Uso de la morfometría, dieta y estratos de forrajeo de aves tropicales en la resolución de hipótesis de nicho

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Resumen

Título: Uso de la morfometría, dieta y estratos de forrajeo de aves tropicales en la resolución de hipótesis de nicho.
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Palabras clave: Aves tropicales, Especialización, Morfoespacio.
Descripción:

Las hipótesis clásicas basadas en nichos argumentan que la composición de las especies locales está relacionada con la variedad de recursos disponibles, que se distribuyen entre ellas para reducir la competencia y permitir así su coexistencia. Sin embargo, los trópicos albergan la mayor diversidad de especies, lo que implica una mayor cercanía de las especies en el espacio de nicho y potencialmente generando nichos de especies más pequeños o una mayor superposición de nichos interespecíficos. Se ha formulado la hipótesis de que una mayor especialización facilita la coexistencia en comunidades de gran diversidad. El análisis de la distribución y la composición de los rasgos funcionales en las comunidades, ha tratado de abordar las funciones de la especialización ecológica y las interacciones de las especies en el ensamblaje de las comunidades locales a partir de grupos de especies regionales. Aquí, proponemos tres clasificaciones de especialización que describen el uso de los recursos a nivel de especie: a) especialización en la dieta, b) dieta principal y c) prevalencia de forrajeo. De esta manera, exploramos cómo la dieta y la especialización en el forrajeo pueden dar lugar a la diferencia de tamaño y a la superposición de un espacio de rasgos octadimensionales (morfoespacio). Encontramos que las especies con mayor especialización en su dieta o prevalencia de forrajeo, presentaban una menor ocupación y superposición del morfoespacio en comparación con las especies generalistas. Nuestros resultados demuestran que los nichos ecológicos de las aves pueden inferirse utilizando los rasgos morfológicos en las aves tropicales y cuantificarse mediante el análisis de hipervolúmenes. Estudios adicionales, teniendo en cuenta una mayor reserva de especies y la ocupación morfoespacial de las aves extratropicales pueden revelar si la ocupación de los nichos es mayor en las aves tropicales, contribuyendo a la comprensión de cómo se genera y mantiene la hiperdiversidad tropical.

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[1] Trabajo de grado

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Abstract

Title: Answering niche-based hypotheses about tropical birds through morphometric, diet and forage stratum data.
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Keywords: Tropical birds, Specialization, Morphospace.
Description:

Classical niche-based hypotheses argue that local species composition is related to the variety of available resources, which are distributed among species to reduce inter-species competition and thus enable coexistence. However, the tropics hold the greatest species diversity, implying that species are more tightly packed into niche space and potentially indicating either smaller species niches or greater interspecific niche overlap. It has been hypothesized that increased specialization facilitates local coexistence in high diversity communities. Analysing the distribution and composition of functional traits in communities has attempted to address the roles of ecological specialization and species interactions in the assembly of local communities from regional species pools. Here, we proposed three classifications of specialization that describe species-level resource use: (a) diet specialization, (b) main diet and (c) foraging prevalence. Whereby, we explore how the avian diet and foraging specialization can shape the difference in size and overlap among an eight-dimensional trait space (morphospace). We found that species with higher specialization in their diet or foraging prevalence presented a smaller morphospace occupation and overlap as compared to generalist species, also taking into account differences in sampling intensity. Our results highlight that avian ecological niches can be inferred using morphological traits of tropical birds and quantified using the analysis of hypervolumes. Further studies, taking into account a bigger species pool and morphospace occupation of extratropical birds may reveal if niche space occupation is higher in tropical birds contributing to the understanding of how tropical hyperdiversity is generated and maintained.

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[1] Bachelor Thesis

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Introduction

Ecological niche

Since the introduction of the term niche in the ecological context by Grinnell (1917), niche theory has become one of the fundamental concepts of ecology (Pocheville, 2015). Despite the differences between the multiple meanings of the concept, the niche has been widely used for studying the relationship between organisms and their environment (Chase & Leibold, 2003; Pocheville, 2015). For Grinnell, the niche encompasses everything that conditions a species in its habitat, including abiotic factors such as temperature, humidity, precipitation and biotic factors such as the presence of food, competitors, predators, refuges, among others (Grinnell, 1917). Grinnell's definition of niche led him to propose an ecological hierarchy in which species were divided according to the distribution of biotic and abiotic factors into biogeographical categories. In this context, the niche was seen as the “ultimate” unit of association between species distribution or occurrence. The comparison of communities also led Grinnell to bring his attention to ecological equivalents that, by evolutionary convergence, are driven to occupy similar niches in different geographical areas (Grinnell, 1924). Charles Elton (1927) also focused on individuals with ecological equivalence in different areas of study but defined the niche primarily by the trophic position and eating habits of the individual.

While Grinnell and Elton emphasized the similarities of niches occupied by ecological equivalent species in different geographic areas, Hutchinson (1957) focused on the similarities in niches of species found in the same location. This last concept was due to the idea, already described by Darwin (Darwin, 1859) that two species coexisting in the same place should occupy different niches. Once established as the principle of competitive exclusion (Gause, 1934; Hardin, 1960), it provided the context for Hutchinson's redefinition of the term niche. Hutchinson formalized the niche of a species as a volume, in the space of environmental variables, where the species can survive indefinitely (id., fundamental niche), or the volume, limited because of interaction with present competitors, where the species actually survives (id., realized niche) (Hutchinson, 1957). Because this niche volume exists within a space of n dimensions, where axis represents variables required by the organism, Hutchinson laid the foundations for quantifying the differences in species'niches. This allowed estimating the niche differences that enable species to coexist, or those that lead to their exclusion (Pocheville, 2015).

To quantify the fundamental niche of species, Hutchinson originally proposed the n-dimensional hypervolume (Hutchinson, 1957). In his approach, hypervolumes exist within a space defined by a set of n variables that represent biologically important and independent axes. The hypervolume is then defined as a subset of this space, i.e. an n-dimensional geometric form. Although this framework has been proposed 60 years ago (Hutchinson 1957), just recently, it became accessible quantitatively through the development of statistical approaches that calculate the size and overlap of these n-dimensional hypervolumes (Blonder et al., 2018; 2014; Swanson et al., 2015; Junker et al., 2016). In combination with the availability of large data sets about species traits, such as PanTHERIA, TRY, EltonTraits 1.0 (Jones et al., 2009, Kattge et al., 2011; Wilman et al., 2014) needed to estimate hypervolumes.

Trait Hypervolumes

By transferring the niche concept from a geographic to a geometric context (Colwell & Rangel, 2009) allowed the definition of the niche in terms of a limitless number of ecological dimensions, and as such its quantification using n-dimensional hypervolumes. Even though hypervolume concepts have been successful use in functional ecology, where traits are often taken as proxies for the niche axes (Blonder, 2018; Bregman et al., 2016; Echeverría-Londoño et al., 2018; Kraft, Valencia, & Ackerly, 2008; Pigot, Trisos, & Tobias, 2016) there must be an understanding about how selected traits and niches are actually related. For instance, the selection of axes is an essential step in the definition of trait hypervolumes, and strategic axes of the taxa of interest should be selected (McGill et al., 2006) In addition, these axes must be formed by continuous variables, necessary to perform operations that allow the estimation of hypervolumes size and overlap or the functional richness of the trait axes (Blonder, 2018). Consequently, efforts in consistency compilation and standardized collection of trait and ecological data have made more accessible the analysis of trait hypervolumes. Noteworthy examples of the implementation of standardized data for the definition of ecological niches have been the distribution of plant forms by Díaz et al. (2016), and trophic level niches on birds by Pigot et al., (2020).

Applications on birds' studies

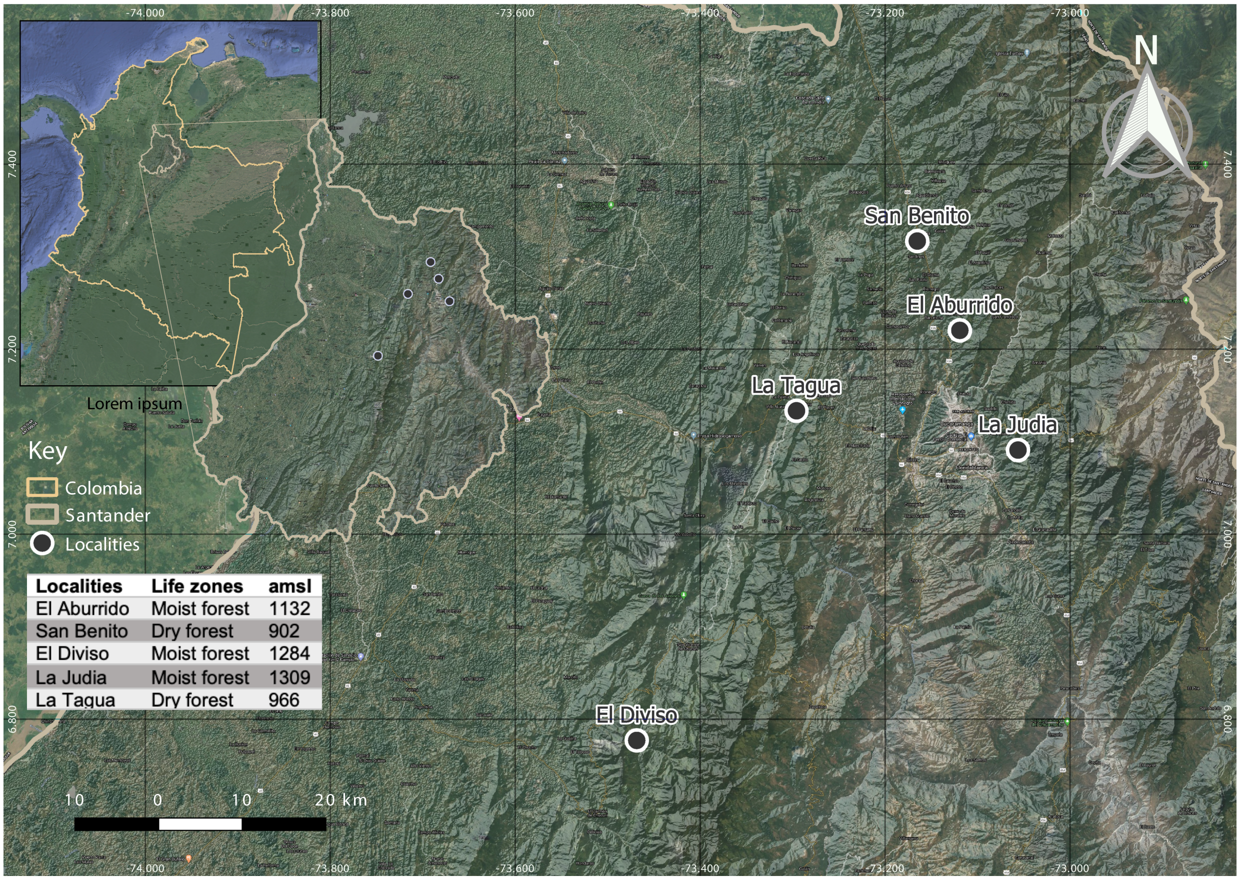
Bird studies have a long tradition in the development of niche concepts and ecomorphology (Miles & Ricklefs, 1984; Grinnell, 1917) and provide a rich template for understanding the relationship of form and function of avian species (Wilman et al., 2014). Most of the distinguishing features of birds, such as their flight adaptations, elaborate courting and parental care behaviours, vocal skills, and variety of eating habits, can be reflected in features of individuals'external anatomy. Among these, the following easily measured and obtained features have been highlighted (Luck et al., 2012; Negret et al., 2015): (1) The bill, whose variation in shape and size, has been directly related to the type of food consumed, and the strategies for handling and obtaining it. For example, some species of insectivorous birds have flattened beaks with a large mouth opening that allows them to catch insects (Schulenberg, 1983), while frugivorous birds have higher, thicker beaks for swallowing fruit (Moermond & Denslow, 1985). The bill has also been related to other aspects such as sexual selection (Rico-Guevara & Araya-Salas, 2015), and processes such as pollination (Rodríguez-Flores & Stiles, 2005) and seed dispersal (Bouffard & Brooks, 2014). (2) The wing, whose length, area and size ratio between its feathers has been related to dispersal capacity, migration, flight manoeuvres and foraging strategies (Claramunt et al., 2012). (3) The length of the legs has been mainly related to foraging behaviours and strategies. For example, tarsal length has been used as a predictor of foraging behaviour in insectivorous birds and their ability to catch prey through multiple strategies (Carrascal et al., 1990). (4) The tail, whose size and shape have been related to flight manoeuvres (Maybury et al., 2001), forage specialization (Clark, 2010) and sexual selection (Clark & Dudley, 2009). Most of the above-mentioned traits are closely related to the trophic aspects of bird species, as birds have diversified into a wide variety of morphological forms by exploiting a complex configuration of trophic niches. The concept of hypervolume allows the integration of these traits for the inference of the ecological niche of birds with different degrees of specialization. In the aim of exploring the role of specialization in the size and overlap of tropical bird ecological niches.

Using hypervolumes, we explore how avian diet and foraging can shape the differences among an eight- dimensional trait space (morphospace) in a high diversity assembly in Santander, Colombia. Using eight morphometric traits, we test the relationships between the morphology and (a) diet specialization, (b) main diet and (c) prevalence in foraging stratum among a tropical bird assemblage. We hypothesize that (i) occupation in the morphospace will be larger in more generalist species (regarding their diet or foraging stratum) and (ii) that these generalist species share more morphospace with other species than species with more specialized diets or foraging prevalence.

1 Methods

1.1 Morphological trait data

We assembled a dataset of morphometric measurements from 3568 live-caught individuals from existing datasets. In total, our dataset represents 185 species of the 971 bird species (19%) recognized in Santander, Colombia (SiB Santander, 2020). For each individual, we obtained morphological traits involving measurements from the bill (culmen length, bill width and depth), wing (length, wingspan), tail (length), tarsus (length), and total body length. The majority of the sampling for the existing dataset was conducted by one researcher following standard protocol for bill width and depth (Colorado, 2004) and culmen, tail, wing and tarsus length (Winker, 1998). The total sampling for the dataset was performed between 2011 and 2017 in 5 localities (Figure 1) and is available in Hypervolume_Birds_diets github repository.



Localities	Life zones	amsl
El Aburrido	Moist forest	1132
San Benito	Dry forest	902
El Diviso	Moist forest	1284
La Judia	Moist forest	1309
La Tagua	Dry forest	966

Figure 1: The geographical location, life zones and above mean sea level (amsl) of the study sites from which the morphological trait data was obtained.

To match the species-level resolution of our ecological data (see 1.2 Ecological data section),we calculated averaged trait values for each species. This is justifiable because most of the variance in trait values occurs between rather than within species (Pigot et al., 2020). Species with missing information from any of the 8 morphological traits measurements were omitted resulting in a dataset consisting of 179 species.

1.2 Ecological data

We complement the species traits with information on the proportional use of different food categories and prevalence in foraging layer (from 0 to 100% in 10% increments), published in Wilman et al.,(2014). We reorganized some of Wilman's original food categories according to the classification scheme proposed by Lopes et al.(2016) and include or exclude food categories for some species according to local knowledge (see Appendix Information for details). Based on the percentages of these categories and in order to explore the differences in the morphological traits according to the specialization of the species'diet and foraging, we categorize species according to their diet specialization, main diet and foraging prevalence as follows:

(a) Diet specialization

First, we adopted a simple approach, adding up the number of food categories in which the percentage was greater than 0. When a species uses a single food category, we assigned them as Obligatory specialists (n= 45 species). Species using two different food categories were assigned as Facultative specialists (n=97 species). Species with broad diets were assigned as Generalists (n=37 species), when they feed on three or more food categories.

(b) Main diet

Second, based on the standardized protocol outlined in Wilman et al., (2014), we assigned species to the diet group from which they obtained at least 50% of their resources. From this we obtained four specialized groups: Nectar (n= 23 species), Fruits (n=27 species), Invertebrates (n=82 species), Seeds (n=19 species). When no food category comprised more than 50% of the whole species'diet, they were considered an Omnivore (n=28 species).

Although not all species classified in the omnivore group are also generalists in the (a) classification, and vice versa, there is nevertheless a wide overlap (Appendix Fig. A7). Both groups (i.e. Generalist and Omnivore) represent the birds with generalist diets referred to in our hypothesis. For foraging specialization, we categorize species based on the relative prevalence on different foraging layers (Appendix Table A2) as follows:

(c) Foraging prevalence

We assigned species to the foraging group from which their prevalence is at least 50%. From this we obtained five specialist foraging groups: Aerial (n= 3 species), Canopy (n= 22 species), Midhigh (n=35 species), understory (n= 24 species), and ground (n= 25 species). Species using multiple foraging layers in relatively equal proportions were considered ‘foraging generalists’, here called General (n= 70 species), to avoid confusion with the generalist category in (a) diet specialization.

1.3 Data analysis

To estimate the morphological variation within the three classifications, we compared the volume and the overlap of trait hypervolumes. Because the number of species is unevenly distributed across our classifications, we constructed traits hypervolumes by fixing the size of the groups to the smallest sample size inside each classification (i.e. Generalist in (a), Seeds in (b) and Canopy in (c)), which allowed us to correct for possible sampling bias in our results. This procedure was carried out through 1000 iterations, randomly selecting the species in each group according to the fixed size. The trait values for the total bill, the exposed culmen, the bill width and the bill depth, the wing length, the wingspan, the tail length, the tarsus length, and the total body length, originally in (mm), were log-transformed. We then constructed the trait hypervolumes using the R package "hypervolume" (Blonder et al., 2014;2018), using the box kernel density estimation method with the default Silverman bandwidth estimator.We compared the mean of inferred traits hypervolumes through all 1000 iterations, reported in units of standard deviations (sd) to the power of the number of traits used (i.e. sd^8). Due to the low number of species in the Aerial group on the foraging prevalence classification, the resampling was performed considering the number of species in the second smallest category (i.e. Canopy) and the Aerial species were removed from the volume analysis.

To estimate the overlap of trait space among our classifications, we used the complete set of species to calculate a single trait hypervolume (Appendix Fig. A1-A3). We then measure the pairwise overlap of hypervolumes among the groups by estimating the Sørensen similarity index (Eq.1).

$$S(A,B) = \frac{2|A \cap B|}{|A| + |B|} \tag{1}$$

Where A or B corresponds to the proportional volume occupied by the species on a particular hypervolume. Values of S vary from 0 (no overlap) to 1 (complete overlap) and are obtained by doubling the volume of the intersection of A and B divided by the sum of the volumes of both hypervolumes (A, B). As trait hypervolumes were estimated using eight morphological traits we further referred to them as groups 'morphospace', and to their volume as 'morphovolume'. In order to double-check the results obtained from the resampling method as described above, we repeated this analysis. Instead of resampling a fixed number of species, we resampled 50% and 70% of all species in each group. Results are presented in the Appendix Figure A4-A6.

2 Results

(a) Diet specialization

For morphospaces calculated on the diet specialization classification, we found an increase in morphovolume according to the number of food categories included in the diet of the species (Figure 2A). Where the largest morphospace corresponds to the Generalist, with a mean volume of 3.19 sd^8 for the 1000 iterations, followed by the Facultative (2.79 sd^8) and the Obligatory (0.97 sd^8) specialist.

For the overlap among morphospaces according to the Sørensen similarity index, we found that about 42% of the morphospace is shared between Obligatory and Facultative, 28% between Generalist/Facultative, and 24% between Generalist/Obligatory species (Figure 2B).

(b) Main diet

For the main diet classification, we found differences in the volume of dietary group ś morphospaces (Figure 3A). Where the largest morphospaces correspond to the Fruit group, with a mean volume of 3.19 sd^8 for the 1000 iterations, followed by the Omnivore (1.46 sd^8) and Invertebrate (1.12 sd^8) groups. Smaller morphospaces were found for the Seed (0.11 sd^8)

and Nectar (0.05 sd^8) groups.

We also found greater overlap between the largest groups, in particular as regards the Omnivore group (Figure 3B). The highest overlap values according to the Sørensen similarity index were obtained among the Omnivore and Fruit group, which share 33% of morphospace, followed by the overlap between Omnivore/Invertebrate (29%) and Invertebrate/Fruit (22%). The least overlap was found in the pairs that included seed and nectar groups.

(c) Foraging prevalence

For morphospaces calculated on the foraging prevalence classification, we found differences in the morphovolume according to species main foraging stratum (Figure 4A). Were the largest morphospaces corresponding to the General (9.76 sd^8) group, followed by Understory (6.56 sd^8) and Canopy (3.81 sd^8) groups. Smaller morphospaces were found for the Midhigh (1.28sd^8) and Ground (0.43 sd^8) groups. As well as among (b) main diet groups, we found that the overlap was greater among the larger foraging groups (Figure 4B). The highest overlap values according to the Sørensen similarity index were obtained between General and Canopy groups, which share 48% of morphospace, followed by General/Understory (43%) groups. The smallest overlap was found on the pairwise that included the Aerial group.

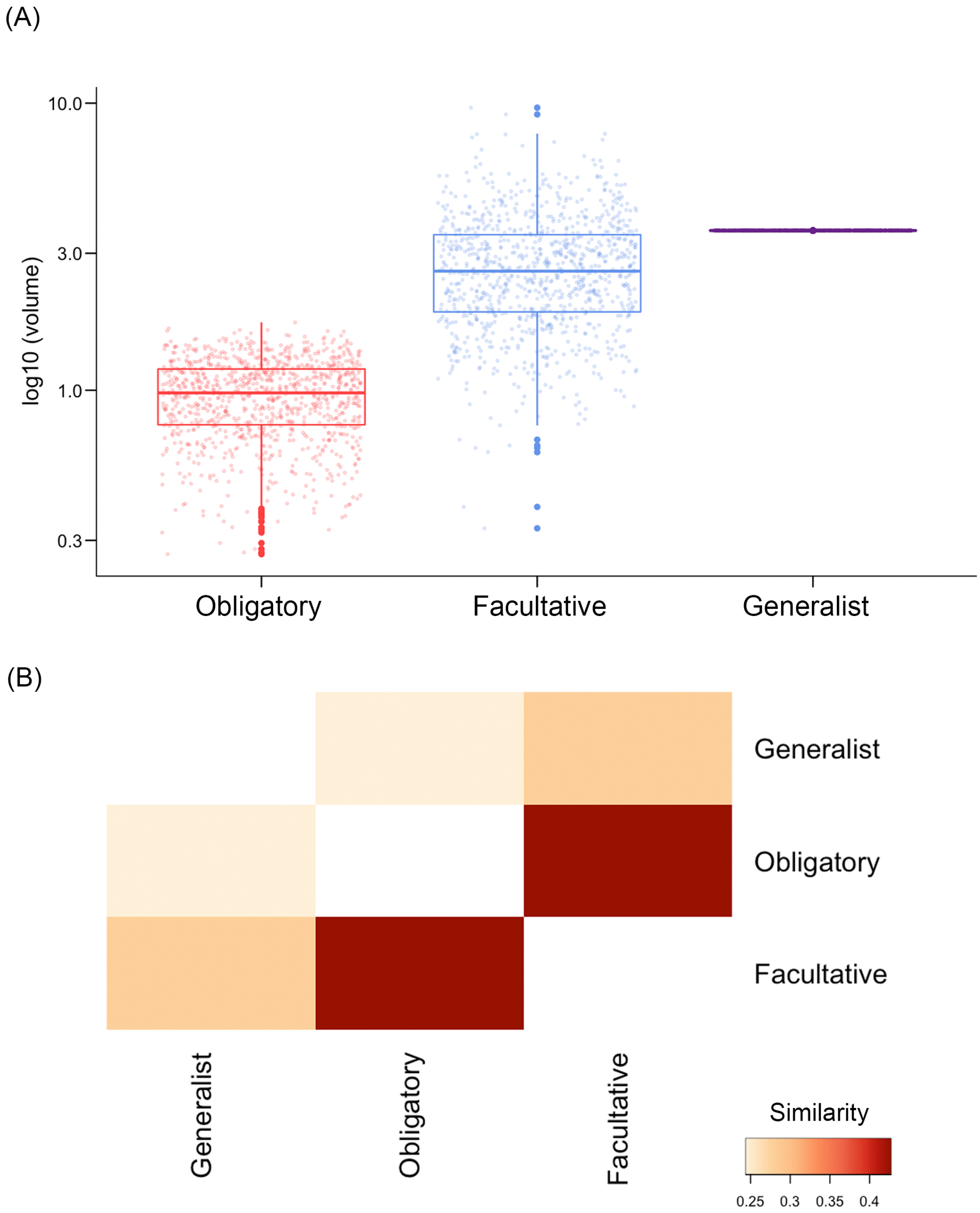


Figure 2: Diet specialization morphovolume and overlap.(A) Boxplot of estimated morphovolume from diet specialization groups morphospaces. Volumes have original units of sd^8 but have been log10- transformed. The light-colored points for each group reflect the volumes obtained in the resampling terations. (B) Pairwise similarity (Sørensen similarity index) in diet specialization groups morphospaces. The darker the cell the greater the overlap.

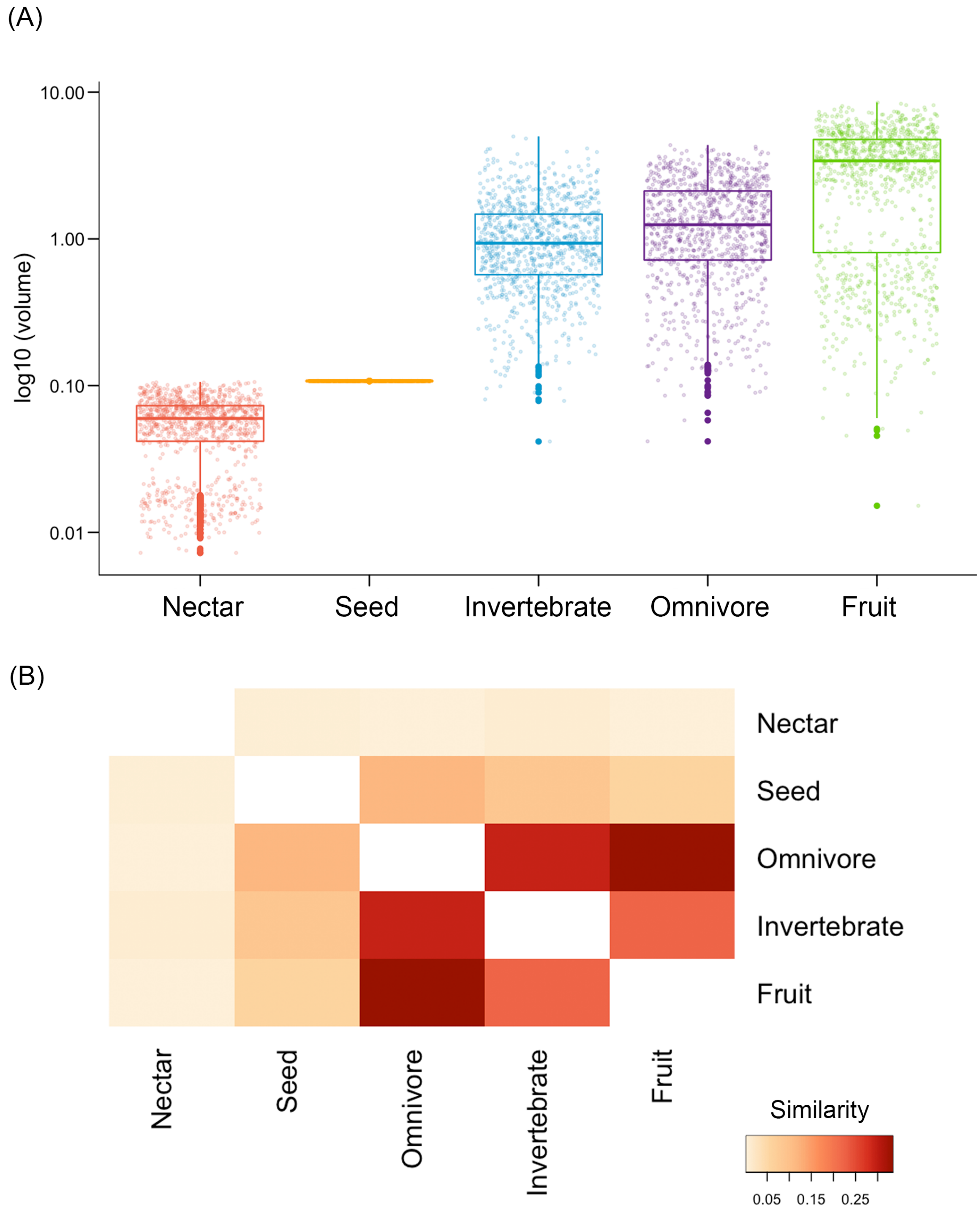


Figure 3: Main diet morphovolume and overlap. (A) Boxplot of estimated morphovolume from dietary groups morphospaces. Volumes have original units of sd^8 but have been log10-transformed. The light-coloured points for each dietary group reflect the volumes obtained in the resampling iterations. (B) Pairwise similarity (Sørensen similarity index) in dietary groups morphospaces. The darker the cell the greater the overlap.

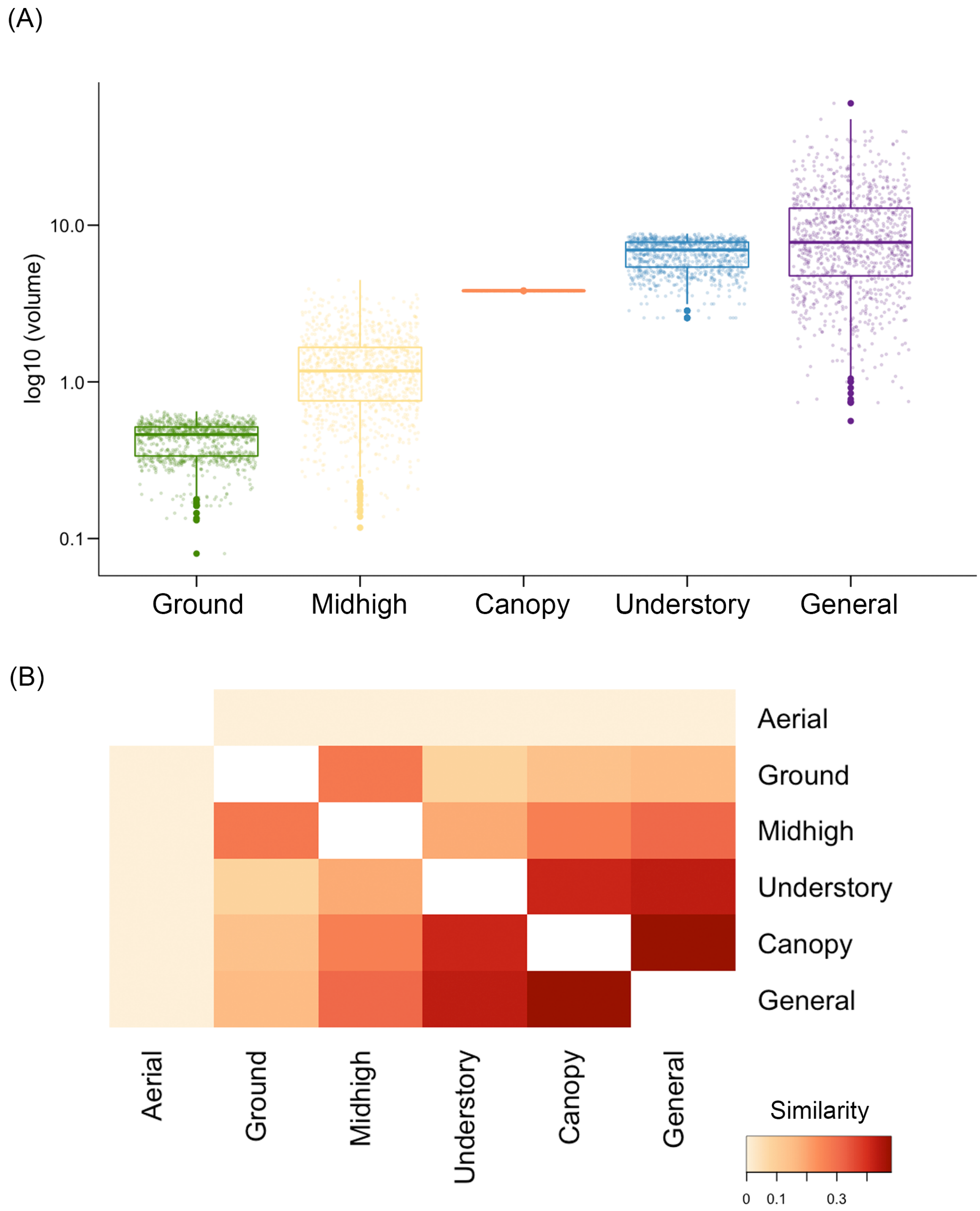


Figure 4: Foraging stratum morphovolume and overlap. (A) Boxplot of estimated volume from foraging groups morphospaces. Volumes have original units of sd^8 but have been log10-transformed. The light-coloured points for each foraging niche reflect the volumes obtained in the resampling iterations. (B) Overlap (Sørensen similarity index) in foraging groups morphospaces. The darker the cell the greater the overlap.

3 Discussion

The presented results confirm our hypotheses about the ecological niches of tropical birds and can be summarized as follows: Species with a broad ecological niche, considering diet specialization (i.e. generalists), main diet (i.e. omnivore species) and foraging prevalence (i.e. species that forage across multiple layers), tend to occupy a larger morphospace than species with specialized diets or foraging prevalence. These groups of generalist species also tend to share a greater fraction of morphospace as compared to species with more specialized diets and foraging prevalence. In the case of high-diversity bird assemblages in the tropics, this suggests a close relationship between form, function and the ecological niche that we were able to uncover using the hypervolume framework.

The assumption that ecological niche spaces can be adequately quantified using a limited set of phenotypic traits is controversial (Didham et al., 2016; Gravel et al., 2016), mainly to the poor definition of direct functional effects of the selected traits. The morphological variables included in this analysis have well- established connections to trophic ecology (Miles & Ricklefs, 1984; Pigot et al., 2020, 2016; Ricklefs & Travis, 1980) and determine the positions of species in ecological space (Ricklefs 2012), specifically considering diet specialization, main diet and foraging prevalence (Pigot et al., 2020, 2016). Hence our results support the idea that the ecological niche cannot only be assessed from the perspective of environmental variables (i.e. following Grinell's and Elton's ideas) but also from the morphological variations among tropical birds. Our a priori functional classification based on diet specialization, main diet and foraging prevalence in combination with the analysis of morphospace occupation using hypervolumes allowed us reconciling these two different perspectives about the ecological niche.

These results might be affected by a biased sampling (i.e. not all groups in the three niche categories are equally well presented). In order to take this into consideration, we calculated morphospace volume in three different ways: (1) using all species present in each group (Figure A1-3), (2) using the number of species in the smallest group and resampling the same number of species in the other groups (i.e. results shown in the main text) and (3) using 70% of the species in each group (Figure A4-A6). The results presented here and discussed below hold for all three methods, which makes us confident that our results are not biased due to differences in sampling intensity. In the following we discuss our results in more detail in view of avian diet specialization, main diet and foraging prevalence:

(a) Diet specialization

Consistent with our first hypothesis (i), we found a smaller occupation of morphospace by species with more specialized diets and broader occupation in generalist species. If morphological differences correspond to differences in resource use (Dehling et al., 2016), this pattern may be explained by species intake on different types of food. For instance, all food types considered in this study are being used by generalists, and almost all generalist species feed on insects and fruits (Appendix Fig S8). Therefore, generalist species exhibit a greater variety of morphological adaptations moulded by their interactions with multiple food resources, adding to the volume of the generalists'morphospace. In particular, we observe an even greater morphospace occupation by those generalist species that feed on fruits and insects, consistent with works at larger scales (Pigot et al., 2020). The difference in morphospace occupation between facultative and obligatory specialists (Figure 2A) can be explained in a similar manner. While facultative species consume all the types of food, obligatory specialists only consume insects, seeds, fruits and nectar (Appendix Fig. A8). Hence, this reduces the number of potential distinct morphological adaptations that increase the total volume of the morphospace of the obligatory species. Although the representation of specialists feeding on vertebrate prey or plant matter in our data set may be limited due to their low capture rate in our methodological design, it is expected that due to the strictness in the obligatory specialist group, it will be very difficult for species in the sampling region to fall into this category. For example, if the work were extended to the national level of Colombia, only one folivore species would be considered a mandatory specialist (Hoatzin, Opisthocomus hoazin). Similarly, species of raptors (e.g., eagles, falcons, and owls) that would be presumed to be carnivores, would not be considered obligatory in our classification due to their intake of invertebrates.

Since generalist species share food resources with multiple specialists, they show a considerable degree of morphological overlap with facultative and obligatory specialists (hypothesis ii). Our results show a lower overlap between specialist and generalist species (Figure 2B). This may indicate that although generalist and specialist species share food sources, they have different adaptations to obtain it. While specialist species target a narrow range of resources, we show that their combinations of morphological traits position them at the periphery of the morphospace, which has been also shown by Dehling et al., (2012) and Pigot et al., (2020). In contrast, generalists show a generalized morphology pattern allowing them to exploit a variety of foraging substrates and prey items, hence they occur clustered toward the centre of the morphological space (Ricklefs, 2012). However, the last is not particularly discernible for this classification, since species are not differentiated by the food they consume, but rather their ability to feed on a certain number of different foods (see methods).

(b) Main diet

By distinguishing specialists according to their diet preferences, we obtained a differential pattern of morphospace occupation between generalists and specialists. Not all specialists show a smaller morphospace occupation than species with more generalist diets (i.e. omnivores). This may be due to the fact that the main diet suggests that the correspondence between form and diet requires a more phylogenetic explanation. Thus, results of average morphovolume analyses can be interpreted by the specific changes in species composition, by the idea that niches with more phylogenetic diversity should have more phenotypic variety (Mazel et al., 2018). Considering the composition of bird families as an explanation for the difference in morphospace occupation in dietary groups we find the larger morphospaces (i.e., Fruit, Omnivore, Invertebrate) correspond to the groups composed of the higher number of families. In contrast, groups with a narrow morphospace (i.e., Seed, Nectar) have species from only two to three different families (Appendix Fig. A10). The large morphovolume we found for fruit feeding species may be driven by unique representation in Toucans (Ramphastidae), New World Barbets (Capitonidae) or Manakins (Pipridae) families. With a relatively small number of species with extreme phenotypes, such as the White- mantled Barbet (Capito hypoleucus) and the Collared Aracari (Pteroglossus torquatus). Species with higher values of beak-related traits (can be seen in Figure A2). On the other hand, the narrow morphospace occupied by nectar specialist species may be explained by its complete representation of the hummingbirds (Trochilidae) family, with the exception of the Bananaquit (Coereba flaveola). Nectar niche species are clearly separated from the rest of species in morphospace by their tarsus length (Appendix Figure A2). Interestingly we found for the invertebrate specialist species, that although composed by the greater number of bird families, do not present values of morphovolume greater than the omnivores or frugivores. This can be due to a greater morphological similarity between the species classified in this group (can be seen in the conservation in the resampling results, Appendix Fig. A5), that although the invertebrate niche is populated by distantly related clades, these lineages are far more tightly packed in morphospace (i.e. suggesting morphological convergence) than would be expected based on their evolutionary relatedness (Pigot et al., 2020).

Considering the overlap of morphospace among groups, we found support for our second hypothesis. Morphospaces of the specialized groups show higher overlap with the omnivorous morphospace than with any of the other morphospace among the specialized groups (Figure 3B). Although species are morphologically adapted to exploit different resources, their morphologies can be broadly similar, in particular when sharing resources. Moreover, the morphospace overlap of almost all omnivores includes at least some species feeding on insects and fruits as well as seeds (Appendix Fig. A9) but rarely nectar and other food categories. Thus, the food types most consumed by omnivores are those shared with species that show the greatest morphological overlap with them. Meanwhile, the foods used in smaller proportions by omnivores correspond to those shared with the species which they overlap the least. Furthermore, the intake of insects by frugivorous species or vice versa might be an explanation for the high morphological overlap found between these two groups. It has been observed that birds'diets comprise a continuum between some extremes commonly treated as distinct categories, such as insectivores and frugivores (Lopes et al., 2003; Remsen, 2003; Zimmer & Isler, 2003). Interestingly we found that birds feeding on nectar also presents a significant intake of invertebrates (especially by hummingbirds), which is not reflected in a high morphospace overlap with the invertebrate group. This may be due to the fact that some of the variables related to invertebrate intake in hummingbirds were not taken into account in this work, such as sexual dimorphism and beak curvature (Stiles, 1995).

(c) Foraging prevalence

Morphospace differences due to foraging prevalence were less consistent than those for diet, in which similar estimates of morphovolume were obtained regardless of the resampling method (compared Figure 2-3 with Figure A4-A5). Nevertheless, we found greater morphospace volume for canopy, understory dwelling species and generalists in the overall and resampling results. Moreover, species with a foraging prevalence at midhigh and ground obtained the lowest morphovolume. With regard to phylogenetic diversity, the wide coverage of species with generalist foraging habits, which are represented in almost all bird families in the data set, seems to be related to the major occupation of morphospace. However, we also found large differences in morphospace volume for groups that do not vary much in the number of families, making it difficult to link phylogenetic diversity with morphospace occupation for foraging prevalence. Altogether, there seems to be no clear pattern between species composition and differences in morphospace occupation, contrasting our results with diet classifications where we found this relation. Most families are well represented among foraging groups and few seem to be linked directly to a particular group. With the exception of the unique presence of swifts (Apodidae) and swallows (Hirundinidae) in the aerial niche.

In terms of morphospace volume overlap, we found that the majority of specialized foraging groups showed higher overlap with foraging generalists (i.e. species that forage across multiple layers) than with any other specialized foraging group (Figure 4B). Almost all overlap values seem to be linked to the group morphospace volume (i.e. groups that have a greater volume show a greater overlap) and not to ecological similarities between the species. The reason for the poor morphological differentiation in the foraging groups may be due to the fact that species are not distinguished by more specific habits, but only by their preference for a certain feeding layer. Studies that found closer relationships between morphometrics and foraging included traits associated with foraging techniques (Pigot et al., 2020) or by comparing the level of species sharing the same food source (Pigot et al., 2016). This may be due that our morphological traits do not determine foraging behaviour and that the inclusion of more body measurements, such as bill-shape (Cooney et al., 2017) or cranial (Felice et al., 2019) measurements may reveal further morphological variation between species according to their foraging prevalence.

4 Conclusions

Our results highlight that the ecological niches of tropical birds can be inferred using morphological traits and quantified using hypervolumes. Advancing the understanding of avian niches hence requires compilations of standardized traits, as well as information about the species life history, from an ecological and phylogenetic perspective. Future studies, taking into account morphospace volume and overlap at a larger spatial scale and species assemblage (i.e. for entire Colombia) or comparing morphospace occupation with those of extratropical birds may reveal if niche space occupation is higher in tropical birds. This will advance the understanding of avian ecological niches and the generation of biodiversity.

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Appendices

Appendix A. Group classification and assignment protocol

(a-b) Main diet and diet specialization

Based on dataset quantifying the relative proportion of the diet made up of 8 different food categories (Table A1; columns 3-4), we assigned species obtaining half or more ($\geq 50\%$) of their food from a single category as specialists to the corresponding dietary groups (Nectar, Fruit, Invertebrate, Seed). The remaining species were classified as non-specialists (Omnivore). Only 5 of 8 possible dietary groups were included in our analyses because no study species specialized on any vertebrate prey or other plant material. For diet specialization classification, we further combined some of the original food categories according to Lopes's proposal classification scheme for avian diet types (Table A1; columns 1-2). By summing up the number of these new food categories on species diet, we assigned species with 1 or 2 food categories as specialists (1: Obligatory and 2: Facultative specialists respectively). The species with 3 or more food categories were classified as Generalists. We modified de presences or absence of some food categories for several species according to the local knowledge of species diets (can be seen the public data set available in Hypervolume_Birds_diets github repository)

(c) Foraging groups

To calculate specialization of foraging substrates, we used the extensive data on the relative use of different foraging niches (scored in 10% intervals) available in Etontriats1.0 dataset.

we assigned species to the foraging niche from which their prevalence is at least 50%. Leaving us with 5 specialist foraging niches: Aerial, Canopy, Midhigh, Understory and Ground. The remaining species were classified as foraging non- specialists (i.e. General). Only 5 of 7 possible foraging niches were included in our analyses because no study species specialized on foraging below a water surface (for further description see Table A2).

Table A1: Description of food categories according to the classification scheme proposed by Lopes et al.(2016), used for the Main diet and Diet specialization classifications, and further equivalent in EltonTraits 1.0 data set.

	Description (Lopes et al. 2016)	Variable (Eltontriaits1.0)	Description (Eltontriaits1.0)
Insectivore	Hexapoda (insects and their kin; e.g., springtails, dragonflies, cockroaches, termites, locusts, true bugs, beetles, flies, butterflies, ants, bees, and wasps), including the benthic aquatic forms (e.g., dragonflies, stoneflies, and mayflies). This category also includes birds that feed on other terrestrial arthropods, such as Chelicerata (e.g., ticks, spiders, and scorpions) and Myriapoda (e.g., centipedes and millipedes).	Diet-Inv	Per cent use of Invertebrates-general, aquatic invertebrates, shrimp, krill, squid, crustaceans, molluscs, cephalopods, polychaetes, gastropods, orthoptera, terrestrial Invertebrates, ground insects, insect larvae, worms, orthopterans, flying insects
Carnivore	Tetrapoda (e.g., amphibians, reptiles, birds, and mammals). Prey must be obtained alive to be considered a carnivore. Eggs of tetrapods (e.g., turtles, snakes, and birds) are also included in this food category because nest predators usually eat eggs and young.	Diet-Vend	Per cent use of Mammals, Birds
		Diet-Vect	Per cent use of Reptiles, snakes, amphibians, salamanders

Piscivore	All kinds of fish, from the, most frequently eaten Actinopterygii (ray-finned fishes) to Myxiniformes (hagfishes), Petromyzontiformes (lampreys), Chondrichthyes (sharks, rays, skates, and chimaeras), and Dipnoi (lungfishes). Fish must be captured alive. Fish eggs are also included here.	Diet-Vfish	Per cent use of Fish
Frugivore	Fleshy fruits, including berries, drupes, pomes, aggregated fruits, multiple fruits, and accessory fruits. Seeds, when ingested, are usually regurgitated or defecated whole	Diet-Fruit	Per cent use of Fruit, drupes
Nectarivore	nectar of flowers.	Diet-Nect	Per cent use of Nectar, pollen, plant exudates, gums
Granivore	Seeds, grains, nuts, and dry fruits, such as that of pines, grasses, sedges, composites, oaks, and palms.	Diet-Seed	Per cent use of Seed, maize, nuts, spores, wheat, grains
Folivores	Leaves, stems, shoots and buds, flowers, whole aquatic plants, ferns, clubmosses, and mosses.	Diet-PlantO	Per cent use of Other plant material, Grass, ground vegetation, seedlings, weeds, lichen, moss, small plants, reeds, cultivated crops, forbs, vegetables, fungi, roots, tubers, legumes, bulbs, leaves, above-ground vegetation, twigs, bark, shrubs, herbs, shoots, aquatic vegetation, aquatic plants

Table A2: Description of Foraging groups based on an estimated percent of foraging stratum recorded in EltonTraits 1.0 data set.

Foraging groups	Description
Aerial	Species where more than 50% of foraging activity occur above vegetation or any structures.
Canopy	Species where more than 50% of foraging activity occur in or just above (from) tree canopy.
Midhigh	Species where more than 50% of foraging activity occur in mid to high levels in trees or high bushes (2m upward), but below the canopy.
Understory	Species where more than 50% of foraging activity occur below 2m in the understory in the forest, forest edges, bushes or shrubs
Ground	Species where more than 50% of foraging activity occur on the ground
General	species where less than 50% of foraging activity occur on any single stratum

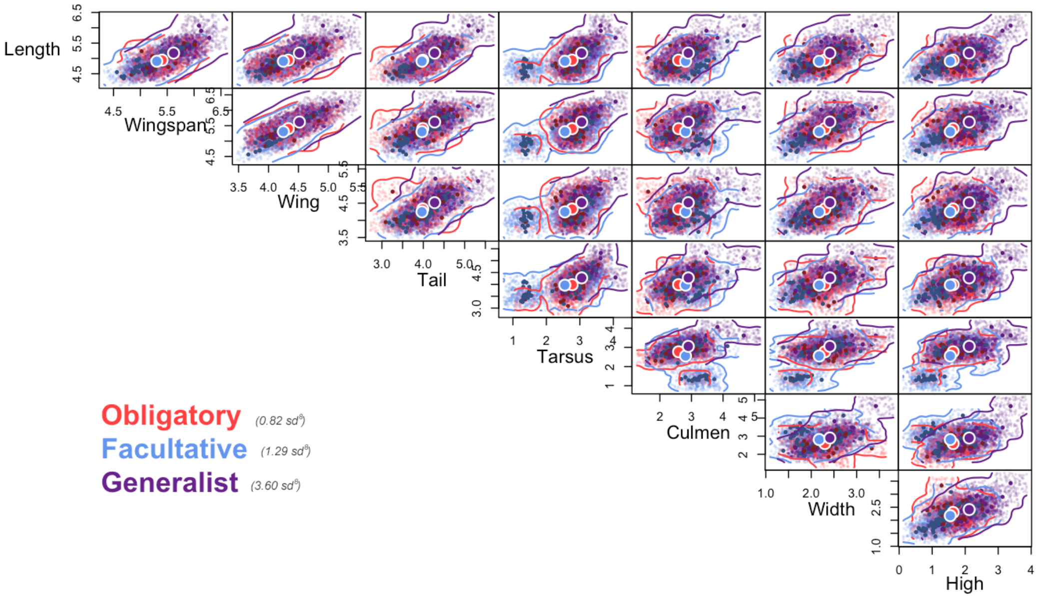

Figure A1: Diet specialization morphospace. Trait hypervolume (i.e. morphospace) for diet specialization groups using the whole pool of species. Morphospace is shown in a 2D projection using the combination of all eight morphological traits implemented in this study. All morphological traits were log-transformed.

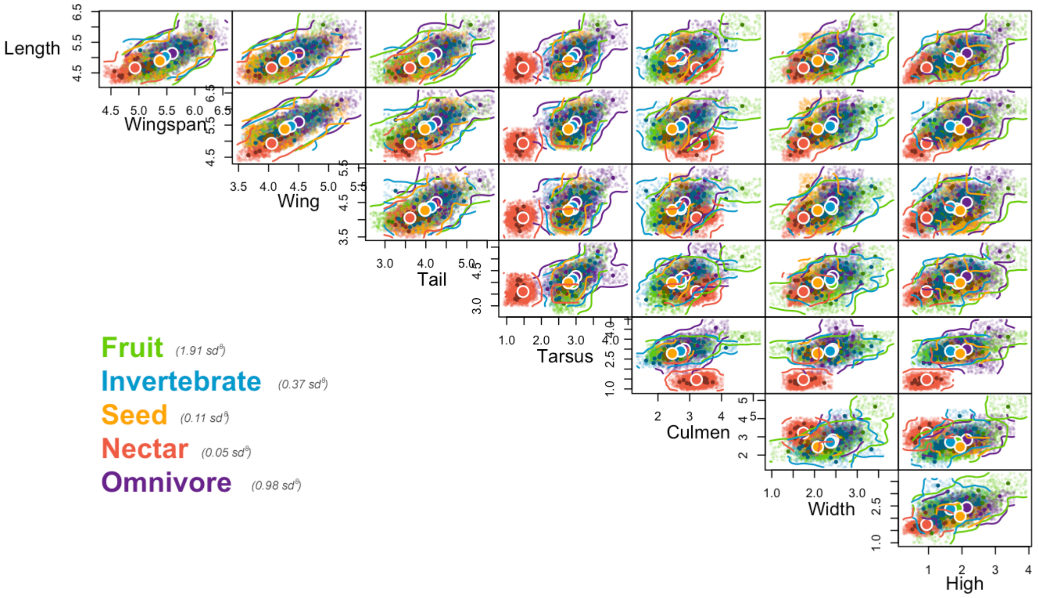

Figure A2: Main diet morphospace. Trait hypervolume (i.e. morphospace) for main diet groups using the whole pool of species. Morphospace is shown in a 2D projection using the combination of all eight morphological traits implemented in this study. All morphological traits were log-transformed.

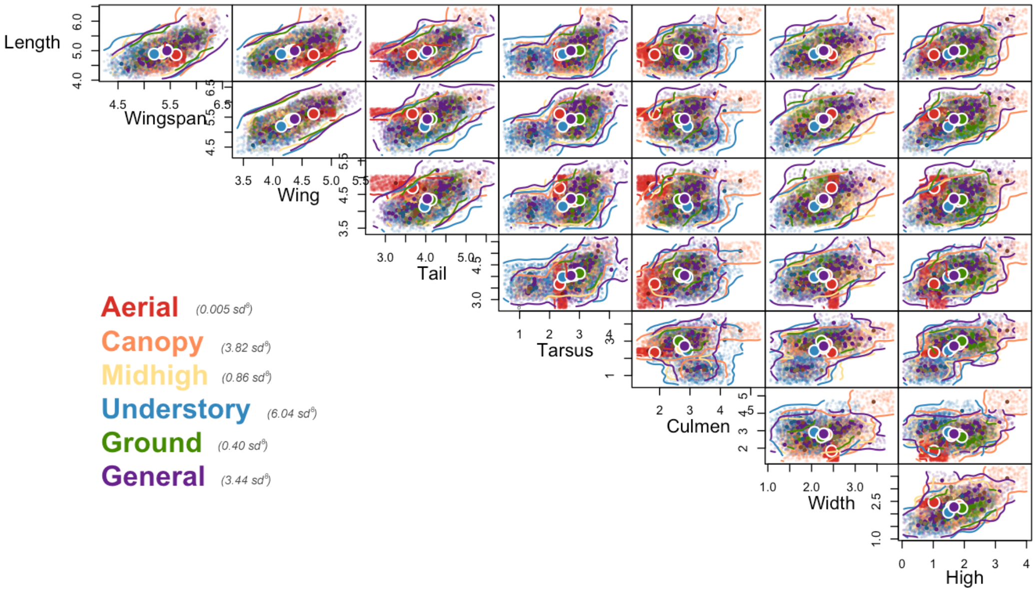

Figure A3: Foraging prevalence morphospace. Trait hypervolume (i.e. morphospace) for foraging groups using the whole pool of species. Morphospace is shown in a 2D projection using the combination of all eight morphological traits implemented in this study. All morphological traits were log-transformed.

Figure A4: Diet specialization re-sampling by percentage. Boxplot of the inferred volumes in the 1000 re-sampling iterations. For each iteration, we took a random sample of 50% (left) and 70% (right) of the species in each group.

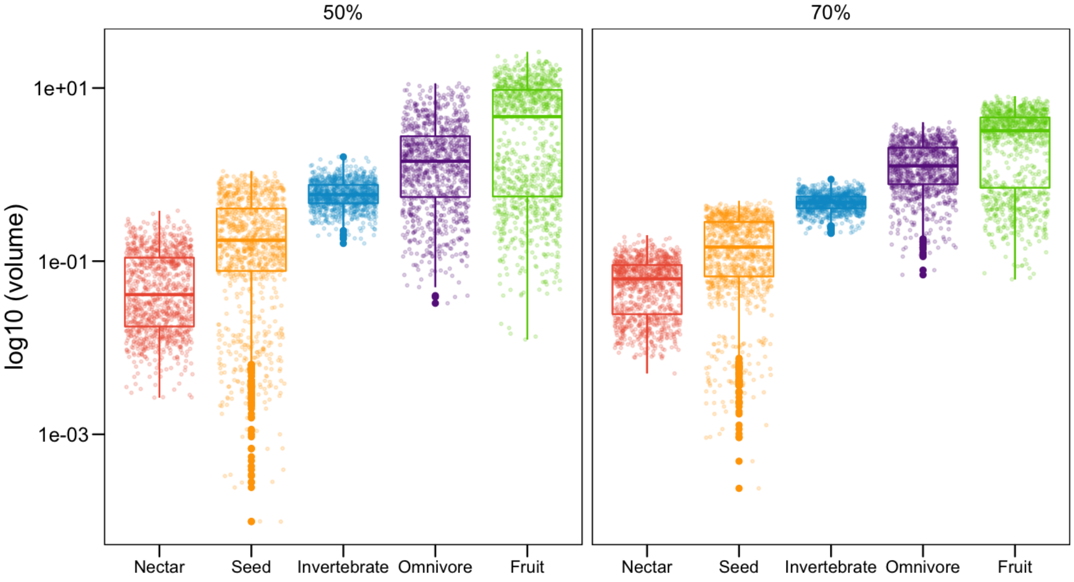

Figure A5: Main diet re-sampling by percentage. Boxplot of the inferred volumes in the 1000 re-sampling iterations. For each iteration, we took a random sample of 50% (left) and 70% (right) of the species in each diet group.

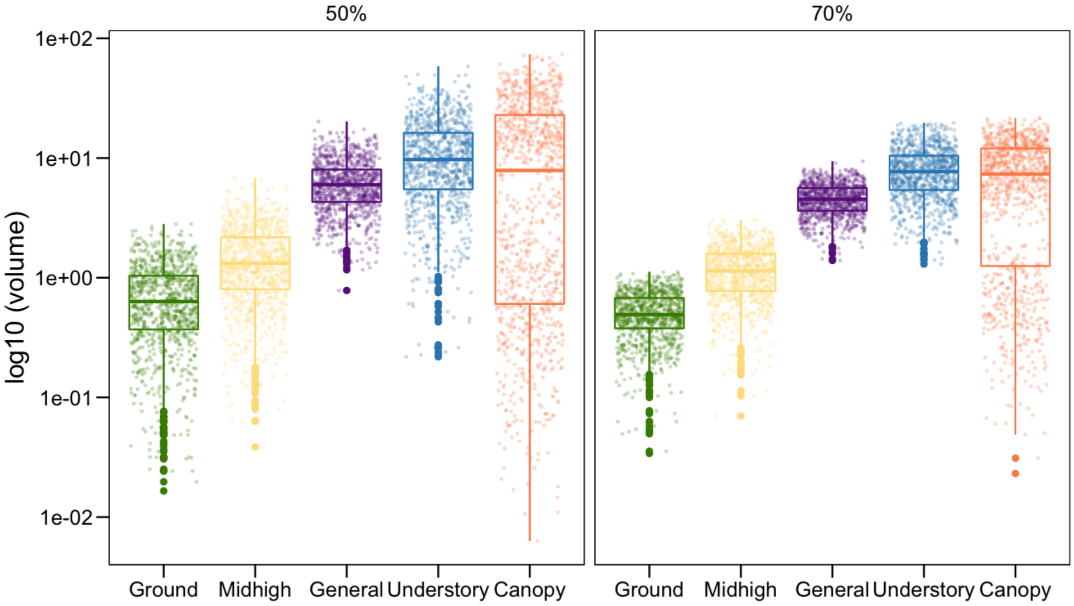

Figure A6: Foraging prevalence re-sampling by percentage. Boxplot of the inferred volumes in the 1000 re-sampling iterations. For each iteration, we took a random sample of 50% (left) and 70% (right) of the species in each foraging group.

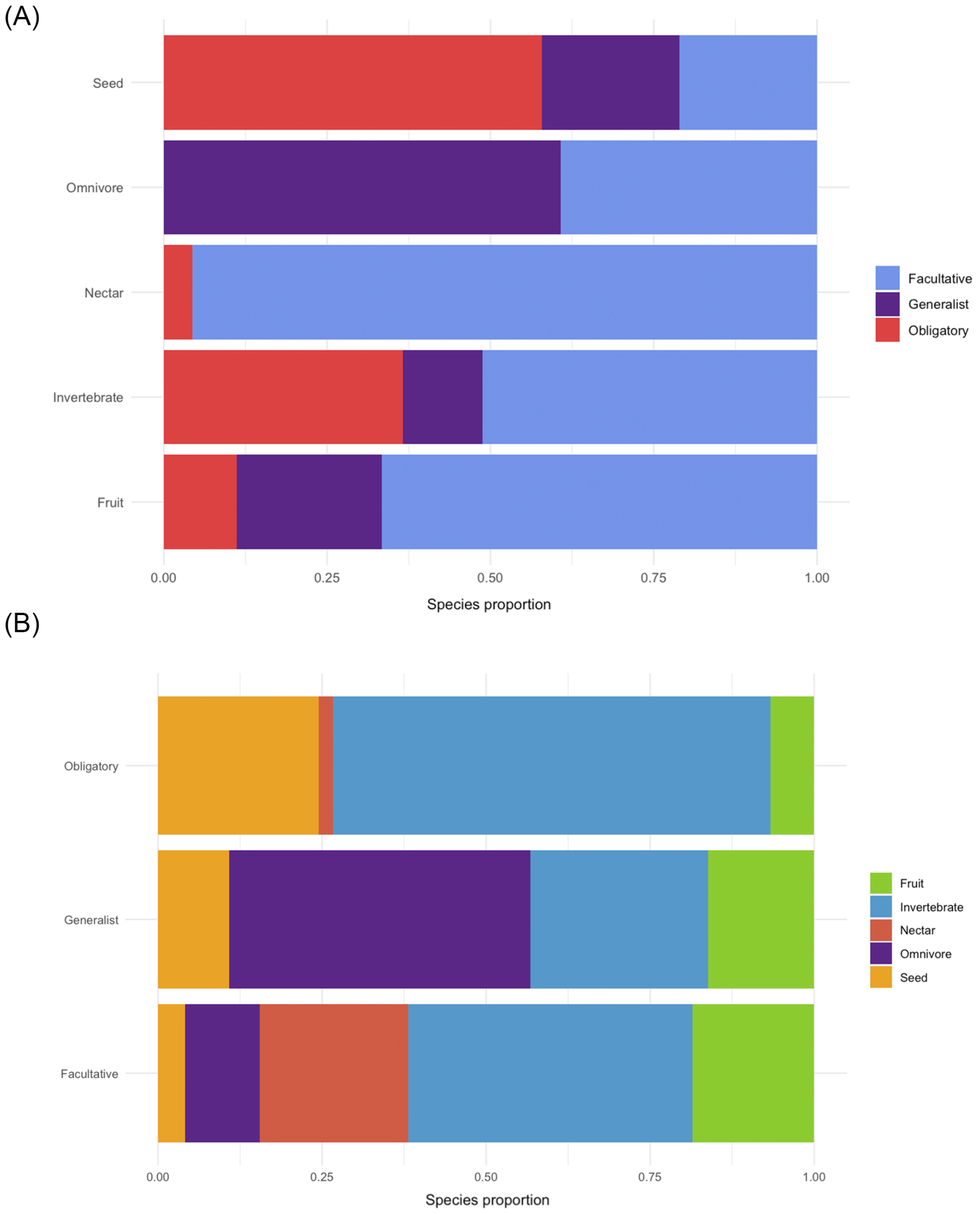

Figure A7: Relation between diet specialization and main diet categories. (A) The proportion of generalist and specialist species in each diet group (B) Proportion of diet groups species in each diet specialization group.

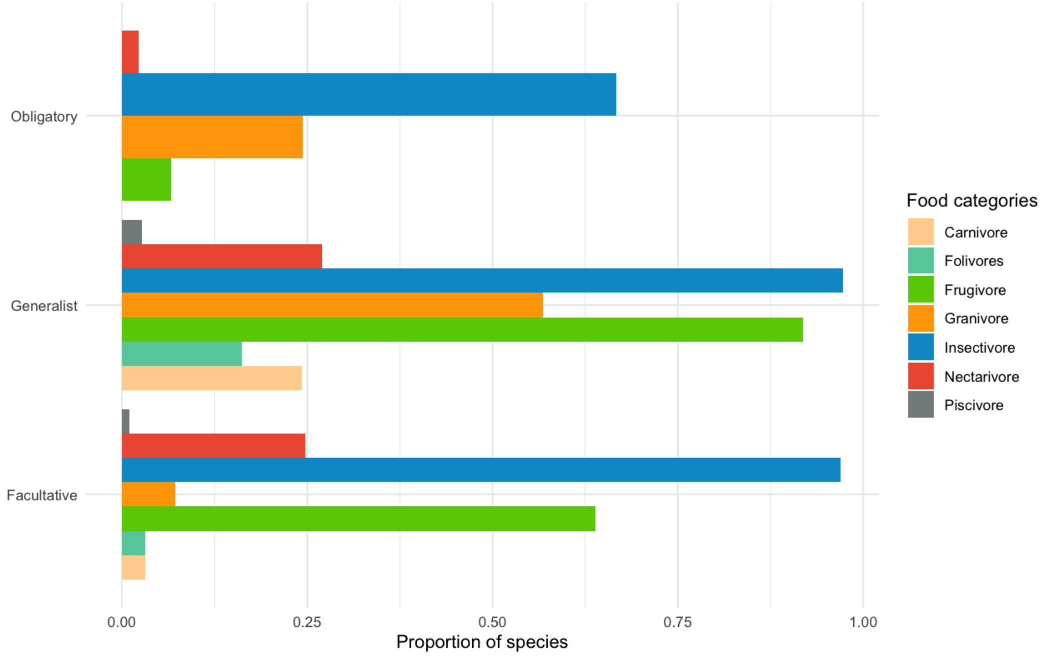

Figure A8: Food categories used by generalists and specialists. The proportion of species using food categories in each diet specialization groups.

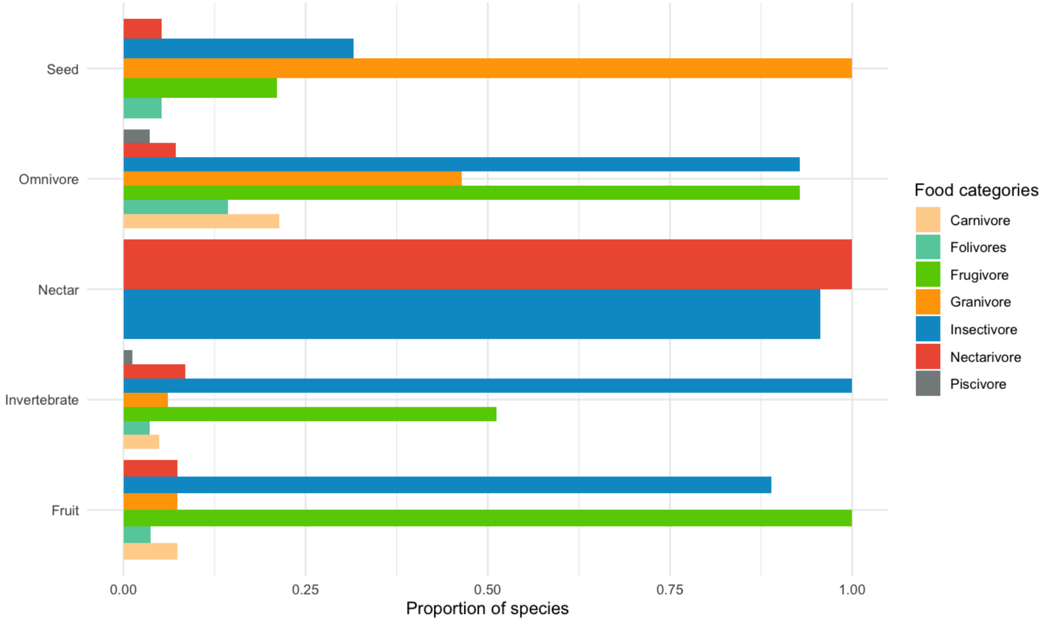

Figure A9: Food categories used by main diet groups. The proportion of species using food categories in each diet group.

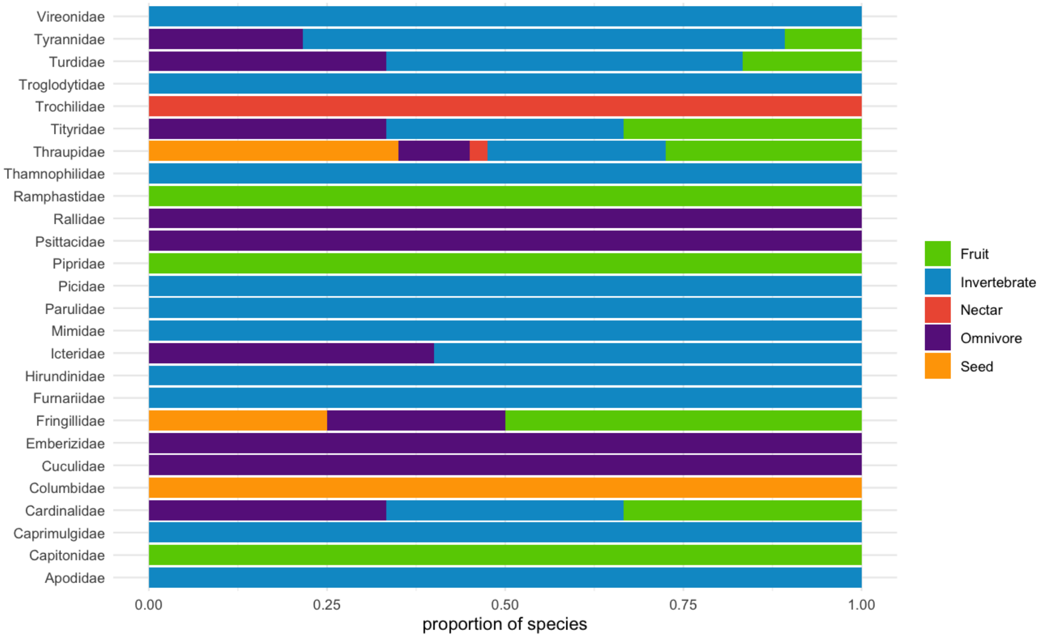

Figure A10: Family composition in main diet groups. The proportion of species in each family by diet groups.

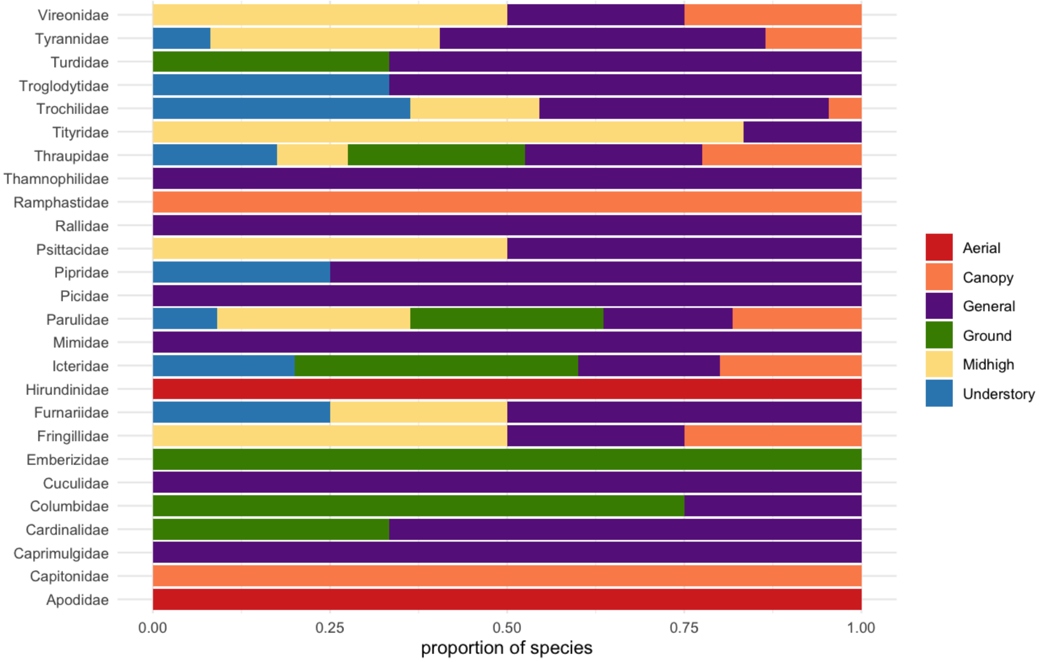

Figure A11: Family composition in foraging groups. The proportion of species in each family by foraging groups.