UNIVERSIDADE FEDERAL DE SÃO CARLOS CENTRO DE CIÊNCIAS HUMANAS E BIOLÓGICAS DEPARTAMENTO DE BIOLOGIA BACHARELADO EM CIÊNCIAS BIOLÓGICAS

MARIANA MALOSTI IUKSZ

BIRD-ARTHROPOD INTERACTIONS NETWORK: FEEDING PATTERNS WITHIN THE BRAZILIAN ATLANTIC FOREST

REDE DE INTERAÇÕES AVES-ARTRÓPODES: PADRÕES DE ALIMENTAÇÃO NA MATA ATLÂNTICA BRASILEIRA

SOROCABA - SP 2024

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RESUMO

As redes de interações são utilizadas para fornecer uma melhor compreensão sobre comunidades ecológicas e suas estruturas. Neste estudo, nós analisamos interações aves-artrópodes na Mata Atlântica brasileira. O levantamento dos estudos foi feito nas plataformas Web of Science e Google Scholar utilizando de maneira combinada as seguintes palavras-chaves: "birds", "Atlantic Forest" e "diet". Nossas hipóteses são: (1) aves irão consumir uma quantidade pequena das presas em relação ao número total encontrado na rede, com menos da metade de conexões (links) possíveis com artrópodes, apresentando um baixo valor para o índice de especialização para a rede (H2'); (2) O núcleo de generalistas da rede deve incluir menos de 50% das espécies de aves detectadas consumidoras de artrópodes; (3) A rede vai apresentar uma estrutura modular. Todas as análises foram feitas pelo software R na versão 4.3.2. Nós encontramos 16 artigos/teses publicados de 2001 a 2020. A rede de interações presa-predador inclui 185 espécies de aves e 37 grupos de artrópodes. A rede teve um total de 1,011 conexões (C = 0.148). O aninhamento total foi N =60.163. A modularidade foi Q = 0.2328. Os resultados corroboram com a hipótese que a especialização da rede seria baixa (H1). O núcleo de generalistas englobou apenas 33 espécies de aves (17.84%) e 6 táxons de artrópodes (16.22%) (H2). No entanto, a rede de interações não apresentou uma estrutura modular, como esperado para redes presa-predadores (H3). A rede de interações permite uma nova visualização da relação entre espécies de aves predando grupos de artrópodes na Mata Atlântica, apresentando uma comunidade com alta sobreposição de nichos e instável devido à ausência do padrão modular.

Palavras-chave: Consumo de artrópodes; Dieta de aves; Floresta Neotropical; Interações predador-presa

ABSTRACT

The interaction networks are used to provide a better understanding of ecological communities and their structure. Here, we analyzed bird-arthropod predation interactions in the Brazilian Atlantic Forest. We searched for studies on the Web of Science and Google Scholar, using the combination of the keywords "birds", "Atlantic forest", and "diet". Our hypotheses were: (1) birds would consume a small amount of prey in relation to the total number of arthropod groups found in the network, with less than half of the total number of possible interactions (links) with arthropod groups, with low values of network specialization index (H2'); (2) the generalist core might include less than 50% of the arthropod eater bird species; (3) The network would present a modular structure. All the analyses were made through R version 4.3.2. We found 16 papers/thesis published from 2001 to 2020. The predator-prey interaction network includes 185 bird species and 37 arthropod groups. The network had a total of 1,011 connections (C = 0.148). The total nestedness was N = 60.163. The Modularity was Q = 0.2328. The results corroborate with the hypothesis that network specialization would be low (H1). The generalist core found only 33 bird species (17.84%) as part of the core and only 6 arthropod groups (16.22%) (H2). However, the network did not present a modular structure, as expected for a predator-prey interaction network (H3). The interaction network provides a novel view of bird species predating arthropod groups in the Atlantic Forest, exhibiting a community with high niche overlap and unstable due to the non modular pattern.

Keywords: Arthropod consumption; Birds' diet; Neotropical forest; Network structure; Predator-prey interactions

1. INTRODUÇÃO AO TRABALHO

O presente Trabalho de Conclusão de Curso foi elaborado no formato de um manuscrito seguindo as regras de formatação da revista brasileira Ornitology Research (ANEXO A; <u>https://link.springer.com/journal/43388/submission-guidelines</u>) visando sua futura submissão e publicação. A formatação seguiu todas as orientações das normas da revista, com exceção das figuras que foram colocadas em tamanhos diferentes de maneira a adequar a visualização destas no documento. A escolha da revista em questão para a submissão por tratar-se da única revista brasileira voltada exclusivamente à Ornitologia e com ênfase na região Neotropical, sendo a revista da Sociedade Brasileira de Ornitologia, antigamente conhecida como Revista Brasileira de Ornitologia.

2. ARTIGO

Bird-arthropod interactions network: feeding patterns within the Brazilian Atlantic Forest

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Abstract

The interaction networks are used to provide a better understanding of ecological communities and their structure. Here, we analyzed bird-arthropod predation interactions in the Brazilian Atlantic Forest. We searched for studies on the Web of Science and Google Scholar, using the combination of the keywords "birds", "Atlantic forest", and "diet". Our hypotheses were: (1) birds would consume a small amount of prey in relation to the total number of arthropod groups found in the network, with less than half of the total number of possible interactions (links) with arthropod groups, with low values of network specialization index (H2'); (2) the generalist core might include less than 50% of the arthropod eater bird species; (3) The network would present a modular structure. All the analyses were made through R version 4.3.2. We found 16 papers/thesis published from 2001 to 2020. The predator-prey interaction network includes 185 bird species and 37 arthropod groups. The network had a total of 1,011 connections (C = 0.148). The total nestedness was N = 60.163. The Modularity was Q = 0.2328. The results corroborate with the hypothesis that network specialization would be low (H1). The generalist core found only 33 bird species (17.84%) as part of the core and only 6 arthropod groups (16.22%) (H2). However, the network did not present a modular structure, as expected for a predator-prey interaction network (H3). The interaction network provides a novel view of bird species predating arthropod groups in the Atlantic Forest, exhibiting a community with high niche overlap and unstable due to the non modular pattern.

Keywords: Arthropod consumption; Birds' diet; Neotropical forest; Network structure; Predator-prey interactions

2.1. Introduction

The Atlantic Forest is a Neotropical forest domain occupying 15 Brazilian states along the coast (IBGE, 2019). Recognized as one of the 25 biodiversity hotspots (Myers et al., 2000), it boasts one of the largest rates of endemisms and diversity among tropical forests (Meira et al., 2008). However, this domain has experienced extensive fragmentation in Brazil (Dario, 2021) and currently is characterized by a mosaic of native forests and human-modified landscapes (Grelle et al., 2021), mostly fragments smaller than 50 hectares, under intense pressure from the edge effect (Pizo and Tonetti, 2020). The Brazilian Atlantic Forest hosts over 930 bird species (Dario, 2021), standing as the second richest South American domain in bird diversity, trailing only the Amazon Forest (Pizo and Tonetti, 2020). The domain shelters 75.6% of Brazilian threatened and/or endemic bird species (Grelle et al., 2021) therefore, its conservation is central for bird conservation (Marini and Garcia, 2005).

Birds are the most well-known and studied terrestrial vertebrates (Sekercioglu 2006), in both natural and anthropogenic environments (Wenny et al. 2011), and their role in structural complexity and functional diversity is essential to forest dynamics (Mariano-Neto and Santos 2023). They may act as *mobile links*, connecting different areas and delivering ecosystem services to different fragments (Emer et al. 2018). More than 50% of bird species are arthropod consumers (Piratelli and Pereira 2002; Wenny et al. 2011), and analyzes of trophic guilds have revealed that use insects as their primary food source (Durães and Marini 2005; Piratelli and Pereira 2002; Sabino et al. 2017; Duca et al. 2023). Bird insectivory plays a central role in regulating populations of foliage-gleaning arthropods, economically relevant for decreasing damages in both agricultural crops and natural ecosystems (Otieno and Mukasi 2023), being responsible for ~70% of total consumption of these prey in forested areas (Nyffeler et al. 2018). However, the habitat- and connectivity losses within the Atlantic Forest have directly affected bird diversity and might lead to huge changes in functional traits and ecosystem services (Mariano-Neto and Santos 2023).

Arthropods have a notable ability to employ active and highly effective strategies to evade predation, surpassing the defensive mechanisms of seeds, fruits, and leaves. (Sekercioglu et al. 2002), thus increasing the need of specialization for insectivorous birds (Şekercioğlu et al. 2004; Alves et al. 2023). Also, these birds tend to have reduced dispersal ability, mostly remaining in their territories (Manhães and Dias 2008; Duca et al. 2023). Therefore, many insectivorous birds are highly sensitive to forest fragmentation and disturbance, including several species under population declines in the Neotropics (Jirinec et al, 2022).

To model the dynamic of ecological interactions, the science of networks may be exported to ecology, allowing the creation of interaction networks to provide a better understanding about biological systems and their dynamics (Cemini et al. 2019). Thus, the ecological communities can be modeled by interaction networks, where a set of nodes (which might represent several biological entities, such as species) are connected by links (in different kinds of interactions, such as pollination, dispersal, and predation) depicting interactions into these communities (Guimarães 2020). These representations use graph theory to better understand the ecological structure, providing network and statistical metrics that can be used to elaborate inferences about the properties of ecological communities (Poisot et al. 2021).

Interaction networks are useful tools to better understand the ecological interactions and the ecological functions involved in these relationships (Pigozzo and Viana 2010; Poisot et al. 2021), unraveling evolutionary patterns within communities (Carlo and Yang 2011). Moreover, the analysis of interaction networks deliver practical insights for guiding conservation strategies, focusing on protecting complex interactions within ecosystems. Recognizing that species connections and interactions are central for promoting species coexistence and supporting essential ecological functions, these networks provide a foundation for targeted conservation efforts (Vitekere et al. 2020). They could be used to analyze mutualistic interactions, such as pollinator-plant (Bascompte et al. 2006), frugivores and seed dispersal (e.g. Emer et al. (2018)), and predator-resources interactions, as in food webs (Melián and Bascompte 2004). Although it is an useful and necessary tool for understanding community ecology and interactions, the ecological networks have been mostly described and published in the Northern hemisphere, having restricted coverage in South America (Poisot et al. 2021). Studies describing bird interaction networks are mainly focused on mutualistic relationships (Guimarães Jr. 2020), e.g., between frugivorous and plants (Bascompte et al. 2003; Carlo and Yang 2011; Dugger et al. 2019; Emer et al. 2018). There is sparse information about predator-prey systems in tropical areas (Mansor et al. 2018), with limited application of interaction networks for conservation strategies in the southern hemisphere (Poisot et al. 2021), especially interactions between birds and arthropods (Otieno and Mukasi 2023).

In this study, we aim to describe a predator-prey interaction network for bird species and arthropod groups within the Atlantic Forest, providing a comprehensive view of food webs and their interactions, bringing information about the topological structure of this network. We tested the following hypothesis:: (1) Birds would consume a small amount of available prey in relation to the total number of arthropod groups found in the network, with less than half of the total number of possible interactions (links), with low values of network specialization index (H2') Bird species will have less links than the half of the total number of possible interactions with the arthropod groups (Araújo et al. 2008; Pascual and Dunne 2006). Based on this assumption, it is expected that the network specialization index (H2') presents a low value, i. e. the number of connections will not diverge significantly among bird species (Bascompte et al. 2006). 2) Since it is expected that most bird species would not consume a large amount of prey, the generalist core of this network would include less than 50% of the bird species. 3) The interaction network will present a modular pattern since antagonistic networks, such as predator-prey interactions, share a more modular structure, while mutualistic networks tend to share a more nested pattern (Cagnolo et al. 2011; Morrison and Dirzo 2020).

2.2 Methods

2.2.1 Data collection

This study was carried out based on a survey for published papers about insectivorous birds within the Brazilian Atlantic Forest, using the combination of the following keywords: "birds", "Atlantic forest", and "diet". The data were extracted using "Web OF Science" and Google Scholar databases. Due to the paucity of publication regarding the interaction of insectivorous birds and arthropods in the Brazilian Atlantic Forest, no date range was applied, and the survey was carried out until november 2023. The studies found through the survey and used to build the network matrix included papers published in both scientific peer reviewed journals, and dissertations, considering only studies that were developed within this biome. The studies included in the analysis had a minimum of one arthropod consumption detected for at least one bird species (Fig. 1). In every publication we analyzed, the arthropods were classified to the lowest taxonomic level possible, mostly to orders, except for Formicidae (Order Hymenoptera), and suborders Heteroptera (order Hemiptera), Mallophaga

(Order Phtiraptera), and Blattaria (Order Blattodea). For the matrix, the categories of arthropods considered the adult-life stage, while interactions including eggs, larvae, oothecas, and cocoons were treated as categories with no taxonomic distinction.

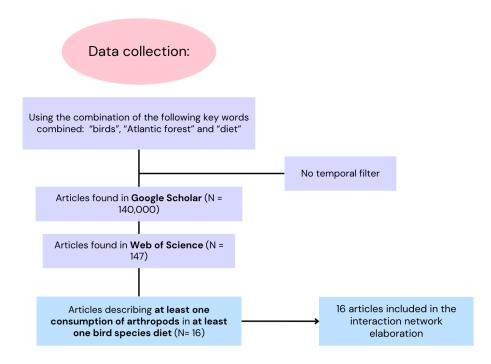


Fig. 1. Flowchart of data collection used to plot the interaction network. Representing the publications' search and the number of articles selected to have their data included in the interaction network, describing the process using the key words and no temporal filter in the survey and how many articles were returned from the databases.

2.2.2 Interactions network

Based on the results compiled in the selected bibliography, we elaborate a matrix of bird-arthropods interactions (Online Resource 1), with the bird species organized in columns and the arthropods in rows. The intersection cell between a bird species and an arthropod group was filled with "1" every time an interaction was recorded in at least one study, and "0" when in absence of interactions; thus, creating a binary database for qualitative analysis (Bascompte et al., 2003; Emer et al. 2018; Oliveira et al. 2015) . The version 4.3.2 R software (Mrvar and Batagelj 2022) was used to plot and analyze the network. The bipartite package (R Core Team 2022) was used to analyze the structure and organization of the network.

2.2.3 Data analysis

To test the hypothesis (1), we first calculated the connectivity, i.e., the number of interactions for each species and the whole matrix, and the network connectance (Jordano 1987), estimating the proportion of a species interactions and the total number of possible interactions (Silva 2021). The network specialization (H2') (Blüthgen et al. 2006) was chosen to analyze how a given bird species may interact with a specific food resource, exhibiting the level of specialization in this binary network for two different biological groups. This metric is a measure of the specialization, in terms of the interaction preferences of predators in relation to prey. The H2' index derived from the Shannon entropy, based on the deviation from the expected probability distribution of interactions (Dáttilo and Vasconcelos 2019; CaraDonna and Waser 2020; Giffu 2020), and ranges from 0 to 1, with 1 representing a highly specialized network.

To test the hypothesis (2), we used the Gc index for generalist cores to determine whether species were part of the core or peripherical species components of the network, calculated by $Gc = (k_i - k_{mean})/z$, where Gc is the generalist index, k_i is the number of links of each bird/arthropods, k_{mean} is the mean number of all birds and arthropods links in the network and z is the standard deviation of the number of links for birds/arthropods species (Dáttilo et al. 2013).

To test hypothesis (3) the Modularity (Q) was selected to detect whether any group of species interacts more among themselves than with outside components, considering the frequency of interactions in the network (Giffu 2020), using the QuanBiMo algorithm (Dorman and Strauss 2014) and, due to variations in the results after different runs, we used the highest value after 50 independent runs (Dáttilo and Vasconcelos 2019). Modularity (Q) implies a community with species interacting strongly within a compartment and weakly with other compartments or species outside of the one it is included in, forming a non-overlapping and strongly interacting species subsystem in the network (Delmas et al. 2018), a pattern visible in food webs (Bascompte and Jordano 2006; Sheykhali et al. 2020), ranging between 0 (no modules) to 1 (fully separated modules) (Li et al. 2023)

A positive value of Q¹ suggests that the network has a modular structure, while values close to zero indicate a less modular structure, and negative values suggest a more random or non modular structure (Giffu 2020). The modularity was later compared to the Q value obtained from 100 null models, used to statistically compare the value to their expected random equivalents, in order to analyze its dependence on network size and sampling density

(Dormann and Strauss 2014). The use of null models allows us to indicate if this metric is an explanatory variable for the structure and dynamic of the network, checking if they are statistically significant (Cimini et al. 2019). The nestedness, modularity and specialization were calculated using the bipartite package (Dormann et al. 2009) available in R software in the 4.3.2 version (R Core Team 2022). The nestedness was estimated by the NODF metric (Nested metric Based on Overlap and Decreasing Fill) (Almeida-Neto et al. 2008), to understand the interactions between specialist and generalist species (CaraDonna and Waser 2020). In a nested system, more specialized species interact with a smaller subset of species that also interact with more generalists (Valverde et al. 2020).

The scripts used to plot the network and run the analysis are available in Online Resource 2.

2.3 Results

The survey relied on 16 studies that included at least one interaction between birds and arthropods (Figure 2; Online resource 1), including studies from 2001 to 2020. The references for the studies can be found in the Online Resource 2. We found 185 bird species interacting with 37 arthropod groups (Figure 3). The total number of interactions of the network was 1,011 different connections, with 6,845 possible connections.

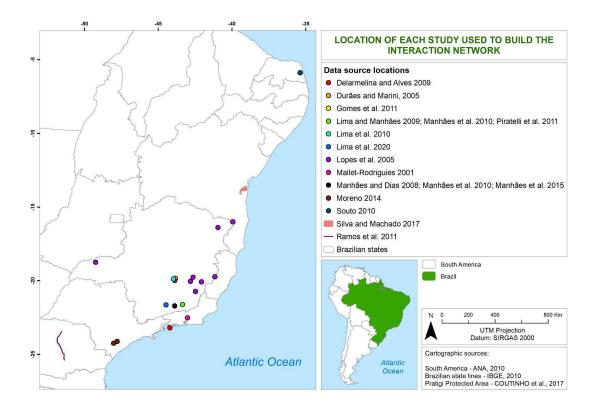


Fig. 2. Location of each study used to build the interaction network.

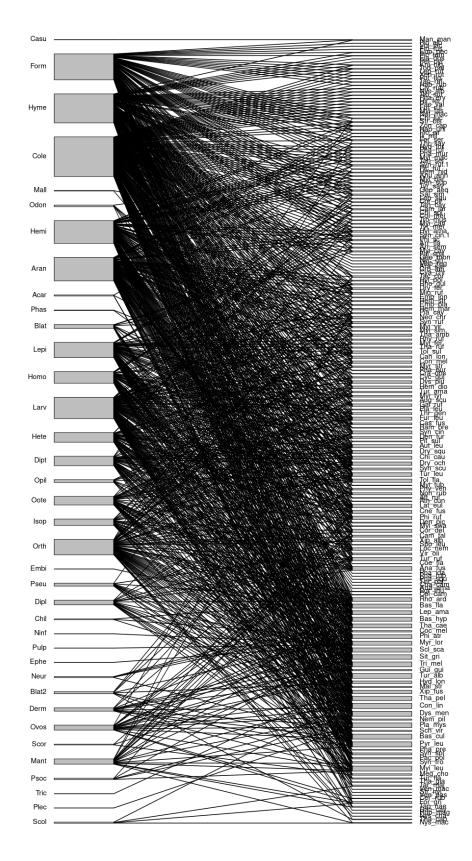


Fig. 3. Interaction network between birds and arthropods in the Brazilian Atlantic Forest. Arthropods are on the left and bird species on the right side of the network. Acronyms for the names are given in Online Resource4. A better resolution for the network is available in Online Resource 5.

The most interactive bird species was *Conopophaga lienata*, with 19 interactions, followed by *Dysithamnus mentalis*, *Pyriglena leucoptera*, *Basileuterus culicivorus*, and *Myiothlypis leucoblephara*, connecting with 18 different arthropods groups each. On the other hand, 25 bird species interacted with only one group of arthropods.

The arthropod group recorded as the main prey for birds was Coleoptera, interacting with 143 predator species, followed by Hymenoptera with 105 connections. Formicidae was the third group most used as a food resource, with 94 connections, Aranae was found interacting with 85 bird species and Hemiptera had 82 connections. There were seven arthropods groups that only connected with one predator species, the orders Embioptera, Ephemeroptera, Plecoptera, Trichoptera and nymph, pulp and cocoon groups.

The network had 6,845 possible connections. The whole network connectance was C = 0.148. The nestedness in the NODF metric for the whole network was N = 60.163, while for bird species (i.e. columns) was N = 60.731 and for arthropod groups (i.e. rows) was N = 45.656. The Modularity result is Q =0.2328, and the result after running the null models was -6.31543 standard deviations (lower than would be expected from random networks). The specialization index result was H_2 '= 0. The Gc index for generalist cores found 33 bird species (17.84%) being part of the core, while 152 species (82.16%) were considered peripheral, i.e. specialists. For the arthropods, only 6 taxons (16.22%) were in the generalists core and 31 taxons (83.68%) were peripheral in this analysis. In order to better visualize the interactions of the top consumers of the network, a network was built with those bird species belonging to the generalist core (Fig. 4).

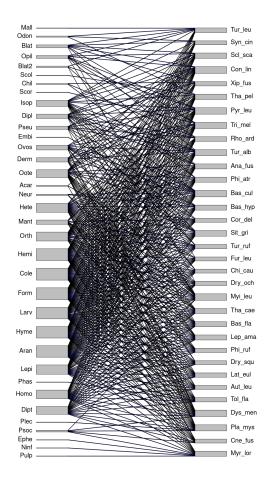


Fig. 4: Interaction network including the bird species belonging to the generalist core from the previous interaction network, with bird species on the right side of the network and arthropod groups on the left. The acronyms for bird species and arthropod groups can be found in Online Resource 3.

Most bird species in the network were considered by Wilman et al. (2014) belonging to the insectivorous guild (129 species, representing 70.9% of all sampled species), followed by 27 birds as omnivorous (14.8%), 22 frugivores and nectarivores (12;1%), 4 granivores (2.2%) and 3 carnivores (1.62%). The majority of bird species considered as insectivores (Wilman et al. 2014) predated Coleoptera (109 bird species), which is the arthropod group most frequent in the diet of these species (more than 50% of the bird species) and the most consumed prey for bird species in all trophic guilds. Embioptera, Ephemeroptera, nymphs, Plecoptera, Trichoptera, cocoons and pupas were part of the diet of only one bird species each. In addition, 12 bird species belonging to this guild had only one arthropod group belonging to its diet in this analysis.

2.4. Discussion

We confirmed the first hypothesis, about bird species consuming a small amount of prey groups, despite the number of possible connections in the network. The mean number of interactions of the species was $M = 5.4649 \pm 4.5572$ DP in 37 possible connections, and the specialization for the whole network was H'2 = 0. We also confirmed the second hypothesis, based on the Gc index for generalists core, in which the species found in the generalist core were those with most interactions, and there were only 17.84% of bird species included in the generalist core. On the other hand, the third hypothesis was not confirmed, since this interaction network did not reveal a modular pattern (Q = 0.2328).

2.4.1. Connectance and specialization

The specialization of a network represents how distinguished the sets of each vertex interactions are from each other (Bascompte et al. 2006). Therefore, a zero specialization network (H2 = 0) means that the interactions for each bird species does not diverge significantly, which matches the low number of interactions for each bird species, even for the most-recorded bird (*C. lineata*; preying on 19 arthropod different groups). The value of specialization for this network indicates that the bird species found in this survey present a high degree of niche overlap (Dugger et al. 2019).

The results of connectance (C=0.148) represent a low value for this measure (Vianna 2010), given the high number of bird species found in this study. Thus, it could be considered as a disconnected network (Guimarães Jr. 2020), with a small mean of interactions per species ($M=5,465\pm4,557$ DP), with few variations across the species. The stability in predator-prey networks may increase with higher connectance in biological communities (Angelis 1975; Russo and Stout 2023), since connectance decreases the observed effects of perturbations under different types of disturbance. Additionally, in antagonistic networks, high values of connectance represent that the predators may consume a larger range of resources, allowing a compensatory effect in eventual fluctuations in resource abundance (Baumgartner 2020). However, the relationship between connectance and conservation is still controversial (Russo and Stout 2023) and the connectance itself should not be considered an indicator of stability, since its value is associated with specific features of each ecological community and, therefore, should not be interpreted on its own (Vitekere et al. 2020).

Bird species tend to consume a small amount of prey groups, regardless of the diversity of prey, as arthropods in the Atlantic Forest (Araújo et al. 2008; Pascual and Dunne 2006). Prey items that are very abundant may not be consumed as expected since the predator may need less nutrients than the available on the environment (Manhães and Dias 2008), as Lima and Manhães (2009) also observed *B. culicivorus* consuming Coleoptera less than expected. Duca et al. (2023) verified that Formicidae was not consumed as expected in comparison to other studies.

2.4.2. Generalist species and Gc index

We found a wider range of links for the few species, such as *C. lineata*, *D. mentalis*, *B. culicivorus*, *M. leucoblephara*, and *P. leucoptera*. Our results also corroborate with the idea that most species have more interactions, with both frequent and non-frequent arthropod groups in the network (Xi et al. 2020). Coleoptera and other arthropod groups such as Formicidae, were some of the most predated groups, and *C. lineata* and *M. leucoblephara*, both common understory bird species (Manhães et al. 2015) were some of the predators with higher degree of interactions. All of the bird species with at least 11 interactions were included in the generalist core according to the Gc index, consuming a wider range of prey in comparison with ten or less interactions. Considering that this represents 17.84% of the total number of birds registered in the survey, the result confirms the general view of the network where it seems to have lots of vertices in a peripheral area, predating a few arthropod groups.

More generalist predator species tend to interact with several prey groups whereas specialist bird species tend to consume a narrower range of prey. Our results corroborate with this idea, since the generalist core birds, such as *D. mentalis* and *C. lineata*, were found predating a wider number of arthropods groups, while species such as *Florisuga fusca* and *Coereba flaveola*, both non insectivore species, with a diet predominantly based on fruits and nectar, with arthropods being less frequent (Almada et al. 2016; Aximoff and Freitas 2009), were found interacting with arthropods groups for predation, but in a reduced amount of interactions, with only one detected for each. Also, omnivore species such as *Geotrygon montana* and insectivore species such as *Veniliornis maculifrons* were also found interacting with only one arthropod group. All of these interactions were found with the arthropods groups with most predating rates, where *F. fusca* and *C. flaveola* interacted with Formicidae and Hemiptera, respectively. *G. montana* consumed only Coleoptera and *V. maculifrons*

consumed only larvae; Thus, this suggests that species with a more specialist feeding habit may interact with central species, i.e. most most detected prey in the network, while generalist predator interacts with both generalist and peripheral prey, i.e. both detected or not prey. The results of a narrow generalist core with most of the bird species being part of the periphery of the network confirm the previous idea of predators choosing some specific prey for consumption in a scenario with considerable food resources availability. On the other hand, it is important to understand that the used of different studies describing birds diet by different approaches and the presence of studies describing only one species diet might compromise the number of interactions found for each bird species, in a way that most sampled birds may have more interactions and fewer interactions for some bird species might be related to sampling less frequently throughout all studies.

Insectivores and omnivores birds are predominant in small sized forest fragments, since their food resources might be more stable throughout the year than seeds and fruits (Dario 2021). They have more homogeneous spatial distribution compared to fruits, due to its abundance, arising in a more stable bird population than frugivorous species (Dario 2021; Manhães and Dias 2011). On the other hand, bird species move through the habitat in function of food resources availability, but its spatial distribution may be more related to vegetation structure and species behavior than prey density (Lopes et al. 2006; Manhães and Dias 2011). Moreover, different bird species may share resources mainly based on prey size, instead of its taxonomic composition; thus larger bird species are able to consume prey of different sizes, while smaller predators generally choose smaller prey (Cagnolo et al. 2011; Manhães et al. 2015; but see Mansor et al. 2018. Additionally, the consumer-resource body mass ratio declines with increasing consumer size, due to the higher energy demands for larger organisms. Therefore, bird species tend to rely mostly on proportionally larger prey instead of a larger number of different arthropod groups (Eskuche-Keith et al. 2023).

2.4.3. Modularity and nestedness

Modularity (Q) implies a community with species interacting strongly within a compartment and weakly with other compartments or species outside of the one it is included in, forming a non-overlapping and strongly interacting species subsystem in the network (Delmas et al. 2018), a pattern visible in food webs (Bascompte and Jordano 2006; Sheykhali et al. 2020), ranging between 0 (no modules) to 1 (fully separated modules) (Li et al. 2023). The interaction network found Q =0.2328, considered a low to medium modularity (0.15 < M < 0.45) (Li et al. 2023). The use of null models allows us to indicate if this metric is an explanatory variable for the structure and dynamic of the network, checking if they are statistically significant (Cimini et al. 2019). The transformation of Q value into a z-score after running 100 null model networks resulted in an observed modularity 6 standard deviations lower than expected from random networks, not being considered significantly modular (Dormann and Strauss 2014). The modularity is likely to be correlated with specialization, since a low degree of specialization for the whole network means some interactions might be random, leading to a low presence of modularity in this network (Dormann and Strauss 2014), which corroborates with the observed in this study, since the overall specialization was H2'=0 and the modularity was M=0.2328, less than expected from random networks. The presence of modules within the network may promote stability in the community by limiting perturbation within a module, avoiding its spread throughout the rest of the community (Delmas et al. 2018). The presence of a less modular network goes in the contrary direction of the knowledge that modularity leads to continued and specific coevolution between predator and preys (Morrison and Dirzo 2020), indicating that this pattern found for the birds and arthropod community in the brazilian Atlantic Forest may compromise its coevolutionary patterns and predator-prey specializations. Additionally, body mass, foraging habitat, mobility and prey capture strategy are some traits that may directly affect the modularity composition in a food web (Eskuche-Keith et al. 2023).

The nestedness pattern results in a highly cohesive network with asymmetric interactions, in which specialists tend to interact with more generalist species and also specialist species, there is a core of generalists to which specialists are linked (Morán-lopez 2020). The nested pattern is an important tool to understand which species might be more responsible for the evolution forces of the whole community (Bascompte and Jordano 2006). The bird-arthropod network is considered nested, considering that its value exceeds N=50 indicating that there is a main core in the network, but not in the same level as mutualistic networks that are typically nested (Guimarães Jr. 2020), since it does not contain as many interactions as a mutualistic interactions network core might contain (Bascompte et. al 2003), so the evolutionary patterns and ecological functions are determined by this group of more generalist bird species, although this core is not that dense and the forces exerted on other species outside of this core is not determined mainly by these groups of nested species.

The non modular pattern found in this interaction network might be related to some limitations found during the data collection, since the absence of taxonomic resolution for some arthropod groups in the studies included in the matrix might compromise the specialization that could be found among birds and some prey groups. The presence of several insectivorous birds in the Neotropics implies in interspecific competition which leads to feeding specializations between predator and prey species (Sherry et al. 2020), that could be reflected in the interaction network as a modular structure. The arthropod groups classified mainly until the order level in this study hampers the insights about birds feeding specialization with specific arthropod taxa, which could be better visualized if the arthropod groups were taxonomically classified until the lower level, being one possible explanation for the absence of a modular pattern, since the prey classification as orders prevents the detection of specialized predator-prey relationships in this network. Thus, this enhances the importance of partnerships among ornithologists and taxonomists, in order to enable studies about bird diets in the best taxonomic resolution possible.

The results found for both nestedness and modularity do not corroborate with the literature, which infers that antagonistic networks, such as in predation interactions, show a modular pattern and less nested (Cagnolo et al. 2011). This structure might be related to coevolutionary patterns between predator and prey resulting in higher specialization between consumers and resources (Morrison and Dirzo 2020). The nested pattern contributes to robustness of the network and communities, due to the fact that the extinction of specialist prey may be compensated by the consumption of other prey, since in a nested pattern, the predator species still have others to interact with (Baumgartner 2020). The non modular and relative nested pattern in the present network suggests that this community is not that as stable as it would be if the antagonistic network pattern of modularity instead of nestedness was shown, since the nested topology for antagonistic network does not promotes local stability and, on top of that the non modular pattern in a predator-prey network decrease its stability (Morrison and Dirzo 2020).

2.4.2. Insectivory within the Atlantic Forest

Many species may inhabit anthropogenic environments, changing bird communities composition due to the loss of Atlantic Forest areas (Dario 2021). Although competition among bird species in the same habitat is imminent, when there are multiple factors which affect birds' predation, it is more plausible that competition decreases and allows different bird species to coexist and consume the same prey groups (Allesina et al. 2011). Considering the Brazilian rainforest scenario, where biodiversity is directly affected by different factors,

such as fragmentation, deforestation, anthropic pressures and spatial heterogeneity, the results of the interaction network allowing different bird species to consume similar prey items with a low variation in prey consumption diversity from the bird species with most interactions to the species with least connections indicates that predation might not be the strongest factor in prey consumption. In view of the endemism degrees, diversity and abundance of arthropods in Brazilian Atlantic Forest, and the forest vulnerability, generally many bird species are able to coexist in the same regions and consume the same food resources (Allesina et al. 2011).

Birds are commonly known for exchanging ecosystem services between different ecosystems in a singular way due to its ability to fly and its foraging interactions in those different regions (Gagetti 2015), providing ecosystem functions and services such as herbivory control and pollination. The same habitat modifications that may guarantee the survival of some generalist species might negatively affect the ecological functions of other species; generalists may not be so compromised in controlling herbivory by predation than specialists can with habitat loss or anthropic disturbance (Sekercioglu et al. 2016). Thus the reduction or loss of some specialist bird species in some ecosystems may alters some specific arthropod populations. In the present study, some arthropod groups, such as Ephemeroptera and Trichoptera were consumed by a single bird species – *Myrmeciza loricata*. Although this bird species is not considered a specialist species in the Gc index, they might play a particular role in the dynamics of those arthropod populations.

Conopophaga lineata can be considered less restricted in terms of substrate (Manhães and Dias 2011), foraging mainly on the forest floor and considered a syntopic species (Manhães et al. 2015) and six different studies analyzed registered its diet (Durães and Marini 2005; Lopes et al. 2005; Lima et al. 2010; Manhães et al. 2010; Piratelli et al. 2011; Manhães et al. 2015). It is one of the understory endemic birds to the Atlantic Forest (Dantas et al 2015). *Pyriglena leucoptera* is an insectivore bird (Wilman et al. 2014) that lives most commonly in understory areas in rain forests and also occupies forest edges (Lopes et al. 2006), being less sensitive to disturbances in the environment, which could explain the frequency of registers for its diet and the number of preys consumed (48.65% of the arthropods groups are part of the species diet), since it might occupy a wider area. It is also from the Thamnophilidae family and one of the army-ant following birds (Souza et al. 2001). Being an army-ant follower indicates that its distribution and frequency may be wider due to the need to follow these insects in larger scales than other species (Modena et al. 2013). In a study by Modena et al. (2013), *P. leucoptera* was one of the most abundant species sampled in a 40 years old forest. *Myiothlypis leucoblephara* generally forages on the forest floor and

seems to feed in an opportunistic way. The consumption by *M. leucoblephara* of preys such as Blattodea and Psocoptera, both arthropod groups with few connections (six and five, respectively) might be explained by the fact that they often have their diet based on the resources most available in the environment (Manhães et al. 2015).

Dysithamnus mentalis is an insectivorous bird from the Thamnophilidae family, one of the main components of Neotropical avifauna (Lopes et al. 2006). It is a species that consumes mostly abundant arthropods and those which are found in the foliage (Piratelli and Pereira 2002). A substrate generalist forager (Lopes et al. 2006; Manhães and Dias 2008), which may contribute to the higher number of interactions in comparison to substrate specialist species. In addition, it is one of the most abundant and frequent bird species registered in different studies about abundance of insectivorous birds in Atlantic Forest (Lopes et al. 2006; Manhães and Dias 2011), being registered in six out of the 15 studies analyzed. Besides its apparent generalist character, Manhães and Dias (2008) found some preference for some prey taxas and for larger prey, aiming at maximizing energy intake. Durães and Marini (2005) found mainly as food resource for *D. mentalis* the groups of Coleoptera and Hymenoptera Formicidae, but did not find any interactions with Aranae, an abundant group of arthropods, while other studies (Lima et al. 2010; Lopes et al. 2005, Manhães and Dias 2008; Manhães et al. 2010) registered this group as a food resource for this bird species.

Another bird with highest interactions was *Basileuterus culicivorus*, an insectivore bird from the family Parulidae widely spread throughout South and Center America (Lima and Manhães 2009), and it is mainly a live-foliage gleaner and it is found restricted to forest areas (Pomara et al. 2007). Throughout variations of the environment, Santana et al. (2012) found no differences in abundance of the species, suggesting that it is more generalist than other species of *Basileuterus* in terms of occupancy of forestal strata and less sensitive to variations in vegetation structure. This inference may explain why this species had more links in the interaction network than others from the genus, since *B. flaveolus* and *B. hypoleucus* registered 14 interactions with the arthropods groups.

The bird species belonging to the frugivorous guild (22 species) had few connections, the three species with highest connections for this group had only five links and seven of them predated only one arthropod group, with the most connected frugivorous species interacting with only 13.51% of the arthropods included in the study. Few frugivorous birds exclusively rely on vegetal material in their diet and the majority of them change their food resources due to several ecological and seasonal factors (Riehl and Adelson 2008). Due to the seasonality

impling in variations in fruit resources throughout the year, bird species that mainly consume fruits may use arthropods as secondary food resources and, in some periods of the year, they might use arthropods as primary food resources (Duca et al. 2023), having less spatial stability and being less site-attached than insectivorous birds (Dario 2021). The consumption of arthropods by fruit-eating birds is a way these species complement their diet in order to obtain higher amounts of protein ingestion (Nazaro and Bledinger 2017), which is aso observed for nectarivorous birds, specially in the breeding season (Lima et al. 2010).

The use of arthropod items by omnivorous birds in this study reveals that out of 27 bird species in this trophic guild only 10 of them consumed more than 10% of the arthropods groups included in the network, with the majority consuming three or less arthropod items in their diet, with Coleoptera as the most frequent prey item in omnivorous birds diet. The omnivorous birds exploit feeding resources based on their habitat, fluctuations on resources or seasonal changes, relying mainly on arthropods during the breeding season, despite the abundance of fruit in order to obtain a higher amount of nitrogen content (Riehl and Adelson 2008), in a way that associate the consumption of arthropods and vegetal material benefits the survival of this species in periods of fruits scarcity (Lima et al. 2010). Differing from vegetal items, arthropods have more antipredatory traits such as cryptic coloration, resulting in more time spent in foraging behavior and, therefore, more energy (Naoki 2003) which reinforces the importance of arthropods in omnivorous birds diet for supplying nutritional resources, since although they need to send more time foraging arthropods than fruits, they still have arthropod items in their diet and use them as food resources frequently.

The carnivorous birds included in the interaction network revealed a low percentage of consumption of all the arthropods in the analysis, with *Guira guira*, the carnivore with highest interactions, predating only 5 arthropod groups (13.51% of the total possible connections). All of the three carnivorous birds (*Guira guira*, *Athene cunicularia* and *Strix hylophila*) interacted with the 10 most frequent consumed arthropod groups, which may indicate the use of arthropods as food resources in an opportunistic way for the carnivorous birds when other food resources are not available.

Invertebrates can be considered ecosystem engineers, since they are able to shape the environment in which they are included (e.g. ants creating a network of above and below-ground nests or the herbivory by Coleoptera and Hemiptera and its transference of energy from plants to the next trophic levels), changing the availability of resources for other species, such as bird species that depend on arthropod eating as their main food source (Kotze et al. 2022). Furthermore, the relatively homogeneous distribution of arthropods in tropical

forests allows different bird species to consume the same food resources using different strategies, enabling a wider diversity of insectivorous species to coexist in these forests (Duca et al. 2023).

Manhães et al. (2015) found Coleoptera and non-Formicidae Hymenoptera as most frequent items consumed by *M. leucoblephara* and *C. lineata*. They did not found Isoptera and Hemiptera Heteroptera in the diet of *M. leucoblephara*, and suggested that it indicates greater ability to tolerate chemical defenses from these arthropods groups for C. lineata, which does not corroborate with the results found in the network, since Manhães et al. (2010) and Manhães et al. (2010) found both arthropods groups consumed by the first bird species. Although Coleoptera has a great ability to use chemical defenses, it is one of the most numerous groups of arthropods in the forests, proposing that its availability overcomes its defenses when birds choose their food resources. The availability overcoming its defenses when they are bird's food resources corroborates with the results in the network in which Coleoptera was the most frequent prey item in the diet for all trophic guilds included in the survey. Also, Coleoptera and Hymenoptera, the most consumed prey items, are usually consumed by bird species that forage for prey hidden inside the vegetation, a behavior observed in several insectivorous birds families (Lima et al 2010), explaining its high consumption. Manhães and Dias (2011) found Coleoptera and Aranae as the most representative groups of arthropods in understory. Representativity of Coleptera, Aranae, Hymenoptera non-Formicidae and Hemiptera non-Heteroptera in other studies (Duca et al. 2023; Lima and Manhães 2009; Manhães and Dias 2011; Sekercioglu et al. 2002; Souza et al. 2001) suggests that those species may be more captured as prey for the bird species as a consequence of its abundance and availability. This relation between prey abundance and consumption is due to interactions resulting from random encounters between food resource and predators with locally abundant arthropod groups in a site or across localities by wide-spreaded prey groups (Cagnolo et al. 2011). Coleoptera, the most consumed food resource in the network, holds a high diversity and abundance in forest areas, explaining its importance in birds' diet (Duca et al. 2023). Furthermore, bird species with higher body mass tend to consume larger arthropods, such as Coleoptera (Manhães et al. 2015). The insectivorous birds are essential to exert a top-down control of abundant arthropod species, shaping the community they live in (Kotze et al. 2022), traits and ecosystem services (Mariano-Neto and Santos 2023).

Our findings enable us to visualize the structure of ecological communities as interaction networks, allowing different topological and mathematical analysis about how species interact with each other within a community, providing insights for further conservation and ecology studies. The interaction network provides a novel view of the relationship between bird species predating arthropod groups in the Atlantic Forest and provides information for further studies about these interactions in the biome.

2.5. Supplementary Information

The online version contains supplementary material available at:

Online Resource 1: Description of each study included in the network including sampling methods, location and study period:

https://docs.google.com/spreadsheets/d/1GpJko1uoQ2eAUxdnUevRBR_eodYVL3De5D1IS wF66tE/edit?usp=sharing

Online resource 2.: Matrix used for elaborating the interaction network: <u>https://docs.google.com/spreadsheets/d/1hEXPZd9rly1t0BJUvF-ozqfhTNYt33qEwhU2jdEeVnE/edit?</u> <u>usp=sharing</u>

Online Resource 3: R script used to plot the interaction network and obtain the nestedness, connectance and specialization index, including the codes used to determine the modularity and its transformation into z-scores after using the null models:

https://docs.google.com/document/d/e/2PACX-1vSR-H_nrOZwkIHQrw6X8V31P1-5vYh43zdTPtE5D xXU4DONUrJlhf1mX8sTaFbH5bj5EhHWO3-0S0Ax/pub

Online resource 4: Acronyms for bird species and arthropod groups included in the interaction network:

https://docs.google.com/spreadsheets/d/1a1YG8n5LE9YT0-6toTTPsilHFPQJbJbjJsccdS3YNM8/edit? usp=sharing

Online resource 5: Bipartite interaction network in a better resolution: https://drive.google.com/file/d/1tKcIBelLx6JGAQ9P0o653c011UdB3vBr/view?usp=sharing

2.6. Author contribution

All authors contributed substantially to the writing of this manuscript.

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2.8. Data availability

All the data related to this article are given as supplementary files along with this article.

2.9. Declarations

All the authors consent to participate in this study.

2.10. Conflict of interest

The authors declare no competing interests.

2.11. References

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ANEXO A - REGRAS DE FORMATAÇÃO PARA SUBMISSÃO DA REVISTA ORNITOLOGY RESEARCH

Instructions for Authors

Article Types

ORIGINAL ARTICLES should not exceed 50 doubled-spaced pages, including tables, figures and references. The sections of the original articles should be: Abstract, Keywords, Introduction, Methods, Results, Discussion, Acknowledgments, and References. In case manuscripts do not adhere to the size or general structure indicated, please contact the journal for a previous analysis on suitability.

REVIEWS should not exceed 15,000 words, excluding tables, figure legends and references.

SHORT COMMUNICATIONS should not exceed 1,500 words, excluding abstract and references, with up to 2 figures and 2 tables. Short communications should not have subheadings, and should have the sections Acknowledgments and References.

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Submission of a manuscript implies: that the work described has not been published before; that it is not under consideration for publication anywhere else; that its publication has been approved by all co-authors, if any, as well as by the responsible authorities – tacitly or explicitly – at the institute where the work has been carried out. The publisher will not be held legally responsible should there be any claims for compensation.

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Please note that Author Contribution information and Competing Interest information must be provided at submission via the submission interface. Only the information submitted via the interface will be used in the final published version. Please make sure that if you are an editorial board member and also a listed author that you also declare this information in the Competing Interest section of the interface. Please see the relevant sections in the submission guidelines for further information on these statements as well as possible other mandatory statements.

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Please make sure your title page contains the following information.

- Title
- The title should be concise and informative.
- Author information
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For authors that are (temporarily) unaffiliated we will only capture their city and country of residence, not their e-mail address unless specifically requested.

Large Language Models (LLMs), such as <u>ChatGPT</u>, do not currently satisfy our <u>authorship criteria</u>. Notably an attribution of authorship carries with it accountability for the work, which cannot be effectively applied to LLMs. Use of an LLM should be properly documented in the Methods section (and if a Methods section is not available, in a suitable alternative part) of the manuscript.

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Please provide an abstract of 150 to 250 words. The abstract should not contain any undefined abbreviations or unspecified references.

For life science journals only (when applicable)

- Trial registration number and date of registration for prospectively registered trials
- Trial registration number and date of registration, followed by "retrospectively registered", for retrospectively registered trials

Keywords

Please provide 4 to 6 keywords which can be used for indexing purposes.

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The following statements should be included under the heading "Statements and Declarations" for inclusion in the published paper. Please note that submissions that do not include relevant declarations will be returned as incomplete.

• Competing Interests: Authors are required to disclose financial or non-financial interests that are directly or indirectly related to the work submitted for publication. Please refer to "Competing Interests and Funding" below for more information on how to complete this section.

Please see the relevant sections in the submission guidelines for further information as well as various examples of wording. Please revise/customize the sample statements according to your own needs.

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- Do not use field functions.
- Use tab stops or other commands for indents, not the space bar.
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- Use the equation editor or MathType for equations.
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Please use no more than three levels of displayed headings.

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Abbreviations should be defined at first mention and used consistently thereafter.

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Acknowledgments

Acknowledgments of people, grants, funds, etc. should be placed in a separate section on the title page. The names of funding organizations should be written in full.

References

Citation

Cite references in the text by name and year in parentheses. Some examples:

- Negotiation research spans many disciplines (Thompson 1990).
- This result was later contradicted by Becker and Seligman (1996).
- This effect has been widely studied (Abbott 1991; Barakat et al. 1995a, b; Kelso and Smith 1998; Medvec et al. 1999, 2000).

Reference list

The list of references should only include works that are cited in the text and that have been published or accepted for publication. Personal communications and unpublished works should only be mentioned in the text.

Reference list entries should be alphabetized by the last names of the first author of each work. Please alphabetize according to the following rules: 1) For one author, by name of author, then chronologically; 2) For two authors, by name of author, then name of coauthor, then chronologically; 3) For more than two authors, by name of first author, then chronologically.

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• Journal article

 Gamelin FX, Baquet G, Berthoin S, Thevenet D, Nourry C, Nottin S, Bosquet L (2009) Effect of high intensity intermittent training on heart rate variability in prepubescent children. Eur J Appl Physiol 105:731-738. <u>https://doi.org/10.1007/s00421-008-0955-8</u>

Ideally, the names of all authors should be provided, but the usage of "et al" in long author lists will also be accepted:

- Smith J, Jones M Jr, Houghton L et al (1999) Future of health insurance. N Engl J Med 965:325-329
- Article by DOI Slifka MK, Whitton JL (2000) Clinical implications of dysregulated cytokine production. J Mol Med. https://doi.org/10.1007/s001090000086
- Book
 South J, Blass B (2001) The future of modern genomics. Blackwell, London
- Book chapter Brown B, Aaron M (2001) The politics of nature. In: Smith J (ed) The rise of modern genomics, 3rd edn. Wiley, New York, pp 230-257
- Online document Cartwright J (2007) Big stars have weather too. IOP Publishing PhysicsWeb. http://physicsweb.org/articles/news/11/6/16/1. Accessed 26 June 2007
- Dissertation Trent JW (1975) Experimental acute renal failure. Dissertation, University of California

Always use the standard abbreviation of a journal's name according to the ISSN List of Title Word Abbreviations, see

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If you are unsure, please use the full journal title.

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All tables are to be numbered using Arabic numerals. Tables should always be cited in text in consecutive numerical order. For each table, please supply a table caption (title) explaining the components of the table. Identify any previously published material by giving the original source in the form of a reference at the end of the table caption. Footnotes to tables should be indicated by superscript lower-case letters (or asterisks for significance values and other statistical data) and included beneath the table body.

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- Supply all figures electronically.
- Indicate what graphics program was used to create the artwork.
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- Name your figure files with "Fig" and the figure number, e.g., Fig1.eps.

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- All lines should be at least 0.1 mm (0.3 pt) wide.
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- No punctuation is to be included after the number, nor is any punctuation to be placed at the end of the caption.
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