ANIMAL SCIENCE

Searching for food in a concrete jungle: feeding ecology of a Psittacine assemblage (Aves, Psittacidae) in a major Amazonian city

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Abstract: The efficient use of food resources is a precondition for wild species´ survival in urban environments. The feeding ecology of animals in tropical cities, however, remains poorly investigated. Here we study the feeding ecology of parrots in Manaus, a major Amazonian city, and compare the results with a parrot assemblage living in undisturbed habitats. We recorded 203 feeding bouts from eight parrot species, which consumed parts of 51 plant species. Parrot diets were dominated by native palm species (Arecaceae). Exotic plants, however, constituted an important portion of the diet of some parrots. Levin's indices, a measure of food niche width, varied from 0.40 to 0.83, indicating an overall tendency to generalist diets. Diet overlap between species was small, indicating broad resource partitioning between members of the assemblage. The diversity of plants consumed in the natural environment was greater than in the urban environment (71 species vs. 52). However, the diversity of plants consumed was similar for parrot species recorded both in natural and urban environments, indicating that occupation of the city does not imply an impoverishment in parrot diets. Creation of municipal protected areas and increasing the city afforestation would provide complementary strategies for Manaus parrot conservation.

Key words: Diet, niche breadth, parrot ecology, urban adaptation, urban birds.

INTRODUCTION

The worldwide expansion of cities is one of the fastest and most impactful changes affecting natural ecosystems, causing dramatic alterations to biodiversity, including species loss and biotic homogenization (Czech et al. 2000, McKinney 2006, Sol et al. 2014). However, a variety of animal and plant taxa have adapted to living in cities, making understanding the effects of urbanization on biodiversity relevant to global conservation, especially in poorly-investigated tropical cities (Aronson et al. 2014, Lepczyk et al. 2017).

Efficient food resource use is a key factor for the successful survival of animal species in cities. The supply of novel types of food in urban environments may result in changes in the diet of such species, including consumption of domestic animals, exotic plants and human-provided foods (Athreya et al. 2013, Murray et al. 2015, Plummer et al. 2015). In addition, urbanization functions as a selective filter for species with different competitive capacities (Shochat et al. 2004, Palacio 2020).

Birds are the most-studied taxonomic group for assessments the impacts of urbanization (Aronson et al. 2014, Bellocq et al. 2017, Lepczyk et al. 2017). However, studies have concentrated on temperate regions, and urban bird ecology has been poorly investigated in the tropics

which, ironically, harbors the greatest diversity of bird species (Lepczyk et al. 2017). Parrots (family Psittacidae) is an appropriate bird group with which to assess the effects of urbanization on birds, as some species are both abundant and appear well adapted to urban environments (Davis et al. 2012, Martens et al. 2013, Le Louarn et al. 2018, Luna et al. 2018). Additionally, parrots show great morphological variation and are recognized for their intelligence and behavioral flexibility, which facilitates adaptation to new environments (Pitter & Christiansen 1995, Sol & Lefebvre 2000, Nunes & Galetti 2007).

Parrot diets are plant-based, although items such as invertebrate larvae and clay are also consumed (Sick 2001, Barnett et al. 2018, Winkler et al. 2020). Differences in parrot body size delimit the consumption of certain types and sizes of food items, often via simple biomechanics effects (Benavidez et al. 2018). Large, hard seeds, for example, dominate the diet of larger Neotropical parrots (*Amazona*, *Ara*), while flowers, nectar and fleshy fruits are more frequently consumed by smaller species (*Forpus*, *Pionus*) (Renton et al. 2015, Benavidez et al. 2018).

While feeding behavior and parrot diets have been frequently studied in natural environments (e.g. Ragusa-Netto & Fecchio 2006, Paranhos et al. 2007, Da Silva 2013), feeding ecology of parrots in urban context have received less attention (Santos & Ragusa-Netto 2014, Silva & Cordeiro 2016, Marques et al. 2018), limiting our understanding of the adaptation of such species to intensely human-modified environments. Here we describe the feeding ecology of a psittacine assemblage recorded in Manaus, an Amazonian city with remarkable diversity of parrot species (Fragata et al. 2022).

Our main objectives were to provide a preliminary assessment of the plant diversity consumed by parrots and quantify some dimensions (e.g. foraging height) of their feeding niches. We examine the diversity of parrot diets and their overlap between species, and investigate whether these attributes are linked to species morphology. In addition, our results were compared with a similar study carried out in Amazonia natural environments (Roth 1984) to investigate the general differences in feeding niches of parrots inhabiting two highly-contrasting environments.

The study focused on the following questions:

i)   How variable are dietary niche breadth and overlap within parrot assemblage in Manaus? The quantity and diversity of food sources in a city is expected to be highly variable in space and time. Under such circumstances those species with generalist diets and low overlap with other species for items consumed could be favored.

ii) Apart to diet composition, does niche partitioning occur between urban parrot species in other foraging dimensions? Syntopic parrot species living in natural habitats forage in different vegetation strata and in small flocks (Roth 1984, Simão et al. 1997, Chapman et al. 1989). We predicted that the parrot assemblages in urban and natural environments would retain the same behavioral patterns even though major differences might exist between them in the structure of their occupied habitats.

iii) Does morphological dissimilarity among species affects parrot niche breadth? Previous analysis indicated that diet composition is associated with parrot body mass (Benavidez et al. 2018). Accordingly, we expected that diet breadth would be related to species morphology.

iv) Do species similar in morphological attributes also have higher levels of diet overlap? It is likely that morphologically-similar

species will share more food items than morphologically distinctive species.

v) Are patterns of feeding niche breadth and overlap distinct in parrot assemblages from urban and natural environments? The quantity and diversity of available food is likely to be higher in near-undisturbed forests than in urban habitats. Based on this premise, it is expected that diversity of plants used by parrots will be higher in natural habitats compared to urban environments. In addition, the higher number of parrot species in natural habitats is expect to result in smaller niche breadths and reduced overlap between individual species in parrot assemblages in natural compared to urban environments.

MATERIALS AND METHODS

Study area

Manaus has an urbanized area of 377 km², and a current population of more than 2.2 million people (IBGE 2019). The city is located in central Amazonia, near the confluence of the Negro and Solimões rivers. Most of the growth in population and urban infrastructure in Manaus has occurred since the 1970s when a free trade zone was implemented in the region (Monte Rey 2019).

The Manaus region has a humid tropical climate with average temperatures around 27° C, and air humidity generally above 80% (INMET 2019). Precipitation shows marked annual variation, with a rainy season from January to June (average monthly rainfall of 240 mm), and a dry season from July to December (average monthly rainfall of 118 mm) (INMET 2019, Fragata et al. 2022).

We identified five areas as suitable for systematic parrot observations (Fig. 1). These sampling sites were located in the south-central region of Manaus, and were chosen because they contained habitats commonly used by tropical urban parrots, such as borders along the forest fragments, interior of forest fragments, streets, avenues, and domestic gardens with variable tree cover levels. All study sites were visited at least once a month, with observations occurring from 06:00 to 09:00 and 16:00 to 18:00. The visit order of each site was changed regularly to ensure parrots were observed at each site at different times of the day.

Bird sampling

Parrot sampling extended from April 2019 to February 2020, and totaled 253 hours of field observation. During field work, the researcher (CSS) walked slowly along trails and roads searching for parrots, and recorded feeding activities with binoculars (10 x 42). We used the feeding bout method (Galetti et al. 2002) to quantify dietary events, with the following information collected for each feeding bout: geographical coordinates, parrot species, number of individuals in the flock, plant species, foraging height and part of the plant consumed (categorized as: fruit, flower, nectar, leaves, seed or pulp). Mean group height was obtained by averaging the lowest and highest individuals in a foraging group. Height estimates of trees and parrots were collected using an electronic clinometer (Haglof, Sweden), with readings being taken at a distance of ten meters from the base of the focal tree.

Fruits or pieces of fruit left by the parrots were collected and photographed with a Canon PowerShot Sx510 camera. The identification of plant species was based on photographs obtained in the field, and collections of plants for later identification. Identifications were made using the literature (Lorenzi et al. 2003, Lorenzi 2009), and by consulting the website REFLORA - Brazilian Plants: Historic Rescue and Virtual
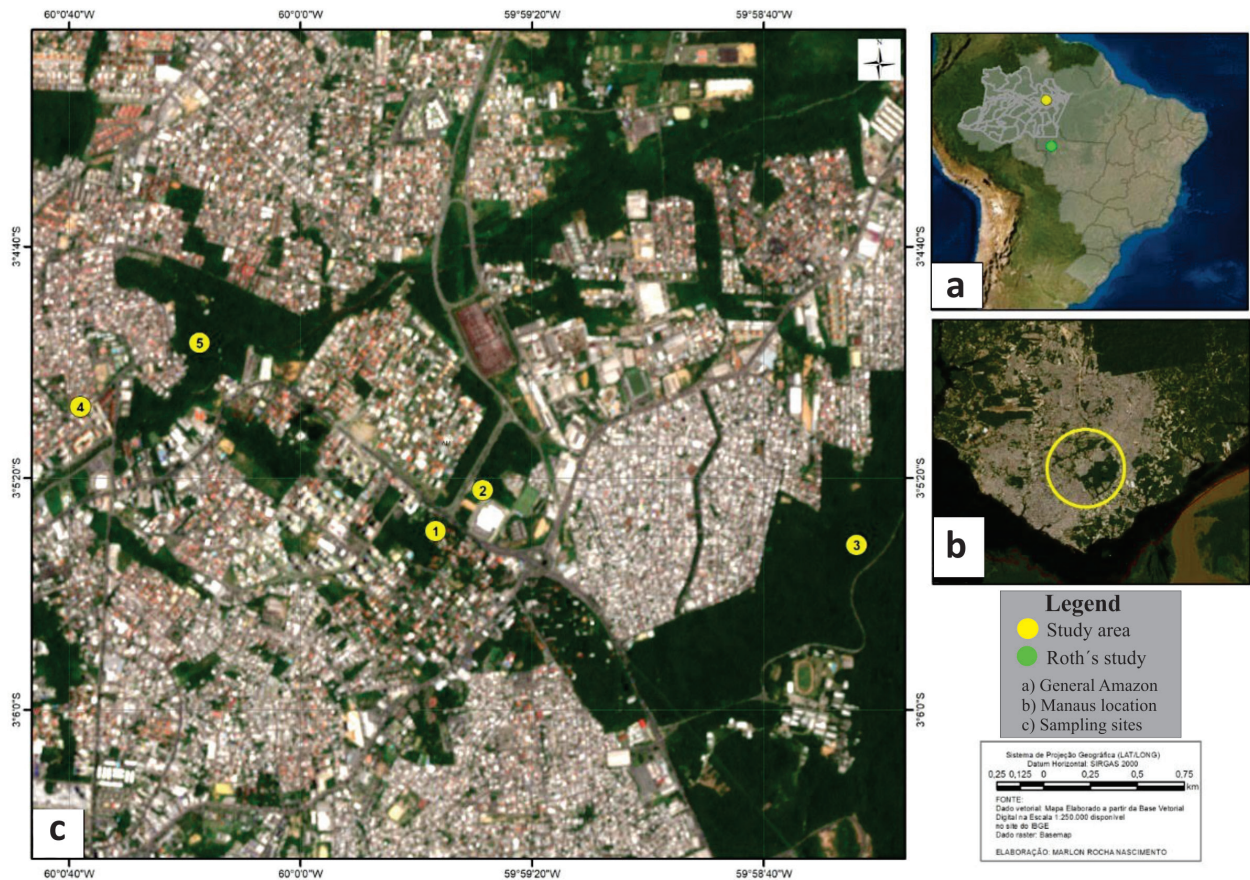
Figure 1. Study region: a) location of Manaus city (yellow bullet) and Aripuanã region (green bullet), b) region where the parrots were sampled within the Manaus urban area (yellow circle), c) detailed of the study landscape showing the five main study sites (yellow numbered bullets).

Herbarium for Knowledge and Conservation of the Brazilian Flora (https://reflora.jbrj.gov.br). Plant identifications were confirmed by one of the authors (VS) with great experience of the central Amazon flora. Only two plants (1% of total) were not fully identified, and were treated as morphotypes during analysis.

Morphometric data of parrots was obtained from specimens deposited in the bird collections of the National Institute of Amazonian Research (INPA; Manaus, Brazil), Museum of Zoology of the University of São Paulo (MZUSP, Brazil), Natural History Museum bird collection (Tring, UK) and Museu Paraense Emílio Goeldi (MPEG; Belém, Brazil). We used rulers, digital calipers and specimen labels to collect the following information: weight (g), total length (mm), tail length (mm), wing length (mm), tarsus length (mm), exposed culmen (mm), beak height (mm), beak width (mm). We obtained measurements of at least two adult individuals *per* species.

Data analysis

We applied Kruskal-Wallis analysis to test for differences in foraging heights and flock size between parrot species. The food niche breadth of each species was estimated with a standardized Levin's index (Hurlbert 1978) that ranges from 0 for specialized diets to 1 for generalist diets. In addition, food niche overlap was estimated with Pianka indices (Krebs 1999), which also range from 0 (no shared resources) to 1 (complete diet overlap).

We tested the hypothesis that the degree of niche overlap between species would be different from null models (Gotelli & Entsminger 2001). Two models were used in the simulations (Gotelli & Entsminger 2001): i) an algorithm where niche width was randomized and the resource usage states were fixed (RA2), and ii) an algorithm where both niche width and the state of resource use were randomized (RA3). The two algorithms gave similar results, and we show only the results of the RA2 model. We used the EcoSim Professional program (http://www.garyentsminger.com/ecosim/) to calculate the Pianka index and apply null models with 1000 iterations.

Parrot body masses were well correlated with other morphological measurements such as tarsus and wing length (R^2 adjusted varying from 0.50 to 0.89, $P < 0.0001$ in all comparisons). Accordingly, we used simple linear regression between species mean body masses and Levin´s indices to test whether larger parrots tended to have greater niche widths. To test whether the most morphologically-similar species had greater niche overlap, we used the morphometric measurements described above to calculate the Euclidean distances between each pair of parrot species.

We compared the matrices of morphological (= Euclidean) distance and niche overlap (= Pianka index) through a Relate analysis using the Primer 6.0 program (Clarke & Gorley 2006). Relate is a non-parametric analogue to the Mantel test and is used to analyze the hypothesis of no agreement in two independently-derived resemblance matrices, and measure their agreement via a Spearman (Rho) rank correlation coefficient (Clarke & Warwick 2001). If diet overlap between parrot species is affected by their morphological attributes, we would expect to find a significant correlation between these matrices.

Ideally, our data should be better compared with undisturbed habitats in a region near Manaus and with similar parrot assemblage. Unfortunately, no such data set was available at the time of the analysis. Consequently, the data we collected were compared with those obtained by Roth (1984), who investigated parrot feeding ecologies in the upper Rio Aripuanã (Fig. 1), a well-preserved region of the southern Amazon dominated by upland forests and rivers environments.

There are major differences in the sampling effort and the assemblage of parrot in Manaus and Upper Aripuanã. Roth (1984) obtained 398 feeding bouts for 15 species of parrots feeding on parts of 98 plant species. Despite these differences between the studies, we consider this comparison is valuable since: i) four parrot species studied by Roth (1984) were also found in Manaus, and ii) the methods used in the two studies were very similar.

To improve comparability between studies we used the same metrics for niche breadth and overlap as Roth (1984). To compare the diversity of plant species consumed by parrots in urban and natural environments, we built cumulative curves of extrapolated species richness to a common sampling effort (Colwell et al. 2012). Feeding bouts were considered as a single entity, and were used to build the cumulative curves using the Estimates (S) program (Colwell et al. 2012). The non-overlap of the confidence intervals with similar sampling efforts indicated significant differences in consumed plant species richness between urban and natural environments.

RESULTS

Parrots diet and foraging behavior

We recorded a total of 203 feeding bouts from eight species of parrots that consumed parts

of 51 plant species from 21 botanical families (Appendix). The number of foraging events varied widely between parrot species, with a high number of observations collected for *Brotogeris versicolurus* (White-winged Parakeet, n = 88), *Psittacara leucophthalmus* (White-eyed Parakeet, n = 35), *Amazona amazonica* (Orange-winged Amazon, n = 27), *Orthopsittaca manilatus* (Red-bellied Macaw, n = 22) and *Ara macao* (Scarlet Macaw, n = 17). In contrast, few food records were obtained for *Amazona festiva* (Festive Amazon, n = 5), *Pionus menstruus* (Blue-headed Parrot, n = 5) and *Graydidascalus brachyurus* (Short-tailed Parrot, n = 4).

Parrot diets were dominated by plants from the families Arecaceae, Anacardiaceae, Fabaceae, Melastomataceae and Myrtaceae (71% of records) (Fig. 2). Native plants dominated the overall parrot assemblage diet, with a smaller contribution from exotic plants (Fig. 3). The species *A. festiva*, *O. manilatus* and *P. menstruus* consumed exclusively native plants, while the diets of *A. amazonica*, *B. versicolurus*, *P. leucophthalmus*, *G. brachyurus* and *A. macao* were complemented with exotics (Fig. 3).

Collectively, the parrot assemblage consumed mainly pulp (64% of records), followed by seeds (20%), whole fruit (8%), flowers (3%), leaves (3%) and nectar (2%). *Brotogeris versicolurus* consumed all plant parts, even though their diet was dominated by fruit pulp (Supplementary Material - Figure S1). Leaves and nectar were consumed only by *B. versicolurus* and *P. menstruus*, while flowers were consumed by four species (Fig. S1).

The average foraging height for all species combined was 16 meters, with only *A. macao* and *A. festiva* foraging at greater heights (Fig. S2 - KW, H = 15.3, *P* = 0.03). The mean group size engaged in foraging activity was four individuals, although larger groups of parrots were seen flying over the study areas. In general, flock size was quite consistent between species, except for the *B. versicolurus* that foraged in larger flocks than *A. amazonica* and *A. macao* (Fig. S2 - KW, H = 50.24, *P* < 0.0001).

Parrot diets: niche amplitude and overlap

The number of plant taxa consumed by parrot species varied from 3 to 25 (Table I). Native açaí (*Euterpe oleracea*, Arecaceae), and exotic
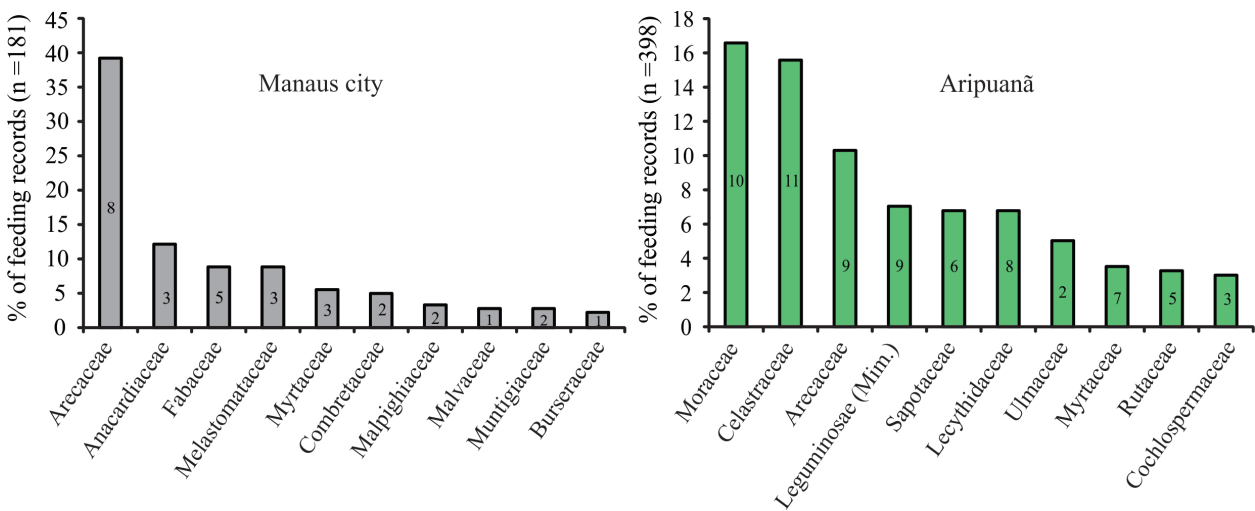
Figure. 2. Principal plant families' whose species were consumed by parrots in Manaus (left graph) and Aripuanã region (right graph). Numbers within the columns indicate the number of parrot species that fed on plants from respective botanical families.

mango (*Mangifera indica*, Anacardiaceae) were the dominant plants in the diet of most species (Table I).

Niche width was quite variable between parrot species (Table I). The lowest Levin´s index value was 0.40 (for *B. versicolurus*), indicating that this species tends to concentrate its foraging activity on a small number of species, even though it consumed a great diversity of plants overall (n = 25 species). In contrast, *A. festiva* and *G. brachyurus* had broader food niches, indicative of a generalist diet (Table I). However, the number of foraging observations for each of these two species was low, making it difficult to interpret this result. Other species had intermediate niche width values (Table I), with some tending to have more specialized (*A. amazonica*, *O. manilatus*), or more generalist diets (*P. leucophthalmus*).

Food niche overlap between species ranged from 0 to 0.74, with a mean value of 0.15 (Table II). Niche overlap was greatest between the following pairs of species: *G. brachyurus*/*P. menstruus*

(0.74), *A. amazonica*/*O. manilatus* (0.62) and *B. versicolurus*/*P. leucophthalmus* (0.54). The other species pairs showed low overlap values, with half of the paired comparisons having values less than or equal to 0.10 (Table II), indicating a broad partitioning of resources.

Observed Pianka index values were significantly higher ($P < 0.001$ in the simulations) than mean and variance of the simulated values (Fig. S3). Diet overlap values were relatively low (between 0.19 and 0.20), but significantly higher than the simulated values, suggesting that food resource use was structured by interspecific competition with broad resource partitioning.

Morphology of parrots and their food niche breadths

No relationships were observed between mean parrot body masses and the number of plant species consumed (F = 0.68, P = 0.55), nor with the Levin´s indices (F = 0.29, P = 0.62) (Table I). Similarly, no relationships between body mass and the number of plant species consumed (F
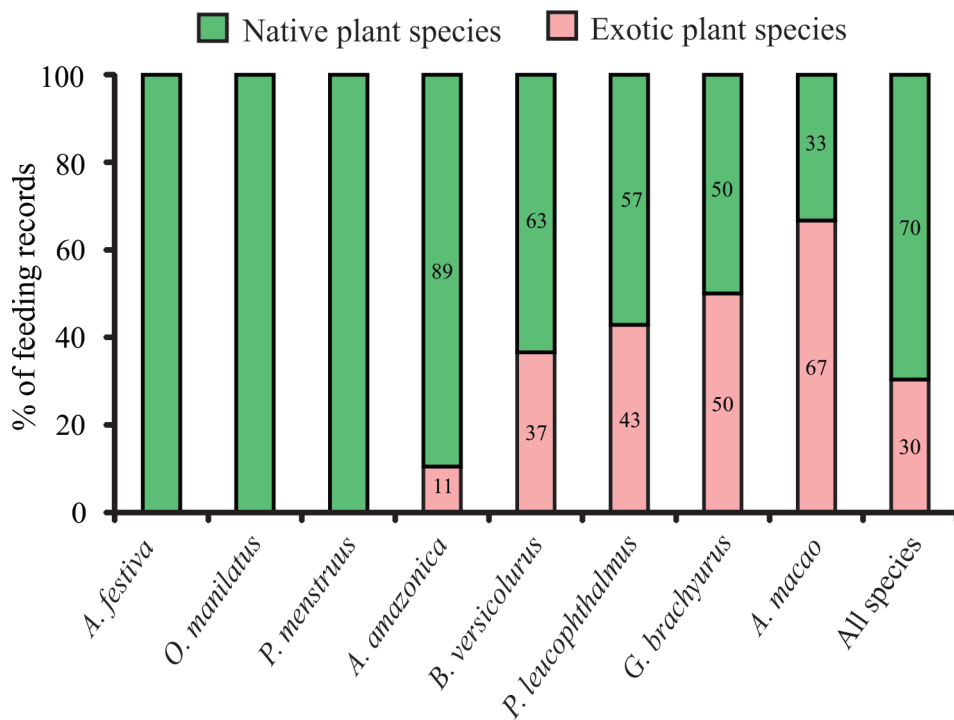
Figure 3. Contribution of native and exotic plant species to the diet of parrots recorded in Manaus city. The current numbers represent percentages of total.

= 1.15, *P* = 0.30), or the Levin´s index (F = 1.36, P = 0.26) were observed for parrots from the natural environment (see below). However, larger species tended to include more seeds in the diet (F = 7.76, *P* = 0.03). This relationship was greatly affected by *A. macao* and, when this species was excluded from the analysis, the effect of body mass on seed consumption disappeared (F = 1.43, *P* = 0.28). These results suggest that food niche breadth is not related to parrot species body mass for either urban or natural environments.

In contrast, we found a negative correlation between the morphological distance between species pairs and Pianka index values (Relate Rho test = 0.39, *P* = 0.03, 999 permutations), indicating that morphologically similar species pairs tended to have higher food niche overlaps (Fig. 4).

Parrot feeding ecology: natural and urban environments

The parrots studied by Roth (1984) fed on plants from botanical families almost completely different from those used in the urban environment, with only Arecaceae and Myrtaceae being consumed by parrots from both studied regions (Fig. 2). Even for these shared plant families, the relative proportions of use were different in the urban and natural environments. The family Arecaceae, for example, was responsible for 35% of records in the urban environment, but represented only 10% of those reported by Roth (1984) from the natural environment (Fig. 2).

The censuses to assess the plant diversity used by parrots were incomplete in the natural and urban environments, even considering the extrapolation to similar sampling effort (Fig. 5). The number of plant species consumed in the natural environment was greater than in the urban environment at a similar level of sampling effort (Fig. 5). However, considering only the four parrot species occurred in both the urban and natural environments, there is no significant difference in the diversity of plants consumed (Fig. 5).

Comparisons of Levin's indices between the urban (Table I) and natural (Supplementary Material - Table SI) environments indicated

Table I. Diet breadth measured by the number of plant species consumed, Levins indices and dominant plant in the diet for each parrot species recorded in Manaus. E for exotic species and N for native species.

Parrot species	N° of feeding records	N° of species	Levins' indices	Dominant plant in the diet
Brotogeris versicolurus	88	25	0.40	*Mangifera indica* E (19%)
Psittacara leucophthalmus	35	15	0.76	*Mangifera indica* E (11%)
Amazona amazonica	27	15	0.45	*Euterpe oleracea* N (29%)
Orthopsittaca manilatus	22	4	0.46	*Euterpe oleracea* N (50%)
Ara macao	17	8	0.74	*Hevea spruceana* N (23%)
Amazona festiva	5	5	1	*Abarema auriculata* N (20%)
Pionus menstruus	5	3	0.64	*Bactris gasipaes* N (60%)
Graydidascalus brachyurus	4	3	0.83	*Bactris gasipaes* N (50%)

differences in the niche breadth of the species recorded in the two study regions. Two species (*P. menstruus*: Levin´s index 0.38 vs. 0.64, and *P. leucophthalmus*: 0.55 vs. 0.78) showed broader diet niche breadths in the urban environment. In contrast, *A. macao* diet niche breadth was greater in the natural environment (0.95 vs. 0.68). Red-bellied Macaw, consumed only one species of plant in the natural environment (*Mauritia* sp., Arecaceae: Roth 1984), and four palm species in the urban environment (*Euterpe oleracea, E. precatoria, Mauritia flexuosa* and *Mauritiella armata*).

Pianka index values were similar between the natural and urban environments (Table SII) (Mann Whitney test, $Z = 1.02$, $P = 0.15$), indicating comparable levels of diet overlap between the parrot species in their respective assemblages. Analogous results were obtained when the Pianka index was compared for pairs of species common to the natural and urban environments (Wilcoxon test, $Z = 0.94$, $P = 0.17$). Some pairs of species, however, had notably different diet overlap values in the two environments. For example, the *A. macao*/*P. menstruus* species pair showed higher diet overlap in the natural

than in the urban environment (Pianka index 0.39 vs. 0.00, respectively), while *O. manilatus*/*P. leucophthalmus* had greater overlap in the urban environment (0.32 vs. 0.00).

DISCUSSION

Parrot diets

We recorded feeding events for eight of the 14 parrot species found in Manaus, a city with the highest recorded diversity of parrot species in Brazil (Fragata et al. 2022). The diversity of plants consumed by these birds in anthropic environments (including cities) ranges from six to 96 plant species (Silva 2013, Santos & Ragusa-Netto 2014, Silva & Cordeiro 2016, Marques et al. 2018, Rico-Silva et al. 2021, Álvarez-Castillo et al. 2022). Although the plant diversity in our study is in line with previous analysis, we emphasize that our survey must be considered as preliminary due to the small overall number of feeding bouts collected. Despite the limitation of incomplete censuses, we documented consistent patterns in the feeding ecology of the studied species.

Parrot foraging events were strongly concentrated on palm trees (Arecaceae). It is

Table II. Values of Pianka indices, measuring the overlap in the diet among paired parrot species recorded in Manaus. Low values (<0.10) are underlined and high values (>0.50) are in bold. Body mass for each species is also shown.

| Parrot species	B	C	D	E	F	G	H
Amazona amazonica **(A)** – 470 g	0.10	0.11	0.51	0.09	**0.62**	0.10	0.33
Amazona festiva **(B)** – 500 g		0.13	0.01	0.37	0.03	0.40	0.14
Ara macao **(C)** – 1250 g			0.12	0.00	0.02	0.00	0.10
Brotogeris versicolurus **(D)** – 72 g				0.28	0.43	0.01	**0.54**
Graydidascalus brachyurus **(E)** – 157 g					0.00	**0.74**	0.30
Orthopsittaca manilatus **(F)** – 329 g						0.00	0.31
Pionus menstruus **(G)** – 140 g							0.00
Psittacara leucophthalmus **(H)** – 149 g							

not possible to know if this pattern reflects fruit selectivity or availability as we do not have quantified data for fruit production and availability across the study period. However, palms are abundant and diverse in forest fragments in Manaus (Serafini 2007), as well as being common in backyards and public spaces in the city, suggesting that palms are consumed as a function of their availability, as happens in natural habitats (e.g. Lee et al. 2014). Nevertheless, palm trees have been identified as an important component of parrot diets in other Brazilian cities (Silva 2013, Santos & Ragusa-Netto 2014, Silva & Cordeiro 2016, Marques et al. 2018).

Native plant species dominated the parrot diets in Manaus and again it is not possible to interpret this pattern in terms of resource selectivity and availability. However, it should be noted that exotic species are important for some of the parrot species. Indeed, exotic plants are generally an important component of the diets of parrots that colonize urban areas in South America (Nunes & Santos-Júnior 2011, Silva 2013, Silva & Cordeiro 2016, Marques et al. 2018). For instance, *Terminalia catappa* (Combretaceae), an exotic plant of Australasian

origin, was responsible for 23% of the total diet of *Ara macao* in our study. The same species is also reported as abundant in the diet of macaws in northwestern São Paulo and Costa Rica (Silva 2013, Matuzak et al. 2008, Hamm et al. 2020).

The consumption of exotic plants may be related to seasonality of fruit production by native species. For instance, exotic plants were important in the diet of the parakeet *Forpus xanthopterygius* only during the dry season in a municipality of São Paulo, Brazil (Silva & Melo 2018). The complementary seasonal production of fruits (and other food items) by exotic and native species may guarantee the availability of food resources throughout the year, favoring the use of urban environments by parrots (Simão et al. 1997, Santos & Ragusa-Netto 2014, Kilpp et al. 2015). Unfortunately, studies of temporal and spatial variation in fruit production of exotic and native species are lacking in our study region. Such data is a clear priority for future research to foster an in-depth understanding of frugivorous feeding ecology in tropical cities, including Manaus.

Another important aspect not explored in our study is the mutualist interaction between parrots and plants (Bascompte et al. 2006,
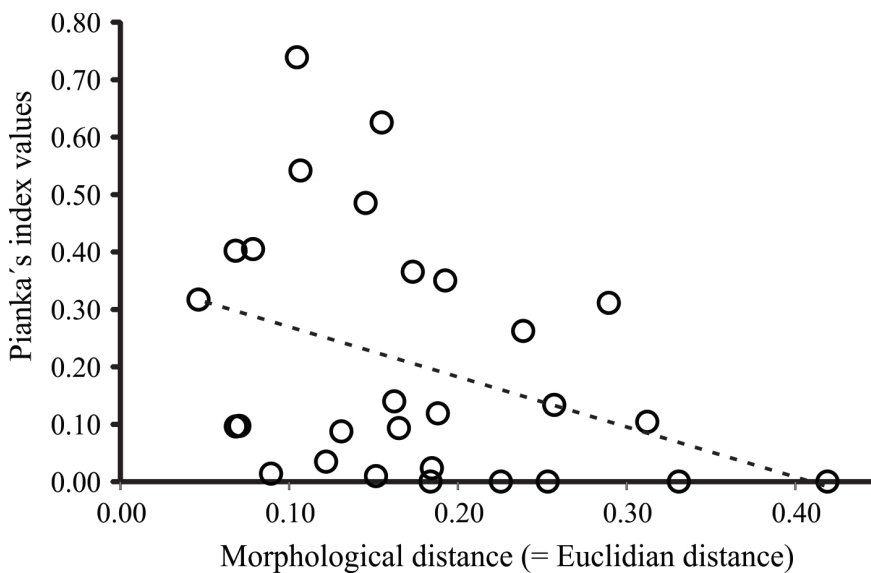
Figure 4. Effect of morphological differentiation in the diet overlap of parrot species. Each point represents a pair of parrot species. Euclidian distances were calculated from seven morphological variables (see Materials and Methods).

Blanco et al. 2015, 2018), Hernández-Brito et. al. 2021). Parrots are recognized by this role as seed predators and seed dispersal of plants in natural environments (Blanco et al. 2021, Hernández-Brito et al. 2021). How these mutualist networks are altered in urban habitats is poorly documented and deserve further attention.

Other food niche dimensions

In accordance with our data, parrot species with contrasting body masses have been reported to forage at different heights, with the largest species tending to occupy the highest vegetation strata (Roth 1984, Simão et al. 1997, this study). Parrots also are social and gregarious animals that show great variation in flock size, which could be associated with food availability, competition, reproduction and foraging strategies (Chapman et al. 1989, Pizo et al. 1995, Masello et al. 2006, Kilpp et al. 2015). In our study, most foraging records involved small parties of four to six birds and a similar pattern has been reported in urban environments in southwestern Brazil (Marques et al. 2018). Foraging in smaller flocks could be a strategy

to diminish food competition among parrots, as suggested by Chapman et al. (1989) for a parrot assemblage from natural habitats in Costa Rica.

Among the parrots in Manaus, *B. versicolurus* was notable for feeding on all plant parts considered in our study. Such flexible foraging behavior has also been documented in other members of the genus *Brotogeris*. For example, *B. chiriri*, which occurs widely in cities in southeastern Brazil, also, consuming many different plant parts (Silva & Cordeiro 2016, Marques et al. 2018). This suggests that the flexible and diversified use of food resources can facilitate the exploitation of urban environments by *Brotogeris* species.

Food niche breadth and overlap

Exploitation of urban environments can be facilitated when assemblages are composed of species with food niches of different breadths, since the food supply in the city may display strong spatial and temporal restrictions and variations (Fuller et al. 2008, Palacio 2020). The niche breadths of parrot species in Manaus varied considerably, with a general trend to
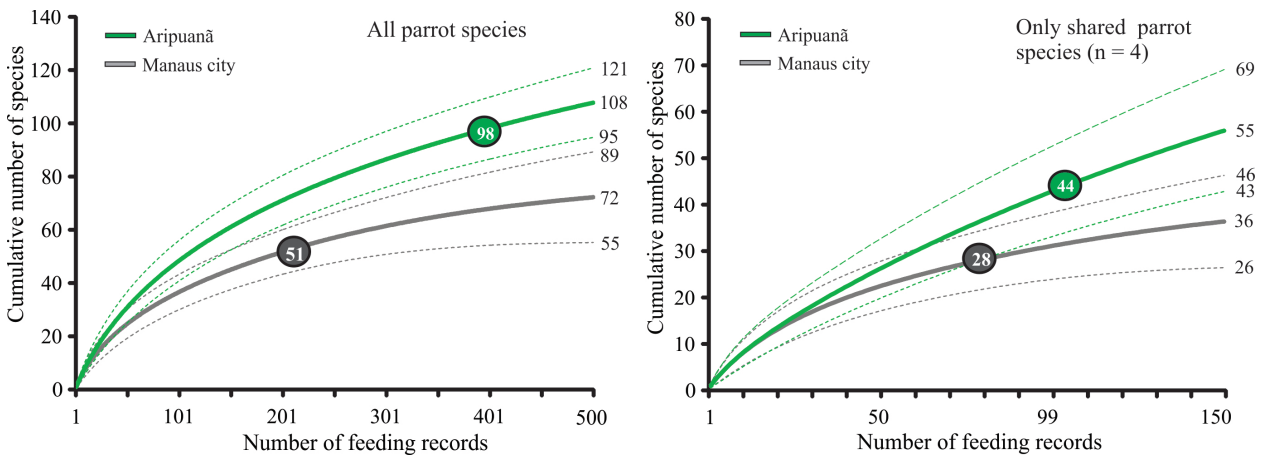
Figure 5. Cumulative curves of plant species in function of the number of feeding bouts collected in urban (Manaus city) and natural (Aripuanã region) environments. The left-hand graph shows data from all parrot species, while the right-hand graph considered only data from the four species that occurred in both urban and natural environments. Numbers inside bullets indicates observed number of species, and numbers in front of each curve show species richness obtained from sampling effort extrapolation. Confidence intervals are indicated by pointed curves.

more generalized diets. Food niche breadth, however, can be highly variable across time. In a year-round study of the *A. ararauna* diet in a city of central Brazil, Santos & Ragusa-Netto (2014) reported Levin´s indexes that varied from 0.05 to 0.96, with low values accompanying intense, but temporally-restricted periods when foraging focused nearly-exclusively on cashew (*Anacardium occidentale,* Anacardiaceae).

The lack of correlation between parrot body mass and niche breadth in both natural and urban environments suggests that larger species do not necessarily have greater food niche breadth. Indeed, diet breadth is largely independent of body mass of Neotropical parrot species (Benavidez et al. 2018). It is possible that the variations in the species diet breadth are more closely associated with behavior and ability to select different food items, than with variation in the measured aspects of parrot morphology.

The extent of diet overlap between species was relatively low in both Manaus and Aripuanã. Such a pattern suggests that interspecific competition may play an important role in structuring parrot assemblage in both natural and strongly modified environments. Diet overlap between parrot species can be attributed, at least in part, to differences in species morphology. Morphologically-similar species tend to show greater food niche overlap, suggesting that the structure of parrot assemblage is influenced by interspecific competition for a wide range of resources (Renton et al. 2015, Benavidez et al. 2018).

Natural and urban environments

The biggest difference in the feeding ecology of parrots in Manaus and the natural environment was the greater diversity of plants consumed by parrots in the latter. However, we did not observe differences in the diversity of plants consumed between the species shared between the two environments, suggesting that the occupation of urban environments does not imply an impoverishment in the diet of the parrot species. It is possible that exotic plants compensate for part of the loss of native species caused by urbanization. In the environments studied by Roth (1984), the contribution of exotic plants to the parrots' diet was almost nil, as might be expected in a little-anthropized area. However, in the current study such species accounted for 30% of foraging events. Another relevant aspect is the marked dominance of a single botanical family (Arecaceae) in the diet of urban parrots compared to those assemblages found in natural environments.

These general comparisons suggest that parrot species which occupy urban environments adjust their diets to exploit plants, such as Arecaceae, with large crop volumes available over extended periods. In addition, exotic species, whose fruit production could potentially coincide with gaps in food availability provided by native species, may help smooth out annual variations in resource availability. The occupation of the urban environment does not imply greater interspecific competition, since the pattern of niche overlap between species in the urban environment studied here closely paralleled that found in the natural environment.

Conservation

The species-rich parrot assemblage of Manaus depends both on the native plants found in the forest fragments and on exotic or native species planted in public or residential spaces. Thus, the protection of fragments of natural habitats and the planting of native or exotic species are complementary strategies for parrot population management in this central Amazonian city. The creation of new municipal protected areas, especially in areas of urban expansion, should

be considered one of the priorities for the protection of parrot species and other native animals and plants in Manaus. In addition, the public administration should encourage the cultivation of plants that are attractive to both birds and other frugivorous animals in public spaces and private residencies. The afforestation initiatives by municipal administration could be beneficed by the data on plants species used by parrots recorded in our study (Appendix).

Acknowledgments

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APPENDIX

List of plant consumed by eight species of parrots (Aves: Psittacidae) in the urban environment of Manaus (Brazil). The numbers refer to the feeding events (feeding bouts) for each species.

Families/Species	*Amazona amazonica*	*Amazona festiva*	*Ara macao*	*Brotogeris versicolorus*	*Graydidascalus brachyurus*	*Orthopsittaca manilatus*	*Pionus menstruus*	*Psittacara leucophthalmus*	Grand total
Anacardiaceae			1	17	1			5	24
Mangifera indica				17	1			4	22
Tapirira guianensis			1					1	2
Arecaceae	11	2	2	20	2	22	3	9	71
Astrocaryum aculeatum	1			3					4
Bactris gasipaes	1	1			2		3		7
Elaeis guineensis								2	2
Euterpe oleracea	8			15		11		4	38
Euterpe precatoria	1	1	2	1		1		3	9
Mauritia flexuosa						9			9
Mauritiella armata						1			1
Roystonea oleracea				1					1
Calophyllaceae		1							1
Calophyllum brasiliense		1							1
Cannabaceae								3	3
Trema micrantha								3	3
Clusiaceae			1						1
Symphonia globulifera			1						1

Families/Species	Amazona amazonica	Amazona festiva	Ara macao	Brotogeris versicolurus	Graydidascalus brachyurus	Orthopsittaca manilatus	Pionus menstruus	Psittacara leucophthalmus	Grand total
Combretaceae			4	5					9
Terminalia catappa			4	5					9
Euphorbiaceae			4	4				1	9
Alchornea discolor				4					4
Croton amazonicus								1	1
Hevea spruceana			4						4
Fabaceae	11	1	5	4			2		23
Abarema auriculata		1							1
Cassia grandis							1		1
Clitoria fairchildiana	1								1
Inga alba	1			1					2
Inga cinnamomea		1							1
Inga laurina				1					1
Inga marginata	1		2						3
Inga vera				1			1		2
Leucaena leucocephala	4			1					5
Pseudopiptadenia sp.	1								1
Schizolobium parahyba	2		2						4
Sp 17 undetermined	1								1
Lecythidaceae				1					1
Bertholletia excelsa				1					1
Loranthaceae				2					2
Passovia pedunculata				2					2
Malpighiaceae				2				6	8
Byrsonima chrysophylla				2				4	6
Byrsonima rodriguesii								1	1
Byrsonima sp.								1	1
Malvaceae				5					5
Pseudobombax munguba				5					5

Families/Species	Amazona amazonica	Amazona festiva	Ara macao	Brotogeris versicolorus	Graydidascalus brachyurus	Orthopsittaca manilatus	Pionus menstruus	Psittacara leucophthalmus	Grand total
Melastomataceae	1			14				1	16
Miconia argyrophylla				4				1	5
Miconia multiflora	1			8					9
Miconia sp.				2					2
Meliaceae	2								2
Cedrela fissilis	2								2
Moraceae				3					3
Artocarpus heterophyllus				1					1
Ficus benjamina				2					2
Muntingiaceae				4				1	5
Muntingia calabura				4				1	5
Myrtaceae				5	1			4	10
Psidium guajava				2	1			4	7
Syzygium malaccensis				3					3
Não identificada	1			1					2
Sp 13 undetermined				1					1
Sp 9 undetermined	1								1
Oxalidaceae								2	2
Averrhoa carambola								2	2
Sapotaceae	1								1
Pouteria caimito	1								1
Siparunaceae								3	3
Siparuna guianensis								3	3
Urticaceae		1		1					2
Cecropia membranacea				1					1
Pourouma cecropiifolia		1							1

SUPPLEMENTARY MATERIAL

Figures S1, S2, S3.
Tables SI, SII.

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