Review

Diet of Neotropical parrots is independent of phylogeny but correlates with body size and geographical range

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Body mass and geographical range are two main drivers of diet in animals, yet how these factors influence diet in the morphologically and ecologically diverse avian group of Psittaciformes is little known. We reviewed current knowledge of the diet of Neotropical parrots and assessed the relation between diet (breadth and composition), phylogeny, body mass and geographical range. Diet has been documented for 98 of 165 species, but information is available only for 34 of 59 threatened species, and countries with high species diversity (> 20 species) had few studies (one to seven). Neotropical parrot species consumed 1293 plant species of 125 families. When assessing the relative frequency of different food items in the diet (seed, fruits, flowers, leaves, nectar, bark and stems), we found that parrots mostly exploited seeds (41.9%) and fruits (38.3%) of native species. Diet overlap was very low among genera (0.006–0.321). At the species level, geographical range and body size explained the variation in diet composition. In particular, small parrots of restricted distribution had a distinct diet composition relative to either large or widely distributed species. Although body size and geographical range showed phylogenetic inertia, diet was independent of phylogenetic history. Our review not only reveals ecological factors explaining diet in a generalist group but also exposes information gaps across the Neotropical region.

Keywords: conservation, diet composition, generalists, Psittacidae.

Several physiological and ecological factors affect diet in animals (Karasov 1986). Among these factors, body size and geographical range emerge as two main drivers of both diet breadth and diet composition. Body size is frequently described as one of the most important factors explaining variation in diet, as it determines metabolic rate, digestive efficiency and energetic requirements (Schmidt Nielsen 1984, Peters 1986). Fundamentally, larger species have more energetic requirements than smaller species, given that metabolic rate relates positively to body mass (Nagy 2005). Accordingly, it is expected that both diet breadth and diet composition will vary as a function of body size. In particular, body size may be positively related to food item size (Ashmole 1968, Wheelwright 1985, Dickman 1988, Gionfriddo & Best 1996, Scharf *et al.* 2000), and to diet breadth

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(Brown & Maurer 1989, Barclay & Brigham 1991) because large animals can capture and consume both small and large food items, whereas small animals are limited to small items (Barclay & Brigham 1991). This simple relation between body size and diet breadth has been found in many taxa including birds (Brändle *et al.* 2002), mammals (Robinson & Redford 1986, Fleming 1991, Tershy 1992, Fa & Purvis 1997), fish (Hyndes *et al.* 1997) and arthropods (Sloggett 2008).

The hypothesis linking diet breadth and geographical range is that by exploiting a higher number of resources and being able to maintain viable populations across a wider variety of conditions, a species with a broader diet should become more widespread (Brown 1984, Dennis *et al.* 2005). However, a positive relation is also predicted if larger-bodied species have greater dispersal abilities that translate into larger geographical ranges (Reaka 1980, Brown & Maurer 1989, Arita *et al.* 1990, Laube *et al.* 2013, but see Gaston & Blackburn 1996). In this case, widely distributed species simply encounter a greater variety of foods compared with species with more restricted ranges (Costa 2009). In a meta-analysis, Slatyer *et al.* (2013) found a positive relation between range size and diet breadth in several plant and animal groups, supporting this general pattern in nature but not distinguishing between the above hypotheses.

Parrots (Order Psittaciformes) are one of the largest groups of birds, with 398 species distributed in tropical and subtropical areas of the world (IUCN 2017). The high diversity of morphology, body mass and foraging behaviour, as well as wide variation in range provide a suitable model for testing the relation between diet, body size and geographical range (Blanco *et al.* 2018). Approximately 30% of parrot species are threatened by habitat loss, fragmentation and the pet trade (Olah *et al.* 2016, Berkunsky *et al.* 2017, Collar 2017, IUCN 2017). In ecological terms, parrots play a key role in the functioning and maintenance of biodiversity by establishing antagonistic and mutualistic interactions with numerous plant species (Dirzo & Miranda 1991, Coates Estrada *et al.* 1993, Blanco *et al.* 2015, 2018, Tella *et al.* 2015, Baños Villalba *et al.* 2017, Montesinos Navarro *et al.* 2017). In a worldwide review of the resource requirements of parrots, Renton *et al.* (2015) found that parrots are trophic generalists with a high plasticity in diet, consuming a wide variety of food items such as seeds, fruits, flowers and nectar from a high diversity of plant species (Lee *et al.* 2014, Blanco *et al.* 2015, 2018, Renton *et al.* 2015). Furthermore, they employ a variety of foraging strategies, adjusting their behaviour to seasonal food availability and even adapting to alternative and novel food sources in modified environments (Matuzak *et al.* 2008). Body size is also related to diet composition in this group. For example, Matuzak *et al.* (2008) found that smaller species tend to feed more on fleshy fruits, seeds and flowers, whereas in parrot assemblages from Costa Rica, larger species tend to feed more on hard seeds and dry fruits.

Despite numerous diet studies in parrots, it remains unclear how ecological factors, including body mass and geographical range, contribute to explaining diet composition and diet breadth patterns at a regional scale. In this study, we carried out a review of the diet of Neotropical parrots (tribe Arini), because a high species diversity of parrots occurs in the Neotropics (165 species, 41.5% of all species) and data are available for all genera in this region (Renton *et al.* 2015). This allowed us to account for a high interspecific variation in body mass and geographical range size to explore factors associated with variation in diet. Data on other attributes that could contribute to explaining diet patterns (e.g. migratory behaviour and beak shape) are lacking for most species.

Based on the theoretical background described above, we predicted that diet breadth and composition are additive functions of both body mass and geographical range, and that larger species with broad distributions are expected to have both broader and different diets compared with smaller species with narrow geographical ranges. Although we made no *a priori* predictions of possible synergistic effects between geographical range and body size, we also explored this possibility by assessing the interaction between both traits. Finally, we also aimed to identify critical diet information gaps with respect to conservation status and country of origin of individual species.

METHODS

Data compilation

Diet information was collected from the virtual library of The Working Group Psittaciformes from the International Ornithologist's Union, with a

database of approximately 2650 publications. One of the authors (A. Benavídez) reviewed all the studies in the Neotropical biogeographical realm, covering a period from January 1970 to November 2017. We also consulted the ISI web of knowledge with keywords 'parrots', 'diet' and 'parrot', and the scientific names of individual parrot species. All studies including quantitative and descriptive data on diet of parrots in their natural range were considered. The following data were obtained from each study (whenever possible): (1) country and year of the study, (2) parrot species studied, (3) number and part of plant species consumed, (4) plant growth form (tree, treelet, shrub, herb, cactus, liana and epiphyte), (5) distribution range of plant species consumed (native or exotic), (6) length of the study, (7) methodology (systematic design or casual observations), (8) biogeographical region and (9) season (dry, wet, breeding and/or non-breeding). Furthermore, data on conservation status (classification of species at high risk of global extinction) were obtained from IUCN Red List Categories (IUCN 2017), which has nine categories: Extinct, Extinct in the wild, Critically endangered, Endangered, Vulnerable, Near threatened, Least concern, Data deficient and Not evaluated. The biogeographical region (hierarchical system of geographical areas in terms of their biota) in the Neotropics was obtained from Morrone (2001). The Neotropical region comprises seven dominions (Mesoamerican, Pacific, Boreal Brazilian, Southwestern Amazonian, Southeastern Amazonian, Chacoan and Parana) and 53 provinces. We quantified body mass (g) as a surrogate for body size and geographical range at the spatial extent of occurrence (ha) in a given species (IUCN 2017). Data on each variable were obtained from Dunning (1992) and Birdlife International (2017).

Diet composition and data analysis

Diet data were extracted from primary studies on a presence/absence basis. The relative frequency (proportion of studies in which a food item was recorded) of different food items in the diet (seed, fruit, flower and others) was computed as the total number of records of item i (e.g. seed) divided by the total number of records of all items (seed, fruit, flowers and others). This value was computed for each parrot species. The relative importance of a given plant family in the diet of each parrot species was estimated as the number of plant species consumed per parrot species divided by the number of plant species recorded in the family. The relative frequency of plant growth form consumed was calculated as the number of plant species consumed per plant growth form. We estimated diet breadth at the parrot species level using the Shannon–Wiener measure (Shannon 1948) and characterized diet composition with non-metric multidimensional scaling (NMDS; Kruskal & Wish 1978) based on a presence/absence Bray–Curtis dissimilarity matrix. The presence of a given plant family in the diet was used instead of the number of plant species of a given plant family because of the bias that could result from differences in sampling effort between parrot species, probably due to abundance and geographical range. NMDS is a non-parametric ordination technique that iteratively minimizes the difference between distance in the original matrix and distance in the reduced ordination space ('stress'; Legendre & Legendre 1998). The lower the stress, the better the approximation in reduced space. Empirical evidence and simulation studies have shown that a stress value of < 0.2 gives an ordination sufficient for interpretation in ecological terms (Clarke & Warwick 2001). Parrot species that had only one taxon in their diet were excluded from this analysis. We subsequently used NMDS axes 1 and 2 as variables accounting for diet composition (e.g. Moleón *et al.* 2009, Boyle *et al.* 2012, Gow *et al.* 2013), as they gave an acceptable ordination with a low number of dimensions (see Results).

To assess diet overlap among parrot genera, we calculated the Morisita niche overlap index (Morisita 1959), which ranges between 0 (no overlap) and 1 (total overlap). We included all parrot genera to calculate niche overlap, and to test for significance in niche overlap values, we computed 95% confidence intervals (CI) with 999 bootstrap samples for each species pair (De Caceres *et al.* 2011). We decided not to analyse diet overlap at the species level because our aim was to search for general patterns of diet variation and also because of the large amount of data which would have resulted from a 98 × 98 matrix (4753 overlap values).

To analyse relations between diet breadth, diet composition (represented by the NMDS values), body mass and geographical range at the species level, we fitted regression models both controlling and not controlling for phylogeny. We first fitted

ordinary least squares (OLS) models with the Shannon–Wiener measure, NMDS 1 and 2 axes as response variables, and body mass and geographical range as explanatory variables (main effects and their interaction). We controlled for sampling effort using the number of studies as a covariate. Explanatory variables including the number of studies were log-transformed due to right-skewed distributions. To account for shared phylogenetic history among parrot species, we used phylogenetic generalized least squares (PGLS), which incorporates dependence among species as a phylogenetic variance-covariance matrix of the residuals (Pagel 1999, Freckleton *et al.* 2002). To this end, we used a recent phylogeny of the Psittaciformes from Provost *et al.* (2017), which includes phylogenetic relation of 307 extant species from a 30-gene supermatrix. In PGLS, Pagel's λ is a measure of the autocorrelation among the residuals due to a shared phylogeny, which ranges from 0 (no phylogenetic signal) to 1 (perfect phylogenetic signal according to a Brownian motion model of evolution; Pagel 1999). If λ values (estimated by maximum likelihood) were not significantly different from 0, we considered the OLS regression to be the most parsimonious model. Finally, we estimated λ values for body size and geographical range using PGLS by considering each variable as a response in intercept-only models (without covariates).

All analyses and graphs were performed/constructed in R 3.2.1 (R Development Core Team 2016), using the packages vegan (Oksanen *et al.* 2015), spaa (Zhang & Zhang 2013), ape (Paradis *et al.* 2004), caper (Orme *et al.* 2012) and visreg (Breheny & Burchett 2017).

RESULTS

Diet studies

A total of 156 published studies met the criteria to assess diet composition of Neotropical parrots (Appendix S1). Most studies were focused on descriptive and quantitative studies of diet composition (119 studies), and a smaller number provided data on consumption of flowers, fruits or seeds by parrots, other birds and other vertebrates (37 studies). From the 119 studies quantifying the diet of Neotropical parrots, 84 were conducted following a systematic design, 16 described casual observations of plant species consumed, nine

lacked sampling information, six described inventory monitoring, three used stomach contents and only one assessed diet through faecal analysis. For those studies following a systematic design, sampling duration was variable: 0–1 months (four studies), 2–6 months (22 studies), 7–12 months (28 studies), > 13 months (27 studies) and no information (three studies). Information on plant species consumed by Neotropical parrots has been published for 98 of 165 species (59.4%) from 19 Neotropical countries (Appendix S2). From these studies, 44.9% were conducted in Brazil, the country with the greatest parrot species richness (85 species, Piacentini *et al.* 2015), followed by Argentina (10.1%) and Mexico (7.0%). Many countries with a high diversity of parrots provided little information on diet (Bolivia, Colombia, Ecuador, Guatemala, Nicaragua, Paraguay, Peru and Venezuela) or lacked any studies (e.g. French Guiana, Guyana, Honduras, Panama and Surinam). Most studies were conducted in the Caribbean (28.2%) and Amazonian (22.4%) biogeographical subregions. Many studies (46.2%) covered all seasons (wet, dry, breeding or non-breeding) in their respective study areas. Several species with large geographical range sizes only had studies in a small portion of their range (e.g. White-fronted Amazon *Amazona albifrons*, Yellow-naped Amazon *Amazona auropalliata*, Yellow-crowned Amazon *Amazona ochrocephala*, Orange-winged Amazon *Amazona amazonica*, Great Green Macaw *Ara ambiguus*, Orange-chinned Parakeet *Brotogeris jugularis*, Red-fan Parrot *Deroptyus accipitrinus*, Brown-throated Parakeet *Eupsittula pertinax*, Red-bellied Macaw *Orthopsittaca manilatus*, Black-headed Parrot *Pionites melanocephalus*, White-eyed Parakeet *Psittacara leucophthalmus* and Sapphire-rumped Parrotlet *Touit purpuratus*). Of the 165 parrot species in the Neotropics, 59 are considered under some threat level, but there was information on diet for only 34 of the threatened species. The number of studies per threatened species ranged from one to five.

Diet composition

Neotropical parrots consumed 1293 plant species of 125 families. The relative importance of plant family varied among parrot species (Appendix S3). Percentages express the total number of records of an item divided by the total number of records of all items. In terms of plant growth form, parrots

mostly exploited trees (59.8%) and treelets (17.7%), and a small percentage of shrubs (9.7%) and herbs (6.4%). Furthermore, parrots were infrequently (< 2%) reported consuming other plant growth forms (cacti, liana and epiphytes). Most plant species were native (96.7%), with a minor percentage of exotic species (3.3%). Diet in terms of plant parts consumed varied greatly among parrot species (Table 1). Seeds were the most common food (41.8%), followed by fruits (38.3%), flowers (11.9%), leaves (5.0%), nectar (3.1%), bark (1.7%) and stems (0.3%). Invertebrates were observed in 13 genera: *Aliopsitta*, *Amazona*, *Ara*, *Aratinga*, *Brotogeris*, *Enicognathus*, *Eupsittula*, *Myiopsitta*, *Pionites*, *Pionus*, *Psilopsiagon*, *Pyrrhura* and *Thectocercus*.

The NMDS provided a fair representation of diet composition of Neotropical parrots (stress = 0.168; Fig. 1) but showed a clear pattern only in axis 1. The positive extreme of this axis described a larger proportion of the plant families Hypericaceae, Juglandaceae, Musaceae, Myricaceae, Poaceae and Selaginaceae. These families (except for Selaginaceae, which are ferns) are characterized by three fruit types: (a) fleshy fruits with small seeds (< 1 cm), (b) dry fruits with small seeds and (c) nuts or fruits with large seeds (> 1 cm) (Every & Baracat 2009, Milliken 2009, Milliken *et al.* 2009, Longhi Wagner & Oliveira 2011). Parrots consuming these families included large (> 1000 g; Great Green Macaw and Military Macaw *Ara militaris*), intermediate sized (Yellow-shouldered Amazon *Amazona barbadensis*, Yellow-crowned Amazon and Red-fronted Macaw *Ara rubrogenys*) and small (< 150 g; Rose-crowned Parakeet *Pyrrhura rhodocephala*, Blue-crowned Parakeet *Thectocercus acuticaudatus*, Monk Parakeet *Myiopsitta monachus* and Cliff Parakeet *Myiopsitta luchsi*) species (Fig. 1). The negative extreme of axis 1 showed an increase of the plant families including Brunelliaceae, Clethraceae, Melastomataceae, Pinaceae, Protaceae and Usneaceae, which are characterized by two fruit types: fleshy and dry fruits with small seeds (Gonzalez Villarreal 2009, Orozco 2009, Prance 2009, Woodgyer 2009), with two exceptions: the family Pinaceae, whose species have seeds of > 1 cm (Farjon & Styles 1997), and Usneaceae, which are lichens. Parrot species consuming these families (Brunelliaceae, Clethraceae, Melastomataceae, Pinaceae, Protaceae and Usneaceae) had a body mass ranging from 85 g (Santa Marta Parakeet *Pyrrhura viridicata*)

to 337 g (Thick-billed Parrot *Rhynchopsitta pachyrhyncha*), with an average of 151 g, and had geographical ranges of between 460 and 572 000 km^2. At the genus level, diet overlap ranged from 0.006 (*Graydidascalus*, *Amazona*) to 0.321 (*Psittacara*, *Thectocercus*) with a mean of 0.032 ± 0.059, but no genus pair showed perfect overlap, suggesting that all parrot genera had different diet compositions (Table S1 and Fig. S1). At the species level, diet breadth (Shannon–Wiener index) ranged from 0 (one plant species consumed; e.g. Blue-fronted Parrotlet *Touit dilectissimus*, Sapphire-rumped Parrotlet, Manu Parrotlet *Nannopsittaca dachillae*, Short-tailed Parrot *Graydidascalus brachyurus*, Brown-throated Parakeet) to 5.389 (219 plant species consumed for Scarlet Macaw *Ara macao*; Table S2).

Relations between diet composition, body size and geographical range

Phylogenetic signals were detected for body mass ($\lambda = 1.00$, $P < 0.0001$, 95% CI: 0.98–1.00) and geographical range ($\lambda = 0.29$, $P = 0.02$, 95% CI: 0.03–0.66). In contrast, no significant phylogenetic signal was detected for diet breadth ($\lambda = 0.00$, $P = 1.00$, 95% CI: 0.00–0.66), NMDS 1 ($\lambda = 0.00$, $P = 1.00$, 95% CI: 0.00–0.70) or NMDS 2 ($\lambda = 0.35$, $P = 0.10$, 95% CI: 0.00–0.78). As no phylogenetic signal was detected for the response variables (diet breadth and composition), relations between diet, body mass and distribution were interpreted based on OLS regression models (Revell 2010). Diet breadth was largely explained by the number of published studies, but not by body mass or geographical range ($R^2 = 0.51$, $F_{4,92} = 23.99$, $P < 0.0001$; Table 2, Fig. 2). By contrast, both body mass and geographical range size accounted for variation in diet composition (NMDS 1), although with little explanatory power ($R^2 = 0.11$, $F_{4,92} = 2.80$, $P = 0.03$). NMDS 1 was positively associated with both body size and geographical range (Table 2). Also, a significant negative interaction between body size and geographical range was found (Table 2, Fig. 3). This suggests that large or widely distributed parrots (red area in Fig. 3; e.g. Blue-and-Yellow Macaw *Ara ararauna*, Red-and-Green Macaw *Ara chloropterus*, Southern Mealy Amazon *Amazona farinosa*, Yellow-crowned Amazon, Blue-winged Parrotlet *Forpus xantopterygius*, Dusky-billed Parrotlet *Forpus modestus*, Golden-winged

Table 1. Percentages of items consumed by Neotropical parrots.

Parrot species	Seed	Fruit	Flower	Leaf	Stem	Bark	Nectar	No. of studies
Alipiopsitta xanthops	25.00	40.63	15.63	15.63		3.13		5
Amazona aestiva	40.00	42.61	13.04	1.74	0.87	0.87	0.87	14
Amazona albifrons	66.68	9.52	23.80					3
Amazona amazonica		100.00						1
Amazona auropalliata	29.00	37.72	22.44	9.10		1.74		1
Amazona autumnalis	29.16	37.50	20.83	8.34		4.17		3
Amazona barbadensis	10.54	68.42	15.78				5.26	3
Amazona brasiliensis	33.80	59.15	5.65	1.40				3
Amazona farinosa	48.90	42.22	2.22	2.22	–	–	4.44	5
Amazona festiva							100.00	1
Amazona finschi	88.89	7.41	3.70		–			2
Amazona kawalli	60.00	10.00	10.00	10.00	–	–	10.00	1
Amazona ochrocephala	30.95	26.19	26.19	7.14	2.38	–	7.15	4
Amazona rhodocorytha	100.00							1
Amazona tucumana	52.64	26.31	21.05					2
Amazona vinacea		100.00						5
Amazona viridigenalis	38.46	53.84	7.69					1
Anodorhynchus hyacinthinus	100.00							1
Anodorhynchus leari	33.33	55.55	11.11					5
Ara ambiguus	35.30	35.30	17.64	5.88	–	5.88	–	2
Ara araurana	51.28	33.35	5.12	5.12	–	-	5.12	9
Ara chloropterus	51.48	38.90	5.18	2.22	-	2.22	-	12
Ara glaucogularis	36.36	18.18	27.27	18.19	-	-	-	2
Ara macao	48.86	29.54	9.46	6.06	0.75	4.92	0.32	14
Ara militaris	56.45	33.87	3.22	6.46	–	–	–	4
Ara rubrogenys	50.00	50.00						5
Ara severus	29.41	35.29	17.64	5.88	-	3.94	7.84	4
Aratinga weddellii	44.00	28.00	28.00					4
Bolborhynchus ferrugineifrons	40.00		60.00					1
Brotogeris chiriri	37.27	36.36	15.47	–	–	–	10.90	12
Brotogeris cyanoptera	21.73	30.43	21.75	8.69	4.36	–	13.04	3
Brotogeris jugularis	36.84	12.28	28.07	14.03	–	8.77	0.00	3
Brotogeris pyrrhopterus		10.00	90.00					1
Brotogeris sanctithomae	10.52	47.36	10.52	5.26	–	5.26	21.05	2
Brotogeris tirica	53.48	32.55	11.62	–	–	–	2.32	6
Brotogeris versicolorus	90.00						10.00	4
Cyanoliseus patagonus	76.93	7.69	7.69	–	–	–	7.69	6
Deroptyus accipitrinus	50.00	50.00						3
Diopsittaca nobilis	50.00	50.00						3
Enicognathus ferrugineus	33.33	33.33	33.33					7
Eupsittacula aurea	64.87	18.93	–	8.10	–	–	8.10	14
Eupsittacula cactorum	44.44	38.90	11.11	5.55	–	–	–	1
Eupsittacula canicularis	31.16	18.03	26.22	14.75	–	9.84	–	4
Eupsittacula pertinax		100.00						1
Forpus modestus	10.00	90.00						3
Forpus xanthops		100.00						1
Forpus xanthopterygius	44.44	33.33	22.22					4
Graydidascalus brachyurus							100.00	1
Guaruba guarouba	10.00	80.00	10.00					2
Hapalopsittaca amazonina	10.00	90.00						1
Hapalopsittaca fuertesi	30.43	52.17	13.04	4.34	–	–	–	1
Leptosittaca branickii		80.00	10.00	10.00				2
Myiopsitta monachus	46.07	32.35	9.80	2.96	–	0.98	7.84	8
Nannopsittaca dachilleae	100.00							1
Nandayus nenday	34.48	37.93	6.90	–	–	–	20.68	2

(continued)

Table 1. (continued)

Parrot species	Seed	Fruit	Flower	Leaf	Stem	Bark	Nectar	No. of studies
Orthopsittaca manilatus	12.00	76.00	4.00	4.00		4.00		4
Pionites leucogaster	60.56	23.95	15.49					1
Pionites melanocephalus	55.00	30.00	5.00	5.00	–	–	5.00	1
Pionopsitta pileata	100.00							3
Pionus fuscus	90.00	10.00						1
Pionus maximiliani	54.66	24.00	17.34	–	–	–	4.00	10
Pionus menstrus	62.08	31.03	6.89					4
Primolius couloni	90.00	10.00						1
Primolius maracana	23.08	76.92						2
Priomolius auricollis	73.07	19.23	3.84	–	–	–	3.84	3
Psittacara holochlora	48.15	51.85						2
Psittacara leucophthalmus	30.43	39.13	17.40	–	–	–	13.04	1
Psittacara mitratus		100.00						2
Pyrilia barrabandi	42.85	35.71	21.42					4
Pyrilia caica	100.00							2
Pyrilia haematotis	50.00	50.00						1
Pyrrhura albipectus	28.57	57.14	14.28					1
Pyrrhura cruentata	100.00							1
Pyrrhura devillei	40.00	40.00					20.00	1
Pyrrhura frontalis	58.18	20.00	14.55	7.27				1
Pyrrhura lepida		100.00						1
Pyrrhura leucotis	54.18	37.50	4.16	4.16				1
Pyrrhura molinae	42.10	42.10	5.26	–	–	–	10.52	5
Pyrrhura picta	15.79	63.17	15.78	–	–	–	5.26	2
Pyrrhura rhodocephala	10.00	90.00						1
Pyrrhura rupicola	20.75	67.92	9.44	1.89				2
Pyrrhura viridicata	36.36	27.28	18.18	-	18.18			1
Rhynchopsitta pachyrhyncha	100.00							1
Thectocercus acuticaudatus	46.15	30.76	15.38	–	–	–	7.69	7
Touit purpuratus		100.00						1
Triclaria malachitacea	59.26	37.04	3.70	–	–	–	–	3

Parakeet *Brotogeris chrysoptera*, Cobalt-winged Parakeet *Brotogeris cyanoptera*, Orange-chinned Parakeet), had a different diet composition compared with small bodied species of restricted range (blue area in Fig. 3; e.g. Grey-hooded Parakeet *Psilopsiagon aymara*, Santa Marta Parakeet, Plain Parakeet *Brotogeris tirica*). Finally, no variable explained variation in NMDS 2 ($R^2 = 0.08$, $F_{4,92} = 1.92$, $P = 0.11$; Table 1), and no significant relation between body size and geographical range was found after accounting for phylogenetic relationships ($R^2 = 0.04$, $F_{1,87} = 3.33$, $P = 0.07$).

DISCUSSION

We found that diet composition correlated with body size and geographical range, yet was independent of shared phylogenetic history. Furthermore, we found a low diet niche overlap between parrot genera, suggesting trophic segregation among them. These results suggest that ecological and life history traits explain variation in diet in a trophic generalist group, although with low explanatory power. Differences in body size limit or facilitate the consumption of certain sizes and types of seeds, fruits and flowers, because body size is strongly linked to energetic requirements and abilities in terms of food searching, harvesting and processing (Bowers & Brown 1982, Brown *et al.* 2004, Palacio *et al.* 2017). Several studies have found that seeds make up the largest proportion in the diet of large Neotropical parrots (Galetti 1997, Matuzak *et al.* 2008, Lee *et al.* 2014, Renton *et al.* 2015), whereas flowers, nectar and fleshy fruits make up the largest proportion in small species (Pizo *et al.* 1995, Cotton 2001, Ragusa Netto & Fecchio 2006, Botero-Delgadillo *et al.* 2010, Renton *et al.* 2015). These differences have been attributed to different energetic requirements among species. For instance, seeds contain high
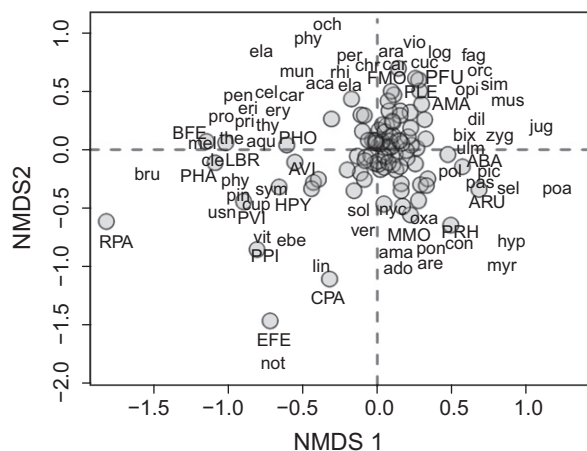
Figure 1. Non-metric multidimensional scaling (NMDS) based on a Neotropical parrot species (upper case letters) by plant families (lower case letters) presence–absence matrix. Species with scores greater than 0.5 or lower than −0.5 are shown for clarity. Species abbreviations: (ABA) *Amazona barbadensis*; (AMA) *Ara macao*; (ARU) *Ara rubrogenys*; (AVI) *Amazona vinaceae*; (BFE) *Bolborhynchus ferrugineifrons*; (CPA) *Cyanoliseus patagonus*; (EFE) *Enicognathus ferrugineus*; (FMO) *Forpus modestus*; (HPY) *Hapalopsittaca pyrrhops*; (LBR) *Leptosittaca branickii*; (MMO) *Myiopsitta monachus*; (PFU) *Pionus fuscus*; (PHA) *Pyrilia haematotis*; (PHO) *Psittacara holochlorus*; (PLE) *Pyrrhura lepida*; (PPI) *Pionopsitta pileata*; (PRH) *Pyrrhura rhodocephala*; (PVI) *Pyrrhura viridicata*; (RPA) *Rhynchopsitta pachyrhyncha*. Plant family abbreviations: (ado) Adoxaceae; (ama) Amaranthaceae; (aqu) Aquifoliaceae; (ara) Araliaceae; (are) Areaceae; (bru) Brunelliaceae; (car) Caricaceae; (con) Convolvulaceae; (cup) Cuppressaceae; (dil) Dilleniaceae; (ebe) Ebenaceae; (ela) Elaeocarpaceae; (eri) Ericaceae; (ery) Erythroxylaceae; (fag) Fagaceae; (hyp) Hypericaceae; (jug) Juglandaceae; (lin) Linaceae; (log) Loganiaceae; (mel) Melastomataceae; (mun) Muntingiaceae; (mus) Museaceae; (myr) Myricaceae; (not) Nothofagaceae; (nyc) Nyctaginaceae; (och) Ochnaceae; (opi) Opiliaceae; orc) Orchidaceae; (oxa) Oxalidaceae; (pas) Passifloraceae; (per) Peraceae; (phy) Phyllanthaceae; (pht) Phytolaccaceae; (pic) Picrodendraceae; (pin) Pinaceae; (poa) Poaceae; pol) Polygonaceae; (pon) Pontederiaceae; (pri) Primulaceae; (pro) Proteaceae; (sel) Selaginaceae; (sim) Simaroubaceae; (sym) Symplocaceae; (thy) Thymelaeaceae; ulm) Ulmaceae; (usn) Usneaceae; (vio) Violaceae; (vit) Vitaceae; (zyg) Zygophyllaceae.

levels of protein and are more critical for large birds which need more protein for maintenance (Gilardi 1996, Klasing 1998). By contrast, small birds need more carbohydrates, because they display higher mass-specific metabolic rates (Suarez & Gass 2002). Although seeds and fruits are the main food of Neotropical parrots (Renton *et al.* 2015), differences in item size could reflect differences not only in body size but also in other morphological traits (e.g. beak size and shape). These

factors would also help explain the patterns of diet composition in this group.

Diet composition was also explained by an interaction between body size and geographical range. In particular, large or widely distributed species had a different diet composition compared with small-bodied species of restricted range. This may relate to the fact that numerous plant families and food types occur in wide distribution ranges within the Neotropics (Maitner *et al.* 2018). Therefore, widely distributed parrot species can access many of the same plant species. In contrast, small species of restricted geographical range may have a significantly lower range of food resources available.

We found a low diet overlap among parrot genera, which may contradict with the idea of high diet plasticity in parrots, as many genera showed similar body sizes and overlapping geographical ranges, thus having access to the same plant species. However, genus diet composition largely depends on the number of parrot species in a given genus (i.e. the higher the number of species, the broader the diet), so extrapolations to the species level may be misleading and niche overlap values should be viewed with some caution. Moreover, diet breadth and composition represent different facets of diet ecology, as two species may show similar diet breadth yet be completely different in terms of the identity of the plant species consumed (Krebs 1998). Although niche overlap is a simple descriptive measure, it may provide insights into the identification of species fulfilling similar functional roles within ecosystems (Rosenfeld 2002, Palacio *et al.* 2016), and thus this should be taken into consideration in further studies.

After accounting for sampling effort, neither body size nor geographical range were related to diet breadth. This agrees with Laube *et al.* (2013), who found that body size, but not diet breadth, was strongly associated with geographical range in an analysis of 165 European passerines. In contrast, Slatyer *et al.* (2013) found a positive relation between range size and diet breadth in a meta-analysis of several plant and animal groups including birds, supporting this hypothesis as a general pattern in nature. Our results, however, support the view that large-bodied and widely distributed parrot species may avoid smaller items due to optimal foraging constraints (Costa 2009), although an analysis using the whole Order may shed light on

Table 2. Factors explaining diet breadth and diet composition in Neotropical parrots. Results of ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS) regressions are shown. Explanatory variables (body mass, geographical range and number of studies) were log-transformed. Coefficients in bold were significant at $P < 0.05$. se, standard error.

|	OLS estimate	se	t	P	PGLS estimate	se	t	P
Diet breadth (Shannon–Wiener index)								
Intercept	**1.452**	0.587	2.475	0.015	**1.515**	0.617	2.454	0.016
Body mass	0.074	0.115	0.638	0.525	0.057	0.118	0.479	0.633
Geographical range	−0.181	0.123	−1.473	0.144	−0.168	0.130	−1.291	0.200
Number of studies	**1.100**	0.131	8.411	< 0.0001	**1.166**	0.133	8.778	< 0.0001
Body mass × geographical range	0.029	0.022	1.287	0.201	0.025	0.023	1.071	0.287
Diet composition (NMDS 1)								
Intercept	**−1.496**	0.593	−2.523	0.013	−0.273	0.234	−1.168	0.246
Body mass	**0.233**	0.106	2.211	0.030	0.037	0.045	0.831	0.408
Geographical range	**0.113**	0.050	2.253	0.027	0.064	0.049	1.289	0.201
Number of studies	0.068	0.053	1.285	0.202	0.072	0.050	1.435	0.155
Body mass × geographical range	**−0.018**	0.009	−2.000	0.048	−0.010	0.009	−1.125	0.264
Diet composition (NMDS 2)								
Intercept	−0.817	0.539	−1.514	0.133	**−0.539**	0.252	−2.138	0.035
Body mass	0.123	0.096	1.280	0.204	0.095	0.051	1.872	0.065
Geographical range	0.033	0.046	0.733	0.465	0.048	0.042	1.147	0.255
Number of studies	−0.050	0.048	−1.032	0.305	−0.031	0.044	−0.703	0.484
Body mass × geographical range	−0.003	0.008	−0.354	0.724	−0.005	0.007	−0.642	0.523
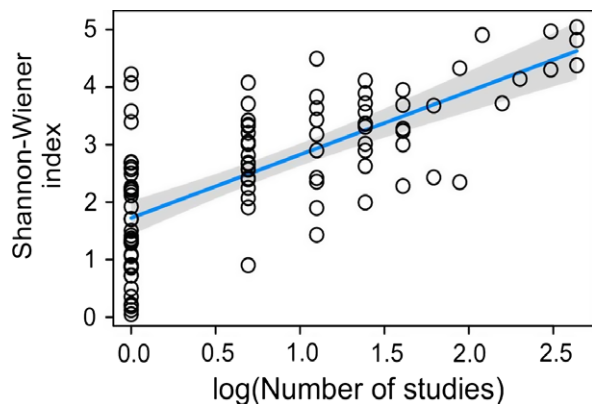
Figure 2. Factors explaining variation in diet breadth (Shannon–Wiener index) of Neotropical parrots. Predictions are derived from ordinary least-squares regressions conditional on the mean of log(body mass) and log(geographical range), and the log(number of studies), respectively.

Figure 3. Factors explaining variation in diet composition (NMDS axis values). Predictions are derived from ordinary least squares regressions conditional on the mean of log(body mass) and log(geographical range), respectively. A response surface between body size, geographical range and diet composition is shown. The response variable (depicted by the vertical bar) is NMDS 1. Open circles represent parrot species. The same colour indicates similar NMDS values, and therefore diet composition.

this pattern. Both body size and geographical range showed phylogenetic inertia, indicating a prominent role of phylogeny in shaping both traits. In contrast, diet did not show a phylogenetic signal, which could explain the ability of parrots to adjust their behaviour to seasonal food availability and novel food resources. In other words, the ecological and phylogenetic independence between body size, geographical range and diet might explain
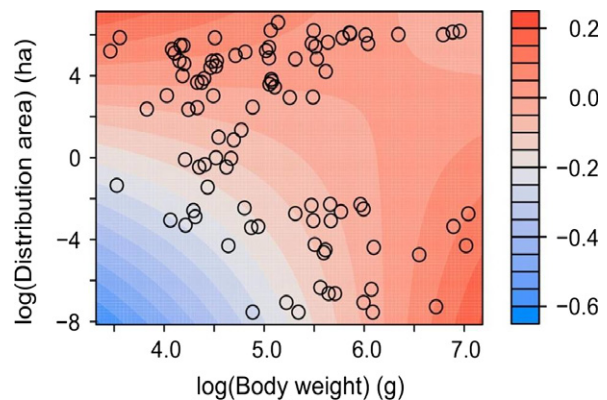
diet plasticity in this group (e.g. Matuzak *et al.* 2008, Bucher & Aramburu 2014).

Although our review highlights important aspects of diet of Neotropical parrots, we also expose the lack of information on 67 of 165 parrot

species (*c.* 42%). Of these species, 34 are listed as threatened, indicating that there is still a large gap in knowledge of their basic biology. This lack of information is problematic and urges diet studies, as the conservation of psittacids depends on knowledge of their natural history (Collar 2017). Several studies have shown that the decline of some parrot populations is linked to a decrease or elimination of key food resources (Saunders 1990, Berg *et al.* 2007) and inadequate nutrition (McDonald 2003). In particular, greater efforts to address different aspects of diet (diet breadth and composition, food resource selection) are needed in countries with high parrot diversity (Bolivia, Colombia, Ecuador and Honduras). In addition, more studies covering the complete distribution of widespread species are necessary for understanding variation in their diet. In this sense, all this information may be essential for long-term conservation of threatened parrot species.

For the first time, relations between diet, body size and geographical range have been tested in a phylogenetic framework across Neotropical parrot species. Our results provide an important ecological view at a regional scale of diet patterns in Neotropical parrot species. These mainly suggest that ecological factors and life history traits partly explain diet of Neotropical parrots. The restriction of the study to the Neotropical region is also a limitation. Other patterns may arise if the complete Order of Psittaciformes are analysed. Moreover, our dataset included widespread species where data were only available for a small fraction of their distributions. This could explain the low explanatory power of the ecological variables analysed. Our assessment of information gaps on parrot species and geographical regions underscores the need for diet studies across broader ranges of parrot distributions. Overall, our review supports the idea that diet composition, rather than diet breadth, is partly driven by body mass and geographical range at the macro-scale. Although such a finding reveals a link between diet composition and life history traits in a trophic generalist group, this pattern should be explored in other taxa by future studies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Heatmap showing niche overlap (Morisita index) between parrot genera.

Table S1. Diet overlap among parrot genera using the Morisita index. Bootstrap confidence interval in parentheses.

Table S2. Values of diet breadth for each species of parrot using the Shannon–Wiener index.

Appendix S1. Data source of diet studies of Neotropical Parrots used for this study (n = 156).

Appendix S2. Summary of gaps in information on Neotropical Parrots.

Appendix S3. Importance of plant family in the diet of parrot species.