Relationship between morphology and trophic ecology in an assemblage of passerine birds in riparian forests of the Paraná River (Argentina)

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ABSTRACT

We describe the ecomorphology of an assemblage of bird species found in riparian forests of the Middle Paraná River, Argentina. We sought to determine (1) the more important morphological characteristics that separate coexisting species, (2) whether such separation was related to the trophic ecology of each species and (3) whether *a priori* guilds showed morphological similarity. We tested the hypotheses that (a) a species' morphology is related to the trophic ecology of that species and (b) that species of *a priori* guilds are morphometrically more similar to each other than to species of different *a priori* guilds. For this, we considered an assemblage of 29 species of birds from riparian forest that were sampled with mist nets during the 2011 and 2014 breeding seasons. We obtained morphometric measurements of captured individuals and supplemented those data with measurements from museum specimens. Trophic characterisation (diet and trophic microhabitat) was based on a literature review. Results showed a separation of bird species as a function of variables related to trophic ecology (diets and trophic microhabitats) and morphology. After controlling for phylogenetic constraint, species' morphology partially reflected the trophic ecology of the species, supporting the central hypothesis of the ecomorphological discipline and showing that the use of trophic and morphometric data provides complementary data to improve the guild organisation of riparian bird assemblages.

Keywords: ecomorphology, guild, riparian birds, riparian forest

1. INTRODUCTION

Ecomorphology can be defined as the science that deals with the functional relationships between the morphological design of an organism and its ecology (Ricklefs and Miles, 1994). Specifically, under the premise that organisms' adaptations demonstrate their ecological relationships, ecomorphological studies deal with the morphological similarities and differences that species present (Ricklefs and Travis, 1980; van Valkenburgh, 1995). Many studies (e.g. Karr and James, 1975; Ricklefs and Cox, 1977; Pianka, 1986; Carrascal *et al.*, 1990) examined the predictive value of a morphological trait for its ecological function, based on the premise that morphological similarity is correlated with ecological similarity (Ricklefs and Travis, 1980; Ricklefs *et al.*, 1981; Mesquita *et al.*, 2007). Such analyses may help determine the degree of specialisation exhibited by different species as a consequence of natural selection and may help to explain the mechanisms of segregation in the use of different resources (Jones, 1997; Rodríguez-Flores and Stiles, 2005; Zapata *et al.*, 2008).

A combination of ecological mechanisms and phylogenetic history determine organismal design (França *et al.*, 2008); thus, species can show similarities in the ecomorphological pattern as a consequence of the phylogenetic legacy. This has led some to suggest that some patterns of ecomorphology may be an artefact of phylogenetic relationships rather than environmental processes (Douglas and Matthews, 1992; França *et al.*, 2008). Thus, phylogenetic influence must be quantified when assessing the relationship between ecology and morphology, especially when addressing studies of local assemblages that include species with different degrees of phylogenetic relatedness.

A guild is a group of species that use the same class of environmental resources in a similar way (Root,

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1967). Once proposed, guild studies proliferated quickly (Hawkins and MacMahon, 1989). This interest in the guild concept came from the need for ecologists to delimit groups of species that were not defined by their taxonomic affinities but only by their ecology and with an emphasis on the use of resources (Hawkins and MacMahon, 1989; Wilson, 1999). The classification of species into guilds, however, is not without controversy, because the criteria used to define guilds may be varied.

Usually, guilds are categorised based on prior information on diet and feeding substrate of the species (*i.e. a priori* guilds; *e.g.* Marone, 1992; Cueto and López de Casenave, 2000; Ronchi-Virgolini *et al.*, 2011). Ecomorphology can make important contributions with regard to the criteria for the classification of species into different guilds. The idea that niche utilisation is correlated with or constrained by phenotype is an underlying assumption of ecomorphology (Bower-Piller *et al.*, 2015). Given the assumption that morphology reflects ecology, and that guilds are made up of ecologically similar species, ecomorphology can provide background information for the classification of species into guilds, including morphology as an additional variable in guild classifications.

Birds have been the subject of various ecomorphological studies at both species and assemblage levels. For example, studies have shown that the shape of the beak and limbs is related to foraging behaviour and habitat use (Moreno, 1991; Woodall, 1991; Moreno and Carrascal, 1993, 1994). However, there is a need for corroborative information supporting the occurrence of correspondence between ecology and morphology in local assemblages of neotropical avifauna because studies testing ecomorphological correspondence at local scales remain scarce for many bird groups (Botero-Delgadillo and Bayly, 2012). Recently, this last author assessed the correspondence between morphology and foraging behaviour based on data from a local assemblage of tyrant flycatchers (Tyrannidae) in Colombia and found that morphology could predict the ecology of the constituent species. The results also showed that the shape and size of the beak, wing length and tarsus were the traits best suited to predict foraging behaviour of species in an assemblage.

Riparian forests of the Paraná River in Argentina host diverse bird assemblages that include resident and migratory species represented by a variety of trophic guilds. Various prior studies have focused on structure and composition of bird assemblages in Paraná River riparian forests (*e.g.* Rosseti and Giraudo, 2003; Ronchi Virgolini *et al.*, 2010, 2011; Berduc *et al.*, 2015). None of these studies, however, have described these assemblages from an ecomorphological perspective, despite the fact that ecomorphology can provide valuable information regarding the structure of such assemblages. Ecomorphological studies may, for example, allow a better understanding of the trophic structure of communities, which may be useful for conservation and management.

The overall objective of this study was to describe the ecomorphology of an assemblage of bird species found in riparian forests of the Middle Paraná River. More specifically, we sought to determine (1) the more important morphological characteristics that separate coexisting species, (2) whether such a separation was related to the trophic ecology of each species and (3) whether species in *a priori* guilds were morphologically similar. Thus, we tested the hypotheses that a species' morphology is related to the trophic ecology of that species and that species of *a priori* guilds are morphometrically more similar to each other than to species in different *a priori* guilds.

2. METHODS

2.1 Study area

We studied ecomorphology of birds found in a riparian forest in the middle section of the Paraná River, Santa Fe Province, Argentina (31°39′40″S, 60°35′33″W). The study site is a partially flooded area that belongs to the Delta and Paraná islands ecoregion (Burkart *et al.*, 1999). The climate is humid-subtropical, with a long-term average annual temperature of 18 °C (Panigatti *et al.*, 1981).

2.2 Bird sampling

We focused the study on 29 bird species from 11 families (Table 1) captured with mist nets (6 or 12 m long, 2 m high, either 36 or 60 mm mesh) during the reproductive season from September 2011 until March 2012 and from September 2014 until March 2015. Although these 29 species represent only about half of the species recorded in these types of riparian forests (*e.g.* 48% of 60 species recorded by Rossetti and Giraudo, 2003), they do represent an assemblage of species that coexist locally during the spring/summer season studied. Ten nets were operated for 4 h, starting at sunrise, one day a week during the study period (Ralph *et al.*, 1996; Painter *et al.*, 1999). Nets were checked every 30 min or more often (15 min) depending on temperature (too cold or too hot). Nets were opened only on days with good conditions and were closed early if bad weather (*e.g.* rain) developed. Net locations were changed at random to prevent birds learning net locations and avoiding nets. Once captured, birds were measured and released quickly to avoid injury and excessive stress (Ralph *et al.*, 1996; Painter *et al.*, 1999). We recorded weight (to the nearest 0.1 g), tarsus (tarsometatarsus) length, beak (height, width and length) and head length, excluding the beak, for each capture following Gosler (2004). Measurements were taken to the nearest 0.1 mm.

To supplement data from captures, we measured specimens housed in Ameghino Museum in the city of Santa Fe, acknowledging that there may be morphological variability between populations from different areas.

Nonetheless, we assume that variation among individuals within a species would be less than variation among species, so that any differences within species among populations would not affect results.

2.3 Data analyses

2.3.1 Morphological analyses

We used a principal components analysis (PCA) to describe morphological variation among the species and, subsequently, to determine if species segregated in morphological space. PCA is an ordination technique (Jongman *et al.*, 1995) that reduces the information of the original variables by forming a linear combination of variables (the principal components) that explain the greatest amount of variation among those variables, generating multidimensional axes (principal components) with which the variables are correlated. PCA was performed on the morphometric measurements made for each of the species, so it was based on continuous variables. Variable 'weight' was eliminated before the analysis because of its high correlation with the variable 'bird length'.

2.3.2 Trophic analyses

Non-metric multidimensional scaling (NMDS) was used to describe trophic variation among the species and, subsequently, to determine if species segregated in trophic space. NMDS was performed on a trophic matrix based on categorical variables (e.g. used or not used) of diet (seeds, fruits, invertebrates and vertebrates) and trophic microhabitat (e.g. stratum in which a species most commonly fed), according to information available in the literature (Beltzer, 1987, 1988; Latino and Beltzer, 1999; Ordano *et al.*, 1999; De la Peña, 2001, 2002, 2006; Alessio and Beltzer, 2003; De la Peña and Pensiero, 2003; Horlent *et al.*, 2003; Beltzer *et al.*, 2004b; Del Barco and Beltzer, 2005; Andreau and Fernández, 2010). The NMDS ordination was created using the 'metaMDS' function in the 'vegan' package (Oksanen *et al.*, 2015) for R (R Core Team, 2015). The bird dissimilarity matrix was based on the Sorensen index. The trophic matrix was relativised through Wisconsin double standardisation where species are first standardised by maxima and then trophic variables by trophic variables totals (Oksanen, 2011). The ordination was evaluated by the coefficient of determination based on stress (R^2; Oksanen, 2011).

2.3.3 Phylogenetic analyses

Phylogenetic constraint on trophic variation among the species was accounted for in the analysis of morphometric influence by the use of a phylogenetic distance matrix. The phylogenetic matrix contained orders, families and genera of species based on Remsen *et al.* (2016), each one coded separately as a dummy variable. Through a Euclidean-based distance matrix on taxonomic data, species phylogenetic relatedness was accounted for in the analysis.

2.3.4 Association between morphometric and trophic data

We used a partial Mantel analysis to assess if trophic and morphometric data constrained by phylogeny were more or less similar to each other than expected by chance. Euclidean-based distance matrices of morphology and phylogeny were used alternatively as control matrices in the analysis to determine the effect of each one. The significance of the Mantel coefficient (H^0: $r = 0$) was assessed through 999 permutations. Partial Mantel analysis was implemented by package *vegan* (Oksanen *et al.*, 2015) in R (R CoreTeam, 2015).

2.3.5 Location of a priori *guilds in morphometric space*

An *a priori*-guild classification (*sensu* Wiens, 1989) was performed to assess the positioning of species in the morphometric space in relation to guild classification commonly used in the study area (e.g. Beltzer, 2003; Beltzer *et al.*, 2004a; Ronchi-Virgolini *et al.*, 2008, 2011). Species were grouped into trophic guilds according to the concept of 'functional guild', a group of species that use the same resources in the same way (Gitay and Noble, 1997). This term fits the original definition of Root (1967) as a group of species that use similar types of resources. Although we did not study guilds in a strict sense, because we only considered bird species (see Jaksić, 1981), we are still using the term guild because we use this approximation to study resource use among bird species. We defined bird guilds based on their main diet, the main substrate used for foraging and, for some species, the method of obtaining food, based on literature accounts (Capurro and Bucher, 1986; Beltzer 1988a,b, 1990a,b; Canevari *et al.*, 1991; Marone, 1992; Caziani, 1996; Cueto, 1996; Darrieu *et al.*, 1996; López de Casenave *et al.*, 1998; Cueto and López de Casenave, 2000; De la Peña, 2001, 2002, 2006; Beltzer, 2003; Marateo, 2009; Ronchi-Virgolini, 2011). While in some cases the feed substrate is mentioned in the name of the guilds, in others, where the species of the guild include various substrates, the substrate is not included in the guild name. In general, species included in the same guild overlap at least one of the substrates. As a result, bird species were divided into 10 guilds (Table 1).

The species assigned to the same guild were located in the morphometric space generated by the principal component analysis to graphically assess the relationship between trophic and morphometric similarities. A permutational multivariate analysis of variance (PERMANOVA) was

Table 1 Classification of bird species in *a priori* guilds

Species	Trophic guilds
Columbina picui	Soil granivore
Zonotrichia capensis	Soil granivore
Agelaioides badius	Granivore–insectivore
Molothrus rufoaxilaris	Soil granivore–insectivore
Molothrus bonariensis	Soil granivore–insectivore
Volatinia jacarina	Herbivore–granivore
Saltator aurantiirostris	Herbivore–granivore
Saltator coerulescens	Herbivore–granivore
Phacellodomus ruber	Foliage insectivore
Vireo olivaceous	Foliage insectivore
Troglodytes aedon	Foliage insectivore
Polioptila dumicola	Foliage insectivore
Furnarius rufus	Soil insectivore
Lepidocolaptes angustirostris	Bark insectivore
Fluvicola albiventer	Short-flight insectivore
Hemitriccus margaritaceiventer	Short-flight insectivore
Serpophaga subcristata	Short-flight insectivore
Satrapa icterophrys	Short-flight insectivore
Elaenia spectabilis	Insectivore–frugivore
Pachyramphus polychopterus	Insectivore–frugivore
Poospiza melanoleuca	Insectivore–frugivore
Paroaria capitata	Insectivore–frugivore
Paroaria coronate	Insectivore–frugivore
Turdus amaurochalinus	Insectivore–frugivore
Turdus rufiventris	Insectivore–frugivore
Icterus cayanensis	Insectivore–frugivore
Taraba major	Generalist
Pitangus sulphuratus	Generalist
Cyclaris gujanensis	Generalist

performed to assess whether morphometric variables were different among *a priori* guilds. Euclidean distance was used as distance measure of bird morphometry. This analysis was performed using the package 'vegan' (Oksanen *et al.*, 2015) in R (R CoreTeam, 2015).

3. RESULTS

3.1 Morphometric analysis

The first three components of the PCA of the morphological data explained 63%, 16%, and 8%, respectively, of the total variation. Together, these three axes accounted for 87% of the morphological variation among species (Table 2). An ordination based on these three principal components showed that species were relatively well spread out in morphological space. Although some species were closely associated along some component(s), they were separated along others (e.g. *Poospiza melanoleuca* and *Polioptila dumicola* in components 1 and 3 *vs* 1 and 2; Figure 1). Isolation in morphological space occurred only in the case of *Lepidocolaptes angustirostris* because of the long beak (Figure 1).

Table 2 Explained variance and correlation of morphometrical variables with each one of the three principal components

	PC1	PC2	PC3
Bill length	–0.61	0.67	0.36
Bill height	–0.75	–0.59	0.04
Bill width	–0.82	–0.34	0.36
Tarsus length	–0.85	0.13	–0.39
Head length	–0.85	0.07	0.09
Hallux width	–0.84	0.16	-0.34
Variance	1.94	0.98	0.73
Percentage variance	63	16	8
Accumulated variance	63	79	87

The first principal component separated species by size, reflected by negative correlations of all variables with this principal component (Table 2). The second main component reflected primarily the difference between length, width and height of beaks among species, separating species with higher and wider beaks from those with longer beaks. Thus, species with longer beaks (e.g. *Lepidocolaptes angustirostris* and *Furnarius rufus*) were located on the upper part of Figure 1, and species with higher and wider beaks (e.g. *Volatinia jacarina* and *Cyclaris gujanensis*) were located at the bottom of the figure. Finally, the third principal component segregated the species based on the length and width of the beak on one side, and based on tarsus length and width of the hallux on the other side. Thus, species with longer tarsi (e.g. *Furnarius rufus*, *Icterus cayanensis*, *Vireo olivaceous* and *Satrapa icterophrys*) were located in the lower parts of the figure.

3.2 Trophic analysis

NMDS summarised the variation of diet and trophic microhabitat among bird species in three dimensions (Figure 2). The first dimension mainly separated, from the rest of the species, those which include only seeds in their diet (*Columbina picui*, *Zonotrichia capensis* and *V. jacarina*) and that feed on the ground (*C. picui* and *Z. capensis*) or in the herbaceous substrate (*V. jacarina*), and those which mainly include invertebrates in their diet (*Pachyramphus polychopterus*, *Hemitriccus margaritaceiventer*, *Serpophaga subcristata*, *P. dumicola* and *Fluvicola albiventer*; Figure 2). The second axis separated species which feed on invertebrates from different substrates: on the ground (*Furnarius rufus*); in the bark of trees (*Lepidocolaptes angustirostris*); and in flight (*F. albiventer*); and the three species that include vertebrates in their diet (*Pitangus sulphuratus*, *Cyclaris gujanensis* and *Taraba major*). *P. melanoleuca* was also separated because it is the only species that included seeds and fruits from the herbaceous and shrub strata. Finally, the third dimension separated those species which feed

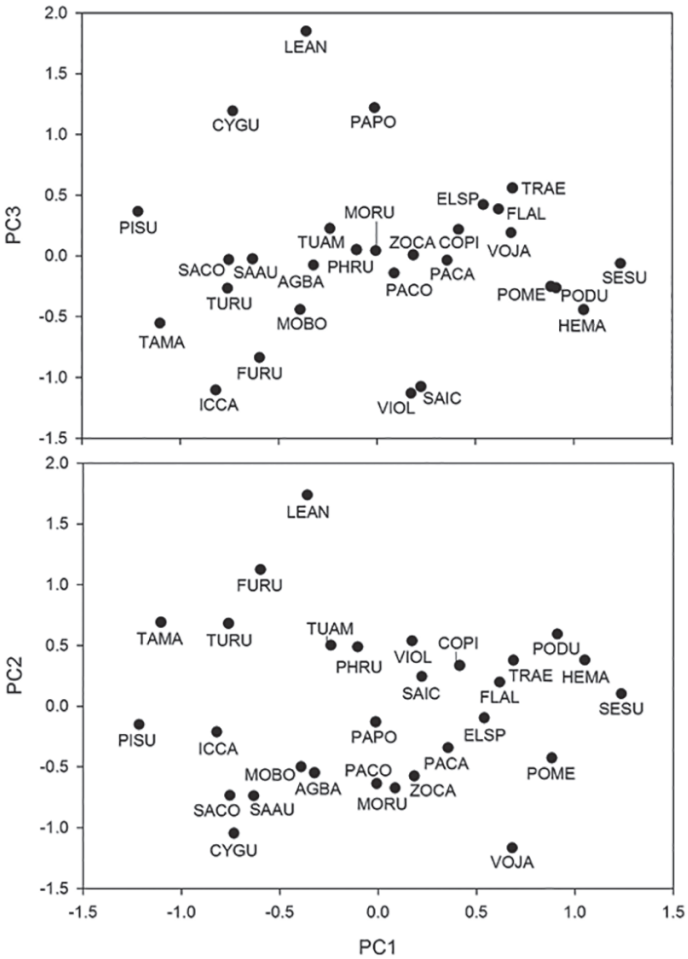

Figure 1 Analysis of principal components based on six morphometric measurements of 29 bird species from riparian forest assemblages.

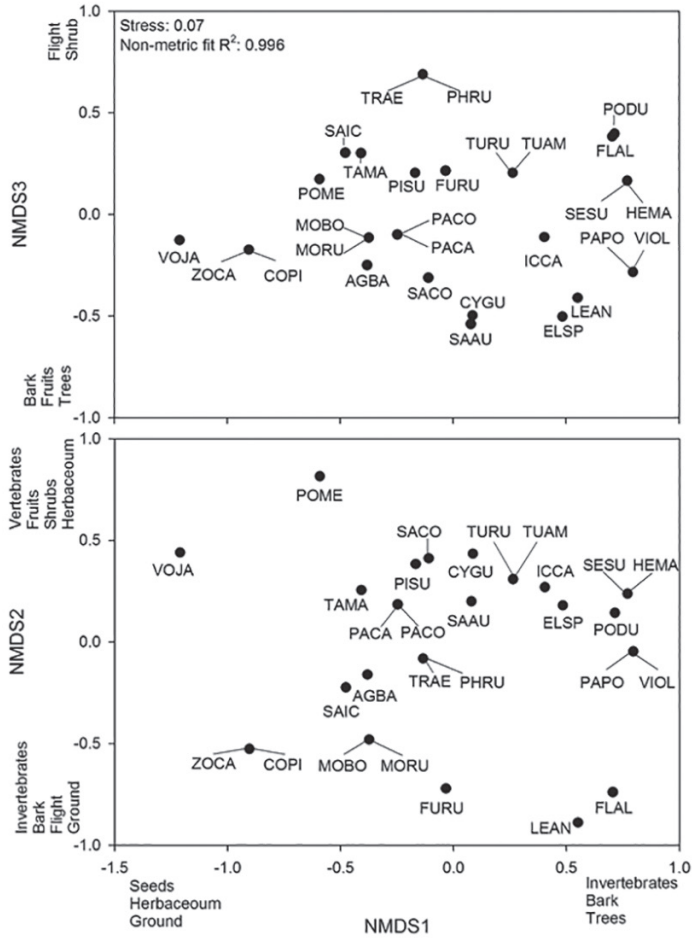

Figure 2 Non-metric multidimensional scaling based on trophic categorical variables of 29 bird species from riparian forest assemblages.

in flight (*Satrapa incterophrys* and *F. albiventer*) and in the shrub stratum (*Phacellodomus ruber and Troglodytes aedon*). Thus, NMDS analysis showed that species can be segregated according to their diet and trophic microhabitat. Although 14 species shared both food items and substrates, groups overlapping in NMDS space were composed of two species at most (*i.e.* in any case three or more species shared trophic items and microhabitat; Table 3).

3.3 Association between morphometric and trophic data

Phylogenetic relationships among species accounted for variation in diet and trophic microhabitat among bird species (partial Mantel test: $r = 0.21$, $P = 0.002$). After controlling for phylogenetic constraint, species with trophic similarities in diet and microhabitat were also morphologically more similar (*i.e.* morphometric and trophic matrices had a positive relationship; partial Mantel test: $r = 0.20$, $P = 0.012$).

Table 3 Species that shared the trophic items of the diet as well as the trophic microhabitat, presenting a similarity of 100% in the NMS analysis

Species	Diet	Trophic microhabitat
Vireo olivaceous	Invertebrates	Arboreal
Pachyramphus polichopterus		
Serpophaga subcristata	Invertebrates	Shrubs
Hemitriccus margaritaceiventer		Arboreal
Turdus rufiventris	Fruits	Soil
Turdus amaurochalinus	Invertebrates	Shrubs
		Arboreal
Paroaria coronata	Seeds	Soil
Paroaria capitata	Fruits	Herbaceous
	Invertebrates	Arboreal
Troglodytes aedon	Invertebrates	Soil
Phacellodomus ruber		Herbaceous
		Shrubs
Zonotrichia capensis	Seeds	Soil
Columbina picui		
Molothrus rufoaxilaris	Seeds	Soil
Molothrus bonariensis	Invertebrates	

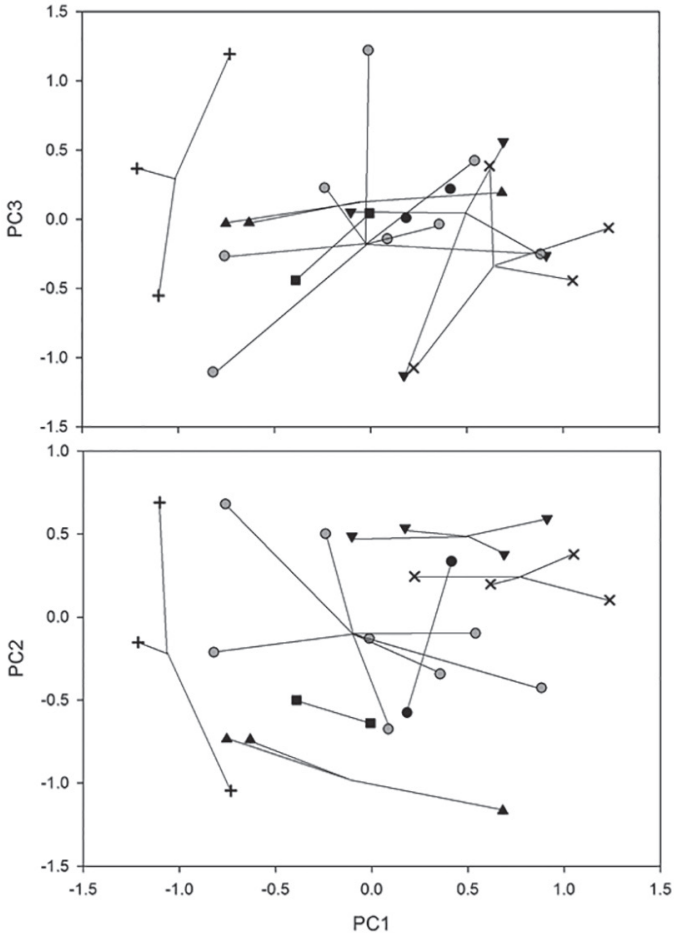

Figure 3 Location of *a priori* guilds on the morphometric space created through principal component analysis. Lines join the species that make up each guild. Symbols represent different guilds: Black circles, soil granivores; black squares, soil granivores–insectivores; black triangles, herbivores–granivores; black inverted triangles, foliage insectivores; X, short-flight insectivores; grey circles, insectivores–frugivores; +, generalists.

3.4 Location of *a priori* guilds in morphometric space

Morphometric variables were different among *a priori* guilds (PERMANOVA: $R^2 = 0.53$, $P = 0.026$). However, location of *a priori* guilds on the morphometric space generated through PCA showed a high morphometric heterogeneity among the species that composed them (Figure 3).

4. DISCUSSION

Studying the existence of ecological and morphological differentiation among synoptic species, and whether there is a correlation between ecology and morphology, is key to assessing the central hypotheses of the ecomorphological discipline (Ricklefs and Travis, 1980). There are few studies that have assessed this relationship in Neotropical bird assemblages (*e.g.* Botero-Delgadillo and Bayly, 2012). This research showed that the structure of bird assemblages found in Paraná River riparian forests can be analysed from an ecomorphological perspective. In this study, species' morphologies partially reflected trophic ecology, supporting the central hypothesis of the ecomorphological discipline (Ricklefs and Travis, 1980) and showing that the use of trophic and morphometric data provides complementary data with which to characterise the guild organisation of bird assemblages.

Results of this study indicate that variables related to diet, trophic microhabitats and morphology were sufficient to separate bird species found in riparian forests into distinguishable groups. This represents a crucial step for ecomorphological studies, since it implies that the concept of 'trophic niche' can be reflected in descriptive ordering analyses (*i.e.* NMDS), which can be used to demonstrate partitioning of resources, whether based on diets or trophic microhabitats. Results also showed that morphological variables used were sufficient to separate species into groups based on morphological differences and similarities. In sum, both procedures (*i.e.* trophic segregation and morphological segregation) represent a vital starting point for testing the core premise for ecomorphological studies, that is, the idea that morphology closely reflects trophic ecology.

4.1 Association between the morphology and the trophic ecology of species

The basis of an ecomorphological approach to understanding the structure of communities is the idea that morphology is related to, or indicative of, the ecological role or niche of an organism in that community (Ricklefs and Miles, 1994). In our study, morphology partially reflected trophic ecology, lending support to the central hypothesis of the ecomorphological discipline (Ricklefs and Travis, 1980). On the other hand, that a correlation should exist between ecological and morphological characteristics is not necessarily obvious. A single shared trait can be the answer to different ecological problems, and that the solution of a given problem can be achieved by different morphological forms (Leisler *et al.*, 1989). Thus, any ecomorphological study must start with the test of a relationship between ecology and morphology.

In this study, morphological and trophic variables did not show a high degree of association. In principle, the lack of a strong association is not surprising as previous studies have reported similar results. As Block *et al.* (1991) pointed out, not all morphological variation can be explained by the way birds search for food. This fact is not surprising either, given that a species' morphology represents a set of phenotypic traits that facilitate all life-history aspects, not simply foraging (Winkler, 1988) and because other factors can influence morphology (Luther and Greenber, 2014). The low degree of association between morphology and trophic ecology seen here also could be related to the nature of the trophic data that were

used. For example, trophic categories used in this and many other studies are largely based on presence–absence matrices that do not provide information on the relative importance of different prey items or foraging substrates. This lack of detailed information can restrict the precision of the association between trophic and morphologic variables. Thus, more detailed evaluations are needed to test whether or not morphological characteristics can serve as an accurate index of niche relationships (Landman and Winding, 1993). Beyond these limitations, the results indicated that there is some association between the trophic and morphological variables. In general, it can be concluded that morphological and trophic characteristics of each of the species are not independent.

Phylogeny has been demonstrated to influence relationships between morphology and ecology (Douglas and Mathews, 1992; Richman and Price, 1992) and in this study, phylogeny accounted for a similar proportion of trophic variation as did morphology. Congeneric species showed a relatively high morphological and ecological similarity (*e.g. Saltator* spp., *Turdus* spp. and *Paroaria* spp.). This phylogenetic effect was accounted for in the analysis of morphological and ecological correlation.

Body mass, length, height and width of beak and tarsus length are the five morphometric measures generally linked with foraging ecology and diet selection (Rotenberry, 1980; Botero-Delgadillo and Bayly, 2012). Body size has been related to trophic ecology (Schoener, 1968; Greenberg, 1979; Rotenberry, 1980). For example, small body size is likely an adaptation for specialised foliage insectivory in parulid warblers because small size allows the exploitation of certain microhabitats by permitting the use of thinner twigs and facilitating agility (Greenberg, 1979; Winker and Leisler, 1985). Accordingly, species that feed on invertebrates associated with the herbaceous, shrub and/or arboreal strata (*S. subcristata*, *H. margaritaceiventer*, *P. dumicola, T. aedon* and *P. melanoleuca*) were segregated from the rest of the species along the first axis of the PCA, based on their relatively small size. In contrast, generalist species (*i.e. T. major*, *P. sulphuratus* and *C. gujanensis*, species that include seeds, fruits, invertebrates and vertebrates in their diet) were the largest in the assemblage. These were the only species included in this study that included vertebrates in their diet, suggesting that only large species can ingest this type of prey. In general, vertebrates that are part of the diet of these species (Lopes *et al.*, 2005; Andreau and Fernandez, 2010), imply that the bird has a relatively large size and strength to achieve capture. For example, the prey size of a predator could be a function of its power to knock the prey down (Grant, 1968). Thus, this result agrees with the idea that bird size could be a better predictor of the size of prey taken than any single bill characteristic (Hespenheide, 1971).

Most studies have attributed variation in beak morphology to differences in trophic ecology, both in terms of the different types of food captured and the different methods of foraging for food (Luther and Greenberg, 2014). Here, species with relatively long beaks were clearly separated from those with shorter and wider beaks. Among the species of small size in this assemblage, the species with longest beaks were mainly insectivorous (*e.g. P. dumicola*, *T. aedon*, *H. margaritaceiventer*, *F. albiventer* and *S. subcristata*) whereas species that include seeds in their diet had shorter and/or higher beaks (*e.g. V. jacarina*, *P. melanoleuca* and *Z. capensis*). The trophic morphology of insectivorous birds is apparently selected more for prey capture than handling, whereas seed-eating birds have a bill morphology selected for food manipulation rather than procurement. Long-billed birds should be able to capture fast moving prey more readily than short-billed birds. The jaw pressures exerted by insectivorous birds need only be great enough to capture and hold prey (Lederer, 1975). In the case of granivorous species, the height and width of the beak are the characters that allow them to apply forces with the beak to compress the seeds, which must be done to husk them (Wilson, 1972; Diaz, 1990).

The length of the tarsus has been historically associated with the feeding microhabitat (James, 1982) particularly the perch type (Grant, 1971). Tarsus length is considered adaptive, in that it is suited to the locomotor needs of the species in the niche(s) it occupies when it is not flying. Tarsus tend to be shorter in most birds that forage on the trunks of trees (Richardson, 1942), such as *L. angustirostris*, the unique bark insectivore included in our study. On the contrary, tarsus tend to be longer in birds that forage on the ground (Dilger, 1956; Rüggeberg, 1960), such as *T. major*, *F. rufus*, *T. rufiventris* and *Molothrus bonariensis* in our study. Beyond these cases, the length of the tarsus was not as important as the morphology of the beak to differentiate the species of the assemblage.

4.2 Association between the morphology and the *a priori* trophic guilds

Estimation of ecological relationships among species from their positions in morphological space, that is, to make ecological inferences from morphological pattern, is one of the goals of ecomorphological analysis (Ricklefs and Miles, 1994). Thus, morphology can help classify species according to ecological criteria. Because classifications of species into guilds is the most widespread approach to classification of species according to their ecological characteristics (Wilson, 1999), consideration of morphological characteristics may help refine guild classifications. Our results showed that, although morphometric measurements were statistically more similar among species included in the same *a priori* guild, there was a large amount of morphometric heterogeneity within guilds. For example, insectivores–frugivores showed a high heterogeneity along the first principal component related to body size differences (*e.g.* Ronchi-

Virgolini *et al.*, 2011). Thus, the results showed that the guild insectivores–frugivores could be re-evaluated, limiting the species that compose them to those within certain ranges of morphological similarity.

The relatively distant positioning in morphological space of species that share ecological characteristics suggests that these species have different niches within the assemblages because morphometry may reflect mechanisms by which species avoid or reduce competition (Hutchinson, 1959; Dayan and Simberloff, 1998). This suggests that species within *a priori* guilds do not overlap in their niches despite sharing trophic characteristics such as diet and feeding microhabitat (*i.e.* despite sharing the characteristics from which they are assigned to a common guild). Thus, the inclusion of morphometry in the context of studies performed at guild level may contribute to a more accurate ecological classification of species.

4.3 Conclusions

In conclusion, this work shows that morphology partially reflects the trophic ecology of bird assemblages of riparian forest from Paraná River, which represents the base concept of ecomorphology. In addition, results showed that ecomorphological studies can help improve *a priori* guild classification of bird species, contributing to a more appropriate approach for the determination of the guild organisation of assemblages.

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6. REFERENCES

Alessio, V. and Beltzer, A. (2003) Biología de la alimentación del Espinero grande *Phacellodomus Ruber* (aves: Furnariidae) en el valle de inundación del río Paraná, Argentina. *Rev. Nodo*, **8**, 91–102.

Andreau, M. and Fernández, D.P. (2010) Predación del Juan Chiviro (*Cyclarhis gujanensis*) sobre aves, murciélagos, reptiles y anfibios. *Nuestras Aves*, **54**, 43– 45.

Beltzer, A.H. (1987) Ecología alimentaria de Batará grande *Taraba major* (Aves: Formicariidae) en el valle aluvial del río Paraná Medio, Argentina. *Stud. Neotrop. Fauna E.*, **22**, 137–144.

Beltzer, A.H. (1988a) Consideraciones sobre la ecología alimentaria del chiviro de isla *Saltator coerulescens coerulescens* y el chiviro de corbata *Saltator aurantiirostris* (aves: Emberizidae) en el valle aluvial del río Paraná medio (Argentina). *Stud. Neotrop. Fauna E.*, **23**, 9–23.

Beltzer, A.H. (1988b) Biología alimentaria del tordo mulato *Molothrus badius badius* (Aves: Icteridae) en el valle aluvial del río Paraná medio, Argentina. *Rev. Asoc. Cienc. Nat. Litoral*, **19**, 113–121.

Beltzer, A.H. (1990a) Biología alimentaria del verdón común *Embernagra platensis platensis* (Aves Emberizidae) en el valle aluvial del río Paraná medio, Argentina. *Ornitol. Neotrop.*, **1**, 25–30.

Beltzer, A.H. (1990b) Biología alimentaria del halconcito común *Falco sparverius* en el valle aluvial del río Paraná medio, Argentina. *Hornero*, **13**, 133–136.

Beltzer, A.H. (2003) Aspectos tróficos de la comunidad de aves de los Esteros del Iberá. In: Alvarez, B.B. (ed.), *Fauna del Iberá*, pp. 257–272. Universidad Nacional del Nordeste, Corrientes.

Beltzer, A.H., Quiroga, M.A. and Bortoluzzi, A.L. (2004a) Variación estacional de la comunidad de aves en un ambiente lenítico del valle de inundación del río Paraná. *Nat. Neotrop.*, **34/35**, 33–37.

Beltzer, A.H., Quiroga, M., Latino, S. and Comini, B. (2004b) Feeding ecology of the Grayish Saltator *Saltator coerulescens* (Aves: Emberizidae) in the Paraná river floodplain (Argentina). *Orsis*, **19**, 91–99.

Berduc, A., Lorenzón, R.E. and Beltzer, A.H. (2015) Patrones de diversidad de aves a lo largo de un gradient latitudinal de bosques ribereños del río Paraná medio, *Argentina. R. Mex. Biodivers.*, **86**, 419-430.

Block, W.M., Brennan, L.A. and Gutierrez, R.J. (1991) Ecomorphological relationship of a guild of ground-foraging birds in northern California, USA. *Oecologia*, **87**, 449458.

Botero-Delgadillo, E. and Bayly, N.J. (2012) Does morphology predict behavior? Correspondence between behavioral and morphometric data in a tyrant-flycatcher (Tyrannidae) assemblage in the Santa Marta Mountains, Colombia. *J. Field Ornithol.*, **83**, 329–342.

Bower, L.M. and Piller, K.R. (2015) Shaping up: a geometric morphometric approach to assemblage ecomorphology. *J. Fish Biol.*, **87**, 691–714.

Burkart, R., Bárbaro, N.O., Sánchez, R.O. and Gómez, D.A. (1999) *Eco-regiones de la Argentina, Buenos Aires*. Administración de Parques Nacionales, Buenos Aires.

Canevari, M.P., Canevari, G.R., Carrizo, G., Harris, J., Rodríguez, M. and Straneck, R.J. (1991) *Nueva guía de las aves Argentinas*, Tomo I y II. Fundación Acindar, Buenos Aires.

Capurro, H.A. and Bucher, E.H. (1986) Variación estacional en la comunidad de aves del bosque chaqueño de chamical. *Physis (Secc. C)*, **44**, 1–6.

Carrascal, L.M., Moreno, E. and Telleria, J.L. (1990) Ecomorphological relationships in a group of insectivorous birds of temperate forests in winter. *Holarct. Ecol.*, **13**, 105–111.

Caziani, S.M. (1996) Interacción plantes – aves dispersoras en un bosque chaqueño semiárido. PhD thesis, Universidad de Buenos Aires, Argentina.

Cueto, V.R. (1996) Relación entre los ensambles de aves y la estructura de la vegetación. Un análisis a tres escalas espaciales. PhD thesis, Universidad de Buenos Aires, Argentina.

Cueto, V.R. and López de Casenave, J. (2000) Seasonal changes in bird assemblages of coastal woodlands in east-central Argentina. *Stud. Neotrop. Fauna E.*, **35**, 173–177.

Darrieu, C.A., Camperi, A.R. and Cicchino, A.C. (1996) Ecología alimentaria de *Pseudoleistes virescens* (Vieillot 1819) (Aves, icteridae), en ambientes ribereños del nordeste de la provincia de Buenos Aires, Argentina. *Serie Informe C.I.C.*, **51**, 1–14.

Dayan, T. and Simberloff, D. (1998) Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Rev.*, **28**, 99–124.

De la Peña, M.R. (2001) Observaciones de campo en la alimentación de las aves. *FAVE*, **15**, 99–107.

De la Peña, M.R. (2002) Nuevas observaciones en la alimentación de las aves. *R. FAVE - Cs Vet.*, **1**, 60–64.

De La Peña, M.R. (2006) *Lista y distribución de las aves de Santa Fe y Entre Ríos*. Literature of Latin America, Buenos Aires, Argentina.

De La Peña, M.R. and Pensiero, J.F. (2003) Contribución de la flora en los hábitos alimentarios de las aves en un bosque del centro de la provincia de Santa Fe, Argentina. *Ornitol. Neotrop.*, **14**, 499–513.

Del Barco, O.D. and Beltzer, A.H. (2005) Ecología alimentaria del Tordo Músico, *Agelaioides badius* (Aves: Icteridae) en el valle de inundación del Rio Paraná. *R. FABICIB*, **9**, 41–46.

Diaz, M. (1990) Interspecific patterns of seed selection among granivorous passerines: effects of seed size, seed nutritive value and bird morphology. *Ibis*, **132**, 467–476.

Dilger, W.C. (1956) Adaptive modifications and ecological isolating mechanisms in the thrush genera "Catharus and Hylocichla". *Wilson Bull.*, **68**, 170–199.

Douglas, M.E. and Matthews, W.J. (1992) Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. *Oikos*, **65**, 213–224.

França, F.G.R., Mesquita, D.O., Nogueira, C.C. and Araújo, A.F.B. (2008) Phylogeny and ecology determine morphological structure in a snake assemblage in the Central Brazilian Cerrado. *Copeira*, **2008**, 23–38.

Gitay, H. and Noble, I.R. (1997) What are functional types and how should we seek them? In: Smith, T.M., Shugart, H.H. and Woodward, F.I. (eds), *Plant functional types: their relevance to ecosystem properties and global change*, pp. 3–19. Cambridge University Press, Cambridge.

Gosler, A. (2004) Birds in the hand. In: Sutherland, W.J., Newton, I. and Green, R.E. (eds), *Bird ecology and conservation: a handbook of techniques*, pp. 85–118. Oxford University Press, Oxford.

Grant, P.R. (1968) Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. *Syst. Biol.*, **17**, 319–333.

Grant, P.R. (1971) Variation in the tarsus length of birds in island and mainland regions. *Evolution*, **25**, 599–614.

Greenberg, R. (1979) Body size, breeding habitat and winter exploitation systems in Dendroica. *Auk*, **96**, 756–766.

Hawkins, C.P. and Macmahon, J.A. (1989) Guilds: the multiple meanings of a concept. *Annu. Rev. Entomol.*, **34**, 423–451.

Hespenheide, H.A. (1971) Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. *Ibis*, **113**, 59–72.

Horlent, N., Juárez, M.C. and Arturi, M. (2003) Incidencia de la estructura del paisaje sobre la composición de especies de aves de los talares del noreste de la provincia de Buenos Aires. *Ecología Austral*, **13**, 173–182.

Hutchinson, G.E. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.*, **870**, 145–159.

Jaksić, F.M. (1981) Abuse and misuse of the term "guild" in ecological studies. *Oikos*, **37**, 397–400.

James, F.C. (1982) The ecological morphology of birds: a review. *Ann. Zool. Fenn.*, **19**, 265–275.

Jones, M. (1997) Character displacement in Australian dasyurid carnivores: size relationships and prey size patterns. *Ecology*, **78**, 2569–2587.

Jongman, R.H.G., Ter Braak, C.J.F. and Van Tongeren, O.F.M. (1995) *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge.

Karr, J.R. and James, F.C. (1975) Ecomorphological configurations and convergent evolution in species and communities. In: Cody, M.L. and Diamond, J.M. (eds), *Ecological and evolution*, pp. 258–291. Belknap Press, Cambridge, MA.

Landmann, A. and Winding, N. (1993) Niche segregation in high-altitude Himalayan chats (Aves, Turdidae): does morphology match ecology? *Oecologia*, **95**, 506–519.

Latino, S. and Beltzer, A.H. (1999) Ecología trófica del benteveo *Pitangus sulphuratus* (aves: Tyrannidae) en el valle de inundación del río Paraná, Argentina. *Orsis*, **14**, 69–78.

Lederer, R.J. (1975) Bill size, food size, and jaw forces of insectivorous birds. *Auk*, **92**, 385–387.

Leisler, B., Ley, H.-W. and Winkler, H. (1989) Habitat, behaviour and morphology of Acrocephalus warblers: an integrated analysis. *Ornis Scand.*, **20**, 181–186.

Lopes, L.E., Fernandes, A.M. and Marini, M.Â. (2005) Predation on vertebrates by Neotropical passerine birds. *Lundiana*, **6**, 57–66.

López de Casenave, J., Pelotto, J.P., Caziani, S.M., Mermoz, M. and Protomastro, J. (1998) Responses of avian assemblages to a natural edge in a chaco semiarid forest in Argentina. *Auk*, **115**, 425–435.

Luther, D.A. and Greenberg, R. (2014) Habitat type and ambient temperature contribute to bill morphology. *Ecol. Evol.*, **4**, 699–705.

Marateo, G., Povedano, H. and Alonso, J. (2009) Inventario de las aves del Parque Nacional El Palmar, Argentina. *Cotinga*, **31**, 47–60.

Marone, L. (1992) Seasonal and year-to-year fluctuations of bird populations and guilds in the monte desert, Argentina. *J. Field Ornithol.*, **63**, 294–308.

Mesquita, D.O., Colli, G.R. and Vitt, L.J. (2007) Ecological release in lizard assemblages of neotropical savannas. *Oecologia*, **153**, 185–195.

Moreno, E. (1991) Musculature of the pelvic appendages of the tree-creepers (Passeriformes: Certhiidae): mycological adaptations for tail-supported climbing. *Can. J. Zool.*, **69**, 2456–2460.

Moreno, E. and Carrascal, L.M. (1993) Leg morphology and feeding postures in four Parus species: an experimental ecomorphological approach. *Ecology*, **74**, 2037–2044.

Moreno, E. and Carrascal, L.M. (1994) Ecomorphological patterns for aerial feeding oscines. *Biol. J. Linn. Soc.*, **50**, 147–165.

Oksanen, J. (2011) Multivariate analysis of ecological communities in R: vegan tutorial. http://www.cran.r-project.org [accessed 15 November 2017].

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. and Wagner, H. (2015) Vegan: community ecology package. R package, v. 2.3-0. https://CRAN.R-project.org/package=vegan.

Ordano, M., Bosisio, A., Boscaro, B., Beltzer, A.H. and de Amsler, G.P. (1999) Stomach contents of thirty six bird species from Northern Argentina. *R. Ceres*, **46**, 555–563.

Painter, A., Little, B. and Lawrence, S. (1999) *Continuation of bird studies at Blyth Harbour Wind Farm and the implications for offshore wind farms*. Border Wind Limited DTI, ETSU W/13/00485/00/00, Harwell.

Panigatti, J., Weber, J. and Pillati, O. (1981) *Estado actual y futuro de los problemas de suelos de Santa Fe*. INTA Rafaela, Santa Fe.

Pianka, E.R. (1986) *Ecology and natural history of desert lizards*. Princeton University Press, Princeton, NJ.

R Core Team (2015) *R: A language and environment for statistical computing, v. 3.2.1*. R Foundation for Statistical Computing, Vienna, Austria.

Ralph, C., Geupel, G., Pyle, P., Martin, T., De Sante, D. and Mila, B. (1996) *Manual de métodos de campo para el monitoreo de aves terrestres*. General Technical report, PSW-GTR 159. Pacific Southwest Research Station, US Forest Services, Department of Agriculture, Albany, CA.

Remsen, J.V., Jr., Areta, J.I., Cadena, C.D., Claramunt, S., Jaramillo, A., Pacheco, J.F., Pérez-Emán, J., Robbins, M.B., Stiles, F.G., Stotz, D.F. and Zimmer, K.J. (2016) A classification of the bird species of South America. American Ornithologists' Union. http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm [available 15 November 2017].

Richardson, F. (1942) Adaptive modifications for treetrunk foraging in birds. *Univ. Calif. Publ. Zool.*, **46**, 317–368.

Richman, A.D. and Price, T. (1992) Evolution of ecological differences in the Old World Lea Warblers. *Nature*, **355**, 817–821.

Ricklefs, R.E., Cochran, D. and Pianka, E.R. (1981) A morphological analysis of the structure of communities of lizards in desert habitats. *Ecology*, **62**, 1474–1483.

Ricklefs, R.E. and Cox, G.W. (1977) Morphological similarity and ecological overlap among passerine birds on St. Kitts, British West Indies. *Oikos*, **29**, 60–66.

Ricklefs, R.E. and Miles, D.B. (1994) Ecological and evolutionary inferences from morphology: an ecological perspective. In: Wainwright, P.C. and Reilly, S.M. (eds), *Ecological morphology. Integrative organismal biology*, pp. 13–41. The University of Chicago Press, Chicago.

Ricklefs, R.E. and Travis, J. (1980) A morphological approach to the study of avian community organization. *Auk*, **97**, 321–338.

Rodriguez–Flores, C.I. and Gary Stiles, F. (2005) Análisis ecomorfológico de una comunidad de colibríes ermitaños (TROCHILIDAE, PHAETHORNINAE) y sus flores en la amazonía colombiana. *Ornitol. Colomb.*, **3**, 7–27.

Ronchi-Virgolini, A.L., Beltzer, A. and Manzano, A. (2008) Bird communities in wetlands along the lower Paraná River. *Avian Biol. Res.*, **1**, 153–163.

Ronchi-Virgolini, A.L., Blake, J.G., Lorenzón, R.E. and Beltzer, A. (2011) Bird assemblages in two types of forests in the floodplain of the lower Paraná River (Argentina). *Ornitol. Neotrop.*, **22**, 387–404.

Ronchi-Virgolini, A.L., Lorenzón, R.E., Beltzer A. and Alonso, J. (2010) Ensambles de aves en el Parque Nacional Pre-Delta (Diamante, Argentina): un análisis de la importancia ornitológica de distintas unidades ambientales. *Hornero*, **25**, 27–40.

Root, R.B. (1967) The niche exploitation pattern of the Blue-gray Gnatcatcher. *Ecol. Monogr.*, **37**, 317–350.

Rossetti, M.A. and Giraudo, A. (2003) Comunidad de aves de bosques fluviales habitados y no habitados por el hombre en el rio Paraná Medio, Argentina. *Hornero*, **18**, 89–96.

Rotenberry, J.T. (1980) Dietary relationships among shrubsteppe passerine birds: competition or opportunism in a variable environment? *Ecol. Monogr.*, **50**, 93–110.

Rüggeberg, T. (1960) Zur funktionellen Anatomie der hinteren Extremität einiger mitteleuropäischen Singvogelarten. *Z. Wiss. Zool.*, **164**, 1–106.

Schoener, T.W. (1968) Sizes of feeding territories among birds. *Ecology*, **49**, 123–141.

van Valkenburgh, B. (1995) Tracking ecology over geological time: evolution within guilds of vertebrates. *Trends Ecol. Evol.*, **2**, 71–76.

Wiens, J.A. (1989) Spatial scaling in ecology. *Funct. Ecol.*, **3**, 385–397.

Willson, M.F. (1972) Seed size preference in finches. Department of Zoology, Univeristy of Illinois, USA. https://sora.unm.edu/sites/default/files/journals/wilson/v084n04/p0449-p0455.pdf [available 15 November 2017].

Wilson, J.B. (1999) Guilds, functional types and ecological groups. *Oikos*, **86**, 507–522.

Winker, H. and Leisler, B. (1985) Morphological aspect of habitat selection in birds. In: Cody, M.L. (ed.), *Habitat selection in birds*, pp. 415–431. Editorial, Ciudad.

Winkler, H. (1988) An examination of concepts and methods in ecomorphology. In: Ouellet., H. (ed.), *Acta XIX International Ornithological Congress*, pp. 2246–2253. National Museum of Natural Sciences, Ottawa, Ontario.

Woodall, P.F. (1991) Morphometry, diet and habitat in the kingfishers (Aves: Alcedinidae). *J. Zool.*, **223**, 79–90.

Zapata, S.C., Travaini, A., Delibes, M. and Matínez-Peck, R. (2008) Identificación de morfogremios como aproximación al estudio de reparto de recursos en ensambles de carnívoros terrestres. *Mastozool. Neotrop.*, **15**, 85–101.