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ORIGINAL ARTICLE

Black Manakin (*Xenopipo atronitens*) as a keystone species for seed dispersal in a white-sand vegetation enclave in Southwest Amazonia

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Abstract

Mutualistic interactions between plants and birds entail benefits for both organisms. While the birds obtain a nutritional resource when feeding on fruit, for example, the plant species benefits from having its seeds dispersed away from the mother-plant. Campinarana ecosystems grow on the white-sand substrates found irregularly within the Amazon basin. We conducted the present study in an enclave of campinarana in the municipality of Mâncio Lima, in the western extreme of the Brazilian state of Acre. We used mist-nets to capture birds, from which we also collected fecal samples. The seeds encountered in these samples were identified and used to establish a bird–plant interaction network, through which we analyzed the connectance, nestedness, centrality analysis, and robustness of the interactions. We recorded 69 of the 648 possible interactions, in which 12 bird species interacted with 54 plant taxa, with intermediate connectance ($C = 10.65\%$) and non-significant nestedness ($N = 11.36$; $p = 0.1$). The bird–plant interaction network of the campinarana enclave sampled in the present study had a random robustness of $R_r = 0.52$ and robustness of the degree of connectivity of $R_d = 0.15$. Based on its centrality analysis and robustness, black manakin, *Xenopipo atronitens*, was the most central bird species, responsible for the maintenance of the stability and structure of the interaction network. Given these findings, and its disproportionate mutualistic interactions with the plant taxa, in comparison with the other local frugivorous bird species, we consider *X. atronitens* to be a keystone species in this white-sand vegetation ecosystem.

Keywords Interspecific interaction · Interaction network · Mutualistic networks · Seed dispersal · The white-sand vegetation

Introduction

Between 50 and 90% of the plant species found in tropical forests are estimated to be dispersed by animals, while 20–50% of the mammals and birds found in these forests feed on fruit during at least part of the year (Fleming et al., 1987). As most tropical plants need animals to disperse their seeds, and thus complete their reproductive cycle (Morellato & Leitão-Filho, 1992), frugivores play an important ecological role as seed dispersers, which influences both the survival and the spatial distribution of the plant species (Fadini & Marco-Jr, 2004). These interactions can be represented using bipartite graphs, which are known as interaction networks (Lewinsohn et al., 2006), and define a system composed of multiple connected elements (Bascompte & Jordano, 2014) that can be used to identify keystone species (Mello et al., 2014).

The keystone species concept was proposed by Paine (1969) and is easily understood. Since its inception, however, the concept has been adapted, amplified, and even redefined, according to the target community, creating a certain degree of confusion and ambiguity (Cottee-Jones & Whittaker, 2012). The original concept defines a keystone species as an organism that plays a central role in the community, maintaining the community stable over time (Paine, 1969). This implies that, if the keystone species were to disappear locally, the whole ecosystem would collapse (Mills et al., 1993). Young (1980) describes the community structure of an ecosystem as a house of cards, which will collapse if the wrong card is removed. While the keystone species

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concept was applied originally to the example of a top predator (*Pisaster ochraceus*) in coastal rock pools (Paine, 1969), all manner of keystone species have now been identified in both aquatic and terrestrial ecosystems (Bond, 1994; Cottee-Jones & Whittaker, 2012), including plants (Gilbert, 1980; Terborgh, 1986) and terrestrial animals such as pollinators, large predators (Ashton, 2010), parasites, and seed dispersers (Mello et al., 2014).

Identifying the keystone species of an ecosystem is a complex task (Mills et al., 1993; Paine, 1995; Young, 1980). Mello et al. (2014) evaluated the role of keystone species in seed dispersal interaction networks and concluded that, to identify a keystone species in a mutualistic interaction network, it is necessary to quantify the relative importance of the different species in the community. This quantification can be based on centrality, that is, the role of a given element in the maintenance of the whole system (Lewinsohn & Cagnolo, 2012; Mello et al., 2014; Schleuning et al., 2014). The application of measures of centrality to Neotropical bats and birds indicates that specialized frugivores may be fundamental mutualists in the seed dispersal network (Mello et al., 2014).

In Brazil, most of the studies that have focused on the interactions between frugivorous birds and fruiting plants have been conducted in the Atlantic Forest, Cerrado, and Caatinga biomes (Baldiviezo et al., 2019), with only very limited research, up to now, in the Amazon biome (Alencar & Guilherme, 2020; Hawes & Peres, 2014). A unique type of ecosystem is found within the Amazon biome, in particular in the western Brazilian state of Acre, which is known regionally as the "campina" or "campinarana," whose ecological interactions are virtually unknown. The white-sand vegetation is a type of ecosystem associated with white-sand soils, which are poor in nutrients and rich in humic acids. The ecosystem white-sand is typically formed by a high density of thin-stemmed trees, a low understory, and few emergent trees (Anderson, 1981; Medina et al., 1990), while the campinas are shrubby formations dominated by herbaceous plants, shrubs, and exposed soil (Anderson, 1981). These systems are found in disjunct enclaves, surrounded by typical Amazonian forest, which are scattered irregularly throughout the Amazon biome (Anderson, 1981; Daly et al., 2016).

In Acre, the white-sand vegetation is concentrated in the western portion of the state (Daly et al., 2016). The local campinarana environments have large numbers of endemic plants and birds (Borges et al., 2016; Daly et al., 2016; Guilherme & Borges, 2011). One of the endemic birds of these ecosystem is black manakin (*Xenopipo atronitens*), a frugivorous species with an irregular distribution in the Amazon biome, where it is restricted to forests that grow on white-sand soils (Borges et al., 2016).

In the present study, we describe the bird–plant interactions observed in a campinarana in the southwestern Amazon, based on the analysis of the seeds found in the feces of birds captured in mist-nets. We confirmed the robustness of the established interaction network by simulating the removal of bird species from the network through hypothetical extinctions, with the aim of identifying a possible keystone species of seed disperser in the campinarana enclave.

Material and methods

Study area

We conducted the present study in an enclave of campinarana habitat in the western extreme of the Brazilian state of Acre, using the permanent trail of the local Biodiversity Research Program (PPBio/Acre), located in the community of Santa Bárbara, on the BR 307 federal highway, in the municipality of Mâncio Lima, Acre state, Brazil (7° 28′ 00″ S, 72° 54′ 00″ W; Fig. 1). Based on IBGE (2012), the vegetation associated with this trail has three principal phytophysiognomic formations, that is, arboreal and forested campinarana, and shrubby campina. The arboreal campinarana is dominated by thin-stemmed trees of small size and a flexible layer of roots on the ground surface (Daly et al., 2016). The forested campinarana has a well-formed canopy with emergent trees and abundant palms, while the shrubby campina has no emergents, but thick undergrowth and areas of exposed soil (Anderson, 1981).

Data collection

Capture of the birds

We captured birds using 10 mist-nets (12 m × 2.5 m with a mesh of 36 mm). For this, we established 36 transects 120 m long perpendicular to the PPBio trail at intervals of 30 m. We capture birds between April and September 2019, on a total of 90 days. We identified all the birds to species, using field guides whenever necessary (Schulenberg et al., 2007). We followed the Brazilian Committee of Ornithological Records (Pacheco et al., 2021) for the scientific nomenclature. Each captured bird was banded with an aluminum ring provided by the Brazilian National Center for Wild Bird Research and Conservation (CEMAVE), through project 4386, coordinated by Edson Guilherme (senior bander, license number 324654).

Collection and identification of the seeds

We placed the captured birds in cloth bags containing absorbent paper for up to 15 min for the collection of fecal

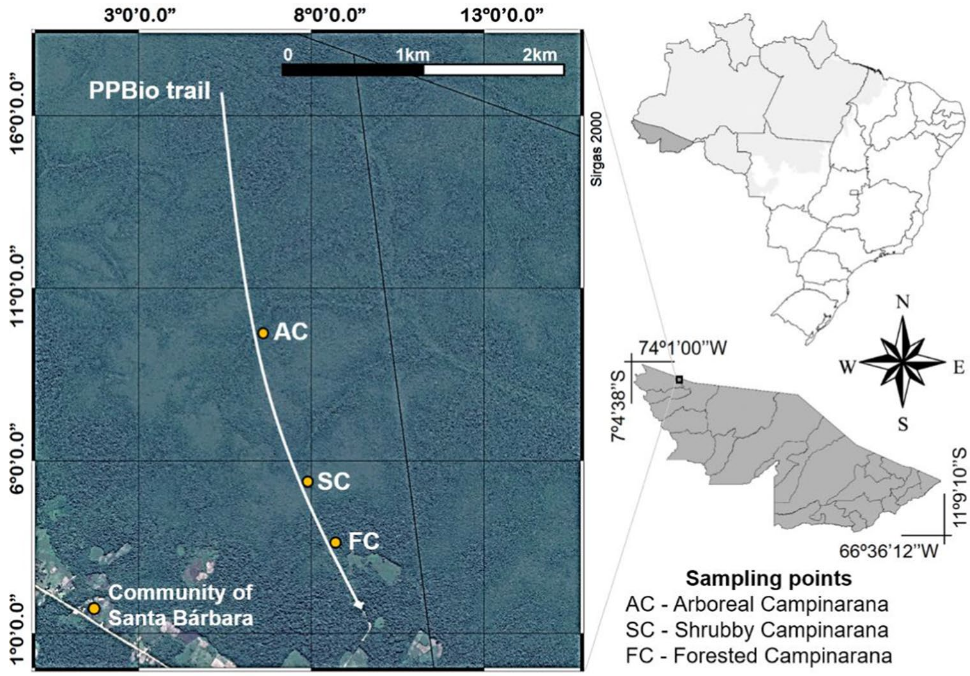

Fig. 1 The PPBio trail and the sampling points in the community of Santa Bárbara, in the municipality of Mâncio Lima, Acre, Brazil. Image: Google Earth. FC = Forested Campinarana; SC = Shrubby Campinarana; AC = Arboreal Campinarana

samples, after which, the birds were released near the capture site. The fecal material containing the seeds was stored in individual packages labeled with the name of the bird species, its band number, and the date. In the laboratory, we cleaned the seeds manually to remove the fecal material and remains of insects. Once cleaned, the seeds were arranged according to their morphological similarities (morphospecies), counted, and photographed. The morphospecies identified in this way were subsequently re-examined and identified with the assistance of researchers from the Botany and Plant Ecology Laboratory (LABEV) at the Federal University of Acre (UFAC) in Rio Branco, supported by reference works on the region's plant diversity (Daly & Silveira, 2008; Daly et al., 2016).

Data analysis

Interaction network we organized the data in a binary presence/absence matrix, with the plant species in the lines and the frugivorous/generalist birds in the columns. In this matrix, the element aij is equal to 1 if bird i interacts with plant j or 0, when there is no interaction (Bascompte et al., 2003). We generated the interaction networks in the R software, using the *bipartite* (Dormann et al., 2009), *sna* (Carter, 2010), and *igraph* packages (Csardi & Nepusz, 2006).

Architecture of the bird–plant interaction network

Connectance (C) estimates the percentage of the interactions recorded between the bird and plant species in terms of all the possible interactions, with a value of between 0 and 100 (Jordano, 1987). The connectance is calculated by the formula: $C(\%) = I \times 100/(F \times P)$, where I = the number of interactions observed, F = the number of frugivorous species, P = the number of plant species, and $(F \times P)$ = the total number of possible interactions between birds and plants in the study area.

Nestedness (N) nestedness occurs when specialist species interact with a well-defined subset of generalist species (Bascompte et al., 2003; Guimarães et al., 2006; Jordano et al., 2003; Memmott et al., 2004). We calculated nestedness using the formula: $N = (100 - T)/100$ (Bascompte et al., 2003) where N = the degree of nestedness, with values that range from 0 to a maximum of 100, and T = the temperature of the network, which estimates the deviation of the unpredicted presence or absence, with values of between 0° and 100° (Atmar & Patterson, 1993). We calculated the temperature in the Nestedness Temperature Calculator program, which applies the null model that assumes that each cell of the interaction matrix has the same probability of being occupied (Atmar & Patterson, 1993, 1995).

Analyses used to identify the keystone species of the campinarana enclave

Measures of centrality we used three different measures of centrality to determine the relative importance of each bird species in the interaction network (Mello et al., 2016), with the principal aim of identifying a keystone species in this network (Martín-González et al., 2010).

Degree centrality (DC) this is an informative measure, weighted only by the number of actual interactions of a species, that is, the number of interactions along a vertex (the degree) in relation to the total number of interactions that this species could possibly maintain in the network (Nooy et al., 2005). We calculated this measure from the bipartite network (bird and plant species).

Closeness centrality (CC) measures the proximity of a species to the other species in the interaction network (Freeman, 1979). A species will have a high level of closeness centrality when it interacts with plant species that are also consumed by many other frugivores in the same network and a low level of closeness centrality when its diet is more restricted (Mello et al., 2014). We calculated the CC in the *Closeness* function of the Pajek32 5.13 program, based on the weighted bipartite network, in which the strength of each link is based on the number of interactions (Mello et al., 2016).

Betweenness centrality (BC) measures the importance of a vertex within the network, such as an important connector species (Freeman, 1979). Species with BC values of greater than 0 are considered to be connector species (Martín-González et al., 2010). We calculated the BC in the *Betweenness* function of Pajek32 5.13, in which the strength of each link is based on the number of interactions (Mello et al., 2016).

Resistance of the interactions following species removal

Robustness (R) considers the stability of a system following the removal of a target species (Landi et al., 2018). We calculated the Robustness (*R*) of the interaction network in the *robustness* function of the bipartite package (Burgos et al., 2009), considering the secondary extinction of the plant species that resulted from the primary extinction of the bird species, based on both the removal of species with the most interactions (degree of connectivity) and the random removal of species. This index varies from 0 to 1, where $R = 1$ indicates that most of the plant species remain following the removal of the bird, whereas $R = 0$ presents the collapse of the community following the removal of only a few bird species.

Results

We recorded 69 of the 648 possible bird–plant interactions in the campinarana enclave monitored during the present study, in which 12 bird species interacted with 54 plant taxa (Fig. 2), generating an intermediate level of connectance ($C = 10.65\%$) and non-significant nestedness ($N = 11.36$; $p = 0.1$). The bird species with the most interactions was *Xenopipo atronitens* with 42 (60.8% of the total), of which, 33 were exclusive, followed by *Elaenia parvirostris* with seven interactions (10.1%), one of which was exclusive,

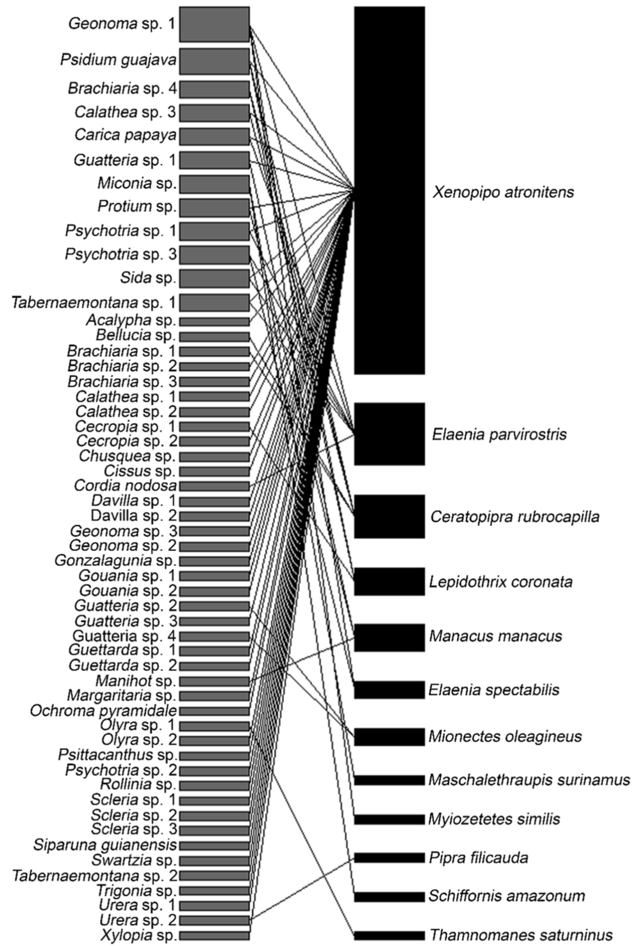

Fig. 2 Bird–plant interactions recorded in the present study based on the birds captured and the seeds obtained from their feces in a campinarana located in the municipality of Mâncio Lima, Acre, Brazil. Black bars = bird species and gray bars = plant taxa

and *Ceratopipra rubrocapilla* with five interactions (7.2%), including two exclusive interactions.

The degree centrality (DC) ranged from 0.01 to 0.60, reflecting a high level of variability in the number of interactions involving the different species in the network (Table 1). *Xenopipo atronitens* (Fig. 3) presented the highest DC value overall. The closeness centrality (CC) ranged from 0.34, with *Mionectes oleagineus* as the most peripheral bird, to 0.73 with *X. atronitens* as the most central species (Table 1). The betweenness centrality (BC) ranged from 0.00 to 0.85 (Table 1), this time with *Myiozetetes similis* as the most peripheral species, while *X. atronitens* continued as the most central species. In summary, *X. atronitens* was the most central species in the three metrics analyzed (Table 1). The bird–plant interaction network of the campinarana enclave surveyed in the present study had a random robustness of $Rr = 0.52$ and a degree of connectivity robustness of $Rd = 0.15$.

Table 1 Values recorded for the measures of centrality calculated for the bird/plant interaction network of a campinarana in southwestern Brazilian Amazonia

Bird species	Degree centrality (DC)	Closeness centrality (CC)	Betweenness centrality (BC)
Xenopipo atronitens	0.60	0.73	0.85
Elaenia parvirostris	0.10	0.52	0.15
Manacus manacus	0.04	0.48	0.03
Schiffornis amazonum	0.01	0.47	0.05
Lepidothrix coronata	0.04	0.47	0.07
Thamnomanes saturninus	0.01	0.45	0.03
Maschalethraupis surinamus	0.01	0.45	0.04
Myiozetetes similis	0.01	0.45	0.00
Elaenia spectabilis	0.02	0.44	0.02
Ceratopipra rubrocapilla	0.07	0.35	0.07
Pipra filicauda	0.01	0.35	0.03
Mionectes oleagineus	0.02	0.34	0.07

Discussion

In tropical forests with highly diverse communities, a relatively large number of interactions will be expected between birds and plants, although overall connectance is normally low (Jordano, 1987). Connectance was intermediate in the enclave of campinarana surveyed in the present study, which may reflect the isolation of this ecosystem within the predominant Amazon forest. This isolation is associated with a reduced diversity of species and a high level of local endemism (Adeney et al., 2016; Borges, 2004; Daly & Silveira, 2008; Daly et al., 2016), which increases the probability of interactions between the bird and plant taxa that coevolved in this unique environment. Intermediate levels of connectance are also typical of fragmented tropical forests and in environments that have suffered some level of alteration, in which the plants and remaining frugivores, which tend to be more resistant, will eventually interact and establish more connections than would be expected for a forest whose niches and microhabitats are intact (Alencar & Guilherme, 2020; Fadini & Marco-Jr., 2004). The nestedness of the interaction network of the campinarana enclave was non-significant, which indicates that the bird–plant interactions in this ecosystem do not follow the pattern typical of other environments (Alencar & Guilherme, 2020; Purificação et al., 2020). Bascompte et al. (2003) concluded that significant nestedness is typical of interaction networks with at least 30 species or ecosystems of reduced complexity. Relatively simple environments are more susceptible to species loss because they form fragile interaction networks (Bascompte et al., 2003; Bastolla et al., 2009; Memmott et al., 2004). This was clear from the interaction network obtained in the present study, in which a single species was responsible for 60.8% of all the interactions. The mutualistic relationships in this enclave of white sand vegetation seem to work exactly as in fragmented forests where the central species is the most abundant and had the smallest body size, contrary to what is expected in pristine forests (Montoya-Arango et al. 2019). This is a potentially preoccupying finding, given the ongoing exploitation of the natural resources found in the campinarana enclaves of western Acre, such as the extraction of white sand for the construction industry and logging to supply firewood for manioc processing ovens. These activities are contributing to the degradation of this unique ecosystem, not only in Acre (Daly et al., 2016), but throughout the Amazon biome (Demarchi et al., 2019; Ferreira et al., 2013; Guilherme et al., 2018).

The findings of the centrality analysis employed in the present study showed clearly that black manakin (*Xenopipo atronitens*) is the most central species of the local bird–plant interaction network, indicating that it is a keystone species in the mutualistic seed dispersal network

Fig. 3 Black manakin (*Xenopipo atronitens*) a keystone species for seed dispersal in our white-sand vegetation enclave. Male (left) and female (right). Photographs: Maíra Santos

of the campinarana ecosystem (Martín-González et al., 2010). *Xenopipo atronitens* clearly acts as a hub, given its large number of interactions, including 33 that are exclusive to this bird, as well as being a connector, linking other sectors of the network (Mello et al., 2014). Hypothetically, if *X. atronitens* were removed from the interaction network, the plant species that interact exclusively with this bird would also be excluded, eventually, from the network. This would destabilize the network and alter its structure, which is exactly what happens when a keystone species is excluded from an ecosystem, given that species with a high level of closeness centrality tend to have a profound impact on other species in the network (Martín-González et al., 2010). In turn, the plant species that depend on *X. atronitens* to disperse their seeds in the campinarana enclave may eventually become locally extinct or at least have their seed dispersal greatly reduced (Koh et al., 2004; Traveset et al., 2017).

The analysis of robustness simulates extinctions (Evans et al., 2013) and indicated that the interaction network of the campinarana enclave is more stable when species are lost randomly than when those with a large number of interactions are excluded, which can lead to the extensive dismantling of the network. This indicates that *X. atronitens* maintains the structure and stability of the interaction network. When generalist species, that is, the species with the largest number of interactions, are excluded, the network becomes vulnerable to secondary extinctions. The loss or extinction of some species from the interaction network may trigger a cascade of co-extinctions, impacting community structure and function which will, in turn, have a direct influence on ecosystem function (Symstad et al., 1998; Colwell et al., 2012; Valiente-Banuet et al., 2015).

Campinas and campinaranas are considered to be relict environments within the Amazon biome, in which most plant species are endemic, demanding a certain degree of adaptation of the associated fauna over the long term (Capurucho et al., 2013; Rossetti et al., 2019). This is likely the case of *X. atronitens*, whose evolutionary history is linked intimately with the shrubby vegetation of the campinaranas, which formed during the glacial cycles of the Pleistocene (Capurucho et al., 2013). This would account for the adaptation of *X. atronitens* for the exploitation of the fruit of an ample variety of the plant species that are endemic to this unique type of vegetation that grows on the white sand soils of the Amazon biome. It is still unclear, however, how *X. atronitens* disperses between the isolated enclaves of campinarana, which are often separated by hundreds of kilometers of dense Amazon forest, although there appears to be little doubt that this process involves the co-dispersal of the seeds of many of the plant species that are endemic to these ecosystem.

Final considerations

Xenopipo atronitens was the principal bird species responsible for the dispersal of the seeds of the plant species found in the campinarana enclave surveyed in the present study, and thus appears to be a keystone species in this type of ecosystem. This conclusion was supported by the combination of different centrality indices. The combination of indices in mutualistic networks has been recommended in order to offer a greater precision of the real biological meaning (Gouveia et al. 2021). Further research on the interaction networks of other campinarana enclaves located within the lowland Amazon forest will be important to refine our understanding of the bird/plant mutualisms of this unique, but poorly-known environment.

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