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Generalist diets allows opportunism behavior to engage in cleaning interactions among birds and large mammals

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ABSTRACT

Cleaning interactions are interspecific associations in which cleaners benefit from the hosts by feeding on parasites, injured tissues, or blood. All around the globe there is a remarkable diversity of birds that behave as cleaners of large mammals. Here we investigated the drivers shaping the organization of networks formed by cleaning birds and host mammals. We used two cleaner-host networks, one from Brazilian openlands and the other one from African openlands, to explore the relationship between diet generalism and cleaning behavior. We hypothesize that cleaning interactions are often opportunistic and, as a consequence, we expect that generalist species are the main components of cleaner-host networks. We first contrast the diet diversity of cleaner species with their closed related species. For 18 of 26 bird families, cleaners show higher diet diversity than closely-related, non-cleaning species. Then we explored if birds with higher diversity diets are the central species of the cleaner-host networks. The results show that there is no apparent correlation between species centrality in the networks and their diet diversity. We suggest that generalism allows opportunist species to engage in cleaning interactions, but the importance of a cleaner species is affected by other attributes, such as abundance and behavioral traits associated with cleaning behavior. In a broader perspective, these results suggest that the factors that may allow species to participate in ecological networks are not the same that modulate their role in the same networks.

Keywords:

Cleaning-symbiosis, Opportunism, Diet-diversity, Birds, Network-centrality

Introduction

In ecological communities, ecological interactions connect individuals of different species. Ecological interactions have far-reaching consequences for population ecology (Macarthur 1955, Jordano 2016) and evolution (Drossel et al. 2001, Guimarães et al. 2011), affecting the persistence of biodiversity at community level (Paine 1966, Fontaine et al 2006, Hale et al. 2020). At community level, ecological interactions often form networks because pairs of interacting species are linked to each other (Pascual & Dunne 2006; Jordano et al. 2006). Several types of interactions, such as mutualisms among plants and seed dispersers and pollinators (Bascompte et al. 2003), predator and prey interactions among mammals

(Pires & Guimarães 2013), facilitative interactions among plant species (Verdú 2010), and cleaning interactions among fish (Guimarães et al. 2007) form species-rich networks showing a myriad of nonrandom network patterns. These nonrandom network patterns include nestedness (e.g. Guimarães et al. 2007; Bascompte et al. 2003) and modularity (e.g. Olesen et al. 2007).

Nestedness patterns implies that the networks show asymmetries, in which species with many interactions form a core of interactions, and species with fewer interactions usually do not interact with each other (Bascompte et al 2003). In contrast, modularity patterns imply that most interactions are organized in modules, i.e., semi-isolated and densely connected groups of interacting species (Olesen et al. 2007, Pimm & Lawton 1990). These nonrandom patterns of the network reflect (i) the variation in the average levels of specializations and generalism and (ii) the nonrandom patterns of niche overlap across different types of interaction (Guimarães 2020). In this sense, the structure of ecological networks may partially encode the processes shaping the ecological interactions and affecting the organization of ecological communities (Jordano et al. 2003; Bastolla et al. 2009; Guimarães 2020).

In the simplest scenario, individuals of different species are generalists, interacting with partners in an opportunistic way, e.g., feeding on resources in the frequency they are available in the environment. Although there is compelling evidence of departures of the patterns of interaction expected by the availability of resources (Olesen et al. 2011; Kuebbing et al. 2013; Pekkonen et al. 2013), the assumption that individuals interact as opportunistic foragers allows insights on the organization of ecological networks. Specifically, opportunism at the individual level implies that, at the species level, variation in number of interactions across species would be correlated with species abundances (Vazquez et al. 2007; Krishna et al. 2008).

Indeed, a number of network patterns can be explained by differences in abundance among species (Vázquez et al. 2005, 2007; Lewinsohn et al. 2006) which suggest, in turn, that opportunism has a central role in the organization of many ecological networks. Opportunism may allow species to engage in new types of interactions, exploring novel resources and structuring, at the community level, networks of interacting species. To engage in new interactions, those species should be able, by their traits and behavior, to interact with a broad diversity of individuals and species. Thus, not only resource availability would determine the engagement of new interactions and the opportunistic behavior, but also the diversity of resource consumption.

Although opportunism may be a central component of some ecological networks, opportunistic species coexist with highly specialized lifestyles that are also part of the network. Some highly specialized lifestyles are extreme specialists that interact with single partners, such as some gall-making insects, floral parasites, myrmecophytes, and anemonefishes. Other highly specialized lifestyles are highly connected species which rely upon a diversity of partners (i.e., a network) to persist. Examples of these highly connected lifestyles include obligate nectarivorous insects, obligate frugivorous birds, cleaner fishes, hypercarnivores, and highly specialized cleaning birds, such as the oxpeckers. By exploring how ecological networks combine opportunists and specialized lifestyles we may obtain insights on how ecological and evolutionary processes built up species-rich assemblages of interacting species.

Here, we used cleaning interactions among birds and mammals as a study system to explore the role of opportunism and specialized lifestyles in structuring ecological networks. Cleaning interactions are ecological interactions that involve clients and cleaners and occur in a number of marine and terrestrial ecosystems. In terrestrial systems, a number of bird species engage in cleaning interactions of mammalian herbivores. There is a remarkable diversity of birds that show this behavior, all around the globe (e.g. Ruggiero and Ewes 1988, Sazima 2007a). The cleaners (birds) benefit from the hosts (large mammals) by feeding on parasites, injured tissue or blood (Ivan Sazima 2011). These interactions often provide benefits for the cleaner individual, but the effects on clients are variable, including negative, neutral, and positive effects. In the large majority of cases, cleaning behavior is facultative for birds. Having said that, some bird species, such as several caracaras (Falconidae) and some tyranid birds, show a number of stereotyped behaviors associated with cleaning. Moreover, in African savannahs, oxpeckers (Buphagus spp.) are highly specialized cleaners that obtain most of their feeding resources from these interactions. Thus, cleaning interactions show variability in the degree of opportunism and specialization and we used this variation to ask questions about the relative role of opportunism in shaping these interactions.

We hypothesize that opportunism allows species to facultatively engage in cleaning interactions to obtain resources. We derived two predictions from this hypothesis. First, we expect that cleaners show higher diet generalism than closely related species (Fig 1A). If opportunism is the leading factor shaping cleaning interactions, opportunist species that already show generalist diets would add additional resources (mainly mammalian ectoparasites and damaged fleshy tissues) to their diets. Second, we expect opportunistic species to interact with more mammalian hosts and with hosts that are used by most of the other cleaning species, i.e., we expect that opportunistic species are the central species of the network (Fig 1B). We test these two predictions with two continent-level networks that depict information on natural history of cleaning interactions among birds and mammalian hosts in Africa and South America (Sazima et al. 2012; Mikula et al. 2017).

Figure 1 a)

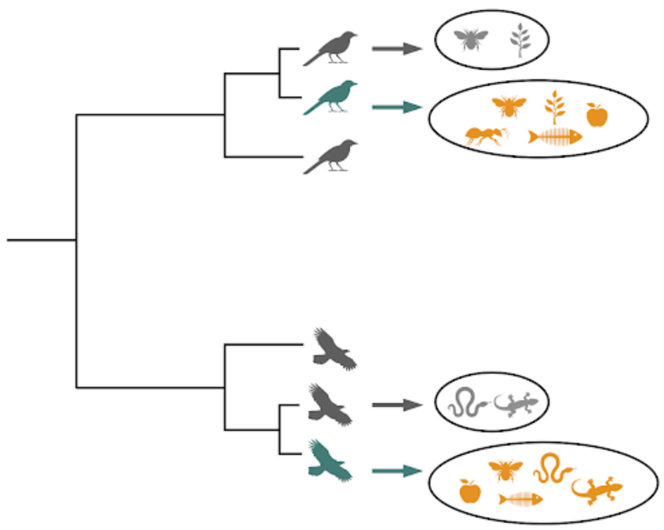

Figure 1 b)

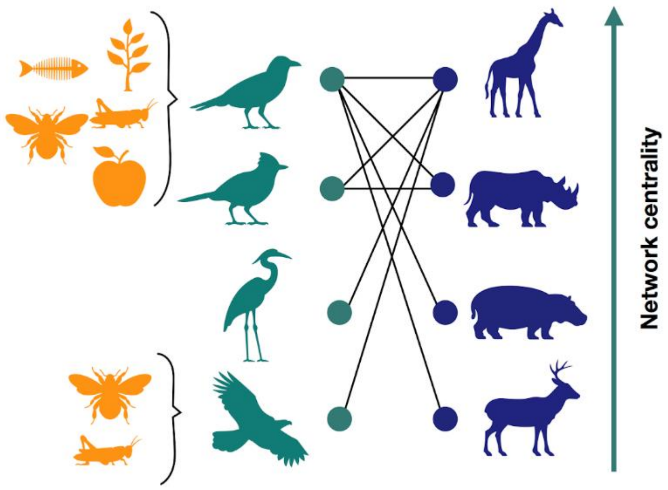

Figure 1 Conceptual framework of the hypothesis. **a)** Does the cleaning habit is related to the diversity of diet in bird's families? Assuming that the green birds in the figure clean mammals, and assuming opportunistic behavior as a response to the tendency of engaging in cleaning interactions, we ask if, in the same bird family, do species that have a generalistic diet (diversification on the feeding resources) also represent the cleaning bird species? **b)** Does the diversity of diet is related to the role of the cleaners in the cleaner-host networks? In the same network, do birds that have a diverse diet represent the central (degree) species? In other words, core cleaning species have a diverse diet?

Material and Methods

To understand how the diversity of diet of birds influences the cleaning associations among birds (cleaners) feed on parasites or injured tissue of mammals (clients), we first calculated a diversity diet index (*H*) for all bird species using the Elton Traits database, *EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals* (Wilman H, et al. 2014). In this database, the diet of each bird species is categorized in terms of broad diet categories (Supplementary figure 1 a). We used these categories to estimate the diet diversity of each bird species by computing the Shannon's Diversity Index (Shannon 1948):

$$H_j = -\sum_{i=1}^{R} p_i \ln p_i$$

in which H_j is the diet diversity of species *j*, *R* is the number of diet categories (resources), p_i is the proportion of diet category *i* in the diet of species *j*. In short, the higher the *H* value of the species, the higher is the diversity of diet resources each individual of the species can consume. Based on the two predictions divided previously (figure 1), we divided the methods in two sections: section (a) and section (b). In section (a) we compared the *H* values of cleaner bird species from Brazilian and African cleaning networks (Sazima et al. 2012; Mikula et al. 2017) with the *H* observed in non cleaning closed-related species. In section (b) we tested if the values of *H* demonstrate a correlation with the centrality degree of both networks. The summary of the methods is represented in figure 2.

(a) Cleaner bird species and families

We calculated the *H* of the cleaning bird species observed cleaning in Brazil and Africa registered in two previous works (Sazima et al. 2012; Mikula et al. 2017). Based on the birds species identified as cleaners, we selected the families that the species belong to. We identified a total number of 26 families. Then we compared the mean *H* of the 26 different bird families without the observed cleaners, with the mean *H* only of the cleaners, in the same given families (Fig 2). Our aim was to uncover a bias of generalist diet habits of cleaners, as we hypothesized that the cleaners would represent the species of their families with more diversification on their feeding habits. The details of the calculated *H* of the species and families can be accessed in Supplementary fig. 1.

To uncover the differences between the means of *H* of families and cleaners, we used a Paired T-Test to determine whether the mean difference between these two sets of *H* is zero. Standard deviation and P-value were also calculated.

(b) Cleaning networks and centrality degree

We analyzed the centrality degree of the Brazilian and African networks (Sazima et al. 2012; Mikula et al. 2017) by computing the number of host species that the cleaners species were interacting. We focused on degree measure, where the nodes (i.e species) that have more diverse interactions, represent the central nodes. Then we compared the centrality degree of each bird species with their *H* value, using a regression analysis. Our prediction was that the bird species that interact with many different hosts (i.e. more links with different mammal species) would be the birds with a higher *H*, meaning a positive correlation between these two measures (Fig 2). The details of hosts species and *H* of each bird species can be accessed in Supplementary fig. 2.

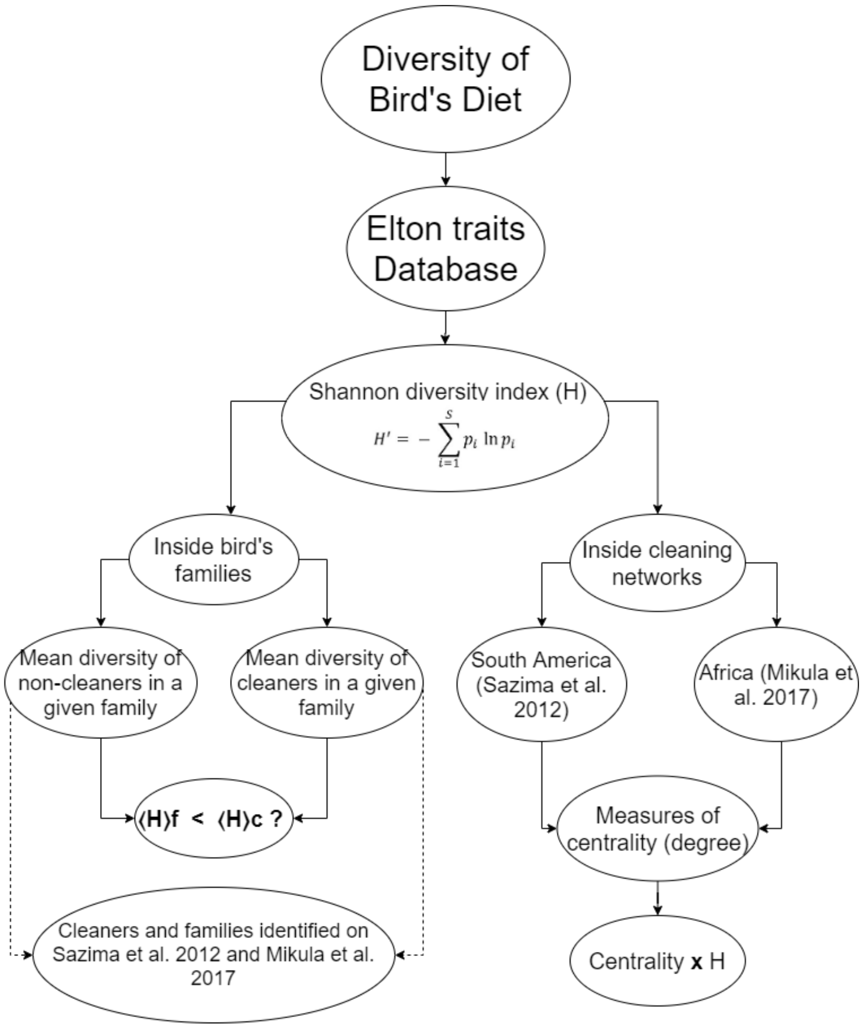

Figure 2 Methods of analysis that include the mean diversity index of diets of non-cleaners in a given family ($<H_f>$) compared with the mean diversity index of diets of cleaners in the same given family ($<H_c>$). Also, using two empirical networks (Sazima et al. 2012; Mikula et al. 2017) we calculated the centrality degree of the bird species and then we analyzed the centrality of these species with their diversity diet index (*H*).

Results

(a) Cleaner bird species and families

The mean diversity of cleaners demonstrate higher values than non-cleaners in most families. For 18 of the 26 families analyzed in Brazil and Africa, the mean diversity was significantly higher for the cleaners (Fig. 3). For example, In Charadriidae family, the *H* mean value was about 0.268 without the cleaners (which in this family, represents about 93% of the members) but, if only considering the cleaners, the *H* value was about 1.265 (which in this family, represents about 6% of the members).

Some families were analyzed only with one species counting as a cleaner species, such as Coraciidae, Cuculidae and Furnariidae. But still, it seems that there is a tendency that the cleaner species have a more diverse diet, when compared with other species in their families. With Furnariidae, for example, the *H* mean value was about 0.113 without the cleaners (which in this family, represents about 99.5% of the members) but, if only considering the cleaner species, the *H* value was about 0.5 (which in this family, represents about 0.45% of the members). All values can be found in Supplementary fig. 1 b).

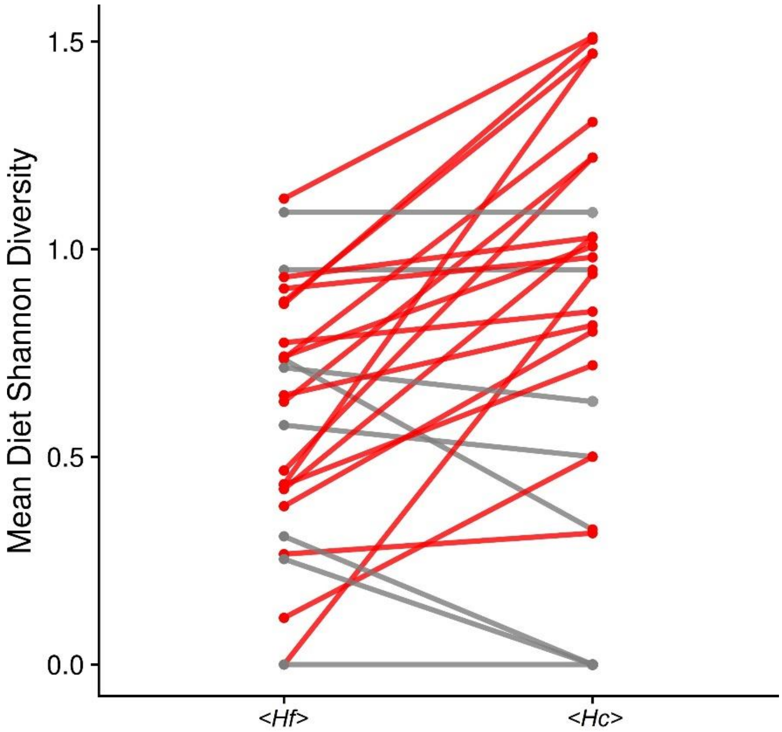

Figure 3 Paired T-Test of the mean diet (Shannon's Diversity Index) of families. Each line represents a different family. $<H_f>$ represents the mean diversity values of families without cleaners. $<H_c>$ represents the mean diversity values only of cleaners in the same given family. The red lines represent the families that demonstrated a positive tendency, where mean H values in cleaners were higher than H values of non-cleaner bird species of the same given family.

Mean: 0.262012; Std Dev: 0.3775; T test: 3.5386; P > t: 0.0008; N: 26

(b) Cleaning networks and centrality degree

Based on Sazima et al. 2012 and Mikula et al. 2017, we reconstructed the networks of cleaning interactions of Brazil (Pantanal) and Africa, using a heat map to identify the diet diversity index of each bird species (Fig. 4). Also, the size of nodes represents the centrality degree of these networks (bigger nodes represent bird species that interact with a higher diversity of host species).

Analyzing the centrality degree of birds in the networks and the H value of the bird species, there is no obvious relation between H and the values of centrality degree, meaning there is no significant results attesting that those values are correlated (Fig. 5).

Figure 4 a)

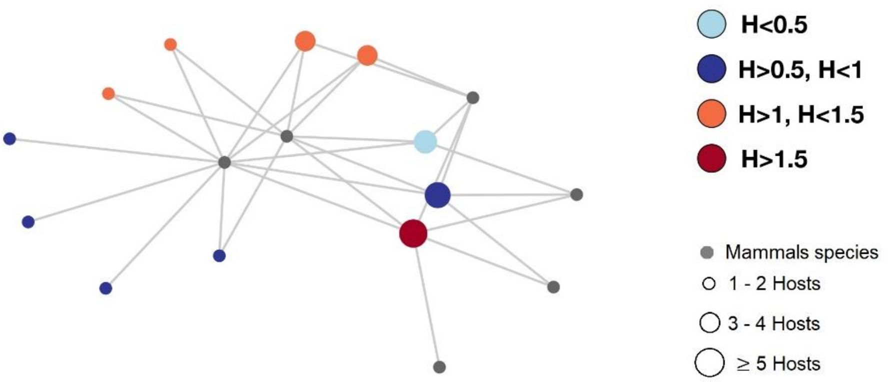

Figure 4 b)

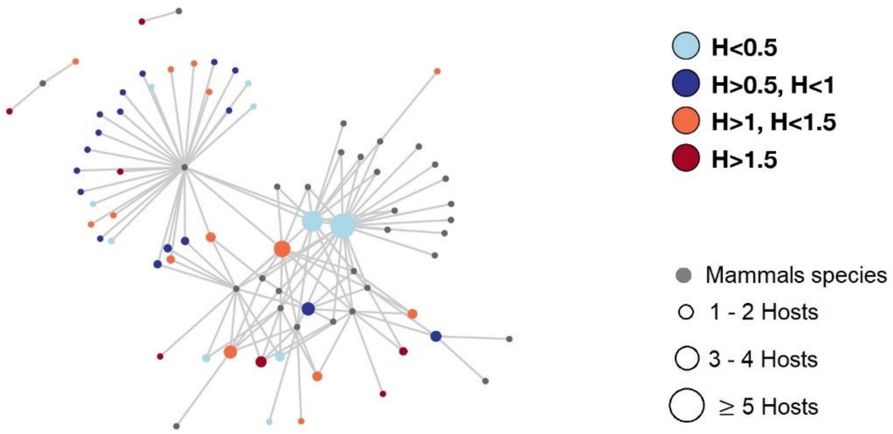

Figure 4 The colored nodes represent the bird species and their *H* value, gray nodes represent mammal species cleaned by birds. Links represent cleaning interactions. The size of the colored nodes represents the centrality degree. The heat map represents the values of *H*, where hot colors represent higher values and cold colors represent lower values. **a)** South America's cleaning network, based on Sazima et al. 2012. **b)** Africa's cleaning network, based on Mikula et al. 2017.

Figure 5 a)

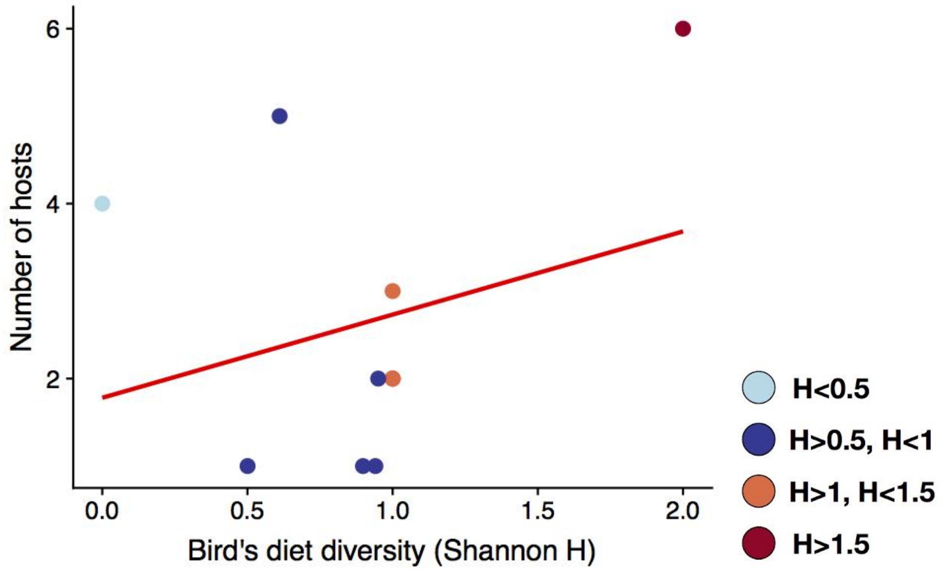

Figure 5 b)

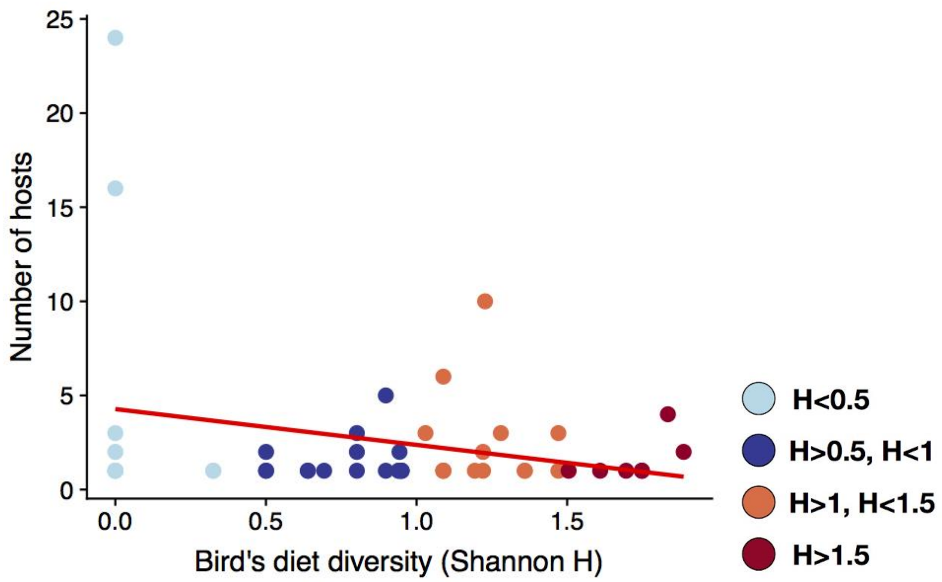

Figure 5 The color of the plots represent the values of H, where hot colors represent higher values and cold colors represent lower values. The regression lines don't exhibit significant tendencies. **a)** South America's cleaning scatter plot; R^2 = 0.01766; p > 0.05 **b)** Africa's cleaning scatter plot; R^2 = 0.01307; p > 0.05.

Discussion

Cleaning interactions among birds and mammals exhibit a great diversity of species and contexts. Analyzing two different networks, of different sizes and different locations, we could identify patterns in a facultative interaction from a broader perspective. Species with a wide repertoire of consumption could potentially engage in different types of interactions, such as facultative interactions like cleaning symbiosis. Once the bird is exposed to an opportunity, here defined as the presence of a mammal that hosts food resources, the ability to use this opportunity is defined by the species natural history. Our results suggest that for the majority of cleaners, the ability to consume different types of resources is an important feature to engage in cleaning interactions. Because the diversity of consumption is important for engaging in the interactions, a structural pattern such as centrality degree could also be influenced by the diversity of consumption. The purpose of this analysis is to understand the implications of resource consumption in the community. The network centrality degree analysis shows that there is no relation between the centrality degree and the diet diversity index of bird species. Which means that the ability of consuming different types of resources do not influence the centrality of the species in the network.

Opportunism is a common behavior between bird species. For example, caracaras (Falconidae) consume a myriad of types of resources, such as fruits, carcasses and eventually arthropods. These birds have been seen interacting with a diverse group of mammals, which raises the idea that they can have a central role in the community network. The caracaras are not only generalists in consumption, but also generalists in interactions with different host species. But, caracaras are an exception to the average opportunistic behavior in cleaning interactions, considering that there is no significant correlation between centrality degree and diversity of diet. The absence of a significant correlation suggests that there is more than one dimension when referring to generalism and specialism behaviors. Indeed, there are different levels of organization that can shape the biodiversity patterns (Levin, 1992). Some cleaner birds are generalists in the networks, when considering the different species of hosts, but in a broader perspective of consumption they are specialized. Some species, like the Oxpeckers (Buphagus sp.), specialized in cleaning interactions, in a way that they consume only parasites that live in large mammals. They are central to the network, demonstrating generalistic associations between different species of mammals, but specialized in consuming small arthropods that live in these mammals. Although these parasites can have a range of differences in morphologies and physiologies, compared to other categories of food resources the Oxpeckers can be defined as a specialist in consumption. Which means that the opportunistic behavior, although being essential to engagement in facultative interactions, can lead to specialized behavior. A strategy that can lead to an intimate relationship between the cleaners and even some of their most frequent hosts.

These individuals rely on the resources provided by the network (here, arthropods, injured tissue or blood) and not on particular hosts. These highly connected species are termed supergeneralists (Jordano et al. 2003, Thompson 2005). They have extremely specialized lifestyles that depend on the network they are embedded to survive. As the supergeneralists occur in the community, they tend to be relatively more important than others for maintaining structure and functioning of the community. The specialization of diet in a central species is not a unique pattern of cleaning networks, since dietary specialization occurs in other supergeneralists. For example, the centrality in seed-dispersal networks happens in species that present a higher centrality degree. Furthermore, centrality was best explained by dietary specialization (Mello et al. 2014).

Here, we have analyzed the structure of interactions and the natural history of bird species in facultative interactions, aiming to unravel the complexity of bird-mammal cleaning communities. Although the history of resources consumed and the centrality degree are important to comprehend the patterns of interactions, each one of them plays a different role in the composition of the community. In a broader perspective, these results suggest that the factors that may allow species to participate in ecological community networks are not the same factors that modulate their role in the same networks. Other factors, such as species abundance, can determine degree centrality. Thus, the role of species does not depend on a global structural generalism. But specifically, the role of species depends on their natural history and their integration into different types of interactions.

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Authors' contribution statement

J.N.A and P.R.G conceptualized the ideas, P.R.G. did the supervision, J.N.A performed the data curation, J.N.A did the investigation, formal analysis and methodology. J.N.A and P.R.G. wrote the original draft, P.R.G did the review and editing.

Conflict of interest statement

The authors declare that there is no conflict of interest.

Research data availability statement

The entire dataset supporting the results of this study was made available at SciELO Data and can be accessed at [https://doi.org/10.48331/scielodata.BLC2ZW].