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Effects of urbanization on plant-animal mutualistic interactions: how do network structure and diversity of interacting partners respond to urban areas?

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Campo Grande

March 2024

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Thesis presented as a requirement for obtaining the PhD title in Ecology, by the Postgraduate Program in Ecology and Conservation, Federal University of Mato Grosso do Sul.

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Dedico este trabalho a minha família e aos
meus orientadores que depositam em mim
apoio, confiança e me incentivam nessa
trajetória acadêmica cheia de desafios.

Agradecimentos

Agradeço a Universidade Federal de Mato Grosso do Sul e ao Programa de Pós-Graduação em Ecologia e Conservação por oportunizar a realização do Doutorado, bem como a CAPES pela bolsa e a Rufford Foundation pelo apoio durante o trabalho de campo. Sou grata a minha orientadora Andréa Cardoso de Araujo por me guiar nessa fase acadêmica onde aprendemos a ser cada vez mais independentes na pesquisa, assim como ao meu co-orientador Pietro, ambos me deram suporte para que esse trabalho tenha chegado até essa fase. Como é gratificante ter essa oportunidade de trabalhar ao lado de pessoas que há tempos admiramos! Agradeço também ao colaborador José Carlos Pena pelas contribuições, troca de ideias, uma pessoa que me ensinou muito sobre ecologia urbana.

Sou grata a minha família, principalmente aos meus pais, Isalete e Valdenir, pelo apoio e confiança. Existem caminhos que percorri até aqui, sem ajuda deles, chegar até essa fase não seria possível.

Agradeço ao Instituto de Meio Ambiente de Mato Grosso do Sul, Associação Nipo Brasileira de Campo Grande, Museu José Antônio Pereira, Secretaria Municipal de Cultura e Turismo, Fundação Municipal de Esportes, Base Aérea de Campo Grande e a Universidade Católica Dom Bosco por dar suporte e autorizar a coleta de dados em suas dependências. Especialmente, a Katiuscia, Adélia, Leonardo, Osias, Heloisa e Paulinho por serem prestativos, viabilizar o meu trabalho e oferecer segurança durante a coleta de dados. Sou imensamente grata também a Simone Mamede e Maristela Benites pelo apoio cultural e pelas dicas na fase de divulgação dos resultados deste trabalho.

Chegar numa cidade diferente para começar um doutorado e ser bem acolhida é uma diferença e tanto! Muito obrigada Karina Paulinelli e Karine Munck pela amizade e por me acolherem e fazerem me sentir melhor no começo da minha estadia em Campo Grande, principalmente em época crítica de Pandemia.

Agradeço as pessoas que me acompanharam no campo, ao fazerem isso me ofereceram segurança e tornaram o campo mais leve. Principalmente, Tainá Boschi, Gabriel Tirintan, Carlos Alberto Castro, Hugo Cabral, Evaldo Benedito de Souza, Beatriz Carneiro e Nayara Morais, que foram repetidas vezes comigo a campo, muito obrigada! O campo se tornou mais divertido com vocês ao meu lado. Além disso, também agradeço aos colegas Fábio Bolzan e ao Pablo Dutra pelas dicas para trabalhar com o QGIS; e ao prof. Rafael Antunes Dias com ajuda para extrair índice de diversidade filogenética.

Sou grata ao prof. Flávio Macedo Alves, uma pessoa querida e que foi muito prestativo para a identificação das plantas, parte fundamental de meu trabalho. Agradeço também ao prof. Jeferson Vizentin-Bugoni, um amigo, que me orientou no mestrado e tem me apoiado desde aquela época até hoje.

Incrível como em quatro anos de doutorado se conhece tanta gente legal. Então, por fim, aos meus colegas Pri, Pablo, Nath, Sofi, Mari, Aléxia, Carol, Giu, Diogo, Hellen, Jeane, Dani, Bogoni, Karen, prof. Rudi, Alêny, Alan, Lili e tantos outros, agradeço pelas risadas, pela amizade, apoio, pelas conversas durante pausa do cafezinho, pela parceira pra ir pro bar chorar, pra celebrar ou mesmo pra rir. Todos foram imensamente importantes para que esse período fosse agradável para mim.

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General abstract

The expansion of urbanization worldwide increases the importance of the management of urban green areas to preserve ecosystem services derived from mutualistic plant-animal interactions. While interactions in urban areas are generally understudied, even less is known in tropical regions. Therefore, the objective of this thesis is to evaluate how mutualistic interactions between plants and animals, and distinct components of diversity (taxonomic, functional, and phylogenetic) of these groups respond to urban landscapes. Specifically, I aimed to (i) evaluate how the urbanization characteristics of different cities around the world affect the occurrence of frugivorous birds; (ii) review studies on the effects of urbanization on mutualistic plant-frugivorous animal interactions in tropical urban areas; and (iii) evaluate how the structure of frugivorous bird-plant interaction networks, and the diversity of interacting species varied among green areas under different landscape contexts in the city of Campo Grande-Brazil. Through the literature review we showed that: (i) most populous cities, recently founded, and at low latitudes harbor a greater richness of obligate and partial frugivores. Furthermore, we showed that (ii) exotic fruits are an important portion of the diet of frugivores, which present a great overlap in the use of resources in tropical urban areas. Finally, (iii) by testing the effects of urbanization empirically we show that landscapes covered by trees and shrubs isolated on impermeable surface matrices positively influence measures of diversity of species in the networks. These, in turn, influence the modularity (partition in the use of resources). Based on the results found across the three chapters, we suggest management actions in urban areas to improve the maintenance of interactions between plants and frugivorous birds. Specifically, we recommend (i) planting native plants to reduce the use, and consequently, the spread of exotic fruits through their consumption by these birds, (ii) considering plants' fruiting phenology to ensure resources are available throughout the year, and (iii) creating habitat patches where wild fauna can take refuge in green areas. Furthermore, filling green areas with plants that have different functional characteristics (such as large and small fruits, tall and small plants) to contribute to a greater partition in the use of resources between species. Finally, the results suggest that green infrastructure is valuable for preserving frugivorous species, especially in tropical cities that retain high species diversity due to general biogeographical patterns, and in recently founded cities where afforestation of green areas is encouraged.

Keywords: frugivory, urban area, urban landscape, city, plant-frugivore bird, ecosystem functions, novel ecosystems.

Resumo geral

A expansão da urbanização em escala global aumenta a importância do manejo das áreas verdes urbanas para preservar serviços ecossistêmicos provindos das interações mutualistas planta-animal. Ainda que essas interações em áreas urbanas sejam geralmente pouco estudadas, menos ainda se conhece nas regiões tropicais. Portanto, o objetivo deste trabalho é avaliar como as interações mutualistas entre plantas e animais e distintos componentes da diversidade (taxonômica, funcional e filogenética) desses grupos respondem a mudanças na estrutura de paisagens urbanas. Especificamente, busquei (i) avaliar como as características de urbanização de diferentes cidades ao redor do mundo afetam a ocorrência de aves frugívoras; (ii) revisar estudos sobre os efeitos da urbanização nas interações mutualistas plantas-animais frugívoros em áreas urbanas tropicais; e (iii) avaliar como variam a estrutura das redes de interações aves-plantas frutíferas e a diversidade de espécies interagindo variaram entre áreas verdes sob diferentes contextos paisagísticos na cidade de Campo Grande-Brasil. Mostramos através da revisão bibliográfica que: (i) as cidades mais populosas, fundadas recentemente e em baixas latitudes abrigam uma maior riqueza de frugívoros obrigatórios e parciais. Além disso, mostramos que (ii) as frutas exóticas são uma parte importante da dieta dos frugívoros, que apresentam grande sobreposição no uso de recursos em áreas urbanas tropicais. Finalmente, (iii) ao testar empiricamente os efeitos da urbanização, mostramos que paisagens cobertas por árvores e arbustos isolados em matrizes de superfície impermeável influenciam positivamente as medidas de diversidade de espécies nas redes. Estes, por sua vez, influenciam a modularidade (partição no uso de recursos). A partir dos resultados encontrados nos três capítulos, sugerimos ações de manejo em áreas urbanas para melhorar o desempenho das interações entre plantas e animais frugívoros. Especificamente, recomendamos (i) o plantio de plantas nativas de modo a reduzir o uso e, consequentemente, a expansão de espécies exóticas através do seu consumo por animais, (ii) considerar a fenologia de frutificação das plantas para garantir a disponibilidade de recursos durante todo o ano, e (iii) criar manchas de habitat onde a fauna silvestre possa se refugiar em grandes áreas verdes. Além disso, preencher as áreas verdes com plantas que apresentam diferentes características funcionais (como frutos grandes e pequenos, plantas altas e baixas) para contribuir na maior partição no uso de recursos entre espécies. Por fim, os resultados sugerem que uma infraestrutura verde é valiosa para a retenção de espécies frugívoras, especialmente em cidades tropicais que retêm alta diversidade de espécies devido aos padrões biogeográficos gerais, e em cidades fundadas recentemente, onde há maior incentivo à arborização de áreas verdes.

Palavras-chave: frugivoria, área urbana, paisagem urbana, cidade, planta-ave frugívora, funções do ecossistema, novos ecossistemas.

General introduction

Urbanization has been rapidly spreading globally, leading to the expansion of impermeable surfaces and human constructions, such as asphalted areas and buildings (Eigenbrod et al. 2011, Ramalho & Hobbs 2012, Forman 2016). The expansion of these densely built and inhabited systems in space (i.e., urban systems) has fragmented natural habitats, resulting in numerous environmental consequences, such as rising temperatures, increased greenhouse gas emissions, occurrence of floods, as well as a decline in the capacity to harbor biodiversity which, in turn, perform several ecosystem functions (Nowak & Walton 2005, Forman 2016, Pickett & Cadenasso 2017, Zari 2019). However, such problems can be alleviated by increasing green areas and implementing actions aimed at sustainability in cities (Eigenbrod et al. 2011). Thus, the expansion of urbanization emphasizes the importance of studies in urban areas, for better planning and management of green infrastructure – defined as a network or set of vegetated areas in urban regions (Breuste et al. 2013, FAO 2016). Such green areas, through the ecosystem services they provide, support human health and environmental quality (Nowak & Walton 2005).

Previous studies have shown patterns of how species diversity response to the spatial gradient to impermeable surface and tree cover within the urban perimeter (Amaya-Espinel et al. 2019, Souza et al. 2019). Particularly, an increase in the coverage of tree (green areas) triggers positive bird richness responses (Amaya-Espinel et al. 2019, Souza et al. 2019). Elements of green areas, such as parks, squares, gardens, vegetation corridors, small remnants, and tree-lined streets, are important places that shelter species performing various ecosystems functions, such as seed dispersal and pollination (Cruz et al. 2013, Maruyama et al. 2019). However, appropriate management strategies are necessary for these elements to fulfill their ecological functions (Aronson et al. 2017, Lepczyk et al. 2017). In this sense, the importance of managing these spaces has been recognized and has become increasingly significant (Cruz et al. 2013, Gelmi-Candusso & Hämäläinen 2019).

The historical development of urbanization varies between different cities, resulting in a heterogeneity of urban landscapes in different regions of the world. These cities differ in aspects such as the period since the beginning of urbanization, size of the urban perimeter, human population size and type of land use, for example (Ramalho & Hobbs 2012, Pickett & Cadenasso 2017). Analyzing aspects that differ between cities on a broader scale is an approach that has provided significant insights into the ecology of urbanized systems (Lepczyk et al. 2017, Richardson et al. 2022). This enables the synthesis of results obtained regarding the anthropic effect on species diversity and mutualistic frugivore-plant interactions in urbanized environments.

The species comprising a community exhibit varying tolerances to withstand environmental changes, such as urbanization (Solé & Montoya 2001, Memmott et al. 2004, Sol et al. 2014). Therefore, changes to the landscape can lead to the local extinction of species unable to tolerate these modified environments (Nowak & Walton 2005, Sol et al. 2014), resulting in the species loss that play crucial functional roles in ecological interactions (Solé & Montoya 2001, Rocha & Fellowes 2018). However, there are few studies that empirically investigate the mechanisms associated with urbanization in mutualistic animal-plant interactions, such as plant-frugivore interactions and the diversity of members of these interactions (Mubamba et al. 2022, Wang et al. 2023, Vissoto et al. 2023).

Birds, when consuming fruits, can perform important ecosystem functions, such as seed dispersal (Sekercioglu 2006), a process that relies on the availability of this food resource to support the persistence of populations of these birds (Jordano et al. 2004).

Similarly, fruit removal by frugivorous birds can have effects on the persistence, distribution, and density of plant populations, influencing species coexistence within the community (Levine & Murrell 2003, Jordano et al. 2004, Parchman & Benkman 2007). Therefore, it is expected that a greater diversity of birds and plants is fundamental for maintaining the stability of ecosystems, even in urban areas.

The matching characteristics between interacting partners (e.g., beak size vs. fruit size, or wing shape vs. foraging stratification) have effects on the structure of interaction networks (Dehling et al. 2014). Therefore, grouping species according to their functional characteristics is essential for understanding the persistence of ecosystem functions, interacting partners and the robustness of interaction networks (Dehling et al. 2016, Pigot et al. 2016). The rapid growth of urbanization strongly affects the loss of wild species and can lead to the functional homogenization of birds in general (Nowak & Walton 2005, Carvajal-Castro et al. 2019). However, there are few empirical studies that test the relationships between urban land use and partition in the use of resources and how the variation in matching characteristics and phylogenetic groupings can be linked to this.

Different spatial contexts have the potential to influence species interactions, as they can affect both animals and plants (Alvey 2006, Dehling et al. 2016, Carvajal-Castro et al. 2019). Densely forested areas tend to harbor a greater diversity of frugivores compared to less forested areas, as a lower supply of resources is expected in more anthropic sites (Carbó-Ramírez & Zuria 2011, Souza et al. 2019). Thus, landscape context influencing species composition and abundance may have implications for the frequency of interactions between pairs of species, as well as the identity of interacting partners (Devictor et al. 2010, Poisot et al. 2012, Pigot et al. 2016, Gleditsch et al. 2017). However, we know little about the effects of this urban gradient, which ranges from densely built urban to green areas (Carvajal-Castro et al. 2019), on the structure of these interactions.

One way to investigate the interactions that occur between birds and fruits is by using bipartite network analysis (Lewinsohn et al. 2006). This approach has been widely employed to detect structural patterns, resource partitioning and to assess specialization of its components, enabling the identification of the mechanisms underlying the maintenance of communities (Blüthgen et al. 2006, Lewinsohn et al. 2006). Several processes can explain the structural patterns of interaction networks, such the complementarity of functional traits or the phylogenetic relationships between component species (Donatti et al. 2011). Analyzing the structural properties of interaction networks provide insights into the stability of communities of interacting organisms (Carlo & Yang 2011), offering support for conservation efforts and guidance in the development of management plans.

Studies have shown that cities with a higher density of buildings tend to have more homogeneous communities, with a predominance of species adapted to living in open and disturbed areas (Sol et al. 2014, Carvajal-Castro et al. 2019, Maruyama et al. 2019). While more preserved areas are home to a greater diversity of species (Schneiberg et al. 2020). Several studies have evaluated the impact of urbanization on animal diversity (Nowak & Walton 2005, Staggemeier & Galetti 2007, Carvajal-Castro et al. 2019, Zari 2019), but there are few studies that show how changes in the landscape structure induced by urbanization can impact the structure of frugivorous plant-bird interaction networks and, specifically, how they affect community descriptors of interacting species (such as taxonomic, functional, and phylogenetic diversity) (Schneiberg et al. 2020, Vissoto et al. 2023).

In this thesis we investigated how urbanization affects the function of seed dispersal, by examining the impact of urban systems on frugivorous animals and their interactions with plants. The thesis is divided into three chapters, each investigating different aspects related to this topic, as follows:

In the first chapter, we evaluated the effects of the period of urbanization, human population size, and impervious surface coverage of cities on the occurrence of frugivorous birds on a global scale. We also tested whether latitude and elevation influence the number of bird species with different levels of fruit dependence.

In the second chapter, we conducted a bibliographical survey to explore the patterns resulting from interactions between plants and frugivorous birds in tropical urban areas. Then, we additionally identify gaps in knowledge. Additionally, we provide recommendations for desirable management actions to conserve biodiversity and its interactions in urban areas.

In the third chapter, we empirically evaluated the effects of impervious surface coverage and tree cover on the metrics of interaction networks associated with partitioning in the use of resources between plants and frugivorous birds. Additionally, we assessed how these landscape characteristics affect the taxonomic, functional, and phylogenetic diversity of the birds and plants in the networks. Finally, we investigated which facets of diversity measured here are important for the robustness of the interaction network, aiming to suggest priority management actions.

Chapter 1 - Increasing human population size, recent urbanization, and lower latitudes relates with higher occurrence of obligate frugivores in urban landscapes worldwide

Increasing human population size, recent urbanization, and lower latitudes relates with higher occurrence of obligate frugivores in urban landscapes worldwide

Abstract

Urban ecology has stimulated interest in understanding patterns and drivers of biodiversity within and across cities. Although it is known that frugivores are a vulnerable group to the expansion of urbanization, few studies have investigated how urbanization affects species with different dependencies on fruits. We conducted a survey in the literature to provide an overview of the occurrence of frugivore birds in urban areas around the world. We investigated how the number of species with different levels of fruit dependence is influenced by period of urbanization, impervious surface coverage (urbanization settings) and by latitude and elevation (biogeographic settings). We found that: (i) urban systems are dominated by opportunistic species in fruit consumption, (ii) obligate and partial frugivores increase in cities with a recent history of urbanization and in low latitudes. Surprisingly, (iii) obligate frugivores increased in cities with larger human population sizes. Our study shows that urban ecosystems are home to a greater number of bird species that tend to consume fruits opportunistically, acting as potential seed dispersers, but may also be home to some specialized species. Finally, our survey suggests that biophilic characteristics of urbanization combined with biogeography govern the number of frugivorous bird species in urban environments.

Keywords: frugivore birds, fruit-eating birds, omnivore birds, opportunist birds, cities.

Resumo

A ecologia urbana estimulou o interesse na compreensão dos padrões e impulsionadores da biodiversidade dentro e entre as cidades. Embora se saiba que os frugívoros são um grupo vulnerável à expansão da urbanização, poucos estudos investigaram como a urbanização afeta espécies com diferentes dependências de frutos. Realizamos um levantamento na literatura para fornecer uma visão geral da ocorrência de aves frugívoras em áreas urbanas ao redor do mundo. Nós investigamos como o número de espécies com diferentes níveis de dependência de frutos é influenciado pelo período de urbanização, cobertura de superfície impermeável e tamanho populacional humano (características de urbanização) e pela latitude e elevação (configurações biogeográficas). Descobrimos que: (i) os sistemas urbanos são dominados por espécies oportunistas no consumo de frutos, (ii) os frugívoros obrigatórios e parciais aumentam em cidades com histórico recente de urbanização e em baixas latitudes. Surpreendentemente, (iii) os frugívoros obrigatórios aumentaram em cidades com maior população humana. Nosso estudo mostra que ecossistemas urbanos abrigam maior número de espécies de aves que tendem a consumir frutos de forma oportunista atuando como potenciais dispersores de sementes, mas podem abrigar também algumas espécies especializadas. Finalmente, nossa pesquisa sugere ainda que as características biofílicas da urbanização, combinadas com a biogeografia, governam o número de espécies de aves frugívoras em ambientes urbanos.

Palavras-chave: aves frugívoras, aves consumidoras de frutos, aves onívoras, aves oportunistas, cidades.

Introduction

Given the rapid rates of human population growth and urbanization, one of the major current ecological challenges is to understand the effects of these anthropogenic changes on biodiversity (Cincotta et al. 2000, Nowak & Walton 2005, Eigenbrod et al. 2011). The conversion of natural habitats into impermeable areas related to human infrastructure, e.g., houses, commercial centers, buildings, streets, and roads, has triggered the extinction of many species, especially those in more vulnerable groups (Solé & Montoya 2001, Nowak & Walton 2005, Sol et al. 2014, Rocha & Fellowes 2018, Souza et al. 2019). In this context, previous studies have shown a reduction in species richness in communities occurring in urban spaces when compared to those recorded in natural areas (Peabotuwage et al. 2019, Gorosito & Cueto 2020). This can result in biotic homogenization (McKinney 2006, Gagné et al. 2016), and in the imbalance of ecosystem functions, such as seed dispersal (Gelmi-Candusso & Hämäläinen 2019, Vissoto et al. 2023).

Fruits are an important food source for many birds (Kissling et al. 2009), and frugivory constitutes the first step for seed dispersal, which is essential for the maintenance and regeneration of vegetation (Coates-Estrada & Estrada 1988; Bascompte & Jordano 2007; Vissoto et al. 2019). Globally, tropical regions with low elevation harbor most of the diversity of frugivorous animals (Fleming et al. 1987, Rahbek 1997). Birds are the numerically the most important group of frugivores (Jordano 2000), and 90% of all frugivorous bird species are distributed in the tropics (Kissling et al. 2009). Despite their importance, frugivorous birds are among the most affected bird guilds when concerning urbanization (Peabotuwage et al. 2019, Souza et al. 2019). The increase of impermeable surfaces decreases the diversity of fruiting plants, while other food items such as insects, grains, pet food, and food scraps may become more available (Ottoni et al. 2009). Therefore, modifications in resource identity related to urbanization may favor omnivorous and opportunistic birds at the expense of more specialized frugivorous species (Chace & Walsh 2006, McKinney 2006, Shochat et al. 2006, Amaya-Espinel et al. 2019, Carvajal-Castro et al. 2019). Because some species depend solely on fruits for their survival, while others depend on this resource on a lesser scale (Walker 2007, Wilman et al. 2014), these changes imply distinct responses of frugivorous birds to urbanization. Despite the importance of fruit-eating birds for the conservation of seed dispersal ecological function, we still lack a synthesis of how urbanization influences birds with different dependencies on fruits in their diets.

In this study, we compiled a global dataset of fruit-eating birds inhabiting cities using published literature to characterize their diversity across urban landscapes. We asked whether birds with different degrees of dependence on fruits are equally affected by urbanization. Specifically, we asked: (1) whether the richness of fruit-eating birds with different levels of dependence on fruits in their diets differ in urban areas across the latitudinal and elevational gradients. Although urban sprawl can cause a decline in species richness, we expect communities at lower latitudes and elevation to have greater numbers of obligate frugivore birds than in higher latitudes and elevation, as the tropical zone encompasses regions with greater productivity and diversity of fruit plants (Kissling et al. 2009). Similarly, elevation is associated with some climatic factors, such as temperature and resource availability, which in turn influence patterns of frugivore bird species richness (Price et al. 2014, He et al. 2019). Therefore, cities located in tropical regions and low elevations should probably still conserve more obligate frugivore birds. We also assessed (2) whether the variation in the diversity of fruit-eating birds among cities is related to the characteristics of the urban settlement, including human population size, period of urbanization, and the impermeable surface cover of the city. Given that obligate frugivores are sensitive to habitat fragmentation and require abundant fruit plants (Walker 2007, Blendinger et al. 2008, Morante-Filho et al. 2018), we would expect them to be more frequent in cities with lower impermeable surface cover. Additionally, cities that have undergone a recent urbanization process and are sparsely populated may still retain a greater diversity of obligate frugivorous birds. Therefore, we expect that cities with lower coverage of impermeable surface, with more recent urbanization time, and less populated will be home to a greater number of obligate frugivores.

Understanding how fruit-eating birds with different dependencies on fruits are affected by urbanization is the first step towards planning biophilic cities that conserve important ecosystem functions, here seed dispersal, essential for maintaining the natural recovery capacity of terrestrial ecosystems. Currently, not much is known about how birds with different dependencies on fruits are affected by urbanization, going beyond broad categorizations that limit a clear assessment of urban ecosystems to maintain essential ecosystem functions across broad latitudinal and altitudinal gradients. Therefore, we hope that the results of this study will contribute to urban planning. Investigating patterns and adjacent processes at the city scale that affect the presence of birds with varying dependencies on fruits, can provide us with insights specifically into how those responsible for consuming the highest and lowest fruit rates respond to urbanization. This may have implications for the spread of propagules in these areas, as many of these birds act as seed dispersers.

Methods

Sampling procedures

We searched for published papers on Scopus and Web of Science using the following keywords: “*avian*” OR “*bird*” AND “*urban*” OR “*anthropic area*” OR “*urbanization*” OR “*urbanisation*” OR “*anthropization*” OR “*city*” OR “*town*”. We additionally checked the references listed in the selected studies in search of other publications related to the topic. We did not impose any restriction on the date of the publications, and the last search was conducted on the 28th of April 2020.

During the systematic review, we applied the following criteria for the inclusion of articles in this survey and included only studies that: (a) were carried out in at least one urbanized area (following the definitions of MacGregor-Fors 2011), (ii) provided primary data (i.e., birds' species list), (iii) included field-based sampling, and (iv) informed the locality sampled (e.g., city or geographic coordinates). We did not include articles that: (i) did not fit the urbanization terms proposed by MacGregor-Fors (2011), i.e., collected data only in transitional sites between peri-urban and non-urban areas or between peri-urban areas and large natural remnants adjacent to city limits; (ii) focused on a single species or a specific group of birds (e.g. migratory species); (iii) used repeated data (i.e., the same authors used the same database to carry out two or more studies in the same urban areas). In these cases, we included only one article and removed the replicates. Furthermore, we did not include articles that (iv) used citizen science data, atlas, literature data, or used other types of data, with little sampling standardization (for example, collected by more than one person with different sampling efforts); (v) reviews; (vi) did not distinguish the listing of birds by area of occurrence in cases where the data collected included non-urban areas (outside city limits); (vii) present a list of birds with only popular names, hence not allowing to consistently identify the species; (viii) carried out on a regional spatial scale (i.e., involving more than one city), but that did not report the distribution of birds among cities; (ix) did not detail the sampling method and/or distribution of samples in the city.

We obtained data on the richness of birds from 157 cities in 199 studies, where the data comes from collections in various types of habitats, such as squares, streets, parks and remnants. Among these cities, 35 of them were duplicates (i.e., data from birds were collected in the same city by two different studies), eight cities were triplicate, four cities were quadrupled, and three cities were quintupled. In these cases, only one study of these cities was kept in our analysis. We used some hierarchical criteria related to the sampling effort and selected the study that presented (i) the largest number of sites sampled, as it potentially has a better description of the richness of birds in the city. In cases in which the studies had a similar number of sampled areas in the same city, we considered other criteria that can affect sampling comprehensiveness of the richness of birds (ii) the greater distance between the sampled areas, (iii) the longer sampling period, (iv) the most recent study, and finally (v) the study that better detailed the sample design.

Data collection

From each selected study we extracted the number of bird species and filtered fruit-eating species using Wilman et al. (2014). Fruit-eating birds included all species consuming fruits, irrespective of the proportion of fruits in their diets. These species were then classified according to their proportion of fruit consumption (Kissling et al. 2009) in (i) obligate frugivores - species that have the largest fraction of their diets composed of fruits (70-100%), (ii) partial frugivores - species in which fruits make up half of their diet (40-60%), and (iii) opportunists - species that include a small fraction of fruits in their diets (less than 30%).

Predictor variables

We recorded the geographical coordinates of the city center point for all study sites to assess their absolute latitude and elevation. We use geographic coordinates to also analyze the distribution of studies across the globe and discuss the knowledge bias across them. We considered ‘tropical’ those areas located between the Tropic of Capricorn (23°26’13.4” S) and the Tropic of Cancer (23°26’13.4” N). To characterize cities, we recorded their human population size (i.e., the number of inhabitants). In addition, their period of urbanization, calculated by subtracting the founding date by the year 2023, was used to describe the historical disturbance of the area; in the case of older cities (i.e., sites dating back to settlement B.C.), we considered the year in which the city started to have a commercial movement as its date of foundation. This information was collected from search engines (Google). Finally, we calculated the impermeable surface cover (km^2) of each city, defining a 50km radius buffer surrounding the centroid of each city. We used the buffer surrounding each city as a mask to extract the land use/land cover classes from the map developed by Hansen et al. (2022) based on Landsat imagery of 2019 with a 30m resolution (we used the strata version, which describes 19 land use/land cover classes). We then converted the raster surface into a shapefile and selected the major urban polygon that was generated and calculated its area size to estimate the continuous impermeable surface cover of each city. For each city, we checked if the main urban area was completely included within the 50km radius buffer before the masking procedure. We made small adjustments for large metropolises, such as Paris (France), as its urban area surpassed the 50km radius buffer.

Statistical analyses

We made lists of all the birds for each city and filtered out all species that consumed fruit (Wilman et al. 2014) and used a binary approach for standardization, as not all surveyed publications presented quantitative information. We then quantified the number of species in each of the three levels of dependence in fruit consumption for each city (Wilman et al. 2014). Next, we used the number of sample areas to analyze if the variation in overall richness of fruit-eating birds and across the three dependency levels is due to sampling bias. First, we performed this correlation for all cities, then we separated tropical and non-tropical cities and tested the correlation again. The results were not significant, that is, the number of locations sampled was not correlated with the number of frugivorous species (Supplementary Material, Table S1).

We used generalized linear models (GLM) to test if (i) the overall richness of fruit-eating birds, (ii) the richness of obligate frugivores, (iii) the richness of partial frugivores, and (iv) the richness of opportunistic fruit-eating birds (response variables) was related to absolute latitude, elevation, the human population size, period of urbanization, and impermeable surface cover (predictor variables). We log-transformed the human population size and impermeable surface cover to avoid data overdispersion. We checked for multicollinearity between the predictor variables using *corrplot* package (Naim et al. 2014) and a variation inflation factor (VIF) test, using *usdm* package (Wei & Simko 2017). We assume VIF ≥ 10 as a benchmark for collinearity (Dorman et al. 2013, James et al. 2013). We highlight here that the predictor variables were not correlated with each other (Supplementary Material, Figure S1). Model fitting was performed using the *glm.nb* function of the R-Package *MASS* (Venables & Ripley 2002), considering a negative binomial distribution for all models because the response variable were zero-inflated.

Results

We recorded 1,917 species of birds across 141 studies distributed in 157 cities all over the world (Fig. 1; Supplementary Material, Table S2). Among them, 793 are fruit-eating species (41.37%), ranging from 3–70 (24.06 ± 14.35), and 1,124 species (58.64%) have diets based on other items. Among the fruit-eating birds, only 8.20% are obligate frugivores and varied from 0–12 (1.22 ± 2.01; n= 65), 20.55% are partial frugivores ranging from 0–21 (3.83 ± 4.22; n=163) and 71.25% are opportunistic fruit-eating species and varied from 1–56 (19.01 ± 11.02; n=565). The city of São Paulo (Southeastern Brazil) presented the greatest overall richness of fruit-eating (n=70), and partial frugivorous (n=21) birds, whereas Palmas (Central West of Brazil) presented the greatest richness of obligate frugivores (n=12), and Ciudad Juárez (Northern Mexico) presented the greatest richness of opportunistic fruit-eating species (n=56). Most of the recorded studies refer to cities in the Temperate zone in the North hemisphere (55%, n = 86 cities, Fig. 1). The Temperate zone in the South hemisphere, and the Tropical zone in the North and South hemispheres presented similar numbers of sampled cities (n=23, n=20, and n=28 cities, respectively).

The period of urbanization of cities ranged from 26 to 3923 years (682.92 ± 719.54), the human population size ranges 10,000 – 24,870,895 inhabitants (1,970,806 ± 3,843,999), impermeable surface cover ranged 5.44 – 22,659.21 km^2 (1,683.36 ± 3,078.34), absolute latitude ranged 1.33 – 66.72 (34.26 ± 14.90), and elevation varied between 3 – 3,773 meters a.s.l. (348.25 ± 576.72). Cities with longer periods of urbanization are concentrated in Europe, the Middle East, and East Asia (including cities with more than 1500 years of continued occupation). The capitals of countries were usually the most populous cities and with more impermeable surface cover since they are usually metropolitan areas.

The richness of obligate frugivores increases with human population size and decreases with the increase in the time since urbanization begins (period of urbanization) and with absolute latitude (Table 1, Figure 2). The richness of partial frugivore species decreased with the increase in the period of urbanization and absolute latitude. The overall richness of fruit-eating birds and the richness of opportunistic fruit-eating birds were not influenced by any predictor. Elevation and the impermeable surface cover was not associated with the richness of any classes of fruit-eating birds.

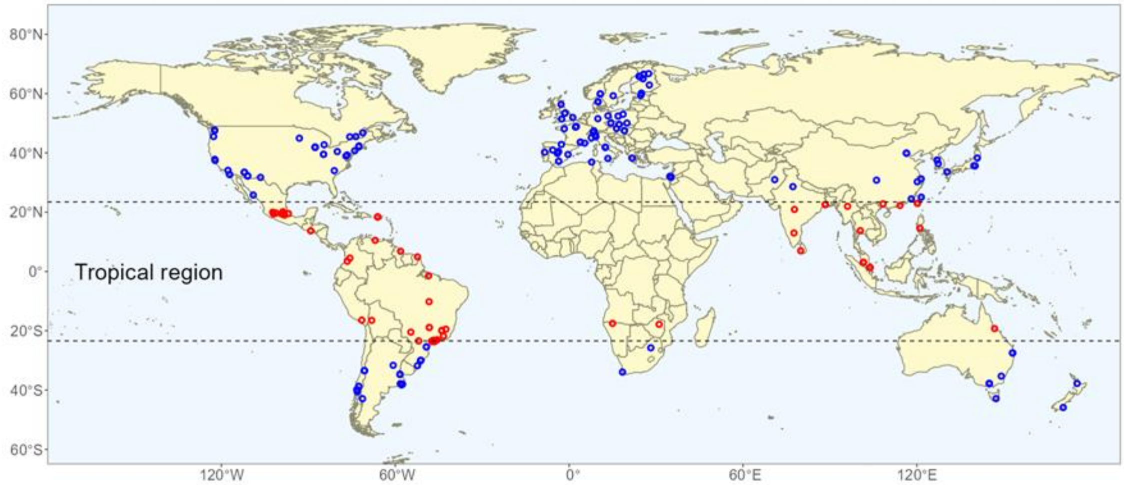

Figure 1 – Global geographic distribution of studied cities included in the analysis of fruit-eating birds across tropical (red circles, n = 48) and non-tropical (blue circles, n = 109) regions. We consider 'tropical' those areas located between the Tropic of Capricorn (23° S) and the Tropic of Cancer (23° N).

Table 1. Influence of urbanization variables: (Impermeable surface cover (log), human population size (log), period of urbanization) and biogeography variables (absolute latitude and elevation) on the richness of fruit-eating birds in the three levels of fruit dependence. Predictive variables that significantly influenced response variables are highlighted in bold.

Response variable	**Predictor variable**									
	Impermeable surface cover (log)		Human population size (log)		Period of urbanization		Absolute latitude		Elevation	
	Estimate	P-value	Estimate	P-value	Estimate	P-value	Estimate	P-value	Estimate	P-value
Overall richness of fruit-eating birds	0.04830	0.1639	0.04460	0.2331	-0.00003	0.6387	-0.00760	0.0583	0.00006	0.4528
Obligate frugivores	-0.04240	0.6014	**0.22230**	**0.0090**	**-0.00170**	**<0.001**	**-0.05300**	**<0.001**	0.00006	0.6496
Partial frugivores	0.01470	0.7761	0.09980	0.0671	**-0.00020**	**0.0444**	**-0.04340**	**<0.001**	-0.00010	0.2688
Fruit-eating opportunistic	0.05750	0.1060	0.03910	0.3080	0.00001	0.8610	0.00190	0.6520	0.00010	0.1490

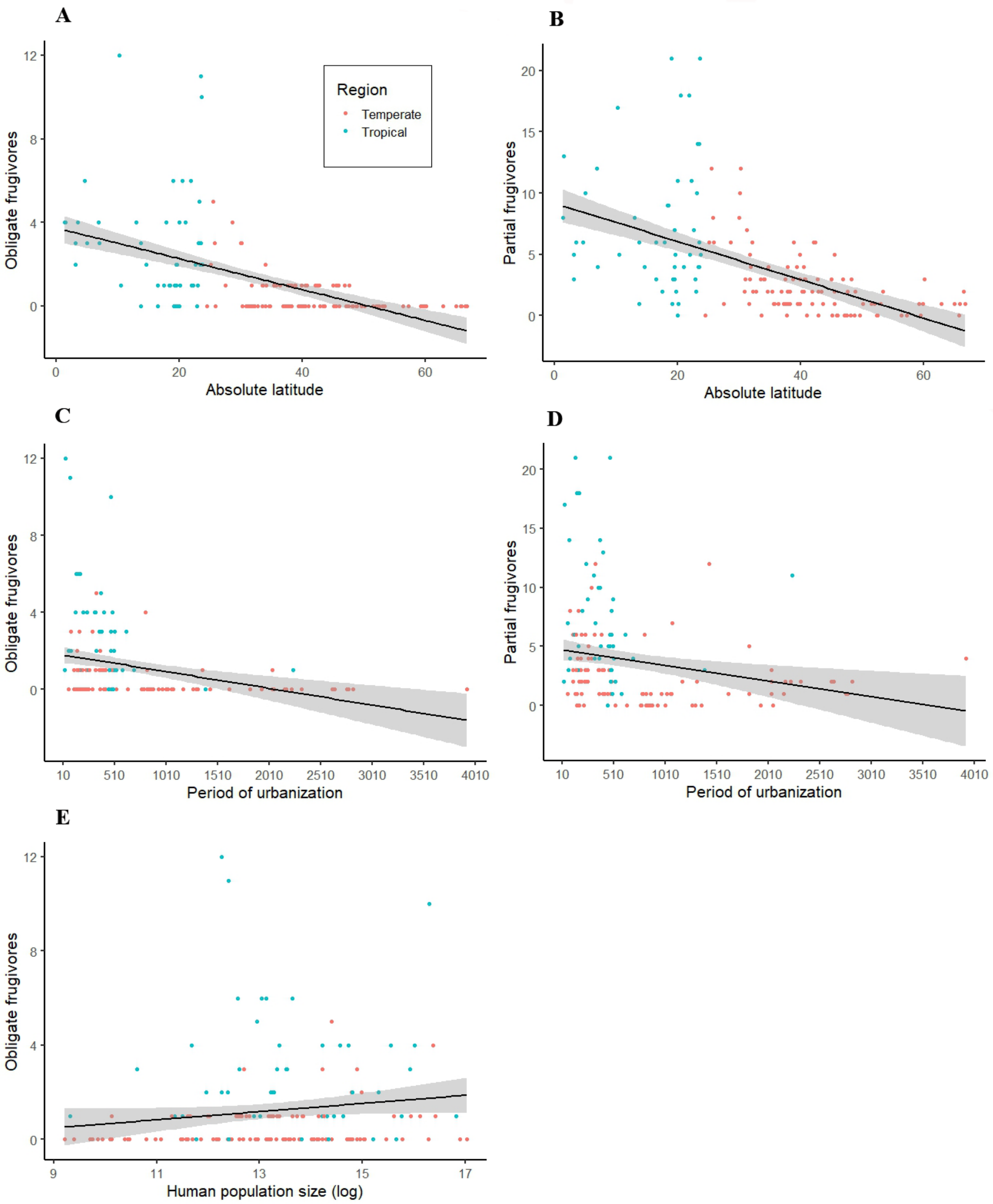

Figure 2 – Relationships between the period of urbanization, absolute latitude, and human population size with the richness of obligate frugivores (A, C, E), and of the period of urbanization and absolute latitude with the richness of partial frugivores birds (B, D) in cities across the world.

Discussion

We showed that the richness of fruit-eating birds varies widely between the levels of dependence on fruits in urban areas, with a lower richness of obligate and partial frugivores than opportunistic species across the world. Therefore, separating the analysis according to dependence of fruits by birds was important in revealing the nuanced responses of birds to urbanization. The high richness of opportunistic fruit-eating birds was already expected and was widely distributed among cities around the world. However, obligate, and partial frugivores need to feed frequently on a wide variety of fruits to meet their energy demands and have great value for the plant community (Walker 2007). It is desirable to have a great diversity of obligate and partial frugivores for the community of plants, but the anthropogenic impacts on these animals are incisive. For example, obligate large-bodied frugivores and plants that depend on these animals to propagate tend to decline with reduced patch size (Bomfim et al. 2018, Emer et al. 2018). Therefore, the persistence of obligate frugivore birds in urban areas it's a challenge, but beneficial to the conservation of several plants that require these animals to propagate.

We showed that the three levels of fruit dependence have different sensitivities to the variables measured here. Opportunistic fruit-eating birds and the overall richness of fruit-eating birds were not influenced by any of the predictor. The opportunists are more numerous and more evenly distributed around the globe and have a stronger weight in total richness of frugivore birds, which explains why total richness was also not influenced by urban predictors. In addition, these opportunist species also consume several resources that are very abundant in cities, such as anthropogenic resources (bread, biscuits, and meat) (Chace & Walsh 2006, Ottoni et al. 2009), so they can persist more often regardless of the impermeable surface cover, the human population size, or the period of urbanization.

We analyzed separately the obligate and partial frugivore groups and found that they are sensitive to the characteristics of urbanization and biogeographic effects. Contrary to our expectations, we show that the number of obligate frugivores increases with human population size. We found three studies that showed an effect of human population size on bird richness (which includes fruit-eating species and birds with diets based on other items). Lepczyk et al. (2017) reported a positive effect of human population size on bird richness, whereas the other two studies have contrasting results (Gagné et al. 2016, Garaffa et al. 2009), showed association negative between human population size on bird richness. When human population size has a strong positive correlation with impermeable surface coverage, both variables have a decreasing effect on bird richness (Gagné et al. 2016). However, we reported that here the correlation between both predictor variables was not strong (r=0.50), perhaps there is some factor existing in populated cities that we did not measure that promotes the diversity of obligate frugivores. We assume that one of the factors is green infrastructure and low-density housing development. For example, finer-scale studies detected a positive effect on the number of houses with the richness of frugivorous birds in a Brazilian tropical city and the island state of Singapore (Lim & Sodhi 2004, Souza et al. 2019). Human dwellings with orchards and gardens may have a greater number of ornamental plants with small fruits that increase the food supply for birds and can be beneficial for frugivores (Lim & Sodhi 2004, Souza et al. 2019). This effect at larger scales still needs to be further explored, but it may indicate that initiatives by city planners associated with strategies to encourage people to maintain private orchards and public parks may be valuable for the conservation of frugivorous birds in the cities (Souza et al. 2019).

Finally, as expected, cities with a shorter history of urbanization showed a greater richness of obligate and partial frugivorous species. This is probably due to the historical configurations of urban planning and management of green areas that are home to great biodiversity. Urbanization has existed for millennia, but green infrastructure was scarce, designed and distributed mainly for imperial spaces in China, and privilege within walls for kings and other urban elites in Near East and Medieval Europe (Shi 1998, Elmqvist et al. 2013, Seto et al. 2013). After many years, following global trends, especially after the industrial revolution, green infrastructure was taking space in the public sphere (Shi 1998, Elmqvist et al. 2013). However, cities with long periods of urbanization have faced challenges in meeting this end (Shi 1998). For example, Beijing is one of the numerous cities that have difficulties in finding enough space to accommodate public parks (Shi 1998). Thus, in the last 150 years, there has been a concern with green areas and their connectivity for the conservation of biodiversity and human recreation (Benedict & McMahon 2002). On the other hand, recently founded cities are being planned with a model that is concerned with the afforestation and conservation of urban green areas, thus retaining greater diversity, such as obligate and partial frugivores.

The impermeable surface cover was not a strong predictor for the dependence levels of fruit-eating birds. Probably this spatial variable has a strong effect on more local scales as reported by previous studies (Reis et al. 2012, Amaya-Espinel et al. 2019, Souza et al. 2019). Cities are very heterogeneous in their landscape contexts, and land use can greatly influence the result on urban species richness (Hahs et al. 2009, Beninde et al. 2015). Indeed, numerous studies have shown that highly impermeable areas on a local scale reduce the number of bird species (Carbó-Ramírez & Zuria 2011, Reis et al. 2012, Amaya-Espinel et al. 2019, Souza et al. 2019, Pena et al. 2023).

However, local-scale green infrastructure likely dampens the impacts of larger-scale urbanization. That is, although highly urbanized places within the city can have fewer frugivores, more wooded places can have a greater diversity of species (Pena et al. 2023). So, there can probably be a balance between green infrastructure and highly impermeable areas within the urban system. In this situation, the size of the impermeable surface area must be less important on a larger scale. Additionally, we did not have control over the location where the birds were observed within the cities. Our survey covered cities of different sizes (from small human settlements to megacities and metropolises) and we did not have the exact coordinates of the sampling units where all the studies were developed to control the effect of habitat type sampled. Thus, the data we gathered was extracted across urban gradients and probably in a large variety of urban habitats, such as conservation units, small public green spaces, or even cemeteries. This can probably mask the effect of a large-scale impermeable surface cover. Therefore, richness of obligate and partial frugivores can be better detected at a finer scale than at a larger scale. In the present study, we can also mention the 30m resolution of the map we used to extract the size of the impermeable surface area, which may have masked small patches of urban vegetation. These results highlight the value of green infrastructure in cities, because otherwise we would probably have detected an impoverishment in frugivore richness with increasing impermeable surface area. Finally, the finding that fruit-eating bird richness in any level of fruit dependence was not influenced by elevation, may be probably because most evaluated cities were distributed in a low elevation range. We included data from only nine cities with elevations between 1000 and 2000 m (the majority in tropical areas), and five cities with elevations higher than 2000 m (all in Neotropics). The remaining cities were all located in altitudes below 1000m.

As expected, cities in lower latitudes, encompassing the tropical zone, have a greater richness of obligate and partial frugivores. This probably reflects their biogeographic species pool, as the tropics are home to more species of obligate frugivores due to their climate stability, productivity, and food availability (Fleming 2005, Kissling et al. 2009). Studies indicate that highly impermeable areas at a local scale are dominated by a few species, generally more opportunistic and this would tend to lead to biotic homogenization. However, our results indicate that biotic homogenization between cities is not yet strong enough to shape patterns on a large scale, because it would probably be reflected in a lower biogeographic force to explain variations in richness patterns of frugivores that are a vulnerable group to the impacts of impermeable surface cover. However, this is probably due to the heterogeneity of land covers within the cities, which present a mix of impermeable areas with green areas. Finally, we emphasize that our dataset includes fewer studies in the tropical zone compared to those in the temperate zone, specifically, cities in Afrotropical regions are underrepresented. These are particularly important locations, as they are home to more obligate and partial frugivores (Kissling et al. 2009).

In conclusion, there are 9993 species of birds in the world, among them 3719 species depend on fruits at some level (Wilman et al. 2014). Fruit-eating birds are an important fraction of existing species and perform important functions. However, we showed that cities harbor a small proportion of these species, as we have recorded only 858 frugivorous birds (less than 10% of bird species) in the evaluated cities. This has implications for the conservation of the ecological functions that cities can support, especially those related to seed dispersal. The richness of opportunistic fruit-eating birds between cities is constant and higher than those of obligate and partial frugivores. This has implications for seed dispersal services, as these species tend to consume fruits at smaller percentages, and to be less efficient than obligate and partial frugivores for seed dispersal, with consequences on the regeneration of green areas within the cities. That is, cities are more prone to depend on bird species that may be insectivores, omnivores, and other opportunistic species than obligate frugivorous birds. Thus, modifications on the habitats and on the availability of resources related to urbanization can favor opportunists birds to the detriment of more specialized species (Chace & Walsh 2006, McKinney 2006, Shochat et al. 2006, Amaya-Espinel et al. 2019, Carvajal-Castro et al. 2019). On the other hand, our results indicate that more recent cities that were founded and projected in a scenario that encouraged wooded areas added with biogeographic characteristics of the region act strongly to shelter more obligate and partial frugivores. Therefore, this can make cities a self-regulating system, as it promotes conservation of obligate and partial frugivores which, by acting as seed dispersers, can maintain the greening of spaces designated for this purpose. The permanence of specialized birds is essential for the conservation of several plants that depend on these animals to propagate.

SUPPLEMENTARY MATERIAL

List of tables

Table S1. Correlation between the richness of fruit-eating birds in the three levels of fruit dependence and number of sites distributed in each city.

Response variable	**P value**	**r^2**
All cities		
Overall richness of fruit-eating birds	0.1397	0.14238
Obligate frugivores	0.3165	-0.09682793
Partial frugivores	0.6963	-0.03780868
Fruit-eating opportunistic	0.1008	0.1579957
Tropical cities		
Overall richness of fruit-eating birds	0.5695	-0.09950694
Obligate frugivores	0.02812	-0.3712368
Partial frugivores	0.1521	-0.2473085
Fruit-eating opportunistic	0.6699	-0.07465835
Non-tropical cities		
Overall richness of fruit-eating birds	0.004483	0.3268199
Obligate frugivores	0.02271	0.2646066
Partial frugivores	0.01014	0.2971623
Fruit-eating opportunistic	0.01457	0.2829572

Table S2. Urbanization and biogeographic settings measured across the 141 studies distributed in 157 cities all over the world.

Journal	Year publication	Author	Absolute Latitude	Region	Ecozone	Country	City	Human population size	Period urbanization	Elevation	Area (km^2)
Revista_Brasileira_de_Ornitologia	2017	Abilhoa_&_Amorin	25.416667	Temperate	Neotropic	Brazil	Curitiba	1800000	330	911	914.92
Ecological_Applications	1996	Blair	37.427483	Temperate	Neartic	EUA	Palo_Alto	64403	254	29	2794.851
PlosOne	2019	Carvajal-Castro_et_al.	4.516667	Tropical	Neotropic	Colombia	Armenia	290000	134	1491	25.399
The_Condor	1998	Clergeau_et_al.	48.113243	Temperate	Paleoartic	France	Rennes	200000	523	42	727.044
The_Condor	1998	Clergeau_et_al.	46.816667	Temperate	Neartic	Canada	Quebec	650000	415	6	1079.714
Urban_Ecosystems	2019	Gorosito_&_Cueto	42.900000	Temperate	Neotropic	Argentina	Esquel	32000	117	598	19.286
Urban_Ecosystems	2017	Dale	59.916667	Temperate	Paleoartic	Norway	Oslo	550000	975	45	1599.91
Urban_Ecosystems	2016	Jasmani_et_al.	3.117841	Tropical	Indomalayan	Malaysia	Petaling_Jaya	550000	73	47	1415.842
Ecological_Indicators	2011	Lizée_et_al.	43.296389	Temperate	Paleoartic	France	Marseille	1605000	2623	14	1181.64
Landscape_Ecology	2013	Meffert_&_Dziock	52.505556	Temperate	Paleoartic	Germany	Berlin	3400000	779	39	2380.11
Landscape_and_Urban_Planning	2014	Paker_et_al.	32.033333	Temperate	Paleoartic	Israel	Tel-Aviv	405300	114	28	1131.339
PlosOne	2017	Pena_et_al.	19.926944	Tropical	Neotropic	Brazil	Belo_Horizonte	2501576	316	884	588.428
Landscape_and_Urban_Planning	2012	Reis_et_al.	10.184444	Tropical	Neotropic	Brazil	Palmas	210000	34	250	60.927
Landscape_and_Urban_Planning	2006	Sandström_et_al.	59.266667	Temperate	Paleoartic	Sweden	Örebro	95400	823	35	340.741
Landscape_and_Urban_Planning	2019	Souza_et_al.	20.464722	Tropical	Neotropic	Brazil	Campo_Grande	840000	151	551	241.525
Urban_Ecology	1986	DeGraaf_&_Wentworth	42.366667	Temperate	Neartic	EUA	Amherst	25000	320	96	76.491
Landscape_and_Urban_Planning	2010	Imai_&_Nakashizuka	38.268222	Temperate	Paleoartic	Japan	Sendai	1033515	423	53	1345.89
Ecological_Indicators	2012	Lin_et_al.	24.479722	Temperate	Indomalayan	China	Xiamen	1400000	636	15	130.843
Biological_Conservation	2009	Loss_et_al.	41.900000	Temperate	Neartic	EUA	Chicago	2695598	243	181	10514.13
Biotic_Homogenization_(Book)	2001	Blair	39.500000	Temperate	Neartic	EUA	Oxford	20864	481	272	35.313
Landscape_and_Urban_Planning	2011	Fontana_et_al.	47.378611	Temperate	Paleoartic	Swiss	Zurich	367000	1933	412	3308.12
Landscape_and_Urban_Planning	2011	Fontana_et_al.	47.050000	Temperate	Paleoartic	Swiss	Lucerne	58000	1273	447	635.297
Landscape_and_Urban_Planning	2011	Fontana_et_al.	46.005000	Temperate	Paleoartic	Swiss	Lugano	49000	1299	279	265.492
Ecology_and_Evolution	2015	Schütz_&_Schulze	48.216667	Temperate	Paleoartic	Austria	Vienna	1800000	2038	166	2656.11
Biodiversity_and_Conservation	2006	Mason	51.934000	Temperate	Paleoartic	England	Harwich	17000	785	11	17.358
Oecologia	2012	Møller_et_al.	57.269444	Temperate	Paleoartic	Denmark	Brønderslev	12000	173	18	48.539
Oecologia	2012	Møller_et_al.	52.408333	Temperate	Paleoartic	Poland	Poznan	856000	770	60	887.883
Oecologia	2012	Møller_et_al.	49.593889	Temperate	Paleoartic	Czech_Republic	Olomouc	110000	1006	223	414.151
Oecologia	2012	Møller_et_al.	47.492500	Temperate	Paleoartic	Hungary	Budapest	2503000	822	115	1927.22
Oecologia	2012	Møller_et_al.	39.856667	Temperate	Paleoartic	Spain	Toledo	298000	1823	497	80.682
Oecologia	2012	Møller_et_al.	37.178056	Temperate	Paleoartic	Spain	Granada	238000	1023	681	150.878
Journal_of_Biogeography	2007	Kark_et_al.	31.783333	Temperate	Paleoartic	Israel	Jerusalem	729900	3923	791	486.542
Landscape_and_Urban_Planning	2008	Caula_et_al.	43.611944	Temperate	Paleoartic	France	Montpellier	244300	823	41	443.989
Frontiers_in_Ecology_and_Evolution	2017	Samia_et_al.	48.699167	Temperate	Paleoartic	France	Orsay	16421	153	96	6376.249
Frontiers_in_Ecology_and_Evolution	2017	Samia_et_al.	59.433333	Temperate	Paleoartic	Estonia	Tallinn	426538	869	25	861.388
Bollettino_di_zoologia	1985	Lo_Valvo_et_al.	38.116667	Temperate	Paleoartic	Italy	Palermo	701782	2759	7	177.22
Bird_Study	1977	Huhtalo_&_Järvinen	65.850000	Temperate	Paleoartic	Finland	Tornio	18900	402	6	148.034
Landscape_and_Urban_Planning	1994	Zalewski	53.022222	Temperate	Paleoartic	Poland	Torun	200000	790	61	227.325
Italian_Journal_of_Zoology	1997	Rolando_et_al.	45.079167	Temperate	Paleoartic	Italy	Turin	962507	2051	242	1961.687

Journal	Year publication	Author	Absolute Latitude	Region	Ecozone	Country	City	Human population size	Period urbanization	Elevation	Area (km^2)
Landscape_and_Urban_Planning	2011	Joo_et_al.	42.733611	Temperate	Neartic	EUA	Lansing	114297	188	256	741.301
Landscape_Ecology	2008	Blair_&_Johnson	44.944167	Temperate	Neartic	EUA	Saint_Paul	285068	169	238	5175.89
Landscape_and_Urban_Planning	2003	Green_&_Baker	33.448333	Temperate	Neartic	EUA	Phoenix	3100000	156	336	3983.34
Urban_Ecosystems	2010	Villegas_&_Garitano-Zavala	16.500000	Tropical	Neotropic	Bolivia	La_Paz	1636000	475	3773	226.156
The_American_Midland_Naturalist	1974	Guthrie	34.110000	Temperate	Neartic	EUA	Claremont	24776	116	405	8158.83
Conservation_Biology	1997	Bolger_et_al.	32.715000	Temperate	Neartic	EUA	San_Diego	1223400	254	16	2344.682
Journal_Biogeography	1976	Vale_&_Vale	37.804444	Temperate	Neartic	EUA	Oakland	34555	171	16	2794.851
Brazilian_Archives_of_Biology_and_Technology	2005	Manhães_&_Loures-Ribeiro	21.776880	Tropical	Neotropic	Brazil	Juiz_de_Fora	456796	173	880	76.56
Biota_Neotropica	2013	Sacco_et_al.	31.771944	Temperate	Neotropic	Brazil	Pelotas	339934	265	11	117.503
Journal_of_Biogeography	2003	Jokimäki_&_Kaisanlahti-Jokimäki	65.736111	Temperate	Paleoartic	Finland	Kemi	25000	154	16	130.377
Journal_of_Biogeography	2003	Jokimäki_&_Kaisanlahti-Jokimäki	66.716667	Temperate	Paleoartic	Finland	Kemijärvi	10000	66	155	35.414
Landscape_and_Urban_Planning	2013	Wang_et_al.	30.266944	Temperate	Indomalayan	China	Hangzhou	5162039	1434	18	3136.373
Journal_of_Ornithology	2012	Zhou_&_Chu	22.266944	Tropical	Indomalayan	China	Hong_Kong	7000000	2237	65	34.965
Annales_Zoologici_Fennici	1971	Nuorteva	60.170833	Temperate	Paleoartic	Finland	Helsinki	500000	473	26	2255.52
Landscape_and_Urban_Planning	1987	Tilghman	42.101389	Temperate	Neartic	EUA	Springfield	310000	387	32	1324.098
Urban_Ecosystems	2006	Donnelly_&_Marzluff	47.609722	Temperate	Neartic	EUA	Seattle	550000	172	77	5191.15
Landscape_and_Urban_Planning	1998	Jokimäki_&_Suhonen	66.500000	Temperate	Paleoartic	Finland	Rovaniemi	34000	223	94	229.156
Landscape_and_Urban_Planning	1991	Degraaf_et_al.	34.000556	Temperate	Neartic	EUA	Columbia	98052	237	92	931.765
Urban_Ecosystems	1997	Hadidian_et_al.	38.910100	Temperate	Neartic	EUA	Washington,_D.C.	572059	233	26	7175.279
Ornis_Scandinavica	1978	Hohtola	62.892500	Temperate	Paleoartic	Finland	Kuopio	65000	370	90	274.744
Urban_Ecosystems	1999	Jokimäki	65.014167	Temperate	Paleoartic	Finland	Oulu	106419	418	15	730.51
Austral_Ornithology	1983	Jones	19.256389	Tropical	Australasia	Australia	Townsville	85000	158	12	110.333
Landscape_and_Urban_Planning	1999	Morneau_et_al.	45.500000	Temperate	Neartic	Canada	Montreal	1017666	381	148	4253.31
Biotemas	2004	Franchin_&_Marçal_Júnior	18.914444	Tropical	Neotropic	Brazil	Uberlândia	500000	135	881	149.089
Landscape_and_Urban_Planning	2011	Carbó-Ramírez_&_Zuria	20.122500	Tropical	Neartic	Mexico	Pachuca	445406	585	2394	67.364
Ecological_Research	2000	Fernández-Juricic	40.416667	Temperate	Paleoartic	Spain	Madrid	2938723	1173	602	2034.11
Ecography	2010	Murgui	39.466667	Temperate	Paleoartic	Spain	Valencia	798033	2161	22	692.022
Biological_Conservation	2009	Suarez-Rubio_&_Thomlinson	18.406389	Tropical	Neotropic	Puerto_Rico	San_Juan	395326	502	11	464.631
Urban_Forestry_&_Urban_Greening	2009	Campbell	45.424722	Temperate	Neartic	Canada	Ottawa	834237	197	77	1596.9
Biological_Conservation	2006	Daniels_&_Kirkpatrick	42.880556	Temperate	Australasia	Australia	Hobart	190000	219	19	98.674
Bird_Study	2010	Baker_et_al.	51.450000	Temperate	Paleoartic	England	Bristol	550000	868	19	477.619
Journal_of_Environmental_Management	2000	Reynaud_&_Thioulouse	4.937222	Tropical	Neotropic	French_Guiana	Cayenne	40993	359	8	33.147
Landscape_and_Urban_Planning	2008	van_Heezik_et_al.	45.874167	Temperate	Australasia	New_Zealand	Dunedin	80000	175	27	118.17

Journal	Year publication	Author	Absolute Latitude	Region	Ecozone	Country	City	Human population size	Period urbanization	Elevation	Area (km^2)
Landscape_and_Urban_Planning	2009	van_Rensburg_et_al.	25.753333	Temperate	Afrotropic	Africa_do_Sul	Pretoria	2921488	168	1350	2869.456
Revista_de_Ornitología_Neotropical	1983	Feninger	34.599722	Temperate	Neotropic	Argentina	Buenos_Aires	2922829	487	36	3745.971
Ararajuba	1995	Matarazzo-Neuberger	23.693889	Tropical	Neotropic	Brazil	São_Bernardo_do_Campo	566893	470	791	1954.65
Ararajuba	1995	Matarazzo-Neuberger	23.483333	Tropical	Neotropic	Brazil	Santo_André_da_Borda_do_Campo	616991	473	729	1954.65
Urban_Ecosystem	2014	Ferenc_et_al.	50.083333	Temperate	Paleoartic	Czech_Republic	Prague	1270000	1622	212	1271.178
Ecological_Applications	2007	Husté_&_Boulinier	48.900000	Temperate	Paleoartic	France	Seine-Saint-Denis	1506466	2323	53	6376.249
Vie_Et_Milieu_-_Life_and_Environment	2012	Arca_et_al.	41.883333	Temperate	Paleoartic	Italy	Rome	2617175	2776	46	2156.094
The_Condor	2003	Hennings_&_Edge	45.520000	Temperate	Neartic	EUA	Portland	529121	178	31	2427.95
Landscape_and_Urban_Planning	2003	Turner	32.221667	Temperate	Neartic	EUA	Tucson	800000	248	754	1051.51
BioRxiv	2018	Muderere_et_al.	17.829167	Tropical	Afrotropic	Zimbabwe	Harare	2500000	133	1485	234.095
Journal_of_Environmental_Biology	2015	Rajashekara_&_Venkatesha	12.978889	Tropical	Indomalayan	India	Bengalore	9000000	486	927	878.198
Ornitologia_Neotropical	2013	Charre_et_al.	19.433333	Tropical	Neotropic	Mexico	Mexico_City	20137152	698	2240	1933.06779
Gayana	2020	Benito_et_al.	33.437778	Temperate	Neotropic	Chile	Santiago	6000000	482	571	356.067
European_Journal_of_Ecology	2017	Leveau_et_al.	37.846389	Temperate	Neotropic	Argentina	Balcarce	35000	147	117	44.566
European_Journal_of_Ecology	2017	Leveau_et_al.	38.266667	Temperate	Neotropic	Argentina	Miramar	24000	135	15	25.874
Landscape_and_Urban_Planning	2020	Barbosa_et_al.	23.547500	Tropical	Neotropic	Brazil	São_Paulo	12000000	469	769	1954.65
Urban_Ecosystems	2012	Toledo_et_al.	23.026389	Tropical	Neotropic	Brazil	Taubaté	300000	378	586	80.092
Biological_Conservation	2011	Husté_&_Boulinier	48.856667	Temperate	Paleoartic	France	Paris	11769000	2323	41	6376.249
Urban_Ecosystems	2016	Escobar-Ibáñez_&_MacGregor-Fors	19.546194	Tropical	Neotropic	Mexico	Xalapa	157614	504	1463	76.935
Ecology_and_Evolution	2016	Silva_et_al.	38.740000	Temperate	Neotropic	Chile	Temuco	282415	142	117	154.501
Ecology_and_Evolution	2016	Silva_et_al.	39.830833	Temperate	Neotropic	Chile	Valdivia	166080	471	13	44.157
Ecology_and_Evolution	2016	Silva_et_al.	40.566667	Temperate	Neotropic	Chile	Osorno	161460	465	22	62.632
Landscape_and_Urban_Planning	2015	Barth_et_al.	27.467778	Temperate	Australasia	Australia	Brisbane	1400000	198	18	2334.53
Revista_Ambiente_e_Agua	2016	Gonçalves_&_Toledo	23.298783	Tropical	Neotropic	Brazil	Jacareí	211214	370	575	164.56
Animal_Biodiversity_and_Conservation	2019	Hera	42.849556	Temperate	Paleoartic	Spain	Vitoria-Gasteiz	250000	842	533	239.362
Landscape_Ecology	2013	Ikin_et_al.	35.309097	Temperate	Australasia	Australia	Canberra	362000	200	594	382.389
Biota_Neotropica	2011	Cruz_&_Piratelli	23.499167	Tropical	Neotropic	Brazil	Sorocaba	580655	369	567	215.347
Pacific_Conservation_Biology	2011	Fitzsimons_et_al.	37.800000	Temperate	Australasia	Australia	Melbourne	3371888	188	20	2406.727
Journal_of_Animal_and_Veterinary_Advances	2014	Lee_&_Rhim	36.351111	Temperate	Paleoartic	Korea	Daejeon	1529292	198	55	454.895
Urban_Ecosystems	2011	Fontana_et_al.	30.032778	Temperate	Neotropic	Brazil	Porto_Alegre	1500000	291	27	723.571
Interciencia	2016	Sainz-Borgo	10.500000	Tropical	Neotropic	Venezuela	Caracas	2245744	456	973	190.672

Journal	Year publication	Author	Absolute Latitude	Region	Ecozone	Country	City	Human population size	Period urbanization	Elevation	Area (km^2)
Urban_Habitats	2011	Nilon_et_al.	39.289444	Temperate	Neartic	EUA	Baltimore	1400000	294	19	7175.279
Ecosphere	2017	Wang_et_al.	1.333333	Tropical	Indomalayan	Singapore	Singapore	5638700	204	30	419.533
Urban_Ecosystems	2018	Canedoli_et_al.	45.466944	Temperate	Paleoartic	Italy	Milan	1345851	2639	133	6718.72
Diversity_and_Distribution	2009	Fuller_et_al.	53.380833	Temperate	Paleoartic	United_Kingdom	Sheffield	513000	2823	82	952.423
Journal_of_Urban_Ecology	2018	Camacho-Cervantes_et_al.	56.340400	Temperate	Paleoartic	Scotland	St_Andrews	16900	883	18	15.853
Tropical_Conservation_Science	2016	Suarez-Rubio_et_al.	21.983056	Tropical	Indomalayan	Myanmar	Mandalay	1500000	166	82	117.597
Inheringia_Série_Zoologia	2018	Rodrigues_et_al.	29.920000	Temperate	Neotropic	Brazil	Canoas	323827	84	20	723.571
Urban_Ecosystems	2019	Moreno-Contreras_et_al.	31.739444	Temperate	Neartic	Mexico	Ciudad_Juárez	1400000	364	1134	1148.439
Journal_of_Urban_Ecology	2018	Kale_et_al.	20.925833	Tropical	Indomalayan	India	Amravati	647000	323	346	51.332
International_Journal_of_Zoology	2019	Bellanthudawa_et_al.	6.974456	Tropical	Indomalayan	Sri_Lanka	Colombo	752993	506	10	687.474
Urban_Ecosystems	2018	Chaiyarat_et_al.	13.752500	Tropical	Indomalayan	Thailand	Bangkok	8280925	623	9	3474.916
PlosOne	2018	Partridge_&_Clark	40.712778	Temperate	Neartic	EUA	New_York	8336817	399	29	22659.205
Urban_Ecosystems	2018	Tzortzakaki_et_al.	38.250000	Temperate	Paleoartic	Greece	Patras	200000	2169	3	125.408
Journal_of_Natural_History	2017	Cristaldi_et_al.	31.650000	Temperate	Neotropic	Argentina	Santa_Fe	525093	450	20	86.594
Canadian_Journal_of_Zoology	2018	Palacio_et_al.	34.766667	Temperate	Neotropic	Argentina	Lomas_de_Zamora	613192	159	21	3745.971
Urban_Ecosystems	2017	Ciach_&_Fröhlich	50.061389	Temperate	Paleoartic	Poland	Kraków	774839	1058	216	1002.343
Environmental_Quality_Management	2017	Bonança_et_al.	23.186389	Tropical	Neotropic	Brazil	Jundiai	418962	372	750	145.524
Comptes_Rendus_Biologies	2017	Aouissi_et_al.	36.900000	Temperate	Paleoartic	Algeria	Annaba	257359	2037	3	199.695
Scientific_Reports	2016	Xie_et_al.	39.906667	Temperate	Paleoartic	China	Beijing	21705000	1823	51	5887.61
Urban_Ecosystems	2017	Lees_&_Moura	1.455833	Tropical	Neotropic	Brazil	Belém	1500000	407	7	205.07
Tropical_Conservation_Science	2018	Wolff_et_al.	18.366667	Tropical	Neotropic	Puerto_Rico	Guaynabo	97924	254	46	464.631
Biotropica	2020	Hayes_et_al.	6.801111	Tropical	Neotropic	Guyana	Georgetown	118000	242	4	87.762
Urban_Forestry_&_Urban_Greening	2019	Pal_et_al.	22.572600	Tropical	Indomalayan	India	Kolkata	4500000	333	11	944.289
Urban_Ecosystems	2018	Shih	25.066667	Temperate	Indomalayan	Taiwan	Taipei	2646204	148	10	2964.026
Russian_Journal_of_Ecology	2014	Yu_&_Guo	30.791389	Temperate	Indomalayan	China	Nanchong	7120000	2225	280	41.611
Biosystems_Diversity	2019	Kopij	17.501565	Tropical	Afrotropic	Namibia	Outapi	11000	26	1113	5.437
Urban_Forestry_&_Urban_Greening	2015	Yang_et_al.	31.233333	Temperate	Paleoartic	China	Shanghai	24870895	1077	16	4312.911
Landscape_and_Urban_Planning	2012	González-Oreja_et_al.	19.057356	Tropical	Neotropic	Mexico	Puebla	1700000	492	2171	731.76
Ecological_Indicators	2016	Aida_et_al.	3.033333	Tropical	Indomalayan	Malaysia	Klang	744062	380	8	1415.842
Basic_and_Applied_Ecology	2019	Lee_et_al.	22.816667	Tropical	Indomalayan	China	Nanning	4000000	1391	85	294.397
Urban_Ecosystems	2015	Kang_et_al.	37.537770	Temperate	Paleoartic	South_Korea	Seoul	10000000	2041	32	4862.781
Landscape_and_Urban_Planning	2006	Morimoto_et_al.	35.600000	Temperate	Paleoartic	Japan	Chiba	918364	822	3	16884.52
Landscape_and_Ecological_Engineering	2014	Mikami_&_Mikami	33.589444	Temperate	Paleoartic	Japan	Fukuoka	1538681	1360	13	3244.22
Urban_Ecossystems	2013	Latta_et_al.	40.441667	Temperate	Neartic	EUA	Pittsburgh	300000	265	229	3180.8
Turkish_Journal_of_Zoology	2014	Peris_&_Montelongo	40.970773	Temperate	Paleoartic	Spain	Salamanca	180000	936	817	137.169
Urban_Ecossystems	2016	Chang_&_Lee	22.983333	Tropical	Indomalayan	Taiwan	Tainan	1880000	523	5	229.848

Journal	Year publication	Author	Absolute Latitude	Region	Ecozone	Country	City	Human population size	Period urbanization	Elevation	Area (km^2)
Urban_Ecossystems	2016	Leveau_&_Leveau	38.000000	Temperate	Neotropic	Argentina	Mar_del_Plata	618989	149	25	263.096
European_Journal_of_Forest_Research	2013	Cruz_et_al.	40.223333	Temperate	Paleoartic	Portugal	Coimbra	140796	1312	19	531.767
Ornithological_Science	2019	Riaz_et_al.	30.969300	Temperate	Paleoartic	Pakistan	Layyah	321505	473	147	25.298
Basic_and_Applied_Ecology	2011	MacGregor-Fors_&_Schondube	19.701944	Tropical	Neotropic	Mexico	Morelia	1000000	482	1909	119.637
Basic_and_Applied_Ecology	2011	MacGregor-Fors_&_Schondube	19.409167	Tropical	Neotropic	Mexico	Uruapan	240000	490	1616	43.758
Basic_and_Applied_Ecology	2011	MacGregor-Fors_&_Schondube	19.988056	Tropical	Neotropic	Mexico	Zamora	128000	449	1565	28.484
Landscape_and_Urban_Planning	2009	Vallejo_Jr_et_al.	14.633333	Tropical	Indomalayan	Philippines	Quezon_City	2679450	84	27	1497.94
Ornitología_Colombiana	2007	Muñoz_et_al.	3.440000	Tropical	Neotropic	Colombia	Cali	2119843	487	966	113.418
Biotemas	2008	Fuscaldi_&_Loures-Ribeiro	19.467778	Tropical	Neotropic	Brazil	Ipatinga	239468	59	237	35.276
Notornis	1995	Day	37.783333	Temperate	Australasia	New_Zealand	Hamilton	109043	159	39	149.355
Arnaldoa	2018	Luque_Fernández_et_al.	16.422122	Tropical	Neotropic	Peru	Arequipa	1008290	483	2288	63.281
Urban_Forestry_&_Urban_Greening	2009	Khera_et_al.	28.610000	Temperate	Indomalayan	India	Delhi	13000000	809	214	1525.83779
Ciencia_Ergo-sum	1996	Cupul-Maganã	25.789603	Temperate	Neotropic	Mexico	Sinaloa	2425675	193	14	120.89
Biological_Conservation	2010	Dures_&_Cumming	33.925278	Temperate	Afrotropic	South_Africa	Cape_Town	3200000	371	30	996.798
Ornitologia_Neotropical	2000	Krügel_&_Anjos	23.425000	Tropical	Neotropic	Brazil	Maringá	240292	76	549	128.443
Urban_Forestry_&_Urban_Greening	2016	Matsuba_et_al.	35.689722	Temperate	Paleoartic	Japan	Tokyo	13515271	823	51	16884.52
Huitzil	2017	Vides-Hernández_et_al.	13.690000	Tropical	Neotropic	El_Salvador	San_Salvador	6300000	498	646	177.589
Urban_Ecosystems	2020	Korányi_et_al.	51.541281	Temperate	Paleoartic	Germany	Göttingen	120000	1070	155	254.428

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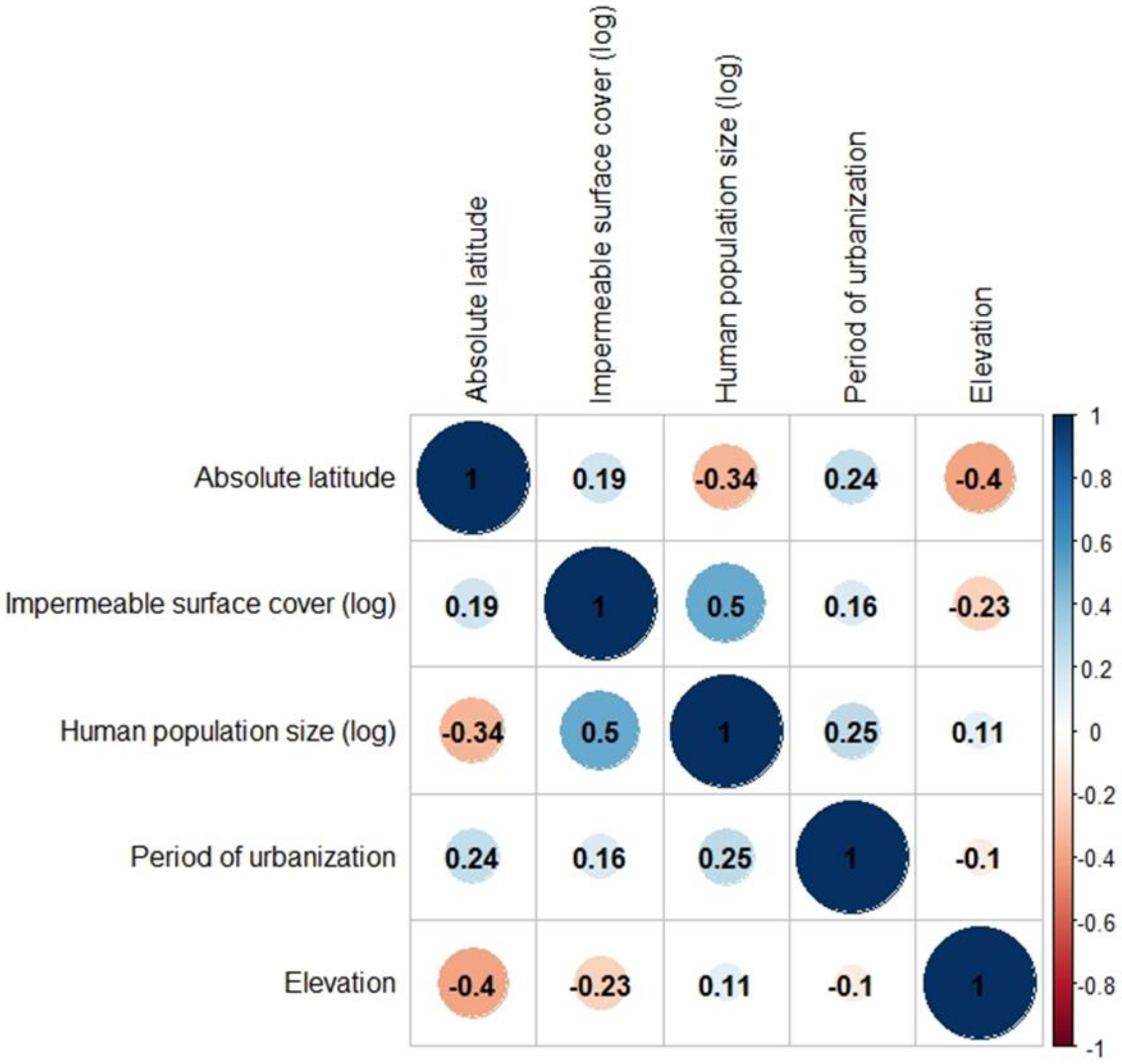


Figure S1. Correlation test among predictor variables (impermeable surface cover (log), human population size (log), period of urbanization, absolute latitude, and elevation).

Chapter 2 - Frugivory and seed dispersal in tropical urban areas: a review

Manuscript accepted for publication in the book “Ecology of Tropical Cities: Natural and Social Sciences Applied to the Conservation of Urban Biodiversity” (In: Angeoletto, F., P. Tryjanowski & M. Fellowes)

Frugivory and seed dispersal in tropical urban areas: a review

Abstract

The diversity of fruits and frugivorous species is especially high in tropical regions where frugivory and seed dispersal interactions are particularly critical for the structure and functioning of terrestrial communities. However, the increasing urbanization in tropical areas has caused profound landscape changes, affecting species interactions and associated ecosystems functions. Here, we present an overview of the studies on frugivory and seed dispersal in tropical urban areas, discussing emergent patterns and processes underlying plant-frugivore interactions as well as major research gaps. Our review highlights an uneven geographical distribution of studies, which are more frequent in the Neotropics in comparison to Indomalayan and Afrotropical regions. We found that in tropical urban areas: (i) the most frequently studied group are flying frugivores (birds and bats), (ii) fruits of Myrtaceae, Moraceae, and Arecaceae are most frequently reported as consumed by frugivores, (iii) introduced plants are often present in frugivores' diets, and become more common with urbanization, (iv) frugivores niche breadths vary with seasonality in fruit availability, (v) a higher diversity of fruits are consumed by frugivores in (or near) habitats that preserve more natural characteristics, such as higher proportion of green areas. Since suitable habitats within cities are highly variable in size, shape, connectivity, patterns of human activity, vegetation management and socioeconomic contexts, we recommend future studies to sample gradients in such variables. Furthermore, as new urban areas are often planned in advance, 'before-after impact' studies may be particularly insightful to understand how frugivores respond to urbanization and how to create frugivore-friendly areas without promoting undesirable (invasive) plants. Although the scarcity of studies and their geographical bias limit generalizations across distinct tropical regions, based on our review we provide a preliminary list of broad recommendations of management practices towards creating biodiversity-friendly urban areas.

Keywords: ecosystem services, novel ecosystems, plant-animal interactions, plant-frugivore interactions, tropical cities, urban landscape, urbanization, zoochory.

Resumo

A diversidade de frutos e espécies frugívoras é principalmente elevada em regiões tropicais onde as interações de frugivoria e dispersão de sementes são particularmente críticas para a estrutura e funcionamento das comunidades terrestres. No entanto, a crescente urbanização nas áreas tropicais causou profundas alterações na paisagem, afetando as interações entre espécies e as funções dos ecossistemas associados. Aqui, apresentamos uma visão geral dos estudos sobre frugivoria e dispersão de sementes em áreas urbanas tropicais, discutindo padrões e processos emergentes subjacentes às interações planta-frugívoro, bem como as principais lacunas de pesquisa. Nossa revisão destaca uma distribuição geográfica desigual dos estudos, que são mais frequentes nos Neotrópicos em comparação como as regiões Indomalaias e Afrotropicais. Descobrimos que em áreas urbanas tropicais: (i) o grupo mais frequentemente estudado são os frugívoros voadores (aves e morcegos), (ii) os frutos de Myrtaceae, Moraceae e Arecaceae são mais frequentemente relatados sendo consumidos por frugívoros, (iii) plantas introduzidas estão frequentemente presentes na dieta dos frugívoros e se tornam mais comuns com a urbanização, (iv) a amplitude dos nichos dos frugívoros varia com a sazonalidade na disponibilidade de frutas, (v) uma maior diversidade de frutos é consumida pelos frugívoros em (ou perto) de habitats que preservam mais recursos naturais, como maior proporção de áreas verdes. Uma vez que os habitats adequados nas cidades são variam muito em tamanho, forma, conectividade, padrões de atividade humana, manejo da vegetação e contextos socioeconômicos, recomendamos estudos futuros para amostrar os gradientes destas variáveis. Além disso, como as novas áreas urbanas são muitas vezes planejadas com antecedência, os estudos de "impacto antes-depois" podem ser particularmente esclarecedores para compreender como os frugívoros respondem à urbanização e como criar áreas favoráveis aos frugívoros sem promover plantas indesejáveis (invasivas). Embora a escassez de estudos e a distribuição geográfica desigual limitam as generalizações em regiões tropicais distintas, com base na nossa análise fornecemos uma lista preliminar de recomendações gerais de práticas de manejo para criação de áreas urbanas amigáveis para biodiversidade.

Palavras-chave: serviços ecossistêmicos, novos ecossistemas, interações planta-animal, interações planta-frugívoros, cidades tropicais, paisagem urbana, urbanização, zoocoria.

Introduction

Cities are socio-ecological systems, where social, economic and cultural factors are strong drivers of the magnitude of physical and biotic changes in the landscape (Schell et al. 2020). Transformation of natural areas to impermeable surfaces (paved streets, roads, and buildings) is increasing globally promoting severe environmental changes (Carvajal-Castro et al. 2019). An increase in urban land cover to 1.2 million km^2 by 2030 is estimated, when 55% of the global population is expected to live in cities (Seto et al. 2012). Since the Tropics harbor most of the global biodiversity, urbanization may be particularly impactful in tropical regions (Cincotta et al. 2000). Greater urban growth is expected in developing countries in these regions, which reinforces the importance of understanding the impacts of urbanization on species interactions to promote biodiversity-friendly urban landscapes. However, few studies so far have investigated how the urban landscape affects biodiversity and species interactions in tropical regions in spite of its considerable biodiversity (Seto et al. 2012, Nascimento et al. 2020, McDonald et al. 2020).

In the Tropics, 70-90% of the woody plants have their seeds dispersed by animals which, in turn, consume fruits as a relevant part of their diet (Jordano 2000; Herrera 2002). Multiple groups of animals are frugivorous, most of them are vertebrates including mammals, reptiles, birds, and fishes (Fleming et al. 1987, Correa et al. 2007), but invertebrates may also be important frugivores and seed dispersers, particularly ants (Camargo et al. 2016). In fact, at least 1230 bird species worldwide consume fruits, of which 90% occur in tropical regions (Kissling et al. 2009). Among the mammals, around 460 species consume fruits, including marsupials, bats, primates, ungulates, and some carnivores (Fleming & Sosa 1994). Furthermore, at least 182 freshwater fish species consume fruits (Correa et al. 2007). While frugivory events may sometimes result in seed predation, it often leads to seed dispersal which exerts critical influence on the distribution, density and persistence of plant populations, ultimately shaping vegetation patterns (Jordano 2000, Sasal & Morales 2012). In turn, the diversity and abundance of frugivores depend on the abundance, diversity and distribution of fruits and seeds across the landscape (Gleditsch et al. 2017). However, increasing loss and fragmentation of natural areas due to urbanization change landscapes and can alter plants and frugivores distribution and affect seed dispersal (Rey & Alcántara 2014, McConkey & O'Farrill 2016, Morante-Filho et al. 2018).

In fact, increasing expansion of cities has generated local extinctions of native species, both plants and animals (Hahs et al. 2009, Ibáñez-Álamo et al. 2016, Sol et al. 2020), with the consequent loss of the interactions in which they engage. Such losses may ultimately translate into a reduced capacity of urban ecosystems to perform critical ecological functions derived from species interactions (Zari 2019), such as seed dispersal (Gelmi-Candusso e Hämäläinen 2019). Despite the increasing interest in evaluating biodiversity in urban ecosystems (Muderere et al. 2018), studies investigating the consequences of urbanization on plant-animal interactions remains geographically concentrated (see below). Here, we present an overview of the studies on frugivory and seed dispersal in urban areas, with a particular focus on understanding the effects of urbanization on plant-frugivore interactions and seed dispersal in tropical areas. Specifically, we (i) examine the global distribution of studies and (ii) in tropical areas, we characterize studies according to the type of environments sampled, taxonomic groups surveyed, methods used to sample interactions, and spatiotemporal coverage; and (iii) review patterns and underlying processes influencing these interactions in urban areas, and whether (and how) they are affected by urbanization. Based on our findings we discuss gaps in the knowledge and provide preliminary recommendations of management practices towards creating biodiversity-friendly urban areas.

Global distribution of urban frugivory and seed dispersal studies

Methods

Our literature search was carried using Scopus and Web of Science employing the following keywords: “*frugivory*” OR “*fruit removal*” OR “*seed dispersal*” OR “*plant- and fruit-frugivor**” OR “*-bat*” OR “*-bird*” OR “*-avian*” OR “*-mammal*” OR “*-monkey*” OR “*-rodent*” OR “*-lizard*” OR “*-vertebrate*” OR “*zoochory*” AND “*urban*” OR “*urbanization*” OR “*urbanisation*” OR “*anthropic*” OR “*anthropization*” OR “*city*” OR “*town*”. In addition, for each study found, we checked the references listed to complement the database. Our search was not restricted by the date of publication, and it was last conducted on 30 October 2020.

Here we included studies that: (i) were carried out in at least one urbanized area (following the definitions of MacGregor-Fors 2011), (ii) considered plant-frugivore interactions in urban green areas, i.e., natural, semi-natural and artificial ecological systems (Cilliers et al. 2013), (iii) included field-based sampling, (iv) informed the locality sampled (e.g. city or geographic coordinates), and (v) presented at least the abstract in English. We excluded studies that: (i) were carried out only in nonurban areas, i.e., rural or natural (*sensu* MacGregor-Fors 2011), (ii) measured plant or animal diversity without relating it to frugivory and/or seed dispersal, (iii) did not specify the distribution of sampling points in urban areas, and (iv) were based only in computational simulations.

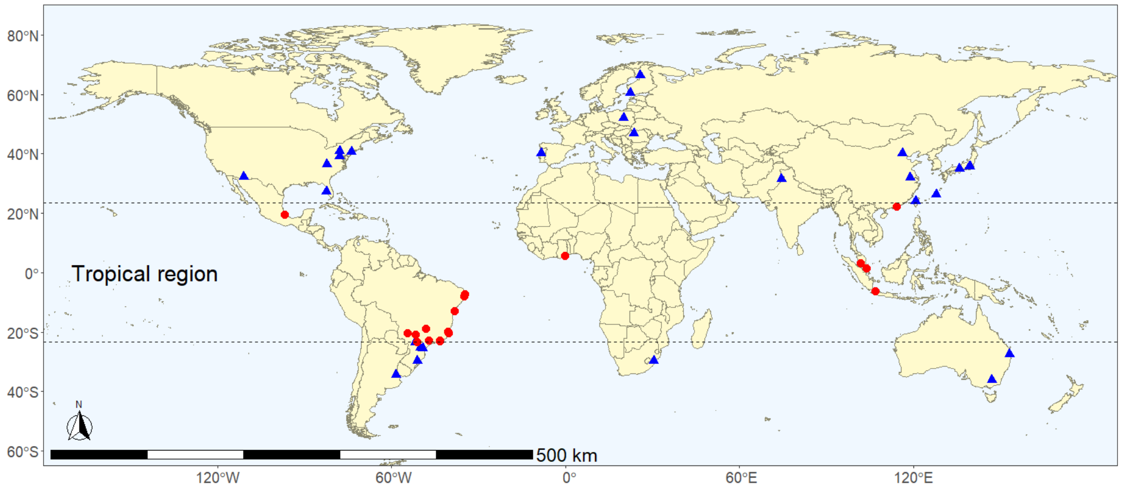
For each study compiled, we extracted the following data: geographic coordinates, city, country, biogeographical region and whether it was conducted in a tropical or non-tropical urban area. For simplicity, we considered ‘tropical’ those areas located between the Tropic of Capricorn (23°26’13.4” S) and the Tropic of Cancer (23°26’13.4” N). In addition, we classified studies into those that ‘directly’, i.e., including a predictor variable related to urbanization or explicit tests of hypotheses related to urbanization (*sensu* Beninde et al. 2015) or ‘indirectly’ (i.e., effects of urbanization are discussed but no direct test is provided) investigated the impacts of urbanization.

Overview

We found 50 studies published on plant-frugivore interactions in urban areas, being 46% in tropical (n = 23) and 54% in temperate regions (n = 27, Fig 1 and Fig. 2A). Altogether, studies encompassed 16 countries and 65 cities (n = 23 in tropical; n = 43 in non-tropical areas; Fig. 1). Of the total, 40 studies were carried out in a single city, eight included more than one city (2 to 11), one included 78 sites in three counties in the United States, and another was on an island (the Singapore city-state). Although the numbers of studies in tropical and temperate regions were similar, they were unevenly distributed within each region (Fig. 1). In the tropics, most studies were in the Neotropics (78.3%; n = 18 out of 23 studies), especially at Eastern South America, with notable gaps in the Amazon, Neotropical Savanna, Andes and Southern Central America. Although Amazon has few large urban settlements, the lack of studies is concerning as it harbors the largest diversity of frugivorous animals and fleshy fruit plants worldwide (Fleming et al. 1987, Kissling et al. 2009) and is an area of high conservation concern (Cincotta et al. 2000). Similarly, there were few studies in the

Indomalayan region (17.4%; n = 4 out of 23 tropical studies), with better coverage of communities in Southeastern Asia, and a gap in the Indian Subcontinent and Southeastern Asia forests. A remarkable gap was also found across the Afrotropical region, where only one study was found. While the Indomalayan region concentrates high diversity of frugivorous birds (Kissling et al. 2009) and bats (Fleming et al. 1987), the Afrotropical region harbours high diversity of frugivore primates, and both regions concentrate high diversity of large-bodied frugivores compared to the Neotropics (Fleming et al. 1987). In the non-tropical region, 44.4% (n = 12) of the studies were conducted in the Palearctic, 22.2% (n = 6) in Nearctic, 18.5% (n = 5) in Southern South America, 7.4% (n = 2) in Australasia, 3.7% (n = 1) in Southern Africa, and 3.7% (n = 1) in the temperate Indomalayan region. These results reveal a sampling bias towards the Neotropical (mainly Eastern Brazil) and Paleartic regions (especially Europe and East Asia). Such geographic gaps constrain generalizations of the patterns discussed below and also indicate places where future studies should be considered in order to achieve a more comprehensive understanding of the spatial variation in the effects of urbanization on plant-frugivore interactions.

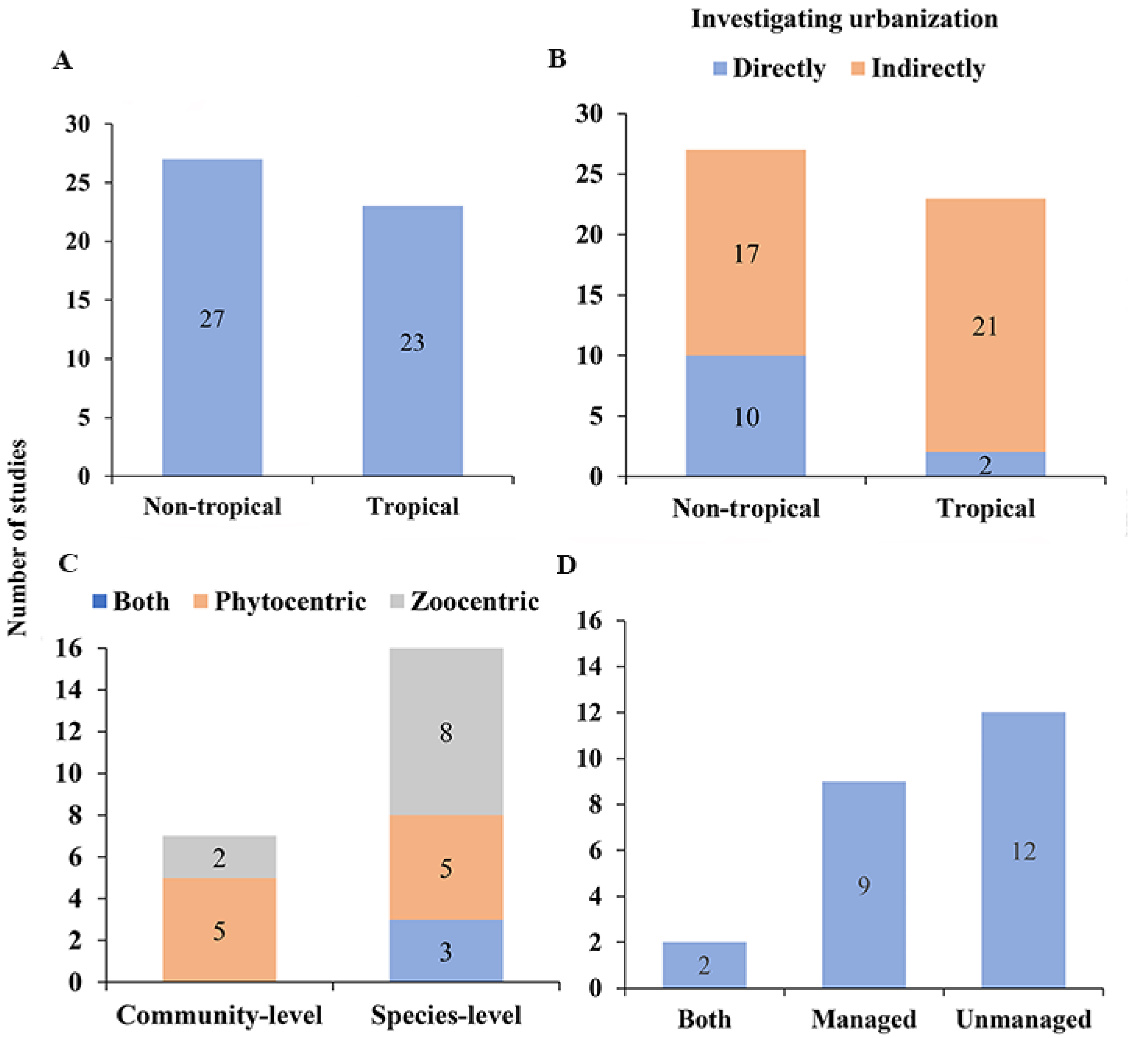
Figure 1 – Global geographic distribution of studies on plant-frugivore interactions across tropical (red circles, n = 28) and non-tropical (blue triangles, n = 22) regions. Seven studies in the tropical region were developed in the same city and therefore circles overlap.



Characteristics of the studies in the tropical urban areas

Out of the 23 studies of plant-frugivore interactions in tropical cities (Supplementary Material, Table S1), 30.4% were carried out at community-level (n = 7) and 69.6% at species-level (n = 16, Fig. 2C). For the latter, there was a predominance of dietary studies (n = 14), which described fruits consumed by one or a few animal species, while only two studies focused on describing the assemblage of frugivores of one or a few plant species. Nine of these studies (39%) were observational (i.e., only described interactions within urban areas), 61% indirectly discussed urbanization-related effects, and 9% (Afrotropics: n = 1, Indomalayan: n = 1) tested directly the effects of urbanization (Fig. 2B). Surprisingly, in the Neotropics which was the most well-sampled tropical region, no study has directly investigated the effects of urbanization. These results indicate that the current understanding on frugivory and seed dispersal in urban tropical areas is largely based on observational studies that describe the diet of a few animal species and, despite discussing the effects of urbanization, rarely include explicit hypotheses (and tests) of its direct effects. In the following sections, we summarize and discuss the distribution of these studies across distinct urban environments, spatial and temporal gradients, sampling methods, and taxa.

Figure 2 – (A) Number of studies on plant-frugivore interactions in urban areas per region. Studies in the tropical region were classified according to whether they investigated the effects of urbanization directly (blue) or indirectly (orange), (B) whether sampling of interactions was based on zoocentric or phytocentric methods (C), and whether the urban areas studied was managed or unmanaged (D). We note that in D 47.8% (n = 11) of the studies (both in managed and unmanaged areas) were conducted on University campuses.



Types of urban environments studied

Urban vegetation areas can be broadly classified as unmanaged or managed. Here we consider that unmanaged areas include, for example, vegetation remnants and riparian corridors that are relicts of the vegetation pre-urbanization and are not regularly submitted to management practices such as clear-cutting and pruning (Fig. 3A). Managed areas, in turn, may vary considerably in the extent of management received, as it is often the case of squares, parks, public walkways, backyards and gardens (Fig. 3B). Both types of urban green spaces within the urban matrix also vary in size, degree of isolation, vegetation cover and human density (Aronson et al. 2017). Our review reveals that studies on plant-frugivore interactions in tropical urban environments (Fig. 2D) characterized interactions either in a single site (managed: n = 2 studies; unmanaged, n = 9), multiple sites (managed = 7, unmanaged = 3), or compared managed and unmanaged sites (n = 2 studies). Although both managed and unmanaged green urban areas can be important refuges for fauna and flora (Aronson et al. 2017), managed areas usually present considerably lower capacity to harbor biodiversity (Beninde et al. 2015). For example, unmanaged vegetation provides better conditions for specialists, ground-nesting bird species than managed sites (MacGregor-Fors & Ortega-Álvarez 2011). In addition, whether (and to what extent) an urban area is managed may influence species composition, which ultimately influence how variable plant-frugivore interactions are across sites (Chan et al. 2020).

Figure 3 – Examples of urban environments showing an unmanaged forest patch (A) and a managed park (B) in Brazil (Foz do Iguaçu city, Paraná state). Photos by Israel Schneiberg.

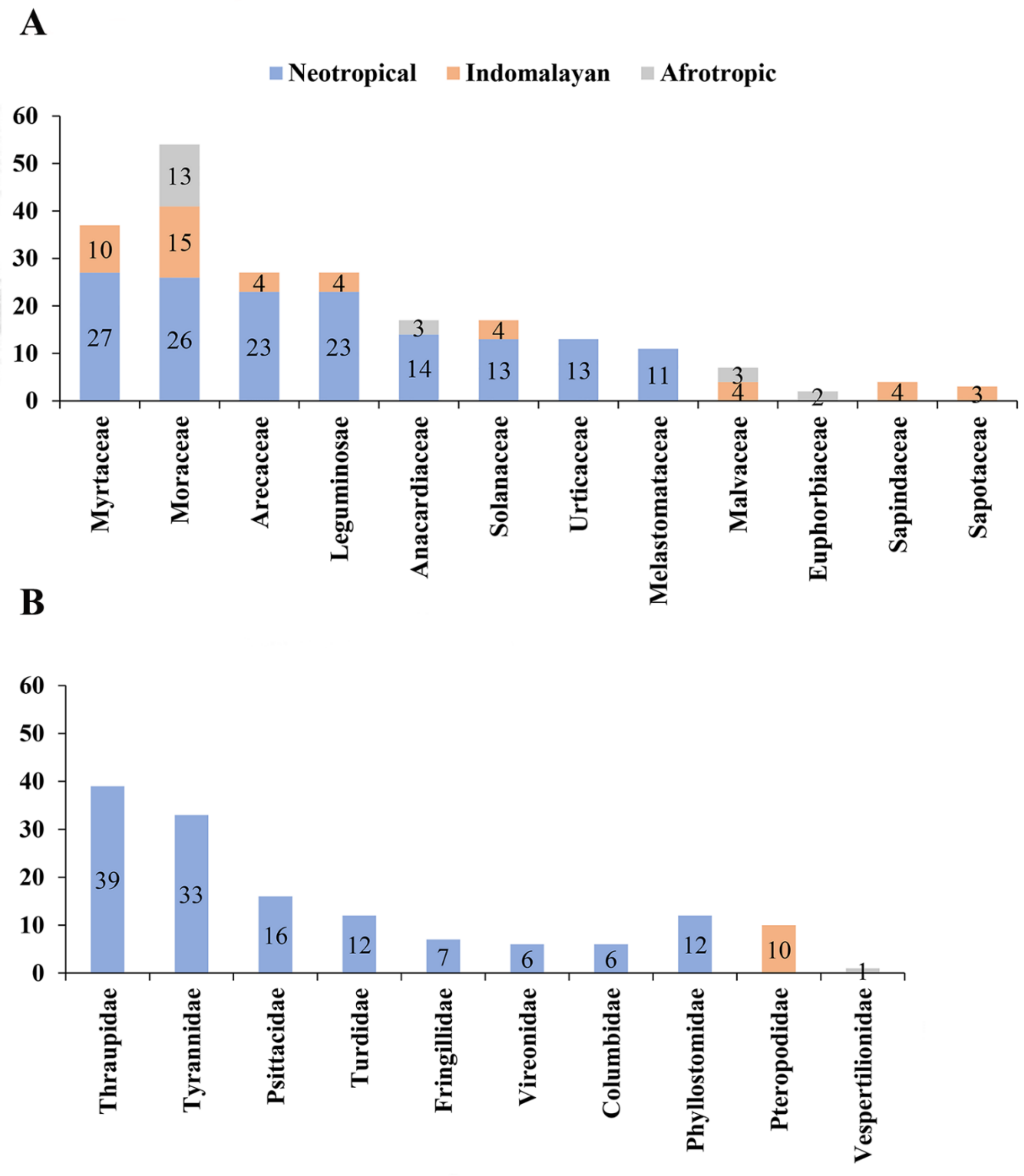
Due to greater habitat complexity and density of vegetation, unmanaged areas can retain “urban avoider” species, such as frugivores with low dispersion (and escape) capacity, and late-successional plant species (McKinney 2002). Because of their habitat requirements, urban avoiders usually do not thrive in highly managed areas. On the other hand, managed areas may harbor “urban exploiters” that are highly synanthropic, and “urban adapters” which are typically omnivorous species that usually inhabiting forest edges and disperse more easily through the urban (usually low quality) matrix, as well as introduced species (McKinney 2002). Furthermore, it is particularly important to consider that spatial overlap is a requirement for the establishment of plant-frugivore interactions (Albrecht et al. 2012, Vizentin-Bugoni et al. 2021), and therefore environmental variables that influence species distributions may also define interactions. In fact, the number of native fruits consumed by bats vary with the distance from natural forests, low impermeable surface coverage and proportion of managed vegetation (Chan et al. 2020). Thus, more studies investigating a broad range of spatial variables that may act as filters of frugivores and their resources in urban landscapes are important to advance the implementation of more biodiversity-friendly cities.

Taxonomic coverage of the studies

Generalist species, i.e., species interacting with a large number of partners, are thought to play a central role in the dynamics and stability of interaction networks, so that identifying these species is important for conservation and management initiatives (Martín González et al. 2010, Messeder et al. 2020, Vizentin-Bugoni et al. 2021). Based on the 23 studies in tropical urban areas, Myrtaceae, Moraceae, Arecaceae, and Leguminosae were the plant families most frequently used as fruit resources by frugivores (Fig. 4A, Supplementary Material, Table S2). *Ficus* was the most frequent genus and the one with the largest number of species across cities in all biogeographic regions. Also, both the Neotropical and Indomalayan regions had *Syzygium* and *Solanum* genera as important resources for frugivores. Species of the genera *Cecropia*, *Piper*, *Syagrus*, *Inga*, *Miconia*, *Myrcia*, *Psidium*, and *Eugenia* were important resource plants in Neotropical cities. While more studies are necessary before generalizations, these plants seem to be often key resources attracting high numbers of frugivores, being especially relevant for urban greening initiatives as long as they are native to the region or introduced species with low risk of becoming invasive. However, we highlight that the knowledge of the flora used by frugivores in local natural areas is desirable to identify appropriate local keystone resources and, thus, to define which plants to use in outplanting initiatives in the urban areas under consideration (Messeder et al. 2020). In addition, our results show that bats and birds are the main fruit consumers in tropical urban areas and, therefore, are important in performing seed dispersal in urban areas (Fig. 4B, Supplementary Material, Table S3). Thraupidae, Tyrannidae, Psittacidae, Turdidae and Fringillidae bird families were the most frequent frugivores groups reported in Neotropical cities, with a high representation of the genera *Turdus*, *Thraupis*, and *Euphonia*. Among mammals, Phyllostomidae (especially *Artibeus*) and Pteropodidae (especially *Cynopterus*) were the frugivore bat families most frequently reported across Neotropical and Indomalayan studies, respectively. Due to their high flight capacity, these groups are probably less affected by low connectivity and low permeability of the urban matrix and can more easily avoid urban disturbance (such as flow of humans and vehicles) than other terrestrial or arboreal frugivores, such as Primates. However, we emphasize that several other groups of frugivorous animals have been little studied in urban areas so far, such as non-flying mammals and lizards (Valido & Olesen 2019), frugivore fishes and chelonians (Falcón et al. 2019), as well as ants

(Camargo et al. 2016) and, thus, their importance as primary or secondary seed dispersers in urban areas remain poorly understood.

Figure 4 – Most diverse plant (A) and frugivore (B) families in tropical urban areas across different biogeographical regions. Numbers indicate the total number of species summed up across studies.



Sampling: methodological approaches and spatiotemporal coverage

Several studies (n = 8, 34.8%), aiming to describe the diet of single animal species in cities, used a zoocentric approach (quantification of interactions through the identification of seeds obtained from droppings; Voigt et al. 2009). On the other hand, five (21.7%) community-level studies used phytocentric approaches (plants observed to quantify fruit consumption by animals). Combination of both methods was never used to characterize interactions at the community-level and only used in one single-species phytocentric, and two single-species zoocentric studies (Fig. 2C). Both methods have pros and cons and may inform about distinct nuances of plant-frugivore interactions. While the phytocentric approach does not inform whether seeds that go through animals' gut will come out intact nor allows investigation of seed germination, it has the advantages of being spatially explicit (the area inside which interactions are measured is known). It also enables the observation of consumers' behavior (Schupp 1993), including the determination of seed predation events (Côrtes et al. 2009), and also allows the identification of frugivory on fruits that despite not having their seeds dispersed by animals frequently, are important food resources (e.g., banana *Musa* spp., mango *Mangifera indica*, kaki *Diospyros kaki*) (Gosper et al. 2005, Buckley et al. 2006). For the zoocentric approach, the spatial scale is unknown as home ranges and dispersal capacity may vary among consumer species from a few meters to several kilometers, but it has the advantage of better characterizing consumers' diets in a broader spatial scale (Vitorino et al. 2022). Since researchers have access to the seeds consumed, this method also allows a more appropriate inference of the outcome of an interaction as, for instance, via investigation of seed germination rates after gut passage (Traveset 1998). Owing to these differences, distinct sampling approaches may inform distinct aspects of frugivory and/or seed dispersal in urban areas.

Evaluation across urban gradients would help to understand how species composition and diversity of interactions vary with urbanization (Schneiberg et al. 2020), however, so far few studies were designed to cover such gradients. Specifically, our review revealed that only one study covered urban + rural environments, another covered urban + rural + natural environments, and four spread sampling points across urban + suburban environments (Supplementary Material, Table S1). As one moves away from highly urbanized areas, major physical changes in the environment occur as human population density, proportion of paved areas, level of soil compaction and average temperature decrease (McKinney 2002). Downtowns with high impermeable surface cover are often isolated by low quality matrices and high pedestrian and vehicle flow (MacGregor-Fors 2011). In contrast, suburban areas tend to present increased tree cover on sidewalks as well as backyards and gardens, therefore, providing habitat and food resources for frugivores (Lim and Sodhi 2004). Since such differences in land use may occur both within and between cities (Ramalho & Hobbs 2012), more studies assessing urban landscape gradients are needed before the generalization on the effects of urbanization can be made.

Temporal distribution of species and resources are also critical factors influencing sampling of plant-frugivore interactions and can vary at distinct scales, from hours or days to seasons, years and decades (Carnicer et al. 2009, CaraDonna et al. 2021). While tropical communities usually have fruits available year-round, with plants often showing staggered fruiting periods, animals in these areas may perform seasonal (latitudinal or altitudinal) migrations. In this scenario, the temporal sampling coverage may considerably influence the detection of species and interactions. In fact, fruit availability was shown to vary over space and time in a tropical urban area (Freitas et al. 2020). Although we found multiple studies sampling interactions restricted only to a portion of the year, 13 studies (56.5%) covered the seasonal variation throughout the year. Moreover, seven studies included multi-year sampling, and none so far has included diurnal variation in plant-frugivore interactions. Importantly, studies have evidenced that the scarcity of resources in some seasons led to increasing overlap in the use of fruits by frugivores (Sartore & Reis 2013, Santos & Ragusa-Netto 2014, Pereira et al. 2019), which is only detectable by sampling that covers the annual cycle of the study system. In the context of urbanization, finer time scales such as those related to the diurnal variation in the flow of vehicles and pedestrians, can also be important by, for example, creating specific temporal windows of opportunity for foraging without implying in higher risk of predation, collision with vehicles or energetic costs associated with the disruption of the feeding activity. On the other hand, longer time scales may also be important as vacant lots, gardens and private backyards may provide complementary but somewhat unreliable supply of resources for frugivores owing to sudden management (e.g. mowing). Thus, well-thought sampling and comprehensive spatiotemporal coverage of studies can be important to advance the understanding of species interactions in the urban landscape.

Effects of urbanization in plant-animal interactions: patterns and processes

Temporal variation

Plants with longer fruiting seasons tend to interact with more frugivorous animals (Vizentin-Bugoni et al. 2021) and interaction frequencies depend on the extent of phenological overlap between partners (Machado-de-Souza et al. 2019). We found five studies that tested the effects of seasonal fruit availability on plant-frugivore interactions in urban areas. They found periods of low fruit availability associated with lower consumers' niche breadths (Santos & Ragusa-Netto 2014; Pereira et al. 2019, but see

Chan et al. 2020), and high niche overlap among frugivores (Sartore & Reis 2013). During periods of high fruit availability, besides increasing niche breadths and decreasing niche overlap, evidence suggests increase in species richness (Corral et al. 2020) and in the proportion of fruits included in the diet (Oliveira-Silva et al. 2018). Thus, in order to support high diversity of frugivores in urban environments, prioritizing the planting of native species and/or non-invasive introduced species that maximize fruit availability throughout the year, are recommended (Fig. 5). This includes consideration of plants with long fruiting periods and/or multiple species with sequential fruiting periods, in order to promote continuous supply of food for frugivores over time (DeWalt et al. 2003).

In this context, gardening may contribute to the network of urban green areas by promoting fruiting plant diversity over time that favors plant-frugivore interactions. For example, in some developed countries from temperate regions, residents have engaged in oriented gardening practices aiming to increase the complexity of vegetation and providing suitable habitats for wildlife, including removal of weeds, outplanting of native shrubs/trees, protection of trees with nest, etc (Mumaw & Bekessy 2017). Gardening also constitutes an opportunity to increase and complement the local plant diversity through cultivation of epiphytes and herbs, since public urban green spaces tend to favor trees and shrubs. These are examples of “ecomimicry” initiatives, in which greening aims to mimic the local natural landscape and renaturalize urban green spaces, making them more biodiversity-friendly, functional and self-sustainable (Rumble et al. 2019). Furthemore, initiatives aiming to educate and guide citizens and policy makers about good practices related to the effects of gardening on species interactions and ecosystem services may benefit from incorporating cultural and socioeconomic factors that may influence gardening patterns (Kinzig et al. 2005, Goddard et al. 2013, Mumaw & Bekessy 2017).

Spatial variation

Plant-frugivore interactions depend on how animals respond to the structure of surrounding habitats (landscape) and their modification (Miguet et al. 2016, Bovo et al. 2018). Studies at this scale are still generally scarce in natural areas, and this is also true for urban areas. Specifically, frugivore bats travel longer distances within urban than rural landscapes, but disperse fruits across longer distances in rural areas (Abedi-Lartey et al. 2016) which highlights the influence of the landscape on seed dispersal. Because long-distance dispersal is an important component of effective seed dispersal (Schupp 1993, Godínez-Alvarez et al. 2002), this indicates a negative effect of urbanization on this ecosystem function. On the other hand, despite short-distance seed dispersal may also be detrimental to the propagation of native plants, it may prevent introduced species from spreading beyond the city limits or at least decelerate biotic invasions.

Furthermore, the size and proximity of native patches, their connectivity within the urban environments through riparian corridors, as well as increased vegetation cover make the landscape more permeable to animals (Beninde et al. 2015, Dale 2017, Gelmi-Candusso & Hämäläinen 2019, Schneiberg et al. 2020). In fact, in Singapore, bats increased fruit richness in their diet with proximity of native forests within urban areas (Chan et al. 2020). Thus, well-connected patches and the presence of large patches with native vegetation within the urban matrix are likely critical to maintain the diversity of frugivores (Fig. 5). Furthermore, theoretical and empirical studies suggest that not only coexistence of multiple species (high diversity), but also the stability (rates of secondary extinctions) of plant-frugivore interaction networks in natural areas depend on how species share resources (Burgos et al. 2007, Bastolla et al. 2009, Thébault & Fontaine 2010, Donatti et al. 2011). Associated with empirical studies that found high resources partitioning among frugivores in unmanaged peri-urban forest patches (Corral et al. 2020, Salazar-Rivera et al. 2020), these results reinforce the value of unmanaged forest patches within urban areas for interaction stability. Therefore, patches of natural areas favor frugivore animals and are essential for maintenance of seed dispersal interactions.

While still important shelters for the fauna and acting as steppingstones that increase connectivity between higher quality habitats, smaller and managed patches are arguably less valuable for frugivores and seed dispersal compared to large unmanaged patches (Beninde et al. 2015, Chan et al. 2020). In fact, anthropogenic disturbances such as noise and presence of potential predators (e.g. dogs and cats) may influence spatial patterns of animal activities (Fernández-Juricic 2001, Blumstein et al. 2005). For example, birds occupy more frequently internal sites of urban parks where foraging activity is disrupted less often than at park edges (Fernández-Juricic 2000). Similarly, in the suburbs of a temperate city, frugivores are less abundant on roadsides and take longer to feed owing to traffic (Suhonen et al. 2017). Although to the best of our knowledge no study so far has investigated these aspects in tropical cities, we argue that it is possible to increase the quality of such areas by applying, for instance, ecomimicry strategies in order to create “pockets” of more complex natural areas. Also, to avoid disruption of frugivores activity and facilitate seed dispersal, initiatives may consider creating “traffic-free zones” within parks by building walkways far from the natural areas.

Functional matching

Morphological traits of plants and frugivores such as fruit and seed sizes and bill gape are important factors defining fruit consumption by animals (Wheelwright 1985). Small fruits are accessible to a wider variety of frugivores and plants with this trait, as well as small seeds, tend to play a central role in communities (Sebastián-González 2017, Torres et al. 2018, Vizentin-Bugoni et al. 2021). Thus, outplanting of native plants with small fruits (and seeds) may be an interesting strategy to attract and support a greater diversity of frugivores. On the other hand, large-bodied frugivores – which often have larger gapes and play important roles as seed dispersers – may feed preferentially on large-seeded fruits which in turn rely exclusively on such animals for dispersal as they are able to swallow the seeds (Dehling et al. 2016, Oliveira-Silva et al. 2018). However, landscape modification and habitat loss increase the risk of local extinction of interactions of such large-bodied animals and large-seeded plants (Bovo et al. 2018, Emer et al. 2018, Vizentin-Bugoni et al. 2019). In fact, defaunation is often biased towards large-bodied frugivorous birds such as Motmots (Momotidae), Chachalacas (Cracidadae) and Hornbills (Bucerotidae), and Mammals such as Gibbons (Hylobatidae) and Civets (Viverridae) which are often important seed dispersers (Corlett 2017, Emer et al. 2018, 2019). Thus, high diversity and complementarity of frugivore and fruit functional traits are critical to maintain high diversity of seed dispersal interactions (Bovo et al. 2018), but remain poorly investigated in the context of urban communities. If urbanization causes homogeneity in functional traits (Sol et al. 2020) it may affect community functioning (Alberti et al. 2017). This means that urbanization can accelerate local extinctions of interactions, and ultimately, extinctions of species that depend on mutualistic partners. In this sense, the existence of urban areas with high fruit and seed trait diversity (including larger fruits) may be an important requirement for the area to support functionally diverse frugivore faunas.

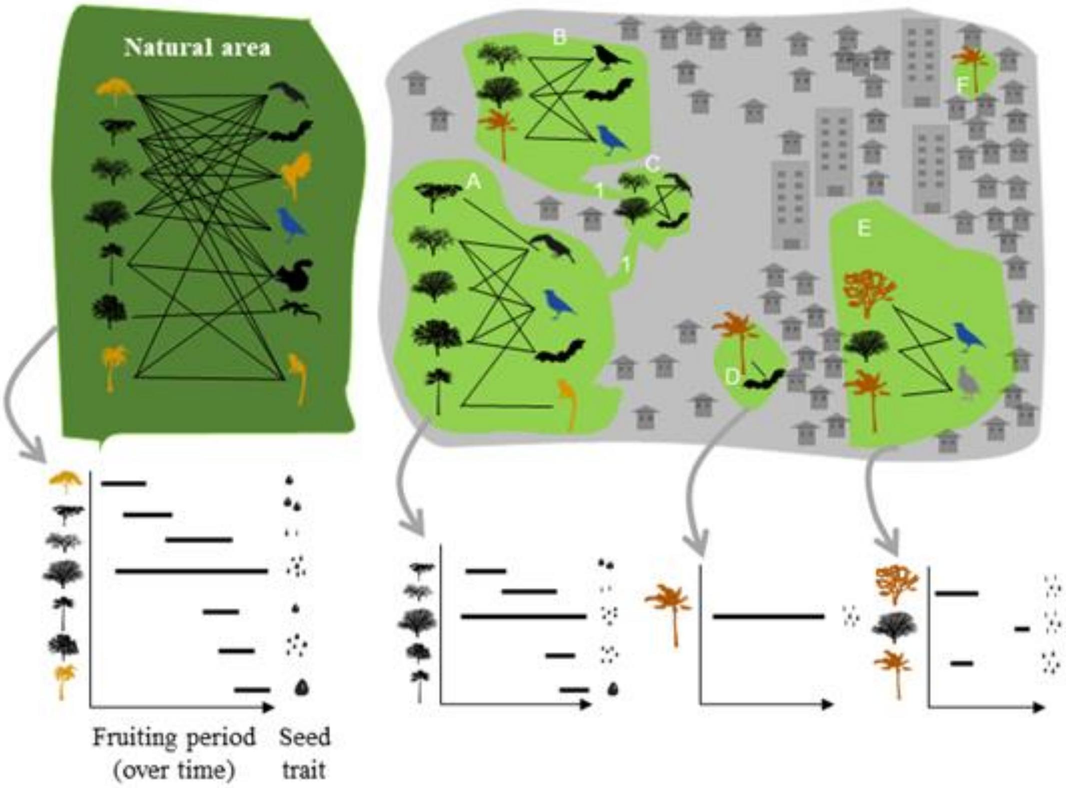
Ecosystem disservices promoted by frugivores: spread of invasive species and other undesirable plants

Introduced plants are commonly cultivated as ornamentals, occupying backyards, gardens, orchards, squares, and parks across the urban landscape (Freitas et al. 2020, Silva et al. 2020). Introduced invasive species often have traits that allow them to spread easily, including small fruits and seeds, and long fruiting periods (see Sperry et al. 2021 and references therein), and frugivores may end up providing 'ecosystem disservices' by spreading seeds of these plants (Vilá & Ibáñez 2011, Saunders 2020). Frugivores are protagonists in this scenario, as they may favor consumption of introduced species in urban areas (e.g., Chan et al. 2020, Laurindo & Vizentin-Bugoni 2020) and accelerate invasion by dispersing the seeds. In fact, more than half of the studies (56.5%, n = 13) reported the consumption of introduced fruits by animals in tropical cities, reporting from 1 to 20 (6.23 ± 6.30, mean ± s.d.) introduced species consumed. This suggests that introduced plants are an important component of animals' diets in cities (Lim et al. 2018, Chan et al. 2020) which, in turn, contribute to their invasion across the landscape. Although preferences were tested for only two frugivore bird species, both fed more frequently on native than introduced species (Santos & Ragusa-Netto 2013, 2014), while another study recorded a bat diet constituted exclusively of introduced species (Chan et al. 2020).

However, not all introduced species are invasive and some of them, such as large-fruited species with high-nutrient pulp (i.e. banana, mango, and kaki), may be beneficial by attracting frugivores and facilitating dispersal of native plant species

(Buckley et al. 2006). In fact, the effect of some plant species on increasing frugivore richness has already been reported for urban areas (Peabotuwage et al. 2019), leading to a potential facilitation process among plants in the community. On the other hand, if such highly attractive introduced plants monopolize frugivores, they may have a competitive effect on native species which face limitations in seed dispersal. The neighborhood effects may be especially relevant for investigation, in which facilitation processes occur when fruiting neighbors increase the chance of removing introduced fruits (Gleditsch et al. 2017) and competition when the availability of frugivores is limited (Carlo & Morales 2008) and introduced trees and their neighbors compete for seed dispersal. In sum, selection of introduced plants for outplanting need to consider not only if they will support frugivore populations but also whether they have potential to become invasive and whether they may facilitate or compete native plants. Moreover, since cities are sources of introduced seeds that are dispersed to adjacent habitats by frugivores, we stress that urban spaces may contribute with the emergence of novel ecosystems, such as those reported for other highly modified semi-natural ecosystems (Cruz et al. 2013, Vizentin-Bugoni et al. 2019). Finally, other ecosystem disservices associated to frugivory and seed dispersal in urban areas involve the spread of parasitic plants, i.e., mistletoes, which can cause economic loss to urban forestry by inducing host mortality (Maruyama et al. 2012, Díaz-Limón et al. 2016), but so far general assessment of these impacts is missing.

Figure 5 – Hypothetical configuration of plant-frugivore interactions in an urban landscape. Large patches of native vegetation (dark green) near the urban matrix (grey area) act as important sources of species and interactions for urban green spaces (light green). Patches near natural and less urbanized areas (A-C) tend to hold higher diversity than small (D, F) or large (E) patches isolated by impermeable urban matrix. Green corridors (1) may facilitate dispersion of species among patches. Introduced species (orange) tend to be more frequently detected in the diet of frugivores in heavily urbanized areas (D-F). While some species are "urban avoiders" (yellow), highly synanthropic may be "urban exploiters" (gray) or "urban adapters" (blue). Urban green spaces with high plant diversity and fruits available over time (without temporal gaps) and encompassing high variation in fruit and seed sizes (compare A versus D and E, in the bottom) are more likely to retain high diversity of plant-frugivore interactions and seed dispersal.



Considerations on management towards urban green spaces friendly to animal-dispersed plants, frugivores and their interactions

While we acknowledge the study of plant-frugivore interactions and their associated ecosystem functions in urban areas are still incipient and generalization may be taken cautiously, we use the existing knowledge discussed in this study and previous reviews (Buckley et al. 2006, Gelmi-Candusso & Hämäläinen 2019, Rumble et al. 2019) to produce a list of measures that may help urban ecosystems to retain diversity of fruiting plants and frugivores as well as the seed dispersal function:

1. Outplanting of local native species whose fruits are consumed by frugivores, especially those with long fruiting seasons and small seeds which may help to support high frugivore abundances and richness and promote seed dispersal

2. Avoiding the outplanting of introduced fleshy-fruits, especially those species with small seeds, as they may be dispersed to natural areas by frugivores and become invasive. However, introduced species with no invasive potential may be considered since they may provide abundant resources and contribute to sustain animal populations

3. Outplanting should consider fruiting phenology in order to avoid (and fill) temporal gaps when fruits are absent or little abundant

4. Creation of “human-free zones” and “high-quality habitat pockets” within managed parks where species more sensitive to human and pet activity may take shelter and/or face less disruption of their activity

5. Urban planning should aim to increase connectivity among urban green spaces via creation of green corridors and implementation of closer green areas which can be used as stepping-stones by frugivores
6. Adoption of the ecomimicry approach with wildlife-focused gardening to foster vegetation structure suitable for frugivores that require greater habitat complexity

Conclusions

While our review highlights the existence of remarkable geographical and methodological biases in the studies of plant-frugivore interactions in tropical urban areas, it reveals important knowledge gaps that should be addressed by future studies. As urbanization rate increases, filling such gaps through comprehensive investigations on the effects of urbanization on species interactions and their mitigation, become urgent for urban planning aiming at the creation of biodiversity-friendly cities. Even though we stress that more studies are required, and caution is needed before generalizations, the evidence accumulated so far (both in urban and non-urban environments) allow the identification (or prediction) of some of the major effects of urbanization on frugivory and seed dispersal in tropical areas. Based on such evidence, we propose a preliminary list of recommendations that may benefit frugivores and the native plants they disperse in tropical cities. We reinforce that the initiatives recommended would benefit from an integrative approach that considers other groups of organisms such as pollinators, for instance, since fruit set often depends on animal pollination. Beyond the inherent value of plant and frugivore biodiversity, seed dispersal interactions underlie other ecosystem services provided by nature such as flood mitigation by increasing soil permeability, carbon sequestration, and temperature regulation (McKinney 2002, Eigenbrod et al. 2011). Furthermore, greater contact with wildlife and outdoor activities benefit human mental and physical health, and promote opportunities for social cohesion and reflection (Davies et al. 2009, Mumaw & Bekessy 2017). Thus, promoting urban green spaces areas goes beyond conserving species and their interactions as, ultimately, biodiversity-friendly cities are critical for maintenance of the health of contemporary and future generations.

SUPPLEMENTARY MATERIAL

Table S1 - https://figshare.com/s/e610f42e264430489809

Table S2 - https://figshare.com/s/8ab91995adb344ad8fb1

Table S3 - https://figshare.com/s/38b80a474c5f7cf6cf79

Chapter 3 – Green areas in urban landscapes favor diversity and resource partitioning among plants and frugivorous birds

Green areas in urban landscapes favor diversity and resource partitioning among plants and frugivorous birds

Abstract

Although urban ecology has stimulated interest in understanding patterns of diversity in the cities, few studies have explored interactions between species in these environments. Specifically, variations in the structure of interactions networks between plants and frugivorous birds remain poorly understood. We quantified interactions between plants and frugivorous birds in Campo Grande, Brazil and tested whether network specialization, modularity, and the components of diversity (taxonomic, functional, and phylogenetic) are influenced by impermeable surface and tree and scrub cover. Secondarily, we evaluated which diversity components are most strongly associated with interaction network metrics. We conducted the study in 24 green areas in the urban-suburban gradient from October 2020 to December 2022. Based on the birds-fruiting plants interactions recorded through fruit consumption, we built 24 quantitative matrices, one for each studied site. We used buffers of different sizes around each sample unit to characterize the landscape through satellite images. In each buffer we calculated tree and impervious surface cover. We recorded 68 species of birds interacting with 81 species of plants, especially frugivorous birds from tanagers, thrush, but including large frugivores such as Bare-faced Curassow and Blue-and-yellow Macaw. We found that: (i) plant diversity increased on well-forested islands (i.e., tree cover at a smaller scale – 200 m) within an urban matrix (1000 m), (ii) green areas in an urban matrix (1000 m) increased the phylogenetic diversity of frugivorous birds, (iii) plant diversity and functional traits are more important in the formation of interactions modules, and (iv) networks of interactions in green areas with high impermeable coverage have greater dominance of some alien, and early successional plant species.

Our study brings insights that may assist management decisions, such as using a greater diversity of plant species with complementary morphological traits associated with frugivory in urban greening. Additionally, it is important to consider the tree and shrub coverage at the smaller scale, as these plants comprise greater diversity of fruiting plants. We show here how some landscape features are associated with different components of diversity and permeate the robustness of interaction networks.

Keywords: frugivory, urban area, urbanization, network structure, resource partitioning.

Resumo

Embora a ecologia urbana tenha estimulado o interesse na compreensão dos padrões de diversidade de espécies nas cidades, poucos estudos exploraram as interações entre as espécies nesses ambientes. Especificamente, as variações na estrutura das interações entre plantas e aves frugívoras permanecem pouco compreendidas. Medimos as interações entre plantas e aves frugívoras em Campo Grande, Brasil, e testamos se a especialização da rede, a modularidade e os componentes da diversidade (taxonômico, funcional e filogenético) são influenciados pela cobertura de superfície impermeável e cobertura arbórea. Além disso, avaliamos quais componentes da diversidade estão mais fortemente associados às métricas da rede de interação. Realizamos o estudo em 24 áreas verdes no gradiente urbano-suburbano de outubro de 2020 a dezembro de 2022. Com base nas interações planta-ave frugívora registradas por meio do consumo de frutas, construímos 24 matrizes quantitativas, uma para cada local de estudo. Utilizamos buffers de diferentes tamanhos ao redor de cada unidade amostral para caracterizar a paisagem através de imagens de satélite. Em cada buffer calculamos a cobertura arbórea e superficial impermeável. Registramos 68 espécies de aves interagindo com 81 espécies de plantas, com destaque para aves frugívoras como saíras, sabiás, mas incluindo grandes frugívoros como mutum-de-penacho e arara-canindé. Descobrimos que: (i) a diversidade de plantas aumentou com a cobertura arbórea em menor escala (200 m) dentro de uma matriz urbana (1000 m), (ii) as áreas verdes em uma matriz urbana (1000 m) aumentaram a diversidade filogenética de aves frugívoras, (iii) a diversidade de plantas e características funcionais são mais importantes no formação de módulos de interações, e (iv) redes de interações em áreas verdes com alta cobertura impermeável têm maior dominância de algumas espécies de plantas exóticas e de sucessão inicial. Nosso estudo traz insights que podem auxiliar em decisões de manejo, como a disponibilização de maior diversidade de espécies vegetais com características morfológicas complementares associadas à frugivoria para plantio nas áreas verdes urbanas. Além disso, nessas decisões é importante considerar a cobertura arbórea e arbustiva em escalas menores, pois essas espécies compreendem a maior diversidade de plantas frutíferas. Mostramos aqui como algumas características da paisagem estão associadas a diferentes componentes da diversidade e permeiam a robustez das redes de interação.

Palavras-chave: frugivoria, área urbana, urbanização, estrutura de rede, particionamento de recursos.

Introduction

Urban areas are spreading quickly around the world (Ramalho & Hobbs 2012, Forman 2016), especially in tropical regions (Cincotta et al. 2000). The transformation of natural areas to impermeable surfaces is one of the major landscape changes, often resulting in significant species loss (Hagen et al. 2017, Carvajal-Castro et al. 2019, Sol et al. 2020). In fact, ecological studies have rapidly advanced to improve our understanding of how biodiversity persists in urban ecosystems, highlighting the role of urban green areas in promoting biodiversity (Reis et al. 2012, Toledo et al. 2012, Silva et al. 2016, Hagen et al. 2017, Souza et al. 2019). Yet, we still know very little about the mechanisms that influence how species interactions are structured, specifically, the partitioning in resource use between species across urban landscapes (Vissoto et al. 2023).

Cities are formed by a heterogeneous landscape, comprising distinct types of land use at different intensities (Pickett & Cadenasso 2017). For example, there may be densely populated areas with a high coverage of buildings combined with green areas, such as small gardens or vegetation corridors, or even large remnants of natural vegetation (Pickett & Cadenasso 2017, Carvajal-Castro et al. 2019). In this sense, discovering the spatial arrangement in which vegetation cover operates to increase biodiversity indices and minimize the impacts of urbanization is valuable for the friendly management of biodiversity (Beninde et al. 2015, Pena et al. 2017). Therefore, the maintenance of green areas in cities function for the conservation of native species and their ecological functions (Nowak & Walton 2005, Alvey 2006, Cruz et al. 2013, Hagen et al. 2017, Pickett & Cadenasso 2017), such as those resulting from interactions between plants and frugivorous animals.

A great diversity of birds consumes fruits and establishes seed dispersal mutualisms with plants (Kissling et al. 2009). These interactions are characterized as complex networks of interactions, illustrating resource sharing among frugivores (Solé & Montoya 2001, Almeida & Mikich 2017). This partitioning of resources, leading to specialization in networks, is due to several processes, such as trait-matching (e.g., large fruits consumed by large beak bird species), phylogenetic inertia (i.e., a shared evolutionary history between interaction partners), and spatial context (e.g., land use cover) (Vázquez et al. 2009, Pigot et al. 2016, Emer et al. 2019b). Otherwise, when there is a significant overlap in resource use, bottlenecks related to the performance of ecological functions may emerge (Dehling et al. 2016). As urbanization leads to greater impoverishment of functional attributes (Smith 2007, Carbó-Ramírez & Zuria 2011, Sol et al. 2014), this can result in interactions being carried out by only a few species. Thus, matching traits such as "large fruits consumed by species of birds with large beaks" may be extinct in these areas. In this way, functional roles can become redundant, making interaction networks smaller and less complex. Thus, to preserve ecological functions it is necessary to examine the processes and mechanisms that are associated with the organization of interaction networks (Vázquez et al. 2009). In urban areas, there seems to be a greater resource overlap in bird-fruiting plants interactions (Sartore & Reis 2013, Santos & Ragusa-Netto 2013, Pereira et al. 2019, Corral et al. 2020). However, the mechanisms underlying this process, for example the environmental gradients existing in the urban perimeter (such as land use), have been little explored (Vissoto et al. 2023).

Bird species have different tolerances to changes in the environment (Solé & Montoya 2001, Memmott et al. 2004, Sol et al. 2014), therefore species specialized in certain resources may be more easily lost depending on the human impact (Chace & Walsh 2006, McKinney 2006, Carvajal-Castro et al. 2019). Indeed, areas with higher cover of trees and bushes generally harbor more robust interaction networks, since they have greater diversity and availability of fruits, being more attractive for birds (Herrera et al. 2011, Emer et al. 2018). If functional diversity also increases in these areas, divergent ecological roles will likely operate to strengthen the network. On the other hand, in another scenario with high impervious surface and low trees and bushes cover, networks can be more simplified, possibly because (i) the community is formed by few plant species and birds, (ii) the high impermeable matrix prevents many animals from reaching these communities, since they are more exposed to predators and have few places to shelter (Fernández-Juricic 2000, Blumstein et al. 2005).

In this study, we aimed (i) to identify birds that consume fruits in green areas and natural patches of urban vegetation, evaluating how metrics associated with the specialization of the interaction networks vary in different landscape contexts. Furthermore, (ii) to evaluate how the taxonomic diversity of fruiting plants, phylogenetic diversity of birds, and functional diversity of both vary across these locations. Finally (iii) to assess which components of diversity – functional, phylogenetic and taxonomic – best describe resource use partitioning. Assuming that landscape features, such as high tree cover and decreased impervious surface areas, in the landscape can cushion the impacts of urbanization, we expect that (1) in more preserved landscapes, interaction networks will be more specialized and have a modular structure. We also expect that (2) in more urbanized landscapes, the taxonomic diversity of plants, phylogenetic diversity of birds, and functional diversity of both will be lower. Finally, the connections that occur in the network of interactions can be formed by processes associated with the spatial context but can also be related with different components of diversity. Thus, we also expect that (3) the modular structure and the specialization of the networks will reflect the greater taxonomic diversity of plants and birds, the greater phylogenetic diversity of birds and/or the complementary functional characteristics of birds-fruiting plants.

Methods

Study area

The study was conducted in the urban area of Campo Grande (Fig. 1, 20°27’53” S; 54°36’58” W), capital of the state of Mato Grosso do Sul, Brazil. The municipality covers an area of 8,082 km^2, with 252 km^2 of urbanized space (IBGE 2022). Campo Grande was founded in 1872 and is undergoing rapid urban expansion, currently with a population of 898,100 inhabitants (111.11 inhabitants/km^2) (IBGE 2022). The climate is characterized by well-defined dry and humid seasons, with average annual temperature of 23.4 °C and average annual rainfall of 1449 mm. The city is located at altitude 592 m and is inserted in the Cerrado domain (IBGE 2004), with native vegetation formed by *cerrado, cerradão, seasonal semideciduous forests* as well as *gallery forests* and *riparian forests* surrounding water bodies.

Selection of sampling areas

In this study, we evaluated the landscape context around of parks, squares and remnants of native vegetation with varying degrees of built-up areas (buildings and other anthropic elements). First, we obtained a list of 181 public green areas in the city (including squares and parks) from the Sistema Municipal de Indicadores de Campo Grande (SISGRAN, 2019). Concomitantly, using Google Earth Pro, we also searched for remnants of native vegetation within the urban area. Then, we selected the study sites from this list according to three preliminary criteria: (i) each sampling unit must be at least 2 km apart, (ii) personal safety, and (iii) permission to access at dawn and dusk for data collection. This resulted in 24 green areas (12 unmanaged sites: natural remnants; and 12 managed sites: city squares and parks) in the urban-suburban gradient.

The unmanaged sites varied in size with four patches of 1-10 ha, five patches of 20-40 ha, one patch of 40-80 ha, and two patches of > 80 ha. The size of the managed sites ranged between < 1 ha and > 10ha (three with 0-1 ha, six with 1-3 ha, one with 3-10 ha, two with > 10 ha). In particular, unmanaged areas consist of patches of native vegetation within the urban matrix, with demarcated trails, but pedestrian circulation occurs less frequently than in managed areas. In contrast, managed green areas selected can be considered representative of other green areas in many tropical cities, which included squares and parks with a mix of sidewalks (some include basketball, soccer fields and playgrounds), lawn and arboreal areas, with scarce native and exotic trees.

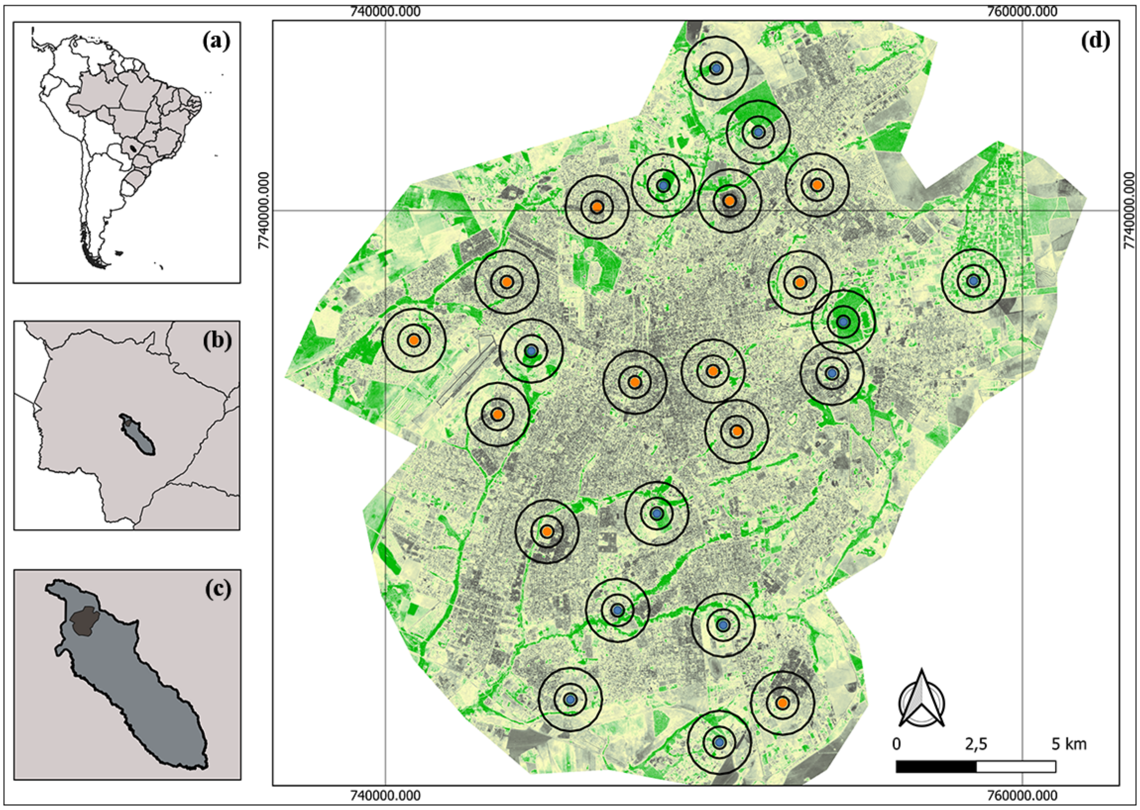


Figure 1. (a) Location of Campo Grande in South America and Brazil, (b) location of the municipality of Campo Grande in the state of Mato Grosso do Sul, and (c) location of the urbanized area in the municipality of Campo Grande. In (d) the 12 managed green areas are represented by orange dots and 12 unmanaged green areas by blue dots, surrounded by their respective buffers (i.e. landscape sizes) of 200m, 500m and 1000m (black circles).

Landscape characterization

Birds that compose a community may vary in their responses to spatial scale in urban areas (Imai & Nakashizuka 2010, Litteral & Wu 2012, Greig et al. 2017). The home range of several Passeriformes has been reported to be around 200 and 500 m (Spurr et al. 2010, Rechetelo et al. 2016), while large frugivorous birds generally have wide home ranges (≥ 1000 m) in which the availability of their food resources is spatially and temporally variable (Ragusa-Netto 2006, Imai & Nakashizuka 2010). The scale-related landscape characteristics should affect interactions that occur in urban areas. Therefore, we used buffers of 200, 500 and 1000 m around each sample unit to characterize the landscape through satellite images. We calculated for each buffer the percentage of the Normalized Difference Vegetation Index (NDVI) (Bonthoux et al. 2018), in July 2022. Although landscape metrics were only computed for 2022, there was no variation in these metrics during the data collection years. The NDVI ranges from -1 to 1, but we use values between 0.60 to 0.90, which represent dense vegetation (Othman et al. 2018), as a proxy for tree and shrub cover. Furthermore, we calculated the percentage of urbanized area for each buffer using the Built-up Index (Zha et al. 2003). Built-up index is an improvement to the Normalized Difference Built-up Index (NDBI), that prevents other land uses from being classified as impervious areas (Zha et al. 2003). Its output results in pixels with a range of values, positive values indicating built-up areas. The Sentinel-2 images were produced with a resolution of 10-m (Fig. 1). Other types of land use, such as lawns, pastures and exposed soil were disregarded in the analysis.

Sampling procedures

Sampling was carried out bimonthly from October 2020 to December 2022, being each site sampled for 13 times. Only one of the sites could not be accessed once in October

2020, because of admission restrictions during the COVID-19 pandemic. We followed the sampling procedure proposed by Jordano (2016), which combines two methods, focal observation and transect sampling. In all sites, we established a nonlinear transect of variable extent (0.40 to 2.65 km) depending on the size of the area. Thus, in some cases, the trails could be longer than the diameter of the sampled area. We conducted an active search along the transects for fruiting plants up to 10 m to each side of the transect. The transect sampling was delimited by time (from 06:00 to 09:00 am and 15:00 to 18:00 pm, interspersing the morning or afternoon period between visits to a given area) encompassing the periods of highest bird activity (Aschoff 1966). When a fruiting plant was recorded in the transect, we carried out focal observation to record frugivory events for 15 minutes. We defined a “frugivory event” as a visit by an individual bird to a focal tree in which the bird was directly observed eating fruit. For observation and identification of frugivorous birds consuming fruits on the fruiting plants, we used 10x42 mm binoculars.

Diversity measures

Fruit-eating bird community counts were conducted during traversing the transects with 15-min survey points, preventing double counting of birds. On each visit to a given site we made lists of birds. Then, amongst the 13 visits performed to a given site in the period of this study we selected the maximum count of a species to describe its abundance in the area. The abundance of observed plant species was quantified through active search in the transect. Phylogenetic diversity reflects the extent to which species in a community share their evolutionary histories, so that more phylogenetically distant species are, the more evolutionary history is represented in the community. As it was not possible to identify some plants at the species level (only genus), we did not calculate the phylogenetic diversity of plants. The phylogenetic relationships among birds were assessed by extracting phylogenies from the BirdTree database (Jetz et al. 2012) and using the backbone tree from Hackett et al. (2008). Since BirdTree offers multiple equally plausible phylogeny hypotheses for a set of species, we generated 999 phylogenies, of which we use the "*consensus*" function of the “*ape*” package to generate a consensus and select only one phylogeny (Paradis et al. 2004). To assess the degree of evolutionary history of birds in the phylogeny of their respective species assemblages in networks, we adopted an originality index based on Rao’s quadratic entropy (Rao PD). This index decomposes the contribution of each species of a phylogenetic tree to the total Rao’s quadratic entropy calculated from the phylogenetic distances between all pairs of species. The Rao 's quadratic entropy of the species was measured with the “*raoD*” function of the “*picante*” package (Kembel et al. 2010) available in the R software (<www.r-project.org>).

To evaluate the functional diversity of bird species, the following morphological measures were taken from the AVONET database (Tobias et al. 2022): (i) beak length, (ii) beak width, (iii) body mass, and (iv) Kipp’s distance. Kipp’s distance is a metric to measure wing elongation in birds and corresponds to the distance between the tip of the longest primary feather and the tip of the first secondary feather of the wing; its values reflect the maneuverability for foraging in different strata of the forest (Pigot et al. 2016). These attributes were chosen due to their relevance for fruit selection by frugivorous birds (Dehling et al. 2014, Pigot et al. 2016). Plant morphological traits were chosen based on characteristics that are important for their selection by frugivorous birds, as described in the literature. These data were recorded only for plants in which frugivory events were observed. In the field we recorded plant height and crop size. Plant height was estimated from the base to the tip of the tallest branch;

crop size, was calculated by counting the total number of fruits in ten randomly selected branches and extrapolating the sum to the remaining branches of each plant. We also measured some attributes of the consumed fruits such as fruit length and diameter. Fruit traits were measured in the laboratory from 10 fruits collected from each individual plant, we then calculated mean values for each species. For abundant plant species, we extracted the average values and obtained a value (plant's height, crop size, fruit length, and fruit diameter) for each species.

We used the four functional traits of birds (beak length, beak width, Kipp’s distance index and body mass) and the four corresponding functional traits of the plants (plant's height, crop size, fruit length, and fruit diameter) to calculate the functional richness (FRic) and functional evenness (FEve) of birds and plant assemblages, respectively. To calculate functional diversity metrics, species occurring across all the communities were first projected into a multidimensional trait space. Then, metrics were derived for each community based on the specific species that occurred in it (Villéger et al., 2008). The first metric, FRic measures the volume of a convex hull formed by connecting all species in a community, in other words, it measures the amount of functional space filled by a community (Villéger et al., 2008). FRic ranges from 0 to 1, with lower values indicating that some functional traits present in the larger pool of species are not present in the specific community. Because FRic does not incorporate the abundance of species we also used the FEve, which measures regularity of the distribution of abundances in the functional space (Villéger et al., 2008). FEve varies between 0 and 1, values close to 1 indicating that abundance is distributed in a similar way between species/traits, or that there is greater functional complementarity. We extract the indices, FRic and FEve, using the “*dbFD*” function from the "*FD*" package (Laliberté & Legendre, 2010).

To further focus on the resources available for birds, we used a taxonomic diversity approach and extracted Shannon-Wiener index values to characterize the diversity of plants included in each interaction network. In this index, values close to 0 indicate low diversity and higher values indicate high diversity (Ortiz-Burgos 2016). We also extracted the Equitability Pielou index (J) which allows us to represent the uniformity of the distribution of individuals among the plant species observed in each network. This index varies from 0, indicating minimum uniformity, to 1, indicating maximum uniformity.

Statistical analyses

Based on the birds-fruiting plants interactions recorded, we built 24 quantitative matrices, one for each studied site, representing the frugivorous species in columns and the fruiting plants in rows. Cells were filled with the frequency of interactions between a pair of species (Bascompte et al. 2003). The frequency of interactions was described by the quantity of fruits consumed by each species of bird. For each network we calculated the network-level metrics that are associated with the partition of resources – Specialization index (H_2') and the weighted Modularity (Q_w). H_2' weights the frequency of interactions, indicating how strongly species interact with each other, and ranges from 0 (low specialization and high overlap of interactions between species, i.e. all species interacting with the same partners) to 1 (high specialization and low overlap of interactions). The modularity indicates the tendency of a network to be organized into clusters, with subsets of species interacting more among themselves than with other subsets of species in the network. Modularity was calculated using the Beckett algorithm (Beckett 2016), and its significance was evaluated comparing values obtained with those generated after 1000 randomizations using vaznull models (Vázquez et al.

2007). The observed value was considered significant if it exceeded the 95% confidence interval, obtained randomly by the null model. The metrics were extracted using *networklevel* and *computeModules* functions of the *bipartite* package in R (R Core Team 2023).

Sampling completeness was evaluated using an interaction accumulation curve for each studied network (Chacoff et al. 2012). Analogous to species community accumulation curve, for interaction networks each link between a plant and an animal species is the equivalent to a “species”, and the frequency of interactions of each pair is considered as its “abundance” (Vizentin-Bugoni et al. 2016).

To evaluate the effects of landscape cover on the structure of interaction networks and on the diversity indexes (taxonomic, functional, and phylogenetic) we followed two steps. Firstly, we assessed multicollinearity among predictor variables (six landscape coverages: percentage of built-up area in 200, 500, 1000-m, percentage of area covered by trees and shrubs in 200, 500, and 1000-m) using *corrplot* package (Naim et al. 2014). Then, to avoid biased parameter estimations and inference among predictors, we calculated the variation inflation factor (VIF) using R-package *usdm* and excluded those variables with VIF ≥ 10 (Dorman et al. 2013, James et al. 2013, Wei & Simko 2017). After this evaluation, we removed the percentage of built-up area in 500-m and percentage of area covered by trees and shrubs in 500-m from the analyses, because they were highly ($r = 0.83$) correlated with percentage of area covered by trees and shrubs in 200-m and 1000-m (Supplementary Material, Figure S1-S2).

In the second step, we used Generalized Linear Models (GLM) to investigate the effects of the predictive variables urbanized coverage (Built-up index) and trees and shrubs coverage (NDVI) in two buffers (200 and 1000 m) on nine response variables: (i) network specialization (H_2'), (ii) modularity (Q_w), (iii) FRic of plants, (iv) FRic of birds, (v) FEve of plants, (vi) FEve of birds, (vii) Rao 's quadratic entropy of birds, (viii) Shannon diversity of plants, (ix) Pielou equitability of plants. Each response variable was analyzed in a separate model, totaling nine models with the four predictors variables (Supplementary Material, Table S1). Model fitting was performed using the *glmmTMB* function of the R-package *glmmTMB* (Brooks et al. 2017) considering a beta type error distribution and a logit link function for eight response variables. For the model that includes Shannon-Wiener diversity, we performed a multiple linear model (lm). For all models, we built a set of candidate models containing all combinations of predictor variables (see global models on Supplementary Materials, Table S1), plus an intercept-only model. Model performance was quantified within an Information Theoretic approach using the second-order small-sample corrected Akaike information criterion (AIC_C; Burnham & Anderson 2002). Models with low AIC_C values and high AIC_C weights ($wAIC_C$) have relatively higher support (Burnham & Anderson 2002). Models for which $\Delta AIC_C \leq 2$ were considered to have similar empirical support. Model selection was carried out using the function *dredge* of the R-package MuMIn (Barton 2018). The importance of individual predictor variables was assessed by deriving model-average parameter estimates and their confidence intervals (Galipaud et al. 2017). Predictor variables are inferred to have a strong effect upon response variables whenever 95% confidence intervals for model-averaged effects do not overlap zero (Burnham & Anderson 2002).

Finally, to evaluate the importance of components of diversity for network specialization (partition in resource use), we evaluated the effects of the diversity measures – taxonomic, functional, and phylogenetic – on the network-level metrics. For this analysis we constructed 14 models, seven models for H_2' and seven models for Q_w as response variables, and (i) FRic plants, (ii) FRic birds, (iii) FEve plants, (iv) FEve birds, (v) Rao 's quadratic entropy birds, (vi) Shannon diversity plants, (vii) Pielou equitability plants, as the predictor variables (Supplementary Material, Table S1). The adjustment of the models was the same as previously described for the second stage.

Results

We recorded 2002 frugivory events and consumption of more than 14,000 fruits by 68 bird species on 81 plant species in 24 green areas within the city of Campo Grande, Brazil. Interaction networks were generally specialized and presented low functional diversity (Table 1; Supplementary Material, Figure S3). Sample sufficiency varied of 39.68 – 100% (Supplementary Material, Figure S4).

Specialization H_2' and modularity Q_w were not associated with any of the landscape predictor variables. The Shannon-Wiener diversity index of plants increased with both impermeable surfaces cover in the 1000 m buffer, and tree and shrub cover in the 200 m buffer ($r^2 = 0.46$, Table 1, Figure 2A-B). Pielou equitability index of plants decreased with impermeable surfaces cover in the 200 m buffer (Nagelkerke’s pseudo $r^2 = 0.4213$, Table 1, Fig. 2C). Finally, Rao 's quadratic entropy of birds was positively associated with the impermeable surfaces cover buffer in 1000 m (Nagelkerke’s pseudo $r^2 = 0.32$, Table 1, Fig. 2D). The other diversity metrics evaluated were not affected by landscape metrics. The results of all models are presented in Supplementary Material (Table S4-S21).

By testing diversity measures that are important to interaction network metrics, we show that modularity increased with Shannon-Wiener diversity of plants (Nagelkerke’s pseudo $r^2 = 0.85$, Table 2, Fig. 2E) and with FRic of plants (Nagelkerke’s pseudo $r^2 = 0.34$, Table 2, Fig. 2F). However, H_2' was not significantly influenced by any of the evaluated diversity metrics (Supplementary Material, Table S22).

Table 1. Variation on the values (Min = minimum, Max = maximum, Mean and Standard deviation) obtained for the response and predictor variables.

Variables	**Mín**	**Max**	**Mean**	**Standard deviation**
Specialization of networks interactions (H_2')	0.45	0.96	0.75	0.15
Modularity of network interactions (Q_w)	0.20	0.77	0.46	0.14
Functional richness (FRic) of plants	0.001	0.24	0.07	0.06
Functional richness (FRic) of birds	0.00003	0.12	0.028	0.037
Functional evenness (FEve) of plants	0.19	0.79	0.58	0.15
Functional evenness (FEve) of birds	0.29	0.81	0.56	0.17
Phylogenetic diversity (Rao 's quadratic entropy, PD Rao) of birds	0.45	0.71	0.63	0.072
Shannon-Winer index	0.63	2.52	1.55	0.53
Pielou equitability index	0.43	0.95	0.83	0.14
Area covered by impermeable surface in the 1000 m buffer	0.55	48.83	19.24	13.04
Area covered by impermeable surface in the 500 m buffer	0	57.38	18.76	15.71
Area covered by impermeable surface in the 200 m buffer	0	62.90	14.21	18.10
Area covered by trees and scrub in 1000 m buffer	4.96	64.80	25.72	18.18
Area covered by trees and scrub in 500 m buffer	3.76	91.19	30.92	24.17
Area covered by trees and scrub in 200 m buffer	1.61	99.19	45.26	31.83

Table 2. Influence of landscape settings on the components of diversity. *P* values are indicated for variables whose confidence intervals (95% CI) did not overlap zero. Here the response variables that had a significant effect by predictor variables are presented.

	Coefficient (β)	95% CI	Weight (w)	*z* value	*P* value
Shannon-Winner diversity of plants					
Impermeable surfaces cover (buffer 1000 m)	0.027524	0.005 to 0.050	0.70	2.422	0.015
Tree and shrub cover (buffer 200 m)	0.014466	0.004 to 0.025	0.70	2.705	0.007
Pielou equitability (J) of plants					
Impermeable surfaces cover (buffer 200 m)	-0.023009	–0.044 to –0.002	0.60	2.141	0.032
Rao’s quadratic entropy of birds					
Impermeable surfaces cover (buffer 1000 m)	0.014597	0.0004 to 0.029	0.42	2.008	0.04

Table 3. Comparison of components of diversity that most affected the modularity in birds-fruiting plants networks in a tropical urban area. Bold indicates predictors variables that significantly influenced the increase in modularity ($p < 0.05$).

Predictors	**Coefficient (β)**	***z* value**	***P* value**	**AIC**	**Pseudo R^2**
Functional richness of plants	**3.7603**	**2.218**	**0.027**	**-26.4**	**0.171**
Functional richness of birds	1.7656	0.583	> 0.05	-22.3	0.014
Functional evenness of plants	0.1974	0.267	> 0.05	-22.0	0.003
Functional evenness of birds	0.9866	1.531	> 0.05	-24.2	0.091
Rao's quadratic entropy of birds	1.524	0.958	> 0.05	-22.8	0.037
Shannon-Wienner diversity of plants	**0.6359**	**3.524**	**< 0.01**	**-32.2**	**0.345**
Pielou equitability (J) of plants	1.2083	1.538	> 0.05	-24.3	0.095

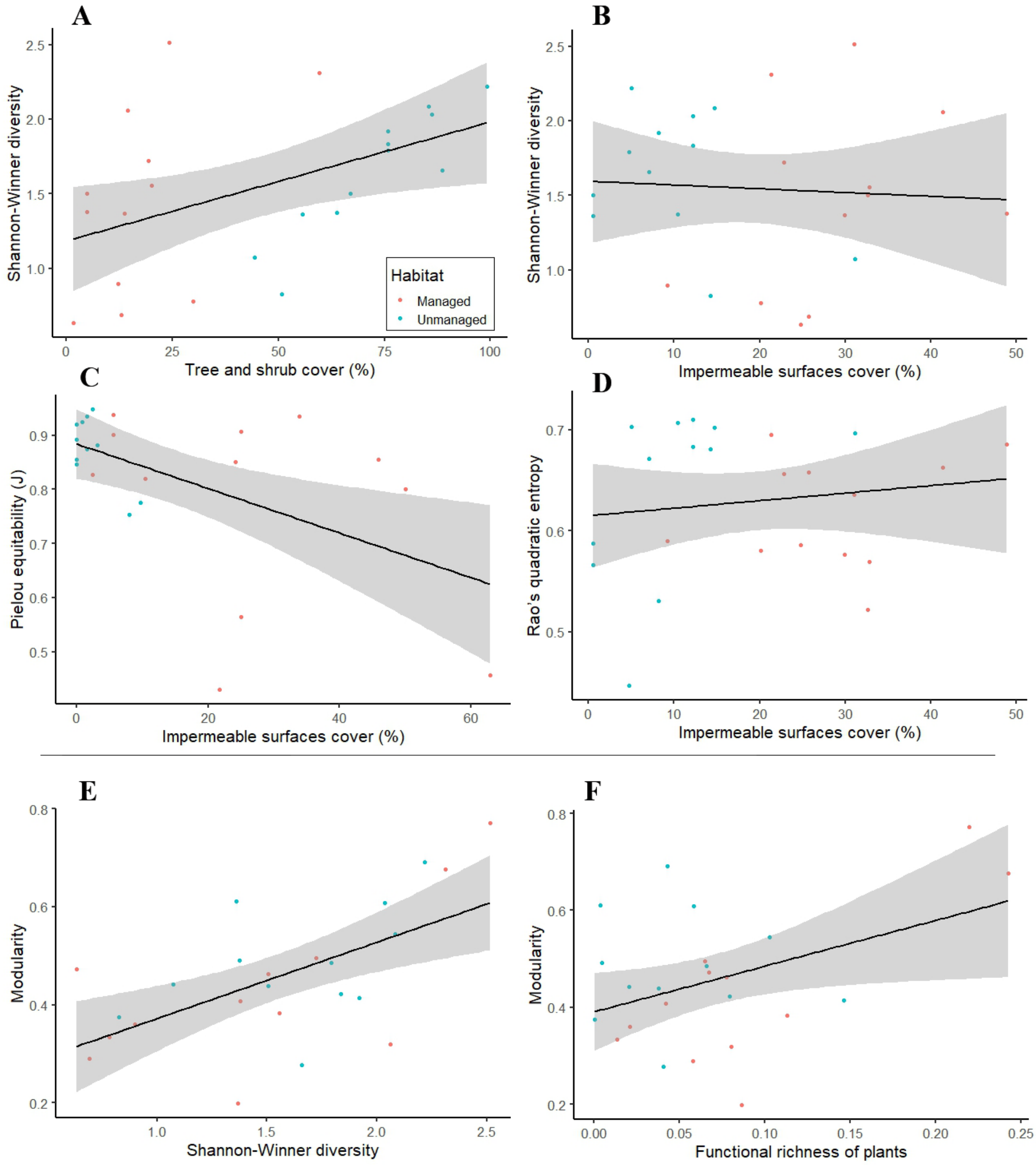


Figure 2. Relationship between landscape descriptors and Shannon-Wiener diversity of plants (A-B), Pielou equitability of plants (C), Rao's quadratic entropy of birds (D). Effects of components of diversity (Shannon-Wienner and Functional richness of plants) on Modularity (E-F) in urban areas in Campo Grande, a tropical city in Brazil.

Discussion

Here we showed that the specialization in all the 24 sampled urban areas (H_2') presented medium to high values, whereas modularity had a greater variation among them. Contrary to our predictions, both the modularity and specialization were not directly associated with impermeable surface and tree cover. On the other hand, impermeable surface cover influenced diversity measures which, in turn, were associated with the modularity of the interaction networks. This suggests that there may be an indirect effect of landscape cover on the structure of interaction networks, mediated by its effects on diversity indices. The increased tree and shrubs cover in a smaller scale resulted in an increase in the diversity of fruiting plants, and plant species diversity was positively associated with modularity. Given that the assembly and dynamics of interaction networks reflect the structure of communities, frequency and intensity of interactions can be driven by changes in species composition and abundance (Ohlmann et al. 2019). Once networks composed by a greater diversity of plants can represent a higher variety of food resources for frugivorous birds with different preference criteria, it could be expected greater specialization on the use of food resources by these birds, thus resulting in networks with a modular structure (Wheelwright 1993, Pizo et al. 2020). Thus, variation in the diversity of fruits across land use gradients has effects on the composition and on the structure of interaction networks, with consequences on ecosystem functioning.

We showed that the diversity of fruiting plants increased with tree and shrub cover, specifically on a small spatial scale (200 m radius buffer). Our results are congruent with other studies and indicate that the presence of green areas is valuable for retaining a greater number of plants inhabiting urban landscapes (Chan et al. 2020, Schneiberg et al. 2020) besides provisioning numerous ecosystem services, such as reducing local temperature and mitigating floods (Nowak & Walton 2005, Eigenbrod et al. 2011). However, contrary to our predictions, plant diversity is also positively associated with impervious surface cover. This result is interesting from the management point of view, indicating that well-forested “islands” (at a scale of 200 m radius buffer) in an impervious surface matrix (at a scale of 1000 m radius buffer) are efficient to harbor diversity and to improve seed dispersal performance.

The finding that plants equitability decreased with impermeable surface cover in the 200 m radius buffer indicates that in these areas the networks present a greater dominance of some species, which are mostly alien, pioneer, and initial secondary plants species. These results are congruent with the reported by other studies (Freitas et al. 2020, Toledo-Garibaldi et al. 2023), and can be related to the fact that locations with lower tree cover and receiving higher irradiation as well as exhibiting higher temperatures present favorable conditions for early succession plants (Toledo-Garibaldi et al. 2023). Furthermore, the introduction of alien species has turned cities into immigration centers, explaining the high dominance of exotic species (Kowarik 2008, Freitas et al. 2020). This may result in increased availability of some fruiting plants to the bird community. Such as some alien species (e.g., *Syzygium cumini*), and early successional plant species (such *Cecropya pachystachya*). Finally, contrary to our expectations, areas with greater impervious surface coverage (at a scale of 1000 m radius buffer) presented greater phylogenetic diversity of birds, but we emphasize that the relationship was weak. This is probably due to the heterogeneous environment in the landscape, composed of built-up areas and areas covered by trees and shrubs, which could provide resources for frugivorous bird in different phylogenetic groups.

Modularity increased with functional richness and diversity of plants, which has important implications for the management of green areas within the city. This relationship has already been reported in natural areas involving birds-fruiting plants and plant–hummingbird interactions (Dehling et al. 2016, Maruyama et al. 2018). This result indicates that in areas with greater heterogeneity of functional traits, is more likely to occur greater number of links between birds-fruiting-plants in networks, resulting in modular networks with subsets of species interacting more than with other sets of species. In these networks we observed that plants with the smallest fruit size (the mistletoe *Phoradendron piperoides*) interacted strongly with the bird with the smallest beak size (*Euphonia chlorotica*). Plants with fruits measuring between 11 and 15 mm interacted with Passeriformes with beaks ranging from 15 and 25 mm in length. Additionally, tall plants (above 15 m) interacted with birds that fly over the treetops (such as Psittaciformes). However, we emphasize that the variation in the functional richness of plants was low. On the other hand, we highlight that the taxonomic diversity of plants was of greater importance in increasing modularity. This highlights the importance of the maintenance of a high diversity of plants presenting also complementary phenotypic traits in urban areas, to provide robustness of the network of interactions (Dehling et al. 2014) and to promote a greater diversity of frugivorous birds in the cities. Results presented here have valuable implications for management decisions, specifically filling gaps linked to functional traits, for example, stimulating the selection of plant species for urban greening, in order to support and enhance functional diversity of fruiting species. This is important for resource sharing among birds and, consequently, the conservation of seed dispersal and interacting communities.

Specialization H_2' index was not associated with any of the evaluated predictors (land use and components of diversity). This result is congruent with another study in the urban area in a Brazilian city (Schneiberg et al. 2020), where the H_2' index also did not differ in the urbanization gradient. Here, some green areas presented networks with intermediate specialization values, whereas other resulted in high values. Possibly, other factors that we did not measure could explain the variation in H_2', such as the temporal change in resource availability, and the variation in the complexity of the vertical structure of vegetation between green areas. In fact, in natural areas it has been reported that vegetations with higher complexity harbors a greater diversity of forest-dependent frugivorous birds (Morante-Filho et al. 2018). Additionally, seasonal fluctuations in fruit composition and availability can influence birds-fruiting plants interactions, and increase their diversity (Malizia 2001, Carnicer et al. 2009). Therefore, we suggest that future studies investigate the role of temporal variation and vegetation structure in the structure of interaction networks across green areas.

In conclusion, our results provide some insights that may assist management decisions in urban areas aiming to maintain the ecosystem functions in the cities. We showed that in a tropical city, well-forested islands in impermeable matrices are efficient in promoting diverse plant species diversity. This, in turn, promotes an increase in the resource sharing between species, as showed by the modular structure of the networks. Additionally, filling gaps associated with functional traits in green areas (i.e., prioritizing plant species with complementary functional traits in urban greening) contributes to generating more robust interaction networks, with the formation of clusters of species that interact with each other, resulting in a greater partition of resources between species. Therefore, for a better performance of ecological functions it is desirable to stimulate the selection of plant species for urban greening, to support and enhance functional diversity of fruiting species. Possibly landscape heterogeneity can explain diverse frugivore bird phylogenetic lineages. Finally, green areas that are locally very impermeable showed high dominance of some plant species. Such areas need attention to promote the planting of a greater diversity of plant species to enhance bird species diversity.

SUPPLEMENTARY MATERIAL

List of tables

Table S1. Final structure of the Generalized Linear Models (glm). Eight models in the second step and all remaining models by third step were fitted using the *glmmTMB* function of the R-package *glmmTMB* (Brooks et al. 2017) considering a beta type error distribution and a logit link function. For the model that includes Shannon-Wiener diversity, we performed a multiple linear model (lm).

	Second step
1	H_2' ~ NDVI 1000-m + NDVI 200-m + Built-up 1000-m + Built-up 200-m
2	Q_w ~ NDVI 1000-m + NDVI 200-m + Built-up 1000-m + Built-up 200-m
3	FRic of plants ~ NDVI 1000-m + NDVI 200-m + Built-up 1000-m + Built-up 200-m
4	FEve of plants ~ NDVI 1000-m + NDVI 200-m + Built-up 1000-m + Built-up 200-m
5	FRic of birds ~ NDVI 1000-m + NDVI 200-m + Built-up 1000-m + Built-up 200-m
6	FEve of birds ~ NDVI 1000-m + NDVI 200-m + Built-up 1000-m + Built-up 200-m
7	Rao 's quadratic entropy ~ NDVI 1000-m + NDVI 200-m + Built-up 1000-m + Built-up 200-m
8	Shannon diversity ~NDVI 1000-m + NDVI 200-m + Built-up 1000-m + Built-up 200-m
9	Pielou equitability ~ NDVI 1000-m + NDVI 200-m + Built-up 1000-m + Built-up 200-m
	Third step
1	H_2' ~ FRic of plants
2	H_2' ~ FRic of birds
3	H_2' ~ FEve of plants

4	H_2' ~ FEve of birds
5	H_2' ~ Rao 's quadratic entropy
6	H_2' ~ Shannon diversity
7	H_2' ~ Pielou equitability
8	Q_w ~ FRic of plants
9	Q_w ~ FRic of birds
10	Q_w ~ FEve of plants
11	Q_w ~ FEve of birds
12	Q_w ~ Rao 's quadratic entropy
13	Q_w ~ Shannon diversity
14	Q_w ~ Pielou equitability

Table S2. Geographic location (Lat = latitude and Long = longitude) of the 24 sampling units and their respective values of modularity values (Q_w), and confidence intervals generated by the null model (95% CI).

Sites	Lat	Long	Modularity	Null Model
Managed sites (public parks and squares)				
Parque Olímpico Ayrton Senna	20°30'47.1"S	54°38'59.5"W	0.3187766	0.027–0.499
Bosque da Paz	20°26'30.0"S	54°34'29.6"W	0.6762061	0.191–0.530
Praça Estrela do Sul	20°25'08.8"S	54°35'46.7"W	0.3836413	0.131–0.480
Praça Itanhangá	20°28'02.9"S	54°36'03.6"W	0.7716194	0.329–0.555
Parque Jacques da Luz	20°33'39.4"S	54°34'42.9"W	0.4949317	0.084–0.180
Praça rua Sessenta	20°27'35.3"S	54°41'27.5"W	0.3609023	0.097–0.234
Monumento aos desbravadores	20°28'15.6"S	54°37'27.2"W	0.4078236	0.056–0.117
Praça do Panamá	20°26'34.6"S	54°39'47.4"W	0.1981369	0.051–0.083
Praça do Peixe	20°29'04.0"S	54°35'35.1"W	0.4625075	0.102–0.282
Praça Generoso Benevides	20°28'50.3"S	54°39'55.3"W	0.3343253	0.117–0.286
Praça Coophasul	20°25'16.7"S	54°38'10.7"W	0.4730508	0.197–0.513
Praça da Poesia	20°24'50.4"S	54°34'12.5"W	0.2897486	0.084–0.193
Natural remnants				
Base aérea	20°27'45.6"S	54°39'19.8"W	0.4221226	0.127–0.270
Rodovia BR 262	20°34'22.2"S	54°35'50.8"W	0.4913868	0.171–0.537
RPPN Cerradinho – Universidade Federal de Mato Grosso do Sul	20°30'29.1"S	54°37'01.6"W	0.5450745	0.096–0.266

District Chácara dos Poderes	20°26'25.6"S	54°31'22.5"W	0.4388850	0.058─0.523
Instituto São Vicente	20°22'52.2"S	54°36'06.2"W	0.6109129	0.151─0.563
District Jardim Los Angeles	20°33'40.9"S	54°38'32.7"W	0.485175	0.179─0.447
Boulevard Gury Marques	20°32'21.1"S	54°35'49.7"W	0.6084501	0.272─0.595
Museu José Antônio Pereira	20°32'08.3"S	54°37'42.4"W	0.3753445	0.051─0.118
Clube de Campo Associação Nipo Brasileira de Campo Grande	20°28'05.6"S	54°33'55.1"W	0.4422441	0.059─0.495
Parque Estadual do Prosa	20°27'09.1"S	54°33'43.1"W	0.6916631	0.318─0.588
Parque Estadual Matas do Segredo	20°23'55.8"S	54°35'17.0"W	0.4144038	0.117─0.280
Universidade Católica Dom Bosco	20°24'51.4"S	54°37'00.1"W	0.2777976	0.074─0.175

Table S4. Top models on the influence of the landscape predictor variables on the network-wide specialization (H_2') in the urban area of Campo Grande, a tropical city in Brazil.

Model	**d.f.**	**logLik**	**AICc**	**ΔAICc**	**Weight (w)**
Intercept	2	13.82	-23.08	0.00	0.36
Built-up (buffer 200 m)	3	14.17	-21.14	1.94	0.14
NDVI (buffer 1000 m)	3	13.90	-20.60	2.48	0.10
Built-up (buffer 1000 m)	3	13.90	-20.60	2.48	0.10

Table S5. Influence of the landscape predictor variables on the network-wide specialization (H_2') in Campo Grande, a tropical city in Brazil. Model averaged results for the variables that influence specialization. **Bold** indicates variables whose confidence intervals did not cross zero.

Model	**Coefficient (β)**	**Adjusted S.E.**	**Lower 95% CI**	**Upper 95% CI**	**Relative importance**	***z* value**	***P* value**
Intercept	**1.098**	**0.3556**	**0.401**	**1.794**	**0.36**	**3.087**	**0.002**
Built-up (buffer 200 m)	-0.01006	0.01101	-0.032	0.012	0.14	0.914	> 0.05
Built-up (buffer 1000 m)	0.01045	0.01523	-0.019	0.040	-	0.686	> 0.05
NDVI (buffer 200 m)	-0.0000229	0.007397	-0.015	0.014	-	0.003	> 0.05
NDVI (buffer 1000 m)	0.004746	0.01141	-0.018	0.027	-	0.416	> 0.05

Table S6. Top models on the influence of landscape predictor variables on the Modularity of birds-fruiting plants networks in the urban area of Campo Grande, a tropical city in Brazil.

Model	**d.f.**	**logLik**	**AICc**	**ΔAICc**	**Weight (w)**
NDVI (buffer 200 m)	3	15.44	-23.69	0.00	0.25
Intercept	2	13.97	-23.36	0.33	0.21
Built-up (buffer 1000 m)	3	14.48	-21.77	1.92	0.09
NDVI (buffer 1000 m)	3	14.45	-21.71	1.98	0.09
Built-up (buffer 200 m)	3	14.38	-21.56	2.13	0.08

Table S7. Influence of the landscape predictor variables on the Modularity of the birds-fruiting plants networks in the urban area of Campo Grance, a tropical city in Brazil. Model averaged results for the variables that influence Modularity. **Bold** indicates variables whose confidence intervals did not cross zero.

Model	**Coefficient (β)**	**Adjusted S.E.**	**Lower 95% CI**	**Upper 95% CI**	**Relative importance**	***z* value**	***P* value**
Intercept	-0.2936169	0.3049044	-0.891	0.304	0.21	0.963	> 0.05
Built-up (buffer 200 m)	-0.0017161	0.0092452	-0.020	0.016	-	0.186	> 0.05
Built-up (buffer 1000 m)	-0.0040460	0.0128153	-0.029	0.021	0.09	0.316	> 0.05
NDVI (buffer 200 m)	0.0071528	0.0049515	-0.003	0.017	0.25	1.445	> 0.05
NDVI (buffer 1000 m)	0.0003898	0.0111317	-0.021	0.022	0.09	0.035	> 0.05

Table S8. Top models on the influence of landscape predictor variables on the FRic (Functional Richness) of fruiting plants in the urban area of Campo Grande, a tropical city in Brazil.

Model	**d.f.**	**logLik**	**AICc**	**ΔAICc**	**Weight (w)**
Built-up (buffer 1000 m)	3	41.20	-75.20	0.00	0.23
Intercept	2	39.86	-75.14	0.06	0.22
Built-up (buffer 200 m)	3	40.47	-73.74	1.45	0.11
Built-up (buffer 1000 m) + NDVI (buffer 200 m)	4	41.79	-73.48	1.72	0.10
NDVI (buffer 1000 m)	3	40.15	-73.10	2.10	0.08

Table S9. Influence of the landscape predictor variables on the FRic (Functional Richness) of fruiting plants in the urban area of Campo Grande, a tropical city in Brazil. Model averaged results for the variables that influence FRic. **Bold** indicates variables whose confidence intervals did not cross zero.

Model	**Coefficient (β)**	**Adjusted S.E.**	**Lower 95% CI**	**Upper 95% CI**	**Relative importance**	***z* value**	***P* value**
Intercept	**-2.896911**	**0.593929**	**-4.061**	**-1.733**	**0.22**	**4.878**	**< 0.001**
Built-up (buffer 200 m)	0.008804	0.012727	-0.016	0.034	0.11	0.692	> 0.05
Built-up (buffer 1000 m)	0.024332	0.016660	-0.008	0.057	0.33	1.460	> 0.05
NDVI (buffer 200 m)	0.005498	0.010111	-0.014	0.025	0.10	0.544	> 0.05
NDVI (buffer 1000 m)	-0.001311	0.014712	-0.030	0.028	-	0.089	> 0.05

Table S10. Top models on the influence of landscape predictors on the FEve (Functional Evenness) of fruiting plants in the urban area of Campo Grande, a tropical city in Brazil.

Model	**d.f.**	**logLik**	**AICc**	**ΔAICc**	**Weight (w)**
Intercept	2	12.17	-19.76	0.00	0.21
Built-up (buffer 200 m)	3	13.41	-19.61	0.15	0.19
NDVI (buffer 200 m)	3	13.19	-19.18	0.58	0.16
NDVI (buffer 1000 m)	3	12.93	-18.66	1.10	0.12
Built-up (buffer 1000 m)	3	12.75	-18.30	1.46	0.10
Built-up (buffer 200 m) + NDVI (buffer 200 m)	4	13.50	-16.89	2.87	0.05

Table S11. Influence of the landscape predictor variables on the FEve (Functional Evenness) of fruiting plants in the urban area of Campo Grande, a tropical city in Brazil. Model averaged results for the variables that influence FEve. **Bold** indicates variables whose confidence intervals did not cross zero.

Model	**Coefficient (β)**	**Adjusted S.E.**	**Lower 95% CI**	**Upper 95% CI**	**Relative importance**	***z* value**	***P* value**
Intercept	0.335857	0.290238	-0.233	0.905	0.21	1.157	> 0.05
Built-up (buffer 200 m)	0.009919	0.008403	-0.007	0.026	0.19	1.180	> 0.05
Built-up (buffer 1000 m)	0.005949	0.012621	-0.019	0.031	0.10	0.471	> 0.05
NDVI (buffer 200 m)	-0.004843	0.005278	-0.015	0.006	0.16	0.918	> 0.05
NDVI (buffer 1000 m)	-0.005930	0.009190	-0.024	0.012	0.12	0.645	> 0.05

Table S12. Top models on the influence of landscape predictor variables on the FRic (Functional Richness) of frugivore birds in the urban area of Campo Grande, a tropical city in Brazil.

Model	**d.f.**	**logLik**	**AICc**	**ΔAICc**	**Weight (w)**
NDVI (buffer 200 m)	3	74.93	-142.67	0.00	0.24
NDVI (buffer 1000 m)	3	74.55	-141.90	0.76	0.17
Intercept	2	72.99	-141.41	1.26	0.13
Built-up (buffer 1000 m)	3	74.07	-140.94	1.73	0.10
Built-up (buffer 200 m)	3	73.89	-140.58	2.09	0.09

Table S13. Influence of the landscape predictor variables on the FRic (Functional Richness) of frugivore birds in the urban area of Campo Grande, a tropical city in Brazil. Model averaged results for the variables that influence FRic. **Bold** indicates variables whose confidence intervals did not cross zero.

Model	**Coefficient (β)**	**Adjusted S.E.**	**Lower 95% CI**	**Upper 95% CI**	**Relative importance**	***z* value**	***P* value**
Intercept	**-3.293604**	**0.611994**	**-4.493**	**-2.094**	**0.13**	**5.382**	**< 0.01**
Built-up (buffer 200 m)	0.007349	0.013198	-0.032	0.004	-	0.557	> 0.05
Built-up (buffer 1000 m)	0.012695	0.021592	-0.048	0.014	0.10	0.588	> 0.05
NDVI (buffer 200 m)	-0.013833	0.009303	-0.030	0.055	0.24	1.487	> 0.05
NDVI (buffer 1000 m)	-0.017369	0.015794	-0.019	0.033	0.17	1.100	> 0.05

Table S14. Top models on the influence of landscape predictors on the FEve (Functional Evenness) of frugivore birds in the urban area of Campo Grande, a tropical city in Brazil.

Model	**d.f.**	**logLik**	**AICc**	**ΔAICc**	**Weight (w)**
NDVI (buffer 200 m)	3	11.96	-16.73	0.00	0.27
Intercept	2	10.04	-15.51	1.22	0.15
Built-up (buffer 200 m)	3	11.21	-15.22	1.51	0.13
NDVI (buffer 1000 m)	3	10.80	-14.40	2.33	0.08

Table S15. Influence of the landscape predictor variables on the FEve (Functional Evenness) of frugivore birds in the urban area of Campo Grande, a tropical city in Brazil. Model averaged results for the variables that influence FEve. **Bold** indicates variables whose confidence intervals did not cross zero.

Model	**Coefficient (β)**	**Adjusted S.E.**	**Lower 95% CI**	**Upper 95% CI**	**Relative importance**	***z* value**	***P* value**
Intercept	0.031156	0.392474	-0.738	0.800	0.15	0.079	> 0.05
Built-up (buffer 200 m)	-0.008559	0.009939	-0.028	0.011	0.13	0.861	> 0.05
Built-up (buffer 1000 m)	0.001321	0.016370	-0.031	0.033	-	0.081	> 0.05
NDVI (buffer 200 m)	0.009303	0.005852	-0.002	0.021	0.27	1.590	> 0.05
NDVI (buffer 1000 m)	0.002283	0.013157	-0.024	0.028	-	0.174	> 0.05

Table S16. Top models on the influence of landscape predictors on the Rao 's quadratic entropy (Phylogenetic divergences represented by Rao's quadratic entropy) of frugivore birds in the urban area of Campo Grande, a tropical city in Brazil.

Model	**d.f.**	**logLik**	**AICc**	**ΔAICc**	**Weight (w)**
Built-up (buffer 1000 m) + NDVI (buffer 200 m)	4	33.96	-57.82	0.00	0.29
Built-up (buffer 1000 m) + Built-up (buffer 200 m) + NDVI (buffer 200 m)	5	34.74	-56.14	1.67	0.13
Intercept	2	30.24	-55.92	1.90	0.11
Built-up (buffer 1000 m) + Built-up (buffer 200 m)	4	32.95	-55.80	2.02	0.11

Table S17. Influence of the landscape predictor variables on the Rao 's quadratic entropy (Phylogenetic divergences represented by Rao's quadratic entropy) of frugivore birds in the urban area of Campo Grande, a tropical city in Brazil. Model averaged results for the variables that influence Rao 's quadratic entropy. **Bold** indicates variables whose confidence intervals did not cross zero.

Model	**Coefficient (β)**	**Adjusted S.E.**	**Lower 95% CI**	**Upper 95% CI**	**Relative importance**	***z* value**	***P* value**
Intercept	0.199578	0.325685	-0.439	0.838	0.11	0.613	> 0.05
Built-up (buffer 200 m)	-0.006863	0.004795	-0.016	0.003	0.13	1.431	> 0.05
Built-up (buffer 1000 m)	**0.014597**	**0.007268**	**0.0004**	**0.029**	**0.42**	**2.008**	**0.04**
NDVI (buffer 200 m)	0.006032	0.003150	-0.0001	0.012	0.42	1.915	> 0.05
NDVI (buffer 1000 m)	0.002104	0.006632	-0.011	0.015	-	0.317	> 0.05

Table S18. Top models on the influence of the landscape predictor variables on the Shannon-Winner diversity index of fruiting plants in the urban area of Campo Grande, a tropical city in Brazil.

Model	**d.f.**	**logLik**	**AICc**	**ΔAICc**	**Weight (w)**
Built-up (buffer 1000 m) + NDVI (buffer 200 m)	4	-11.93	33.97	0.00	0.48
Built-up (buffer 1000 m) + Built-up (buffer 200 m) + NDVI (buffer 200 m)	5	-11.11	35.55	1.58	0.22
Built-up (buffer 1000 m) + NDVI (buffer 1000 m) + NDVI (buffer 200 m)	5	-11.90	37.14	3.17	0.10

Table S19. Influence of the landscape predictor variables on the Shannon-Winner diversity index of fruiting plants in the urban area of Campo Grande, a tropical city in Brazil. Model averaged results for the variables that influence Shannon-Winner diversity index. **Bold** indicates variables whose confidence intervals did not cross zero.

Model	**Coefficient (β)**	**Adjusted S.E.**	**Lower 95% CI**	**Upper 95% CI**	**Relative importance**	***z* value**	***P* value**
Intercept	0.503419	0.528218	-0.532	1.539	-	0.953	0.34056
Built-up (buffer 200 m)	-0.010367	0.008315	-0.027	0.006	0.22	1.247	0.21245
Built-up (buffer 1000 m)	**0.027524**	**0.011364**	**0.005**	**0.050**	**0.70**	**2.422**	**0.01544**
NDVI (buffer 200 m)	**0.014466**	**0.005347**	**0.004**	**0.025**	**0.70**	**2.705**	**0.00683**
NDVI (buffer 1000 m)	0.003770	0.011468	-0.019	0.026	-	0.329	0.74235

Table S20. Top models on the influence of the predictor variables on the Pielou Equitability index (J) of fruiting plants in the urban area of Campo Grande, a tropical city in Brazil.

Model	**d.f.**	**logLik**	**AICc**	**ΔAICc**	**Weight (w)**
Built-up (buffer 200 m)	3	23.12	-39.04	0.00	0.20
Built-up (buffer 1000 m) + Built-up (buffer 200 m) + NDVI (buffer 1000 m)	5	26.02	-38.70	0.34	0.17
Built-up (buffer 1000 m) + Built-up (buffer 200 m)	4	24.13	-38.15	0.89	0.13
Built-up (buffer 1000 m) + Built-up (buffer 200 m) + NDVI (buffer 200 m)	5	25.47	-37.61	1.43	0.10
NDVI (buffer 200 m)	3	22.37	-37.54	1.50	0.09
Built-up (buffer 1000 m) + NDVI (buffer 200 m)	4	23.49	-36.88	2.16	0.07

Table S21. Influence of landscape predictor variables on the Pielou Equitability index (J) of fruiting plants in the urban area of Campo Grande, a tropical city in Brazil. Model averaged results for the variables that influence Equitability Pielou (J) index. **Bold** indicates variables whose confidence intervals did not cross zero.

Model	**Coefficient (β)**	**Adjusted S.E.**	**Lower 95% CI**	**Upper 95% CI**	**Relative importance**	***z* value**	***P* value**
Intercept	1.197258	0.666757	-0.110	2.504	-	1.796	0.0726
Built-up (buffer 200 m)	**-0.023009**	**0.010748**	**-0.044**	**-0.002**	**0.60**	**2.141**	**0.0323**
Built-up (buffer 1000 m)	0.029486	0.017655	-0.005	0.064	0.40	1.670	0.0949
NDVI (buffer 200 m)	0.010612	0.008146	-0.005	0.027	0.19	1.303	0.1927
NDVI (buffer 1000 m)	0.018669	0.013790	-0.008	0.046	0.17	1.354	0.1758

Table S22. Effects of taxonomic (Shannon Diversity and Pielou Equitability indexes), functional (FRic=Functional Richness and FEve=Functional Eveness), and phylogenetic (PDRao) diversity indexes on the network-wide specialization (H_2') of birds-fruiting plants interaction networks in the urban area of Campo Grande, a tropical city in Brazil.

Predictors	**Coefficient (β)**	***z* value**	***P* value**	**AIC**	**Pseudo R^2**
FRic of plants	-0.8661	-0.358	> 0.05	-21.8	0.006
FRic of birds	-2.1276	-0.526	> 0.05	-21.9	0.012
FEve of plants	0.5378	0.506	> 0.05	-21.9	0.009
FEve of birds	1.4391	1.431	> 0.05	-23.6	0.065
Rao 's quadratic entropy	2.2334	1.020	> 0.05	-22.6	0.038
Shannon	0.3119	1.056	> 0.05	-22.7	0.043
Equitability	1.9254	1.920	0.055	-24.8	0.107

List of figures

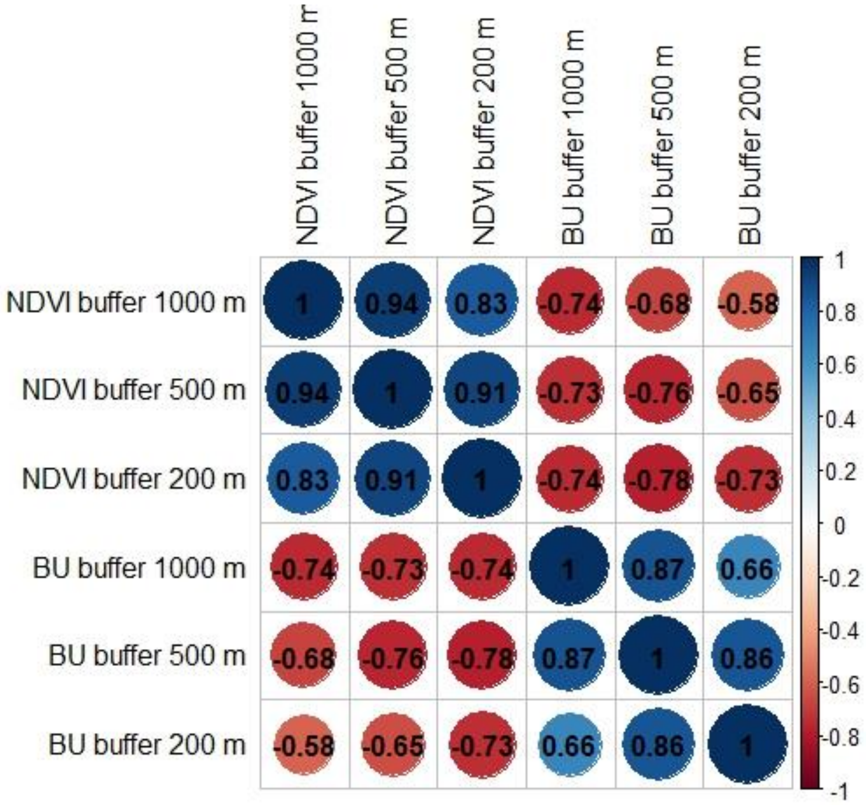
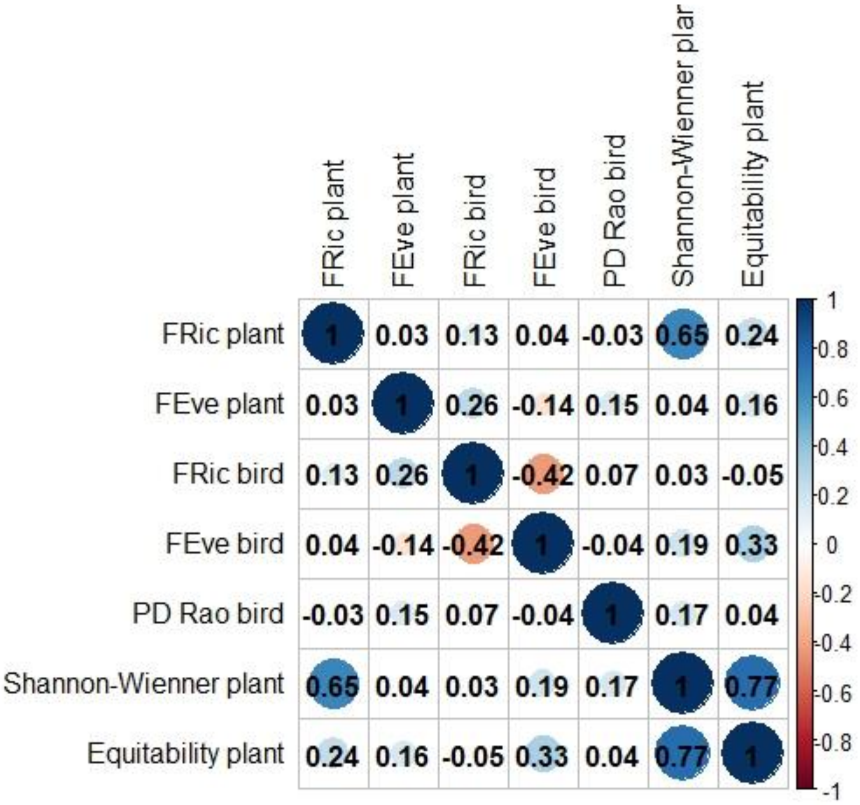


Figure S1. Correlations among predictor variables tree and shrub cover (in buffers 1000 m., 500 m., and 200 m.) and Impermeable surfaces cover (in buffers 1000 m., 500m, and 200 m).



	FRic plant	FEve plant	FRic bird	FEve bird	PD Rao bird	Shannon-Wienner plar	Equitability plant
FRic plant	1	0.03	0.13	0.04	-0.03	0.65	0.24
FEve plant	0.03	1	0.26	-0.14	0.15	0.04	0.16
FRic bird	0.13	0.26	1	-0.42	0.07	0.03	-0.05
FEve bird	0.04	-0.14	-0.42	1	-0.04	0.19	0.33
PD Rao bird	-0.03	0.15	0.07	-0.04	1	0.17	0.04
Shannon-Wienner plant	0.65	0.04	0.03	0.19	0.17	1	0.77
Equitability plant	0.24	0.16	-0.05	0.33	0.04	0.77	1

Figure S2. Correlations among predictor variables functional richness (FRic: plants and birds), functional evenness (FEve: plants and birds), rao's quadratic entropy (PD Rao: phylogenetical divergence of birds), Shannon-Wienner diversity (plants), Pielou equitability (plants).

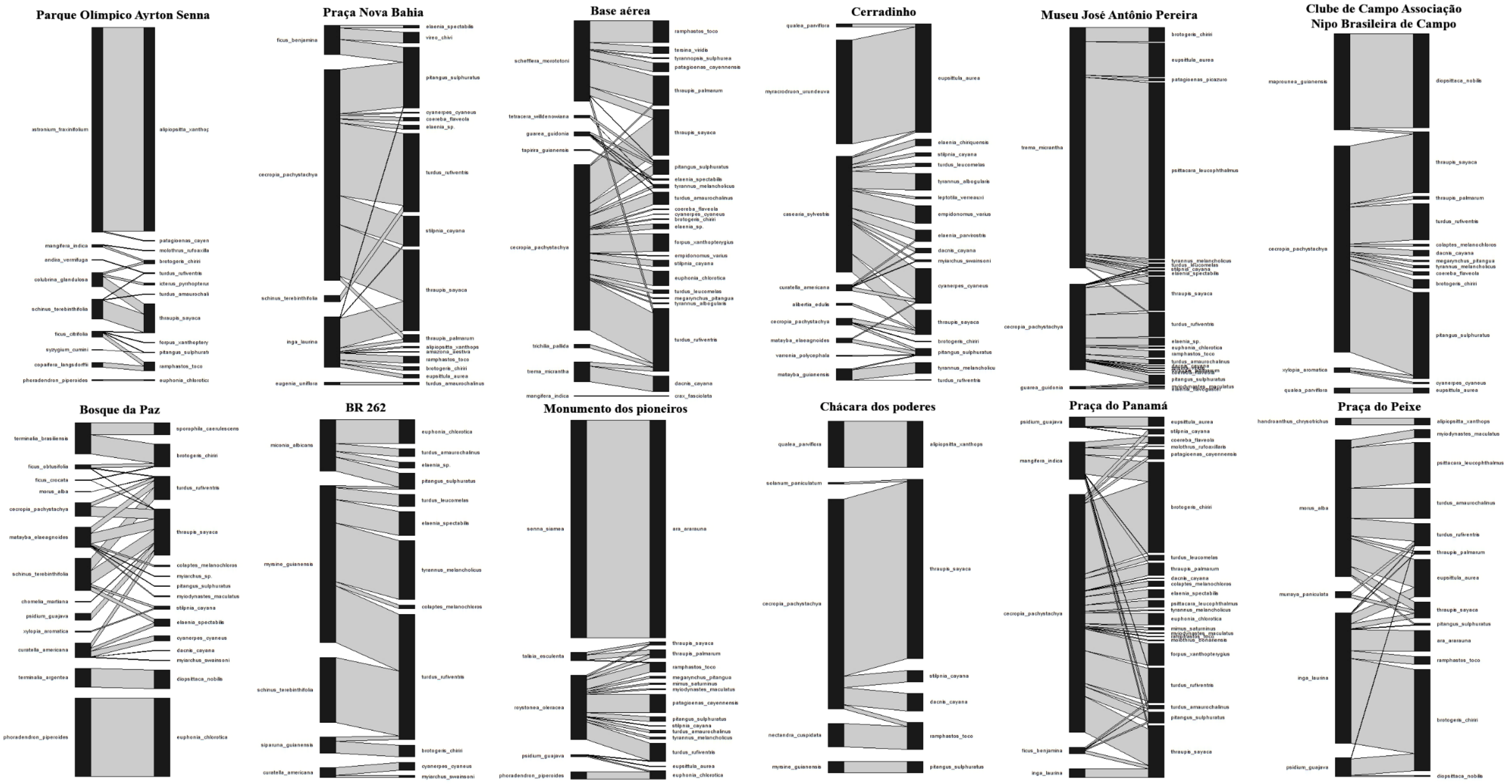
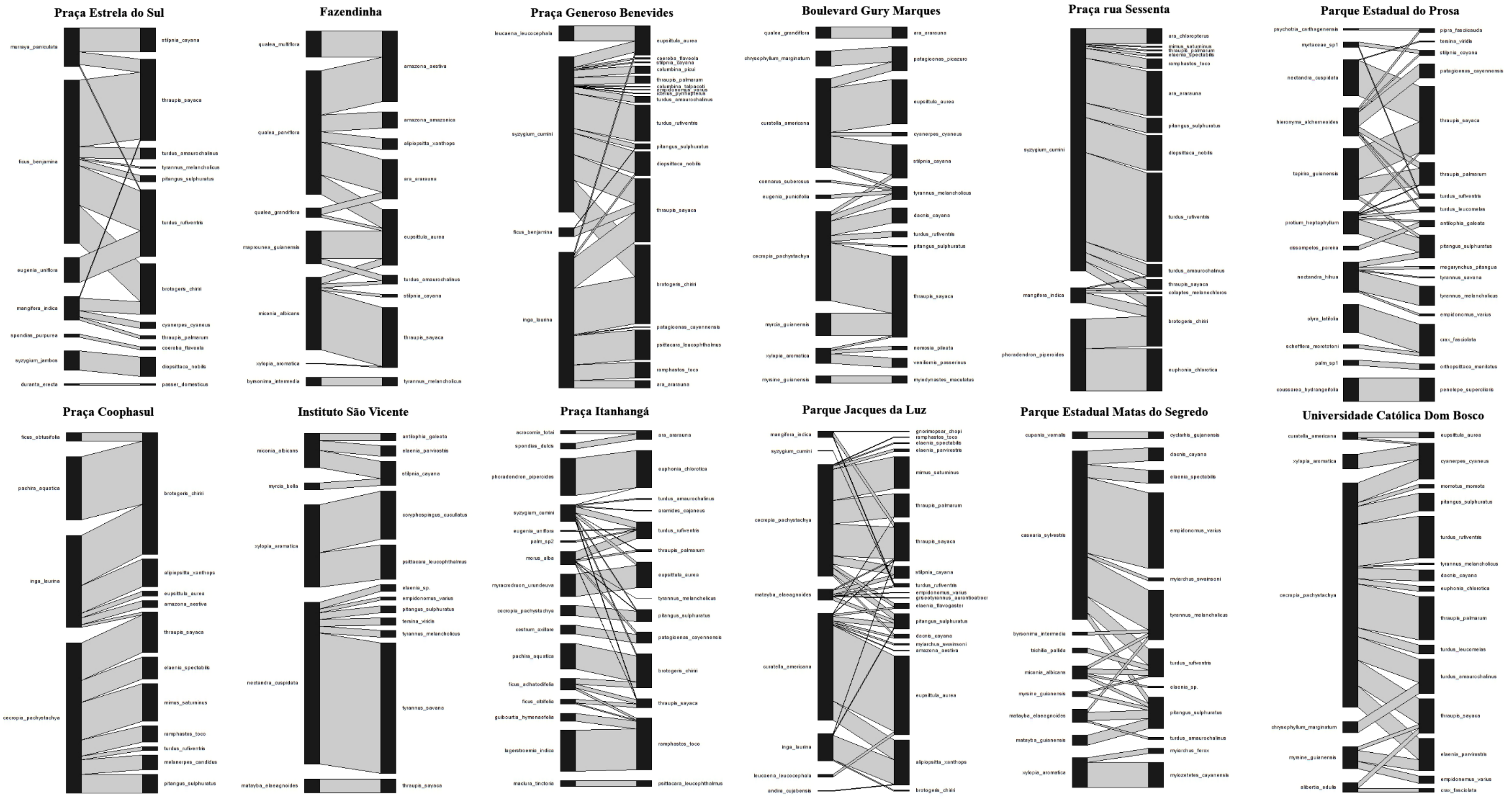


Figure S3. Birds-fruiting plants interactions networks sampled at the 24 green areas in Campo Grande, Brazil. Vertices (in black) represent plant species (on the left), and bird species (on the right). Edges (in gray) represent the frequency of interactions between a pair of species.



Praça Estrela do Sul

Fazendinha

Praça Generoso Benevides

Boulevard Gury Marques

Praça rua Sessenta

Parque Estadual do Prosa

Praça Coophasul

Instituto São Vicente

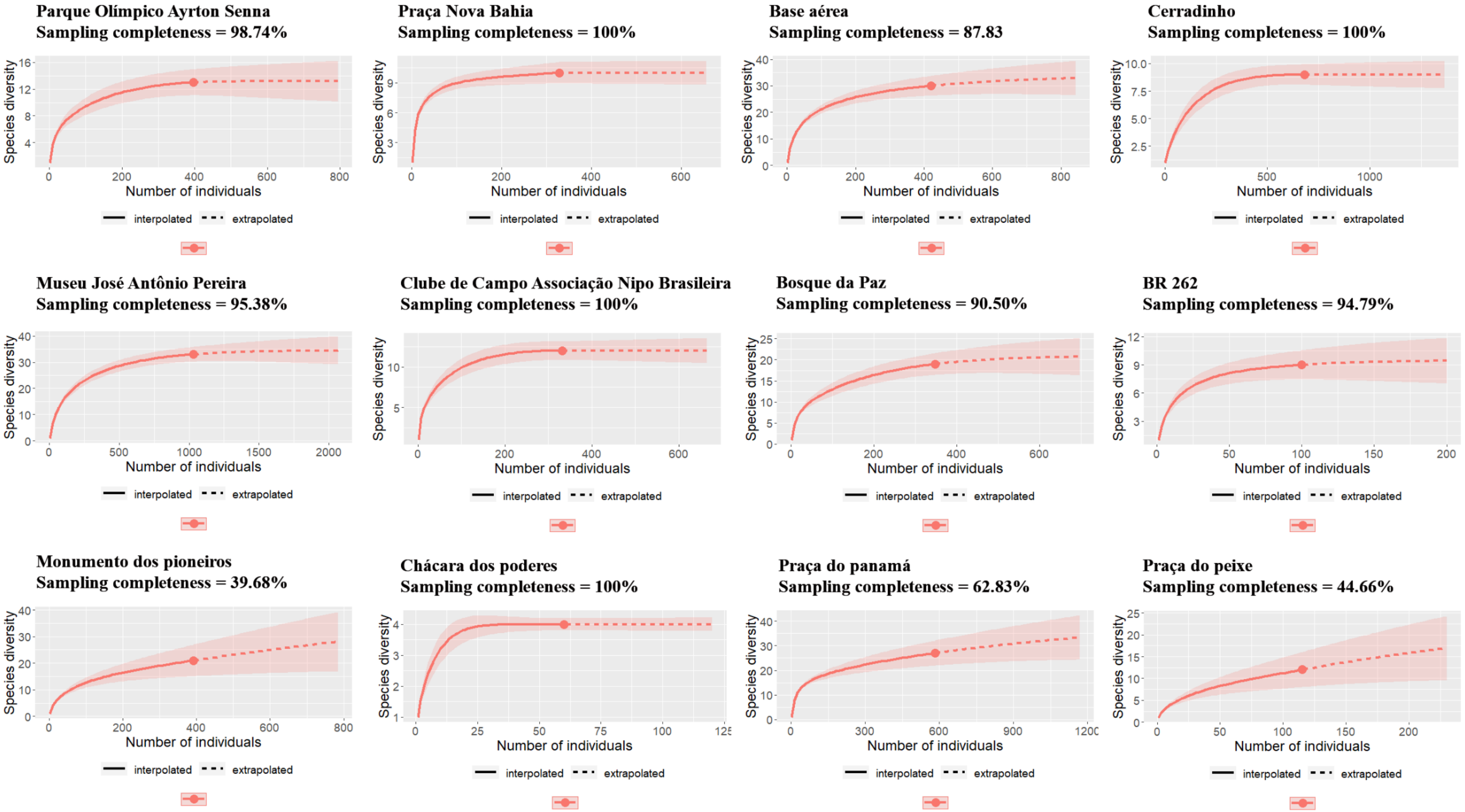
Praça Itanhangá

Parque Jacques da Luz

Parque Estadual Matas do Segredo

Universidade Católica Dom Bosco

Figure S3. Continued.


Parque Olímpico Ayrton Senna
Sampling completeness = 98.74%

Praça Nova Bahia
Sampling completeness = 100%

Base aérea
Sampling completeness = 87.83

Cerradinho
Sampling completeness = 100%

Museu José Antônio Pereira
Sampling completeness = 95.38%

Clube de Campo Associação Nipo Brasileira
Sampling completeness = 100%

Bosque da Paz
Sampling completeness = 90.50%

BR 262
Sampling completeness = 94.79%

Monumento dos pioneiros
Sampling completeness = 39.68%

Chácara dos poderes
Sampling completeness = 100%

Praça do panamá
Sampling completeness = 62.83%

Praça do peixe
Sampling completeness = 44.66%

Figure S4. Sampling completeness evaluated using an interaction accumulation curve for each studied network. Sample sufficiency varied of 39.68 – 100%.

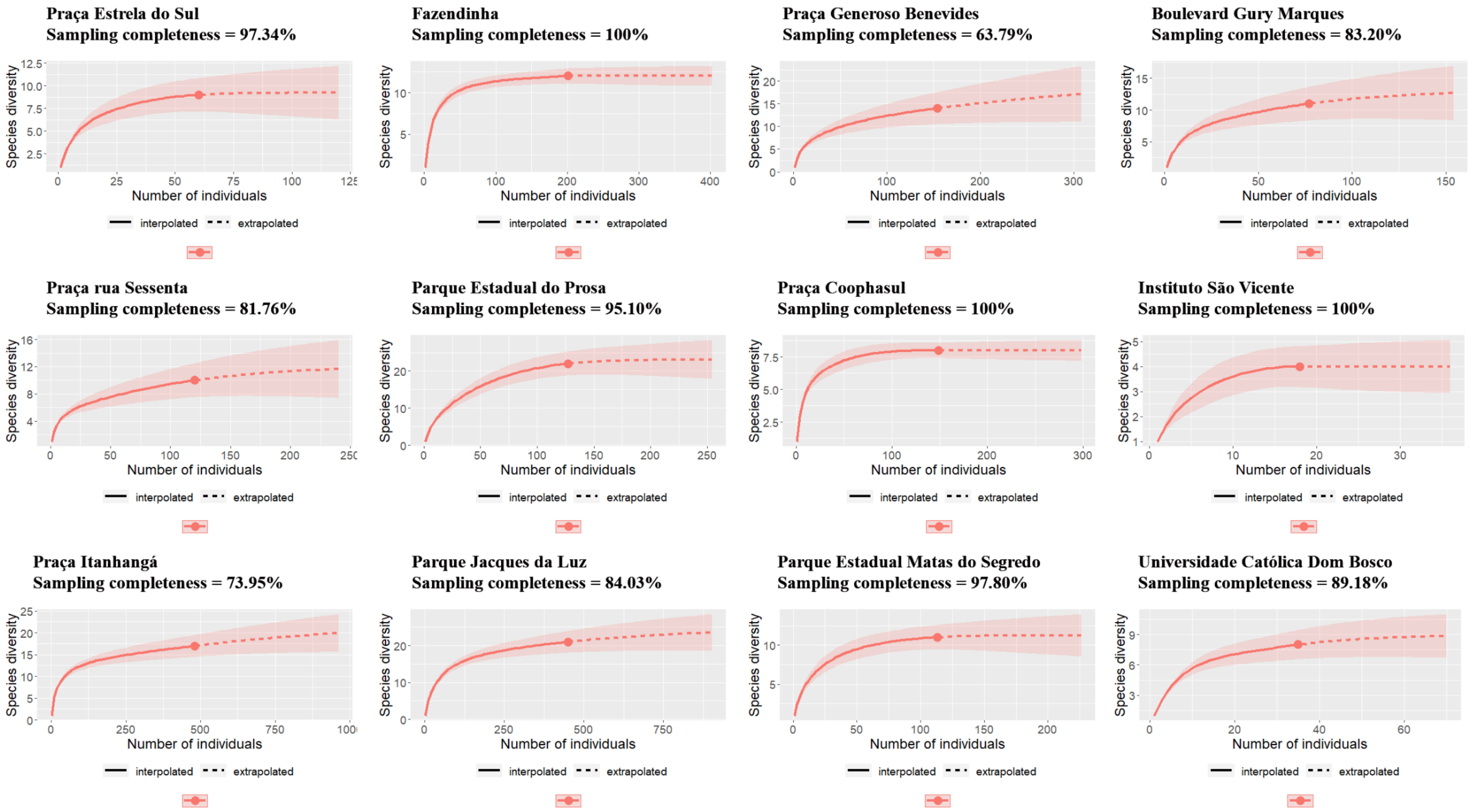


Figure S4. Continued.

General conclusion

In the first chapter, we demonstrated that the number of opportunistic frugivores birds is much higher in cities around the world. We found that the short period of urbanization, low latitudes and increased human population size positively influence the occurrence of obligate frugivores. Additionally, we found that low altitude and a short period of urbanization also positively influence the occurrence of partial frugivores. From these findings, we concluded that urban areas established during the post-industrial Revolution period (150 to 200 years ago) were situated in a context that encouraged the afforestation of green areas, with significant implications for the conservation of fruit-eating birds. Furthermore, the biogeographic characteristics of the region remain an important driver that defines the maintenance of patterns for frugivores, even within cities. Finally, when growth in human population size is not accompanied by an increase in impervious surface coverage, it can positively influence fruit-eating birds.

In the second chapter, we identified a limited number of studies evaluating the mechanisms and processes associated with urbanization that directly influence interactions in tropical urban areas. We detected potential risks linked to urbanization, such as a high consumption of exotic fruits by frugivorous animals, and increased resource overlap among bird species. Drawing from these patterns found in the literature, we suggest several management actions to enhance the performance of ecosystem functions resulting from plant-frugivorous interactions in urban areas. First, we propose encouraging the planting of native fruit trees that produce fruits throughout the year to prevent a shortage of food resources for fruit-eating fauna inhabiting urban spaces. Furthermore, promoting management practices that conserve species diversity in general should prioritize supporting the interactions between species. Establishing urban impact buffer zones in green areas, characterized by high environmental quality, as wild refuges is recommended, as these areas can harbor species less tolerant to urbanization. Moreover, adopting an "ecomimicry" approach to gardening in private spaces can also be beneficial. This approach mimics natural ecosystems, providing refuge for wildlife, offering resources for frugivorous fauna, and fostering interactions between species.

In the third chapter, we examined the direct effects of urban landscape coverage on interaction network metrics – Specialization (H_2') and Modularity (Q_w) – as well as on the taxonomic, functional, and phylogenetic diversity of networks members, in the urban area of Campo Grande, state of Mato Grosso do Sul. We demonstrated that the landscape characterized by a core of tree and shrub cover within a 200 m, surrounded by an impermeable surface cover matrix extending to 1000 m, positively influenced the taxonomic diversity of plants. Furthermore, this taxonomic diversity positively influenced modularity, indicating potential indirect effects of the spatial context on the structure of interaction networks. We observed that the phylogenetic diversity of frugivorous birds was higher in green spaces with impermeable surface cover at the 1000 m scale. From this finding, we concluded that islands of vegetation within urbanized landscapes can effectively promote the persistence of species and sustain interactions between them, particularly in terms of partitioning the use of resources. We also found that although not influenced by landscape context, the functional richness of plants positively influenced modularity. However, in comparison to taxonomic diversity of plants, functional richness had a smaller effect on modularity. Additionally, we observed that plant’s equitability decreased with impervious surface coverage at a local scale (200 m), indicating that interaction networks in these landscape contexts are dominated by a few plant species. In short, our results suggest that when selecting plants for afforestation it is important to consider multiple species and prioritize filling gaps associated with morphological characteristics that have significant implications for interactions between species.

We conclude that increasing the availability of native plant species in the public sphere is already an important step towards increasing the number of native species in the city. In this sense, promoting cultural events to attract the local community in favor of ecosystem services and encourage the planting of such species can be a significant advance. Based on our study, the selection of such species may prioritize greater taxonomic and functional diversity, i.e., several plant species with distinct morphological characteristics associated with consumption by animals (such as large and small fruits, tall trees, shrubs, lianas, and herbs). This could have important implications for greening and conservation of fauna that feed on fruits and act in propagules propagation. Thus, we suggest selection of some species, such as *Cecropia pachystachya*, *Ficus citrifolia*, *Trema micrantha*, and *Schinus terebinthifolia*, which have extended fruiting periods and produce fruits that are consumed by several species in the studied city, within the Cerrado domain. Furthermore, it is important to fill seasonal gaps, and provide resources throughout the year. Additionally, it is favorable that such resources have different morphological characteristics that allow them to be consumed by various species of birds. So, for the dry season we suggest the following native plants: *Schefflera morototoni*, *Pachira aquatica*, *Alibertia edulis*, *Terminalia brasiliensis*, *Maprounea guianensis*, *Nectandra cuspidata*, *Inga laurina*, *Myracrodruon urundeuva*, *Colubrina glandulosa*, *Miconia albicans*, *Astronium fraxinifolium*, *Qualea parviflora* and *Q. grandiflora*. Finally, plants that were important resources in the rainy season were: *Guarea guidonia*, *Nectandra hihua*, *Matayba guianensis*, *Myrsine guianensis*, *Protium heptaphyllum*, *Eugenia uniflora*, *Chrysophyllum marginatum*, *Casearia sylvestris*, *Andira cujabensis* and *Xylopia aromatica*.

In summary, while the spatial characteristics of urbanization have been extensively studied to investigate their effects on biodiversity (e.g., bird diversity), we emphasize the need for further studies on species interactions, particularly frugivory, in other urban areas, specifically in tropical areas, which harbor the highest diversity of frugivores. Obligate frugivores increase with human population size, and we encourage future studies to investigate the relationships between this pattern and house orchards and gardens, which could offer more insights into species interactions in urban areas. Additionally, studies focusing on the vertical structure of green spaces that reflect the complexity of vegetation could also offer information on the management of green areas in favor of the conservation of species and their interactions. Finally, we expect that by increasing the number of empirical studies it will also be possible to investigate multiple networks between several urban systems.

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