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ASPECTOS ECOLÓGICOS E EVOLUTIVOS DA ESCOLHA DOS FRUTOS: FATORES DETERMINANTES E VARIAÇÕES INDIVIDUAIS

Luís Paulo Pires

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Tese apresentada à Universidade Federal de Uberlândia, como parte das exigências para obtenção do título de Doutor em Ecologia e Conservação de Recursos Naturais.

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UBERLÂNDIA

Fevereiro - 2019

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INTRODUÇÃO

O estímulo para o desenvolvimento desta tese, intitulada “ASPECTOS ECOLÓGICOS E EVOLUTIVOS DA ESCOLHA DOS FRUTOS: FATORES DETERMINANTES E VARIAÇÕES INDIVIDUAIS”, surgiu ainda na graduação, quando descobri na Ecologia de Interações o foco do meu interesse científico. Ainda naquela oportunidade, tive a oportunidade de conduzir meus primeiros estudos no tema, dentro dos programas de iniciação científica, sob a orientação do Prof. Dr. Kleber Del-Claro. A experiência me possibilitou estudar mais a fundo o tema e isso direcionou a minha curiosidade para as interações mutualísticas frugívoro-planta, bem como suas representações a partir das redes ecológicas. Ainda na infância do meu amadurecimento acadêmico, os questionamentos giravam em torno do “se dentro de um habitat existe uma variedade de frutos maior do que aquela que de fato é consumida por um frugívoro, qual é o fator de seletividade ou escolha? Existe alguma preferência? Essas preferências são constantes entre diversos grupos ou variam conforme os diferentes organismos? Como essas preferências impactam as comunidades biológicas”.

Com tais questionamentos em mente, parti para o mestrado, onde me propus, juntamente com o Prof. Kleber, a estudar uma pequena parte deste amplo espectro investigativo. Na ocasião, estudei como o tamanho dos frutos de uma espécie de Piperaceae no Cerrado poderia influenciar o comportamento de forrageio de uma espécie de morcego. De fato, houve um critério seletivo pelos morcegos em relação ao tamanho do fruto e a busca por discutir este resultado estimulou ainda mais a curiosidade sobre o tema. Será que o padrão se repetiria para outras espécies de plantas e outros frugívoros? Será que se manteria em outras áreas com características diferentes? E se acrescentássemos outros fatores, será que seriam tão ou mais importantes que o tamanho? Obviamente, tantas questões não poderiam ser respondidas no curto tempo de um mestrado, mas serviram de combustível para o aprofundamento no tema.

Passei os anos seguintes desenvolvendo a proposta do doutorado. A ideia sempre foi abranger o escopo do que foi estudado no mestrado, como é de se esperar dos doutorandos. Por isso, defini as perguntas seguintes como as norteadoras do projeto: como diferentes fatores atuam separadamente e em conjunto para definir as interações frugívoro-planta? Existe algum fator de seletividade dos frutos ou as interações acontecem ao acaso? Os indivíduos dentro de uma mesma espécie se comportam da mesma forma que a população no uso dos recursos? Como esses padrões respondem às alterações ambientais e qual a sua importância ecológico-evolutiva? Com tais perguntas, elaborei uma proposta e a apresentei à Profa. Dra. Celine de Melo, que colaborou com a melhoria da ideia e aceitou o pedido de orientação.

Ingressei no curso de doutorado em março de 2015 com o projeto "REDES DE INTERAÇÕES ESPÉCIE-RECURSO E INDIVÍDUO-RECURSO ENTRE AVES FRUGÍVORAS E PLANTAS NO CERRADO: VARIAÇÕES INDIVIDUAIS NA ECOLOGIA DE COMUNIDADES", dando então continuidade à linha de pesquisa iniciada no mestrado. No intuito de responder às perguntadas listadas anteriormente, a Tese a seguir foi estruturada em quatro capítulos, com os seguintes objetivos:

I) Revisão teórico-conceitual da evolução das interações frugívoro-planta, na qual foi abordado o papel da pressão seletiva direcional exercida pelos frugívoros sobre as características de plantas zoocóricas;

II) Determinar se as interações entre aves frugívoras e plantas zoocóricas são estabelecidas de acordo com regras biológicas (hipótese determinista) ou pela abundância das espécies de plantas e aves (hipótese neutral) através dos parâmetros estruturais das redes ecológicas;

III) Investigar se existe variação interindividual do nicho em uma espécie de ave generalista e, caso exista, quais os fatores responsáveis pela origem desta variação, a partir de uma abordagem de redes ecológicas;

IV) Investigar como a cor de frutos artificiais pode influenciar a escolha o comportamento de forrageio de aves frugívoras e como esta influência se altera em um gradiente de efeito de borda.

Cada um destes capítulos serve a seu propósito. No primeiro capítulo, pretendemos situar o leitor na temática da Tese e, além disso, possibilitar a compreensão integrada dos demais capítulos, através do estabelecimento do arcabouço teórico sobre mecanismos evolutivos das interações animal-planta, que é comum a todos os capítulos da tese. O segundo capítulo apresenta o papel de diferentes fatores na estruturação das redes e suas implicações para as comunidades biológicas. O terceiro é um desafio à teoria ecológica vigente que considera os organismos em uma mesma espécie como funcionalmente equivalentes, ignorando variações individuais que afetam a estrutura das redes de interação. Por fim, o último capítulo avalia como os fatores que determinam as interações ecológicas podem sofrer variações em relação às perturbações ambientais. Juntos, porém, estes capítulos colaboram para a discussão sobre a origem e a conservação das interações mutualísticas entre aves e plantas nos ambientes tropicais, estes que, não raro, se encontram em avançado grau de degradação.

Os capítulos I, II e III seguem as normas gerais de formatação da revista Oecologia, que serve como base para vários outros periódicos na área de Ecologia. O capítulo IV, por sua vez, está formatado de acordo com as normas da revista Acta Scientiarium – Biological Sciences, na qual o capítulo está publicado.

RESUMO

Pires, Luís P. 2019. Aspectos ecológicos e evolutivos da escolha dos frutos: fatores determinantes e variações individuais. Tese de doutorado em Ecologia e Conservação de Recursos Naturais. UFU. Uberlândia-MG. 71p.

As interações entre frugívoros e plantas são fundamentais para a manutenção do equilíbrio ecológico dos ecossistemas. As plantas fornecem recurso alimentar para os animais que, por sua vez, atuam como dispersores das sementes. Nos ambientes tropicais, as aves se destacam como o grupo mais importante de dispersores de sementes das angiospermas, em número de espécies. Considerando a relevância desse serviço ecossistêmico, esta tese teve como objetivos: 1) discutir a abordagem coevolucionista das interações frugívoro-planta; 2) investigar o papel de fatores neutros e determinísticos na estruturação das redes de interações entre aves frugívoras e plantas; 3) avaliar o grau de especialização individual em uma espécie de ave frugívora generalista e 4) investigar como perturbações ambientais (*i.e.* efeito de borda) podem afetar a percepção de cores e a seleção de frutos pelas aves. Para alcançar o primeiro objetivo, foi feita uma revisão bibliográfica acerca da evolução das interações frugívoro-planta, com foco na convergência temporal dos padrões de evolução e diversificação dos grupos de frugívoros e das angiospermas. Nesta análise, nós concordamos com autores que afirmam que as pressões seletivas entre esses grupos acontecem em pulsos de coevolução, com períodos onde elas são mais fortes e direcionais intercalados por outros nos quais as forças coevolutivas são fracas. Com relação ao segundo objetivo, foi aplicada uma abordagem de redes ecológicas e nós encontramos que a restrição de tamanho imposta pela abertura do bico e a sobreposição temporal entre frugívoros e recursos explicam as interações par-à-par, porém a abundância relativa das espécies explica melhor as métricas de redes. No capítulo 3, novamente utilizou-se a abordagem de redes ecológicas, porém considerando que os nós de um dos lados da rede representavam indivíduos de uma mesma espécie frugívora. Identificou-se que esta população generalista é composta pela soma do nicho de indivíduos especialistas e que a variação sazonal na disponibilidade dos recursos afeta a amplitude do nicho individual. Por fim, no capítulo 4 realizou-se uma abordagem experimental para avaliar se a cor dos frutos e a distância em relação à borda do fragmento influencia a escolha dos frutos. Os resultados demonstraram que nenhum desses fatores explicou satisfatoriamente o consumo de frutos, o que acreditamos ser devido à predominância de espécies frugívoras oportunistas nos fragmentos estudados. Em seu conjunto, os dados e discussões apresentados nesta tese sugerem que: 1) mais informações sobre a coevolução entre frugívoros e plantas são necessárias para predizermos como as espécies irão responder às perturbações ambientais 2) modelos explanatórios das redes mutualísticas entre plantas e frugívoros devem considerar as restrições fenotípicas e a abundância das espécies, ao passo que as interpretações dos parâmetros das redes devem ser condicionadas aos fatores que os geram; 3) variações intraespecíficas no uso dos recursos são importantes na determinação das interações ecológicas e que redes no nível dos indivíduos apresentam propriedades que não se repetem no nível das espécies; e 4) a influência do efeito de borda sobre a escolha das cores dos frutos pelos frugívoros é principalmente indireto, através da modificação da estrutura do habitat e da composição das guildas tróficas.

Palavras-chave: mutualismos, interações ecológicas, frugivoria, dispersão de sementes.

ABSTRACT

Pires, Luís P. 2019. Ecological and evolutionary aspects of fruit choice: determinant features and individual variation. PhD Thesis. UFU. Uberlândia-MG. 71p.

Interactions between frugivores and plants are fundamental for the stability of ecological communities. Plants provide food for frugivorous animals and these disperse the seeds to suitable sites. In tropical ecosystems, birds are the most relevant seed dispersers of angiosperms, in terms of species richness. Considering the importance of this ecosystem service, this thesis aimed at: 1) discuss the coevolutionary approach of plant-frugivore interactions; 2) investigate the role of neutral and deterministic processes in assembling plant-frugivore networks; 3) assess the degree of individual specialization in a generalist bird species and 4) evaluate how environmental disturbances (*i.e.* edge effect) may influence color perception and fruit choice by frugivorous birds. To achieve the first goal, we did a review on the evolution of plant-frugivore interactions, focusing on the temporal congruency in the evolution and diversification patterns of frugivores and angiosperms. In this review, we agreed with authors who suggest that the selective pressures between these groups happens in pulses of coevolution, defined by periods when reciprocal evolution is strong and directional interspersed by others when coevolutionary forces are weak and diffuse. For the second objective of this study, we applied an ecological network approach and found that size constraints and temporal overlap between frugivores and resources explain pairwise interactions, but that species relative abundance performed better at explaining aggregate network metrics. In chapter 3, we once again used network theory but this time we considered the consumer nodes as different individuals in the same population. We identified that the generalist diet of the population is the sum of the niches of dietary specialist individuals and that seasonal variation in resource availability influences the dietary width of individual niche. Finally, in chapter 4 we designed an experimental study to assess if fruit color and the distance from forest borders influence fruit choice. Results showed that neither of these predictors explained fruit consumption and we believe this is due to the prevalence of opportunistic frugivorous species in the study sites. In its whole, the data and discussions presented in this thesis suggest that: 1) we need more information on the evolution of plant-frugivore interactions in order to better predict how environmental disturbances will affect species evolutionary trajectories; 2) models explaining plant-frugivore mutualistic networks should consider biological constraints and species relative abundance, but that these may not equally explain different processes of network assembling; 3) intraspecific variations in resource use are important for the establishment of biological interactions and that individual-level networks may contain properties that, albeit existent, are not evident in species-resources networks; and 4) the influence of edge effect of color-based fruit choice is mainly indirect, by modifying habitat structure and guild composition.

Keywords: mutualisms, ecological interactions, frugivory, seed dispersal.

CAPÍTULO I

A REVIEW ON THE EVOLUTION OF ANGIOSPERM-FRUGIVORE INTERACTIONS

A REVIEW ON THE EVOLUTION OF ANGIOSPERM-FRUGIVORE INTERACTIONS

Luís Paulo Pires and Celine de Melo

ABSTRACT

The evolution of fruits largely contributed to the dominance of angiosperms and they provided new ecological opportunities for frugivore vertebrates to evolve and diversify. However, it is not yet clear whether reciprocal coevolution drove the evolution of plant-frugivore interactions. This review aimed at discussing major events of the evolution of fleshy-fruited angiosperms and their seed dispersers, in order to elucidate if and how they responded to mutual selective pressures. Angiosperms evolved between the Mid and Late Cretaceous and they experienced a large diversification from the latter to a peak in the early Eocene. All main lineages of extant frugivores originated from the Eocene onward. Frugivorous birds evolved in the Eocene but diversified in the Oligocene, primates evolved in the early Eocene and frugivorous bats diversified in the Oligocene-Miocene. Incongruence in the times of the origins and diversification of angiosperm and their modern seed dispersers suggest that other animals interacted with early angiosperms, and the likely candidates are the multituberculates. Several studies investigated how plant-frugivore mutualistic interactions contribute to the diversification in both plants and animals and we can draw two main hypotheses from them: the plant-frugivore coevolutionary hypothesis and the neutral hypothesis. There are consistent evidences supporting each of these hypotheses, which suggest that they may not be mutually exclusives. An alternative is that plant-frugivore coevolution happens in pulses. Times of high environmental disturbances promote significant changes in mutualistic interactions and release new niche spaces for emerging species, which in turn exert stronger selective pressures and adaptive changes on fruit and frugivores traits. As those niches become occupied by evolving frugivores, interactions become more stable and coevolution is weak and diffuse. We are currently undergoing a new period of unstable plant-frugivore interactions and we need more information on plant-frugivore coevolution in order to predict how species will respond to a changing world.

Keywords: paleoecology; coevolution; mutualism; dispersal syndromes; fleshy fruits.

INTRODUCTION

Frugivory, or the interactions between fleshy fruits and frugivores, is a widespread biological process in nature. A wide range of plant families exhibit fleshy fruits and they may represent over 30% of the woody species in temperate forests and up to 90% in the tropical forests (Jordano 2017). These plants, in turn, are consumed by many vertebrate animals, including not only the three major extant frugivores, birds, bats and monkeys (Jordano 2017), but also rodents (Sunyer et al. 2013), elephants (Bunney et al. 2017), ungulates (Albert et al. 2015), carnivores (Corlett 2017), fishes (Correa et al. 2018), reptiles (de Miranda 2017) and many others. For instance, a single plant genus, *Ficus*, is supposed to be consumed by 10% of all bird species and 6% of all mammal species (Shanahan et al. 2001). Not only it is widespread, but frugivory also plays a pivotal role in sustaining and renewing biological populations because many frugivores are actually seed dispersers and carry seeds away from parental plants, thus increasing seedling survival and promoting the colonization of new sites (Jordano 2017). Fruits and seed dispersal, together with flowers and their interactions with pollinators, were two of the most important features that allowed the evolutionary success of angiosperms (Gómez and Verdú 2012).

Traditional theories on the evolution of plant-frugivore interactions were based on the theoretical framework developed for the study of pollination (Tewksbury 2002), and so they relied on the assumption that fleshy fruits evolved sets of traits that match the biology of their respective frugivores, through coevolution (Gautier-Hion et al. 1985). These sets of matching traits are known as fruit syndromes (van der Pijl 1969). For example, bird-dispersed fruits are often colorful because birds are visually-oriented while many mammal-dispersed fruits are dull-colored since many species forage using olfactory cues (Lomáscolo and Schaefer 2010). The assumptions underlying the dispersal syndromes has allowed ecologists to test hypotheses on plant-frugivore coevolution, but findings are often controversial (Renoult et al. 2014). Some studies found correlations between the traits of frugivores and those of the fruits they eat, thus suggesting coevolution (Schaefer et al. 2007; Lomáscolo et al. 2008; Lomáscolo and Schaefer 2010) but many others found strong phylogenetic signals in the distribution of fruit traits and question the ability of frugivores to exert sufficient selective pressure on them (Herrera 1998; Cazetta et al. 2012; Correa et al. 2015a; Valenta et al. 2018) (Valenta and Chapman 2018). For example, the evolution of dispersal syndromes would require consistent directional selective pressure, but very few animals are obligate frugivores and most of them only consume fruits opportunistically (Jordano 2017). As a consequence, plant-frugivores interactions, as well as the coevolution between them, are weak and diffuse (Herrera 1985; Bascompte and Jordano 2007). Under a diffuse coevolutionary process, the selective pressure exerted by many different frugivores would produce generalized sets of fruit traits (Valenta and Chapman 2018).

Coevolutionary hypotheses are hard to test, because they rely on a series of predictions that are often difficult to find in the fossil record (Althoff et al. 2014). However, a fundamental requirement of these hypotheses is the temporal congruence in species evolution and diversification, because the time scales of plant and animal evolution can be quite different and species cannot coevolve if they are temporally too far apart from each other (Valenta and Chapman 2018). Therefore, if the mechanism behind the changes in the diversity of plants and frugivores through time is mutual coevolution between them, we might expect to find evolutionary convergence in the timing of phylogenetic and ecological radiation of fleshy-fruited angiosperms and frugivores (Eriksson 2014).

Therefore, in this review we aim at discussing the evolution of the mutualism between fleshy-fruited angiosperms and frugivores. We do not intend to make an exhaustive review on the issue but rather focus on the timing of the evolution and diversification of these mutualisms and how angiosperms and frugivorous vertebrates responded to distinct selective pressures. Therefore, we address three major questions: 1) when did fleshy-fruited angiosperms originated and how did fruit traits evolved through time? 2) was there congruence in the timing of the evolution and radiation of fleshy fruits and their major extant frugivores? and 3) what role did mutualistic interactions play in the evolution of fleshy-fruited angiosperms and frugivores? Here we concentrate mainly on the interactions between fleshy fruits and birds, bats and monkeys, the three major groups of vertebrates that have been the most important seed dispersers after the peak in the diversification of fruit types in the Eocene up to the modern era. Moreover, throughout this review we use the term “fruit” in a broad sense, regarding its ecological and functional rather than its botanical definition, in order to include different kinds of diaspores that could be consumed by vertebrate frugivores.

ORIGIN AND EVOLUTION OF FLESHY FRUITS AND FRUGIVORES

Fleshy fruits

Defining the exact origins of fleshy-fruited angiosperms and the interactions with their seed dispersers is not an easy task because fruits are hardly well preserved in the fossil record (Colinvaux and De Oliveira 2001). Therefore, the endeavor of gathering evidences on angiosperm evolution and the traits of ancient fleshy fruits rely largely on records of fossil seeds, because these are often better preserved than soft tissues, and correlations with traits of extant lineages (Eriksson 2008). This is a trustworthy approach because in modern angiosperms there is a strong positive correlation between seed size and fruit complexity and, thus, paleobotanists are able to use seed size as a surrogate of plant diversity (Bolmgren and Eriksson 2010). Analogously, inferring plant-frugivore interactions from the fossil record relies on the same biological uniformitarism (Tiffney 2004).

The fossil record shows that the origin of angiosperms happened somewhere around 130Mya, between the Mid and Late Cretaceous (Soltis and Soltis 2004; Butler et al. 2009). Fleshy tissue around the seeds, however, appeared long before that and it can be found in some old lineages of gymnosperms (*e.g.* cycads, *Ginkgo* spp.) (Tiffney 2004). Notwithstanding, it was in angiosperms that fruit diversity met its evolutionary success, expressed as the vast number of extinct and extant families that possess fleshy fruits and depended, or depends, on biotic seed dispersal. It is widely accepted that fruits did not have had a single origin and that they evolved independently and convergently many times in the history of angiosperm evolution (Bolmgren and Eriksson 2010). For instance, in Rubiaceae, fruits have evolved at least 12 times independently (Kainulainen et al. 2010) and in Solanaceae capsular fruits and berries evolved independently in different lineages (Särkinen et al. 2013). Arguably, the mainstream hypothesis of the evolution of fruits assumes that they are adapted to attract seed dispersers, even if originally they may have had other functions (Mack 2000; Tiffney 2004).

By the time of the origin of angiosperms, fruits and seeds were very small and lacked specific adaptations to seed dispersers, and they remained relatively unchanged for the next 50Myr (McLoughlin and Pott 2018). This period (*i.e.* the Cretaceous) was marked by constant habitat disturbances which greatly influenced early angiosperm evolution. Dinosaurs, the largest herbivores of the Cretaceous, inflicted strong disturbances in the vegetation (Bakker 1978), just as modern large herbivores do (Omeja et al. 2014) and wildfires also had a significant impact on Earth ecosystems during the Cretaceous (Brown et al. 2012). These disturbances most likely set the evolutionary stage for primitive angiosperms, selecting for small, fast-growing plants with corresponding small fruits, more suited for disturbed habitats (Brodribb and Feild 2010). However, at approximately 80Mya, angiosperm seed size, fruit size and fruit type started to diversify (Bolmgren and Eriksson 2010). This radiation accelerated following the largest mass extinction event on Earth's history, which wiped out all nonavian dinosaurs at the end of the Cretaceous-Paleogene (K-Pg) boundary around 65Mya. Vegetation structure changed drastically and angiosperms experienced a diversification burst until the early Eocene, around 50Mya, when fruit diversity reached its peak (Brown et al. 2012) and all modern fruit types (dehiscent/indehiscent, dry/fleshy, apocarpous/syncarpous) were already set (Eriksson 2014). The transition between the Paleocene and the Eocene (~55Mya) as well as the early Eocene were marked by increases in Earth's temperature (Paleocene Eocene Thermal Maximum and early Eocene Climatic Optimum, respectively) (Smith et al. 2012) and during most part of this phase, the landscape changed and highly diverse subtropical to warm temperate angiposperm-dominated forests extended as far as the high latitudes in the northern hemisphere (Townsend et al. 2010). This changing environment provided new, unexplored niches for evolving organisms and marked the first stage of the evolution of plant-frugivore interactions.

The diversification of angiosperms during the late Cretaceous can be explained by, at least, three different processes (Eriksson 2014). The coevolution between new plants and animals (especially small mammals) emerging at the early Eocene could somehow have favored large seeds. Alternatively, the vegetation transition from open habitats to closed forests in the early Tertiary increased competition for light in the understory and larger seeds were probably better competitors in these environments due to their larger reserves (Tiffney 2004). Finally, the angiosperms evolving in the forests of the early Tertiary could have been taller than their ancestors in the late Cretaceous and, consequently, had also larger seeds that could not be dispersed abiotically. It is not yet clear, however, which of these processes was the main driver of angiosperms diversification (Fleming and Kress 2011), but it seems that plant size, seed size and biotic dispersal are coadapted traits that evolved together in the early Tertiary (Eriksson 2008).

This floral scenario remained until the Eocene-Oligocene transition (between ca. 34 ~ 33.5Mya), when Earth's environment suffered another drastic change, followed by the most significant mass extinction event since the end of the Cretaceous (Pound and Salzmann 2017). Earth became much cooler and the southern hemisphere became drier (Bowen 2007). Lower temperatures, associated with strong tectonics and sea-level fall (Pound and Salzmann 2017), changed plant diversity and the distribution of forests worldwide, with a pronounced contraction of tropical forests to low latitudes and the emergence of temperate forests in the northern hemispheres and grasslands at higher latitudes (Jaramillo et al. 2006). The large rainforests from the Tertiary were replaced by more open woodlands and savannas, with lower vegetation (Abello et al. 2018). In consequence of such massive changes in Earth ecosystems and the subsequent turnover in flora diversity, animal communities also experienced a significant transformation (Lindow and Dyke 2006; Buerki et al. 2013; Pound and Salzmann 2017). The most prominent frugivores of the late-to-mid Eocene, which included small browsers and arboreal forest-dwelling mammals went extinct, releasing niche space for other species to exploit, such as flying frugivores (Eriksson 2014).

We can summarize three major moments in the evolution of fleshy fruits that stands out in the history of angiosperms from the Cretaceous up to the Eocene-Oligocene transition in the Tertiary: *1)* an initial phase from the origins of angiosperms ca. 130Mya to approximately 80Mya, when fruits and seeds were small and lacked adaptations for seed dispersers; *2)* a radiation phase from 80Mya until the early Eocene (*ca.* 50Mya) when seed size and fruit diversity reached its peak, rainforests covered much of the Earth's land surface and the first groups of modern frugivores appeared; and *3)* a turnover phase following the Eocene-Oligocene transition, when tropical forests were replaced by temperate forests in the higher latitudes and the major lineages of extant frugivores evolved and diversified. In the next sections we will discuss the evolution of frugivores in each of these three moments and, finally, if they played any role in the evolution and diversification of fruit traits.

Frugivores

Vertebrate seed-dispersal is much older than the rise of fleshy-fruited angiosperms, going back 300 Myr (Tiffney 2004). For instance, herbivore dinosaurs possibly dispersed the seeds of cycads and conifers in the early Cretaceous (Fleming and Kress 2011). Even after the origin of angiosperms, many plant families evolved much earlier than their seed dispersers (Fleming and Kress 2011). However, these associations were rather fortuitous (Tiffney 2004) and, until the late Cretaceous fruits and seeds lacked adaptations for vertebrate seed dispersal, which only evolved during the radiation phase of angiosperms between 80Mya and the early Eocene (Eriksson 2008). Therefore, the evolution of 'legitimate' frugivory occurred only at the end of the first phase of angiosperm diversification (80~50Mya) (Eriksson 2014), and with a few exceptions frugivores only began to interact with fruiting plants after the latter had already evolved (Fleming and Kress 2011). For example, the most important modern frugivores, in terms of species richness, are arguably birds, monkeys and bats (Jordano 2017) an yet these vertebrates only became important seed dispersers long after the peak in angiosperm diversification in the early Eocene and especially during the Oligocene and the Miocene (34~10Mya), when many of the modern lineages of frugivores evolved (Fleming and Kress 2011).

Birds are the main consumers of fleshy-fruits and they interact with twice as many plant families than bats and monkeys (Fleming and Kress 2011). Frugivory can be found in all major clades of birds (Palaeognathae, Galloanserae and Neoaves) and it is supposed to have evolved multiple times in the group (Cracraft et al. 2003). Considering the representativeness of birds in the extant frugivore fauna, they were suggested to have laid the basis for the evolution of frugivory in other groups, especially euprimates (Fleming and Kress 2011), but this hypothesis does not find much support (Eriksson 2014). The first records of bird evolution date back to the Late Jurassic (Xu et al. 2014), but the major orders that include extant frugivores evolved much later, in the rapid diversification of the group following the mass extinction of the K-Pg boundary (Jarvis et al. 2014). Nonetheless, clear evidences of frugivory in birds just appeared in trogons of the early Eocene (Kristoffersen 2002). Furthermore, passerines, the most speciose order of birds which includes ca. of 60% of all living avian species and most of the frugivorous species, are even younger, dating back to the late Oligocene (Lindow and Dyke 2006, but see

Ericson et al. 2003 for a discussion on an earlier origin of passerines in Australia). Birds were the first frugivores to exploit a flying niche, which they would later share with bats, and it clearly provided them with many advantages, specially the ability to easily access a resource that became more patchily distributed in the late Eocene (Eriksson 2014).

Primates are the second most important seed dispersers and fruits are found in 91% of more than 504 living primate species (Lambert 2011). In the tropical forests, primates may represent 25% to 40% of all frugivore assemblages (Chaves et al. 2018). According to Sussman et al. (2013), euprimates (*i.e.* "primates of modern aspect") evolved in the Paleocene-Eocene transition (~55Mya), roughly at the same time of the first frugivorous birds. They were considerably fruit eaters, which can be attributed to early morphological adaptations (grasping feet, low-crowned molar teeth, orbital convergence) to a frugivorous diet (Bloch and Boyer 2002). Euprimates evolved in a very close relationship with fleshy-fruited angiosperms, because speciation and diversification rates were higher and extinction rates were lower in those lineages that established mutualistic interactions with fleshy-fruits (Gómez and Verdú 2012). The importance of these interactions for the evolution and diversification of euprimates is deeply expressed in the prevalence of fruits in the diets of most extant primates (Chapman and Dunham 2018).

Finally, bats belong to the second most diverse order of mammals, with *ca.* of 20% of all living mammal species. The two families in which frugivory evolved as the main feeding habit are the Pteropodidae (Old-World fruit bats), with 171 frugivorous species, and Phyllostomidae (leaf-nosed bats), with approximately 96 frugivorous species (Dumont 2003). Together, these two families account for over 350 species and nearly a third of all bat species (Rojas et al. 2012). The evolutionary history of bats is poorly understood because their fragile bones are hardly preserved in the fossil record and their phylogenies are conflicting (Jones et al. 2005). Nevertheless, the oldest known fossil bat (*Icaronycteris index*) is supposed to be at least 53 million years old (Simmons and Geisler 1998) and, thus, their origins can be traced back to the early Eocene. Many lineages of extant and extinct bats were already established by the middle Eocene, suggesting a rapid diversification of the group (Simmons 2005). However, unlike birds and primates, which already displayed frugivory by the early Eocene, the first bats were small and insectivorous (Simmons and Geisler 1998; Simmons and Conway 2003). Pteropodids diverged from this primitive ancestral lineage at sometime around 28 to 18Mya, in the Oligocene (Teeling 2005). Phyllostomid bats evolved in the early Oligocene

(30.8~33.3Mya) (Rojas et al. 2016), but frugivorous lineages evolved even later, during the late Oligocene and early Miocene (~20Mya) (Rojas et al. 2012; Baker et al. 2016). The congruence in the origins of frugivory in phyllostomids and pteropodids supports the hypothesis that global shifts in the distribution of tropical forests facilitated the evolution of frugivory in these two lineages (Baker et al. 2012). As for primates, the evolution of frugivory in bats opened new adaptive niches for the evolution of the group and has driven accelerated diversification within both phyllostomids and pteropodids (Dumont et al. 2012; Shi and Rabosky 2015).

CONVERGENCE IN THE TIMING OF THE ORIGINS OF FLESHY-FRUITED ANGIOSPERMS AND THEIR SEED DISPERSERS

All major extant frugivores, birds, monkeys and bats, evolved throughout the Eocene (55~34Mya) and later in the Oligocene/Miocene (34~10Mya), when angiosperm diversity was already high. However, seed size, fruit size and plant diversity started to increase much earlier, in the late Cretaceous, and continued to increase into the transition with the Tertiary (Bolmgren and Eriksson 2010; Eriksson 2014). This evidence suggests a mismatch of tens of millions of years in the timing of the evolution of modern seed dispersers and their core food plants (Fleming and Kress 2013). For example, the bat subfamily Stenodermatini is largely recognized as a specialist on fruits of Moraceae, especially *Ficus* (Sánchez and Giannini 2018). However, Stenodermatini evolved at 16.8Mya (Rojas et al. 2016), while *Ficus* is nearly 75 millions of years old (Särkinen et al. 2013). Altogether, these evidences imply that other groups of frugivores participated in the early phase of interactions with fleshy-fruited angiosperms.

Dinosaurs have been suggested as such frugivores (Bakker 1978; Barrett 2014), but there is considerable debate on this assumption, mainly because it is unlikely that these large animals relied heavily on the small fruits of early angiosperms (Butler et al. 2009). Fishes were among the first frugivorous of the Late Cretaceous, but their role on the evolution of fleshy fruits is still largely conjectural and, if at all, it was obviously restricted to wetland plants (Correa et al. 2015b, 2018). Some other animals, like small lizards (Olesen and Valido 2003) and marsupials (Tiffney 2004), were potential candidates of frugivores and dispersal agents of early angiosperms until the K-Pg boundary, but these animals were omnivorous and probably consumed only fruits occasionally (Tiffney 2004).

Notwithstanding, compelling evidences indicate that the most important early frugivores of fleshy fruits were the now-extinct plesiadapiforms and mainly the multituberculates (Eriksson 2014). Plesiadapiforms were primate-like arboreal mammals of the Paleocene (Bloch et al. 2007). Their fossil morphology suggest that they were omnivorous, but that they occasionally included fruits in their diet (Boyer et al. 2010; Chester and Beard 2012). Given that they were an abundant and highly diversified clade, they were probably casual seed dispersers of early angiosperms fleshy fruits. Likewise, multituberculates were small, rodent-like mammals that evolved in the middle Jurassic (~165Mya) and were the most successful lineage of mammals in the Mezosoic (Wilson et al. 2012; Yuan et al. 2013). Their unique dental complexity indicates that they had a high range of feeding habits, including carnivory, insectivory, omnivory, granivory and also frugivory, among others (Wilson et al. 2012). This group started to diversify around 20Mya before the K-Pg boundary, which coincides with the growing diversification of angiosperms and fruits, and they shifted toward a plant-dominated diet throughout the end of the Cretaceous and in the early Paleocene, at least partially due to the growing availability of new and unexplored plant-feeding niches (Wilson et al. 2012). The demise of plesiadapiforms and multituberculates by the Eocene released a frugivore niche space that was gradually occupied by the evolving lineages of modern frugivores (Boyer et al. 2012)

WHAT IS THE ROLE OF MUTUALISTIC INTERACTIONS IN THE (CO)EVOLUTION OF FLESHY-FRUITED ANGIOSPERMS AND FRUGIVORES?

Ecological interactions are one of the most powerful forces driving species coevolution (Thompson 1999; Hembry et al. 2014). For instance, interspecific competition is supposed to be one of the main causes of coevolutionary divergence among species (Connell 1980; Schluter 2010) and predation promote evolutionary diversification of both predator and prey species (Zu et al. 2016; Pontarp and Petchey 2018). On the other side, mutualistic interactions between animals and plants comprise some of the putative examples of species coevolution, such as yucca and yucca moths (Pellmyr and Leebens-Mack 1999), figs and fig wasps (Wiebes 1979), ants and myrmecophytes (Brouat et al.

2001) and many others. Despite being tightly related to coevolutionary processes, obligate mutualisms are relatively uncommon in nature and, therefore, the role of facultative mutualisms (*e.g.* plant-frugivore interactions) on species evolution is much less clear (Rojas et al. 2016). Several studies investigated how plant-frugivore mutualistic interactions contribute to the diversification in both plants and animals, but their findings are highly controversial (Eriksson 2008; Lomáscolo and Schaefer 2010; Lotan and Izhaki 2013; Nevo and Valenta 2018; Ramos-Robles et al. 2018b). From these divergent results, we can draw to main hypotheses concerning the evolutionary relationship between angiosperms and frugivores: the plant-frugivore coevolutionary hypothesis and the neutral hypothesis.

The neutral hypothesis arouse as the assumptions underlying the dispersal syndromes were rarely confirmed in the field (Valenta and Chapman 2018). Early studies on plant-frugivore coevolution hypothesized that dispersal syndromes would be a widespread phenomenon in nature (Tewksbury 2002), but they failed to support this hypothesis because tight associations between frugivores and fleshy-fruits are not common (Herrera 1985). In fact, most plant-frugivore interactions are weak and diffuse (Bascompte and Jordano 2007), *i.e.* plant and frugivores do not depend highly on each other and interact in a group-wise manner (Eriksson 2014). Consequently, any possible directional selective pressure exerted by a frugivore on a plant trait would be attenuated by other frugivores, which in turn would make paired coevolution between them unlikely (Bascompte and Jordano 2007). Diffuse coevolution is advantageous for fruiting plants because relying on multiple partners provides functional redundancy of seed dispersal services and promote its continuity even after the loss of one frugivore species (Rother et al. 2015).

There are considerable evidences supporting the neutral hypothesis of plant-frugivore evolution. To name only a few examples, the first phase of angiosperm diversification (80~50Mya) happened before, not rarely by a great amount of time, the origins of modern frugivores (Fleming and Kress 2011), and, thus, they can be excluded from any potential coevolution with early angiosperms (Eriksson 2014). Moreover, the astonishing diversity of fruit traits may be attributed to phylogeny (Valenta et al. 2018), climate (Buerki et al. 2013) and geographic distribution (Hampe 2003). Also, transformations of fruit types may not depend on strong selective pressure by frugivores because their ontogenies are very similar and can happen without major changes in their genetic structure (Seymour et al. 2013; Eriksson 2014). Some recent ecological studies using network approach added to the amount of evidences supporting the neutral hypothesis and demonstrated that many plant-frugivore interactions are randomly established, *i.e.* the probability of interaction between species is a product of their relative abundances (Fort et al. 2016).

Regarding the plant-frugivore coevolution hypothesis, despite the scarcity of evidences supporting strong correlations among fruit traits, many studies found that frugivores may influence at least some of them (Herrera 1985, 1998; Yoder and Nuismer 2010; Day and Kokko 2015; Brodie 2017). Fruit size is probably the example that stands out, because there is a significant trend towards a positive correlation between frugivores body size and fruit size, suggesting that the latter is an important feature mediating plant-frugivore interactions (Wheelwright 1985; Bach and Kelly 2004; Lord 2004; Burns 2013; Pires and Melo, unpub. data). For instance, Galetti et al. (2013) demonstrated that the loss of large-bodied frugivorous birds (*i.e.* toucans) led to a reduction of seed size of a keystone palm species in less than 100 years, and they suggested that human-induced defaunation of large frugivores may cause changes in the evolutionary trajectories of animals and plants. Other fruit traits, such as coloration, odor and display evolved as a response to the sensorial biology of frugivores (Lomáscolo et al. 2008; Lomáscolo and Schaefer 2010; Baker et al. 2012; Valenta et al. 2013; Stournaras and Schaefer 2016; Nevo and Valenta 2018). From the animal perspective, the evolution of specialized structures such as teeth morphology in mammals (Corlett 2017) and some bill shapes in birds (Jordano 2017) are also the outcome of directional selection towards frugivory. Moreover, despite the fact that extant frugivores only appeared after the origins of their plant resources, plant-frugivore interactions may have prompted diversification of bats (Rojas et al. 2012), primates (Gómez and Verdú 2012), birds (Kissling et al. 2009) and crown lineages of plans (Fleming and Kress 2011; Sánchez and Giannini 2018).

The large amount of credible evidence supporting either the plant-frugivore coevolutionary hypothesis or the neutral hypothesis may indicate that they are not mutually exclusive and advocate for the need of an integrative theoretical framework of the dynamics of angiosperm-frugivore evolution. In this sense, Eriksson (2014) proposed that the coevolution between fleshy-fruited angiosperms and frugivores occurs in pulses. According to this proposal, coevolutionary plant-frugivore interactions are stronger in periods of high environmental disturbances, *e.g.* climate change, orogeny, tectonics, species turnover, etc. These disturbances often promote significant changes in mutualistic interactions and release new niche spaces (*i.e.* ecological opportunity) for emerging species, which in turn exert stronger selective pressures and adaptive changes on fruit and frugivores traits (Eriksson 2014). This in accordance with paleontological evidence, because the phylogenetic radiation of modern frugivores happened after the mass extinction of the K-Pg boundary and converged with the peak of angiosperm diversification in the Eocene (Fleming and Kress 2011), and their ecological radiation happened throughout the drastic changes in the Eocene-Oligocene (Pound and Salzmann 2017) and the Oligocene-Miocene (Beddow et al. 2016). Moreover, considering that we are facing times of strong human-induced environmental changes and unparalleled rates of species loss (Barnosky et al. 2011), the hypothesis of pulses in coevolution can also explain why the evolutionary response of seed size to defaunation happened in such a short time (Galetti et al. 2013; Brodie 2017). These periods of strong coevolution between frugivores and fleshy-fruited angiosperms are interspersed by periods of more stable and weaker interactions, as the previously opened niches become saturated by evolving frugivores, decreasing subsequent co-diversification (Eriksson 2014; Price et al. 2016). The stability of plant-frugivore interactions undermines the strength of directional selective pressures, thus promoting diffuse, group-wise coevolution, rather than pairwise coevolution (Costa et al. 2018).

Eriksson (2014) argued that the first phase of angiosperm diversification from the Late Cretaceous to the Eocene (80~55Mya) may represent a long pulse of strong reciprocal coevolution between fleshy-fruits and the multituberculates and that since then coevolutionary pulses became more localized in space and time. He also suggests that we are currently undergoing a new period of unstable plant-frugivore interactions, which started with the extinction of large-bodied mammals in the Late Quaternary (Lorenzen et al. 2011). If this holds true, evolutionary information on plant-frugivore interactions can be used for conservational purposes as we can predict that fruit and animal traits will rapidly respond to the loss of interacting partners (Galetti et al. 2013). Therefore, future research will benefit as more refined phylogenies of fleshy-fruited angiosperms and frugivores become available, which will allow to test for taxon-specific patterns and identify more accurately when coevolution drives plant-frugivore interactions (Eriksson 2014)

CONCLUSIONS

The evolution of fleshy-fruited angiosperms marked a novel time in the history of life on Earth and, therefore, understanding the dynamics of plant-frugivore evolution is fundamental for the conservation of these mutualistic interactions in face of the severe environmental changes that threatens biodiversity worldwide. The dispersal syndromes hypothesis predicts that fruiting plants and frugivores coevolved, which can be observed by tight associations between their morphologies. Nonetheless, field studies only rarely find strong trait matching between them, casting doubt on coevolutionary interpretations of plant-frugivore interactions. Although birds, monkeys and bats, the three major extant frugivores, only evolved after angiosperm diversity was already high, there is considerable congruence on the radiation of many modern frugivore lineages and that of the plants they consume. These evidences suggest that angiosperm-frugivore coevolution may happen in pulses and that it is stronger in times when interaction networks face strong disturbances. This is of particular interest for biological conservation, because human activities are greatly impacting species interactions around the world, which can result in profound evolutionary consequences for biodiversity.

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CAPÍTULO II

SPECIES TRAITS EXPLAIN PAIRWISE INTERACTIONS BUT NOT THE AGGREGATE METRICS OF A PLANT-AVIAN FRUGIVORE NETWORK

SPECIES TRAITS EXPLAIN PAIRWISE INTERACTIONS, BUT NOT THE AGGREGATE METRICS, OF A PLANT-AVIAN FRUGIVORE NETWORK

Luís Paulo Pires and Celine de Melo

ABSTRACT

Interactions between plants and frugivores are important for the maintenance of biological communities, but it is still controversial if and how different factors contribute to the establishment of species interactions. This study investigated the role of trait-matching (temporal overlap and size constraint) and species relative abundance in determining pairwise interactions and the parameters of the network between birds and fresh-fruited plants in a semidecidual forest from the SE, Brazil. We used a likelihood approach and built probability matrices based on each factor and all possible combinations among them and compared these matrices with the frequency and structure of the observed network. We also investigated if pulp content and fruit color can influence species-level network metrics and species role in the observed network using generalized linear models. We found that biological constraints explain the detailed structure of the network, but they fail to predict aggregate network metrics, which are better explained by models that included abundance. A combination of fiber, lipids and water contents, explain plant species degree, strength and closeness centrality but none of fruit chemicals can explain their contribution to overall nestedness. Fruit color did not influence any species-level metrics. This study adds to the ongoing debate on the relative contribution of biological constraints and neutralism to the structure of biotic interactions and we demonstrated that the processes generating these interactions were based on rules defined by species traits, but the configuration of the network is defined by neutral processes. Therefore, our ability to understand patterns and processes in ecological networks, as well as species functional role, depends on combining both species traits and their relative abundances. We urge that researchers should be cautious when summarizing the complexity of ecological interactions into aggregate metrics that may not clearly reflect the processes responsible for generating them. How pervasive these results are among different mutualisms and at different regions is a promising avenue for future studies.

Keywords: ecological interactions; frugivory; graph theory; biological constraints; neutral theory.

INTRODUCTION

Interactions between flesh fruited plants and frugivores play a pivotal role in shaping, sustaining and renewing biological communities, especially in the tropics where up to 90% of angiosperms depend on frugivores to disperse their seeds (Fleming and Kress 2013). Over the last two decades, ecologists have unraveled and discussed the importance of many recurring and invariant patterns of plant-frugivore interactions using network approach (Vieira and Silva 1997; Bascompte and Jordano 2007; Ings et al. 2009; Carlo and Yang 2011; Pires et al. 2011; Guimarães and Deyn 2016; Jordano 2016; Delmas et al. 2018), such as their nestedness (Sebastián-González et al. 2015), modularity (Silva et al. 2016; Sebastián-González 2017; Ramos-Robles et al. 2018a), asymmetry and low degree of specialization (Schleuning et al. 2011; Fort et al. 2016). More recently, interest is focused in the mechanistic determinants of such patterns and species role in ecological networks (Dehling et al. 2016; Muñoz et al. 2016; Bender et al. 2018) and there is considerable debate on the relative importance of different drivers of species interactions in structuring biological networks (Vázquez et al. 2009a, b; García 2016).

Interactions between frugivores and fruiting plants may be determined by trait matching among species (*i.e.* complementarity between species morphology, phenology and spatial distribution). This deterministic paradigm states that frugivores interact with plants whose fruit characteristics match their morphology and behavior, whereas mismatches in corresponding functional traits impose exploitation barriers for interactions (*i.e.* forbidden links, Jordano et al. 2003; Olesen et al. 2011). For example, fruit size may limit the number of consumers that are efficiently capable of exploiting it (Wheelwright 1985; Burns 2013; Pires et al. 2015) and species only interact if they co-occur in space and time (Blendinger et al. 2016). Trait-mediated interactions have evolutionary and conservational implications, mainly if species depend highly on their counterparts (*i.e.* species strength; Bascompte and Jordano 2007), because the loss of phenotypic matching may cause the loss of pairwise interactions and/or distinct functional roles in species assemblages whenever morphological and functional specialization are related (Dehling et al. 2016).

Size-coupling is maybe the most widespread pattern in plant-frugivore interactions (Wheelwright 1985; Lord 2004; Flörchinger et al. 2010; Burns 2013; Pires et al. 2015; Guerra et al. 2017). Large gaped frugivores generally interact with a wider diversity of fruit sizes whereas narrow gaped frugivores are constrained to small-sized fruits (Bender et al. 2018). Therefore, the probability of a pairwise interaction between a frugivore and a plant is as high as the degree of size matching between gape and fruit size. Expectedly, size-structured networks are mainly nested, with large gaped generalist frugivores consuming a set of plant species with different fruit sizes and small gaped frugivores specializing in smaller fruits (Olesen et al. 2010). On the other hand, fruit size may only set a threshold on consumption and frugivores may forage randomly for fruits smaller than their gape width (Burns 2013). Furthermore, even small gaped animals can consume bigger fruits by crushing them or stretching their jaws (Kelly et al. 2010). Hence, the degree to size matching shape network structure is still a matter of further debate.

Moreover, interactions in seasonal habitats are highly dynamical (Jordano et al. 2003; Carnicer et al. 2009) particularly due to the phenological cycles of plants and animals (Plein et al. 2013; Gonzalez and Loiselle 2016). The timing of life history events such as fruiting and migration determine whether interactions can occur at all and, in many situations, may influence interactions quantitatively (Johansson et al. 2015b). For instance, when the interacting life-stage is long, species tend to interact with more partners, whereas short temporal availability of species generally produce only a few, already existing interactions (Yang et al. 2013). Also, frugivores may seasonally shift their diets according to the temporal availability of fruits (Carnicer et al. 2009; Yang et al. 2013) and the seasonal arrival of new species in the system may alter network structure (Ramos-Robles et al. 2016). Thus, species phenology is a major life-history trait that may influence plant-frugivore interactions and determine properties of ecological networks (Vázquez et al. 2009b; Yang et al. 2013; Johansson et al. 2015b; Gleditsch et al. 2017).

Fruit chemistry is also an important driver of plant-frugivore interactions (Herrera 1987; Lotan and Izhaki 2013; Blendinger et al. 2015). Water, carbohydrates, lipids, proteins and fibers are important fruit contents that avian frugivores need for migration (Smith et al. 2007), reproduction and molting (Moermond and Denslow 1985; Walker et al. 2014), and pulp composition varies widely among different plant species (Blendinger et al. 2016). To the extent of our knowledge, so far only a few, very recent studies investigated if and how the chemical compounds of fruits shape plant-frugivore networks (González-Castro et al. 2015; Ramos-Robles et al. 2018a, b), hence it still remains unclear whether fruit chemistry alone is an structuring feature in trait-mediated networks.

Network properties, however, can also be generated by random interactions among species, a neutral process of network assembling (Burns 2006; Vázquez et al. 2009a). Neutrality is an evolutionary-free hypothesis that assumes that species are functionally equivalents and that the likelihood of interactions between plants and frugivores is proportional to their relative abundances, *i.e.* abundant species are likely to be more connected than rare ones, because random encounters between common species happen more frequently (González-Castro et al. 2015; Fort et al. 2016). Thus, it is expected that differences in species abundances would affect aggregate network properties such as connectance, nestedness and interaction strength (Burns 2006; Krishna et al. 2008; Vázquez et al. 2009a; Fort et al. 2016).

Nonetheless, deterministic and neutral processes are not mutually excludents and may work simultaneously in network assembling (Vázquez et al. 2009a). Extensive studies which evaluated both hypothesis demonstrated that some metrics (*e.g.* connectance and nestedness) are best predicted when neutrality and trait matching are considered together (González-Castro et al. 2015; Minoarivelo and Hui 2015; Olito and Fox 2015; Sebastián-González et al. 2015). In order to assess the relative importance of each mechanism, Vázquez et al. (2009b) developed a conceptual framework that compares how well hypothetical networks assembled by different predictors (*e.g.* size and temporal overlap, abundance, etc.), as well as combinations between them, explain topological properties of the observed network (but see Olito and Fox 2015, for a discussion on the limitations of the framework). This approach has been used to unravel drivers of network architecture mainly in plant-pollinator interactions (Vizentin-Bugoni et al. 2014; Olito and Fox 2015; Fort et al. 2016; Gonzalez and Loiselle 2016), but up to date no other study has applied this framework in other kinds of mutualisms, such as plant-frugivore interactions.

Our aim was to investigate the relative role of size, phenological coupling, fruit chemistry and species abundance in shaping the structure of an interaction network between frugivorous birds and plants, to explain whether these interactions are assembled by deterministic or neutral processes, or a combination of both, using the conceptual framework of Vázquez et al.(2009b) and generalized linear models. We asked the following questions: 1) is abundance more important than species traits in determining pairwise interactions and network parameters (*i.e.* connectance, nestedness, modularity and species strength); 2) does fruit color and the contents of water, lipids, carbohydrates and proteins in fruit pulp predict-species level network metrics?

METHODS

Study site

The study was conducted in the semidecidual forest of Fazenda Experimental do Glória (FEG: 18.95ºS, 48.20°W) from July 2015 to June 2017. The forest has ~30 ha and is surrounded by a gallery forest, pastures and crops (see Lopes et al. 2011, for a detailed description of the area). The climate is markedly seasonal, with a dry winter (April to September) and a rainy summer (October to March) (Bueno et al. 2018).

Fruits abundance, morphology, phenology and nutritional compounds

In this paper, we use the term “fruit” in a broad sense, regarding what is actually eaten by the frugivores (*i.e.* diaspore) rather than its botanical definition. We counted the number of individuals (D) of each plant species with ornitochorical fruits (*sensu* Fleming and Kress 2013) along a 450m x 5m transect. From each species recorded, we selected five individuals and every 15-20 days we counted the number of ripe fruits if plants had less than 100 fruits or estimated it by multiplying the number of fruits in a single branch by the number of branches in the plant (Melo et al. 2013). We then calculated the mean number of mature fruits (n) per individual/month. The relative fruit abundance (F_{rel}) of species i was defined as: $Di\ x\ ni/\sum_{j}^{i}(Di\ x\ ni)$. The length of the fruiting season (l) of each species was defined as the number of months that at least one individual displayed mature fruits.

We also measured eight variables for each plant species: fruit size (width, mm), fresh fruit weight (g), hue (nm - wavelength at reflectance midpoint), and the contents of water (%), lipids (% of dry mass), proteins (% of dry mass) and carbohydrates (% of dry mass). For measurements of fruit size and weight, we used 10 fruits of each species. Fruit size was measured using a digital caliper (0.01mm) and fruit weight was measured in an analytical balance (0.001g). Reflectance spectra of each species were calculated using a spectrophotometer (Jaz, Ocean Optics Inc., Dunedin, FL, U.S.A.) between 300–700 nm, which corresponds to the visible spectrum for birds (Hart 2001). We measured the reflectance spectra of five fruits of each species inside a black box. We measured reflectance as the proportion of a standard white reference tile (WS-1-SS; Ocean Optics, Dunedin, FL, U.S.A.). The distance between the fruit and the optical sensor was held constant for all measurements and the angle of illumination and reflection was set at 45°. All reflectance measurements were processed with SpectraSuite® software. We derived the mean hue for each species using function *summary.rspec* in *pavo* package (Maia et al. 2013). Chemical analyses of fruits were conducted at LaborNutri© (http://www.labornutri.com.br/). Humidity was determined as the difference between dry fruit weight (g) and fresh fruit weight. Protein content was measured with Kjeldahl method and lipids with Soxhlet extraction with hexane. Fibers were defined by acid detergents. After defining these contents, carbohydrate was determined as the remaining dry fruit weight:

$$Carbohydrates \ = 100 - water - lipids - proteins - fibers$$

Birds phenological and morphological traits

To estimate the abundance of bird species, we randomly established 10 observational points of 10m radius along small trails in the area, distant at least 150m from each other (adapted from Burns 2005). Each point was visited for 10 min from 06h00 to 12h00 twice per month. Every frugivorous birds seen or heard within each point during observations were recorded. We waited five minutes after arrival in each point to start counting birds to avoid oversampling individuals that moved from one point to the next. Bird abundances were defined as the mean number of individuals from each species registered per month. Bird species spotted interacting with fruiting plants were not accounted in abundance measures, to avoid sampling redundancy (Krishna et al. 2008). We measured gape width (mm - the width across the outside of the bill at the base of the upper mandible) from three specimens of each species deposited in the Coleção Ornitológica Marcelo Bagno from University of Brasília.

Plant-frugivore interactions

We recorded interactions between birds and plants through focal observation of fruiting individuals (260h, 20h/plant species) from 06h00 to 12h00. We stood at ~10m distant from each focal plant and recorded every bird that approached it. We only started recording interactions one minute after arrival on focal plant to minimize the influence of the observer presence on bird behavior. Each different approach that resulted in a fruit being eaten (whole or in pieces) was considered a single record. From these observations, we constructed a bipartite interaction matrix (*O*) in which each cell *oij* was the number of fruits that bird species *i* consumed from plant species *j*. We conducted a rarefaction analysis based on links in the network in order to estimate sampling sufficiency using function *ChaoSpecies* on *iNext* package.

Network determinants: constructing interaction probability matrices

We constructed different interaction probability matrices of the same size as *O* which assumed that network structure was determined by the relative abundance (*A*), size-coupling (*S*) and temporal overlap among species (*T*), following Vázquez et al. (2009b).

In the abundance probability matrix (*A*) the likelihood of species interactions *aij* is the product of the relative abundances of bird *i* and plant *j* (Vizentin-Bugoni *et al.* 2014). The size-matching probability matrix (*S*) was constructed so that species would only interact if fruits were less than 1.5 times the size of the gape width of birds**.** We did not constrain fruit size to exactly match gape width in order to consider intraspecific variation in bill morphology and also to consider some elasticity of the commissure. If this requirement was met, then the likelihood of species interactions *sij* was the proportion fruit size *i* / gape width *j*.. We developed the temporal overlap probability matrix (*T*) so that each cell entry *tij* was the number of months that bird species *i* co-ocurred with mature fruits of plant species *j*. We normalized matrices *A*, *S* and *T* by dividing each cell by the sum of the matrix.

We also constructed probability matrices based on the joint influence of all possible combinations of *A, S* and *T*. For instance, matrix *AS* denotes the combined effects of abundance and size, so that the likelihood of interactions is proportional to species relative abundances given the constraint imposed by size. Each cell entry in the combined matrices *AS*, *AT*, *TS* and *ATS* was calculated by the Hadamard product of the corresponding matrices. We normalized all matrices as done for each one of them individually. Finally, we constructed a null model (*Null*) in which all species had the same probability of interactions (*i.e.*, all cell values in the matrix are equal to 1/*ij*, where *i* and *j* are the number of bird and plant species in the observed matrix, respectively)

The ability of probability matrices to predict pairwise interactions

To evaluate the relative contribution of species traits and neutrality to the structure of the observed network (*O*), we mostly followed Vázquez et al. (2009b) and used a likelihood approach in which the best predictors are those probability matrices whose highest scoring cells match the cells with higher number of interactions in the observed matrix. For that, we assumed that the probability of interaction between an avian frugivore and a plant followed a multinomial distribution. However, unlike Vázquez et al. (2009b), we defined the number of species in each probability matrix as the number of parameters used to weight different models' complexities, which is more conservative than using the number of matrices in the model (Vizentin-Bugoni et al. 2016). Therefore, models with a single predictor (*Null*, *A, S, T*) had 38 parameters each (25 bird species and 13 plant species); models with two predictors (*AS, AT* and *TS*) had 76 parameters and the full model (*ATS*) incorporated 114 parameters. We calculated the Akaike Information Criteria (AIC) for each matrix as AIC = L - 2*k*, where *k* is the number of parameters used in each model. Then, we defined the AIC of the best-fitting probability matrix as 0 and compared it with other models using ΔAIC.

Network metrics

We assessed network properties using five aggregate metrics: connectance, specialization, interaction evenness, interaction asymmetry (for plants and birds separately) and weighted nestedness. Connectance is the proportion of all possible interactions that actually occur and varies from 0 when there are no interactions in the network to 1 when each single species is linked to every other species (García 2016). We measured specialization at network level using H2’ index (Blüthgen et al. 2006), which ranges from 0 when interactions are generalized to 1 when there is a high degree of specialization. In bipartite networks, interaction evenness measures the distribution of interactions, so that a high skewed distribution indicates an uneven network. We calculated interaction evenness following Tylianakis et al. (2007). Interaction asymmetry quantifies the strength (dependency) of the interaction from one side to the other of the network and it ranges from -1 when resources are completely dependent on specific consumers to 1 in the opposite situation. Interaction asymmetry was calculated separately for birds and plants following (Vázquez et al. 2007). Nestedness is a network property in which most links are concentrated in a group of generalist species that interact among themselves, whereas low connected species form a subgroup of interactions inside the first group. It was calculated using weighted nestedness (WNODF) proposed by (Almeida-Neto et al. 2008). WNODF varies from 0 to 100 (totally nested networks). Metrics were calculated using function *networklevel* and *specieslevel* in package *bipartite*.

The ability of probability matrices to predict aggregate network metrics

To test the degree to which our models predict network metrics, we generated 1000 randomizations of each model (*Null, A, S, T, AS, AT, TS* and *ATS*) of the same size of *O* (467 interactions) using *mgen* function in *bipartite* package, constraining all species to receive at least one interaction (Vázquez et al. 2009b). We calculated the mean and 95% confidence interval of connectance, H2’, interaction evenness, asymmetry and WNODF of all generated networks and considered that predictors could explain the corresponding observed metrics calculated from *O* whenever we found overlap between them. Comparisons were computed using function *confint* in *bipartite*.

The contribution of fruit colour and pulp content on plant-level networks statistics

In addition to the metrics at network levels presented so far, we asked whether and how fruit traits can influence plant species roles in the observed network. We constructed generalized linear models (GLM) in order to determine if color and nutritional content of fruits (*i.e.* water, protein, fibers, lipids and carbohydrates) can affect plant species degree, species strength, nested contribution and closeness centrality (CC). Degree is the number of observed links (interactions) of a node (Dormann, 2011). Species strength is the sum of the dependencies of each species across all its counterparts, *i.e.* it measures the importance of a species to their partners (Ramos-Robles et al. 2018). Nested contribution measures how much each plant species contribute the nested pattern of the network (Ramos-Robles et al. 2018). CC is an index that measures the proximity of a node to all other nodes in the network (Dormann, 2011). For each response variable, we defined a full model that contained all fruit traits and then built several models with all combinations among them. All models were built using function *dredge* in R package *MuMln* and compared by their values of the AIC, while corrected for small sample sizes. We reported only the models with ΔAICc ≤ 2.

RESULTS

Birds and plant species in the FEG

We observed 25 bird species (7 families) consuming fruits of 13 plant species (10 families) in the FEG (Appendix 1). Fruits were a year-round resource and for most months (21, 75%) at least two plant species could be found fruiting simultaneously (Table 1). *Psychotria prunifolia* was the most abundant plant species, but *Nectandra membranacea* was the plant with the highest fruit abundance per individual and also the most visited (Table 2). Mean fruit size was 7.27mm (range: 4.01mm – 10.21mm) and mean fruit weight was 0.20g (range: 0.03g – 0.66g). Fruits of bird-dispersed plants exhibited a wide variety of color displays, such as black (*e.g. Miconia* spp.), white (*Protium* spp.) and multicolored (*Siparuna guianensis*). The contents of fruit pulp from different species varied, but for all species water (57.57% of fruit weight, range: 35.44% – 84.77%) and carbohydrates (31.21% of fruit weight, range: 7.70% - 53.25%) were the main contents of fresh fruits (Table 2).

We recorded 944 individuals from 25 bird species (Table 3). From these, only *Antilophia galeata* was the most abundant species, with 402 recordings (42.58%). Most species (76.00%) counted less than 15 encounters. Bill size ranged from the small gaped *Dacnis cayana* (4.80mm) to the very large gaped *Ramphastos toco* (33.27mm) (Figure 1).

Table 1. Fruiting phenology of plants consumed by frugivorous birds in the Fazenda Experimental do Glória, SE Brazil. Black filled cells are months in which at least one individual of the species presented ripe fruits.

Species	2015					2016												2017					
	Aug	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**
Siparuna guianensis		■	■	■	■	■	■	■	■									■	■	■			
Miconia affinis		■		■	■	■	■	■	■							■	■	■					
Rubiaceae sp1	■	■	■							■	■	■	■	■	■	■							
Nectandra membranacea			■	■	■							■	■	■	■	■	■	■					
Miconia nervosa		■	■	■	■	■							■	■	■	■							
Protium heptaphyllum				■	■	■								■	■	■	■	■					
Psychotria prunifolia										■	■	■	■	■								■	■
Cardiopetalum calophyllum																			■	■	■	■	
Protium ovatum														■	■	■	■						
Birsonima intermedia																			■	■	■		
Virola sebifera														■	■								
Aegiphilia sp.																			■	■			
Mataiba guianensis																		■	■				

Table 2: Fruit traits of plant species consumed by birds in the Floresta Experimental do Glória, SE Brazil. ***n***: mean number of fruits per individual/month; ***D***: number of individuals; **F_{rel}:** relative fruit abundance; ***l***: mean length of the fruiting season.

Family	Species	Visits (%)	*n*	*D*	*Frel (%)*	*l (months)*	Fruit width (mm)	Weight (g)	Hue (nm)	Water (%)	Protein (%)	Lipid (%)	Carbohydrates (%)
Annonaceae	*Cardiopetalum calophyllum*	4.92	1672.05	3	2.79	4	7.26	0.11	519	35.44	1.73	1.09	53.25
Burseraceae	*Protium heptaphyllum*	9.02	1027.66	5	2.86	5	10.21	0.11	368	54	1.24	1.65	34.76
	Protium ovatum	0.41	66.33	1	0.04	4	10.61	0.03	368	70	1.77	1.76	19.24
Lamiaceae	*Aegiphila* sp.	2.05	1297.50	1	0.72	2	8.31	0.24	579	56.3	5.00	1.00	28.03
Lauraceae	*Nectandra membranacea*	22.75	5398.05	10	30.00	7	6.62	0.05	388	60	5.60	0.78	30.68
Malpighiaceae	*Birsonima intermedia*	1.64	267.27	3	0.45	3	9.27	0.04	680	58	2.19	1.65	30.5
Melastomataceae	*Miconia affinis*	8.20	1637.59	21	19.11	8	5.28	0.13	374	76	3.00	0.65	16.63
	Miconia nervosa	3.28	3.18	38	0.07	6	6.26	0.21	687	84.77	1.32	1.76	7.70
Myristicaceae	*Virola sebifera*	3.69	367.00	2	0.41	2	10.21	0.17	613	36	2.34	2.54	50.57
Rubiaceae	*Psychotria prunifolia*	9.43	56.73	370	11.67	6	6.61	0.61	609	65.53	6.39	1.34	23.09
	sp. 1	15.16	238.88	92	12.21	8	4.01	0.17	374	61	4.55	2.04	29.33
Sapindaceae	*Mataiba guianensis*	8.61	138.00	10	0.77	2	9.27	0.13	519	45.77	4.34	3.00	41.56
Siparunaceae	*Siparuna guianensis*	10.86	508.05	67	18.92	8	10.49	0.66	498	45.67	7.90	1.78	40.35

Table 3. Monthly occurrence of fruit-eating bird species from Fazenda Experimental do Glória, SE Brazil, from August 2015 to July 2017.

Family	Species	Abundance	Relative Abundance	2015					2016													2017					
				Ago	Set	Out	Nov	Dez	Jan	Fev	Mar	Abr	Mai	Jun	Jul	Ago	Set	Out	Nov	Dez	Jan	Fev	Mar	Abr	Mai	Jun
Icteridae	*Icterus pyrrhopterus*	9	0.010																		■	■	■			
Mimidae	*Mimus saturninus*	3	0.003														■									
Pipridae	*Antilophia galeata*	402	0.427	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
Psitacidae	*Forpus xantopterigius*	2	0.002								■															
Ramphastidae	*Ramphastus toco*	24	0.025	■		■		■				■			■		■	■	■	■	■	■	■	■	■	■
Thraupidae	*Dacnis cayana*	16	0.017		■	■					■										■	■		■		
	Saltator maximus	14	0.015												■		■			■		■	■	■	■	■
	Saltator similis	111	0.118	■	■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	■	■	■	■		
	Tangara cayana	102	0.108	■	■	■		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
	Tangara palmarum	7	0.007		■										■	■	■									■
	Tersina viridis	19	0.020		■	■										■		■	■			■				
	Tangara sayaca	5	0.005												■		■		■			■				
	Pipraeidea melanonota	2	0.002														■									
Turdidae	*Eucometes penicillata*	2	0.002					■												■						
	Nemosia pileata	10	0.011			■					■		■				■					■				
	Turdus leucomelas	83	0.088	■	■	■	■	■		■	■		■		■	■	■	■	■	■	■	■	■	■	■	■
	Turdus rufiventris	34	0.036		■		■								■		■	■	■		■			■		
Tyrannidae	*Myarchus ferox*	10	0.011								■	■					■					■	■	■		
	Elaenia sp.	11	0.012								■										■	■			■	
	Megarhynchus pitangua	46	0.049															■	■	■	■	■	■	■	■	
	Tyrannus savana	1	0.001																■							
	Myiozetetes similis	13	0.014																			■	■	■		
	Pitangus sulphuratus	8	0.008																				■	■	■	
	Tyrannus melancholichus	6	0.006																			■	■		■	
	Suiriri suiriri	2	0.002	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-	-	-

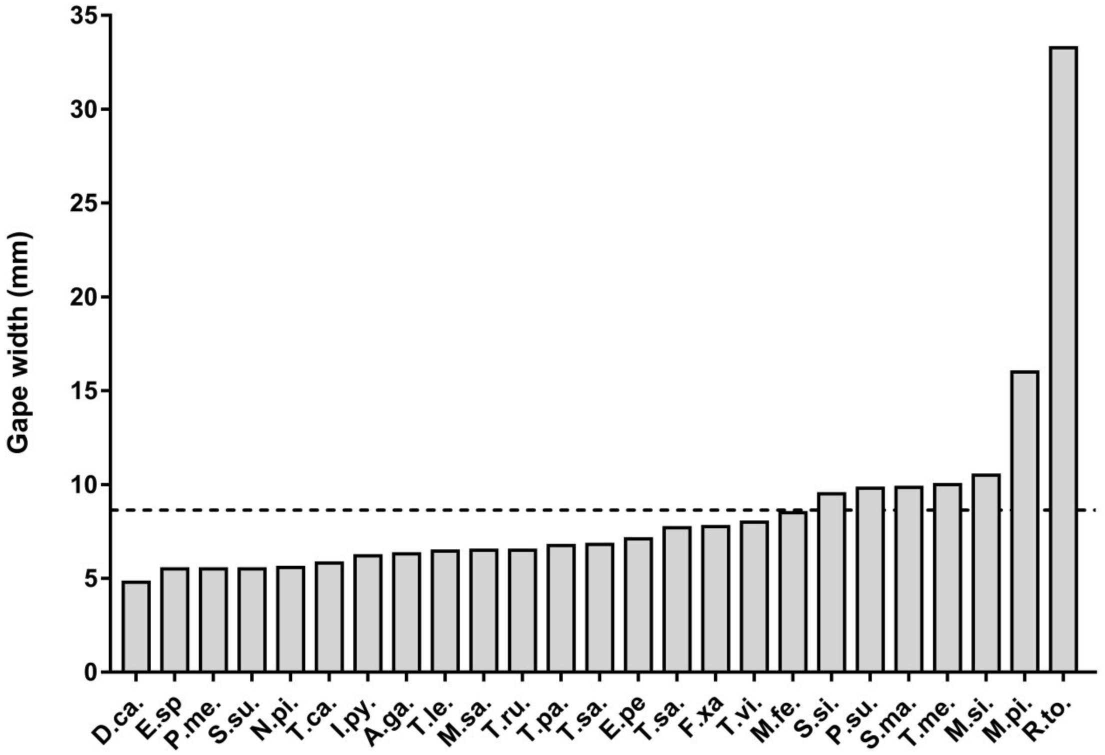

Figure 1. Gape width of 25 bird species recorded consuming fruits in the Fazenda Experimental do Glória, SE Brazil. Dashed line is the mean fruit size. Full species names are given in Appendix 1.

Pairwise interactions and aggregate network metrics

We recorded 467 interactions between birds and fresh-fruited plants in the FEG (Figure 3), which represents *ca.* 77% of the estimated interactions in the area. *A. galeata* was the bird species which had the highest number of interactions (237, 50.75%) with most plant species (10, 76.92%) (Figure 2). The observed network had many fewer interactions than possible (connectance = 0.23) and it was slightly more nested than expected by chance (WNODF = 23.95). Moreover, it was moderately specialized (H2' = 0.43) and highly uneven (0.61).

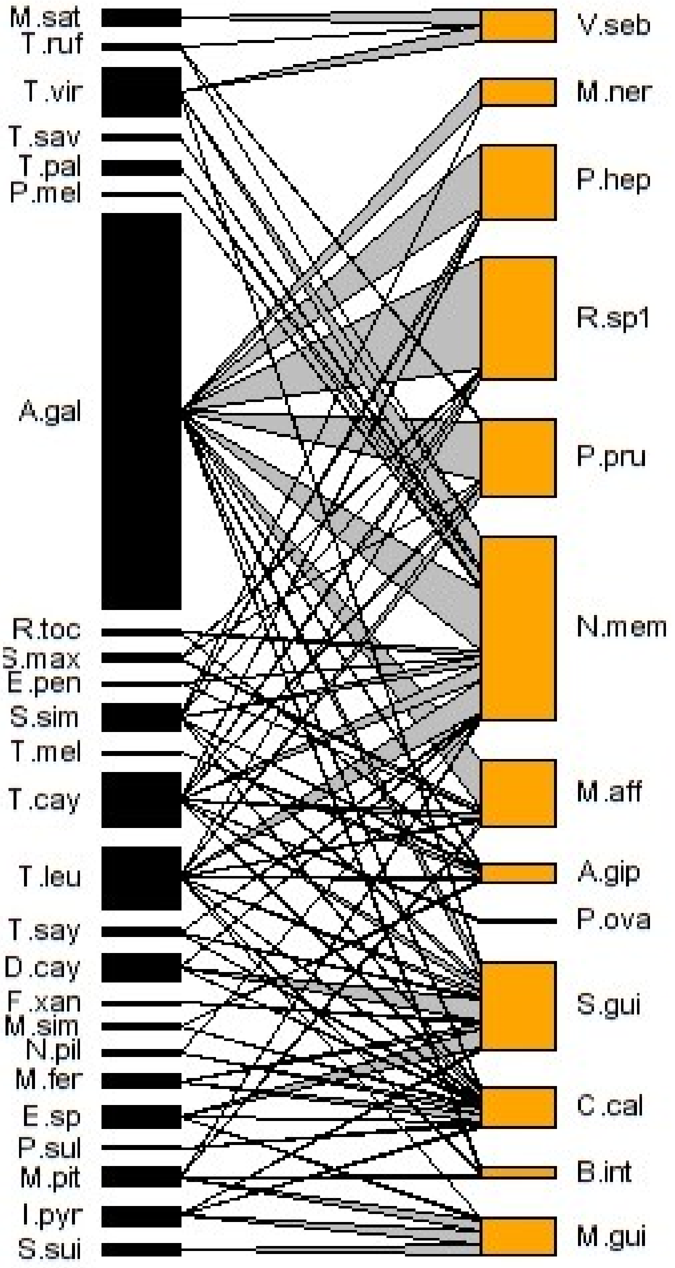

Figure 2. Interaction network between fruit-eating birds (black boxes) and plants (orange boxes) in the Fazenda Experimental do Glória, SE Brazil. Grey lines pairwise interactions and the thickness of the line represents the frequency of interactions. species names are given in Appendix 1.

Temporal overlap and size-matching between pairs of species were the most important drivers of the frequency of observed interactions. The model which had the best fit was the one that combined temporal overlap and size-matching (*TS*), followed by the models based solely on temporal overlap (*T*) and size matching (*S*), respectively. The explanatory power of each model declined when relative abundance of species was added as a factor.

Consequently, the probability matrix based on the relative abundance alone had the worst fit to the observed network (Figure 3).

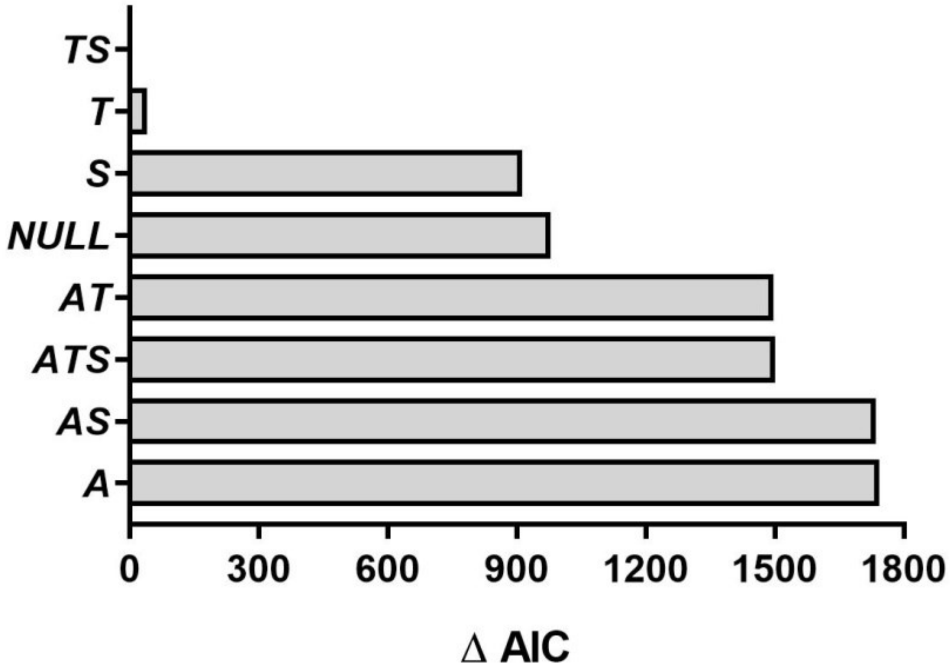

Figure 3. ΔAIC values of the predictors (probability matrices) of the observed interactions between fruit-eating birds and plants in the Fazenda Experimental do Glória, SE Brazil. NULL: same probability of interactions; A: abundance; T: temporal overlap; S: size-matching and all combinations among them (AT, AS, TS, ATS). The best fitting model (TS) is set at ΔAIC = 0.

In general, aggregate network metrics were poorly explained by size-matching and temporal overlap (Figures 4a-4f). Exception is made for nestedness, which was best predicted by the null model and the model including only size-matching (Figure 4b). On the other hand, models including species relative abundance were good predictors of connectance, interaction evenness and interaction asymmetry for birds, although this latter was explained by the model that also included size-matching (Figure 4a, 4c and 4f). None of our models were capable of accurately predict network specialization and the asymmetry of interactions for plants (Figures 4d-4e).

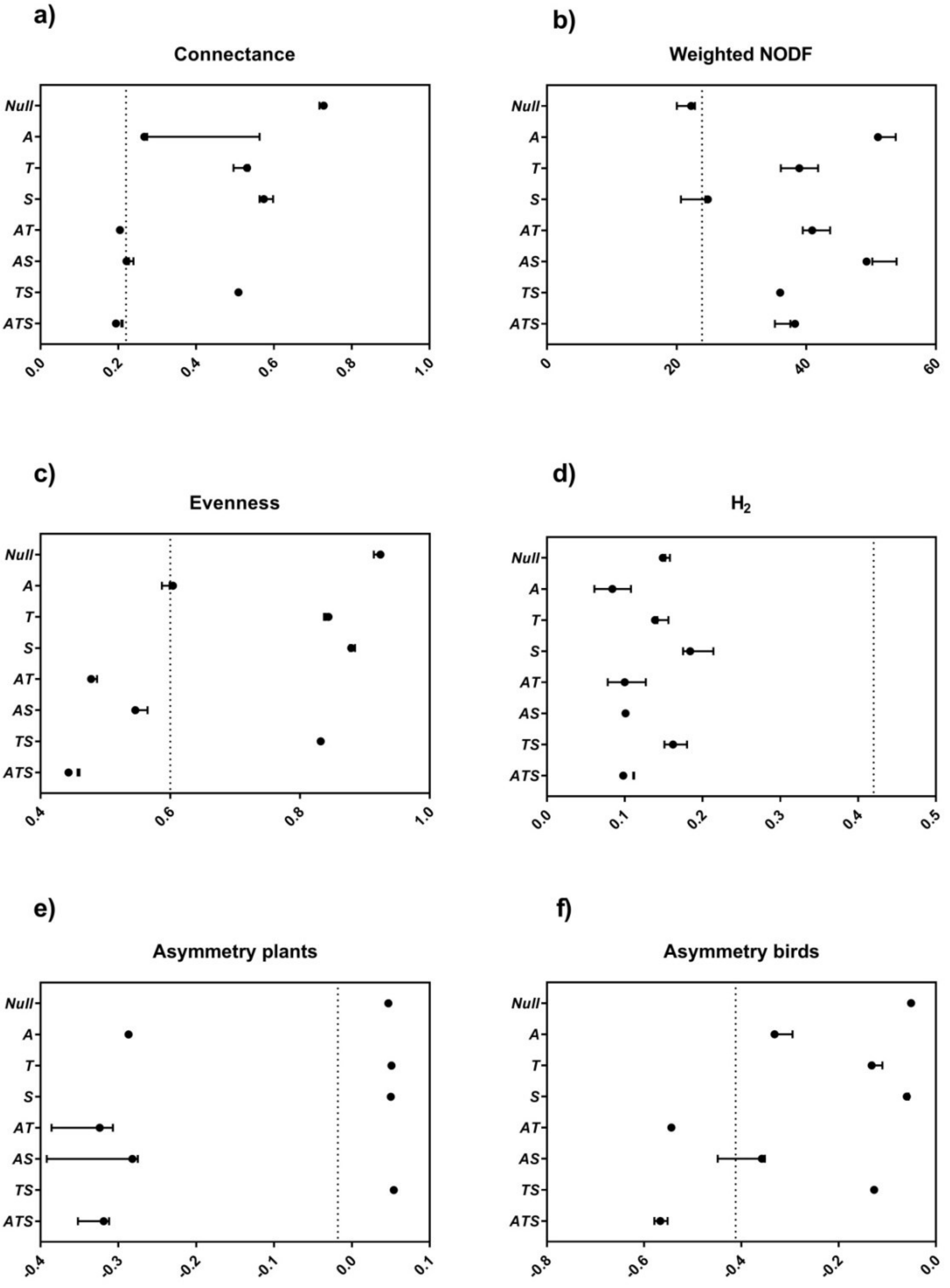

Figure 4. Comparisons between values of aggregate network statistics (mean and 95% confidence interval) of the randomizations of the probability matrices and the observed values (dashed vertical lines inside boxes) in the Fazenda Experimental do Glória, SE Brazil. A model is able to predict the structure of the observed network when there is overlap between the predicted and the observed values. *NULL*: same probability of interactions; *A*: abundance; *T*: temporal overlap; *S*: size-matching and all combinations among them (*AT*, *AS*, *TS*, *ATS*).

Species-level network metrics

N. membranacea was the plant with the highest number of interacting partners (*i.e.* species degree), the one that most contributed to network nestedness and it also had the highest species strength (Table 4). The number of interacting partners and species strength were influenced by pulp content (Table 5). Species degree and strength were negatively affected by a combination of fiber, lipid and water content (Figure 5). Fibers also negatively affected closeness centrality. None of the fruit traits were able to explain the contribution of plant species to the overall observed nestedness. Carbohydrates and fruit color, in turn, did not play any role in the determination of species-level parameters.

Table 4. Species-level metrics of plants consumed by avian frugivores in the FEG, SE Brazil.

Family	Species	Degree	Species strength	d'	Nested contribution	Closeness centrality
Annonaceae	*Cardiopetalum calophyllum*	*12*	*3.96*	*0.42*	*0.86*	*0.04*
Lamiaceae	*Aegiphila*sp.	*6*	*1.83*	*0.47*	*0.42*	*0.02*
Burseraceae	*Protium heptaphyllum*	*3*	*0.45*	*0.21*	*1.05*	*0.09*
	Protium ovatum	*1*	*0.06*	*0.42*	*0.87*	*0.01*
Lauraceae	*Nectandra membranacea*	*15*	*7.27*	*0.25*	*2.79*	*0.12*
Malpighiaceae	*Birsonima intermedia*	*3*	*0.25*	*0.17*	*1.12*	*0.02*
Melastomataceae	*Miconia affinis*	*6*	*1.55*	*0.16*	*0.73*	*0.08*
	Miconia nervosa	*2*	*0.13*	*0.12*	*1.06*	*0.04*
Myristicaceae	*Virola sebifera*	*3*	*1.64*	*0.79*	*-0.50*	*0.03*
Rubiaceae	*Psychotria prunifolia*	*5*	*0.94*	*0.15*	*0.92*	*0.09*
	sp. 1	*5*	*0.70*	*0.25*	*1.67*	*0.12*
Sapindaceae	*Mataiba guianensis*	*5*	*2.38*	*0.81*	*0.32*	*0.02*
Siparunaceae	*Siparuna guianensis*	*11*	*3.84*	*0.41*	*1.66*	*0.07*

Table 5. AIC value and statistics of the best models generated by GLMs regarding the influence of pulp composition on species-level network parameters. FIB = fibers, LIP = lipid, WAT = water, INT = intercept.

Response variable	Predictors	AIC	R^2	F	P
Degree	LIP + WAT + FIB	69.27	0.76	13.99	<0.05
Species strength	LIP + WAT + FIB	58.65	0.56	2.96	<0.05
Closeness centrality	FIB	-45.36	0.29	5.99	<0.05
Nestedness contribution	INT	34.50	0.56	3.56	0.07

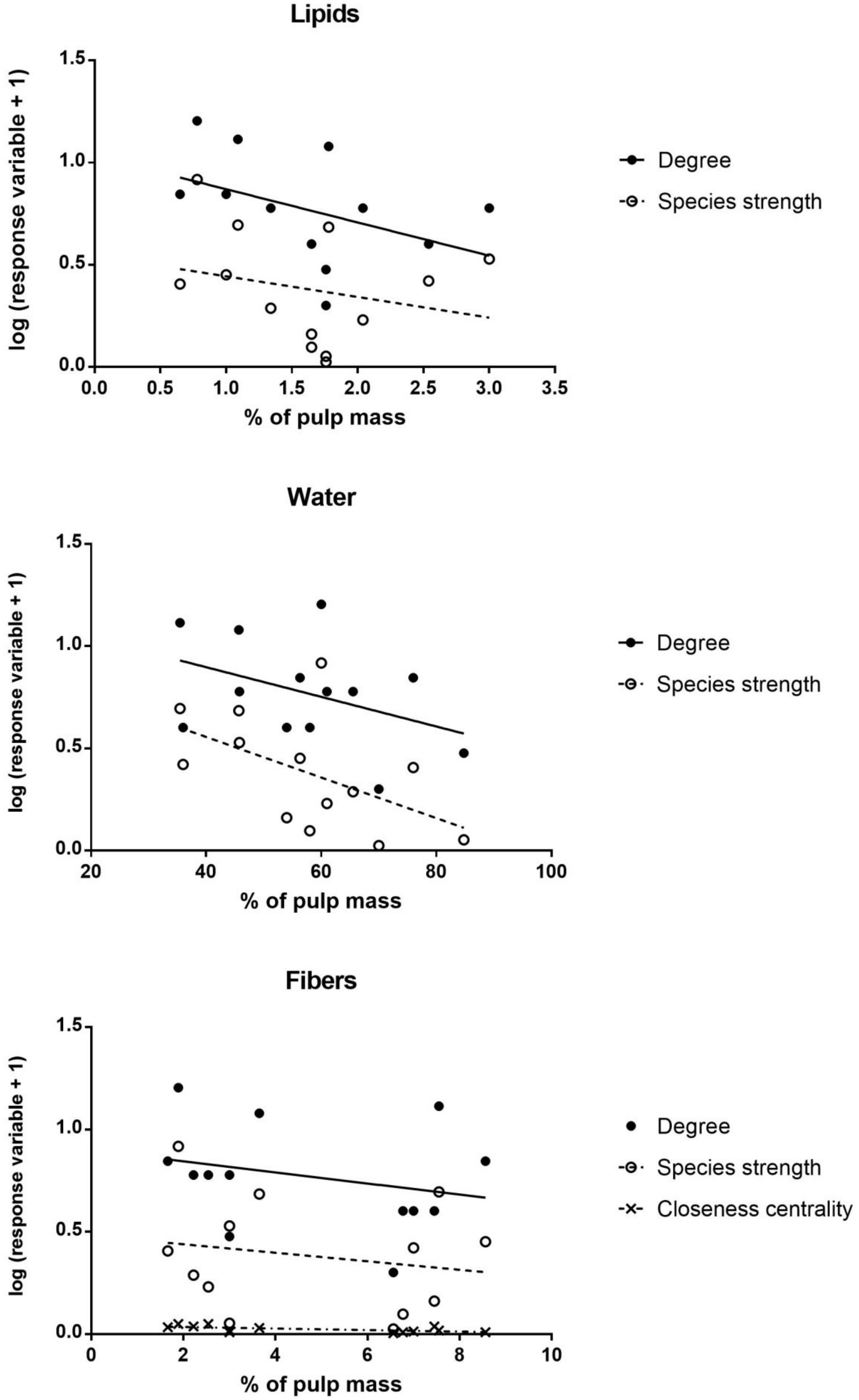

Figure 5. Relationship between fruit nutrients (% of pulp mass) and species-level network parameters (for plants) in the FEG, SE Brazil. We only report nutrients available in the best models

DISCUSSION

The ability of species traits and abundance to explain bird-plant network structure

Our findings suggest that trait-matching between birds and plants explains the observed pairwise interactions between birds and fruiting plants, providing further evidence of the ecological and evolutionary determinants of biological interactions in tropical ecosystems (Blendinger et al. 2016; Dehling et al. 2016; Muñoz et al. 2016). However, neutral processes (*i.e.* species relative abundance) performed better than biological constraints in explaining aggregate network parameters, such as connectance, interaction evenness and interaction asymmetry (for birds). Given that network metrics are insensitive to the actual configuration of pairwise interactions (Olito and Fox 2015), our results indicate that models predicting network metrics may not predict with the same accuracy the underlying mechanisms of the detailed structure of biotic interactions, which is the main focus of ecological research.

The probability matrix that best predicted the frequency of pairwise interactions in the FEG contained both temporal overlap and size-matching (*TS*), which indicates that interactions are non-random and are established based on underlying ecological and evolutionary mechanisms. Given that we sampled a significant amount of the estimated interactions, we conclude that unobserved links are the result of constraints imposed by species morphology and phenology (*i.e.* forbidden links) and they will remain unobserved even with increasing sampling effort (Olesen et al. 2010). Birds can only consume fruits of an upper limiting size (<1.5 x gape width) and more often visit plants with long fruiting seasons. For that reason, plants with smaller fruits and long fruiting seasons, such as *N. membranacea* and Rubiaceae sp1., had the highest visitation rates because their fruits are often much smaller than the gape width of birds and because they can be consumed by both short and long-term bird species. We stress that these results are important for theoretical and conservational purposes because unraveling the mechanisms of pairwise interactions allow us to elaborate more accurate models of species interactions and to focus on plant traits that increase network complexity and, consequently, community persistence (Blüthgen 2010).

The next best-fitting model explaining the frequency of interactions included only species phenology (*i.e.* temporal overlap). This finding adds to the growing evidence that temporal coordination of species activities is one of the main drivers of plant-frugivore interactions in seasonal habitats (Vidal et al. 2014; Ramos-Robles et al. 2018b). Obviously, the lack of temporal overlap between pairs of species determine strong forbidden links, but we've shown that phenology plays a quantitative role and that the probability of two species interact in the FEG is as high as the number of months in which they co-occur. This is particularly evident because plants with long fruiting periods, such as *N. membranacea*, established stronger interactions with many partners. These plant species are keystone resources for the maintenance of avian frugivores because they provide fruits over long periods and may be consumed by birds with short-term phenologies (Ramos-Robles et al. 2016), such as rare resident species like *Nemosia pileata* and migratory species like *Tyrannus savanna* and *Pipraeidea melanonota*.

Plants in tropical forests exhibit a large diversity of fruiting strategies and these may influence the architecture of plant-frugivores networks (De Castro et al. 2012). In our study we identified a continuum of phenological strategies spanning from plant species whose individuals asynchronously produce large fruit crops over long periods (*e.g. N. membranacea* and *S. guianensis*) to species that synchronously produce small crops over short or long periods (*e.g. Mataiba guianensis* and *Miconia nervosa*, respectively). In general, interactions of the plants in the former side were a subset of the interactions established by plants of the other side, and these latter contributed more to network nestedness. Only a few species tend to contribute strongly to nestedness (Rohr et al. 2014; Pawar 2014) and although we did not directly evaluate how the length of the fruiting season influences plant species contribution to the nested structure of the network, we suggest that it may do so, as it was previously demonstrated in other studies (Vidal et al. 2014; Gonzalez and Loiselle 2016) and, consequently, their importance to the conservation of species interactions.

Phenology is deeply associated with specific abiotic conditions, such as temperature and rainfall (Bendix et al. 2006). Therefore, interactions that are strongly determined by temporal overlap among species, such as in the FEG, are susceptible to disturbances that may affect the timing that species are available as partners and how long they remain so, such as climate change (Rafferty et al. 2015). Our limited information on how species respond to phenological shifts suggests, for example, that mismatches in species phenology caused by changing environmental conditions can result in a failure for migratory bird populations to adapt to the new schedule of resource availability (Day and

Kokko 2015) and that seasonal, short-term and facultative mutualisms are more likely to become extinct due to phenological disruption (Rafferty et al. 2015). We know that global warming has already caused changes in biotic conditions of many environments and, consequently, affected the phenology of many organisms (Johansson et al. 2015a) but we don't know how these changes cascade through entire interaction networks and we suggest that evaluating these consequences is a promising and much needed avenue for future studies (Câmara et al. 2018).

Size-coupling between avian frugivores and fruit size is a strong determinant of mutualistic interactions (Burns 2013; González-Castro et al. 2015) and we also found that the model containing size-matching was one of the most significant drivers of pairwise interactions. The deterministic hypothesis of the evolution of fruit size in angiosperms states that it is supposed to have evolved as a response to frugivores selective pressure (Lord 2004). For example, most small and medium bodied avian frugivores exhibit a strong preference for smaller and spherical fruits which are easier to swallow whole (Herrera 1987). This is the case of *N. membranecea*, which was the most visited plant species and also had the highest number of partners in the FEG. This also explains why the size-constraint matrix had the closest nestedness value to the observed network. Nestedness arises when specialized interactions are a subset of the generalized ones (Bascompte et al. 2003). Our size-matching criteria predicted that species should interact proportionately to the fruit width/bill width ratio and it was so for the most specialized bird species in our system, *Forpus xanthopterygius* and *Tyrannus melancholichus*. These two specialists interacted with plant partners (*Siparuna guianensis* and *Aegiphilia* sp., respectively) that also participated in interactions with generalists and, thus, defined the nested structure of the observed network.

Despite that, even if gape-width determine the ability of birds to interact with fruits, which is the case in our study, caution must be taken when considering unobserved interactions based on size-matching as forbidden links. Many studies consider that a bird is unable to consume a fruit larger than its gape-width (Wheelwright 1985; Lord 2004; Burns 2013), but this constraint is true only for species that swallow fruits whole. Many generalists, however, are peckers and can consume fruits much larger than their capacity to stretch jaws, by removing fruit pieces (Kelly et al. 2010). Notwithstanding, feeding behavior has important implications for seed dispersal, because peckers are known to crush seeds, while swallowers generally maintain seeds intact in their guts (Zwolak 2017). For that reason, we suggest that in order to understand how size-constraints structures pairwise interactions and influence birds functional role, it is important to distinguish fruit choice from seed dispersal, because albeit being interconnected processes, frugivores in the interaction network may or may not be effective seed dispersers (Donoso et al. 2016).

Neutrality assumes that all individuals have the same probability of interaction and that encounters among them happen randomly (Vázquez et al. 2009a). Being so, abundant species will establish more interactions with more partners while rare species will only participate in a few interactions (Krishna et al. 2008). In our study, we found that species relative abundance played no significant role in predicting the detailed network structure (*i.e.* the frequency of interactions). We believe that this is a ‘true’ pattern of species interactions and not the result of sampling bias (see Fründ et al. 2016, for a dicussion on the issue) because: 1) our abundance measures were independent from interaction frequencies and 2) abundant birds (*e.g. Saltator similis* and *Tangara cayana*) and scarce plants (*e.g. Miconia nervosa*) did not interact proportionately to their relative abundances. This finding is in accordance with previous studies (Vázquez et al. 2009b; Vizentin-Bugoni et al. 2014, 2016; Olito and Fox 2015; Gonzalez and Loiselle 2016) and, hence, our study corroborates the deterministic hypothesis that species traits explain the ability of species to interact with each other more than their relative abundances, suggesting underlying ecological and evolutionary causes of species interactions (Vázquez et al. 2009b).

Network metrics

Only a small proportion of the interactions between avian frugivores and plants in the FEG were actually realized. Moreover, interactions were generalized, nested and highly uneven. These are common trends in plant-frugivore networks and have ecological implications for community persistence and stability (Sebastián-González et al. 2015; Fort et al. 2016). For example, in generalized and nested assemblages birds most probably disperse seeds of many plants, ensuring that seed dispersal endures even if some interactions are lost (Bascompte et al. 2003). Interaction asymmetry may also promote stability and coexistence, because species can be more resistant and resilient to disturbances by relying on generalist partners that also depend on other species (Bascompte and Jordano 2007).

Contrarily to what we described for pairwise interactions, in general species traits poorly predicted network metrics, with the exception of nestedness, which was best explained by size-matching. In fact, models containing abundance were much closer to the parameters of the observed network. For instance, connectance, interaction evenness and interaction asymmetry for birds were more accurately predicted by abundance alone or in combination with species traits than models that did not include it. Aggregate network metrics can illustrate general attributes of species interactions and their ecological consequences. Nonetheless, different distributions of the frequency of interactions in the matrix can result at the same network parameters (Olito and Fox 2015). What we demonstrated in this study is that some different networks built using only species relative abundance have similar aggregate metrics as the observed network, but these networks fail to equally predict pairwise interactions. Therefore, summarizing the complexity of ecological interactions into a single number can be misleading especially if they are constrained by biological traits and, hence, caution must be taken when comparing networks through their aggregate metrics in an effort to unite patterns with the underlying mechanisms responsible for generating them (Vázquez et al. 2009a; Blüthgen 2010).

This statement is particularly evident when we look at the H2’ of the observed network. None of our models could accurately predict this network index of specialization, because all of them were considerably more generalized than the observed network. The conceptual framework of Vázquez et al. (2009b) has systematically demonstrated that hypothetical probability matrices based on species traits and their relative abundances fail to explain the degree of specialization of the observed matrix (Vizentin-Bugoni et al. 2014; Olito and Fox 2015; Gonzalez and Loiselle 2016). This recurring pattern is possibly an outcome of how H2’ is calculated, because it is based on the Shannon-Wiener index, which takes into account the distribution of interaction frequencies (Blüthgen et al. 2006). Therefore, once again we suggest that network aggregate metrics, like H2’, should be used with caution, because our research adds to the growing evidence that it is not a suitable network metric to depict interactions based on biological constraints.

The effects of pulp composition and fruit color on plants species-level metrics

Pulp composition mainly affected plant degree, species strength and closeness centrality. Fruit chemistry is an important feature mediating plant-frugivore interactions (Blendinger et al. 2015, 2016) and we demonstrated that fat, juicy and fibrous fruits were only consumed by a handful bird species and only established weak interactions. Also, plants with fibrous fruits occupied peripheral positions in the network. Fibers and lipids are generally hard to digest and, therefore, they are retained at birds gut for longer periods (Levey and Martínez del Rio 2001; Smith et al. 2007; González-Castro et al. 2015). Although fruit retaining may be advantageous for seed dispersal because seeds are dispersed over longer distances, it does affect interaction frequencies since birds are satiated earlier if they consume fruits of low digestibility, which in turn reduces the number of interacting partners and affects species-level parameters such as species strength and closeness centrality. For instance, *N. membranacea*, the most visited species in the FEG, had fruits with low fiber and fat contents, which allows birds not only to consume larger crops of the same species but also to visit other plants to obtain enough nutrients. Just like we demonstrated in this study, González-Castro et al. (2015) found that water content negatively affected species-level parameters in a seasonal forest from Mexico. Although we did not evaluated seasonal shifts in birds diets, we believe that they may influence fruit preferences and, as such, species-level metrics because abiotic conditions may shape the nutritional composition of fruits (Lotan and Izhaki 2013) .

Fresh-fruits from the FEG exhibited a wide variety of colors, as measured by hue, but we found that it was not a good predictor of species-level metrics for plants, and, thus, it was a poor driver of bird-plant interactions. One of the evolutionary hypotheses to explain the color diversity of fruits in angiosperms is that it evolved as a response to the selective pressure of frugivores on the most conspicuous fruits (Valenta et al. 2018). Notwithstanding, fruit detectability also depends on the contrast against the background (Camargo et al. 2013, 2014), which wasn't measured in this study. However, in a previous research conducted in the same site using artificial fruits we observed that fruit choice was not based on color preferences (Pires et al. in press), corroborating that birds forage on fruits irrespective of fruit colors. We suggest that for generalized biotic systems, such as the bird-plant interaction network from the FEG, the diversity of fruit colors have little impact on fruit choice of frugivorous birds and that the importance of plant species on the diet of avian frugivores depends on other traits, such as the nutritional compound of the pulp, constrained by fruit size and plant phenology.

CONCLUSIONS

This study provide evidences that the network of interactions between avian frugivores and plants are assembled through biological constraints and trait complementarity among species and that relative abundance becomes more important when predicting network parameters. Therefore, we add that in order to understand the determinants of species interactions, researchers such consider models that include both species traits and their relative abundance and be cautious with the use of network aggregate metrics that may not clearly reflect the processes responsible for generating them. To the extent of our knowledge, this is the first study to apply a likelihood approach to evaluate the determinants of plant-frugivore interactions and it demonstrates that assembling rules are pervasive through different kinds of mutualistic networks. We believe that other parameters could increase the explanatory power of our models, such as the role of phylogenetic signal and we suggest that this is an important step to distinguish if and to what degree network patterns are the result of current ecological processes or species evolutionary history. Finally, we propose that defining the rules of network assembling and how common these rules are among different kinds of interactions may improve our capacity to predict how network of interactions will respond to micro and macro scale environmental disturbances, such as habitat fragmentation and global warming.

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Appendix I: Bird (rows) – plant (columns) interactions in in the Floresta Experimental do Glória, SE Brazil.

Species	*Aegiphilia* sp.	*Birsonima intermedia*	*Cardiopetalum calophyllum*	*Mataiba guianensis*	*Miconia affinis*	*Miconia nervosa*	*Nectandra membranacea*	*Protium heptaphyllum*	*Protium ovatum*	*Psychotria prunifolia*	Rubiaceae sp1.	*Siparuna guianensis*	*Virola sebifera*
Antilophia galeata	1	3	2		29	15	37	39		35	67	9	
Dacnis cayana			2				1					13	
Elaenia sp.			1	1								11	
Eucometes penicillata					1		1						
Forpus xantopterigius												2	
Icterus pyrrhopterus			2	8								1	
Megarhynchus pitangua		2		6	2		1						
Mimus saturninus													8
Myarchus ferox			4									3	
Myiozetetes similis	1		2										
Nemosia pileata			3				1						
Pipraeidea melanonota							1						
Pitangus sulphuratus			1										
Ramphastus toco	1						3						
Saltator maximus					3					1	1		
Saltator similis	3		1			1	4	4			1	2	
Suiriri suiriri				7									
Tangara cayana			3		3		1	1	2	3	4	6	
Tangara palmarum							8						
Tangara sayaca			2				2					1	
Tersina viridis							19					1	9
Turdus leucomelas	2	2	1	1	2		19			6	1	3	
Turdus rufiventris							1			1			1
Tyrannus melancholichus	2												
Tyrannus savana							3						

CAPÍTULO III

INDIVIDUAL SPECIALIZATION AND SEASONAL VARIATION IN THE TROPHIC NICHE OF THE HELMETED MANAKIN

INDIVIDUAL SPECIALIZATION AND SEASONAL VARIATION IN THE TROPHIC NICHE OF THE HELMETED MANAKIN

Luís Paulo Pires and Celine de Melo

ABSTRACT

Many ecological studies presume individuals in a population are ecologically equivalent, but natural populations may be highly heterogeneous in the use of resources, which deeply affects the stability and persistence of biological communities. In this study we investigated the seasonal dynamics of individual niche in the Helmeted manakin, *Antilophia galeata*, a generalist bird species, following three models of interindividual diet variation, through the parameters of ecological networks. We found low connectance and nestedness for both networks. Notwithstanding, dry season network was more nested, while wet season network was more modular. Null models were consistently different from all observed parameters, which indicates mechanistic basis underlying the patterns we found. Therefore, we demonstrated that individuals of *A. galeata* behave as dietary specialists and that seasonality of resources affects ecological network parameters at the individual level. We conclude that intraspecific variations in resource use are important in determining ecological interactions and that downscaling ecological networks to the individual level may reveal emergent properties that, albeit existent, are not evident in species-resources networks.

Keywords: ecological interactions; frugivory; foraging; ecology of individuals; Optimal Diet Theory.

INTRODUCTION

Most generalist species use resources opportunistically, expanding or contracting niche width in response to population density and spatio-temporal availability of resources (Bolnick et al. 2003). When not constrained by resource availability, the frequency distribution of each item in the diet of a generalist individual is heterogeneous because resources with high-nutritional rewards are consumed more often than low-quality ones (Tim Tinker et al. 2012). Therefore, according to Optimal Diet Theory (ODT - MacArthur and Pianka 1966) individuals rank preferential and alternative resources in order to maximize net energy intake (Pulliam 1974). Traditionally, most of biological research considers conspecific individuals as ecologically equivalents and hence ignore intraspecific variation that may affect resource ranking (Violle et al. 2012; Tur et al. 2015).

Actually, research evidences suggest that many natural populations are quite heterogeneous in resource use (Bolnick et al. 2003), owning to interindividual phenotypical variations in morphology, physiology, behaviour (Svanback and Bolnick 2005; Araújo et al. 2011) and, consequently, energetic balance during foraging. Thus, when such variations are considered, the niche of individuals is expectedly different than the total population niche, promoting differences in the ability to rank resources and individual specialization (Costa-Pereira et al. 2017). Over decades, many studies revealed that individual specialization affects the stability and persistance of populations and, therefore, should be considered in order to understand niche dynamics and resource use in biological communities (Van Valen 1965; Camargo et al. 2014; Costa-Pereira et al. 2017).

Svanbäck and Bolnick (2005) proposed three conceptual frameworks to unveil the underlying mechanisms causing interindividual diet variation: the Shared Preference Model (SPM), the Distinct Preference Model (DPM), and the Competitive Refuge Model (CRM). In SPM individuals rank resources (preferred and less preferred) similarly when these are abundant, but differ at the rate that they add alternative resources in their diet in such a way that some individuals shift from top-ranked to less preferred resources more quickly than others. On the other hand, in the DPM individuals have different preferential resources, but they add secondary itens to their diets when the availability of the preferred is reduced, which would increase niche overlap. At last, the CRM predicts the same ranking for preferred resources at high availability, but different ranking for alternative resources at low abundance.

The models of Svanbäck and Bolnick (2005) assume two premises: 1) that individuals are heterogeneous in their ability to exploit resources and 2) that resource availability varies in space and time. For that reason, temporal availability of resources is crucial for population niche dynamics, and it is highly influenced by the seasonality of natural environments (Marshall and Burgess 2015; Costa-Pereira et al. 2017). In this regard, Pires et al. (2013) demonstrated that in a marsupial species interindividual differences in resource exploitation were responsible for changes in population niche width between dry and wet seasons, whilst intraindividual niche width remained unchanged. In that manner, understanding how seasonality shapes population niche through intra and interindividual variations are important to unravel how populations adapt to environmental disturbances that have impact on resource availability (Cantor et al. 2013; Miguel and Campos 2018).

Complex Network Theory has been used as a tool for analyzing and interpreting data on animal-plant interactions, shedding light on emergent ecological patterns of biological communities (Bascompte and Jordano 2007; Olesen et al. 2011; Dehling et al. 2016; Lemos-Costa et al. 2016; Dalsgaard et al. 2017). More recently, it has been incorporated in the studies of population niche dynamics (Dupont et al. 2014; Tur et al. 2015; Miguel and Campos 2018), and have demonstrated some recurring patterns (e.g., nestedness and modularity) of intraspecific variation in resource use (Tim Tinker et al. 2012; Muylaert et al. 2014; Guerra et al. 2017).

The way in which individual specialization affects parameters of interaction networks allows us to test hypothesis regarding the models proposed by Svanbäck and Bolnick (2005). For instance, it is expected that networks depicting the CRM scenario would exhibit high modularity, because individuals avoid competition at low resource availability by shifting to different, less preferred resources. On the contrary, SPM networks are expected to be highly nested, since individuals include the same alternative resources in their diets, but at different rates, so that specialized interactions represent a subgroup of more generalized interactions. Low specialization and some degree of compartmentalization are expected for DPM networks, because individuals reduce niche overlap by moving from top-ranked resources to different, less preferred ones.

Despite being largely utilized to depict species-level interactions, so far network approach has only been applied in a few studies that investigate individual-level interactions (e.g., Araújo et al. 2008; Tur et al. 2014; Miguel and Campos 2018) and, as far as we know, fewer have demonstrated how seasonality shapes population niche dynamics and the structure of individual-resource networks in plant-frugivore mutualisms (Pires et al. 2013; Tur et al. 2015; Costa-Pereira et al. 2017). In this sense, this study investigated the seasonal dynamics of the intraspecific niche in the Helmeted manakin (*Antilophia* *galeata*, Pipridae, Lichtenstein, 1823), a generalist species, following the models proposed by Svänback and Bolnick (2005) and using the ecological network approach. We tested the following hypothesis: 1) individuals of the Helmeted manakin are dietary specialists and 2) the degree of individual specialization in *A. galeata* varies seasonally, with higher modularity occurring in the dry season due to reduced availability of resources and higher nestedness in the wet season.

MATERIALS AND METHODS

Study Area

The study was conducted in the semidecidual forest of Fazenda Experimental do Glória (FEG: 18.95ºS, 48.20°W) from July 2015 to June 2017. The forest has ~30 ha and is surrounded by gallery forest, pasture and crops (see Lopes et al. 2011, for a detailed description of the area). The climate is markedly seasonal, with a dry winter (April to September) and a rainy summer (October to March) (Bueno et al. 2018).

Abundance and Phenology of Bird-Dispersed Plants

In order to quantify seasonal availability of resources, we selected five individuals of each plant species with ornitochorical fruits (sensu Fleming and Kress 2013) along a 450m x 5m transect. Every 15-20 days, we counted the number of ripe fruits per individual when plants had less than 100 fruits or estimated it by multiplying the number of fruits in a single branch by the number of branches in the plant (Melo et al. 2013). Fruiting season of each species was defined as the number of months that at least one individual displayed mature fruits.

The Helmeted manakin

The Helmeted manakin is an obligate, abundant, generalist and endemic frugivore species from the forests of Cerrado (Marini 1992). Individuals of the species have been documented to use different foraging and feeding behaviours, such as vertical stratification of the understorey (see Marini 1992; Silva and Melo 2011, for a detailed description of foraging strategies in the species). Such array of behavioural traits allow individuals to access and exploit resources differently and variations in the efficiency of these strategies that affect the realized reward of resources (*i.e.* net energy intake) may promote individual specialization (Estes et al. 2003).

Monthly Abundance of the Helmeted manakin

To estimate the abundance of *A. galeata*, we randomly established 10 observational points of 10m radius along small trails in the area, distant at least 150m from each other (adapted from Burns 2005). Each point was visited for 10 min from 06h00 to 12h00 twice per month. Every frugivorous birds seen or heard within each point during observations were recorded. We waited five minutes after arrival in each point to start counting birds to avoid oversampling individuals that moved from one point to the next. Abundance was defined as the mean number of individuals registered per month during dry and wet seasons.

Niche Dynamics in the Helmeted manakin

The diet of the individuals of the Helmeted manakin was determined solely by the analysis of fecal samples. We used 20 mist nets (12m x 3m) to capture birds. Samplings were conducted for consecutive four days every two months from June 2015 to May 2017. Mist nets were set from 06hr 30min to 16hr 30min and were checked every 30 min. To collect fecal samples, birds were kept in fabric sacks for 10-20 min. After that, birds were banded using metal bands following standardized procedures from CEMAVE/ICMBio and then released. In the lab, we searched for seeds in fecal samples and we considered that an interaction between an individual of *A. galeata* and a plant species occurred whenever we found seeds in feces.

Multiple observations of the diet of an individual are necessary to determine the degree of individual specialization because niche width cannot be defined by a single feeding bout since resources are scattered in space and time (Lemos-Costa et al. 2015). Hence, diet was recorded by recapturing banded individuals. In order to assure data independency and that each recording represented a different feeding choice, we only considered those recaptures that occurred in different mist netting campaigns.

We built individual-resources interaction matrices M in which each cell mij is 1 when individual i interact with plant j or 0 otherwise. We chose to depict interactions in binary matrices due to the qualitative dietary data obtained through fecal content, because the number of seeds in feces may not be used as a proxy for the frequency of consumption seeing that most fruits have more than one seed. Although weighted matrices often provide more accurate data on network parameters (Jordano 2016), the models of Svanback and Bolnick (2005) as well as the predictions of ODT on which they lie upon, are qualitative, so the binary approach is fit for analyzing and interpreting our data (Pires et al. 2011).

The population niche dynamics of the Helmeted manakin was determined by the network parameters of individual-resource networks. We investigated the following parameters:

1) d': species index of specialization, based on its discrimination from random selection of partners (Blüthgen et al. 2006). It varies from 0 (complete generalization) to 1 (complete specialization). d' was derived from the whole network for each season, considering all species captured in the mist netting (Online Resource 1).

2) Connectance ($\bar{C}$): proportion of all possible interactions that actually occur (García 2016a). In individual-resource networks, higher connectance means higher niche overlap and that individuals are generalists, whereas lower values indicate niche differentiation (Pires et al. 2011);

3) Nestedness ($\bar{N}$): it is a network property in which most links are concentrated in a group of generalists that interact among themselves, whereas low connected species form a subgroup of interactions inside the first group (Almeida-Neto et al. 2008). In individual-resource networks, nested interactions means that specialist individuals interact with a subset of species that generalist consume (Pires et al. 2011). We calculated nestedness using Almeida-Neto et al. (2008) "nestedness metric based on overlap and decreasing fill" (NODF) for binary networks, separately for plants and individual. Henceforward we report only measures of nestedness for individuals. We normalized NODF values by dividing them by 100. Therefore, it varies from 0 (non-nested networks) to 1 (totally nested networks).

4) Niche overlap: mean similarity in interaction pattern between species of that level, calculated by Horn's index. Values near 0 indicateno common use of niches, 1 indicates perfect niche overlap.

5) Modularity ($\overline{M}$): property of networks in which interactions are compartmentalized in well-defined groups (Guimerà et al. 2007). In individual-resource networks, modularity occurs when a group of individuals interact more frequently with a set of plants that are less frequently consumed by other groups of individuals (Tur et al. 2015). Modularity was calculated using Simulated Annealing Algorithm (Guimerà and Amaral 2005), that divides the network in compartments and determines a modularity index for each one of them and then computes the best fit for the entire network by direct maximization. $\overline{M}$ index varies from 0 when individuals are randomly distributed in modules in the network or when all individuals fall into the same compartment to 1 when there are no links among different modules.

We performed 1000 randomizations of each network using mgen algorithm (in bipartite package). Firstly, we transformed the observed networks into probability matrices by dividing each cell by the matrix sum. Then, we constrained null models so that each randomized network had the same size as the observed matrices and interactions were distributed regarding the probability in the observed probability matrices.

Statistical Analyzes

Analysis were conducted in RStudio 2.4-4 (R Core Team, 2017), using circular (Lund and Agostinelli 2013), bipartite (Dormann et al. 2009), rnetcarto (Doulcier and Stouffer 2015) and RInsP (Zaccarelli et al. 2013) packages. We investigated seasonal variation in resource availability using circular statistics and compared mean vector size (*i.e.* fruiting intensity) under the Watson-Williams test (Zar 2010). We compared the number of fruiting individuals and species and the abundance of the Helmeted manakin in the dry and wet seasons were using Mann-Whitney tests (Zar 2010). Finally, parameters generated by the null models were compared to the ones from the observed matrices using One Sampe T-tests (Zar 2010). Descriptive statistics are presented as mean ± SD, unless specified otherwise, and were considered significant if $P < 0.05$.

RESULTS

Mature fruits were available through the whole year in the FEG, but their frequency varied along months (Figure 1). In the dry season, fruiting individuals had 80% less fruits (57.00

± 19.98) than in the wet season (283.17 ± 149.08; Watson-Williams, $P < 0.01$). The number of fruiting species (dry: 15.91 ± 3.70, wet: 14.42 ± 4.44; $U = 77$, $P = 0.52$) and individuals (dry: 22.82 ± 9.32, wet: 22.00 ± 6.74; $U = 87.5$, $P = 0.18$) did not vary between seasons (Figure 2).

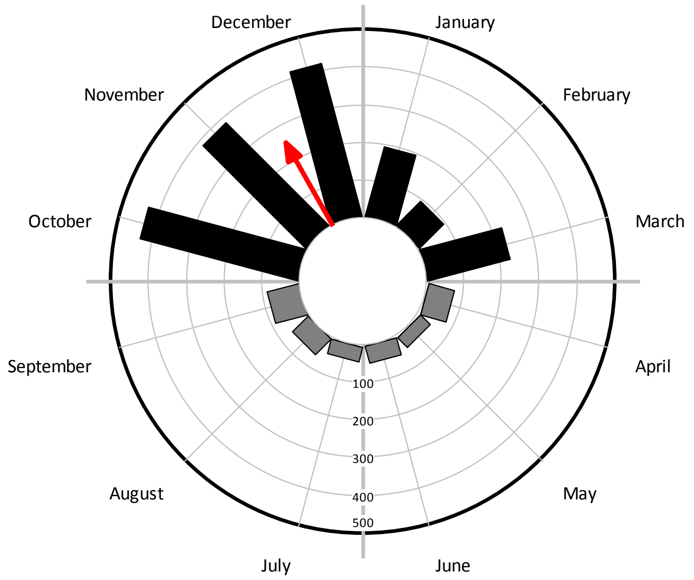

Figure 1. Circular histogram of mean fruit availability per month in the Fazenda Experimental do Glória. Black bars represent mature fruit availability in the wet season and grey bars in the dry season. Red arrow is the mean angle (*i.e.* time of the year most likely to find mature fruits) and the arrow length corresponds to the mean vector (r) value. Each concentric circle represents 100 matures fruits.

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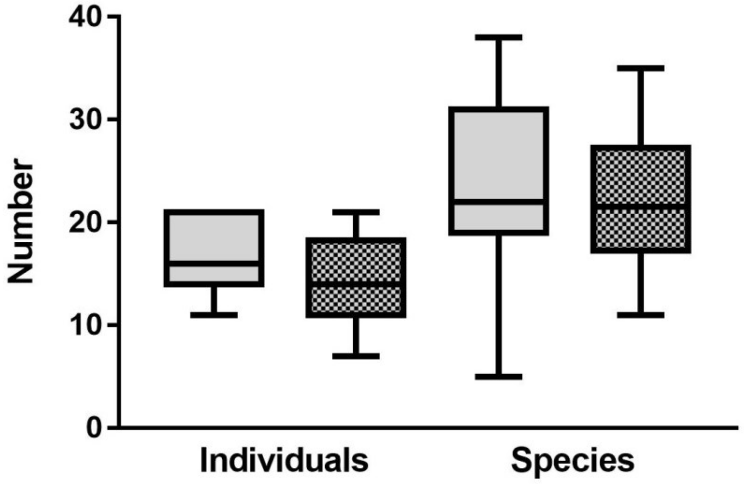

Figure 2. Boxplot of the number of individuals (left grey boxplots) and species (right grey boxplots) during dry (plain grey) and wet (squared grey) seasons.

We recorded 453 individuals of the Helmeted manakin, 225 (20.45 ± 9.88 registers/month) in the dry season and 228 (19.00 ± 5.49 registers/month) in the wet season, and there was no difference in monthly abundance between them (*U* = 58.5; *P* = 0.66). Using mist nets we captured 115 individuals during dry season and 64 in the wet season, from which we obtained 61 fecal samples (19 recaptured individuals in the dry season and 12 in the wet season).

The diet of the Helmeted manakin was predominantly composed of fruits (96.64%). The species behaved as a generalist consumer, *i.e.* we found seeds from 17 species in the feces of captured individuals, 12 in the dry season and 10 in the wet season (Figure 3) and d' of this species was considerably low in the FEG species-resource networks. Both seasonal individual-resource networks were low connected and nested, notwithstanding nestedness and niche overlap were higher in the dry season (Table 1). Despite that, interactions in the wet season were more modular (Table 1).

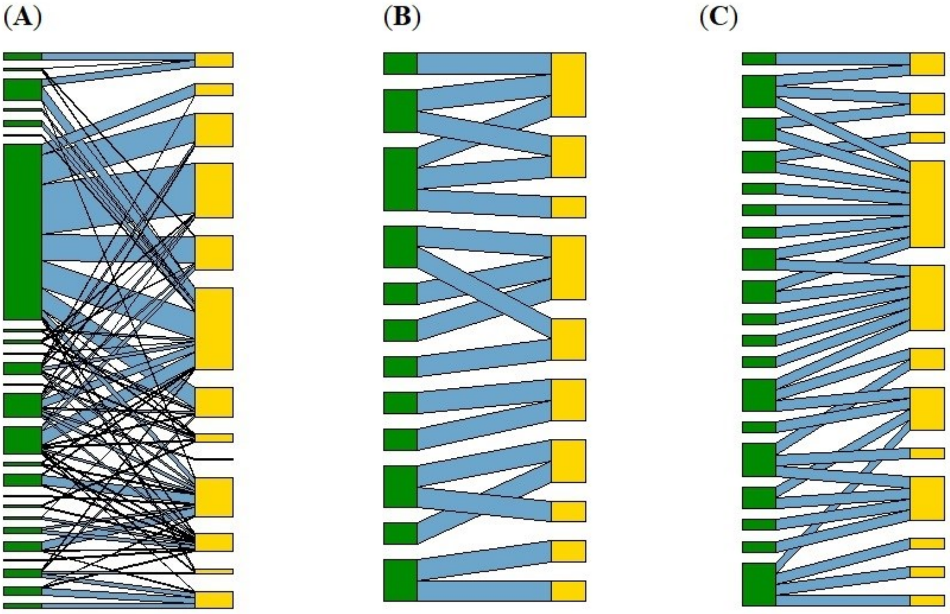

Figure 3. Consumers-resources bipartite networks in the Fazenda Experimental do Glória. Green boxes are consumers, yellow boxes are resources and blue connectors are interactions between them. (**A**) Weighted interactions between bird species and fruiting plants. The largest green box is the Helmeted manakin; (**B**) unweighted interactions between individuals of the Helmeted manakin and fruiting plants in the wet season; and (**C**) unweighted interactions between individuals of the Helmeted manakin and fruiting plants in the dry season.

Table 1. Parameters of the observed and null interaction networks between individuals of the Helmeted manakin and plants. All parameters were different from those expected by the null models (p<0.001).

Parameter	**Dry season**		**Wet season**	
	Obs	**Null**	**Obs**	**Null**
d’	0.08	---	0.08	---
$\bar{C}$	0.14	0.13	0.15	0.14
$\bar{N}$	0.21	0.13	0.10	0.06
Niche overlap	0.10	0.08	0.20	0.16
M	0.52	0.572	0.85	0.746

DISCUSSION

Similarly to many other previous studies (Marini 1992; Silva and Melo 2011; Purificação et al. 2014; Gonçalves et al. 2015; Silva et al. 2016), we recorded a generalist diet for the Helmeted manakin, because in both seasons the species interacted with many partners and d’ was considerably low. Nevertheless, if all individuals in a generalist population were themselves generalists and shared similar resources, then connectance should have been high. Despite that, we observed that networks derived from both seasons were low connected, that is, only a few of all possible interactions actually occurred. Low values of connectance indicate diet differentiation and specialization, because the likelihood of two individuals sharing the same resources is smaller when there are fewer interactions in the network (Pires et al. 2011). Therefore, we present evidence that the dietary niche width of the individuals of *A. galeata* is different from the total population niche. We suggest that increased diet dissimilarity among individuals is caused by resource patchiness (Dupont et al. 2014; Tiribelli et al. 2017). Adult males of the Helmeted manakin are territorialists (Marini 1992; Marçal 2017), and the resources inside a defended territory become unavailable for other individuals, mainly other adult males. Therefore, male and female (as well as adult and young) individuals have access to different resource patches, thereby increasing interindividual dietary differences (Fretwell and Lucas 1969; Flesch et al. 2015).

Nonetheless, the magnitude of individual specialization varied between seasons, because niche overlap was twice as high in the dry season. The abundance of individuals of the Helmeted manakin did not vary between seasons, but the frequency of resources per fruiting plant did. Plants that fruited between October and March had five times more fruits than the others. This is a recurring phenological pattern in the tropics, where fruiting intensity is usually higher in the rainy season (Bendix et al. 2006; Hawes and Peres 2016), and it may explain the seasonal dynamics of the individual niche width in the Helmeted manakin and the structure of the individual-resource networks. In the rainy season, when plants produce large crops, birds that find a fruiting plant have access to an abundant resource. Following the predictions of ODT, if birds rank this resource preferentially, it would reduce the time (*i.e.* energy) they spent searching for fruits. Therefore, in the rainy season the intraindividual niche is narrower because individuals specialize in different top-ranked resources. In contrast, during the dry season fruiting intensity is smaller and individuals need to spend more time searching for secondary resources which, in turn, increases the intraindividual niche width and dietary overlap.

Nestedness is one of the most recurring pattern of ecological networks in tropical ecosystems (Bascompte and Jordano 2007) and it is expected when generalist species interact with many partners, whereas specialists interact with a subset of these (Olito and Fox 2015; Sebastián-González et al. 2015; Ramos-Robles et al. 2016). In nested individual-resource networks, individuals with narrower niche width are expected to specialize in top-ranked resources while generalists consume both top and less preferred items (Pires et al. 2011; Cantor et al. 2013b, see Ideal Free Distribution Theory, Fretwell and Lucas 1969). In this study, we found that seasonal patterns of resource use were consistent with the Distinct Preference Model proposed by Svanback and Bolnick (2005), which assumes that individuals have different first-choice resources when their availability is high (wet season, in our case). The underlying mechanism of this model is the tradeoff in foraging efficiency: for each resource, there is an optimal foraging strategy that allows individuals to maximize energy intake, but the efficiency of this strategy declines for every other resource (Tim Tinker et al. 2012). Thus, even if some individuals specialize in low-quality resources, the energy payout (*i.e.* net energy reward) is similar compared to that provided by high-quality resources, because the foraging strategies involved in acquiring the latter are often costly, especially due to competition (Estes et al. 2003).

Despite that, the network depicting interactions in the dry season was more nested. As stated before, niche overlap was also higher in the dry season because individuals included secondary resources in their diets by increasing niche width. Therefore, a higher degree of nestedness is expected for the dry season because individuals are also more generalists. This is also in accordance with the DPM (Svanback and Bolnick, 2005) since it predicts that individuals should include novel resources in their diet when resource availability is low (which is the case for the dry season in the FEG), therefore increasing niche overlap and, consequently, nestedness.

Modularity was the most distinct parameter in our study and it was clearly more pronounced in the rainy season. We believe that modules were defined by 1) resource patchiness (Fontúrbel and Medel 2017) inside male-defended territories and 2) higher fruit availability and, consequently, individual specialization in preferred resources. Higher compartimentalization in the wet season is also expected by the predictions of DPM (Svanback and Bolnick, 2005) because increased fruit availability allows individuals to specialize in their first-choice resources, hence defining groups that are composed by few individuals with similar rank preferences.

Compartmentalization has been systematically observed in many animal-plant interactions (Martín González et al. 2012, Krasnov et al. 2012, Fonseca and Ganade 1996, Donatti et al. 2011, Mello et al. 2011, Schleuning et al. 2014, Silva et al. 2017), and it is a common feature of specialized networks, such as many that depicts plant-pollinator interactions (Vizentin-Bugoni et al. 2014, 2016; Dalsgaard et al. 2017). Furthermore, in these mutualisms modularity has been observed to be an emergent pattern in the transition from species to individual-resource networks (Tur et al. 2015). Similarly, we argue that downscaling frugivore-plant networks to the level of individuals may unveil a modular structure that is masked at the species level, especially at the incidence of individual specialization. Hence, it seems reasonable to assume that perturbations in compartimentalized individual-resource networks would not spread homogeneously among conspecifics, which in turn would increase the stability of generalist populations and, consequently, of ecological communities (Silva et al. 2016; Gilarranz et al. 2017).

There is an increasing interest in the ecology of individuals and studies demonstrate that it affects the stability and persistance of natural populations as well as the dynamics of species interactions (Ings et al. 2009, Tur et al. 2015). In this study, we demonstrated that the incidence and seasonal magnitude of individual specialization in a generalist bird species are in accordance with the predictions of the DPM proposed by Svanback and Bolnick (2005) and that they mechanistically affect the structure of ecological networks. Therefore, we provide further evidence that moving from the species-resources to the individual-resources approach is a fundamental step towards understanding emergent patterns that only become clear at the level of individuals, which, in turn, have important implications for higher levels of organization, such as populations and communities. As it is already done for species-resources networks, future studies would benefit from the investigation of how different biological factors can shape the structure of individual level networks (Tur et al. 2014, 2015), such as individual and resource traits (e.g., see Guerra et al. 2017; for trait-mediated interactions from the perspective of resources) and spatial heterogeneity of resources (Dupont et al. 2014).

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CAPÍTULO IV*

FRUIT COLOUR AND EDGE EFFECTS POORLY EXPLAINS FRUGIVOROUS BIRD-PLANT INTERACTIONS IN DISTURBED SEMIDECIDUOUS FORESTS

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Fruit colour and edge effects poorly explains frugivorous bird-plant interactions in disturbed semideciduous forests

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ABSTRACT. Fruit colour is considered an important feature mediating interactions between plants and frugivorous birds. Despite that, colour mediated interactions are context-dependent, and habitat disturbances may affect how frugivorous birds perceive fruit colours. This study assessed the influence of fruit colour and edge effect on the consumption of artificial fruits by frugivorous birds in three disturbed semideciduous forests in southeastern Brazil. In each of those areas, we performed a field experiment in which we placed artificial fruits of three different colours on plants and recorded their consumption by birds. Red-coloured fruits were ingested more often than yellow, but neither of them was consumed differently from dark-blue. Edge effect only affected consumption of yellow fruits. Our data neither support the hypothesis of preferential consumption of the highest contrasting colours nor of increased fruit consumption in the forest interior. These findings indicate that colour and edge effects, as well as the interaction between them, may not be strong predictors of fruit choice by birds in disturbed environments, especially because generalist species, which are less sensitive to the physical alterations in forests, are favoured in these areas.

Keywords: frugivory; behaviour; plant signals; sensory ecology; plant-animal communication.

A COR DOS FRUTOS E O EFEITO DE BORDA NÃO EXPLICAM AS INTERAÇÕES ENTRE AVES FRUGÍVORAS E PLANTAS EM FRAGMENTOS FLORESTAIS SEMIDECÍDUOS ALTERADOS

RESUMO. A cor dos frutos é importante nas interações entre plantas e aves. Apesar disso, as interações mediadas por cores são contexto-dependentes e as alterações no habitat podem afetar a maneira como os frugívoros percebem a coloração dos frutos. Este estudo avaliou a influência da cor e do efeito de borda no consumo de frutos artificiais por aves em três florestas semidecíduas degradadas no sudeste brasileiro. Em cada uma dessas áreas, foi conduzido um experimento no qual foram colocados frutos artificiais de três cores diferentes nas plantas e foi registrado o seu consumo pelas aves. Os frutos vermelhos foram mais consumidos do que os amarelos, mas nenhum deles foi consumido mais frequentemente do que os azul-escuros. O efeito de borda afetou apenas o consumo de frutos amarelos. Nossos dados não suportam as hipóteses de consumo preferencial da coloração mais contrastante nem do aumento do consumo de frutos no interior dos fragmentos. Estes resultados indicam que a cor dos frutos, o efeito de borda e a interação entre estes dois fatores, não são fortes preditores da escolha do fruto por aves em ambientes degradados, principalmente pela ocorrência de espécies generalistas nestas áreas, que são menos sensíveis às alterações físicas nos fragmentos.

Palavras-chave: frugivoria; comportamento; sinais das plantas; ecologia sensorial; comunicação planta-animal.

INTRODUCTION

Fruit choice is a vital component of bird-plant interactions (Muñoz et al., 2016). It depends on the spatial context (Tiribelli, Amico, Sasal, & Morales, 2017), of frugivores' morphology and behaviour and also of plant traits such as phenology, crop size, fruit colour, accessibility, shape and size (Flörchinger, Braun, Böhning-Gaese, & Schaefer, 2010; Sallabanks, 1993; Smith & McWilliams, 2014; Snow, 1971). For instance, fruits consumed by frugivorous birds are generally small, spherical, odourless and colourful (Galetti, Alves-costa, & Cazetta, 2003; Schmidt, Schaefer, & Winkler, 2004). Thus, understanding the underlying mechanisms of fruit consumption is of particular concern for evolutionary and conservation biology, since birds interact with many plant taxa and are the leading seed dispersers in tropical ecosystems (Blendinger, Martín, Osinaga Acosta, Ruggera, & Aráoz, 2016; Fleming & Kress, 2011; Kuhlmann & Ribeiro, 2016).

To be consumed, a fruit must first be detected. In the forest sub-canopy, where shading limits light availability (Endler, 1993; Wicklein, Christopher, Carter, & Smith, 2012), plants that compete for seed dispersers may increase signalling by producing contrasting fruit colours (Schaefer, Schaefer, & Vorobyev, 2007), which are hypothesised to have evolved in response to selection mediated by frugivores (Cazetta, Galetti, Rezende, & Schaefer, 2012). In fact, increased detectability may affect plant fitness through higher fruit consumption rates, enhanced seed dispersal, and plant recruitment (Cazetta et al., 2012; Lomáscolo & Schaefer 2010; but see Stournaras & Schaefer 2016).

Birds have a tetrachromatic vision and are well adapted for colour perception (Osorio & Vorobyev, 2008). Avian frugivores feed on fruits of a wide variety of colours (Fleming & Kress, 2011). Notwithstanding, colour hue alone may not explain patterns of bird-plant interactions because fruit detectability also depends on contrast against the background (*i.e.* conspicuousness) (Burns & Dalen, 2002; Cazetta et al., 2012; Duan, Goodale, & Quan, 2014; Schaefer, Levey, Schaefer, & Avery, 2006; Schaefer et al., 2007; Schmidt & Schaefer, 2004; Silva & Melo, 2011). For example, a particular colour may be conspicuous at close range but cryptic at long distances (Cazetta, Schaefer, & Galetti, 2009). Furthermore, conspicuousness may also vary seasonally, because background (specially foliage) and illumination may vary critically in time (Burns & Dalen, 2002; Camargo, Cazetta, Schaefer, & Morellato, 2013). Therefore, it is crucial to incorporate chromatic (wavelength related) and achromatic (intensity related) aspects of fruit colours for a broader and more elaborate understanding of frugivorous bird-plant mutualisms, since these contrasts take into account the differences in target size, distance from the signal receiver and illuminance intensity that may affect fruit detectability (Schaefer et al., 2006).

Habitat transformation due to anthropogenic disturbances may also affect bird-plant interactions (Donoso, García, Rodríguez-Pérez, & Martínez, 2016; Herrerías-Diego et al., 2008; Martínez & García, 2015; Menezes, Cazetta, Morante-Filho, & Faria, 2016). Such alterations change habitat structure, functioning, and quality, especially near the forest boundaries, where edge effects alter abiotic conditions and create a subset of microhabitats (Aleixo & Vielliard, 1995). For example, Magrach, Santamaría, and Larrinaga (2013) demonstrated that fruit removal by birds increases with distance from forest edges, thus disrupting plant reproduction at forest boundaries (but see Bach & Kelly 2004; Galetti et al., 2003). Investigating how edge effects alter ecological interactions is imperative for habitat conservation, since disrupted interactions in forest edges may trigger negative cascading effects throughout the entire environment (Harper et al., 2005; Magrach et al., 2013).

One would expect that edges may alter biological interactions by changing colour perception in birds (Bach & Kelly, 2004; Cazetta et al., 2009; Galetti et al., 2003). Assuredly, habitat disturbances may change background heterogeneity, light incidence, and cause sight obstruction, influencing fruit visibility and conspicuousness (Camargo, Cazetta, Morellato, & Schaefer, 2014). Light intensity, for example, can vary drastically in forest environments and is usually higher at edges (Endler, 1993). In these environments, achromatic signals may be more important than chromatic ones for foraging birds (Cazetta et al., 2009; Schaefer et al., 2006). Despite that, so far there are no studies assessing the influence of edge effects on colour-mediated interactions between birds and plants.

In this study we aimed at investigating the influence of fruit colour and habitat disturbance on the consumption of artificial fruits by birds. We predicted that 1) highly contrasting colours would be preferred by birds over cryptic ones; 2) fruit consumption would decrease along the edge-interior gradient in forest fragments and 3) highly contrasting fruits would be more detected and consumed in the interior (shaded) than in the edge (brightened) of the forests.

MATERIAL AND METHODS

Study areas

The study was conducted in October 2011 in three semideciduous forests in the Cerrado of Minas Gerais State: Estação Ecológica do Panga (Panga) (19°10’04’’ S and 48°23’41’’ W), Fazenda Experimental do Glória (Glória) (18º57’03’’ S and 48º12’22’’ W) and Fazenda São José (São José) (18°51’35’’ S and 48°13’53’’ W).

The Panga has 409 ha of area, and its vegetation is composed of a mosaic of different formations of the Cerrado, such as grasslands, cerrado stricto sensu, woodland, savanna, dry forests and riparian forests (De Faria Lopes & Schiavini, 2007). The Gloria has ca. 30 ha of area and is mainly composed of woodland and riparian forest surrounded by large agro-pastoral landscapes (Lopes et al., 2011). The São José is a woodland fragment of 20 ha surrounded by eucalyptus forest (Júnior et al., 2011).

Sampling design

We made 594 artificial spherical fruits (about 15 mm wide) using flour, water, vegetable oil, sugar and liquid paraffin (*sensu* Arruda, Rodrigues, & Izzo, 2008). We dyed artificial fruits into three colours: red, dark-blue and yellow. We chose these colours because they contrast distinctly with the background and occur naturally in many ripe fruits and arils that are consumed by frugivorous birds in the study areas and also in the Cerrado, such as those of *Birsonima* sp., *Miconia* sp., *Siparuna* sp., *Protium* sp. and *Calophyllum* sp.

(pers. obs., Camargo et al., 2013). Moreover, these colours produce distinct chromatic and achromatic contrasts.

We attached the fruits to the plant branches by a thin brown polyester line (about 10 mm long). Then, we set all artificial fruits on non-fruiting and/or flowering understory plants with green leaves so that background and fruit presentation was standardised for all experimental colours and among the different areas (*i.e.* Camargo et al., 2014). We hung nine artificial fruits (three of each colour) on the plants. In each area, artificial fruits were set in 22 plants (10m away from one another) along two parallel transects (11 plants per transect), the first at forest edges and the last 100 m away from them (edge-interior gradient).

Fruits were left exposed for 72 hours. Only pecked artificial fruits were considered in the analyses, because either birds or other frugivores, such as monkeys or bats, could have consumed any missing fruits. At forest edges, plants were fully exposed to standard daylight, while from 10 meters onwards plants were under forest shade. We used the illuminance spectra provided by Pavo package (Maia, Eliason, Bitton, Doucet, & Shawkey, 2013), using arguments “forest shade” and “D65”. For all comparisons among fruit colours and the background, contrasts (chromatic and achromatic) did not differ between different illuminant conditions (Table 1), so we used the mean contrast between full sunlight and forest shade for each pair of colours in the analysis.

Fruit colour reflectance

In order to identify the physical properties of the colours studied, reflectance spectra of artificial fruit colours were measured with a spectrophotometer (Jaz, Ocean Optics Inc., Dunedin, FL, U.S.A.) between 300–700 nm, which corresponds to the visible spectrum for birds (Hart, 2001). We measured the reflectance spectra of five fruits of each colour inside a black box, and calculated background reflectance as the mean reflectance of 30 leaves from common shrubs occurring in each area. We measured reflectance as the proportion of a standard white reference tile (WS-1-SS; Ocean Optics, Dunedin, FL, U.S.A.). The distance between the fruit and the optical sensor was held constant for all measurements and the angle of illumination and reflection was set at 45°. All reflectance measurements were processed with SpectraSuite® software.

We analyzed the chromatic and achromatic contrasts using Vorobyev and Osorio (1998) receptor noise-limited model to calculate colour distances. This model takes into account the receptor sensitivity of the four different cones (LWS, MWS, SWS, UVS) that make the visual system of most birds and quantify how each one is stimulated by a given color. Small to medium-sized Passeriformes are the main fruit consumers in the study areas and in the Cerrado, so we used the eye model based on the spectral sensitivities of the blue tit (*Cyanistes caeruleus*) (Cazetta et al., 2009).

In order to calculate single cone stimulation, we estimated quantum catch as:

$$Q_i = R_i(\lambda)S(\lambda)I(\lambda)d\lambda \qquad (1)$$

where the subscript i denotes each single cone, $R_i(\lambda)$ the spectral sensitivity, $S(\lambda)$ the reflectance spectrum of the color and $I(\lambda)$ the illumination spectrum. We corrected for light adaptation and colour constancy by applying the Von Kries transformation (Vorobyev & Osorio, 1998).

To calculate color distances, we first needed to assign a noise value (ω) for each receptor class i, based on its Weber Fraction (v) and on the number of receptors of type i within it (n):

$$\omega_i = \nu_i/n_i \qquad (2)$$

We used the noise values for the blue tit available in Hart, Partridge, Cuthill, and Bennett (2000).

Finally, colour distances can be calculated for tetrachromats by weighting the Euclidean distance of the photoreceptor quantum catches by the Weber fraction of the cones (ΔS).

Table 1. Mean ± SD and p-values of T-tests results for comparisons of chromatic and achromatic contrasts of fruit colours and artificial background under different illuminant conditions (forest shade and standard daylight).

	Chromatic contrast			Achromatic contrast		
	Forest shade	Standard daylight	p	Forest shade	Standard daylight	p
Red	9.041 ± 2.575	9.030 ± 2.553	0.987	7.674 ± 4.100	8.289 ± 4.124	0.599
Yellow	7.910 ± 3.763	8.322 ± 4.041	0.710	14.310 ± 3.428	14.340 ± 3.445	0.969
Dark-blue	5.315 ± 1.002	5.268 ± 1.005	0.869	6.713 ± 3.618	6.879 ± 3.643	0.872

$$\Delta S = \sqrt{\frac{\begin{bmatrix} (\omega_1\omega_2)^2(\Delta f_4 - \Delta f_3)^2 + (\omega_1\omega_3)^2(\Delta f_4 - \Delta f_2)^2 + (\omega_1\omega_4)^2(\Delta f_3 - \Delta f_2)^2 + \\ (\omega_2\omega_3)^2(\Delta f_4 - \Delta f_1)^2 + (\omega_2\omega_4)^2(\Delta f_3 - \Delta f_1)^2 + (\omega_3\omega_4)^2(\Delta f_2 - \Delta f_1)^2 \end{bmatrix}}{[(\omega_1\omega_2\omega_3)^2 + (\omega_1\omega_2\omega_4)^2 + (\omega_1\omega_3\omega_4)^2 + (\omega_2\omega_3\omega_4)^2]}} \tag{3}$$

Colour distances are measured in units of 'just noticeable differences' (jnd). According to Vorobyev and Osorio (1998), discrimination between objects increases as values of ''jnd'' become higher than one.

For achromatic contrasts (ΔL), discrimination among receptors is based solely on brightness differences (Δf_i):

$$\Delta L = \left|\frac{\Delta f_i}{\omega}\right| \tag{4}$$

Data analysis

We performed an ANOVA to assess differences in contrasts among the different fruit colours and the background. We applied a two-way ANOVA on fruit consumption using colour and distance from the edge as factors. We applied a simple linear regression to test the relationship between fruit consumption and the edge-interior gradient. Spectral measurements were analysed on RStudio, using Pavo package (Maia et al., 2013). We used the non-parametric alternatives for the tests described above whenever data did not fit a normal distribution according to Shapiro-Wilk test (Zar, 2010).

RESULTS AND DISCUSSION

The reflectance spectrum of each colour of the artificial fruits is illustrated in Figure 1. All colours used in this study exhibited contrasts higher than one jnd. Red and yellow fruits had the highest chromatic contrasts ($H_{2,72} = 23.49$; $p < 0.001$), and yellow was the highest achromatic contrasting colour ($F_{2,72} = 29.39$; $p < 0.001$; Table 2).

Birds pecked 153 artificial fruits (Table 3). Fruit consumption varied amongst different colours ($F_{2,66} = 6.91$; $p = 0.001$). There was a difference between the consumption of red (2.03 ± 0.15) and yellow fruits (0.96 ± 0.19) ($p = 0.001$) per plant, but no difference between each of them and dark-blue fruits (1.51 ± 0.25) (Figure 2). There was no interaction between fruit colour and distance from the edge ($F_{20,66} = 0.922$; $p = 0.562$). Yellow was the only colour whose consumption varied along the edge-interior gradient, decreasing with distance from the edge (Figure 3).

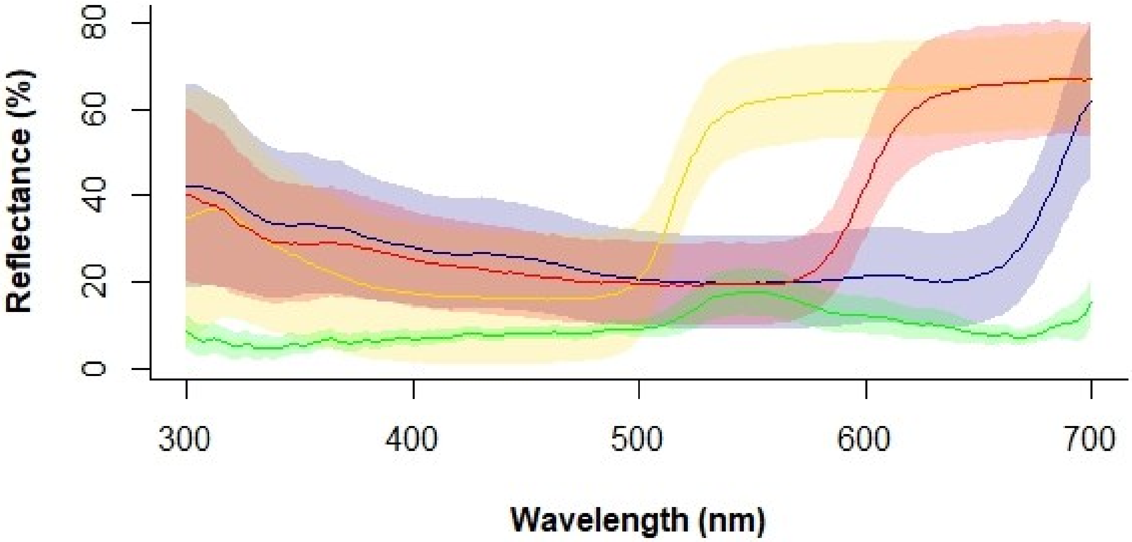

Figure 1. Mean reflectance spectra (lines) and standard deviations (shading) of the yellow, dark-blue and red fruit colours and the green background.

Table 2. Multiple comparisons of mean (±SD) chromatic and achromatic contrasts (*jnds*) between artificial fruit colours and a standardized green background. Calculations were done using data from both illuminance conditions: full sunlight and shade conditions. Different letters in the same column represent statistical significance ($p < 0.05$).

Colours	Chromatic Contrast	Achromatic contrast
Red	9.035 ± 2.564^{A}	7.981 ± 4.108^{b}
Yellow	8.116 ± 3.902^{A}	14.320 ± 3.346^{a}
Dark-blue	5.291 ± 0.201^{B}	6.796 ± 3.624^{b}

Table 3. Number (and percentage) of artificial fruits of four different colours consumed in three semideciduous forests in southeastern Brazil.

	Fruit Colour			
Area	Red	Dark-blue	Yellow	*Total*
Panga	28 (41.79)	20 (29.85)	19 (28.36)	67
Glória	20 (43.48)	11 (23.91)	15 (32.61)	46
São José	19 (47.50)	19 (47.50)	2 (5.00)	40
Total	67 (43.79)	50 (32.68)	36 (23.53)	153

Our results show that each colour had distinct contrasts against the background, albeit colour preferences did not rely on conspicuousness. On the other hand, habitat structure (*i.e.* edge-interior gradient) influenced the role of chromatic and achromatic signals in fruit consumption, at least for yellow fruits.

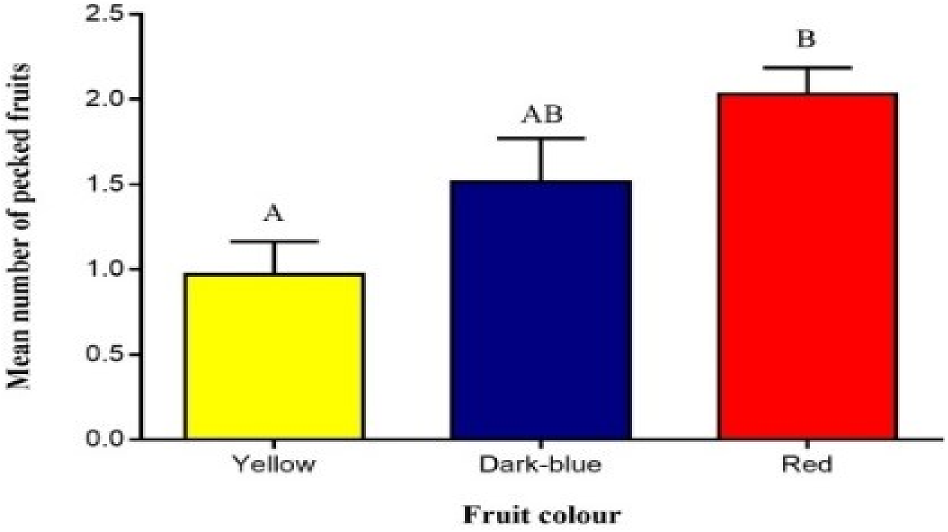

Figure 2. Mean number (±SE) of artificial fruit colours pecked per plant in three disturbed areas in the Cerrado. Different letters represent statistical significance ($p < 0.05$).

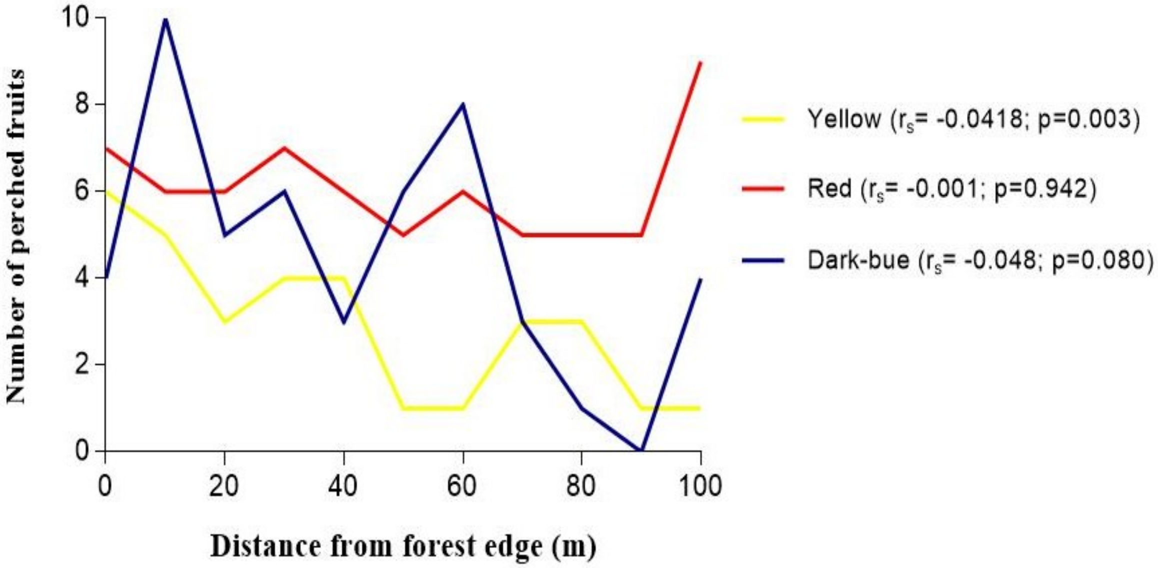

Figure 3. Consumption of three different artificial fruit colours along the edge-interior gradient.

We found that yellow had a high achromatic contrast against the leafy background and that it was the only colour for which consumption reduced along the edge-interior gradient. Birds use achromatic signals when foraging at longer distances and constant light intensity, whereas chromatic signals become more reliable at shorter distances (Schaefer et al., 2006) and at low, inconsistent light intensity (Cazetta et al., 2009). At forest edges, birds have a broader visual field because there are often fewer structures (*e.g.* trees, leaves, branches, etc.) obstructing sight and light is not limited as in the forest interior. This scenario facilitates long distance foraging and the colours with high achromatic contrast, such as yellow, would attract frugivores from a distance. Towards the interior of the forest, foraging activities shift from long-distance to close quarters, owing particularly to limited, poor-quality light availability and denser vegetation in the understory. Therefore, we suggest that, for a single colour, the role of achromatic signals in frugivore attraction is more prominent in edge-like environments, which explains why yellow fruits were consumed less frequently in the forest interior, where high chromatic contrast would be more effective in attracting birds (Camargo et al., 2014; Flörchinger et al., 2010).

Despite its high achromatic contrast, yellow fruits were not consumed preferentially over red and/or dark-blue fruits at forest edges. Although conspicuousness increases the probability of consumption because it allows for easier detection of fruits (Schmidt et al., 2004), colour preferences are much more complex because they also depend on innate and learned behaviours (Burns & Dalen, 2002; Camargo et al., 2015; Honkavaara, Siitari, & Viitala, 2004; Paluh, Kenison, & Saporito, 2015; Schaefer et al., 2007). For instance, some studies show that omnivorous birds have an unlearned preference for red or reddish fruits (Schmidt & Schaefer, 2004; Willson & Comet, 1993) and that fruit preferences match the frequency of natural colours in the community (Duan et al., 2014). Our findings are in accordance with these results, because red was the most consumed fruit colour, followed by dark-blue and yellow. Although yellow is a common fruit colour in the Cerrado (Camargo et al., 2013), red and dark fruits are overrepresented in the forests studied, especially for small, spherical fruits (unpubl. data), which suggests consumption based on learned preference by birds. Other underlying mechanisms for the colour preferences observed in this experiment and that require further investigation are the association of colour and nutritional rewards (Schaefer, McGraw, & Catoni, 2008) and exploitative competition with mammals for yellow fruits (Lomáscolo & Schaefer, 2010; Lomáscolo, Speranza, & Kimball, 2008)

The effects of habitat disturbance on plant-frugivore interactions may go beyond fruit detectability due to physical alterations of the habitat structure, affecting the whole community of foragers (Cordeiro & Howe, 2003; Moran, Catterall, & Kanowski, 2009). Kirika, Farwig, and Böhning-Gaese (2008) demonstrated that environmental disturbances significantly reduced frugivorous richness and functional variation, affecting mainly specialist birds. In disturbed habitats such as those in which this experiment was conducted, generalist, opportunistic, and edge-tolerant species are favoured and may be able to forage in forest edges, as well as in its interior (Cavarzere, Marcondes, Moraes, & Donatelli, 2012), compensating for the loss of disturbance-sensitive species (Menezes et al., 2016). Thus, generalist birds may still overexploit some fruits colours that are predominant in the community (*i.e.* red and dark-blue). Hence, a disruption of seed dispersal may occur since diversity of frugivores foraging in disturbed areas is reduced and dispersal effectiveness varies among different dispersers (Babweteera & Brown, 2009; Li, Li, An, & Lu, 2016).

Advances in the study of sensory ecology have broadened our understanding of how animals sense and interact with their environment (Renoult, Kelber, & Schaefer, 2015). Nonetheless, our knowledge of animal senses and how they mediate plant-animal interactions is still very limited. Although fruit colour is an important feature mediating plant-frugivore interactions, our findings demonstrated that it is not a strong predictor of fruit choice by birds in disturbed areas. Those results demonstrate the need to gather evidence for alternative roles of fruit colour beyond plant-frugivore communication.

CONCLUSION

In this study, we found limited interaction between fruit colour and edge effect in determining frugivorous birds and plants interactions, since only yellow fruits were consumed more often on the edges than on the interior of the fragments. We suggest that the effects of habitat disturbance on the consumption of different fruit colours are mainly indirect, *i.e.* through the alteration of community composition, which would favour the prevalence of generalist species in disturbed environments. Further studies would benefit from the assessment of how edge effects alter habitat structure and whether and how these changes affect light conditions in forest fragments.

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