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The Critical Importance of Old World Fruit Bats for Healthy Ecosystems and Economies

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Despite extensive documentation of the ecological and economic importance of Old World fruit bats (Chiroptera: Pteropodidae) and the many threats they face from humans, negative attitudes towards pteropodids have persisted, fuelled by perceptions of bats as being pests and undesirable neighbours. Such long-term negativity towards bats is now further exacerbated by more recent disease-related concerns, particularly associated with the current COVID-19 pandemic. There remains an urgent need to investigate and highlight the positive and beneficial aspects of bats across the Old World. While previous reviews have summarised these extensively, numerous new studies conducted over the last 36 years have provided further valuable data and insights which warrant an updated review. Here we synthesise research on pteropodid-plant interactions, comprising diet, ecological roles, and ecosystem services, conducted during 1985-2020. We uncovered a total of 311 studies covering 75 out of the known 201 pteropodid species (37%), conducted in 47 countries. The majority of studies documented diet (52% of all studies; 67 pteropodid species), followed by foraging movement (49%; 50 pteropodid species), with fewer studies directly investigating the roles played by pteropodids in seed dispersal (24%; 41 pteropodid species), pollination (14%; 19 pteropodid species), and conflict with fruit growers (12%; 11 pteropodid species). Pteropodids were recorded feeding on 1072 plant species from 493 genera and 148 families, with fruits comprising the majority of plant parts consumed, followed by flowers/nectar/pollen, leaves, and other miscellaneous parts. Sixteen pteropodid species have been confirmed to act as pollinators for a total of 21 plant species, and 29 pteropodid species have been confirmed to act as seed dispersers for a total of 311 plant species. Anthropogenic threats disrupting bat-plant interactions in the Old World include hunting, direct persecution, habitat loss/disturbance, invasive species, and climate change, leading to ecosystem-level repercussions. We identify notable research gaps and important research priorities to support conservation action for pteropodids.

Keywords: bat-plant interactions, double mutualism, ecosystem services, Palaeotropics, pollination, Pteropodidae, seed dispersal

INTRODUCTION

Discrepancies between human perceptions of an animal, and the importance of the animal to broader human well-being, is perhaps most profoundly unbalanced for bats. Old World fruit bats (family Pteropodidae; Simmons and Cirranello, 2020; also referred to as "pteropodids") are particularly threatened, facing multiple environmental pressures not only as a result of exclusion from statutory protection policies, but also due to a lack of necessary conservation attention, even for legally protected species (Aziz et al., 2016). In addition, the COVID-19 pandemic is the latest and worst disease-related concern to have reinforced long-held fears and negative attitudes towards bats (López-Baucells et al., 2018; Rocha et al., 2020; Tuttle, 2020; Zhao, 2020). Bats are persecuted due to misguided fears of viral transmission (Tuttle, 2018; Rocha et al., 2020; Lu et al., 2021), the noise, smell and mess associated with roosts in residential areas (Aziz et al., 2017a), and for their consumption of fruit crops (Aziz et al., 2016); the latter has even induced mass culls of ∼50% of the endemic flying fox (*Pteropus niger*) population in Mauritius (Florens and Baider, 2019). Fruit bats also continue to be intensively harvested for consumption (Mildenstein et al., 2016), despite often dwindling populations, and despite zoonotic disease concerns.

The 201 species of pteropodids range from Africa, the eastern Mediterranean, Madagascar, Indian Ocean islands, across South and Southeast Asia, southern East Asia including Hong Kong and Taiwan, and throughout islands of the Pacific from the Ryukyu Archipelago, to coastal eastern Australia (including Christmas Island), Melanesia, Micronesia, and Polynesia excluding New Zealand and Hawai'i (Mickleburgh et al., 1992). Available data on the status of species suggest serious population declines for many, mainly due to habitat loss and overhunting, with 37% of assessed species being threatened (IUCN, 2020). Pteropodid declines will also result in plant declines, with ecosystem-wide repercussions.

Complex inter-relationships between Pteropodid bats and plants over millennia have resulted in "bat flowers" and "bat fruits" that are reliant on bats for pollination and/or seed dispersal (Marshall, 1983). Bat-plant interactions were first recorded in 1772 and compiled in the mid-1980s (Marshall, 1983, 1985), showing how pteropodids carry out vital ecological functions in diverse habitats, and are thus essential for the healthy functioning of ecosystems and economies (Marshall, 1985; Fujita and Tuttle, 1991; Mickleburgh et al., 1992; Richards, 1995; Lacher et al., 2019). On faunally depauperate islands, pteropodids play keystone roles as principal pollinators and seed dispersers (Elmqvist et al., 1992; Shanahan et al., 2001; Fleming and Racey, 2009; McConkey and Drake, 2015; Florens et al., 2017), while their high abundance on some continents ensures they are important providers of ecosystem services (Redford et al., 2013; Baker et al., 2018; van Toor et al., 2019; Laurindo et al., 2020). Many plants visited by pteropodids are utilised by humans, and thus have economic importance (Fujita and Tuttle, 1991; Kunz et al., 2011; Scanlon et al., 2014).

Although recent decades have seen a huge growth of papers on pteropodid diet and function, their role has likely been underestimated compared to the much more widely studied birds, primates, and large terrestrial mammals (Seltzer et al., 2013; Baker et al., 2018). Further, pteropodid species that can maintain plant populations in degraded areas regularly forage in isolated trees (Schmelitschek et al., 2009), and can be key to catalysing restoration in disturbed habitats (Sritongchuay et al., 2014; Oleksy et al., 2015). A comprehensive understanding of bat-plant interactions in the Old World is essential for defining their importance, and their benefits to humans – which can help foster a much-needed and more favourable balance in public opinion, and direct research to important gaps in knowledge.

The goal of this paper is to synthesise the breadth of our latest knowledge on pteropodid diet and pteropodid-plant interactions, building from previous reviews and spanning more than three decades of research (1985–2020). We use this dataset to: (i) describe the confirmed and potential ecological roles that pteropodids perform, by evaluating studies on diet, foraging movement, pollination, and seed dispersal; (ii) summarise the main threats to these roles; and (iii) identify the most critical research gaps. This review thus covers the current state of knowledge regarding pteropodid-plant interactions.

METHODS

In this review of more recent bat-plant interaction studies, we included interactions described in post-1985 reviews along with the many new studies since. We also included studies that investigated ecosystem services and disservices by pteropodids (Zhang et al., 2007).

With the exception of Pacific island nations and Papua New Guinea, data have been organised according to country and geopolitical regions (United Nations, 2020). We grouped together island nations of the regions Melanesia, Micronesia, and Polynesia as "The Pacific." For Africa, we treated insular and continental nations as separate regions.

Although this review covers all pteropodids across their range, for which the common term "fruit bats" is sometimes used, we use the terms "large pteropodid" and "large fruit bat" to refer only to species with either body weight ≥250 g or forearm length >110 mm (following Pierson and Rainey, 1992; Kunz and Pierson, 1994), which includes the genera *Acerodon, Aproteles, Desmalopex, Dobsonia, Eidolon, Hypsignathus, Pteralopex, Pteropus*, and *Styloctenium* (Pierson and Rainey, 1992; Kunz and Pierson, 1994; genera list compiled by Mildenstein, 2002). We make this distinction as large fruit bats have distinctly different roles and ecosystem interactions compared to the small fruit bats (Richards, 1995), and also tend to be disproportionately targeted by hunters (Mildenstein et al., 2016).

We reviewed research articles worldwide, during the period 1985-2020, that dealt specifically with the following topics:

(1) diet (studies that investigated, identified and documented food plants consumed by pteropodids, including food choice experiments);

(2) foraging movement (studies involving either long-distance tracking of movements, or feeding behaviour at food plants);
(3) pollination (studies involving exclusion experiments, effective pollen transfer, or effect of bat visitors on fruit set);
(4) seed dispersal (studies involving observations of dispersal distances, modelling of seed shadows, direct observations of bats carrying off fruit, ingestion of viable seeds, gut passage times, seed germination experiments, seedling/sapling recruitment, or seed predation observations);
(5) conflict between pteropodids and fruit growers, including owners of non-commercial backyard trees, which can be considered a form of ecosystem disservice (Zhang et al., 2007; Shackleton et al., 2016).

We collated a preliminary list of studies by performing a Boolean search with relevant wildcards on the ISI Web of Science database and Google Scholar (**Supplementary Information 1**).

We then used this database to conduct comprehensive analyses of research trends and information gaps. Other potentially relevant studies may be overlooked because they were unobtainable or inaccessible (e.g., behind paywalls, or in books, workshop proceedings, and local repositories inaccessible to the international community, or in a language other than English).

Scientific and common names of bat species follow the IUCN (2020). We made every effort to update all plant species names to the most current accepted taxonomic revisions rather than using obsolete names listed in the original studies; we used the online database The Plant List (2013) to verify the latest botanical nomenclature. However, we acknowledge that discrepancies still exist, particularly if further taxonomic revisions have occurred during the course of this review. Unresolved plant names, which could not be identified within current taxonomic databases (e.g., misassigned/misspelled names, obsolete names without contemporary equivalents, or synonyms with several matches), were indicated with question marks.

Data Analysis

Research trends from 1985 to 2020 were analysed and visualised based on regional and geopolitical boundaries, in order to understand research efforts across different countries and to inform future priorities and targets. The proportion of plant parts (e.g., fruits, flowers, and leaves) consumed by pteropodids was analysed at the levels of pteropodid genus and plant family. Data visualisation was conducted using the ggplot package in R 3.6.3 (R Core Team, 2021) and Inkscape 1.0.1 (Inkscape Project, 2021).

The overall bat-plant interaction networks were visualised using the bipartite package in R 3.6.3 (R Core Team, 2021). For each network, interactions were summarised as a bipartite matrix, with each cell containing the number of interactions between each plant family and pteropodid genus.

Relationships among body size (in g), foraging distance, and fruit size were assessed using Spearman Rank correlations.

RESULTS AND DISCUSSION

We obtained 311 relevant studies on bat-plant interactions in the Old World published during 1985-2020: 204 from Web of Science, an additional 73 from Google Scholar, and 33 opportunistically. Of the 201 pteropodid bat species, 37% (*n* = 75) have been studied, in 47 countries. Most of the studies documented diet (52% of all studies; 67 pteropodid species), followed by foraging movement (49%; 50 pteropodid species). Relatively few studies have directly investigated the roles played by pteropodids in seed dispersal (24%; 41 pteropodid species), pollination (14%; 19 pteropodid species), and conflict with fruit growers (12%; 11 pteropodid species) (**Figure 1**). The database on all recorded pteropodid-plant interactions from 1985 to 2020 is in **Supplementary Information 2**. Detailed regional summaries of these studies are in **Supplementary Information 3**.

Pteropodids display unique feeding behaviours, and researchers have employed a variety of methods to study them. Pteropodid bats feed by squeezing out the juices of the plant part, which they swallow, and then spit out wads known as “ejecta” that contain the fibres and often seeds of the plant. Nectar is accessed by lapping with the bats’ long tongues. Because only small seeds and juices are swallowed, morphological investigation of faecal samples on their own can generate biased diet accounts. To overcome this, some researchers use direct observations of feeding bats, collect dropped fruits and seeds, and/or record seedlings/saplings under feeding roosts and parent trees, to supplement information collected from faeces under day roosts.

Bat ejecta and partially eaten dropped fruits are distinctive, and provide reliable accounts of diet (**Supplementary Information 4**). Researchers have also used microscope analyses to identify the flower/nectar portion of the diet. More recently, molecular methods have been developed that can putatively detect all plant parts, although the limitation of this technique is that it does not distinguish the plant parts consumed, and therefore should not be used in isolation; these methods can only supplement morphological/microscopic methods but not replace them (Aziz et al., 2017b). As not all studies employed all methods equally, our results are necessarily biased by the different methodological approaches used, and variation in sampling effort (e.g., time period, seasonality, etc.).

Pteropodid Diet

Studies have recorded $\geq$1072 food plant species from 493 genera and 148 families (**Supplementary Information 2**). Most plant taxa were recorded as being consumed for their fruit (71% of species), followed by flowers (28.6%) and leaves (8.9%). For 16 pteropodid genera (including 80% of all pteropodid species) that had sample sizes exceeding 10 consumed plant species, nectarivory (defined as >50% of diet species comprising floral resources following Fleming et al., 1987) was the least common diet type, found in three genera and four species (*Eonycteris spelaea, Macroglossus minimus, M. sobrinus, Syconycteris australis*) (**Figure 2**), all of which are small-bodied (16-59 g) (**Supplementary Information 2**). The large-bodied *Pteropus* (*n* = 67 species) are considered frugivores (>50% of diet

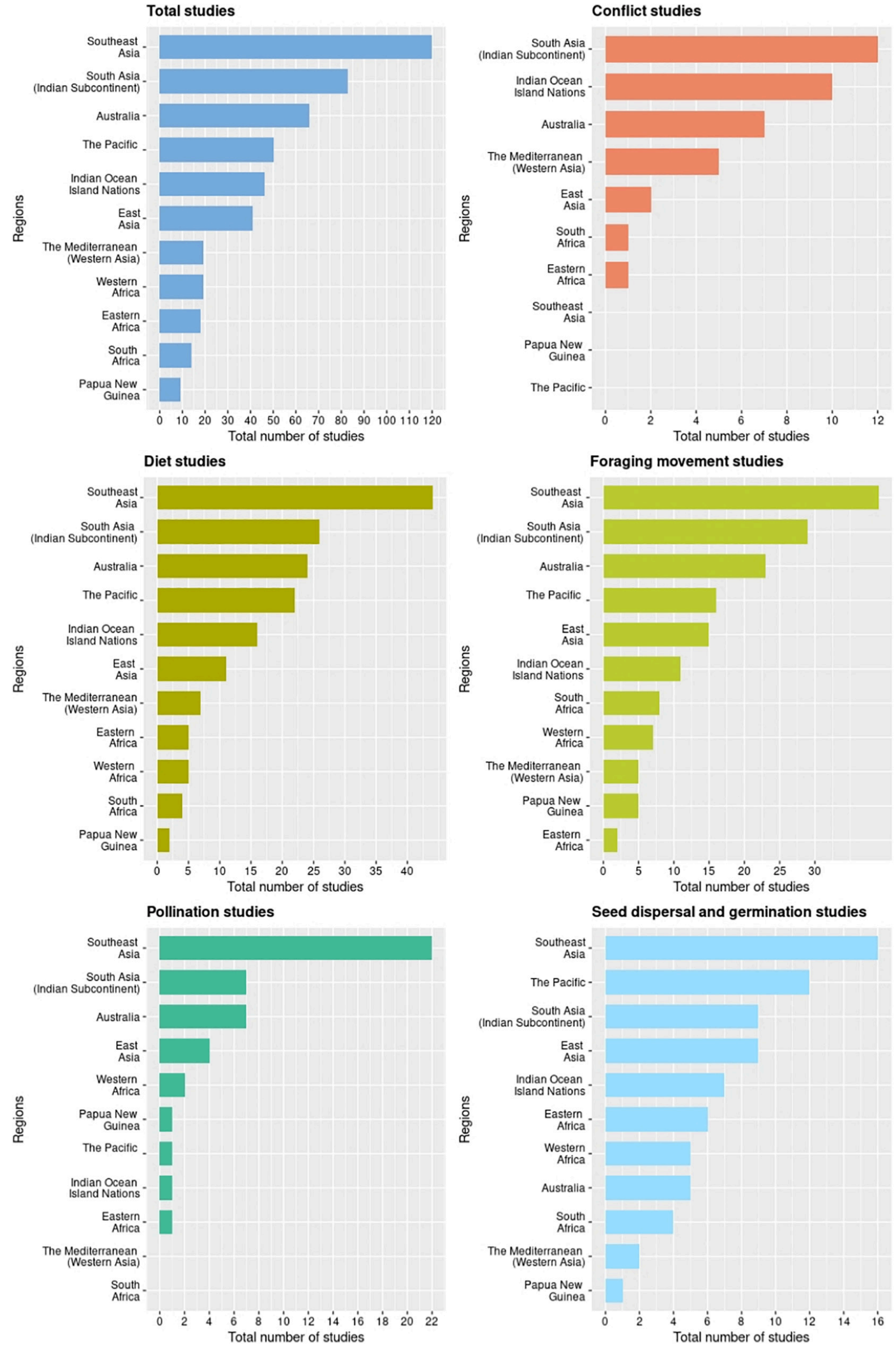

FIGURE 1 | Geographical distribution of research on Old World bat-plant interactions across five major themes during 1985-2020.

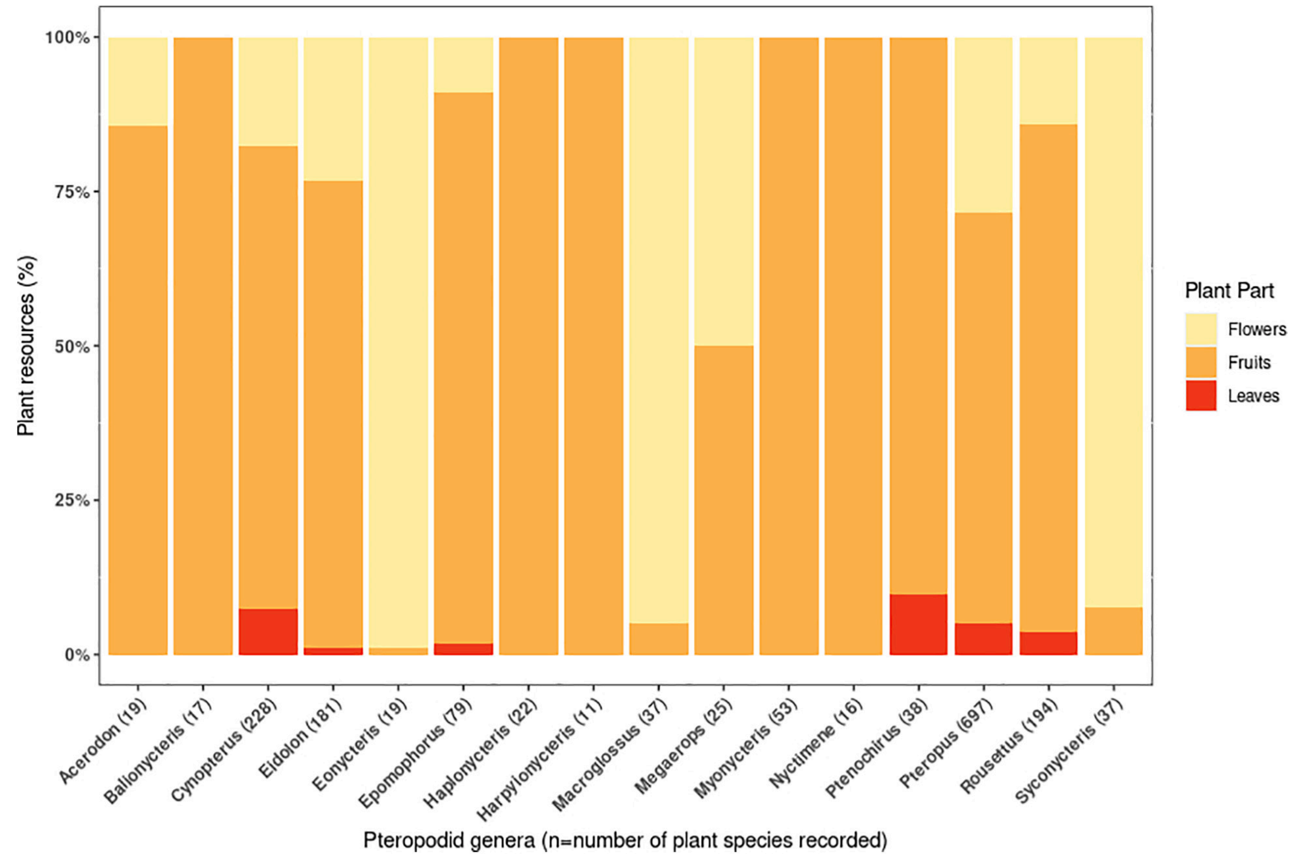

FIGURE 2 | Quantity of fruits, flowers and leaves recorded in the diets of pteropodid bats during 1985-2020. The quantity is represented by the proportion (percentage) of plant species consumed for each plant part, and is recorded for all studied species within 16 pteropodid genera. These genera fed on a minimum of 10 plant species recorded in the literature.

species were fruit) but had the most generalist diet, with >25% of diet as flowers and leaves.

The remaining 12 pteropodid genera (24 species) were also frugivores, covering a wide range of body weights (14-1100 g). However, the majority of pteropodid studies are biased towards detecting fruit, because plant parts are often sampled under day or night roosts, and fruits leave more recognisable remains (i.e, seeds, skin, and pulp) than pollen/nectar and leaves. For this reason, leaf consumption is considered to be more widespread than reported; because of its relatively high protein content, the "juice" of the leaves is the only part swallowed by the bats (Kunz and Diaz, 1995; Nelson et al., 2000b). Also, some pteropodid genera such as *Cynopterus, Megaerops*, and *Pteropus* have been recognised as being frugi-nectarivorous (Stewart et al., 2014; Sritongchuay and Bumrungsri, 2016; Aziz et al., 2017b; Stewart and Dudash, 2018); in one 28-month study, the most frequently occurring food item in *Pteropus rufus* faeces was *Agave sisalana* pollen, and many faecal samples were pure *Agave* pollen (Long and Racey, 2007). Further studies on frugivorous bats, employing a more holistic combination of methods over longer time periods, may reveal more diverse diets than currently recognised.

At least seven other plant parts are consumed by pteropodids, although most of these have only been recorded for the more generalist *Pteropus* spp. (**Table 1**). Twigs are the most common of these other food items, followed by seeds. Seed-eating may often be misinterpreted as fruit consumption, as several plant species with dry fruits (lacking edible pulp) were recorded as fruit consumption in studies. Seed consumption occurred mostly in the leguminous plants from the family Fabaceae. Pteropodids also consumed shoots, sap, petioles, bark and the upper stem of plants.

The plant families Arecaceae (38 genera), Anacardiaceae (18 genera), and Musaceae (all species within the genus *Musa*) provide both floral and fruit resources to multiple bat genera (**Figure 3**). Floral resources were also commonly recorded from the families Fabaceae, Malvaceae, Myrtaceae, and Bignoniaceae, with both Fabaceae and Malvaceae providing multiple resources for the highest number of pteropodid genera. Moraceae and Annonaceae provided the most common fruit resources. *Ficus* was the most commonly consumed genus, with the syconia of 114 species consumed by pteropodids. Several studies have concluded that *Ficus* dominate the diet of pteropodids (e.g., Fujita and Tuttle, 1991; Shanahan et al., 2001; Stier and Mildenstein, 2005; Oleksy et al., 2015; Aziz et al., 2017b), possibly because of the availability and abundance across seasons (Eby, 1998), but determining the accuracy of this finding has been difficult given the sampling bias in field techniques. Small-seeded *Ficus*

TABLE 1 | Plant parts that are a minor component in the diet of pteropodid bats.

Plant part consumed	# plant species	Plant families (Genera)	Bat genera consuming item
Twigs	10	Rubiaceae (*Coffea*) Araliaceae (*Schefflera*) Bromeliaceae (*Ananas*) Elaeocarpaceae (*Elaeocarpus*) Moraceae (*Artocarpus, Ficus, Morus*) Phyllanthaceae (*Bischofia*) Theaceae (*Schima*) Zingerbiaceae (*Alpinia*)	*Cynopterus* *Pteropus*
Seeds	7	Fabaceae (*Acacia, Maniltoa, Parkia, Pithecellobium*) Podocarpaceae (*Podocarpus*) Arecaceae (*Cycas*) Dipterocarpaceae (*Shorea*)	*Cynopterus* *Pteropus*
Shoots	3	Jubulaceae (*Frullania*) Metzgeriaceae (*Metzgeria*) Sematophyllaceae (*Acroporium*)	*Pteropus*
Sap	3	Streliziaceae (*Ravenala*) Arecaceae (*Cocos, Phoenix*)	*Pteropus*
Petioles	1	Fabaceae (*Erythrina*)	*Pteropus*
Bark	1	Moraceae (*Ficus*)	*Pteropus*
Upper stem	1	Poaceae (*Saccharum*)	*Pteropus*

species are more likely to be found in faeces and ejecta samples than large-seeded species, which are not swallowed. Molecular techniques (e.g., Sanger and Next-Generation Sequencing) have been more recently used to investigate pteropodid diet, and this has revealed more diverse diets than determined using traditional morphological or microscope analyses (Aziz et al., 2017b; Lim et al., 2018; Chan et al., 2020).

Foraging Landscape of Pteropodids

Of the 189 pteropodid species with habitat data recorded by the IUCN (2020), 11% were listed as dependent on primary vegetation only. Secondary habitats and agricultural areas (plantations and/or gardens) were used by 56% and 50% of species, respectively. Fifteen species (8%) are reported to use urban landscapes. Hence, the majority of pteropodid species (89%) are using various stages of disturbed habitat, and could be contributing to restoration or plant gene flow via pollination and seed dispersal. They could also serve as essential mutualists that maintain plant populations and ecosystem services in human-modified habitats (Sritongchuay et al., 2014; Oleksy et al., 2015; van Toor et al., 2019). However, this also means that the majority of pteropodids are utilising habitats that potentially bring them into conflict with humans (e.g., Aziz et al., 2016; Oleksy et al., 2018); illegal hunting is known to occur in 50% of foraging areas used by the commensal *Pteropus lylei* (Chaiyes et al., 2017).

Pteropodids use resources over a broad swathe of landscapes, with nightly foraging distances positively related to body size (Spearman Rank, $R = 0.5539$, $n = 25$ species). Movements ranged from an average of 0.1 km for the frugivorous *Cynopterus* spp. to 56 km for *Eidolon helvum*, also a frugivore ($n = 5$ studies, **Table 2** and **Supplementary Information 5**). Within this range of foraging distances travelled, the nectarivorous species generally moved shorter distances, averaging 0.25 to 5.21 km. Maximum distance moved in a night was also positively related to body size ($R = 0.5599$, $n = 22$ studies), with the longest maximum distances recorded for *Eidolon* and *Pteropus* (88 km). Within the landscapes where they forage, pteropodids use cognitive map-based navigation to forage amongst resources (*Rousettus aegyptiacus*, Harten et al., 2020; Toledo et al., 2020); *R. aegyptiacus* flew distances of up to 25 km from day roosts using a fast and straight flight track, showing loyalty to visited fruiting trees and the flight track (Tsoar, 2011). The rest of the night's foraging was spent within the vicinity of the first flight until returning to the roost before sunrise. These flight patterns have consequences for the spatial pattern of defecated seeds, with potentially very different dispersal distances achieved for seeds swallowed earlier in the night compared to those consumed later – but this aspect is currently still unstudied.

At least seven species migrate seasonally to track food resources (*Eidolon helvum, Myonycteris torquata, Nanonycteris veldkampii, Pteropus alecto, P. poliocephalus, P. scapulatus,* and *P. vampyrus*; Thomas, 1982; Richards, 1995; Richter and Cumming, 2008; Epstein et al., 2009; Moussy et al., 2013; Fleming, 2019), potentially resulting in long-distance pollen and seed movement (see below). During migration, distances of up to 370 km were recorded in a single night for *E. helvum*, with individuals travelling more than 2,500 km in total (Richter and Cumming, 2008). The fastest travel was recorded for *P. vampyrus*, moving 130 km in 2 h during migration (Epstein et al., 2009). Indirect evidence for seasonal movements related to food availability has been recorded for two of eight species studied in Malaysian forests (*Cynopterus horsfieldii, Megaerops ecaudatus*) (Hodgkison et al., 2004). Australian *Pteropus* species are highly nomadic with little uniformity among individuals (Welbergen et al., 2020), moving annually around roosts (and presumably feeding resources) across broad swathes of landscapes, with distances ranging from 1400 to 6000 km. Even for the species that do not migrate, single long-distance flights have been recorded; e.g., the 37 g *Cynopterus sphinx* and *C. horsfieldii* flew 10 km over open water to colonise Krakatau Island (Whittaker and Jones, 1994), and many island-dwelling populations move around naturally fragmented landscapes on a nightly basis (McConkey and Drake, 2007; Oleksy et al., 2019).

Pteropodids as Pollinators

Sixteen pteropodid species from eight genera have been proven to function as pollinators (**Table 3**), based on robust scientific evidence obtained from in-depth investigations beyond mere documentation of diet, flower visitation or pollen load. Of these, the genus *Pteropus* appears to include a disproportionately high number of pollinating species within the guild ($n = 7$; 44% of all known pteropodid pollinators), related to seven different plant species, though this likely reflects the high species diversity within this pteropodid genus. The nectarivorous species *Eonycteris spelaea* alone has been proven to be a particularly important pollinator for seven different plant species, and the genus *Macroglossus* appears to be specifically important for wild bananas (*Musa* spp.) and mangrove ecosystems (Momose et al., 1998; Watzke, 2006;

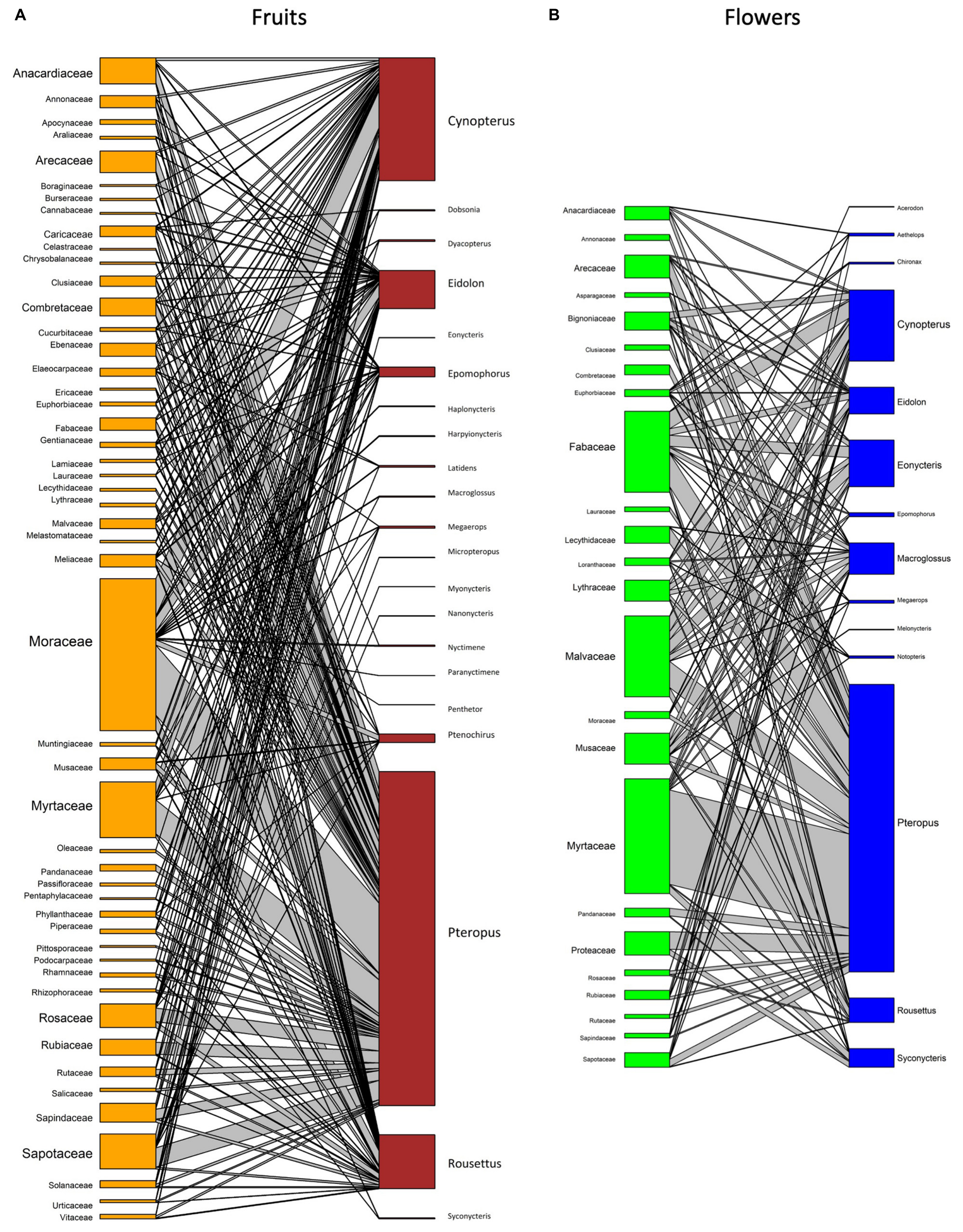

FIGURE 3 | Network graphs showing interactions between pteropodid bats (right) and the plant taxa (left; **(A)** flowers and **(B)** fruit) they interact with. Graphs are based on the number of species within each family consumed by pteropodid genera for five or more interactions recorded.

TABLE 2 | Summary of movement studies on pteropodid genera (1985–2020).

Genera	Diet	Body weight (g)	Distance (km)		No. of studies	Location of study
			Mean	Max		
Acerodon	Fruit	470-1100	21.0	87.0	1	Philippines
Balionycteris	Fruit	14	<1		1	Malaysia
Cynopterus	Fruit	26-58	1.7	6.0	6	China, India, Malaysia
Dobsonia	Fruit	87	0.6	1.2	1	Papua New Guinea
Eidolon	Fruit	250-300	56.1	88.0	5	Burkina Faso, Ghana, Zambia
Eonycteris	Flower	59	5.21	17.9	2	Thailand
Epomophorus	Fruit	80-110	1.44	13.9	3	South Africa
Macroglossus	Flower	16-22	1		1	Papua New Guinea
Melonycteris	Flower	48	0.25	0.4	1	Papua New Guinea
Nyctimene	Fruit	30-49	0.5	1.1	1	Australia
Ptenochirus	Fruit	63-80	0.47	0.48	1	Philippines
Pteropus	Fruit	440-820	9.7	87.5	16	American Samoa, Australia, Cambodia, India, Japan, India, Madagascar, Pakistan, Palau, Thailand
Rousettus	Fruit	45-125	7.2	31.6	8	China, Cyprus, Israel, Madagascar, South Africa,
Syconycteris	Flower	18	1.1	6.8	2	Australia

The main diet of the bat is indicated, according to whether they are nectarivores or frugivores. Mean and maximum movements in a single night are recorded in kilometres. Sources of variation in movement patterns are indicated where these have been described. Data came from 56 studies, but were focused mainly on Pteropus (n = 23). ***Supplementary Information 5*** *has full details on foraging distances.*

Nor Zalipah et al., 2016; Stewart and Dudash, 2016, 2018; Nor Zalipah and Ahmad Fadhli, 2017; Nuevo Diego, 2018; Nuevo Diego et al., 2019), underscoring the obligate pollinator roles of the latter two genera. However, the apparently disproportionate pollinating role of *Eonycteris spelaea* compared to other species may also be a reflection of research effort, as this species is commonly found in human-dominated landscapes across most Southeast Asian countries (Francis et al., 2008), and therefore easily studied in comparison to other species. Further research would be helpful in elucidating the pollinating roles of the comparatively more threatened and rare *Pteropus, Acerodon*, and *Desmalopex*, critical facultative pollinators despite being classified as frugivores. Some of the larger *Pteropus* species have been implicated in the destruction of flowers (Soepadmo and Eow, 1977; Elmqvist et al., 1992; Nathan et al., 2009; Stephenraj et al., 2010), but this has either been incorrectly assumed (Gumal, 2001; Aziz et al., 2017c), or their positive impacts as pollinators have overridden negative effects of their feeding behaviour (Elmqvist et al., 1992; Stephenraj et al., 2010; Toyama et al., 2012). *Pteropus scapulatus* exhibits behaviour and a tongue structure that are more reminiscent of nectar-feeding bats (Birt, 2004), indicating a need to investigate the diet of all pteropodid species in more detail to understand and compare their functional roles. Documented food plants and foraging behaviour of this bat taxon provide clues that should direct future research.

Twenty-one different plant species from eight plant families are now known to be pollinated by pteropodids **Table 3**; families Fabaceae, Lythraceae, Malvaceae, Musaceae and Myrtaceae appear to have particularly important coevolutionary relationships with bats, containing multiple species that are known to be almost entirely dependent on pteropodids for effective long-distance pollen transfer (Crome and Irvine, 1986; Elmqvist et al., 1992; Law and Lean, 1999; Birt, 2004; Boulter et al., 2005; Bumrungsri et al., 2008, 2009; Bacles et al., 2009; Acharya et al., 2015; Groffen et al., 2016; Aziz et al., 2017c; Sheherazade et al., 2019; Sritongchuay et al., 2019). These plant taxa that have close associations with bats display characteristics of chiropterophily: flowers are light-coloured, large, presented on the periphery of the canopy and produce more nectar and pollen at night (Marshall, 1983). In a highly specialised case, the flowers of *Mucuna macrocarpa* in Japan open explosively when triggered by foraging *Pteropus dasymallus*, which allows pollination to occur (Toyama et al., 2012). However, just as bats can be effective dispersers of fruits that are not adapted for bat dispersal, we need improved documentation of their pollination importance for plants that are less specialised for bats.

At a community level, nectarivorous bats have been found to have higher network strength, abundance (Sritongchuay and Bumrungsri, 2016) and generalised degree (number of interactions per species divided by the number of possible interacting partners; Sritongchuay et al., 2019) than other pteropodids. However, the temporal and spatial differences that these bats show in their feeding patterns, when compared to large bats such as *Pteropus* (Aziz et al., 2017c), could suggest complementary roles in pollination. Bats are more effective pollinators than other animals for most of the documented plant species (Ratto et al., 2018; Sheherazade et al., 2019), carrying more pollen and moving across larger landscape areas compared to nectar-feeding birds (Law and Lean, 1999) or native bees (Wayo et al., 2018; Sheherazade et al., 2019). However, this finding also

TABLE 3 | Confirmed pteropodid pollinators and their associated bat-pollinated plant species.

Bat Pollinator	Plant Family	Plant Species	Source/Study
Acerodon celebensis	Malvaceae	*Durio zibethinus*	Sheherazade et al., 2019
Cynopterus sphinx	Fabaceae	*Mucuna championii*	Kobayashi et al., 2020
	Sapotaceae	*Madhuca longifolia* var. *latifolia*	Nathan et al., 2009; Stephenraj et al., 2010
Eidolon dupreanum	Malvaceae	*Adansonia suarezensis*	Baum, 1995
Eonycteris spelaea	Bignoniaceae	*Oroxylum indicum*	Sritongchuay et al., 2008
	Fabaceae	*Parkia speciosa*	Bumrungsri et al., 2008
		Parkia timoriana	Bumrungsri et al., 2008
	Lythraceae	*Sonneratia alba*	Nor Zalipah et al., 2016
		Sonneratia caseolaris	Nor Zalipah et al., 2016
		Sonneratia griffithii	Nuevo Diego, 2018
	Malvaceae	*Durio zibethinus*	Bumrungsri et al., 2009; Aziz et al., 2017b; Chaiyarat et al., 2019; Sheherazade et al., 2019
Macroglossus minimus	Lythraceae	*Sonneratia caseolaris*	Watzke, 2006
		Sonneratia griffithii	Nuevo Diego, 2018
		Sonneratia ovata	Nuevo Diego et al., 2019
Macroglossus sobrinus	Musaceae	*Musa acuminata halabanensis*	Itino et al., 1991
		Musa itinerans	Liu et al., 2002
Pteropus alecto	Malvaceae	*Durio zibethinus*	Sheherazade et al., 2019
Pteropus conspicillatus	Myrtaceae	*Syzygium sayeri*	Boulter et al., 2005
Pteropus dasymallus	Fabaceae	*Mucuna macrocarpa*	Toyama et al., 2012
Pteropus giganteus	Bixaceae	*Cochlospermum religiosum*	Erancheri et al., 2013
	Malvaceae	*Ceiba pentandra*	Nathan et al., 2005
	Sapotaceae	*Madhuca longifolia* var. *latifolia*	Nathan et al., 2009
Pteropus hypomelanus	Malvaceae	*Durio zibethinus*	Aziz et al., 2017c
Pteropus poliocephalus	Myrtaceae	*Corymbia citriodora*	Bacles et al., 2009
Pteropus tonganus	Malvaceae	*Ceiba pentandra*	Elmqvist et al., 1992
Rousettus leschenaultii	Malvaceae	*Ceiba pentandra*	Nathan et al., 2005
Pteropodidae (species unknown)	Fabaceae	*Parkia biglobosa*	Lassen et al., 2012
Pteropodidae spp. (either *Macroglossus lagochilus* or *Syconycteris australis*, or both; indistinguishable in the field)	Myrtaceae	*Syzygium cormiflorum*	Crome and Irvine, 1986
Pteropodidae spp. (*Macroglossus minimus* & *Syconycteris australis* grouped together without species-specific diet)	Myrtaceae	*Syzygium sayeri*	Boulter et al., 2005
Pteropodidae (species unknown)	Malvaceae	*Adansonia digitata*	Djossa et al., 2015

reflects the choice of plants studied, which have been primarily crop or timber plants important to humans that were already suspected to be bat-pollinated. To understand the importance of bat pollination at the community level, we require more studies in wild ecosystems, but the cost, effort and time required to confirm pollination in these environments is likely to be challenging.

Pteropodids as Seed Dispersers

Seed dispersal studies, including seed germination experiments, have been conducted on 41 pteropodid species from 15 genera, but only 29 pteropodid species from 9 genera have been recorded actively dispersing seeds, with documented dispersal for fruits from 311 plant species from 184 genera and 75 families. The genera with the most bat-dispersed species were *Ficus* (60 species), *Syzygium* (14 species), and *Diospyros* (8 species). Bats processed seeds gently in most cases (see below), and therefore most of the 687 species listed as fruit resources in our database (**Supplementary Information 2**) are potentially dispersed by bats. Six methods have been used to document seed dispersal by different pteropodid species (**Table 4**). Direct observations at the parent tree or of fruit being carried away have been observed for most species, followed by investigations of ejecta and faeces under day roosts.

Fruit Selection

The primary cue pteropodids use for finding fruit and determining ripeness is odour Kshitish (Acharya et al., 1998; Luft et al., 2003; Hodgkison et al., 2007, 2013; Raghuram et al., 2009; Shafie et al., 2014), and a strong odour is among the plant traits considered indicative of bat attraction and the bat-fruit syndrome (Bollen et al., 2004; Hodgkison et al., 2013). However, pteropodids also rely, to a significant extent, on vision and have enlarged eyes and a visual cortex (Speakman, 2001). Researchers have suggested "light-coloured" fruit (and probably flowers) are an adaption for bats to find food in dark conditions (Richards, 1990), although bats consume fruit exhibiting a diversity of colours (Hodgkison et al., 2003), and at least some pteropodids are sensitive to the ultraviolet spectrum (Li et al., 2018). Other characteristics of bat-preferred fruits include fruits with high quantities of water and sugar, and low quantities of fats and proteins (Korine et al., 1998; Bollen et al., 2004; Nelson et al., 2005) and an unusual syndrome of dry fruits with a high protein content found in Mediterranean habitats (Korine et al., 1998). Fruit displays, in which the fruits are held away from the foliage and therefore more accessible to bats, are also commonly reported in bat-consumed fruits. These include fruits produced from the trunk (cauliflory), fruits available from leafless main branches (ramicarpy), or fruits on the end of long downward-pointing peduncles (flagelliflory) (Richards, 1995; Hodgkison et al., 2003; Bollen et al., 2004).

Across the studies, information was only available on fruit colour (collected for $n = 141$ plant species) and not fruit odour, chemical composition or display. Bats dispersed seeds from fruits representing a diverse range of colours; here we categorised most species as red (31 species), green (29 species), or yellow (23 species). Fewer fruits were purple (15 species), brown (12 species), orange (11 species), black (10 species), or white (7 species), with just a few species having blue (2 species) or pink (1 species) fruits. While this colour diversity is predominantly light coloured (yellow, orange, or white = 41 species) or with no distinguishing colour against the background (dull: green or brown $n = 41$ species), collectively, the bats show use of a broad range of fruit colours (59 species that are neither dull nor light).

Some pteropodid species are regular visitors to orchards and/or gardens, where they come into conflict with farmers by consuming fruit crops (Aziz et al., 2016). Foraging *Pteropus tonganus* in Fiji was four times more abundant in farmland than in forests, and territorial disputes over food were only documented in farmland (Luskin, 2010). This suggests a potential preference for cultivated landscapes, either because of resource distribution, resource abundance, and/or the nutritional content of the plant resources, which could disrupt natural seed dispersal processes (McConkey and Drake, 2006). However, even though bats can consume large quantities of cultivated fruits (Oleksy et al., 2018), some studies have found that pteropodids prefer to forage on native species rather than on introduced fruits (Korine et al., 1999; Nelson et al., 2000a; Mildenstein et al., 2005; Andrianaivoarivelo et al., 2012).

Fruit Processing

Pteropodids feed by mainly swallowing fruit juices, spitting out fruit fibres and seeds as ejecta. Seeds are dispersed in ejecta, by swallowing and defecating, and by physically carrying the entire fruit; for all dispersal modes researchers report "gentle" seed treatment where seeds are dispersed undamaged. The capacity to swallow seeds is limited to the diameter of the oesophageal lumen, which can extend to 4-5 mm in the larger Australian *Pteropus* (Richards, 1995). Hence, only small seeds (≤ 6 mm width) are dispersed through swallowing and defecation (Shilton et al., 1999; Shanahan et al., 2001; Oleksy et al., 2017). The largest seeds dispersed by defecation were 6 mm wide (*Pteropus rufus* in Madagascar; Bollen et al., 2004), and large fruit bats could disperse slightly larger seeds than small fruit bats in this way (Spearman Rank test significant at 10% level; $R = 0.3934$, $n = 22$ bat species); however, the fruit size of defecated seeds was unrelated to bat size ($R = 0.5003$, $n = 19$ bat species). Seeds dispersed by ejecta were inconsistently reported, so we did not test for a relationship with body size. Maximum widths of 12 mm were noted in ejecta, and often seeds dispersed by defecation were also dispersed in ejecta.

Seeds that are too large to be swallowed are dispersed when bats carry fruits in their mouth away from the parent plant. The largest seed dispersed by pteropodids was for *Mangifera indica* which can reach widths of 71 mm. *Mangifera* was only consumed by large bats (≥ 250 g in body weight), indicative of the positive relationship between seed width and pteropodid body size ($R = 0.6994$, $n = 14$ bat species), and fruit width and pteropodid body size ($R = 0.8299$, $n = 12$ bat species). More important than the width of the fruit is its weight, and pteropodids can carry heavy fruits relative to their body weight. This has rarely been described, but the weight of carried fruits has ranged from 0.5 to 1.6x the body weight of the bat (Nakamoto et al., 2015; Mahandran et al., 2018). Therefore, pteropodids of more than 1 kg could potentially have the capacity to disperse fruits of more than 1.5 kg – though this requires further investigation.

The ability of pteropodids to carry heavy fruits indicates that body mass alone is a poor surrogate of these bats' dispersal abilities, as pteropodids are potential dispersers of fruits consumed by much larger animals – even elephants and rhinoceroses, which disperse mango seeds via defecation (Sridhara et al., 2016). Pteropodids can also consume large quantities of fruit relative to their own body mass; e.g., *Rousettus aegyptiacus* consumes fruit up to a maximum of 150% of its body mass (Izhaki et al., 1995). The high density at which some populations of large pteropodids can occur (Richter and Cumming, 2005; Tait et al., 2014) also implies high rates of consumption at the community level. This has rarely been quantified, but a single colony of *Eidolon helvum,* estimated at 152,000 individuals, was predicted to provide 338,000 dispersal events in a single night (van Toor et al., 2019). Even during the seasonal reduction in colony size, the authors estimated these bats moved 5,500 seeds in a night.

Population abundance is a key factor driving the seed dispersal importance of Neotropical bats (Laurindo et al., 2020), and is likely to be of similar importance for pteropodids. The importance of abundance *per se* has not been investigated in pteropodids, but sufficient population density to induce territorial disputes is essential for effective seed dispersal of large-seeded fruit by *Pteropus* species (Richards, 1995; McConkey and Drake, 2006; Mahandran et al., 2018). *Pteropus* preferentially feed on and defend small territories within fruiting trees. Seed dispersal occurs when newcomers attempting to access the tree cannot forage, because the tree is full of feeding territories already claimed by earlier arrivals – the "raiders versus residents" phenomenon (Richards, 1990). The new arrivals snatch a fruit and fly elsewhere to consume it, hence dispersing the seed from the parent tree. This behaviour has not been reported for other genera apart from *Eidolon* (Racey, pers. obs.), but small pteropodids frequently remove fruit from a parent tree for consumption at regularly used feeding roosts (Utzurrum, 1995; Deshpande and Kelkar, 2015). This feeding behaviour results in more consistent seed dispersal than that by the large 'resident feeder' pteropodids who may usually consume fruit more often at the parent plant, and are thus only effective at dispersing swallowed seeds. Eleven of these small pteropodid species with available seed dispersal information have been noted to use feeding roosts and/or have been observed carrying fruit away from the parent tree (**Table 4**).

Seed Consumption

While researchers report consistently gentle seed processing by pteropodids, some seed-eating has been recorded in at least three *Pteropus* species (involving *Cycas* spp., Cox et al., 2003; *Podocarpus pallidus, Maniltoa grandiflora,* McConkey and Drake, 2015; *Shorea* sp. and an unknown species, Ong, 2020). "Fruit" consumption recorded for plants that have no fleshy portion are potentially also examples of seed consumption. For large seeds, such as *Cycas* spp. and *Maniltoa grandiflora,* consumption does not necessarily prevent effective seed dispersal, since seeds are not entirely consumed and could still germinate (McConkey and Drake, 2015). Seed-eating bats have also been recorded in the Neotropics, where *Chiroderma* spp. have cranio-dental morphology that promotes consumption of fig seeds (Nogueira and Peracchi, 2003; Nogueira et al., 2005); *Centurio senex* has also been recorded eating seeds with soft endocarps (Villalobos-Chaves et al., 2016). It is possible that seed-eating is more prevalent than currently appreciated in pteropodids, as an alternative strategy to folivory and insectivory, to obtain sufficient protein (Courts, 1998; Clulow and Blundell, 2011). Given the lack of apparent morphological adaptations to consume hard items, seed-eating by pteropodids would be expected to be limited to softer seeds; however, *Latidens salimalii* possibly consumes the softer content of nuts by biting through an extremely hard, thick coat (Agoramoorthy and Hsu, 2005).

Dispersal Distances

Some pteropodid species have the capacity to disperse seeds farther than has been recorded for any other animal (**Figure 4**). The maximum dispersal distances recorded for small bats (<250 g) were 30 km for defecated seeds ($n = 6$ studies) with fat-tailed kernels (Tsoar, 2011), while larger bats (≥250 g) defecated seeds over distances up to 24 km (non-migratory) and 88 km (migratory) ($n = 8$ studies) (**Supplementary Information 6**). Most seeds pass through pteropodid guts in 30–116 min, but some seeds are retained for up to 24 h (Shilton et al., 1999; Abedi-Lartey, 2016; Oleksy et al., 2017). If the longer gut retention

TABLE 4 | Seed dispersal study methods according to pteropodid species.

Bat species	Observed in parent tree	Observed carrying fruit away	Ejecta/faecal samples below feeding roost	Seed traps/ejecta/faecal samples below day roost	Ejecta beneath parent tree	Ejecta/faecal samples along transects
Cynopterus brachyotis	x	x	x	x		x
Cynopterus horsfieldii	x	x		x		
Cynopterus minutus	x	x				
Cynopterus sphinx	x	x	x	x		
Cynopterus titthaecheilus	x	x				
Eidolon helvum		x		x		
Epomophorus crypturus	x	x				
Epomophorus wahlbergi	x	x				
Macroglossus minimus						x
Macroglossus sobrinus	x	x				
Nyctimene rabori				x		
Ptenochirus jagori				x		x
Ptenochirus minor						x
Pteropus conspicillatus	x	x		x		
Pteropus dasymallus		x	x		x	x
Pteropus giganteus	x	x		x		
Pteropus mariannus						x
Pteropus niger						x
Pteropus poliocephalus					x	
Pteropus rufus	x		x	x		
Pteropus samoensis		x				
Pteropus tonganus	x			x	x	x
Rousettus aegypticus						
Rousettus amplexicaudatus		x				
Rousettus leschenaultii		x		x		
Rousettus madagascariensis	x	x				

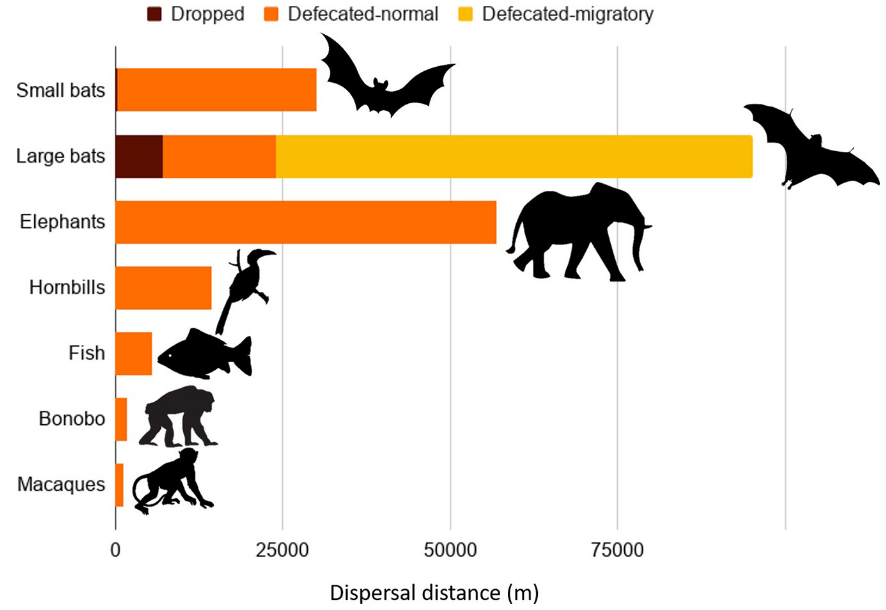

FIGURE 4 | Maximum seed dispersal distances for small (<250 g) and large (≥250 g) pteropodid bats and the comparison with other taxa confirmed to perform long-distance seed dispersal. References for the comparisons are given in the text. Dispersal distances for bats are given for seeds defecated without swallowing (dropped or spat), and defecated seeds during migratory and non-migratory periods.

times are used to estimate dispersal distances, bats can potentially disperse seeds up to 300 km from the parent tree (Shilton et al., 1999), at least for migratory species that traverse such long distances. These dispersal distances are within (or farther than) the maximum range reported for the longest seed dispersers recorded: elephants (6-57 km; Campos-Arceiz and Blake, 2011), fish (5.5 km; Anderson et al., 2011), and hornbills (3.5 to 14.5 km; Kitamura, 2011; **Figure 4**). In comparison, primates in the Palaeotropics have shorter dispersal distances of up to 1.3 km for macaques (McConkey, 2018) and 1.8 km for bonobos (Tsuji et al., 2010).

Seeds that are too large to be swallowed by bats are dispersed much shorter distances than described above, but documenting these patterns accurately has been difficult. Maximum distances of 400 m have been recorded for seeds spat out in ejecta or dropped by small pteropodids ($n = 9$ studies), and 7.2 km for large pteropodids ($n = 7$ studies). In the case of large pteropodids, these distances are still longer than those recorded for many other taxa (**Figure 4**), and qualifies them as long-distance seed dispersers (Cain et al., 2000). Average dispersal distances for seeds across all pteropodids and handling methods is 0-150 m, but it is difficult to determine the frequency of these distances. While dispersal distances of defecated seeds are estimated using gut retention times and movement data, seeds that are dropped or spat out are recorded through direct observations of foraging bats or locations of feeding roosts. Documenting long flights of bats carrying fruits is difficult, and hence has only been reported rarely.

Pteropodids vary in their use of feeding roosts, and this behaviour influences the likelihood of whether seeds are deposited under or away from the crowns of parent plants. Several pteropodid species have been recorded to use feeding roosts (**Table 4**) and could be carrying fruit away from parent crowns regularly, regardless of food-processing behaviour. This is most often observed in small pteropodid species (Bhat, 1994; Hodgkison et al., 2003; Deshpande and Kelkar, 2015), which move seeds 37-200 m for processing in other trees. The large-bodied *Pteropus* species process fruit within the crown, dropping 70% or more of seeds that are too large to be swallowed in this area, and yielding a likelihood of dispersal away from the plant crown that is dependent on the abundance of feeding bats (described above in "Fruit processing") (McConkey and Drake, 2006; Nakamoto et al., 2009; Mahandran et al., 2018).

Seed Deposition and Germination

Bats defecate in flight (Tan et al., 2000), so can theoretically disperse seeds anywhere along their foraging routes. This is particularly relevant for restoration of disturbed areas, as bats only have to pass over habitat to disperse seeds into it (Sritongchuay et al., 2014; Oleksy et al., 2015). However, use of feeding roosts concentrates seed rain in more limited areas. Smaller bodied *Cynopterus* species create small homogenous seed shadows, while the larger bodied *Pteropus* create large heterogeneous patterns (Deshpande and Kelkar, 2015). While these two genera have been recorded facilitating seed dispersal in urban areas (Corlett, 2006; Vendan and Kaleeswaran, 2011; Chan et al., 2020), human activities may impact successful seedling recruitment, e.g., due to seed deposition on unsuitable substrates inhibiting germination, or seedlings crushed by footfall due to higher human traffic.

As *Pteropus* and *Acerodon* spp. are canopy feeders, this dispersal guild may be particularly important to canopy-germinating seeds of strangler figs (Laman, 1995;

Shanahan and Compton, 2001). However, the effects of dispersers on germination are notoriously variable among plant-animal combinations (Traveset, 1998). Pteropodid bats showed the same variable pattern in the 67 bat-plant interactions for which germination tests have been conducted (46 plant species, 25 bat species), but showed an overall tendency for neutral (60%) or positive effects (33%) (**Table 5**). Negative effects were recorded for just four interactions (5%), with three interactions showing a decrease in germination speed, and two interactions showing a decrease in germination rate. Seeds of *Ficus* were most commonly tested (31 interactions), demonstrating mainly positive (14 interactions), or neutral (16 interactions) effects, with one inconclusive test. Two studies compared germination of *Ficus* in ejecta and faeces, and found either positive effects for seeds in faeces, or inconclusive results. A further 41 pteropodid-plant interactions were inferred to be successful based on the presence of saplings under feeding roosts.

Double Mutualisms: Bats as Pollinators and Seed Dispersers of the Same Species

Pteropodids act as both pollinators and seed dispersers (**Figure 5**), and are therefore potentially important "double mutualists," i.e., playing a beneficial role in two different functions (Fuster et al., 2019). Double mutualisms have been reported rarely (302 records in a review by Fuster et al., 2019), and appear to occur more commonly on islands (Olesen et al., 2018; Fuster et al., 2019). Here 138 bat-plant interactions were recorded which are potential examples of double mutualisms, involving 26 pteropodid species with 91 plant species from 36 families (**Figure 6**). The plant families Myrtaceae, Sapotaceae, Musaceae, Arecaceae and Anacardiaceae, in particular, may potentially benefit from double mutualisms involving several different pteropodid species across different countries. Many *Pteropus* species are probably double mutualists, reflecting the more generalist diet of the genus. Both bat pollination and seed dispersal have been confirmed for *Musa acuminata* (Itino et al., 1991; Tang et al., 2007b; Meng et al., 2012) and *Madhuca longifolia* (Nathan et al., 2009; Stephenraj et al., 2010; Mahandran et al., 2018), but most of these potential double mutualisms are based on fruit and flower feeding records, some of which are also confirmed seed dispersal records (**Supplementary Information 2**).

As many studies report non-destructive feeding behaviour, diet lists could provide a reasonable suggestion of function, especially for seed dispersal, but most of the potential double mutualisms we report require further investigation in order to confirm this functional role. Given the known examples of plant self-incompatibility (Bumrungsri et al., 2009), flower destruction (Gumal, 2001), and fruit consumption at parent trees (McConkey and Drake, 2006), pteropodid diet on its own cannot, and should not, be used to confirm ecological roles. While seed dispersal potential can be inferred from foraging movements, more in-depth research is needed to determine whether a pteropodid species serves as a pollinator or flower predator; e.g., *P. vampyrus* in Sarawak is reported to destructively consume whole flowers of *Madhuca motleyana* (Gumal, 2001), and *Cynopterus* spp. appear to have limited effectiveness as true pollinators despite non-destructive feeding

TABLE 5 | Summary of results of germination tests on seeds dispersed by pteropodids.

Pteropodid genus	**Number of plant species and the recorded effects on germination speed or rate**				
	Positive	**Neutral**	**Negative**	**Inconclusive**	**Source/Study**
Balionycteris		5		2	Hodgkison et al., 2003
Chironax		1			Hodgkison et al., 2003
Cynopterus	1	7	1		Shilton et al., 1999; Hodgkison et al., 2003; Tang et al., 2007a, Tang et al., 2008, 2012; Mahandran et al., 2018
Dyacopterus		2			Hodgkison et al., 2003
Eidolon	4	23			Webala et al., 2014
Epomophorus	3	4	1		Djossa et al., 2008; Voigt et al., 2011; Jordaan et al., 2012; Helbig-Bonitz et al., 2013
Micropteropus	1				Djossa et al., 2008
Myonycteris	1				Djossa et al., 2008
Nanonycteris	1				Djossa et al., 2008
Nyctimene	1				Utzurrum and Heideman, 1991
Ptenochirus	1				Utzurrum and Heideman, 1991
Pteropus	7	29			Entwistle and Corp, 1997; Bollen and van Elsacker, 2002; Goveas et al., 2006; Vendan and Kaleeswaran, 2011; Scanlon et al., 2014; Chen et al., 2017; Oleksy et al., 2017
Rousettus		9	2		Izhaki et al., 1995; Tang et al., 2007a; Mahandran et al., 2018; Andrianaivoarivelo et al., 2011
Unidentified	1			1	Utzurrum, 1995; Djossa et al., 2008
Total	21	79	4	3	

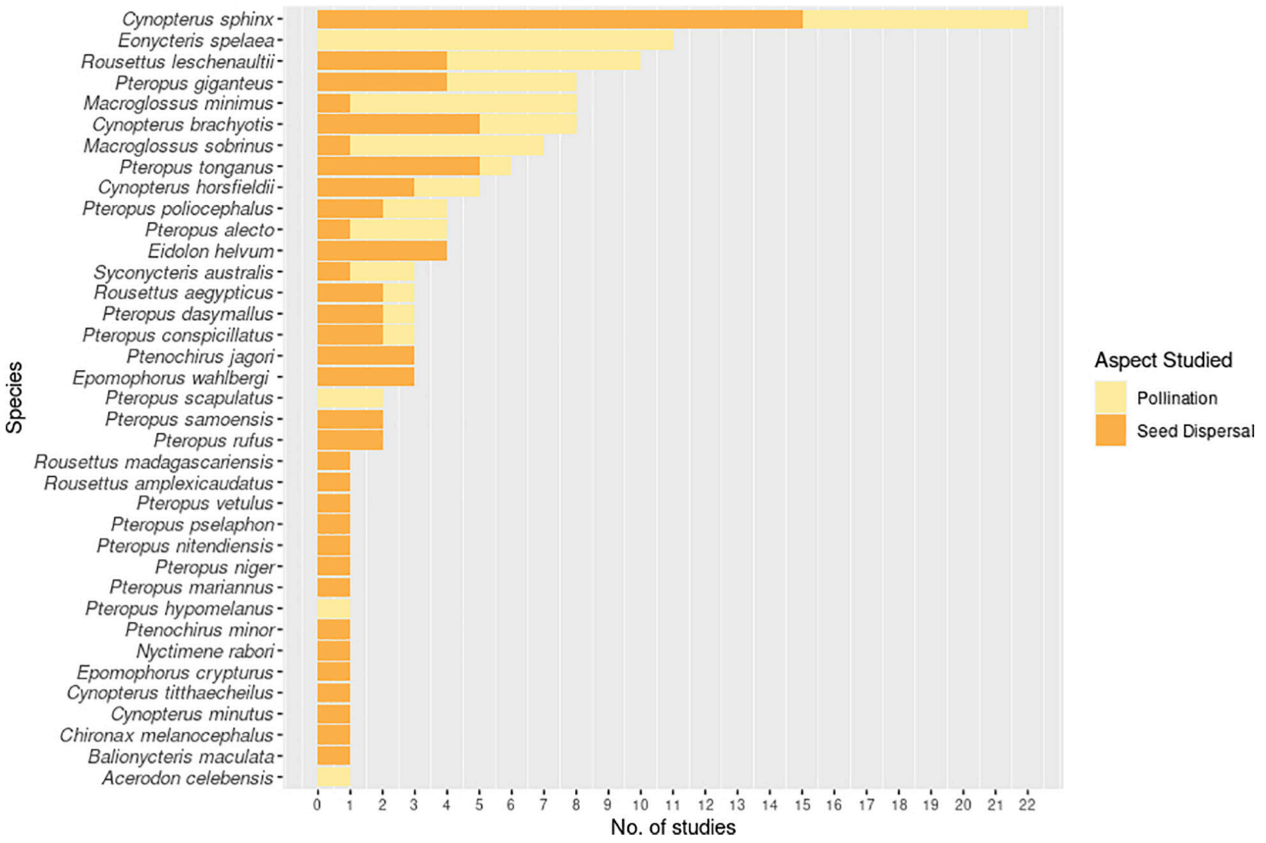

FIGURE 5 | Number of studies investigating the roles of specific pteropodid species as pollinators or seed dispersers during 1985-2020.

(Stewart and Dudash, 2017). However, flower consumption does not necessarily prevent successful pollination from happening for an individual plant, as long as some gynoecia remain intact and have a chance to receive conspecific pollen in the process (Elmqvist et al., 1992; Nathan et al., 2009; Stephenraj et al., 2010; Toyama et al., 2012).

It is also important to note that some plant species that could potentially benefit from both pollination and seed dispersal by bats (e.g., *Agave americana, Diospyros kaki, Eriobotrya japonica, Mangifera indica*, *Manilkara zapota, Musa acuminata, Prunus armeniaca, P. persica, Psidium guajava,* and many *Syzigium* species – although, pollination for all except *M. acuminata* is currently still unconfirmed) are commercially important trees, commonly planted in gardens, orchards and plantations – and as such, bat consumption of these fruits can be perceived as a form of ecosystem disservice (Zhang et al., 2007; Shackleton et al., 2016).

Intra-Specific Variation in Ecological Function

Variation among individuals is important for maintaining diverse seed dispersal and pollination roles at the population level (Zwolak, 2018; Schupp et al., 2019). To our knowledge, intra-specific or intra-population variation in pteropodids has only been described for movement distances, although the independent movement trajectories that individuals from a single roost display (e.g., Tsoar, 2011; Harten et al., 2020; Toledo et al., 2020; Welbergen et al., 2020) could mean considerable variation in foraging choices as well (e.g., Scholesing et al., 2020). Future studies might reveal broad variation in food choice, seed dispersal, and pollination among individuals. Of the 160 studies on pteropodid foraging movements (**Supplementary Information 5**), intra-population variation in movement distances was described for five genera, and for three of these (*Cynopterus, Pteropus*, and *Rousettus*) female bats moved further than males. Sexually immature *Melonycteris* moved further than adults, and seasonal and habitat differences in ranging distances were found for *Eidolon helvum* and *Rousettus aegyptiacus*.

Function of Pteropodids at the Community Level

The role that pteropodids fulfil within the wider pollinator and seed disperser communities is poorly understood. Twenty-six studies have investigated either pollination or seed dispersal roles of bats across multiple plant species, and compared these roles with other animals in the community. While feeding assemblages have been documented for individual plant species, particularly to document pollination of cultivated plants, we cannot interpret the broader community roles from these

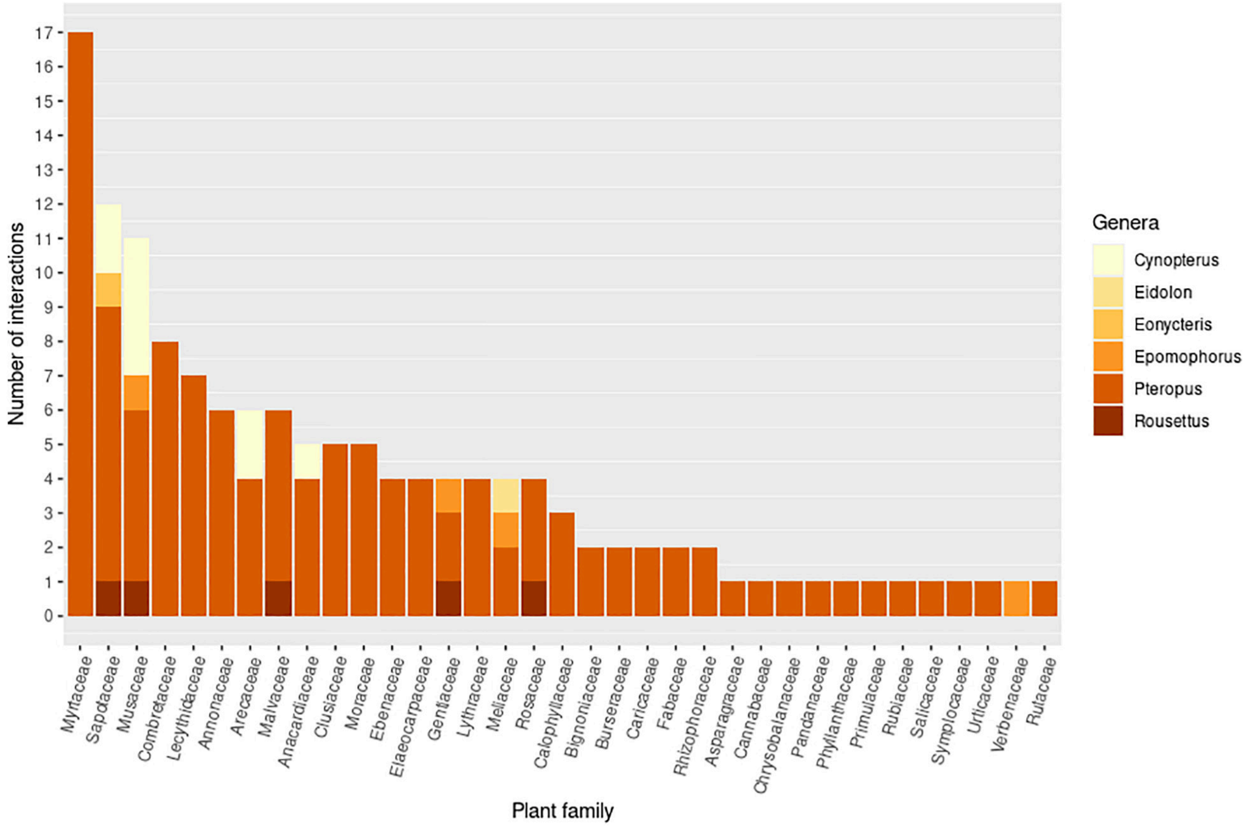

FIGURE 6 | Pteropodid-plant interactions that are potentially double mutualisms, in which a pteropodid species might act as both pollinator and seed disperser for the same plant species. Double mutualisms were assessed at the species level for both plants and bats. The graph shows the number of species-species interactions within each plant family and pteropodid genus. Only families with more than one interaction are shown. Plants in an additional 13 families were recorded for overall pteropodid diet, but only one interaction was recorded for each, and thus not included here.

studies. In the Tongan archipelago, *Pteropus tonganus* was the only effective seed disperser of 57% of the plant species that it consumed, an importance resulting from the prehistoric extinctions of other large dispersers (McConkey and Drake, 2015). The importance of *Pteropus* on islands is also reflected in their large diet breadth. *Pteropus tonganus* and *P. samoensis* interacted with 59% of the forest tree species on Samoa, and about 25% of the woody plant species in Mauritius have their seeds dispersed by *P. niger* (Florens et al., 2017), while *P. ornatus, P. tonganus*, and *P. vetulus* were found to be far more efficient seed dispersers compared to introduced rats on New Caledonia (Duron et al., 2017). In the Philippines, birds dispersed a higher diversity and number of seeds into successional forests (Ingle, 2003; Gonzales et al., 2009), and there was substantial overlap in fruit consumption between birds and bats especially during some seasons (Gonzales et al., 2009). Given the depauperate frugivore and pollinator communities on islands, pteropodid bats are likely to play dominant, keystone roles within these systems wherever their populations have not been decimated by hunting or pest control (Cox et al., 1991). The high *Pteropus* diversity across islands and probable origin of the genus from the islands of Wallacea (Tsang et al., 2020) suggest a long evolutionary history in island ecosystems, which could be reflected in the ecological roles they perform there.

Within continental habitats, the importance of bat pollination and seed dispersal have been studied at the community level in Australia and Thailand (e.g., Birt, 2004; Sritongchuay et al., 2019), but no community-wide studies have been conducted in most regions. In a dipterocarp forest in Peninsular Malaysia, *Pteropus vampyrus* occurred in a different module of a seed dispersal network compared to smaller bats, indicating they tended to interact with a different subset of plant species (Ong, 2020). The large bats shared a module with other large mammals, including elephants and frugivorous primates, while the smaller bats occurred in the same module as squirrels and rats. *Pteropus vampyrus* was found to be among the 10 most important seed dispersers in the community, with smaller bats also playing an important community role. A study focused on bat-used fruit resources in a Malaysian rainforest found that 56% of the resources used by bats were also consumed by primates, civets or squirrels, but the ecological roles were not evaluated (Hodgkison et al., 2003).

In Peninsular Malaysia and Thailand, small pteropodids are important *Sonneratia* pollinators in mangroves (Nor Zalipah et al., 2016; Stewart and Dudash, 2016, 2017; Nuevo Diego, 2018;

Nuevo Diego et al., 2019), with *Pteropus* spp. likely playing a similar role possibly supplemented by seed dispersal (Gumal, 2001; Weber et al., 2015; Wee et al., 2017). Since mangrove health can be crucial for maintaining healthy functioning coral reefs (Mumby, 2006; Yates et al., 2014; Loh et al., 2018; Friess et al., 2020), this suggests that the ecological importance of pteropodids extends beyond terrestrial and even coastal/estuarine ecosystems to potentially influence the health of marine ecosystems too. To fully understand the importance of pteropodid bats at the community level, we need broad studies across a greater breadth of ecosystems. Because pteropodids are important for both pollination and seed dispersal, studies focusing on a single function will underestimate their importance to ecosystems, and hence ambitious studies are needed that measure pollination and seed dispersal jointly.

Population abundance is an important predictor of functional importance for a broad range of animals including bats (Bauer and Hoye, 2014; Winfree et al., 2014; Simmons et al., 2019; Laurindo et al., 2020). Even animals that rarely disperse seeds can be important contributors to community-wide seed dispersal if they occur in very abundant populations, as has been documented for ducks (Soons et al., 2016) and proposed for the now extinct passenger pigeon (Webb, 1986). Hence, the sheer abundance of some pteropodid populations (Roberts et al., 2012; van Toor et al., 2019) combined with their effectiveness as pollinators and seed dispersers suggest vital functional roles within the ecosystems where they occur. The fact that many of these abundant pteropodid species are also migratory, thereby promoting long-distance dispersal of pollen and seeds (Bauer and Hoye, 2014), creates an even greater urgency in understanding the community-level roles of pteropodids.

Assessing the Ecosystem Services for Humans Provided by Pteropodids

Although the majority of studies on the ecological roles of pteropodids have focused on seed dispersal, attempts to document the benefits these bats bring to humans have more frequently focused on pollination, likely because such benefits are more direct and can be more easily quantified in economic terms. The majority of pollination studies have documented the ecosystem services provided by bats for major fruit crops in Asia such as durian (*Durio zibethinus*; Bumrungsri et al., 2009; Acharya et al., 2015; Aziz et al., 2017c; Sheherazade et al., 2019), petai (*Parkia* spp.; Bumrungsri et al., 2008), midnight horror (*Oroxylum indicum*; Sritongchuay et al., 2008), and madhuca (*Madhuca longifolia*; Nathan et al., 2009; Stephenraj et al., 2010), with some Australian research focusing on important timber species (e.g., Bacles et al., 2009). The durian pollination services from pteropodids in Sulawesi, Indonesia alone have been valued at $117 ha/fruiting season or USD 450,000 for a single village (Sheherazade et al., 2019). The only study to place a financial value on seed dispersal was for *Eidolon helvum* and its role in reforestation in Ghana. van Toor et al. (2019) estimated that bats contributed a total annual gross revenue of $11,939 to $858,068 per bat colony depending on season and area. In an unusual case, the fruit foraging behaviour of *Cynopterus* and *Pteropus* in mixed-fruit agricultural landscapes in India was perceived by farmers to be beneficial (Deshpande and Kelkar, 2015); the bats aggregate cashew (*Anacardium occidentale*) and *Areca* palm nuts in accessible places, which reduces the labour required for collection. In addition, their pollination service was recognised for bananas (*Musa* spp.) and kapok (*Ceiba pentandra*), so that overall, farmers perceived that bats brought more benefits than the losses through crop raiding.

Pteropodids have also been implicated in potential ecosystem disservices to humans through their consumption of agricultural fruits (Zhang et al., 2007; Aziz et al., 2016) and the dispersal of exotic plants (Corlett, 2005; von Döhren and Haase, 2015; Vaz et al., 2017; Chan et al., 2020). As such, future approaches to assessing, quantifying and valuing the ecological roles of pteropodids should attempt to more be more holistic in including both services and disservices (Friess et al., 2020).

Threats to the Ecological Roles of Pteropodids

Of the 201 pteropodid species to date, 189 have been assessed by the IUCN (2020), such that 37% are currently threatened (7 species are "Critically Endangered," 27 species are "Endangered," 36 species are "Vulnerable") and 48% are of "Least Concern;" 9% of species are "Data Deficient" (**Figure 7**). However, caution must be exercised when using the assigned Red List status as sole indicator of species extinction risk. The status of many pteropodids are poorly known particularly in more localised contexts, and delays in communicating research result in outdated assessments. Furthermore, pteropodids found on islands pose special challenges when applying the IUCN's habitat-based criteria of extent of occurrence (EOO) and area of occurrence (AOO) to assess status (Mildenstein, 2020). Finally, while "common" pteropodids are studied more than "threatened" species at a rate of 5:1 (Mildenstein, 2012), "common" bat species, particularly those deemed as low conservation priorities based on their widespread distribution at a regional level, can be misinterpreted as not threatened at a country level. This can sometimes conflict with national-level species assessments that have not been captured or reflected by the IUCN Red List in a timely manner; e.g., *Pteropus hypomelanus* and *P. vampyrus* are both classified as "Endangered" in Peninsular Malaysia (PERHILITAN, 2017), but are both only listed as "Near Threatened" by the IUCN Red List (Bates et al., 2008; Tsang, 2020).

Another problem with looking at IUCN species assessments in isolation is that such assessments do not reflect the functional importance of many common and abundant species (**Figure 5**) at an ecosystem or landscape level (Redford et al., 2013; Baker et al., 2018). Since pteropodids are crucial for introducing seed rain into cleared areas and maintaining plant gene flow amongst forest fragments (Sritongchuay et al., 2014; Oleksy et al., 2015; Lim et al., 2018; van Toor et al., 2019; Chan et al., 2020), their disappearance could potentially disrupt reforestation and regeneration processes (Castillo-Figueroa, 2020). Modifications

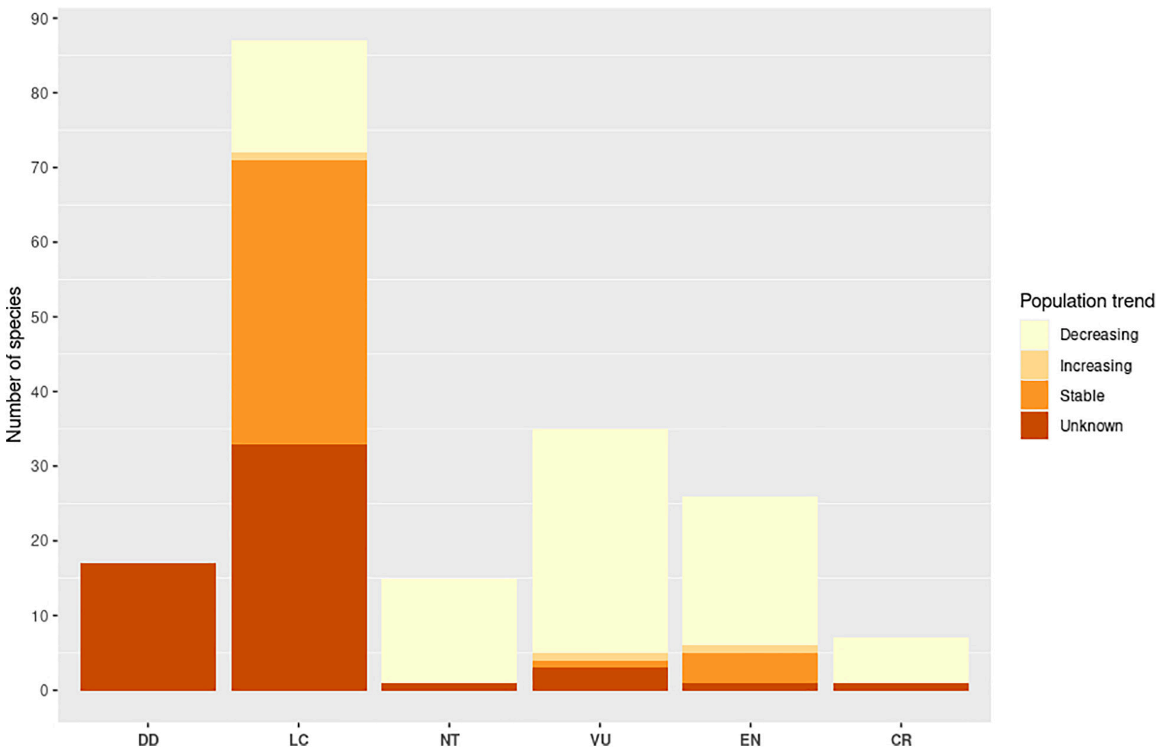

FIGURE 7 | IUCN Red List status and associated population trends of all assessed pteropodids (2020).

of the frugivore community (through logging or hunting of birds and terrestrial mammals) in the Neotropics have already been shown to reduce seed removal at the community level, leading to reduced plant recruitment and sapling density (Boissier et al., 2020). Similar effects can be expected for the Palaeotropics (Osuri et al., 2020), and it is crucial for such assessments to include pteropodids.

Comprehensive reviews have identified a number of major threats to pteropodids (Mickleburgh et al., 1992; Jones et al., 2009; O'Shea et al., 2016; Frick et al., 2019). These include direct and indirect anthropogenically caused mortality. Logging, agriculture (commercial and private or community-based), and hunting were reported by the Red List to present major threats to pteropodids (**Supplementary Information 7**), while fire and pollution have emerged as more recent threats. The following specific drivers are likely to cause major disruptions to pteropodid-plant interactions and their associated ecosystem functions.

Hunting and Harvesting for Consumption and Trade

Bat hunting is widespread across the Old World, affecting about 50% of pteropodid species across 24 pteropodid genera, and particularly prevalent on the large pteropodids in Southeast Asia, and to a lesser extent Africa (Struebig et al., 2007; Epstein et al., 2009; Mildenstein et al., 2016), having already caused the extinction of several *Pteropus* species on islands (Jones et al., 2009; Mildenstein et al., 2016). Bats are hunted for a variety of different reasons, including for bushmeat consumption (either for subsistence or as a perceived delicacy), medicinal value, trade, recreation, and for the decorative and currency values of their teeth (Mildenstein et al., 2016; Lavery and Fasi, 2019). However, hunting for consumption remains the most widespread reason. While bat meat may serve as a necessary source of protein for certain impoverished communities (Mildenstein et al., 2016), elsewhere it is prized as a high-value and high-status meat costing more than poultry (Mohd-Azlan, pers. comm.; Jenkins and Racey, 2008) when it is sold on the black market (e.g., *Pteropus mariannus* is sold by poachers for as much as 150 USD on Guam; Mildenstein, unpubl. data).

Hunting causes changes to bat foraging and roosting behaviour, as well as population declines (Mildenstein et al., 2016). As the ecosystem roles of *Pteropus* become disrupted when their population abundance is too low, their functional extinction in the Asia-Pacific region – where their ecological importance in many countries is still poorly understood – can become a concern long before actual species or population extinction (McConkey and Drake, 2006). Similarly, *Eidolon helvum* travels the longest distance of any known mammal in Africa (van Toor et al., 2019), and its annual transboundary migration likely makes it the most important long-distance disperser of seeds and pollen on the continent (Richter and Cumming, 2008) – yet it is intensively hunted whenever it is found in abundance (Mildenstein et al., 2016; O'Shea et al., 2016). Although most bat hunting and trade is local rather than international, hunting pressure selectively targets the large pteropodids (Mildenstein et al., 2016) that function as the most crucial and often sole long-distance dispersers (Elmqvist et al., 1992; Fleming and Racey, 2009; McConkey and Drake, 2015), which should be a cause for serious concern (Stoner et al., 2007).

These examples underscore how conservation action is imperative even for abundant and/or common species due to their disproportionately important roles in maintaining ecosystem health (Redford et al., 2013; Florens et al., 2017; Baker et al., 2018; Laurindo et al., 2020). The majority of assessed pteropodid species are considered Least Concern by the IUCN Red List, with conservation efforts skewed towards highly threatened species. Yet this approach overlooks common and less threatened species that are often more vulnerable to hunting due to their hyperabundant populations (e.g., *Rousettus amplexicaudatus* in the Philippines), which may lead to a "Passenger Pigeon Fiasco" effect whereby a common and widespread species went extinct over time due to continuous overhunting and the lack of effective statutory conservation attention (Tanalgo and Hughes, 2019).

Killings and Persecution Driven by Conflict and Negative Perceptions

Negative public perceptions of bats have been documented as remnant and long-standing socio-cultural values of Western, Eurocentric cultures that increasingly permeate international media reporting on bats (Thiriet, 2010; Lunney and Moon, 2011; Kingston, 2016). However, specific and localised negative perceptions of bats can also arise through conflict interactions such as crop-raiding and shared living space, often exacerbated by low awareness of bats' ecological importance (Larsen et al., 2002; Kung et al., 2015; Aziz et al., 2016, 2017a; O'Shea et al., 2016). In particular, intentional killings of bats for crop protection purposes can result in multiple species being intensively culled at very high numbers (O'Shea et al., 2016), with the national cullings of *Pteropus niger* on Mauritius being the most recent extreme example (Florens and Baider, 2019). Such massive population reductions are especially damaging at the ecological level, because it directly affects the role of such a keystone island species in maintaining native forests (Florens et al., 2017). Ironically, persecution and culling of pteropodids can also negatively impact the very commercial crops that rely on these bats for successful pollination and fruit production, such as durian (Aziz et al., 2016).

These issues are further compounded by misguided fear over speculated disease risks, which are often sensationalised and exaggerated by the media (Thiriet, 2010; Schneeberger and Voigt, 2016; López-Baucells et al., 2018; Tuttle, 2018). The current COVID-19 pandemic is the latest and worst example of this problem, with premature speculations in the media misleadingly associating the disease with bats, i.e., assuming or implying all bats to be a direct source of human infection (as opposed to one insectivorous genus merely being a possible evolutionary origin of the virus currently causing the disease), stoking even more public backlash (Rocha et al., 2020; Tuttle, 2020; Zhao, 2020). This has even resulted in violent and cruel attempts to cull or eradicate bats in a completely misguided effort to control the disease, despite the fact that the animal host for the SARS-CoV-2 virus is still unknown (Bittel, 2020; Lu et al., 2021).

Habitat Loss and Disturbance

Habitat loss and disturbance affect both roosting areas and food sources for pteropodids. Deforestation is especially a concern in the tropics (Jones et al., 2009; Meyer et al., 2016), and a decreasing abundance of native food plants can drive pteropodids to feed more on introduced exotics in human-dominated areas (Luskin, 2010; Mildenstein, 2012; Aziz et al., 2016; Lim et al., 2018). This could lead to ecosystem disservices (Zhang et al., 2007; von Döhren and Haase, 2015; Vaz et al., 2017) such as the propagation of invasive plants (e.g., Voigt et al., 2011; Jordaan et al., 2012), and also crop-raiding of commercially cultivated fruits (Aziz et al., 2016), but even simple interventions to address habitat degradation, such as invasive alien plant control in native forests, can improve foraging habitat for pteropodids and therefore potentially reduce crop raiding (Krivek et al., 2020).

Land-use change in surrounding areas is also known to alter pollination networks in mixed-fruit orchards, affecting fruit production (Sritongchuay et al., 2019). Moreover, cave-roosting pteropodid pollinators such as *Eonycteris* and *Rousettus* are particularly vulnerable to limestone quarrying activities by the cement and marble industries, land-clearing around caves, and disturbance by human visitors (Clements et al., 2006). The lack of suitable cave roosts can thus have a direct detrimental impact on pollination services, affecting economically significant fruit industries (Sritongchuay et al., 2016).

Habitat modification, fragmentation and urbanisation are already known to affect pollination and seed dispersal by phyllostomid bats (Meyer et al., 2016; Regolin et al., 2020); e.g., in the Neotropics, frugivorous bats avoid areas with too much light, and feed less (on both fruit and nectar) in these areas (Lewanzik and Voigt, 2014). However, the impact of such processes on the ecological roles of pteropodids is still poorly understood. In particular, more studies are needed to document the full seed dispersal cycle, from seed deposition all the way through to plant recruitment, and how this is affected by habitat alteration (Meyer et al., 2016).

Invasive Species

Invasive species are a significant threat to island-dwelling pteropodids, but the impacts of invasions are not well studied (Welch and Leppanen, 2017). Non-native cats, dogs, rats, ants and snakes prey on pteropodids (e.g., Vincenot et al., 2017a; Oedin et al., 2021), but how this threatens pteropodids' population stability and behaviour is mostly unknown. On Guam, predation by the invasive brown tree snake (*Boiga irregularis*) is thought to have contributed to the extinction of the endemic *Pteropus tokudae*, and partially to declines in *P. mariannus* (Wiles, 1987; Mildenstein, 2020). The snake has also caused the extirpation of most forest bird species on Guam (Savidge, 1987), which, in turn, has disrupted plant recruitment (Rogers et al., 2017). How this reduction in fruit bat population size and behaviour has affected the island's ecosystem, in terms of loss of ecological roles, has not been investigated. Invasive yellow crazy ants (*Anoplolepis gracillipes*) on Christmas Island disrupt the activity budgets of *Pteropus melanotus* (Dorrestein et al., 2019), but impacts on foraging and movement behaviour have not been documented.

Invasive species also have indirect effects on pteropodids when they alter habitats either through overgrazing (such as by deer and goats), competition for food resources (e.g. by macaques; Reinegger et al., 2021), or through the spread of non-native plants (Welch and Leppanen, 2017). The effect this has on foraging movement and ecological roles of pteropodids will depend on whether they avoid invaded areas (Krivek et al., 2020) or are attracted to them (Luskin, 2010), and there have not been enough studies to quantify responses.

Climate Change

Climate change can threaten pteropodids through increased frequency and intensity of extreme weather events such as cyclones and intense heat/droughts (Welbergen et al., 2008; Jones et al., 2009). Cyclones are known to have an impact on endemic *Pteropus* spp. on Indian Ocean and Pacific islands, drastically reducing populations (e.g., 80-90% for some island *Pteropus*) and their food sources, and leaving bats vulnerable to increased hunting pressure from humans, conflict due to greater foraging in anthropogenic landscapes, or predation from domestic animals (Craig et al., 1994; Grant et al., 1997; McConkey et al., 2004; Esselstyn et al., 2006; O'Shea et al., 2016; Scanlon et al., 2018). Again, the negative impacts on island ecosystems are likely to be disproportionately high, particularly since the ecological roles of island *Pteropus* cannot be replaced by other animals (McConkey and Drake, 2015; Duron et al., 2017).

Australian *Pteropus* are known to regularly die en masse from extreme heat stress due to ambient temperatures exceeding 42°C (Welbergen et al., 2008; Jones et al., 2009; Daly, 2020), and the most recent bushfires associated with such an extreme weather condition (van Oldenborgh et al., 2020) will likely have far-reaching and long-lasting impacts on the Myrtaceae-dominated forests that rely heavily on pteropodid pollination (Birt, 2004; Boulter et al., 2005; Bacles et al., 2009; Reuters, 2019). Climate change could also lead to increased and intensified precipitation that would depress foraging activity, and perhaps even cause pups to starve or be abandoned, whilst sea level rise could inundate coastal roost sites (Jones et al., 2009).

Temperature changes could alter the timing of flowering and fruit development which could interfere with pollination and seed dispersal relationships (Sherry et al., 2007), particularly for migratory species that follow resource pulses (see Foraging Landscapes section). Pteropodids locate flowers and fruits using olfaction primarily, but the volatile organic compounds (VOCs) that they use as a guide could be altered by climate change (Yuan et al., 2009). However, while impacts of climate change are already being predicted for Neotropical pollination (e.g., Zamora-Gutiérrez et al., 2021) and seed dispersal (e.g., bird dispersal of a palm; Sales et al., 2021), potential effects on the ecological roles of pteropodids have not yet been studied.

Knowledge Gaps and Future Research Directions

Although research efforts on pteropodid-plant interactions have increased markedly over the last three decades (**Figure 8**), the gaps in our knowledge of their ecological roles are large (**Supplementary Information 8**). We propose eleven key priorities for future studies and other efforts to bolster our understanding of bat-plant interactions in the region (**Table 6**). Of the 201 pteropodid bat species to date, only 37% (*n* = 75) have been studied, with the majority of research focused on a few common species. Documenting the role of common or widely distributed species that could be playing major ecological roles (e.g., *Pteropus vampyrus,* Gumal, 2001; *Eidolon helvum*, van Toor et al., 2019) is important, but we have not yet sufficiently understood or recognised the importance of abundance per se, in order to ensure that populations of highly abundant species are maintained at appropriate levels. However, it is also vital to understand the roles of rare species that have dwindling populations. These population declines are often a direct result of human persecution (Aziz et al., 2016; Mildenstein et al., 2016; O'Shea et al., 2016), and strong arguments are required to bolster support for species conservation – especially for those deemed "common" and "abundant" (Redford et al., 2013; Baker et al., 2018).

Most of the countries with highly diverse pteropodid assemblages have had few studies, hindering our understanding of how these diverse bat communities are structured with respect to their ecological roles. The highest diversity of pteropodids is found in Indonesia (77 species), Papua New Guinea (36 species), and India (13 species) (**Figure 9**), but only India features in the five countries that have had more than 20 studies published on pteropodids, while African bats have been particularly poorly studied. Forested and cultivated habitats have received the most research effort, yet pteropodids inhabit other habitats, such as caves and urban areas, where more research attention is required.

A paucity of studies on the ecological roles of pteropodids has hindered a broader understanding of their importance. The majority of studies we report were focused only on diet, followed by foraging movement. Relatively few studies have directly investigated the roles played by pteropodids in pollination and seed dispersal (**Figure 1**). Pteropodids in Africa, the Mediterranean and Papua New Guinea are especially poorly studied in these aspects. Also, even with pteropodid species for which some documentation of diet exists, more comprehensive and detailed dietary records are still needed.

A research focus on pollination of cultivated plants is an important conservation need for countering persecution and negative opinions against bats. Yet robust empirical evidence is still lacking for confirming the role of bats in pollinating more commercially important plants, even though some of these plants have been erroneously cited as examples of bat pollination services (e.g., *Artocarpus, Palaquium*; Lee et al., 2002). Bat diet, flower visitation and pollen load identification/quantification, on their own, are insufficient for determining pollination success. In order to confidently determine pollinator effectiveness and pollination services of individual pteropodid species, investigations must employ appropriate exclusion experiments, identify relevant floral biology traits (including timings of anther dehiscence and stigma receptivity), document bat feeding behaviour, assess successful pollen transfer, and/or analyse the effect of bat visits on mature fruit set; without the use of these methods, any conclusions about the pollinating

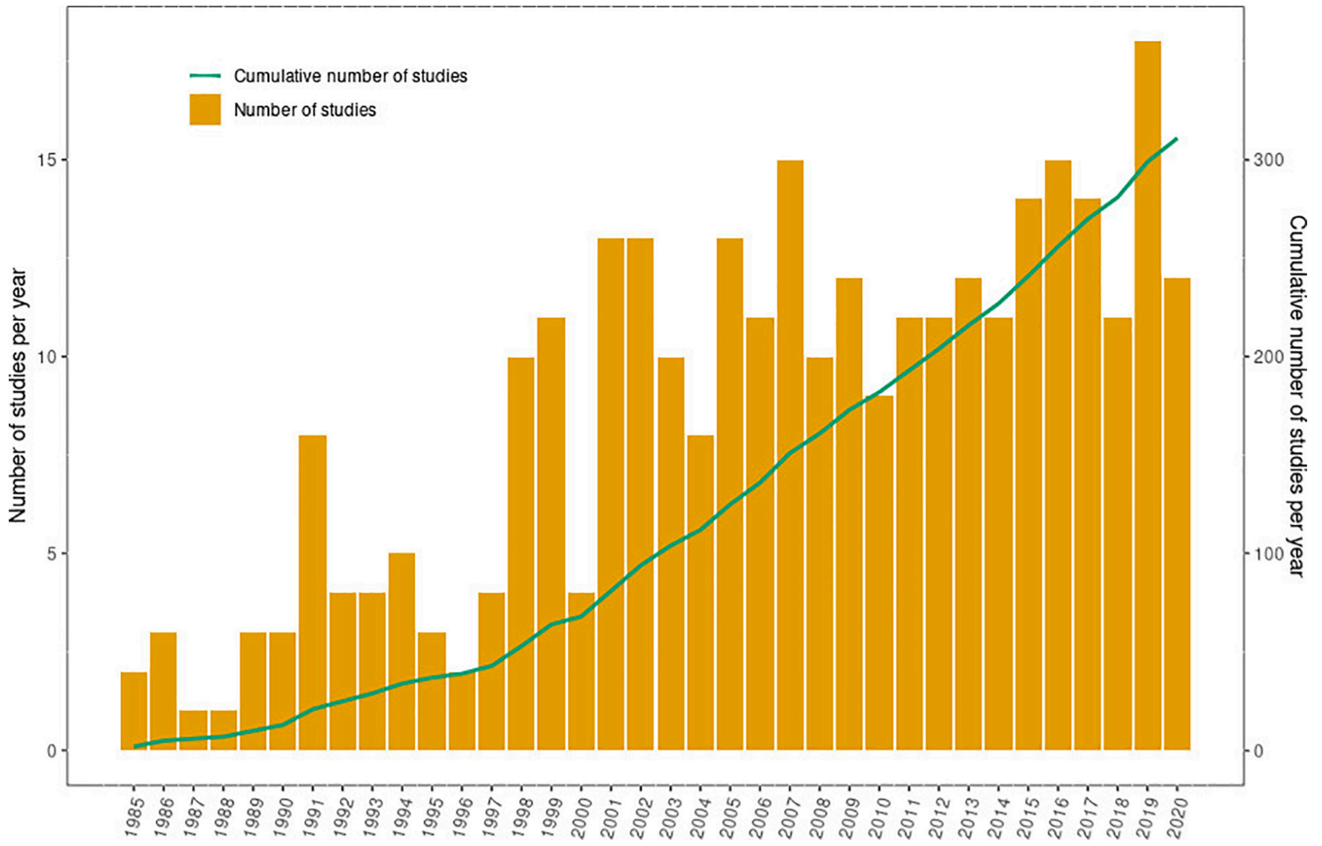

FIGURE 8 | Research effort on Old World bat-plant interactions during 1985-2020.

TABLE 6 | Directions for future research directions and other efforts to bolster progress on understanding pteropodid-plant interactions.

Future directions	Description	Type
Understudied species and in understudied regions and habitats	Studies in mega-diverse countries (e.g., Indonesia and Papua New Guinea), understudied geographical territories and habitat types (e.g., caves, urban areas, mangroves, peat swamps).	Research
Value of abundance	Importance of abundance *per se* to the maintenance of bat-plant interactions. Understanding how reductions in highly abundant bats could impact ecological roles.	Research
Pollination and seed dispersal roles	Pollination studies for more commercially important and wild plant species; studies across a broader range of bat species; confirming the role of bats as double mutualists; assessment of the role pteropodids play in restoration.	Research
Community-wide studies	Broader studies encompassing more animal and plant species within communities to more accurately evaluate the importance of bats. Where possible studies should jointly evaluate both pollination and seed dispersal.	Research
Economic evaluation of roles	Quantify the positive contributions of bats via pollination, seed dispersal, habitat restoration and other services. Evaluate positive roles in the context of negative roles, such as crop raiding.	Research
Impact of disturbances and population declines on ecological roles	Determine how changes in population abundance, landscape structure, resource abundance, pollution, climate and other disturbances alter ecological roles	Research
Open data-sharing	Increase research visibility, up-to-date open data-sharing online, and promote responsible and equitable resource exchange amongst scientists, countries, and regions.	Other
Partnerships	Promote equitable and transparent partnerships among scientists, organisations, and conservation practitioners inside and outside the Old World tropics to effectively achieve the set priorities.	Other
Protocols on bat-plant interaction studies	Establish a standardised and easy-to-follow protocol or guide on bat-plant interaction studies. Also, increase capacity-building and training (study design, field surveys, data analysis, science communication) for early-career researchers in the Global South.	Other
Public awareness	Intensify and improve the translation of technical research to be more accessible to the mass public to promote and gain support for species and habitat conservation efforts.	Other

FIGURE 9 | Proportion of studied pteropodid species per country during 1985–2020 (map excludes countries with no pteropodid occurrence).

roles of bats are premature and potentially inaccurate, and therefore cannot be made.

There remains a paucity of data on pteropodid pollination of wild plants. This knowledge deficit must be addressed to better appreciate the role of bats at the community level, and to understand their roles as double mutualists for a variety of ecosystems. Indeed, bat pollination could well be occurring for many plant species that are not currently known or suspected to be chiropterophilous, especially since some *Pteropus* species forage diurnally (Pierson et al., 1996; Richmond et al., 1998; Lavery et al., 2020; Aziz, pers. obs.). Broader studies are required to compare bats with other mutualists (Ong, 2020; Ingle, 2003; McConkey and Drake, 2015); where feasible, such studies should integrate the combined roles of pollination and seed dispersal to more accurately determine the importance of pteropodids. Studies quantifying the ecosystem services and economic contributions of the large-bodied pteropodids most intensively threatened by hunting and conflict (e.g., *Pteropus* spp. and *Eidolon* spp.) are a particularly critical and urgent need.

The frequent conflict between pteropodids and people requires economic assessments of ecosystem services and disservices to fairly and accurately represent the losses and gains that pteropodids generate. This can be done by incorporating cost-benefit analyses into assessments of such bat-plant interactions involving commercial fruit growers. Conflict was the least studied topic in our review (12% of studies) (**Figure 1**), only conducted in 14 countries, and only three of these (Japan, Kenya and Mauritius) also have studies on the ecological roles of the bats. An exception to this imbalance is Mauritius, where supposed losses of cultivated fruit to foraging *Pteropus niger* has resulted in two culls by the Government of Mauritius, causing the deaths of over 90,000 bats (Vincenot et al., 2017b). Researchers here have noted the ineffectiveness of culls (Florens and Baider, 2019), calculated minimal fruit losses to the bats (Oleksy et al., 2018), documented the ecological roles of the species (Nyhagen et al., 2005; Florens et al., 2017), and attempted to identify appropriate mitigation methods to reduce economic loss (Oleksy et al., 2018; Krivek et al., 2020). Such efforts are urgently needed but still lacking in many regions, such as Southeast Asia, East Asia, West Africa, South Africa, and Papua New Guinea. Negative perceptions of bats might be countered by more studies on the roles pteropodids play in pollinating important plants, or restoring habitats via seed dispersal. This restoration role is well recognised in Neotropical regions but represented by less than five studies for pteropodids (Sritongchuay et al., 2014; Oleksy et al., 2015, 2017; van Toor et al., 2019), even though 89% of pteropodid species are tolerant of anthropogenic disturbance (IUCN, 2020).

The final major research gap is our limited understanding of how pteropodids respond to disturbances and threats, and the impacts these have on ecological roles. Disturbance and fragmentation alter pathways used by Neotropical bats (Meyer et al., 2016; Ferreira et al., 2017; Regolin et al., 2020) but is largely unstudied in pteropodids, even though it has consequences for resources used, pollination success, and seed deposition (McConkey and O'Farrill, 2016). Although pteropodids frequently feed on cultivated fruits and flowers, this is influenced by the quality of the native habitat (Krivek et al., 2020) and food abundance (Luskin, 2010), as many pteropodids appear to prefer wild fruits to cultivated ones (Korine et al., 1999; Nelson et al., 2000a; Andrianaivoarivelo et al., 2012). A more in-depth understanding of resource selection can improve our understanding of pteropodid-plant interactions and conflict with humans. Finally, population abundance has been shown to influence seed dispersal capacity for some *Pteropus* species (McConkey and Drake, 2006), and testing for this in more species, as well as how it impacts pollination, is required.

More open, equitable collaborations and data-sharing (e.g., the Bat Eco-Interactions Database[1]) among researchers and other professionals working on pteropodids would enable a more comprehensive documentation of the benefits pteropodids bring to ecosystems and humans. Such collaborations could be used to establish standardised protocols for documenting bat-plant interactions, and to develop training opportunities particularly for Global South researchers. Finally, the translation of research findings into a format accessible to the general public through popular science communication channels is particularly essential for overcoming negative public perceptions of bats, especially in places where awareness and appreciation of bats remains low.

CONCLUSION

Pteropodid bats play vital roles in seed dispersal and pollination, and are implicated as double mutualists for a diverse range of plant taxa. Island species are especially important for ecosystem functioning, but continental species have rarely been studied at a community level despite having the capacity for moving large numbers of seeds over the longest distances recorded for any animal. Well over half the world's pteropodid species remain unstudied in terms of their ecological roles, and many may experience multiple threats in various dimensions and scales. Even species that have been studied remain severely understudied in many aspects, often limited to just one study or single aspect. There is also a need to move away from species-driven research, especially research efforts and funding that focus solely on species diversity or endemism, and instead conduct research highlighting the importance of pteropodid-plant interactions at a landscape level, and their importance for healthy ecosystem functioning, even when common or less threatened species are involved.

We hope the results and findings highlighted by this review will encourage more studies on pteropodid-plant interactions to bolster the knowledge necessary for understanding the conservation values associated with this important animal group. We urge more efforts to be directed towards areas where pteropodid-plant interactions are poorly understood or explored. A comprehensive understanding of pteropodid ecological roles and their implications for human well-being is necessary to initiate effective conservation actions for an animal group that remains one of the least charismatic, and is consistently overlooked in research and conservation efforts.

AUTHOR CONTRIBUTIONS

SA, KM, KT, TS, TM, and PR contributed to the conception and design of the study. SA, KM, KT, M-RL, CN-D, VC-L, and PR performed the literature search and/or organised the database. SA, KM, KT, TS, M-RL, JY, and CN-D produced the figures and/or tables. SA wrote the first draft of the manuscript. SA, KM, KT, JY, TM, CN-D, and PR wrote sections of the manuscript. All authors reviewed and/or analysed the literature and contributed to manuscript revision, read, and approved the submitted version.

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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.2021.641411/full#supplementary-material

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[1] https://batbase.org/

Supplementary Information 1 | Methods and workflow for literature review.

Supplementary Information 2 | Pteropodid-Plant Interactions Database (1985–2020).

Supplementary Information 3 | Regional summaries of research on pteropodid-plant interactions during 1985–2020.

Supplementary Information 4 | Feeding signs of *Pteropus* bats on fruit.

Supplementary Information 5 | Foraging distances of pteropodids.

Supplementary Information 6 | Seed dispersal distances of pteropodids.

Supplementary Information 7 | Threats to pteropodid species as assessed by the IUCN (2020).

Supplementary Information 8 | IUCN Red-Listed pteropodid species with corresponding numbers of species-specific studies documenting aspects of bat-plant interactions during 1985–2020.

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