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DIVERSIDADE TAXONÔMICA E FUNCIONAL DAS AVES DA MATA ATLÂNTICA SOB INFLUÊNCIA DA MAIOR METRÓPOLE DO HEMISFÉRIO SUL, SÃO PAULO, BRASIL

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Diversidade taxonômica e funcional das aves da Mata Atlântica sob influência da maior metrópole do hemisfério sul, São Paulo, Brasil

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A maior parte das pessoas é assim.

Sonham com o voo, mas temem as alturas.

Para voar, é preciso ter coragem para enfrentar o terror do vazio.

Porque é só no vazio que o voo acontece.

O vazio é o espaço da liberdade, a ausência de certezas.

Por isso trocam o voo por gaiolas.

As gaiolas são os lugares que as certezas moram.

Rubem Alves

Resumo

Urbanização cria uma das formas de uso e ocupação do solo mais irreversíveis e comumente resulta em perda de espécies e homogeneização funcional das comunidades de aves, podendo assim afetar o funcionamento dos ecossistemas. O objetivo da presente tese foi compreender, de diferentes maneiras, como a urbanização da megacidade de São Paulo influencia as comunidades de aves e os processos ecológicos. O primeiro capítulo avaliou como parques urbanos e áreas residenciais contribuem com a manutenção das comunidades de aves e diversidade de funções ecossistêmicas comparado com grandes fragmentos florestais (áreas-fontes). Os resultados mostram a necessidade de manter grandes áreas de floresta nativa nos limites da cidade para preservar a rica avifauna e manter o funcionamento dos ecossistemas. Parques urbanos próximos (<10 km) às áreas fontes abrigam maior diversidade funcional de aves, mas não taxonômica, que àqueles distantes (> 10 km). Em habitats urbanos, complexidade vegetacional pode mitigar o impacto da urbanização. O segundo capítulo busca compreender como guildas de aves e toda a comunidade podem ser influenciadas por características bióticas-abióticas das áreas verdes urbanas desta megacidade. Os resultados indicam a importância de grandes áreas-verdes com alta cobertura de arbustos para abrigar rica avifauna regional. Pequenas áreas verdes devem mitigar os possíveis impactos negativos às aves relacionados às vidraças, tráfego de veículos e presença de humanos, cães e gatos, que podem sistematicamente eliminar grupos funcionais e diminuir a provisão de serviços ecossistêmicos de aves (frugívoras-nectarívoras e insetívoras) e também generalistas. O terceiro capítulo testa como as espécies, grupos funcionais e índices de diversidade funcional respondem à quantidade de vegetação (índice vegetação diferença normalizada, NDVI) e telhados de barro vermelho (em inglês: RCR – potencial sítio de nidificação) em áreas residenciais da megacidade de São Paulo. Os resultados indicam que combinações entre alta cobertura de NDVI (> 0.5) e RCR podem aumentar a ocorrência de espécies e funções ecológicas nas cidades Neotropicais. Estes resultados podem direcionar medidas de manejo ambiental e políticas públicas que visem a conservação da biodiversidade e seus serviços ecossistêmicos (essenciais ao bem estar humano) em diferentes habitats urbanos.

Palavras-chave: Aves. Conservação. Funções Ecossistêmicas. Homogeneização Funcional. Mata Atlântica. Urbanização.

Abstract

Urbanization creates one of the most irreversible forms of land use and occupation. Commonly, urbanization results in species losses and functional homogenization of bird communities, thus affecting the functioning of ecosystems. The objective of this thesis was to understand, in different ways, how the urbanization of São Paulo's megacity influences bird communities and ecological processes. In the first chapter, I evaluated how urban parks and residential areas contribute to the maintenance of bird communities and diversity of ecosystem functions compared to large forest fragments (source areas). The results show the need to maintain large areas of native forest on the city limits to preserve the rich avifauna and maintenance of ecosystem functioning. Urban parks next (<10 km) to the source areas show greater bird's functional diversity, but not taxonomic, than those far away (> 10 km). Moreover, vegetation complexity can mitigate the impact of urbanization in urban habitats. In the second chapter, I evaluated how bird guilds and the entire community can be influenced by biotic-abiotic characteristics in São Paulo's urban green areas. The results indicated the importance of large green areas with high shrub cover to shelter rich regional birdlife. On the other hand, small green areas should mitigate the possible negative impacts on birds related to glass panels, vehicle traffic and the presence of humans, dogs and cats, which can systematically eliminate functional groups and decrease the provision of ecosystem services provided by specialist guilds (frugivorous-nectarivorous and insectivorous) and also generalists. In the third chapter, I tested how species, functional groups and functional diversity indices respond to the amount of vegetation (normalized difference vegetation index, NDVI) and red clay roofs (RCR, a potential bird nesting site) in residential areas of the São Paulo megacity. The results indicate that combinations between high coverage of NDVI (> 0.5) and RCR can increase the occurrence of species and ecological functions in Neotropical cities. These results can guide environmental management measures and public policies aimed at the conservation of biodiversity and its ecosystem services (essential to human well-being) in different urban habitats.

Keywords: Birds. Conservation. Ecosystem Functions. Functional Homogenization. Atlantic Forest. Urbanization.

Sumário

1. Introdução Geral

1.1. Urbanização e os impactos ambientais nas esferas global a regional

Urbanização é um processo dinâmico que altera drasticamente as paisagens pré-existentes (natural ou rural), além de consumir grandes quantidades de energias e recursos para satisfazer exclusivamente as necessidades da vida humana moderna (Fontana et al., 2011; Seto et al., 2012; Seto & Ramankutty, 2016). Desenvolvidas de humanos (*Homo sapiens*) para humanos, as cidades são ecossistemas urbanos complexos, as quais se pressupõem a existência de aglomeração física, de pessoas, equipamentos, infraestruturas, fixado em um dado local e mantido por variados fluxos energéticos e mercadológicos (Liu et al., 2013; Santos, 1988). De fato, cidades são construídas com o propósito para facilitar as interações sociais, a administração política e econômica, embora moldadas por padrões culturais, religiosos e sociais (Pauchard et al., 2013; Santos, 1988).

As comodidades e facilidades à vida humana moderna oferecidas dentro do sistema urbano influenciam fortemente o homem a viver em alta densidade demográfica das cidades (Santos, 1988). A forte tendência de um mundo cada vez mais urbanizado pode ser visualizada na mais recente trajetória da população humana, que junto às cidades, tem crescido rapidamente à taxas sem precedentes e, em um curto espaço de tempo (< 100 anos), iniciado logo após ao período da industrialização (Seto et al., 2012; United Nations, 2014). Em 1950, 30% da população humana mundial vivia em cidades (United Nations, 2014); em 2014, a população urbana global já passava da metade (54%), com estimativas de que até 2030, a área urbana global alcançará a marca de 1,2 milhões km², representando quase o triplo da área ocupada nos anos 2000 (Seto et al., 2012). Com o desenfreado crescimento populacional, estima-se que, até 2050, a população urbana planetária atinja 66% - dos mais de 9 bilhões de habitantes (United Nations, 2018). Isto aumentará ainda mais a “geofagia”, ou seja, expansão das áreas urbanas sobre os habitats naturais ou rurais (Morello et al., 2000), resultando em grande destruição ambiental (Wigginton et al., 2016) e perda de biodiversidade (Aronson et al., 2016; McKinney, 2006).

Em escala global, cidades são representadas por manchas isoladas que ocupam apenas 3% da superfície do planeta (Liu et al., 2014), mas que dependem da importação massiva da produção de alimentos, energia, água e matérias primas geradas fora de seu território (Wigginton et al., 2016), fazendo com que seus impactos extrapolem seus limites físicos (Berkowitz et al., 2003). Neste sentido, as cidades alteram profundamente a cobertura do solo, causando a disrupção dos sistemas hidrológicos, biogeoquímicos, alterando os fluxos energéticos, aumentando os níveis de poluições do solo, ar e água (Grimm et al., 2008; Marzluff, 2017; Murgui & Hedblom, 2017). Como consequência, presume-se que a pegada ecológica de uma cidade exceda 200 vezes o seu tamanho (Wigginton et al., 2016), além de aumentar as emissões de gases de efeito estufa, que por sua vez, alteram temperatura e regime de chuvas local e regionalmente, com efeito aditivo às mudanças climáticas (Elmqvist et al., 2013; Tratalos et al., 2007). Invariavelmente, diversos estudos apontam urbanização como uma das mais drásticas e irreversíveis formas de uso do solo (Seto et al., 2012; Seto & Ramankutty, 2016), sendo atualmente considerada uma das maiores causas de extinções de espécies através do globo (Czech et al., 2000; Marzluff et al., 2001; McKinney, 2006).

Preocupantemente, países em desenvolvimento, os quais são responsáveis por abrigar grande parte da biodiversidade global (Myers et al., 2000), têm apresentado altas taxas de urbanização (United Nations, 2018). A América do Sul é a região do globo com a maior (85%) proporção da população vivendo em cidades (United Nations, 2014). A ocorrência de uma mega imigração do campo para as cidades, impulsionada a partir da metade do século XX, fez com que países como o Brasil, Argentina e Colômbia, abrigassem, atualmente, megacidades (> 10 milhões de hab.) como São Paulo e Rio de Janeiro, Buenos Aires e Bogotá, respectivamente (United Nations, 2014). Sem planejamento, suas cidades expandiram rapidamente sobre áreas naturais, gerando grandes problemas socioeconômicos e ambientais (Inostroza et al., 2013; Pauchard et al., 2013), ameaçando cerca de um quinto dos 34 *hotspots* mundial de biodiversidade (Cincotta et al., 2000; Mittermeier et al., 2004).

O Brasil é um dos países mais biodiversos do mundo (Mittermeier et al., 2005). Entretanto, desde a colonização, a costa leste brasileira, a qual encontra-se sob os domínios do bioma Mata Atlântica, foi extremamente impactada por diversos ciclos econômicos que ali converteram mais de 90% de suas florestas em culturas agrícolas, e mais recentemente, em cidades (Cincotta et al., 2000; Mittermeier et al., 2005). O desenvolvimento econômico em detrimento de suas riquezas naturais deu suporte para que a Mata Atlântica tornasse a região mais urbanizada e populosa do país (IBGE, 2015). Por outro lado, a destruição da maior parte de seus habitats nativos resultou em uma das maiores assembleias de espécies ameaçadas do planeta (Instituto Chico Mendes de Conservação da Biodiversidade, 2018), colocando em risco sua alta taxa de espécies endêmicas (Vale et al., 2018). Isto fez com que este bioma viesse a compor o seleto grupo de *hotspot* global de biodiversidade (Myers et al., 2000).

Atualmente, a Mata Atlântica é considerada uma das regiões de alta prioridade para a conservação da biodiversidade (Brooks et al., 2006; Mittermeier et al., 2011). Entretanto, a dinâmica de ocupação do solo na Mata Atlântica, a qual reúne extensas regiões metropolitanas (i.e., São Paulo e Rio de Janeiro: 22 e 13 milhões de hab., respectivamente), mas também diversos outros aglomerados urbanos, com população entre (> 500 mil e < 4 milhões de habitantes) distribuídas ao longo do seu território, reflete o mega desafio para alcançar de maneira efetiva a conservação dos recursos naturais e de sua rica biodiversidade (Cincotta et al., 2000; IBGE, 2015; Pauchard et al., 2013).

O desenvolvimento das cidades brasileiras sobre áreas ricas em vida silvestre associado à enorme desigualdade social cria paradoxos ambientais únicos. Assim, seus impactos sobre a biodiversidade carecem de avaliações sistemáticas ou encontram-se parcamente avaliados. Apesar da maioria dos estudos em ecologia urbana estar concentrada em regiões temperadas (MacGregor-Fors & Escobar-Ibáñez, 2017), a condição única dos habitats urbanos sulamericanos, especialmente brasileiros, não permite extrapolações dos resultados obtidos em outras regiões. Portanto, sendo de alta prioridade a realização de estudos *in loco*. Desse modo, as nossas cidades são laboratórios de pesquisa a céu aberto, prontas para serem cientificamente avaliadas (MacGregor-Fors & Escobar-Ibáñez, 2017) para assim produzir conhecimento das principais características das cidades que influenciam na manutenção de biodiversidade (Barbosa et al., 2017; Fontana et al., 2011; Reis et al., 2012; Toledo et al., 2012), consequentemente, guiar ações de conservação de biodiversidade dentro dos espaços urbanos e criar cidades mais biodiversas (ou “bird-friendly”) (Piratelli et al., 2017).

1.2. Avifauna em um mundo cada vez mais urbanizado

A urbanização é um processo contínuo que produz variações nos padrões e densidades de ocupações humanas, influenciando significantemente os ecossistemas locais (Alberti, 2005; Chace & Walsh, 2006; Marzluff et al., 2001; Vitousek et al., 1997). Embora centros urbanos ocupem apenas 3% da superfície terrestre e distribuídos em manchas isoladas, seu ecossistema heterotrófico e dissipativo, regido por alta dominância humana e políticas socioeconômicas, têm causado drásticas mudanças na paisagem global (Alberti et al., 2003; Liu et al., 2014; Wigginton et al., 2016). Paisagens naturais e rurais são convertidas com perpetuidade por uma imensa rede de equipamentos e estruturas urbanas (i.e. estradas, ruas, avenidas, edificações, postes, vidraças, fios de energia elétrica, dentre outros (MacGregor-Fors & Schondube, 2011; Shanahan et al., 2013). O rápido crescimento populacional humano e das cidades (Grimm et al., 2008; United Nations, 2018) aumenta a impermeabilização do solo e eleva temperatura e níveis de poluição do ar, água, solo e acústica (Eldredge & Horenstein, 2014). Assim, cidades contribui com a perda e fragmentação de habitats e aumenta efeito de borda (Fernández-Juricic, 2001; Fernández-Juricic & Jokimäki, 2001; Marzluff et al., 2001; McKinney, 2002, 2006), restando apenas pequenos remanescentes de vegetação natural/seminatural, muitas vezes, depauperados, isolados e sem conectividade entre eles (Faggi & Caula, 2017; Fontana et al., 2011).

Comparado a outros grupos animais, as aves são as mais estudadas e mantém relativa diversidade de formas e grupos funcionais em ecossistemas urbanos (Beninde et al., 2015; Chace & Walsh, 2006; Leveau et al., 2019; Marzluff, 2017; Murgui & Hedblom, 2017; Oliveira Hagen et al., 2017; Sol et al., 2014, 2017). Com o propósito de avaliar os efeitos da urbanização sobre as assembleias de aves vivendo em cidades, ecológos urbanos passaram a comparar riqueza de espécies, abundância, e indíces de diversidade e similaridade das avifaunas registradas em diferentes habitats urbanos. Deste modo, as avifaunas de habitats urbanos tem sido comparadas com àquelas presentes em ambientes rurais (Clergeau et al., 1998; Garaffa et al., 2009; McDonnell & Pickett, 1990), naturais (Leveau et al., 2017; Minor & Urban, 2010) e áreas verdes (parques, campos de golfe, cemitérios, praças, etc.) (Blair, 1999; Fernández-Juricic, 2000b; Lussenhop, 1977; MacGregor-Fors & Ortega-Álvarez, 2011; Matarazzo-Neuberger, 1992; Morelli et al., 2018; Peris & Montelongo, 2014). Com a crescente necessidade de avaliar os impactos da urbanização sobre as comunidades de aves de forma sistematizada, ecólogos utilizaram-se de gradientes urbano-rural ou urbano-natural (Clergeau et al., 1998; Ferenc et al., 2013; Garaffa et al., 2009; Kark et al., 2007b; Leveau & Leveau, 2004). Com o reconhecimento da diversidade de habitats existente dentro das cidades, cresce o interesse em avaliar como as aves respondem a determinados níveis de urbanização (Leveau & Leveau, 2004; Reis et al., 2012; Toledo et al., 2012), onde também foram realizadas comparações entre as classes de urbanização (i.e., residencial vs. comercial e/ou industrial) (Lerman et al., 2014; Ortega-Álvarez & MacGregor-Fors, 2009; van Heezik et al., 2008) e entre ruas arborizadas a não arborizadas (Fernández-Juricic, 2000a; Park & Choi, 2005; Young et al., 2007).

Como consequência, diversos trabalhos apontam para uma tendência global de que urbanização afeta drasticamente as comunidades de aves (MacGregor-Fors & Escobar-Ibáñez, 2017; Marzluff, 2017; Murgui & Hedblom, 2017), a qual, em média, elimina 92% das espécies que ocorriam antes da urbanização (Aronson et al., 2016). Comumente, quanto maior a urbanização, menor a riqueza de espécies de aves e maior a abundância (Blair, 1996; Clergeau et al., 1998, 2001; Crooks et al., 2004; Fontana et al., 2011; Ortega-Álvarez & MacGregor-Fors, 2009; Toledo et al., 2012; Villegas & Garitano-Zavala, 2010), muito embora níveis intermediários de urbanização possam manter uma maior diversidade de espécies (Leveau et al., 2018; Rodrigues et al., 2018). Isto indica que as espécies de aves apresentam diferentes sensibilidades aos níveis dispares de distúrbios ambientais provocados por diferentes níveis de urbanização. Neste sentido, as espécies tem sido classificadas conforme sua tolerância à urbanização (Blair, 1996; Crooks et al., 2004; McKinney, 2002), que, após ter sido recentemente revisada (Fischer et al., 2015), as categorias são: i) “urban-dwellers” - *moradores-urbanos*: beneficiam-se do uso de recursos em áreas urbanas, tornando-as mais abundantes neste ecossistema antrópico; ii) "*urban utilizers*" – *usuários urbanos*: são capazes de utilizar facultativamente os recursos em áreas urbanas; e iii) "*urban avoiders*" – *evitadores urbanos*: altamente sensíveis à urbanização, as quais suas densidades máximas são detectadas em ambientes naturais e evitam áreas urbanas.

A capacidade de uma espécie explorar ou evitar o ecossistema urbano tem influência direta com a forma que suas características ecológicas e funcionais interagem com a complexidade estrutural dos habitats e seus recursos (Croci et al., 2008; Møller, 2009). Comparado com os ecossistemas naturais, urbanização promove elevada simplificação estrutural dos habitats que limitam a recolonização e persistência de grande quantidade de espécies nativas especialistas (i.e., habitats, dieta, estrato de forrageio e nidificação) nas cidades, mas beneficia as espécies com alta plasticidade ecológica que usam eficientemente os recursos antropogênicos (Aronson et al., 2014; Sol et al., 2014). Isto significa que cidades de diversas regiões do globo impõe potentes filtros urbanos sobre as comunidades de aves locais, os quais selecionam as espécies de aves por meio de suas características funcionais pré-adaptadas a viver em habitats urbanos (Croci et al., 2008; Hensley et al., 2019). Assim, determinados grupos funcionais tomam vantagem sobre outros em meio urbano. Neste sentido, urbanização favorece as aves de áreas abertas e onívoras (Chace & Walsh, 2006; Fernández-Juricic, 2001), residentes (Barbosa et al., 2020; Bezzel, 1985; Lancaster & Rees, 1979), nidificantes em cavidades e em árvores (Conole, 2014; Emlen, 1974; Gavareski, 1976; Jokimäki, 1999; Jokimäki & Suhonen, 1998), mas prejudica as espécies insetívoras florestais (Chace & Walsh, 2006; Croci et al., 2008; Fernández-Juricic, 2001), migratórias (Barbosa et al., 2020) e nidificantes de solo e construtoras de cavidades 'Picidae" (Conole, 2014; Emlen, 1974; Gavareski, 1976; Jokimäki, 1999; Jokimäki & Suhonen, 1998).

O efeito da urbanização sobre as comunidades de aves é uma filtragem não-aleatória das espécies, restando apenas as aves de determinados grupos funcionais aptas a explorar o ecossistema urbano (Devictor et al., 2007), as quais representam um pequeno conjunto de espécies das comunidades de aves dos habitats naturais e seminaturais periurbanos (Aronson et al., 2016; Maseko et al., 2019). Estas são compostas por espécies nativas-generalistas e exóticas-introduzidas, que podem aumentar substancialmente suas densidades dentro das cidades (Blair, 1996, 2001; Clergeau et al., 2006; Croci et al., 2008; Leveau & Leveau, 2005; Leveau & Leveau, 2004; Marzluff et al., 2001; Rolando et al., 1997; van Rensburg et al., 2009). Por quase quarenta anos, este processo pelo qual urbanização produz alta dominância de poucas espécies em detrimento da drástica perda de espécies nativas foi chamado de homogenização biótica (Beissinger & Osborne, 1982; Blair, 2001; Clergeau et al., 2006; Olden et al., 2004; Olden & Rooney, 2006). Independentemente das características biogeográficas e climáticas, estudos ornitológicos reportaram a ocorrência de homogeneização biótica em cidades da Europa (Clergeau et al., 1998, 2001, 2006; Fernández-Juricic, 2000b; Jokimäki & Kaisanlahti-Jokimäki, 2003; Savard et al., 2000), América do Norte (Blair, 2001; Ortega-Álvarez & MacGregor-Fors, 2009), Oceania (Catterall et al., 2010; Chace & Walsh, 2006), América do Sul (Fontana et al., 2011; Leveau & Leveau, 2005; Leveau & Leveau, 2004; Reis et al., 2012; Toledo et al., 2012; Villegas & Garitano-Zavala, 2010) e África (van Rensburg et al., 2009). Entretanto, habitats urbanizados proporcionalmente favorece um conjunto maior de espécies nativas que exóticas (Sol et al., 2020), ainda que frequentemente compartilhem similares traços funcionais e filogenéticos quando comparadas em diversas regiões do globo (Coetzee & Chown, 2016; Ibáñez-Álamo et al., 2017; Oliveira Hagen et al., 2017; Pagani-Núñez et al., 2019; Si et al., 2017; Sol et al., 2014), sendo atual e conceitualmente mais aceita a ideia de que urbanização causa homogeneização funcional (Sol et al., 2020).

As variadas funções ecológicas das espécies de aves podem refletir diretamente no provimento de serviços ecossistêmicos (i.e., dispersão de sementes, polinização, controle de artrópodes, ciclagem de nutrientes e produção de biomassa) essenciais ao funcionamento do ecossistema (Nyffeler et al., 2018; Sekercioğlu, 2006; Sekercioğlu et al., 2004). Como as funções ecológicas das espécies são estritamente conectadas com a multiplicidade de traços funcionais presente na comunidade (Mason et al., 2005), ecólogos têm utilizado características morfológicas, fisiológicas e/ou fenotípicas (Laliberté et al., 2010) para calcular índices de diversidade funcional (FD) (Laliberté et al., 2014) para avaliar quantitativamente como as aves interagem nos diferentes ecossistemas (Violle et al., 2007), bem como são influenciadas por diferentes tipos de habitats e uso do solo (Coetzee & Chown, 2016; Vaccaro et al., 2019). Neste sentido, homogeneização funcional associada aos habitats urbanos tem implicações diretas à conservação das espécies e diversidade de funções ecossistêmicas (Luck et al., 2013b; Oliveira Hagen et al., 2017). Portanto, homogeneização funcional das comunidades de aves podem impactar negativamente na manutenção dos habitats, produção de alimentos e saúde ambiental, bem como aos aspectos socioeconômicos, culturais e religiosos (Belaire et al., 2015; Margalida et al., 2014; Sekercioglu, 2012; Sekercioğlu et al., 2004; Tratalos et al., 2007), afetando o bem estar da população humana (Tratalos et al., 2007). A proposição de tornar as cidades mais sustentáveis e contribuir efetivamente à manutenção da biodiversidade e serviços ecossistêmicos tem ganhado força em escala global (Sekercioglu, 2012; Vitousek et al., 1997). Para isto, o uso das múltiplas facetas da diversidade taxonômica e funcional tem sido amplamente recomendada (Leveau et al., 2020; Oliveira Hagen et al., 2017; Palacio et al., 2018; Pena et al., 2017; Sol et al., 2020) porque nem sempre áreas com elevada riqueza de espécies apresentam valores altos de diversidade funcional (Bae et al., 2018; Chapman et al., 2018). Apesar disso, a abordagem integrativa entre os componentes de diversidade taxonômica e funcional fornece uma profunda compreensão de como as mudanças ambientais afetam as comunidades e provisão de serviços ecossistêmicos (Villéger et al., 2008), sendo fundamental para propor ações mais efetivas à conservação da biodiversidade e manutenção de suas funções ecossistêmicas (Cadotte & Tucker, 2018).

Dentro das cidades, frequentemente jardins, arborização urbana, cemitérios, campos de golfe, corredores verdes de avenidas e praças assumem um importante papel na manutenção dos habitats e recursos para as aves urbanas e serviços ecossistêmicos (Carbó-Ramírez & Zuria, 2011; Fernández-Juricic, 2000a; Juri & Chani, 2009; Pena et al., 2017). Além disso, estudos tem apontado quais as principais características ambientais que aumentam os índices de riqueza de espécies e diversidade funcional dentro dos habitats urbanos, como (1) elevada taxa de cobertura vegetal (Leveau et al., 2020); (2) aumento de tamanho das áreas verdes (Beninde et al., 2015; Schütz & Schulze, 2015); (3) elevada heterogeneidade ambiental e configuração espacial dos habitats (Oliveira Hagen et al., 2017); e (4) estrutura vegetacional (Campos-Silva & Piratelli, 2020; Maseko et al., 2019; Morelli et al., 2018; Morelli, Benedetti, et al., 2017); (5) riqueza de espécies arbóreas (Campos-Silva & Piratelli, 2020; Silva et al., 2020; Pena et al., 2017), proximidade de recursos hídricos (Barbosa et al., 2020; Morelli, Benedetti, et al., 2017). Contudo, os ecossistemas urbanos apresentam novas ameaças e desafios às espécies de aves (MacGregor-Fors & Schondube, 2011; Pena et al., 2017; Ramalho & Hobbs, 2012; Sacco et al., 2015), muitas vezes distintas dos habitats naturais. Por exemplo, estudos tem reportado diminuição dos índices taxonômicos e/ou diversidade funcional das aves decorrentes do aumento das edificações, impermeabilização do solo e densidade populacional humana (Evans et al., 2018; Palacio et al., 2018; Sacco et al., 2015; Schütz & Schulze, 2015; Wang et al., 2017), bem como aos altos índices de poluição sonora (Barbosa et al., 2020; Silva et al., 2020; Fernández-Juricic, 2001; Fontana et al., 2011; Pena et al., 2017).

Apesar destas variáveis urbanas influenciarem negativamente no nível taxonômico, pouco se sabe como índices de diversidade funcional respondem ao (1) aumento das presenças humana e (2) de animais domésticos (Churcher & Lawton, 1987; Lessa et al., 2016; Loss et al., 2013; MacGregor-Fors & Schondube, 2011), iluminação artificial e estruturas associadas (postes e fios) (Leveau, 2018; Morelli et al., 2018; Seress & Liker, 2015), cabos de energia elétrica e de telecomunicações e presença de antenas (MacGregor-Fors & Schondube, 2011), tráfego de veículos (Carbó-Ramírez & Zuria, 2011; Fernández-Juricic, 2001; Leveau & Leveau, 2016), vidraças (Basilio et al., 2020) e telhados (Emlen, 1974; Pellissier et al., 2012).

Além disso, quando o assunto é a proximidade entre áreas verdes e áreas fontes nos limites das cidades, diferentes respostas foram obtidas em avifaunas de regiões temperadas e tropicais (Clergeau et al., 2001; MacGregor-Fors & Ortega-Álvarez, 2011; Melles et al., 2003; Puga-Caballero et al., 2014; Shih, 2017). Por exemplo, uma meta-análise global encontrou que urbanização em regiões de clima temperado beneficia espécies onívoras e granívoras (Chace & Walsh, 2006), enquanto que cidades neotropicais favorecem espécies onívoras e insetívoras (Ortega-Álvarez & MacGregor-Fors, 2011). Além de regiões neotropicais apresentarem menor compreensão de como a urbanização influencia os componentes da diversidade de suas comunidades de aves (MacGregor-Fors & Escobar-Ibáñez, 2017), cidades latino-americanas tem aumentado demasiadamente e ameaçam seus *hotspots* de biodiversidade (Cincotta et al., 2000; Mittermeier et al., 2011). Tais discrepâncias encontradas entre as biotas e urbanização das cidades neotropicais e de zonas temperadas inviabilizam qualquer tipo generalização dos resultados. Portanto, sendo necessária a realização de estudos que orientem ações de manejo e planejamento do desenvolvimento urbano para criar cidades mais sustentáveis e biodiversas (Leveau et al., 2020; Oliveira Hagen et al., 2017; Sol et al., 2020).

1.3. A ornitologia na grande São Paulo e a lacuna ecológica dos impactos da urbanização sobre as aves

Os primeiros registros de aves conhecidos cientificamente para a região metropolitana (ou megacidade) de São Paulo foram feitos em 1819, sob autoria do naturalista austríaco, Johan Natterer. Em sua expedição pelo rio Tamanduateí, atual região central da cidade de São Paulo, Natterer coletou espécies raras como *Stephanoxis lalandi* e *Circus buffoni*. Desde então, sob diferentes métodos, a ornitologia da região metropolitana (ou megacidade) de São Paulo tem sido incrementada ano a ano, sendo relativamente bem conhecida (Figueiredo & Lo, 2000; Ihering, 1898; Pelzeln, 1871; Schunck, 2008).

Por um longo período (1819-1940), as pesquisas ornitológicas foram marcadas pela passagem de naturalistas-colecionadores e coletores profissionais (Johan Natterer, Hermann von Ihering, Pinder, Ernst Garbe, Adolfo Hempel, João Leonardo Lima, Olivério Pinto e outros) que obtinham registros exclusivamente por meio da coleta científica de aves (Schunck, 2008). A instalação do Museu Paulista no bairro do Ipiranga facilitou a logística dos coletores, culminando em uma das avifaunas mais bem estudadas para época, com destaque à presença de espécies de campos naturais (*Nothura maculosa*), áreas alagadas (*Botaurus pinnatus*) e de matas preservadas (*Glaucidium minutissimum*) (Schunck, 2008). Foi nos campos do Ipiranga que Ihering & Ihering (1907) coletaram o espécime-tipo e descreveram o passeriforme *Emberizoides ypiranganus,* assim homenageando o bairro “Ipiranga” que se destacou pela importância biológica e história do Brasil (Ihering, 1898). Mais tarde, outras localidades na região metropolitana de São

Paulo também tiveram suas avifaunas amostradas pelos coletores do Museu Paulista. Em São Paulo, locais como a Serra da Cantareira, Marsilac, Alto da Serra, Santo Amaro, dentre outras; Guarulhos (Cumbica, área que hoje abriga o aeroporto internacional de São Paulo); Salesópolis (Estação Ecológica de Boracéia), Santo André (Alto da Serra – atual Paranapiacaba), dentre outras (Ihering, 1898; Schunck, 2008; Willis & Oniki, 2003).

Se por um lado houve o declínio das coletas científicas a partir da década de 50, por outro, pesquisadores passaram a investigar as avifaunas em campo principalmente utilizando-se da observação e escuta das aves, com resultados publicados em forma de listas (Figueiredo & Lo, 2000; Schunck, 2008). Na cidade de São Paulo, o primeiro trabalho realizado a partir deste método investigou as comunidades de aves dos bairros do Brooklin e Santo Amaro, de áreas verdes públicas (e.g., praça da República e parques da Água Branca e Tenente Siqueira Campos) e do reservatório Billings, o qual registrou espécies raras como *Phibalura flavirostris* e *Accipiter poliogaster* (Mitchell, 1957). A partir daí, outros estudos foram desenvolvidos na zona norte do município, Serra da Cantareira (Negreiro 1974), bem como a realização de estudo de longa duração realizado na Cidade Universitária Armando Salles de Oliveira (Höfling & Camargo, 1999), e em diversas áreas verdes, parques e unidades de conservação estudadas pelo Centro de Estudos Ornitológicos (Argel-de-Oliveira, 1987; Figueiredo, 2020) e por técnicos da Divisão de Fauna do município de São Paulo – DEPAVE-3 (São Paulo, 2018b).

Mais tarde, Figueiredo e Lo (2000) realizaram a compilação dos registros contidos nestes trabalhos e publicaram a primeira lista de aves deste município. Esta lista foi importante para demonstrar o conhecimento da avifauna regional para a época, subsidiando diversos ornitólogos interessados em contribuir com a realização de novos estudos e complementos à lista de aves do território municipal – (Almeida et al., 2003; Antunes et al., 2008; Figueiredo, 2003; Macarrão et al., 2008, 2014; Melo & Schunck, 2011; Macarrão, 2007). Esta compilação foi revisada e atualizada em 2008, passando de 300 para 373 espécies de aves (Schunck, 2008).

Conforme ocorre a transformação da paisagem, nos níveis local e regional, a matriz florestal torna-se rural-urbana, quebrando as barreiras biológicas. Assim, espécies que não ocorriam antes na região colonizaram os habitats periurbanos e urbanos da região metropolitana de São Paulo, com destaque para as espécies que se beneficiam de áreas abertas degradadas *Patagioenas picazuro* (Höfling & Camargo, 1999), *Fluvicola nengeta* (Lo 2000), *Thamnophilus doliatus* (Antunes et al., 2008), *Furnarius figulus* (Melo, 2010), florestas secas como *Myiothlypis flaveola* e *Ramphocelus carbo* (Perrella et al., 2018; Schunck et al., 2011), florestas de araucária *Leptasthenura setaria* (Melo & Schunck, 2011), áreas úmidas florestadas *Mesembrinibis cayennensis* (Antunes et al., 2008), além de diversas aves aquáticas/limícolas como *Pilherodius pileatus*, *Anas versicolor* e *A. georgica* (Montanhini, 2007), *Podicephorus major* (Schunck et al., 2011), *Netta peposaca* (Melo, 2014). Por outro lado, diversas espécies, anteriormente registradas, mas sensíveis à perda e alteração dos habitats, desapareceram com o crescimento da cidade e não foram mais registradas, como *Nothura maculosa* e *Rhynchotus rufescens* (Figueiredo, 2020; Höfling & Camargo, 1999). O monitoramento realizado por ornitólogos e observadores de aves é fundamental para detectar o reaparecimento de algumas espécies que ficaram longo período de tempo (60-120 anos) sem ser detectada no território paulista, como reportado para *Crypturellus parvirostris* (Melo & Godoy, 2010), *Botaurus pinnatus* (Schunck, Salaroli, et al., 2019) e *Pyrrhocoma ruficeps* (Dores & Melo, 2020), além de registrar a ocorrência de espécies adicionais à municipalidade de São Paulo, nos casos de *Leptasthenura setaria* (Melo & Schunck, 2011) e *Elaenia spectabilis* (Macarrão et al., 2014), indicando novas ocorrências de espécies ameaçadas *Touit melanonotus*

(Melo & Braga, 2021), mesmo em locais bem estudados (Tonetti et al., 2017), ampliando assim o conhecimento da avifauna da região (Figueiredo, 2020).

Uma outra parte das espécies que originalmente não ocorria, mas que hoje mantém populações estabelecidas na região metropolitana de São Paulo, é proveniente de introduções realizadas pelo homem por meio de solturas e/ou escapes de cativeiro. Este é o caso das espécies alóctones, ou seja, espécies nativas de outras regiões brasileiras que, após facilitação humana, vivem nos habitats urbanos da megacidade de São Paulo, como *Brotogeris chiriri, Diopsittaca nobilis*, *Paroaria dominicana* e *P. coronata* (Schunck, 2008), bem como das exóticas introduzidas *Passer domesticus, Estrilda astrild* e *Columba livia* (Sick, 1997). Controversamente, *Myiopsitta monachus,* uma espécie que estabeleceu populações introduzidas em áreas urbanas da América do Norte, Europa, África e Ásia (Burgio et al., 2020), não teve o mesmo êxito com a urbanização de São Paulo (Figueiredo, 2020).

Juntamente com os registros históricos supracitados, o número crescente de estudos a partir dos anos 2000, em regiões bem preservadas da Mata Atlântica, como a reserva Florestal do Morro Grande, em Cotia (Develey & Martensen, 2006), Serra da Cantareira (Tonetti et al., 2017), Área de Proteção Ambiental Capivari-Monos (Melo et al., 2016), núcleo Curucutu do Parque Estadual da Serra do Mar (Schunck, Silveira, et al., 2019) e áreas da represa Guarapiranga (Schunck et al., 2011; Schunck & Rodrigues, 2016), Vila de Paranapiacaba "Alto da Serra", em Santo André (Silveira, 2009) tem revelado uma megadiversidade de aves nos arredores da maior área urbana do hemisfério sul. Estas florestas integram a Reserva da Biosfera do Cinturão Verde da Cidade de São Paulo (Yoshida & Uieda, 2014). Este aumento do esforço amostral nas áreas florestadas e reservatórios da cidade de São Paulo apresenta rica avifauna, com 528 espécies registradas para o município de São Paulo (Figueiredo, 2020). Certamente, o exemplo da capital paulista estimulou outros municípios brasileiros a conhecer sua biodiversidade, contando com a presença marcante da avifauna. Um caso similar na região metropolitana de São Paulo (RMSP) é a cidade de Guarulhos, onde atualmente são conhecidas 375 espécies de aves em seu território municipal (Guarulhos, 2018).

A maioria dos estudos ornitológicos desenvolvido nestes municípios (São Paulo e Guarulhos) foi conduzida por pelo menos um ano, com visitas mensais realizadas em apenas uma área, onde pesquisadores objetivaram exclusivamente conhecer as avifaunas das áreas verdes, desde parques municipais isolados a grandes áreas protegidas com vegetação nativa da Mata Atlântica (Antunes & Eston, 2008; Guarulhos, 2018; Melo et al., 2016; Perrella et al., 2018; Schunck, 2008; Schunck, Silveira, et al., 2019), incluindo também áreas úmidas e represas (Schunck et al., 2011; Schunck & Rodrigues, 2016). Entretanto, pouca atenção tem sido dada para outros tipos de áreas verdes (e.g., cemitérios, terrenos e praças) e áreas residenciais (Argel-de-Oliveira, 1995; Matarazzo-Neuberger, 1992; Mitchell, 1957), os quais, se manejados de modo integrado com outras áreas verdes, podem aumentar a diversidade de aves em áreas densamente urbanizadas (Nolazco, 2012; Pena et al., 2017; Silva et al., 2015).

Apesar da ocorrência de diversos estudos ornitológicos na megacidade de São Paulo, estes apenas sugeriram a influência da urbanização sobre as assembleias de aves. Até 2019, surpreendentemente nenhum estudo havia testado como o processo de urbanização da maior metrópole da América do Sul tem influenciado suas comunidades de aves. Só recentemente, em 2020, a influência da urbanização sobre as aves de diversas áreas verdes foi investigada por (Barbosa et al., 2020). Eles encontraram que altos índices de ruídos e proximidade de recursos hídricos modulam significativamente as comunidades de aves residentes e migratórias da região. Entretanto, as assembleias de aves urbanas neotropicais são sensíveis à proximidade com áreas fontes (Puga-Caballero et al., 2014), quantidade de áreas verdes (Beninde et al., 2015; Leveau et al., 2020), complexidade estrutural vegetacional (Campos-Silva & Piratelli, 2020; Fontana et al., 2011; Reis et al., 2012; Toledo et al., 2012) e presença de espécies arbóreas nativas e exóticas (Campos-Silva & Piratelli, 2020; Silva et al., 2020; Lessi et al., 2016). Além disso, a presença de animais domésticos (Lessa et al., 2016; MacGregor-Fors & Schondube, 2011) e vidraças (Basilio et al., 2020; Chace & Walsh, 2006) são alguns dos novos desafios que a urbanização impõe sobre suas avifaunas regionais (Chace & Walsh, 2006), mas que ainda faltam evidências de como influenciam a assembleia de aves da megacidade de São Paulo. Isto demonstra uma enorme lacuna no conhecimento de como a urbanização da maior cidade do Hemisfério Sul influencia a riqueza, abundância e, principalmente a diversidade funcional de sua avifauna. Esta última é fundamental para entendermos o funcionamento dos ecossistemas (Díaz & Cabido, 2001; Filippi-Codaccioni et al., 2009; Flynn et al., 2009) e propormos medidas mitigatórias aos impactos causados pela urbanização (Donnelly & Marzluff, 2006; Hansen et al., 2005).

Apesar do enorme apelo à conservação das espécies em habitats urbanos e periurbanos (Oliveira Hagen et al. 2017), poucos pesquisadores testaram quais as variáveis ambientais influenciam a abundância e traços funcionais das espécies ou comunidades de aves que vivem nos habitats da megacidade de São Paulo. Dentre eles, ressaltam-se os estudos de densidade e micro-habitat da população de *Phylloscartes eximius* que vive no Parque Estadual Cantareira (Tonetti & Pizo, 2016) e investigações sobre o uso do habitat e tamanho da área de vida de *Myiodynastes maculatus*, no Parque Ecológico Tietê (Vitório et al., 2019), além de aspectos da biologia reprodutiva de *Buteo brachyurus*, no Parque Ibirapuera (Monsalvo, 2012) e frugivoria por aves, no Parque Estadual da Cantareira (Campagnoli et al., 2016; Ikuta & Martins, 2013).

Considerando que, nos próximos trinta anos, 90% da população brasileira viverá em cidades, isto significa que áreas urbanas expandirão ainda mais sobre seus *hotspots* de biodiversidade (Mittermeier et al., 2011). Assim, biomas como a Mata Atlântica, que perigosamente concentra 70% da população e abriga habitats e biotas já ameaçados pela urbanização e atividades humanas (ICMBio, 2018) podem ter o funcionamento do ecossistemas e provimento de serviços ecossistêmicos profundamente impactados (Cincotta et al., 2000; Sekercioglu, 2012; United Nations, 2018). Neste contexto, estudos adicionais são urgentemente necessários para conhecermos quais características ambientais influenciam os variados aspectos da diversidade taxonômica e funcional das comunidades de aves regionais. Deste modo, o presente estudo teve por objetivo avaliar como aspectos contidos na urbanização da megacidade de São Paulo modulam as ricas comunidades de aves das áreas protegidas (Schunck, Silveira, et al., 2019; Tonetti et al., 2017), dos parques e áreas verdes urbanos em meio à matriz urbana (Barbosa et al., 2020) e em áreas residenciais (Argel-de-Oliveira, 1995). Os resultados dessa avaliação serão fundamentais para guiar políticas públicas locais que orientem o manejo ambiental a fim de mitigar os impactos da urbanização sobre as comunidades de aves (Pena et al., 2017) e prover condições ambientais favoráveis à manutenção da biodiversidade e funções ecossistêmicas dentro das cidades neotropicais (Leveau et al., 2020; Oliveira Hagen et al., 2017), importantes para o bem-estar humano e desenvolvimento sustentável (Sekercioglu, 2012; Tratalos et al., 2007).

1.4. Capítulos da tese

No primeiro capítulo, eu avaliei como as assembleias de aves e funções ecossistêmicas por meio de índices de diversidade são influenciados por áreas de alta densidade humana e áreas verdes urbanas comparada com áreas protegidas com vegetação nativa (fonte), bem como a distância da fonte e variáveis vegetacionais (verde) e urbanas (cinza) (ver Faggi & Caula, 2017). No segundo capítulo, eu busquei compreender como índices de diversidade taxonômica e funcional das aves frugívoras, insetívoras, migratórias e residentes são influenciadas por características presentes nas áreas verdes distribuídas dentro da maior cidade do hemisfério sul. Eu testei como o tamanho da área, características vegetacionais e urbanas influenciam sobre os índices de diversidade de cada guilda, discutindo como isto pode impactar o provimento de serviços ecossistêmicos (i.e., controle de insetos, dispersão de sementes) essenciais à manutenção do ecossistema. Por fim, no terceiro capítulo, eu busquei avaliar como as espécies de aves e diversidade funcional são influenciadas pela quantidade de vegetação e presença de telhados de barro – que as aves usam como sítio de nidificação, em áreas densamente habitadas da megacidade de São Paulo. Considerando diferentes escalas locais (50, 100 e 200 m), eu testei como porcentagens do solo urbano contendo produtividade primária (NDVI) e telhados de barro podem influenciar as comunidades de aves em uma matriz altamente urbanizada. Nos três capítulos, eu busquei compreender como as aves e suas funções ecossistêmicas tem sido influenciadas por características locais e da paisagem, para assim gerar diretrizes de manejo ambiental e mitigação dos possíveis impactos sobre as aves que vivem nos três tipos de habitats mais dominantes da megacidade de São Paulo.

2. Área de Estudo

A região metropolitana de São Paulo é a área urbana mais populosa do hemisfério sul e está situada no sudeste do Brasil (23°54W, 46°63S; Figura 1, pag. 59). Ela compreende 39 municipalidades, onde 21,5 milhões de habitantes vivem em um território de aproximadamente 8 mil km² (2,4 mil habitantes por km²) (IBGE, 2020). Destes 39 municípios, São Paulo (23°32’56”S, 46°38’20”W, 12,2 milhões de hab.) e

Guarulhos (23°27’46”S, 46°31’58”W, 1,3 milhões hab.) são as municipalidades que centralizam mais que 60% dos 22 milhões de pessoas e juntos representam o principal centro comercial-financeiro da América do Sul (IBGE, 2020).

O clima é úmido subtropical com inverno ameno e seco, além de verão chuvoso com temperaturas moderadamente altas (Alvares et al., 2013). A vegetação predominante é a floresta ombrófila densa, uma tipologia da Mata Atlântica (Veloso et al., 1991). Originalmente, São Paulo e Guarulhos apresentavam florestas, campos e áreas alagáveis. Entretanto, desde 1940, esta região experimentou intenso processo de urbanização e rápido crescimento populacional, levando à remoção massiva de seus ecossistemas naturais (IBGE, 2015; Instituto Florestal, 2020). A área urbana apresenta 2.100 km² (IBGE, 2015) onde seus principais remanescentes de áreas verdes estão representados por pequenas áreas isoladas na forma de parques urbanos e praças (São Paulo, 2017). Além disso, a megacidade de São Paulo está cercada por grandes remanescentes da Mata Atlântica, que em 1993, foram reconhecidos pela UNESCO como parte integrante da Reserva da Biosfera da Mata Atlântica, a qual protege a rica biodiversidade, paisagens naturais e diversos serviços ecossistêmicos essenciais à vida humana (Tonetti et al., 2017).

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Capítulo 1

Influence of habitat types and distance of source area on bird taxonomic and functional diversity in a Neotropical megacity

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Influence of habitat type and distance from source area on bird taxonomic and functional diversity in a Neotropical megacity

Abstract

Here we investigate how diverse habitat types, vegetation (green)/urban(gray) characteristics, and distance from large patches of native forests (source) drive bird species richness and functional diversity in the megacity of São Paulo in Southeast Brazil. We test for the effects of habitat types and their distance from source areas on each bird index, and the contribution of vegetation and urban characteristics to the observed results. We detected 231 bird species and our data confirmed our predictions: 1) bird species richness and functional richness in urbanized habitats was 50–90% lower than in the source habitats; 2) urban parks near (< 10 km) source areas preserved a similar number of species to distant urban parks, and had higher functional richness than more distant urban parks (>10 km); and 3) shrub and herbaceous cover and tree cover, were positively related to species richness and specialized functional traits related to diet and foraging stratum. The number of buildings and their maximum height were negatively related to bird species richness and functional richness. Functional evenness and functional divergence did not vary across urban and native habitats, yet both were negatively associated with tall buildings. Functional evenness increased with tree cover and number of lamp poles, while functional divergence showed a bimodal response to building number. Our study stresses the need to maintain large-protected areas surrounding megacities and the complexity of vegetation embedded in large Neotropical urban settlements to mitigate the impacts of urbanization on birds.

Keywords: Atlantic Forest. Functional Homogenization. Diet-Foraging Specialist-Generalist Traits. São Paulo Megacity. Urban Parks. Urban Vegetation Characteristics

Introduction

The Neotropical region is home to the rich biodiversity in the world, although it has been subjected to massive urbanization, which poses risks for several global biodiversity hotspots (Cincotta et al. 2000; Myers et al. 2000; Pauchard et al. 2013). South America alone shelters five of the 35 global biodiversity hotspots (Myers et al. 2000; Mittermeier et al. 2011) and nearly one-third of all bird species in the world (Remsen et al. 2018). More than 80% of the 430 million human inhabitants of South American live in urban settlements, which is expected to reach nearly 500 million people by 2050 (United Nations 2018). The rapid urban growth in developing countries poses multiples challenges to social, economic, and environmental sustainability (Andersson 2006; Pauchard et al. 2013). Combined, these factors increase threats to biomes, biodiversity, and ecosystem services (Cincotta et al. 2000; Myers et al. 2000), thus depleting human welfare (Tratalos et al. 2007; Aronson et al. 2014; Vale et al. 2018).

Birds are the most studied animal group in urban settlements worldwide (Marzluff 2017), where they perform central ecosystem functions (e.g., pollination, seed dispersal, arthropod control, and nutrient cycling) for habitat maintenance and sustainability (Sekercioglu 2012; Nyffeler et al. 2018). Ecosystem functions are intrinsically linked to species ecological traits (Mason et al. 2005) and ecologists have been using functional traits (e.g., morphological, physiological, and/or phenological attributes) (Laliberté and Legendre 2010) to calculate several functional diversity (FD) metrics (Laliberté et al. 2014). These metrics help in understanding the way organisms interact in ecosystems (Violle et al. 2007) and clarify how changes to habitat affect biodiversity and the provision of ecosystem services (Villéger et al. 2008). Thus, although FD has been considered to be more accurate than taxonomic indexes (Batisteli et al. 2018) for predicting ecosystem functioning (Petchey and Gaston 2006), there are also central limitations depending on which components of diversity are incorporated into metrics (Cadotte and Tucker 2018).

Urban landscapes filter bird species based on non-randomized functional traits (Croci et al. 2008), benefiting few generalists to the detriment of several habitat- and resource specialists (Devictor et al. 2007; Callaghan et al. 2019). Therefore, urbanization intensifies species loss, biological invasions (Grimm et al. 2008), and functional homogenization, with a decline in the provisioning of ecosystem functions (McKinney 2006; Devictor et al. 2007; Concepción et al. 2016; Leveau et al. 2017), and so is considered one of the main global pressures on biodiversity (Marzluff 2017). Urban landscapes may also have high habitat heterogeneity depending on the size of native patches, the ages of urban and native remnants, land and vegetation cover, gray (urban) structures and population densities, along with socio-economic characteristics (MacGregor-Fors and Schondube 2011; Ramalho and Hobbs 2012; Sacco et al. 2015; Pena et al. 2017). Distinct management actions in urban areas may benefit habitat heterogeneity and resources for birds (Toledo et al. 2012; Beninde et al. 2015; MacGregor-Fors et al. 2016; Oliveira Hagen et al. 2017; Campos-Silva and Piratelli 2020), thus making them richer and/or functionally more diverse than surrounding ecosystems (Sol et al. 2014; Oliveira Hagen et al. 2017).

The size of green (vegetation) patches, habitat structure, vegetation cover (including street trees), and proximity of water bodies are strong positive predictors of high bird species richness (MacGregor-Fors and Schondube 2011; Sacco et al. 2015; Pena et al. 2017; Barbosa et al. 2020; Campos-Silva and Piratelli 2020). Conversely, buildings, impervious surfaces, human density, human activities, bird-window collisions, domestic animals, noise and light pollution are negatively related to bird species richness and positively associated with the abundance of few habitat and diet generalist species

(Leveau and Leveau 2004; Villegas and Garitano-Zavala 2010; Fontana et al. 2011; MacGregor-Fors and Schondube 2011, 2012; Reis et al. 2012; Loss et al. 2014; Pena et al. 2017; Brisque et al. 2017; Pedreros et al. 2018; Basilio et al. 2020; Barbosa et al. 2020). The spatial configuration and interactions among the above-cited factors may affect bird assemblages in urban ecosystems (Oliveira Hagen et al. 2017; Leveau et al. 2020), but there have been contrasting results with regard to how the distance of urban greenspaces from source areas (urban-fringe) drives species richness, abundance, and functional composition of birds (MacGregor-Fors and Ortega-Álvarez 2011; Puga-Caballero et al. 2014; Campos-Silva and Piratelli 2020).

Reducing rates of species losses and maintaining ecosystem services are global concerns in an increasingly urbanized world (Vitousek et al. 1997; Sekercioglu 2012). Although a myriad of ornithological studies has been performed in South American urban areas (MacGregor-Fors and Escobar-Ibáñez 2017; Marzluff 2017; and references therein), little attention has been given to how urbanization affects functional bird traits and their ecosystem functions in Neotropical cityscapes (Sacco et al. 2015; Tomás Ibarra and Martin 2015; Pena et al. 2017; Oliveira Hagen et al. 2017). Components of functional diversity are assumed to be sensitive to noise pollution (Pena et al. 2017), human population size (Gagne et al. 2016), built cover (Luck et al. 2013), limited habitat connectivity (Kang et al. 2015), and invasive species (Latta et al. 2013). This knowledge is a necessity for urban planning and vital to decision makers for the management of environmental characteristics within and around cities to maintain diverse functional traits and preserve ecosystem services (Oliveira Hagen et al. 2017).

Many endemic birds do not find suitable environmental conditions (i.e., habitats, niches, and resources) in urbanized sites (Fontana et al. 2011; Toledo et al. 2012; Sol et al. 2014; Callaghan et al. 2019; Campos-Silva and Piratelli 2020), and habitats near the urban fringe (< 10 km) may play a more important role in bird conservation than those further away (> 10 km) in Neotropical megacities (Puga-Caballero et al. 2014).

Here we investigated how a severely urbanized area, embedded in a global biodiversity hotspot — the Atlantic Forest (Myers et al. 2000) — affects its rich birdlife (Tonetti et al. 2017; Schunck et al. 2019). In comparison to larger native forests (source), we evaluate whether bird species richness (BSR) and functional diversity (FD, represented by diet, foraging stratum, and biomass), taxonomic and functional composition, are distinctly affected by (1) two main urban habitat types (urban parks and high dwelling-density sites) and their (2) proximity to the source, as well as the (3) vegetation (green) and urban infrastructure (gray) characteristics present in each habitat type.

We predict that:

(1) The main intra-urban habitats (e.g., urban parks and high dwelling-density sites) should reflect high losses of bird species and functional richness compared to large native forest remnants (source).

(2) The distance of intra-urban habitats (urban parks and high dwelling-density sites) from large native forests should be a key factor in the maintenance of high BSR and FD metrics, such as functional richness and functional divergence, as (1) many specialist forest birds avoid crossing over non-habitat matrices for long distances (Awade and Metzger 2008; Tremblay and St. Clair 2011; Martensen et al. 2012) and (2) urban habitats act as a potent biological filter (Aronson et al. 2014, 2016). Therefore, increased distance of intra-urban habitats from the forest source should negatively affect bird species persistence and functional trait composition, although incrementing the abundance of few urban-dwellers and thus increasing functional evenness among habitat types.

(3) Green characteristics, represented by tree, shrub, and herbaceous characteristics, should maintain more bird species and diverse functional traits than gray characteristics, those related to urban structures, because the latter lead to a high abundance of a few bird species, thus increasing functional homogenization. This prediction is in accordance with the habitat complexity hypothesis (MacArthur and Macarthur 1961), which assumes that increased vegetation structure improves the provisioning of microhabitats and resources for birds.

Methods

Study area

The São Paulo metropolitan region (hereafter, São Paulo megacity), in Southeast Brazil (23.54°W, 46.63°S; Figure 1) is the most populous urban area of the Southern Hemisphere with 21.5 million inhabitants distributed among 39 municipalities encompassing ~8 mil square kilometers (2.4 thousand inhabitants per square kilometer) (IBGE 2020). The municipalities of São Paulo (23°32’56”S, 46°38’20”W, 12.2 M inhabitants) and Guarulhos (23°27’46”S, 46°31’58”W, 1.3 M inhabitants) concentrate more than 60% of the 21.5 M civilians of the megacity, and together represent the main financial and commercial center of South America (IBGE 2020). The climate is humid subtropical with mild, dry winters, and rainy summers, with moderately high temperatures (Alvares et al. 2013). The vegetation is dense rain forest, a typology of the Atlantic Forest (Veloso et al. 1991).

The municipalities of São Paulo and Guarulhos were originally dominated by floodplains, fields, and forests. Since the 1940s, the region has faced intense urbanization and rapid population growth, leading to the removal of massive portions of native ecosystems (Kronka 2005). The urban area encompasses 2100 square kilometers (IBGE

2015), and the main remaining green areas are small and isolated urban parks and squares (PMMA 2017). São Paulo megacity is surrounded by several protected areas with rich bird communities. To the south there are Morro Grande Forest Reserve (10,870 ha, 198 ssp.; Develey and Martensen 2006), Várzea do Embu State Park (128 ha, 204 spp.; Schunck and Rodrigues 2016), Capivari-Monos Environmental Protected Area (25,000 ha, 250 spp.; Melo et al. 2016) and the Curucutu administrative region of Serra do Mar State Park (36,134 ha, 382 spp.; Schunck et al. 2020), and to the north there are Alberto Lofgren State Park (174 ha, 182 spp.; Antunes and Eston 2008) and Cantareira State Park (7,900 ha, 326 spp.; Tonetti et al. 2017), plus Fontes do Ipiranga State Park (526 ha, 157 spp.), a native forest fragment in an advanced stage of avifaunal declining due to isolation by urban growth (Guix 2004; Perrella et al. 2018). The Serra do Mar and Cantareira state parks preserve Atlantic Forest bird species (Tonetti et al. 2017; Schunck et al. 2019) and are recognized as important bird areas (IBAs - Bencke et al. 2006). To the northeast, Itaberaba State Park integrates the *continuum* of Cantareira. The majority of these areas are included in the Biosphere Reserve of the Green Belt of the city of São Paulo (UNESCO 1993), with the aim of preserving the largest remnants of Atlantic Forest in the region and their rich biodiversity, remarkable natural landscapes, and important ecosystem functions and services (Tonetti et al. 2017).

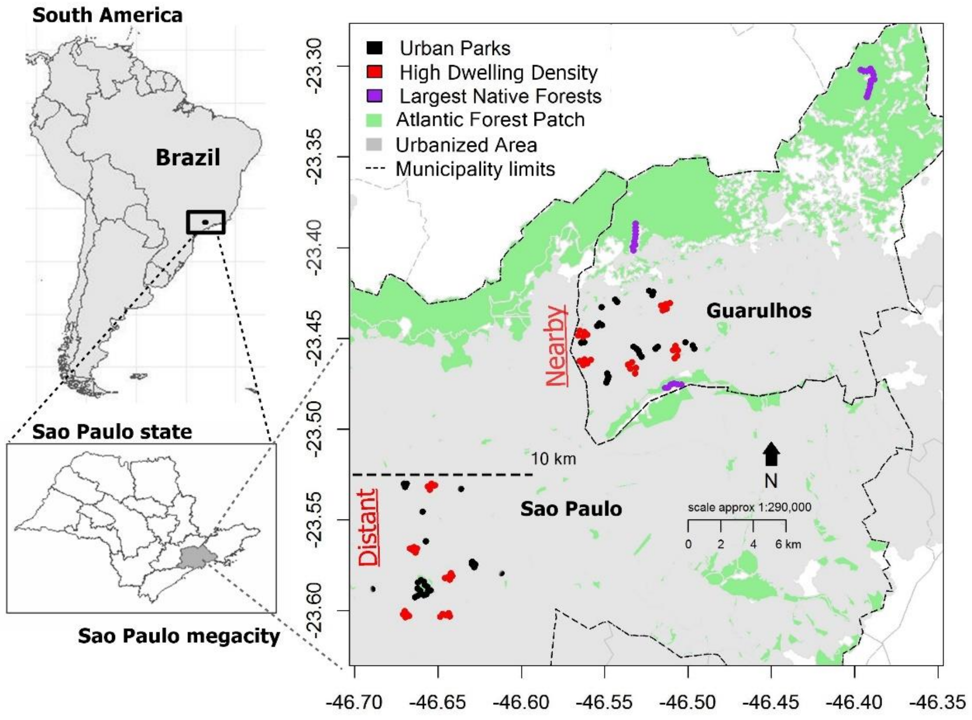

Fig. 1 São Paulo megacity and 126 sampled point-counts in the municipalities of São Paulo and Guarulhos. Urban park (black circles) and high dwelling density (red circles) sampled point-counts were classified according to a 10 km distance threshold (---) from Atlantic Forest source patches (large green patches: Cantareira and Itaberaba state parks and Tiete ecologic park), where their sampled sites (purple circles) are shown. Habitats: urban parks near (UPN: < 10 km) and distant (UPD: > 10 km) and high dwelling density near (HDN: <10 km) and distant (HDD: > 10 km) to the largest native forest (LNF or source).

Habitat types, distance from source forest, and green-gray traits

The densely habited regions of the central and north parts of the São Paulo metropolitan region (IBGE 2020) were selected for study to understand how the rapid conversion of forests to urban settlements affects bird metrics. These regions include a suitable number of urban parks (UPs) isolated by large zones of high dwelling-density sites (HDs) and the largest native forest (LNF) mainly at urban fringes/municipalities limits. The LNFs (here defined as the reference habitat) are the Cantareira State Park, a most preserved Atlantic Forest remnant (Tonetti et al. 2017) in our study region, followed by small UPs (intermediate degradation) with native and/or managed vegetation (PMMA 2017), and HDs (more degraded habitat) covered mainly by paved surfaces, buildings, and other urban structures, as in other urban areas.

Two categories of UPs and HDs were defined to test whether a 10 km threshold distance from the border of the megacity (MacGregor-Fors and Ortega-Álvarez 2011; Puga-Caballero et al. 2014) has significant effects on bird assemblages and respective FD in intra-urban habitats: (1) nearby (< 10 km, UPN and HDN) and (2) distant (> 10 km, UPD and HDD) from the LNF. The habitat categories were established at a minimum distance of ~ 0.8 km from each other to reduce the chances of the same bird being sampled twice (Peris and Montelongo 2014).

Finally, vegetation (green) and urban infrastructure (gray) characteristics were measured to test the relationship between environmental variables and bird species richness and functional diversity. Green and gray characteristics were sampled twice in 20 x 30 m plots settled from the center of each sampling unit (Table 1). All evaluated environmental characteristics were assumed to strongly drive Neotropical bird communities (Ortega-Álvarez and MacGregor-Fors 2009; Fontana et al. 2011; MacGregor-Fors and Schondube 2011).

Table 1 Environmental variables and methods of measurement in three habitats across São Paulo megacity, southeastern Brazil. Measurements methods were based on MacGregor-Fors (2008); Ortega-Álvarez and MacGregor-Fors (2009); Villegas and Garitano-Zavala (2010); MacGregor-Fors and Schondube (2011); and Puga-Caballero et al. (2014).

Category	Variable	Acronimum	Method
Green	Herbaceous cover	Herb.cov	visually estimative (%) of each plot covered by herbaceous plants, grass included
	Maximum height of herbaceous	Herb.h	maximum height (cm) of herbaceous plants in each plot
	Shrub morphorichness	Srb.ric	the number of different morphological shrubs estimated visually at each plot
	Shrub cover	Srb.cov	visually estimative (%) of each plot covered by herbaceous plants
	Maximum height of shrub plants	Srb.h	maximum height of shrub vegetation (cm) within the plot
	Tree abundance	Tree.abu	number of individuals of trees (diameter breast height, DBH > 10 cm) within a plot area
	Tree morphorichness	Tree.ric	the number of different morphological tree individuals visually estimated at each plot
	Tree cover	Tree.cov	the land the surface within of plot covered by canopy trees, which were visually estimated and expressed in percentage
	Maximum height of trees	Tree.h	maximum height of trees (m) within each plot
Gray	Maximum height of buildings	Buil.h.max	maximum height (m) of buildings at each plot
	Minimum height of buildings	Buil.h.min	minimum height (m) of buildings at each plot
	Number of cables	N.cable	visually estimative of number of electricity and telecommunication cables and wires at each plot
	Number of concrete posts	N.conc.post	visually estimative of number of concrete posts at each plot
	Number of wood posts	N.wood.post	visually estimative of number of wood posts at each plot
	Number of pole lamps	N.pole.lamp	visually estimative of number of pole lamps of streetlight
	Number of antennas	N.anten	visually estimative of number of antennas of television, radio, and others

Bird data

Bird assemblages were evaluated by 126 fixed point-counts (Bibby et al. 2000) using a radius of 50 m around (Bibby et al. 1993). These point-counts were settled across the LNF (the source) (28), UPN (< 10 km) (25), UPD (at least > 10 km) (23), HDN (25) and HDD (25) (Online Resource 1). Point-counts represent sampling units of habitat types and were separated by at least 200 m (Vielliard and Silva 2010). The distance among sampling units (see below: point-counts) ranged from 0.2 to 35 km.

Birds were surveyed from September 2017 to March 2018, during the morning of sunny days (30 min after sunrise until 9:30 a.m.). September to March represents the reproductive season for birds in Southeast Brazil (Sick 1997), with the arrival of several migrants (Somenzari et al. 2018). The number of individuals for all bird species heard and seen (8x42 mm binoculars) for a period of 10 minutes was recorded. Individuals in flight were included only when foraging (*e.g.*, Hirundinidae and Apodidae aerial insectivores). To avoid counting bias in forest sites, birds were first detected by their vocal characteristics, followed by visual confirmation of their foraging behavior. All point-counts were surveyed three times in a randomized order, roughly once every four or five weeks, but never repeated in the same month. Only the first author performed bird counts to assure standardization, while another researcher measured the environmental variables described above. Nomenclature follows that of the Brazilian Ornithological Records Committee (Piacentini et al. 2015).

Bird functional traits

Bird traits related to broad variation in the ability of species to exploit habitat and feeding resources were selected. All traits were extracted from a global bird-trait dataset (Wilman et al. 2014) (Table 2).

Table 2 Bird functional traits used in functional diversity analyses of São Paulo megacity, Southeast Brazil. Carnivores = endotherms + ectotherms + fish + other vertebrates.

Functional trait	Range	Definition
Diet	0-100%	percentage of each diet items (e.g., invertebrates, carnivores, carrion, fruits, nectar, seeds, and plants) utilized by bird species
Diet plasticity	1-7	number of diet items (e.g., invertebrates, carnivores, carrion, fruits, nectar, seeds, and plants) used by each species
Foraging strata	0-100%	percentage of each foraging strata levels (i.e. water below the surface, water around the surface, ground, underground, middle, canopy, and aerials) used by the species
Foraging plasticity	1-7	number of foraging strata (i.e. water below the surface, water around the surface, ground, underground, middle, canopy, and aerials) used by each species
Biomass (g)	3-1200	weight in grams (g) of each species

Diet composition and foraging strata are important for understanding how species occupy niches and acquire resources from their environment (Petchey and Gaston 2006), and provide ecosystem services such as seed dispersion, arthropod population control, scavenging, and nutrient cycling (Sekercioglu 2012). Plasticity of diet and foraging strategies reflect the degree to which a taxon can be considered either a generalist or specialist with regard to resource exploitation. Moreover, body mass is positively related to metabolic rate and the number of food resources required for birds (Luck et al. 2013). Bird conservation status was based on regional (São Paulo 2018) and global (IUCN 2019) red lists, but was not considered for calculating FD metrics.

Alpha and beta diversity indices

The following steps were performed to estimate FD indices (Laliberté and Legendre 2010). First, the functional distance between each bird species pair was calculated according to their trait values using Gower’s distance (Gower 1966). A functional distance matrix was then submitted to principal coordinate analysis (PCoA) to obtain a subset of PCoA axes for use used as new “traits”. For this, we used the ‘pcoa’ function of the ape package (Paradis and Schliep 2018). Finally, FD indices were calculated using the new “trait” data and relative abundance data. Both bird species richness (BSR) and three functional diversity (FD) indices were calculated for each point-count (Table 3), using the ‘dbFD’ function of the FD package (Laliberté and Legendre 2010; Laliberté et al. 2014). An approach of accumulated BSR was built as a function of the number of records for each one of the five habitat categories. The FD indices consider distinct components of diversity (Table 3). Functional richness (FRic) is monotonically related to BSR. Functional evenness (FEve) is influenced only by abundance, and functional divergence (FDiv) considers both abundance and species richness (Mouillot et al. 2005; Villéger et al. 2008); more details in Table 3.

Beta diversity was also considered in the analyses because it represents variation in species (or functional trait) composition across bird assemblages. In our case, birds in different habitat types and distance from the LNF. The following were then calculated: (1) total species and trait beta diversity, which was partitioned into (2) turnover, a measure of replacement of species and traits between sites, and 3) nestedness, representing species and trait losses from site to site (Baselga 2010; Villéger et al. 2013). For this, we used the functions “*beta.pair*” and “*functional.beta.pair*” available in the “*betapart*” package (Baselga and Orme 2012). A multivariate dispersion analysis was used to obtain the distances of species and functional traits of each point-count to the centroid of all habitat types separately for total beta diversity, turnover, and nestedness, using the “*betadisper*” function of the “*vegan*” package (Anderson 2006; Oksanen et al. 2018).

Table 3 Taxonomic and functional diversity indices sampled in São Paulo megacity, Southeast Brazil.

Category	**Indices**	**Acronym**	**Explanation**
Taxonomic¹	Bird species richness	BSR	the accumulated number of different bird species recorded
FD²	Functional richness	FRic	the volume of multidimensional space occupied by the community within functional space
	Functional evenness	FEve	evenness of abundance distribution in the functional trait space
	Functional divergence	FDiv	divergence in the distribution of species characteristics within the volume occupied by each functional trait

Sources: 1, Gotelli & Colwell (2011); 2, FD, functional diversity (Mouillot et al., 2005; Villéger et al., 2008).

Data Analysis

Prior to analyses, the data were (1) checked for normality using the Shapiro-Wilk test; (2) evaluated for heteroscedasticity and the presence of extreme outliers by plotting residuals; and (3) assessed for multicollinearity using the "*vif*" function of the *usdm* package (Naimi et al. 2014). Four environmental variables (Srb.ric, Tree.ric, N.cables, and N.conc.post) were excluded because of high values for the variance inflation factor (VIFs > 5) (Menard 2001), while another nine were retained for analysis. To avoid temporal dependence caused by repeated measures at each point-count, and to proceed with the following analysis, bird species abundance was represented by the maximum value of the three point-counts at each site (Sandström et al. 2006).

A principal component analysis (PCA) was performed to investigate visually how habitat types present distinct green and gray characteristics in their compositions, using the package "*factoextra*" (Kassambara et al. 2017). For this, the values of environmental variables present at each point-count was used, which allowed habitat classification based on distinct compositions of green and gray characteristics.

The methods proposed by Chao et al. (2014) were used to estimate and compare species richness among habitat categories. Individual-based rarefaction and extrapolation curves were created for each one of the five habitat categories. The individual-based rarefaction curves were plotted against the number of individuals randomly taken from observed samples until all individuals had been accumulated. Next, sample completeness and extrapolation curves were constructed for species richness of each habitat category to link individual and coverage-based sampling curves, up to double the reference sample size. Extrapolation curves were plotted to double the reference site (Colwell et al. 2012) — in the present case, the largest native forest (LNF) habitats as the most preserved native forests of our study area (Tonetti et al. 2017). Bootstrap with 999 replicates was used to estimate 84% confidence intervals (CI) for all rarefaction curves, for which non-overlapping intervals were assumed to indicate statistical difference. The 84% CI was considered because of its similar effect to that of traditional *p-value* < 0.05 tests, thus avoiding spurious interpretations (Type II errors) associated with overlap of 95% CIs (see MacGregor-Fors and Payton 2013). Estimates were computed using the “iNEXT” function in the homonymous package (Hsieh et al. 2016).

To test whether habitat categories and the 10 km threshold distance from the LNF (Puga-Caballero et al. 2014) affected bird assemblages and functional traits distinctly, alpha and beta taxonomic and FD indices per point-count for each habitat were used. Before analysis, a standardized effect size (ses; see Gotelli and McCabe 2002) of FD metrics was performed (e.g., functional richness, sesFRic; functional evenness, sesFEve; and functional divergence, sesFDiv (Mason et al. 2013). Next, Moran's I test was calculated to explain the absence of spatial autocorrelation for BSR (Moran’s I: 0.29, *p*-

value: <0.001) and sesFRic (Moran's I: 0.24, *p-value*: <0.001). However, both sesFEve (Moran's I: 0.009, *p-value*: >0.05) and sesFDiv (Moran's I: 0.04, *p-value*: >0.05) demonstrated spatial autocorrelation of the data. In accordance to Zuur et al. (2009), generalized linear models (GLMs) were used for BSR, sesFRic and beta diversity indices, and generalized linear mixed models (GLMMs) for sesFEve and sesFDiv, with Poisson or Gaussian distributions. For the models, bird indices were used as response variables and habitat types and distance from LNF (categoric) as predictor variables. Habitat types were used as a random term in GLMMs to avoid possible dependency troubles, using the "glmer" function of the "lme4" package (Bates et al. 2015). Null models were also built for each index and comparisons were made using Akaike's information criterion for small sample sizes (AICc) by calculating the difference in AICc between each model and the model with the lowest AICc (ΔAICc), using the "model.sel" function of the "MuMIn" package (Barton 2019). Models with ΔAICc < 2.0 were considered to have substantial support (Burnham and Anderson 2002) and selected as the most explicative models. Based on the models, the confidence intervas (CIs) estimates for each habitat type were compared using the "*emmeans"* function in the homonymous package (Lenth 2019).

Finally, generalized additive models (GAMs) were used to investigate the relationship between green and gray characteristics (predictor variables) and taxonomic (BSR) and FD indices (sesFRic, sesFEve, and sesFDiv) as response variables. For this, the "gam" function in the "mgcv" package (Wood 2011) was used on the restricted maximum likelihood estimation (REML) and Gaussian or Poisson distribution. The green characteristics were then used as proxy of more structured/preserved habitats, and gray characteristics as indicators of urbanization level/habitat simplification (MacGregor-Fors and Schondube 2011; Sacco et al. 2015; Faggi and Caula 2017). An initial full model was created including green (Herb.cov, Srb.cov, Tree.ric, Tree.abu) and gray (Buil.h.max, N.buil, N.cables, and N.pole.lamp) characteristics. Subsequent models were generated via backward stepwise deletion of non-significant terms ($p > 0.05$) using the “anova” function. The best model for each bird index was selected based on the abovementioned AIC approach. Plots of the regression models were built separately for each environmental variable with the aid of the “*visreg*” function in the homonymous package (Breheny and Burchett 2017), which allowed the contribution of each one of the variables contained in the selected model to be demonstrated. All analyses were run in R version 3.5.2 (R Core Team 2018).

Results

Environmental traits

Green and gray characteristics varied significantly among habitats (Online Resource 1; Figure 2). The first two axes of the PCA (Axes 1 and 2) explained 60% of the variation. Axis 1 alone explained 45% of the variation and was related to tree abundance (*Tree.abu*), shrub cover, shrub morphorichness (*Srb.ric*), shrub maximum height (*Srb.h.max*) and dead trees (*Tree.dead*) and negatively associated with building size (*Buil.siz*), number of pole lamps (*N.pole.lamp*), and number of cables (*N.cables*). Axis 2 explained 15% of the variation and this was positively related to maximum height of buildings (*Buil.h.max*), and negatively associated with number of woody posts (*N.wood.post*) and herbaceous cover (*Herb.cov*). Green and gray characteristics were distinctly distributed across urban and non-urban habitats. Areas of HDN and HDD were arranged in an extreme of lands highly dominated by urban infrastructure (large buildings, cables, pole lamps, *etc.*) with scarce green characteristics. The largest native forest (LNF) was in the other extreme due to containing highly forested sites (abundance of trees, dead trees, high shrub morphorichness, shrub cover, and tall shrubs), and poorly represented by gray characteristics. Urban parks were located in an intermediate position between HD and LNF, due to their intermediate values for green and gray characteristics and were most represented by herbaceous cover. Green and gray characteristics did not differ between UPN and UPD, but HDD and HDN ($p < 0.05$) differed from them due to building structures.

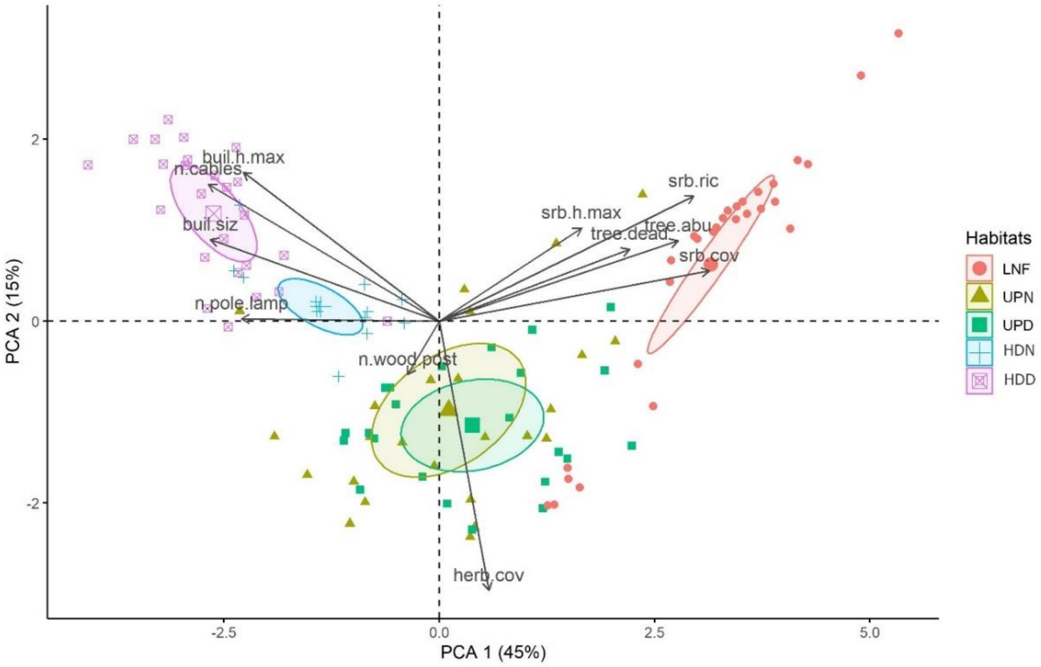

Fig. 2 Habitat segregations based on the distinct composition of green and gray characteristics in São Paulo megacity, according to principal component analysis. Green characteristics: herb.cov, herbaceous cover; srb.cov, shrub cover; srb.h.max, maximum height of shrub, shr.ric, shrub morphorichness; tree.abu, tree abundance; tree.cov, tree cover; tree.ric, tree morphorichness; tree.dead, dead tree. Gray characteristics: n.cables, number of cables; n.pole.lamp, number of pole lamps; n.wood.post, number of wood posts; buil.h.max, maximum height of buildings; buil.siz, building size. Habitats: urban parks near (UPN) and distant (UPD) and high dwelling density near (HDN) and distant (HDD) to the largest native forest (LNF or source).

Bird species richness and abundance

A total of 8442 records of 231 bird species were sampled (Online Resource 2), representing 49.8% and 61.6 % of all birds recorded for the municipalities of São Paulo (464; SVMA 2018) and Guarulhos (375; SEMA 2018), respectively. Large native forest (LNF) sheltered most (205, mean per point-count: 42.4 ± 5.09; 89%) of the bird species richness followed by UPN with 111 (48%) species (26.8 ± 5.0), UPD with 80 (35%) (22.8 ± 5.29), HDN with 35 (15%) (11.2 ± 1.66), and HDD 28 (12%) (12.8 ± 2.0). Yet, LNF was 1.8 to 7.4 times richer than UP and HD sites, respectively.

The highest dominance of specialists was for LNF, while generalists were proportionally more abundant in the intra-urban habitats. Fifty-three percent of the insectivores recorded in LNF were drastically reduced in UP and, mainly, HD sites; both plant-seed eaters and omnivores increased in these urban habitats (Figure 3a). Nearly 30% of the Atlantic Forest endemic bird species recorded in LNF were negatively impacted by habitat loss in intra-urban habitats, while the abundances of exotic and allochthonous birds increased (Figure 3b). Most of the birds that forage on up to two feed items (73%) and in up to two foraging strata types (70%) recorded in LNF severely declined in intra-urban habitats. Species foraging mainly on three diet items and in three foraging strata types had higher abundances in more urbanized habitats (Figure 3c-d).

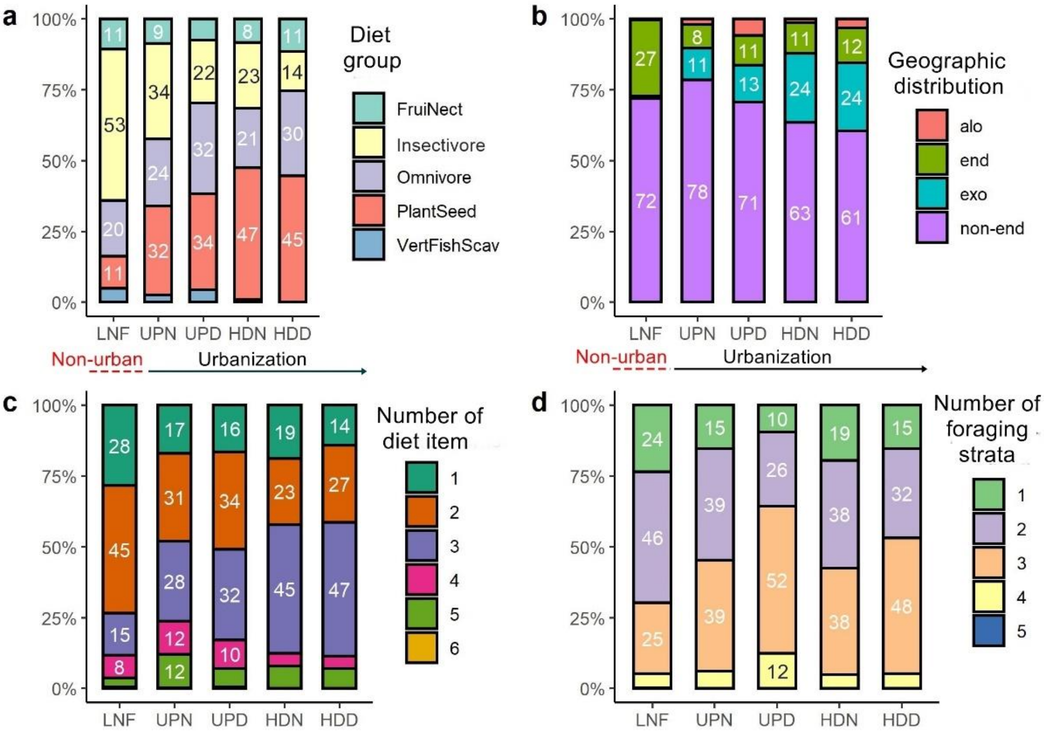

Fig. 3 Abundance (%) of bird guilds per habitat type: (a) Diet group, five Wilman's diet categories; (b) Geographic distribution, alo, allochthonous; end, Atlantic Forest endemic; exo, exotic; and non-end, species distributed in two or more Brazilian biomes; (c) Number of diet items, the quantity of diet items used by bird species in the community; and (d) Number of foraging strata, the quantity of foraging strata used by bird species in the community. Habitats: urban parks (UP) near (UPN) and distant (UPD) and high dwelling density (HD) near (HDN) and distant (HDD) to the largest native forest (LNF or source).

The sample-based rarefaction and extrapolation curves revealed higher bird species richness (BSR) in LNF than in other habitat types, with significant differences (non-overlapping curves) between them. Among the others, UPN had higher BSR than did UPD. Such a difference was also found between HDN and HDD, but only in interpolated data, while extrapolation curves had overlapping 84% confidence intervals (Figure 4) after 2,700 records. Sampling completeness was high for all habitats (0.992 – 0.999), thus few species additions are expected (varying 0.1 - 8 spp.) to reach 100% coverage.

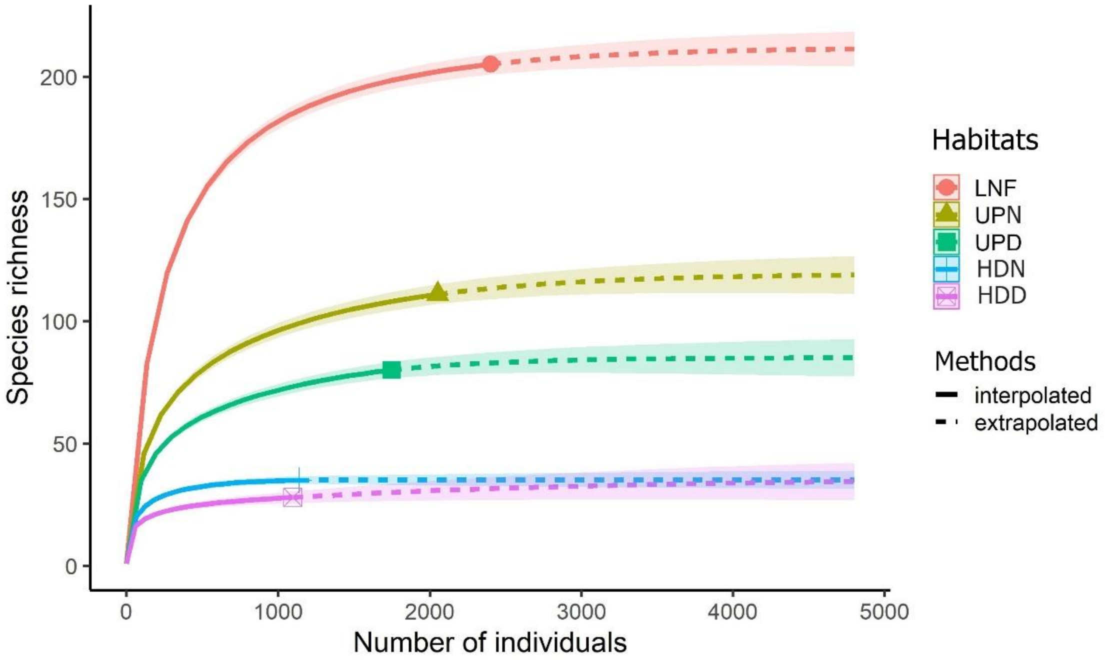

Fig. 4 A comparative rarefaction curves for birds (species ~ abundance) related to distance from source (LNF, largest native forest). Urban parks near (UPN) and distant (UPD) and high dwelling density near (HDN) and distant (HDD) in a Neotropical megacity. Rarefaction curves built based on observed (–) and extrapolation (---) values (up to double of the most preserved habitat, LNF) using the bootstrap method (999 replications), with 84% confidence intervals.

The Solitary Tinamou (*Tinamus solitarius*), Southern Bristle-Tyrant (*Phylloscartes eximius*), Buffy-fronted Seedeater (*Sporophila frontalis*) and Copper Seedeater (*S. bouvreuil*) are listed as threatened with extinction on at least one of the red lists considered (Online Resource 2). Four species are classified as near-threatened, three of which were mainly recorded in LNF while one, the Turquoise-fronted Parrot (*Amazona aestiva*), was found mostly in UP sites. All 55 Atlantic Forest endemic birds live in LNF, among which the Plain Parakeet (*Brotogeris tirica*) is the only one to have higher abundance at UP and HD sites. Exotics (Rock Dove [*Columba livia*], House Sparrow [*Passer domesticus*], and Common Waxbill [*Estrilda astrild*]) and allochthonous birds (e.g., Red-shouldered Macaw [*Diopsittaca nobilis*], Turquoise-fronted Parrot, Yellow-chevroned Parakeet

[*Brotogeris chiriri*], Red-cowled Cardinal [*Paroaria dominicana*], and Red-crested Cardinal [*P. coronata*]) were more represented in UP and HDD sites than in LNF. The Sick's Swift (*Chaetura meridionalis*) and Lesser Yellowlegs (*Turdus flavipes*) are migratory, while the other 23 species are partially migratory. Partially migratory species were well represented by the flycatchers (e.g. Streaked Flycatcher [*Myiodynastes maculatus*], Tropical Kingbird [*Tyrannus melancholichus*], Variegated Flycatcher [*Empidonomus varius*], Piratic Flycatcher [*Legatus leucophaius*], Olivaceus Elaenia [*Elaenia mesoleuca*] and Small-billed Elaenia [*E. parvirostris*]), the Chivi Vireo (*Vireo chivi*), and thrushes (Creamy-bellied Thrush [*Turdus amaurochalinus*] and Eastern Slaty Thrush [*T. subalaris*]).

All comparative models were better than the null models in explaining the variation in alpha diversity for BSR, sesFRic, and sesFDiv. Only sesFEve did not differ from the null model (Table 4). Our results showed that LNF sustained significantly higher BSR (AICc = 708.9, Table 4, Figure 5a) and sesFRic (AICc = 513.2, Table 4, Figure 5b) than other habitat types, and that UP had higher BSR than HD. However, although distance of UPs from LNF did not cause significant differences in BSR (UPN = UPD, Figure 5a), sesFRic was higher in UPN than in UPD (Figure 5b). Distance from the LNF did not cause differences in BSR and sesFRic be (HDN = HDD, Figure 5a-b). Both functional evenness (sesFEve, AICc = 413.6, Table 4, Figure 5c) and functional divergence (sesFDiv, AICc = 415.7, Table 4, Figure 5d) were similar among all habitats; *i.e.* the distance of HD and UP from LNF did not have a significant effect on these two FD metrics.

Table 4 GLMs and GLMMs for alpha taxonomic and functional diversity indices of birds regarding habitat types in São Paulo megacity, Southeast Brazil.

Indice	**Intercept**	**SE**	**AICc**	**ΔAICc**	**wAIC**
bird species richness	3.746	0.02	708.9	0	1.0
functional richness	10.830	0.34	513.2	0	1.0
functional evenness *(null)*	-0.0008	0.61	413.1	0	0.885
functional divergence	-1.842	1.02	415.7	0	0.563

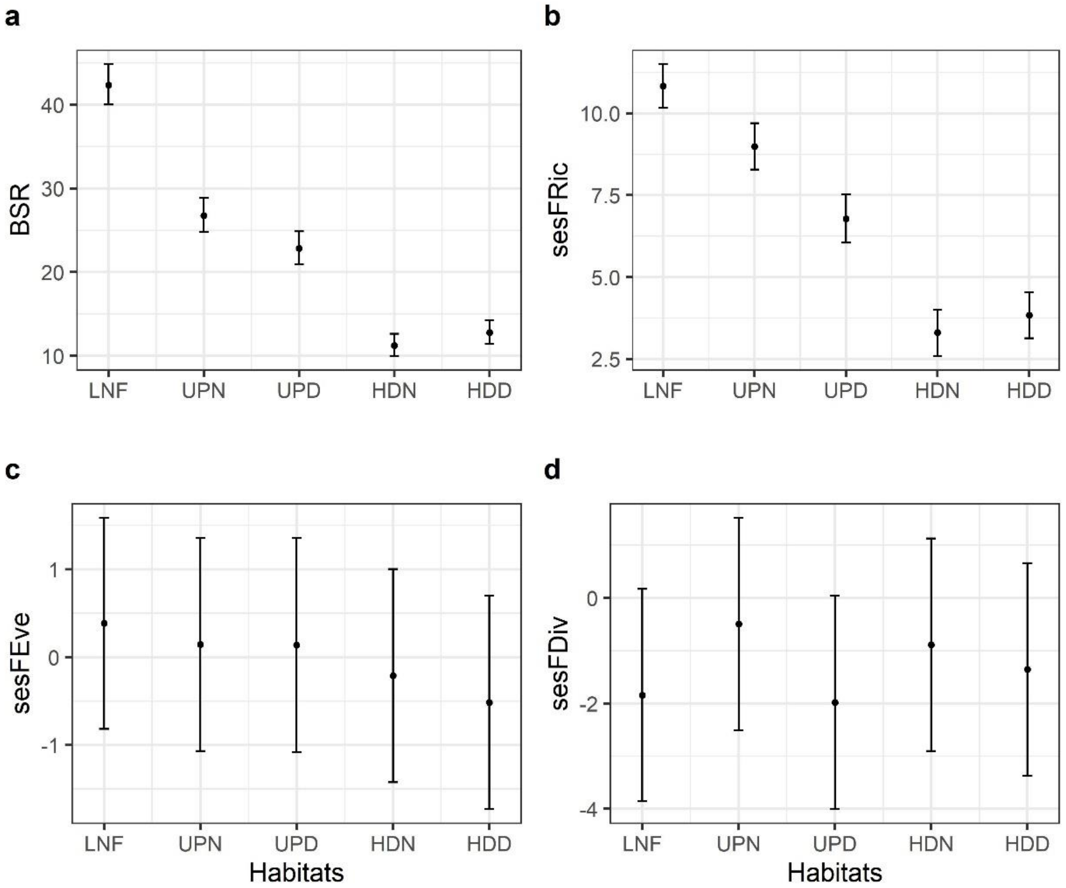

Fig. 5 Comparison of predicted values and confidence intervals of alpha diversity indexes between habitat types and distinct distance from LNF in accordance with the models in Table 4. a) Bird species richness (BSR); b) functional richness (sesFRic); c) functional evenness (sesFEve); and d) functional divergence (sesFDiv). Abbreviations: largest native forest (LNF), urban parks near (UPN) and distant (UPD) and high dwelling density near (HDN) and distant (HDD).

All species and trait models were better than null models in explaining total beta diversity and its two components (Table 5). These results highlight strong species turnover within habitats types (Table 5, Figure 6b), although UPD showed high species nestedness (Table 5, Figure 6c). Beta diversity showed high turnover in HDN (Table 5, Figure 6e), while HDD had less nestedness than did LNF and UPD (Table 5, Figure 6f).

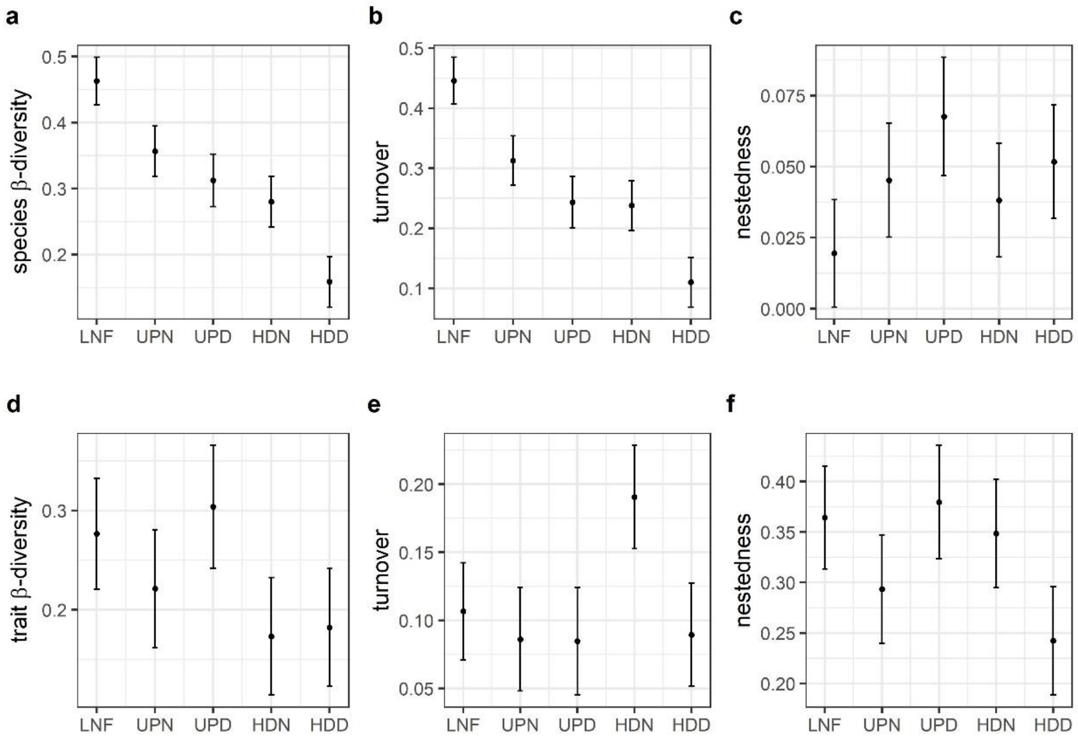

Fig. 6 Comparison of predicted values and confidence intervals of beta diversity indices between habitat types and distance from LNF following models in Table 5. a) species beta-diversity (BSR) and their b) turnover and c) nestedness; d) trait beta-diversity and their e) turnover and f) nestedness. Abbreviations: largest native forest (LNF, source), urban parks near (UPN) and distant (UPD) and high dwelling density near (HDN) and distant (HDD).

Table 5 GLMs for beta diversity indices regarding bird species and traits in three habitat types in São Paulo megacity, Southeast Brazil.

Species	**Intercept**	**SE**	**AICc**	**ΔAICc**	**wAIC**
total diversity	0.463	0.01	-222.0	0	1.0
Turnover	0.446	0.34	-203.0	0	1.0
Nestedness	0.195	0.009	-385.0	0	0.856
Functional traits					
total diversity	0.276	0.02	-111.0	0	0.938
Turnover	0.106	0.01	-223.6	0	0.998
Nestedness	0.364	0.02	-135.4	0	0.982

Some green and gray characteristics were critical in explaining their effects on BSR and FD metrics. The model that best explained variation in BSR was represented by the combination of herbaceous cover, shrub cover, and the number of buildings (wAIC = 0.779). These same characteristics, plus the number of antennas, composed the best model for explaining variation in sesFRic (wAIC = 0.404). Thus, BSR and sesFRic increased with increasing herbaceous cover and shrub cover, and decreased with increasing number of buildings (Table 6, Figure 7 a-f). Only sesFRic was positively related to the number of antennas (Table 6, Figure 7 l). The interaction between the number of buildings and the maximum height of buildings was the best model for explaining variation in sesFDiv (wAIC = 0.565), while the combination of tree cover, maximum height of buildings, and the number of pole lamps was the model that best explained variation in sesFEve (wAIC = 0.444). Yet sesFDiv was negatively related to the maximum height of buildings, and showed a bimodal relationship with it (Table 6, Figure 7 h-i). Finally, sesFEve was positively related to sites with more than 50% of tree cover and number of pole lamps, with a bimodal association with maximum height of buildings (Table 6, Figure 7 l-m).

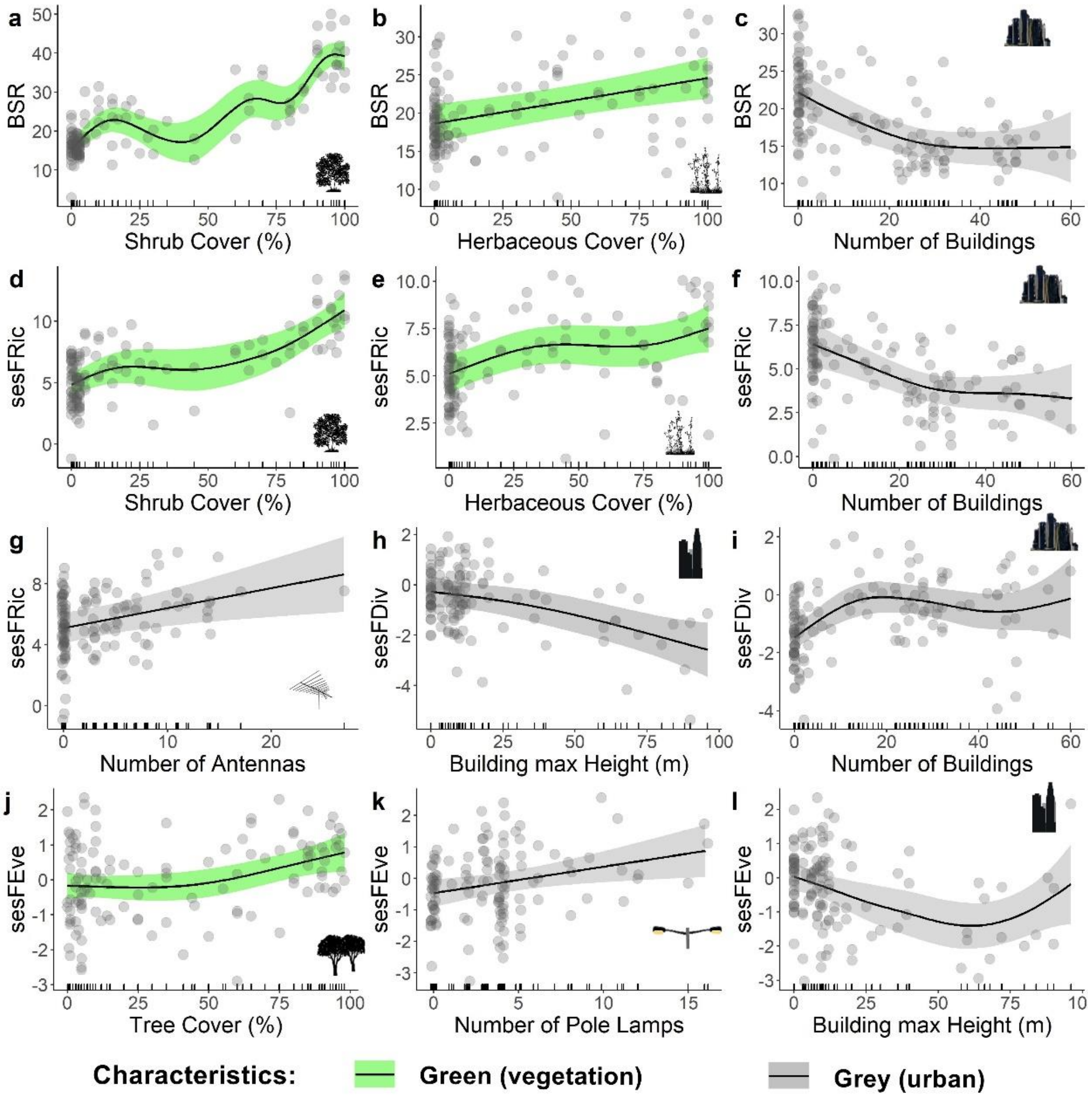

Fig. 7 Relationship between green/gray characteristics and bird species richness (BSR) and functional diversity indices. Abbreviations: functional richness (sesFRic), functional divergence (sesFDiv), and functional evenness (sesFEve) of avian communities in São Paulo megacity.

Table 6 GAMs showing green and gray characteristics as best predictors of taxonomic and functional diversity ndices of birds living in São Paulo megacity, Southeast Brazil.

Response variable	Model	df	logLik	AICc	ΔAIC	wAIC
Bird species richness ~	**herb.cov + srb.cov + n.buil**	14	-365.6	**765.1**	**0.0**	**0.779**
	herb.cov + alt.h.max + srb.cov + buil.siz + n.buil	13	-369.3	769.5	4.4	0.086
	herb.cov + alt.h.max + srb.cov + tree.cov + buil.siz + n.buil	16	-365.6	770.8	5.7	0.045

	herb.cov + alt.h.max + srb.cov + srb.h.max + tree.cov + buil.siz + n.buil	18	-363.5	771.3	6.2	0.035
	herb.cov + alt.h.max + srb.cov + srb.h.max + tree.cov + buil.siz + buil.h.max + n.buil + n.anten	22	-357.8	771.9	6.8	0.026
	herb.cov + alt.h.max + srb.cov + srb.h.max + tree.cov + tree.h.max + buil.siz + buil.h.max + n.buil + n.anten	24	-355.8	772.6	7.5	0.018
	herb.cov + alt.h.max + srb.cov + srb.h.max + tree.cov + buil.siz + n.buil + n.anten	20	-362.5	774.6	9.6	0.007
	herb.cov + alt.h.max + srb.cov + srb.h.max + tree.cov + tree.h.max + buil.siz + buil.h.max + n.buil + n.pole.lamp + n.anten	25	-354.9	775.5	10.4	0.004
	null	1	-494.6	993.4	228.2	0.0
Functional richness ~	**herb.cov + srb.cov + n.buil + n.anten**	14	-256.8	**545.3**	**0.0**	**0.404**
	herb.cov + alt.h.max + srb.cov + n.buil + tree.cov + n.pole.lamp + n.anten	14	-257.7	547.3	2.0	0.149
	herb.cov + srb.cov + n.buil + n.anten	11	-260.8	547.5	2.2	0.136
	herb.cov + alt.h.max + srb.cov + buil.siz + n.buil + n.anten	14	-257.1	547.5	2.2	0.135
	herb.cov + alt.h.max + srb.cov + n.buil + n.anten + tree.cov	17	-253.4	547.7	2.4	0.124
	herb.cov + alt.h.max + srb.cov + tree.cov + tree.h.max + n.buil + n.pole.lamp + n.anten	16	-255.8	550.2	4.9	0.035
	herb.cov + alt.h.max + srb.cov + tree.cov + tree.h.max + buil.siz + n.buil + n.pole.lamp + n.anten	17	-255.8	552.2	6.9	0.013
	herb.cov + alt.h.max + srb.cov + srb.h.max + tree.cov + tree.h.max + buil.siz + n.buil + n.pole.lamp + n.anten	18	-256.1	554.8	9.5	0.003
	herb.cov + alt.h.max + srb.cov + srb.h.max + tree.cov + tree.h.max + buil.siz + buil.h.max + n.buil + n.pole.lamp + n.anten	18	-256.2	557.5	12.2	0.001
	null	2	-334.5	673.1	127.7	0.0
Functional evenness ~	**tree.cov + buil.h.max + n.pole.lamp**	8	-186	**391.3**	**0.0**	**0.444**
(sesFEve)	tree.cov + buil.h.max + n.pole.lamp + n.anten	11	-183.6	391.8	0.5	0.340
	tree.cov + tree.h.max + buil.h.max + n.pole.lamp + n.anten	12	-183	393.5	2.3	0.143
	alt.h.max + tree.cov + tree.h.max + buil.h.max + n.pole.lamp + n.anten	14	-181.9	395.6	4.3	0.051
	alt.h.max + srb.cov + tree.cov + tree.h.max + buil.h.max + n.pole.lamp + n.anten	14	-182	397.8	6.6	0.017
	alt.h.max + srb.cov + srb.h.max + tree.cov + tree.h.max + buil.h.max + n.pole.lamp + n.anten	16	-181.9	400.9	9.7	0.004
	herb.cov + alt.h.max + srb.cov + srb.h.max + tree.cov + tree.h.max + buil.h.max + n.pole.lamp + n.anten	17	-181.7	403.7	12.4	0.001
	herb.cov + alt.h.max + srb.cov + srb.h.max + tree.cov + tree.h.max + buil.h.max + n.buil + n.pole.lamp + n.anten	18	-181.4	406.2	14.9	0.0
	herb.cov + alt.h.max + srb.cov + srb.h.max + tree.cov + tree.h.max + buil.siz + buil.h.max + n.buil + n.pole.lamp + n.anten	19	-181.1	408.2	17.0	0.0
	null	2	-203.2	410.6	19.3	0.0
Functional divergence ~	**buil.h.max + n.buil**	11	-188.9	**403.2**	**0.0**	**0.565**
	tree.h.max + buil.h.max + n.buil + n.anten	12	-189	405.2	2.0	0.211
	buil.h.max + n.buil	8	-194.1	406.1	2.8	0.136
	srb.cov + tree.h.max + buil.h.max + n.buil + n.anten	13	-189	407.5	4.4	0.064
	srb.cov + srb.h.max + tree.h.max + buil.h.max + n.buil + n.anten	15	-187.7	410.1	7.0	0.017
	srb.cov + srb.h.max + tree.cov + tree.h.max + buil.h.max + n.buil + n.anten	17	-185.6	412.8	9.6	0.005
	srb.cov + srb.h.max + tree.cov + tree.h.max + buil.h.max + n.buil + n.pole.lamp + n.anten	18	-185.1	414.8	11.6	0.002
	srb.cov + srb.h.max + tree.cov + tree.h.max + buil.siz + buil.h.max + n.buil + n.pole.lamp + n.anten	19	-185.2	417.0	13.8	0.001
	alt.h.max + srb.cov + srb.h.max + tree.cov + tree.h.max + buil.siz + buil.h.max + n.buil + n.pole.lamp + n.anten	20	-185.3	419.7	16.5	0.0
	herb.cov + alt.h.max + srb.cov + srb.h.max + tree.cov + tree.h.max + buil.siz + buil.h.max + n.buil + n.pole.lamp + n.anten	21	-185.2	422.4	19.2	0.0
	null	2	-210.9	425.9	22.7	0.0

Discussion

Our data confirmed our hypothesis of a massive decline in bird species richness (BSR), functional richness (sesFRic), and functional composition in UP (intermediate values) and, mainly, in HD (lower values) sites, when compared to LNF (high values). Our data also support that green characteristics maintain high bird FD indices, and that gray characteristics are related to functional homogenization, with an exception of the positive relationship between sesFRic and number of antennas. Finally, our assumption of decreasing BSR and FD metrics with increased distance from LNF (source area) was also confirmed, which was more severe in HD, and mitigated by UP. The only exceptions were FD indices including species abundance as functional evenness and functional divergence.

BSR and sesFRic decreased significantly from LNF to urbanized habitats; nearly 50% and 90% of all (231) bird species were not recorded in UP and HD (intra-urban areas), respectively. Many forest birds do not find suitable habitats in small urban green areas (Chace and Walsh 2006; Fontana et al. 2011; Amaya-Espinel et al. 2019; Leveau et al. 2019), suggesting local extinction events. Losses of BSR in HD sites agree with global average rates of extinction (92%) of pre-urban bird species found in cityscapes across of the world (Aronson et al. 2016). However, BSR loss should still be higher compared to bird diversity recorded through long-term studies performed in protected areas of the peri-urban region of São Paulo (Tonetti et al. 2017; Schunck et al. 2019). These findings support our first prediction that protected LNFs are important for the preservation of more diverse ecological niches and resources in an urbanized landscape. This is central to the maintenance of high species diversity (Maseko et al. 2019), including the Atlantic Forest endemic and specialist bird species pool (Tonetti et al. 2017; Schunck et al. 2019), and diverse ecosystem functions (Anjos et al. 2019). Although Ups provided significant intermediate vegetation structure, compared to LNF and HDs, they failed to shelter several endemic and habitat and feeding resource specialist birds. Such species may not find suitable habitats and specific ecological niches in small Ups (Peris and Montelongo 2014; Puga-Caballero et al. 2014; Fischer et al. 2015; Amaya-Espinel et al. 2019). Indeed, habitat loss drives local extinction of specialist species in urban landscapes (Guix 2004; Devictor et al. 2007; Fischer et al. 2015). Yet, Ups may play an important role in the conservation of native bird species and functional richness compared to HD sites within the urban landscapes. Our findings (high sesFRic) highlight that Ups are potentially critical to maintaining the ecosystem functions and resilience of avian communities within Neotropical cities (Ortega-Álvarez and MacGregor-Fors 2009; Carbó-Ramírez and Zuria 2011; Estevo et al. 2017; Faggi and Caula 2017; Amaya-Espinel et al. 2019), and across the world (Fernández-Juricic and Jokimäki 2001; Chace and Walsh 2006; Ikin et al. 2013; Strohbach et al. 2013; Morelli et al. 2016; Tryjanowski et al. 2017).

Proximity to LNF did not influence BSR for UP and HD sites, and sesFRic between HD sites. However, UPNs (i.e., near the forest source areas) had higher sesFRic than did UPDs. This confirms that even Ups having similar BSR, the proximity of UP to the LNF is important in maintaining more diverse bird functional traits. It given us supporting our second prediction, which we predicted that proximity to LNF is key factor in the maintenance of high sesFRic. We found that some species with diet and foraging strata specializations, such as small insectivorous (e.g. Pallid Spinetail [*Cranioleuca pallida*], Golden-crowned Warbler [*Basileuterus culicivorus*], Sharp-tailed Streamcreeper [*Lochmias nematura*], Euler's Flycatcher [*Lathrotriccus euleri*], Variable Antshrike [*Thamnophilus caerulescens*], and Ochre-collared Piculet [*Picumnus temminckii*]) and frugivorous birds (Ruby-crowned Tanager [*Tachyphonus coronatus*], may successfully cross the urban matrix to reach small forest remnants in UPN. Forest birds are predicted to be unable to fly long distances across a non-habitat matrix (Awade and Metzger 2008; Martensen et al. 2012; Cornelius et al. 2017). We provide evidence that proximity to the source forest increased bird functional space in UP, thus representing better resource use by birds than in Ups that are distant from LNF. However, long-term studies are needed to evaluate whether these birds use UPNs just as stepping-stones and/or for local movements (Fernández-Juricic 2000), or as a seasonal source of feeding resources and habitats (Guix 2007; Leveau 2018).

Our study agrees that urbanization has filtered Atlantic Forest birds by functional traits, as in other regions (Croci et al. 2008; Schütz and Schulze 2015; Silva et al. 2016; Aronson et al. 2016) and that BSR in intra-urban habitats is the result of the selection of species based on functional traits that are pre-adapted to tolerate extreme environmental conditions (Croci et al. 2008). The present study found a massive presence of generalists in intra-urban habitats, which also represented more than a third of the LNF bird community. This should have contributed to high species turnover between LNF and intra-urban habitats (except for HDD). However, as generalist species share similar functional traits and life histories selected by urban filters (Devictor et al. 2007; Croci et al. 2008), there was lower divergence of functional trait composition, as shown by our turnover and nestedness beta-diversity trait analyses. Exceptions included high turnover in HDN and lower nestedness in HDD, which can be linked to distinct trait compositions between exotic (Rock Dove, House Sparrow, and Common Waxbill) and allochthonous birds (Yellow-chevroned Parakeet, and Red-shouldered Macaw) across these habitats (see also Oliveira Hagen et al. (2017).

Overall, the high similarity of functional divergence (sesFDiv) and functional evenness (sesFEve) across all habitats and distances from the LNF was caused by low functional trait specialization in our bird assemblages; and only the sesFEve confirmed our predictions. This suggests high niche complementarity and regularity of trait abundances among the intra-urban and non-urban habitats, which was also confirmed by functional trait composition. To our knowledge, this is the first evidence of high similarity of sesFDiv and sesFEve across native and urban habitats in a megacity. It is likely that wide open niches in intra-urban habitats, which specialist birds are unable to fill, were intensively occupied by a high abundance of a few urban-dwellers (Fischer et al. 2015). These generalist birds can effectively use available resources and may provide diverse ecosystem functions. Urban-dwellers in the present study were represented by native (e.g., Plain Parakeet, Blue-and-white Swallow [*Pygochelidon cyanoleuca*], Great Kiskadee [*Pitangus sulphuratus*], and Sayaca Tanager [*Tangara sayaca*]) and allochthonous-exotic birds (e.g. Rock Dove, House Sparrow, and Red-shouldered Macaw), as omnivores, aerial insectivores, and plant-seedeaters with high plasticity in diet and foraging strata (Filippi-Codaccioni et al. 2009; Pena et al. 2017). However, some studies have demonstrated a decline in the quality of ecosystem services provided by generalists replacing specialists (Galetti et al. 2013; Casas et al. 2016; Luna et al. 2018).

As predicted, shrub and herbaceous cover were central green characteristics for maintaining high BSR and bird sesFRic, and tree cover increased sesFEve. Our study agrees with the habitat complexity hypothesis (MacArthur and Macarthur 1961), according to which diverse green characteristics improve functional niche space for birds and likely the ecosystem functions they perform (Batisteli et al. 2018; Melo et al. 2020). Herbs, shrubs, and trees are important green characteristics for increasing vegetation structure of forests, from the ground to the canopy (Crouzeilles et al. 2016). Thus, more structured habitats have positive effects on bird assemblages by providing more food resources and foraging strata for diverse bird species (Palmer et al. 2008; Domínguez-López and Ortega-Álvarez 2014; Leveau et al. 2015; Lessi et al. 2016; Lee and Carroll

2018), increasing BSR and sesFRic in our study. Surprisingly, only sites with more than 50% tree cover (mainly related to UP and LNF) increased bird functional evenness (sesFEve). In an opposite pattern from what is known for other Neotropical cityscapes (MacGregor-Fors and Ortega-Álvarez 2011; Pedreros et al. 2018), this study indicates that a relevant proportion of birds in São Paulo megacity are highly sensitive to tree cover. However, the stability of sesFEve values at sites with less (< 45%) tree cover indicates the efficiency of invasive and urban-dwellers to exploit the less wooded UP and HD sites, as previously reported in other Neotropical cities (Pena et al. 2017; Amaya-Espinel et al. 2019). Thus, the present results support the need to increase tree plantings within Neotropical cities to mitigate urban impacts on birds (Pena et al. 2017). The results also provide evidence that tree cover can improve the regularity of bird abundance and the use of habitat and resources by birds in urban ecosystems.

Contrary to the green characteristics, high number of buildings had a negative effect on BSR and sesFRic, and maximum height of buildings reduced bird sesFDiv. High density of built-up areas eradicate suitable habitats for birds, causing loss of habitat and diet specialists and increased abundance of a few generalists (Fernández-Juricic and Jokimäki 2001; Chace and Walsh 2006; MacGregor-Fors and Ortega-Álvarez 2011; Toledo et al. 2012; Sacco et al. 2015; Marzluff 2017; Sol et al. 2020). In the present study, the removal criticism of key vegetation characteristics (i.e., herbaceous, shrub, and tree cover) in UP and, mainly, HD sites resulted in huge losses and impoverishment of intra-urban habitats. This is directly linked to the loss of foraging and strata specialist birds with unique functional traits, which leads to declines in bird sesFRic across intra-urban habitats. Our findings agree with previous studies that report that tall buildings increase urban-dwelling bird abundance and reduce the abundance of insectivores (Sacchi et al. 2002; Pellissier et al. 2012; Sacco et al. 2015; Amaya-Espinel et al. 2019), which explains the negative relationship between sesFDiv and maximum height of buildings found here. This indicates that the abundance of specialist functional traits is more affected by tall buildings than by the number of buildings. Moreover, sesFEve was high in sites without or with low buildings (i.e., LNF and some UP, respectively), and in those sites having very tall buildings (> 75m height), such as in HDD sites. This means that the regularity of the abundance of bird traits (1) increased in LNF due to the occupation of high functional niches by highly diverse bird species, and (2) increased in HD because of the high abundance of urban dwellers. This last effect likely contributed to decreased sesFDiv due to low functional trait diversification. A similar results was found for Rao's quadratic entropy of birds in a medium size Brazilian city (Pena et al. 2017). Thus, the process of verticalization in São Paulo megacity has a key role in functional homogenization. Furthermore, there are green characteristics (resources) not accessed by birds at HD sites with buildings of 50 – 75 m in height, indicated by the decrease in sesFEve. As a result, the density of high buildings should be a barrier for specific birds (i.e. Western Cattle Egret [*Bulbucus ibis*], Blue-winged Parrotlet [*Forpus xanthopterygius*], Smooth-billed Ani [*Crotophaga ani*], Southern Beardless Tyrannulet [*Camptostoma obsoletum*], Common Waxbill, and Cattle Tyrant [*Machethornis rixosa*]).

The number of antennae and pole lamps, both gray characteristics, increased bird sesFRic and sesFEve, respectively. Birds in HD sites use antennas as resting and foraging perches (Emlen 1974). Thus, alternatively, antennas would favor an increase in functional niche space for urban birds in more urbanized sites. On the other hand, pole lamps may supply perches for foraging by abundant omnivores-insectivores (e.g. Great Kiskadee, Sayaca Tanager, House Sparrow, Tropical Kingbird) and nesting sites for the House Sparrow and House Wren (*Troglodytes musculus*). In the first case, the artificial light of streetlamps serves as a strong insect attractant (Davies et al. 2012), thus benefiting abundant omnivores-insectivores with increased food availability, as previously reported for diurnal urban birds (Morelli et al. 2018; Leveau 2018). Pole lamps may also provide nesting sites for some cavity-nesters such as the House Sparrow (MacGregor-Fors and Schondube 2011) and House Wren (*pers. obs.*), thereby increasing sesFEve across the more urbanized sites. Nonetheless, further studies are needed to investigate whether increment of bird FD based on the number of antennae and pole lamps reflects the low availability of tall trees and tree cavities in HD sites.

Conclusions

This study demonstrates how urbanization in São Paulo megacity has drastically impacted avian communities and functional diversity in one of the greatest global biodiversity hotspots— the Atlantic Forest. We showed the importance of protected areas (LNF) surrounding large urban settlements for reducing species losses and, presumably, increasing the provisioning of goods and ecosystem services (i.e., insect control, seed dispersal, pollination, nutrient cycling, and others) in UP but not in HD sites. We stressed that herbaceous and shrub plants were responsible for increasing the co-occurrence of birds with unique traits, likely due to the increased niche breadth (Mason et al. 2005; Laliberté and Legendre 2010), and that tree cover augmented the abundance of trait regularity in functional niche space, thereby improving the efficient use of resources (Villéger et al. 2008; Mason et al. 2013). As an alternative, the number of antennas can aid to enhance sesFRic of birds living in more urbanized habitats, where sometimes it is impossible to increase tree cover. The number of buildings, tall buildings, and pole lamps (and their likely light pollution effect) and presence of invasive birds, are strong inductors of bird dominance and functional homogenization.

Urbanization in Latin American cities is expected to increase, and urban designers, engineers, and architects need to consider this study in their efforts to create solutions for more sustainable and biodiverse cities. Our findings provide an important hierarchical guide for decision-makers to apply during environmental management directed at increasing bird species and functional trait richness in large Neotropical settlements. We recommend that Neotropical cities should increase vegetation structure in intra-urban habitats to provide additional microhabitats to increase urban bird diversity. For this, we encourage the addition of a diversity of native trees (including tall trees) in intra-urban habitats, as well as shrub and herbaceous cover, to promote richer bird diversity and ecosystem functions within cities. Furthermore, urban planners should rethink the building density and the process of verticalization in Neotropical cities, mainly within a 10 km distance threshold from global biodiversity hotspots.

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Capítulo 2

Large-sized areas and increased in shrub cover improve bird functional diversity in urban greenspaces

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Abstract

We test which biotic and abiotic variables (e.g., size area, vegetation characteristics, water distance, human and domestic animal's disturbances, vehicles, and glass windows) influence functional diversity indices of insectivores, frugivores-nectarivores, migrants, residents, and total bird assemblage of urban greenspaces of the São Paulo megacity, Southeast Brazil. We recorded a rich avian assemblage (235 species) in 25 studied sites. Our GLM analyses showed that large size areas of urban greenspaces and shrub cover are the main characteristics to drive high bird functional diversity in São Paulo megacity. On the other hand, small-sized sites presented restrict environmental conditions to preserve bird functional diversity; this may be linked to possible negative impacts that habitat homogeneity, absence of shrub layer, high impact of traffic, and massive presence of glass windows, pedestrians, and domestic animals deliver for bird communities. We stress that dog and cat abandons may cause declines in bird's ecological functions (e.g., insect control, seed dispersal, and pollination) central for sustaining biodiversity in our study sites. We recommend that urban planners and managers should prioritize large-sized areas with high shrub cover. We also highlighted a need to mitigates the negative impact on birds caused by glass windows, traffic vehicles, human presences, and domestic animals. These management actions are feasible and important tools to improve bird diversity and likely a better provisioning of ecosystem services provided by specific bird guilds.

Keywords: Bird Functional Traits. Functional Richness. Functional Evenness. Functional Guilds. Glass-windows. Human and Animal Disturbances.

Introduction

The rapid global urban growth causes dramatic environmental changes and biodiversity losses (Grimm et al., 2008; McKinney, 2006), posing risks for many global biodiversity hotspots (Cincotta et al., 2000). Urbanization replaces part of preexistent vegetation cover by buildings and impervious surfaces (Eldredge & Horenstein, 2014), creating biological filters that act as barriers for several bird species, related to their functional traits (e.g., body size, biomass, habitat and diet specialization, understory, ground, cavity, and shrub nesters), thus limiting the occurrence of specialists and benefiting generalists (Croci et al., 2008; Sol et al., 2017). Urbanization may catalyze biological invasions (Grimm et al. 2008) and functional homogenization (Concepción et al., 2016; Devictor et al., 2007; Leveau et al., 2017; McKinney, 2006) and so is considered as a threaten for former rich-ecosystems (Leveau et al., 2017).

Many specialist birds (e.g. frugivores-nectarivores and insectivores) perform specific environmental functions in tropical ecosystems, and often are not replaced by generalists (Casas et al., 2016; Menezes et al., 2016). Environmental changes impact bird functional traits, driving failures in ecosystem functions (Mason et al., 2005; Palacio et al., 2018) and ecosystem services they perform (Sekercioğlu et al., 2004). Birds have been well-studied in urban settlements (Beninde et al., 2015; Chace & Walsh, 2006; Leveau et al., 2019; Marzluff, 2017; Murgui & Hedblom, 2017; Sol et al., 2014, 2017; Campos-Silva and Piratelli 2020), where they provide central environmental services as seed dispersal, pollination, arthropod control, nutrient cycling, and biomass production (Nyffeler et al., 2018; Sekercioğlu, 2006; Sekercioğlu et al., 2004). Avian species perform an important role in socio-economic and cultural aspects of human life (Belaire et al., 2015; Sekercioğlu et al., 2004; Tratalos et al., 2007). They are surrogates for bioindication of environment quality (Parker III et al., 1996) and faunal integrity (Amâncio et al., 2008;

MacGregor-Fors et al., 2010; Morelli et al., 2017), including several well-accepted charismatic species, central to bring biological conservation in urban ecosystems (Piratelli et al., 2017).

Urban greenspaces (UGs) have been traditionally the main studied habitats in urban settlements (Fernández-Juricic, 2000b; Fontana et al., 2011; MacGregor-Fors et al., 2016; Zhang et al., 2012). They are often composed by preserved sites, parks, squares, lays, and other public and private green lands (Faggi & Caula, 2017; Campos-Silva & Piratelli, 2020). These sites are "green islands" immersed in a built-up cover and their anthropogenic structures ("gray sea"), providing human recreational and increasing the provision of ecosystem services (Tratalos et al., 2007). Ugs also play an important role providing habitats for bird biodiversity (Fernández-Juricic & Jokimäki, 2001; Puga-Caballero et al., 2014; Tryjanowski et al., 2017; Zhou et al., 2012). Their heterogeneous design (e.g. different sizes, forms, vegetation, connectivity, and spatial configuration) may result in diverse values for bird conservation in urban landscapes (Donnelly & Marzluff, 2006; Fernández-Juricic, 2001).

Latin American cityscapes are growing rapidly (United Nations, 2018) and there is little comprehension of how their green (i.e. vegetation) and gray (i.e. infrastructures) characteristics and human disturbances may impact distinct bird functional groups. Avian species richness (SR) and functional diversity (FD) decrease with urban noise (Barbosa et al., 2020; Pena et al., 2017), impervious surfaces and built cover (Fontana et al., 2011; Luck et al., 2013; Sacco et al., 2015), reduction of habitat connectivity (Kang et al. 2015) and increased invasive species (Latta et al. 2013). On the other hand, they are positively associated to size and density of Ugs (Oliveira Hagen et al., 2017; Schütz & Schulze, 2015), vegetation cover (Sacco et al., 2015), and proximity of water bodies (Barbosa et al., 2020). Studies have shown that insectivores and frugivores are positively correlated to large size areas and vegetation structure, yet omnivores and granivores benefits of small sized sites and habitat simplification (Campos-Silva & Piratelli, 2020; Fontana et al., 2011; MacGregor-Fors & Schondube, 2012; Maseko et al., 2020; Reis et al., 2012). Insectivores and frugivores are also more sensitive to human and pet interferences than other guilds (MacGregor-Fors & Schondube, 2011), and residents and migrants may perform distinct responses to the influence of urban noise and proximity of bodies of water (Barbosa et al., 2020). These studies highlighted that different functional groups need specific conservation strategies (Shanahan et al., 2011). This knowledge is central for mitigating the anthropogenic impacts and to improve bird functional traits and ecosystem services in cityscapes (Oliveira Hagen et al., 2017; Pena et al., 2017). However, few studies have investigated the relation between environmental variables and FD indices in Neotropical cities (Leveau, 2019; Pena et al., 2017; Sacco et al., 2015), revealing a gap of knowledge of their effects on FD across distinct bird guilds.

In this study, we tested whether the local biotic and abiotic variables influence FD indices of both the total bird assemblage and the specific guilds (i.e., insectivores, frugivores-nectarivores, migrants, and residents). We predict that (1) increased in the area of Ugs improve functional richness (Fric) of all bird guilds due to their robust and positive relationship with increase in species richness (Beninde et al., 2015; Fernández-Juricic & Jokimäki, 2001); (2) based on habitat complexity effects (MacArthur & Macarthur, 1961), vegetation characteristics and proximity of water should increase Fric of target guilds (i.e., frugivores-nectarivores, insectivores, and migrants) as a response of their relation with increased microhabitats and food resources (Barbosa et al., 2020; Ikin et al., 2013; Leveau, 2018). Due to the multiples relations that some biotic-abiotic characteristics act specifically on species richness and/or abundance of frugivores, insectivores, and migrants or generically on the residents and the entire assemblage

(Barbosa et al., 2020; Campos-Silva & Piratelli, 2020; Loss et al., 2013; MacGregor-Fors, 2008; Ortega-Álvarez & MacGregor-Fors, 2009; Puga-Caballero et al., 2014); we also predict that (3) human disturbances (i.e., number of pedestrians, cats, dogs, vehicles, and glass windows) and tree cover (Chang & Lee, 2016)) may affect bird functional traits, represented by Fric changes. As these latter variables may also drive contrasting responses in the abundance of habitat generalist *vs.* specialist birds, we predict that (4) they should reduce functional evenness (Feve) and functional divergence (Fdiv) of insectivores, frugivores-nectarivores, and migrants, and increase Feve and Fdiv of residents, reflecting on the entire bird assemblage, due to the presence of several abundant birds with similar functional traits (Melo et al. Chapter 1).

Methods

Study area

The São Paulo metropolitan region (from now São Paulo megacity) is the most human populous urban area of the Southern Hemisphere, in Southeast Brazil (23.54°W, 46.63°S; Figure 1). The megacity encompassing 39 municipalities where approximately 21.5 M inhabitants live in 7 946.84 km² at the density of 2.4 mil inhabitants/square kilometers (IBGE, 2020). The municipalities of São Paulo (23°32'56"S, 46°38'20"W, 12.2 M inhabitants) and Guarulhos (23°27'46"S, 46°31'58"W, 1.3 M inhabitants) concentrate more than 60% of ~22 M inhabitants of the megacity, and together represent the main South American financial center of South America (IBGE, 2020).

The climate is humid subtropical with mild, dry winters and rainy summers, with moderately high temperatures (Alvares et al., 2013). The vegetation is dense rain forest, a typology of the Atlantic Forest (Veloso et al., 1991). The municipalities of São Paulo and Guarulhos were originally dominated by floodplains, fields, and native forests. Since the 1940s, the region had an intense urbanization process and rapid human population growth, leading to the removal of portions of native ecosystems (Instituto Florestal, 2020). The urbanization currently occupies 2100 km² square kilometers (IBGE, 2015) and the remaining green spaces varies from small to large sized areas (1 to >10.000 ha), mainly represented by several small isolated urban parks and squares (see Barbosa et al. 2020). Large and protected areas (i.e., Serra do Mar and Serra da Cantareira state parks) are in the north and south faces, and together preserve a greater part of the regional Atlantic Forest bird diversity (Schunck et al., 2019; Tonetti et al., 2017), recognized as important bird areas – IBAs (Bencke et al., 2006).

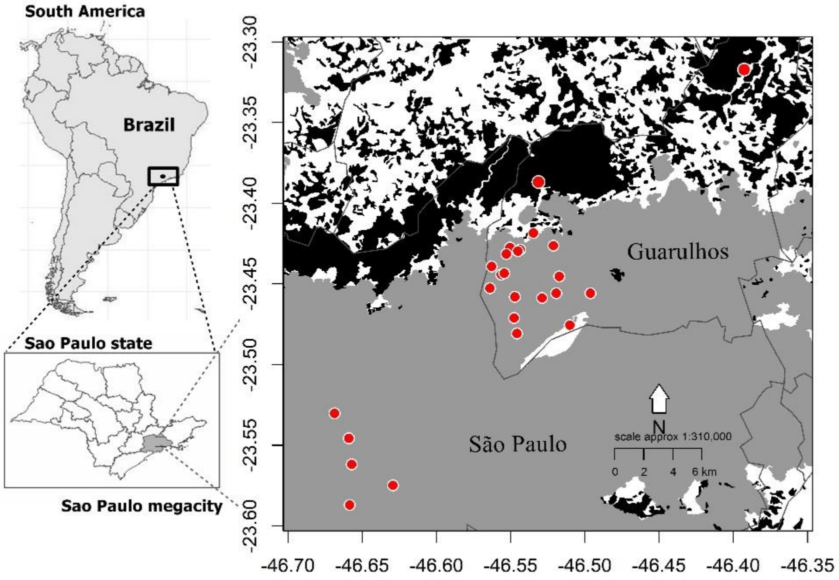

Figure 1 Distribution of 25 urban greenspaces across São Paulo megacity. Legend: *black patches*, Native forest fragments; *gray patches*, urbanized areas; and *red circles*, urban greenspaces considered in our study.

Experimental design

The UGs in municipalities of São Paulo and Guarulhos range from large periurban forest reserves (>1000 ha) to small-sized (<2 ha) and highly isolated patches surrounded by a dense urbanized matrix (Barbosa et al., 2020; Lourenço-de-Moraes et al., 2018), merged in global biodiversity hotspots (Cincotta et al., 2000; Myers et al., 2000). In the two extremes, small and highly isolated sites are degraded UGs, and the large native forest remnants are references for the most preserved UGs. Patterns of isolation and size of UGs changes from the limit of the city to the downtown, providing an interesting landscape parameter to be tested (e.g., distance from the source areas, size, distance from water and large forest sources) (Barbosa et al., 2020; Puga-Caballero et al., 2014). In this context, we plotted the available UGs in a radius of 20 km to select our study sites. We selected the UGs at least 0.8 km far from each other, because avian species probably can easily cross from one site to another at distances lesser 0.7 km (Peris & Montelongo, 2014).

Bird fauna was sampled by the 101 fixed point-count distributed across 25 UGs. The point-count approach is recognized as one of main methods to evaluate bird communities (Bibby et al. 2000; more details in *Bird data* subsection). The influence of local characteristics such as vegetation parameters (including shrub/herbs and tree characteristics), and human disturbances (e.g., pedestrians, car traffic, domestic cats (*Felis catus*) and dogs (*Canis lupus familiaris*), and potential impact of glass windows) were also investigated.

Environmental data

We measured nine vegetation characteristics, size area, and five variables associated to human disturbances within 20 x 30 m plots (Table 1), settled from the center of each one of the 101 sampled point-counts across 25 UGs.

Table 1 Size, vegetation, and bird threat variables sampled in UGs of São Paulo megacity, Southeast Brazil. The variables and measurement methods were based on previous studies (Amaya-Espinel et al., 2019; Basilio et al., 2020; MacGregor-Fors, 2008; MacGregor-Fors & Schondube, 2011; Ortega-Álvarez & MacGregor-Fors, 2009; Puga-Caballero et al., 2014; Villegas & Garitano-Zavala, 2010).

Category	**Variable**	**Acronimum**	**Method**
Landscape	Size area	Size	Patch size area (ha) measured using Google Earth tool.
Green	Herbaceous cover	Herb.cov	visually estimative (%) of each plot covered by herbaceous plants, including tall grasses.
	Maximum height of herbaceous	Herb.h	maximum height (cm) of herbaceous plants in each plot
	Shrub morphorichness	Srb.ric	number of different morphological shrubs estimated visually at each plot
	Shrub cover	Srb.cov	visually estimative (%) of each plot covered by herbaceous plants
	Maximum height of shrub plants	Srb.h	maximum height of shrub vegetation (cm) within the plot
	Tree abundance	Tree.abu	number of individuals of trees (diameter breast height, DBH > 10 cm) within plot area
	Tree morphorichness	Tree.ric	number of different morphological tree individuals visually estimated at each plot
	Tree cover	Tree.cov	land surface within of plot covered by canopy trees, which were visually estimated and expressed in percentage
	Maximum height of trees	Tree.h	maximum height of trees (m) within plot
Human disturbances	Number of glass windows	Glass	number of glass windows (approximately > 0.5 m wide and height) in each plot; for this, we counted the translucid and mirror glasses due to the liability to cause bird strikes
	Number of pedestrians	Pedest	number of pedestrians for three minutes passing along the plot area
	Number of dogs	Dogs	number of dogs passing for three minutes along each plot area
	Number of cats	Cats	number of dogs passing for three minutes along each plot area
	Number of vehicles	Vehic	number of cars, bus, trucks passing for three minutes along each plot

Variables with high amplitude of variation in the studied period (i.e., number of vehicles, human and domestic animals) were counted three times in each point-count for achieving mean values. Variables with few variations in the studied period (i.e., glass windows and vegetation characteristics) were estimated once on each point-count. To standardize the distinct sample size, for all variables we calculated the mean values per each site.

Bird data

We surveyed birds in 25 UGs settled across the São Paulo megacity (Suppl. Mat. 1). We used 101 (50 m limited radius) point-counts (Bibby et al., 1993), with a minimum distance of 200 m between each point (Ralph et al., 1993). The number of points was proportional to the size of UGs, with less points in small (n = 1, Portuguesinha; 1.1 ha) and more in larger sized areas (n = 13, Itaberaba; 5300 ha, Suppl. Mat. 1). We recorded the number of individuals heard and/or seen (8x42 mm binoculars) along 10 min in each point-count. Specimens in flight were included only when foraging (*e.g.* aerial insectivores: Hirundinidae and Apodidae). To avoid bird count bias, we adopted the following proceedings: 1) only the first author performed bird counts; 2) all point-counts were surveyed three times in a randomized order; 3) point-counts were not revisited in the same month; 4) bird surveys were conducted from September to March (2017-2018), in the reproductive season (Sick, 1997) and influx of seasonal migrants in southeastern Brazil (Sick, 1997; Somenzari et al., 2018); and 5) we performed surveys at the first three hours of the day on sunlight enough to perform bird counts and avoided rainy, windy, and foggy days.

Bird functional traits

We selected four morphometric bird traits (body mass, wing and bill length, and bill width) (Rodrigues et al., 2019) and five diet categories (invertebrate eaters, frugivores-nectarivores, omnivores, vert-fish-scavegers, plant-seedeaters) (Wilman et al., 2014), both associated to species' skills to exploit habitats and feeding resources, and the ability to delivery ecosystem services (Suppl. Mat. 2, Sekercioğlu, 2006). Body mass is related to the amount of individual energy intake and metabolic rates, longevity, foraging behavior, and home range size. Wing length is linked to the movement capacity, and the ability to tolerate habitat fragmentation, resource use, seed dispersal, and nutrient cycling. Both bill length and bill width influence pollination effectiveness, handling of fruit and seeds, and use of habitats and microhabitats (Luck et al., 2012). Only adult bird traits were used in our analyses to avoid bias.

Diet is related to the spectrum of items consumed by birds. In our study, we selected 'Invertebrate eaters' (hereafter called insectivores) and "Frugivores-Nectarivores" (Wilman et al., 2014) because they reflect central bird ecosystem functions linked to habitat maintenance (Sekercioğlu, 2006) and human welfare (Luck et al., 2012; Tratalos et al., 2007). Nectarivores and frugivores are related to nectar and fruit consume, respectively associated to pollination and seed dispersal services (Sekercioğlu, 2006); and insectivores perform biological control of arthropods populations (Nyffeler et al., 2018).

We also considered the migratory behavior (Somenzari et al., 2018) which is linked to the ability to perform long-distance movements, and potential to colonize isolated habitats in urban landscapes (Barbosa et al., 2020). Migrant species (MGT) have populations that seasonally move away and return from their breeding sites. Partially migratory (MPR) are species which some of their populations has migratory behavior. Populations of resident (RE) species occupy the same area all year round, including nomadic birds (Somenzari et al., 2018). We based species' distribution range on specific literature, Atlantic Forest endemic (End), species restrict to the biome (Vale et al., 2018); non-endemic (non-End), species occurs in more than one biome (Sick, 1997); exotic introduced (Exo), non-native birds introduced by humans (Sick, 1997); and allochthonous (Alo), native birds introduced by anthropic actions in a region without historic occurrence (Schunck, 2008). The risk of extinction was based on regional (São Paulo, 2018) and global (IUCN, 2019) red lists. We considered the following categories: threatened (TH), taxa classified as vulnerable (VU), endangered (EN), and critically endangered (CR);

near-threatened (NT), species with high probability of becoming endangered in the near future; and least-concern (LC), species unlikely to become extinct in the near future. We followed the nomenclature of the Brazilian Ornithological Records Committee (Piacentini et al., 2015).

Functional diversity indices

Before calculating FD metrics, we carefully performed some transformations in our data set. To avoid over sampling caused by repeated measures in each point, we used the maximum number of records of each species observed in one of the three samplings (Sandström et al., 2006). To standardize the effect of distinct size sample sites, we used the global index of point abundance (IPA) for each site, which represents the total number of records divided by number of points sampled in each site (Bibby et al., 1993). The IPA value was used as measured of relative abundance for each site, being proportional to size area and effort sampling. We used the total accumulated of number of species observed in each site (Gotelli & Colwell, 2011) to achieve species richness (SR).

To estimate FD indices, we performed the following steps (Laliberté & Legendre, 2010): (1) as our data include continuous, categorical, and missing values, we calculated the functional distance between all the bird species pairs according to their trait values using the Gower's distance (Gower, 1966; Podani, 1999); (2) we ran a principal coordinate analysis (PCoA) on this functional distance matrix to get a subset of the PCoA axes and used as a new 'trait', using the *pcoa* function of the *ape* package (Paradis & Schliep, 2018); and (3) we calculated FD indices using the new "trait" data and the relative abundance data. We computed five functional diversity (FD) metrics for each site using *dbFD* function of the FD package (Laliberté et al., 2014; Laliberté & Legendre, 2010). We excluded functional dispersion (FDis) and Rao' Q quadratic entropy (Rao's

Q) of our analyses because they were highly (1.00) correlated (Figure 2). Species richness (SR) and functional richness (FRic), which are monotonically related (Mason et al., 2005; Petchey & Gaston, 2006), also were highly (0.94) correlated (Figure 2). We then used SR only for discuss our FRic findings because it provides a better comprehension of how unique functional traits are associated to changes of species in the community (Oliveira et al., 2020). In our analyses, we used the three FD indices (as following):

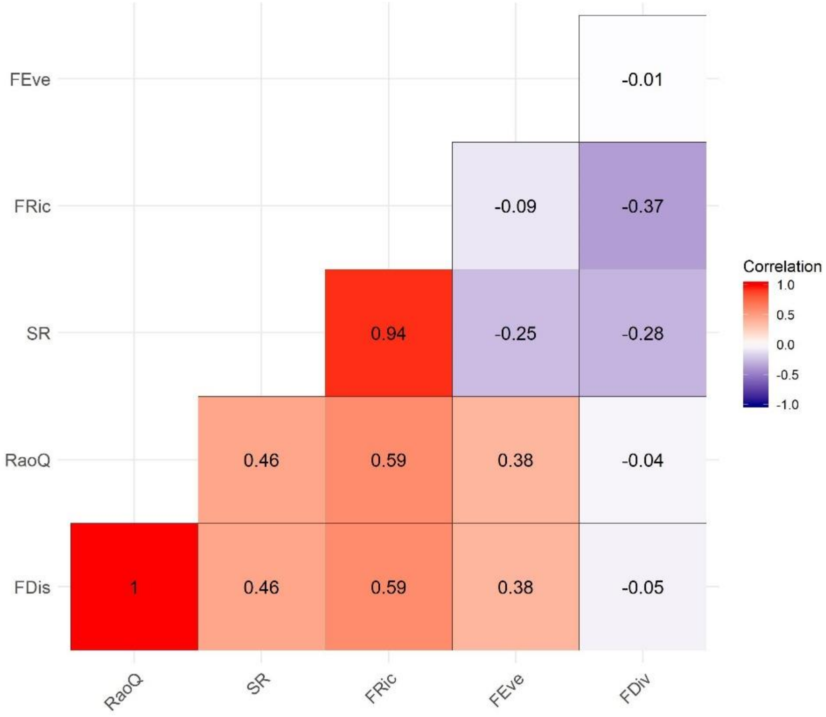

Figure 2 Matrix of correlation (Spearman method) among taxonomic and functional diversity indices. Legend: FEve, functional evenness; FRic, Functional richness; SR, species richness; RaoQ, Rao's quadratic entropy; FDis, functional dispersion; and FDiv, functional divergence.

Functional richness (FRic) is the volume of multidimensional space occupied in the community within the functional space (Villéger et al., 2008). High values of FRic occurs when the available resources are more efficiently used by organisms (Mason et al. 2005).

Functional evenness (FEve) is the evenness of abundance distribution in the functional trait space (Mouillot et al., 2005; Villéger et al., 2008). The FEve

values decrease either when abundance is less evenly distributed among species or when functional distances among species are less regular (Villéger et al., 2008). Functional divergence (FDiv) reflects the divergence in the distribution of abundance in the trait volume and represents niche differentiation in a biological community and increases with the number of species that have unique functional trait values (Villéger et al., 2008).

Data Analysis

We first checked the normality using the Shapiro-Wilk test and plotted residuals to verifying heteroscedasticity. Multicollinearity was checked using the *vif* function of the *usdm* package (Naimi et al., 2014). Tree environmental variables (Tree.ric, Tree.abu, and Shrb.ric) were excluded because the high values of variance inflation factor (VIF > 4). We then proceed with ten variables which were uncorrelated and suitable for analysis (Suppl. Matt. 1). Bird traits were not collinear (VIF < 3) and were integrally used in the analyses. To reduce data dispersion and improve linearity, we used log transformation for size area and arcsine square root for vegetation characteristics expressed by percentage cover (Donnelly & Marzluff, 2004).

Moran's I tests revealed absence of spatial autocorrelation for FRic (Moran’s I: 0.02, *p-value*: 0.24), FEve (Moran’s I: -0.04, *p-value*: 0.96), and FDiv (Moran’s I: 0.05, *p-value*: 0.07). Then, generalized linear models (GLM) with gaussian distribution error was used to test the relation between biotic and abiotic variables (size area, vegetation characteristics, distance of water and forest sources, human and domestic animals disturbances, vehicles and glass windows) and FD indices (FRic, FEve, and FDiv) for each bird guild (residents, migratory, frugivores-nectarivores, and insectivores). First, we constructed a global model including all environmental variables fitted using *glm* function of the *stats* package (R Core Team, 2018). Next, we generated a set of models with all combinations of variables using the *dredge* function of the *MuMIn* package (Barton, 2019). For each model, we computed the Akaike's Information Criterion (AIC) corrected for small sample size (AICc) (Burnham & Anderson, 2002), and the difference in AICc between models and the model with the lowest AICc (ΔAICc). Then, we selected the best models with ΔAICc < 2.0 because they provided substantial support and equally plausible (Burnham & Anderson, 2002), but used only the model with major power weight of inference (wAIC). Finally, we used *visreg* function of the homonymous package (Breheny & Burchett, 2017) to plot the environmental variables that best explained our results. We repeated the procedure above for each bird guilds (residents, migratory, frugivores-nectarivores, and insectivores) to investigate the need of applying of different management strategies in their maintaining in UGs. We carried out all analyses in R program version 3.5.2 (R Core Team, 2018).

Results

We counted a total of 7,886 records from 235 bird species (Suppl. Mat. 3), representing (27%) of all (861 spp.) bird diversity of the Atlantic Forest (Moreira-Lima & Silveira, 2018), or still 44.5% of 528 species recorded in São Paulo municipality (Figueiredo, 2020) and 62.6% of 375 species known to the Guarulhos municipality (Guarulhos, 2018). Fifty-three species (24%) are endemic to this biome (Vale et al., 2018). Most of them were found in the largest Atlantic Forest fragments as Cantareira (39 spp.) and Itaberaba (46 spp.) state parks, and only 11 in the UGs isolated by urbanization. Four species are threatened by extinction (*Tinamus solitarius, Sporophila frontalis, S. bouvreuil,* and *Phylloscartes eximius*) according the global and regional red-lists, and four are near-threatened species (IUCN, 2019; São Paulo, 2018) (Suppl. Mat. 2). The two first threatened birds were recorded in Cantareira and Itaberaba state parks; *P. eximius* only in Cantareira, and *S. bouvreuil* in Tietê ecological park. Five species are allochthonous (Schunck, 2008), three exotic introduced, and 178 have wide geographic distribution (Sick, 1997).

The ten species with more records were *Columba livia* (491 records), *Brotogeris tirica* (375), *Tangara sayaca* (272), *Pitangus sulphuratus* (264), *Pygochelidon cyanoleuca* (252), *Turdus rufiventris* (251), *Coereba flaveola* (207), *Patagioenas picazuro* (186), *Bubulcus ibis* (179), *Troglodytes musculus* (169) (Figure 3a-b), corresponding to (33.5%) of all observed abundance. Singletons (17 spp., e.g., *Scytalopus speluncae*) and doubletons (23 spp., e.g., *Chamaeza meruloides*), together, represented (17%) of total species recorded. Most species (74.5%) had three to 100 contacts; and few (8.5%) of species had more than 100 contacts. More than half of species (124 spp.; 52%) were insectivores, followed by (31 spp.; 13%) frugivores-nectarivores. Most species (90%) were residents and likely to stay all year round in the studied sites. Twenty-six species (11%) showed some migratory behavior. *Turdus flavipes* and *Chaetura meridionalis* were migrants and 24 species (e.g., *Tyrannus* spp., *Empidonomus varius*, *Sporophila lineola*, *Vireo chivi*, *etc.*) were partially migrants. Half species were insectivores and nearly 13% were frugivores-nectarivores.

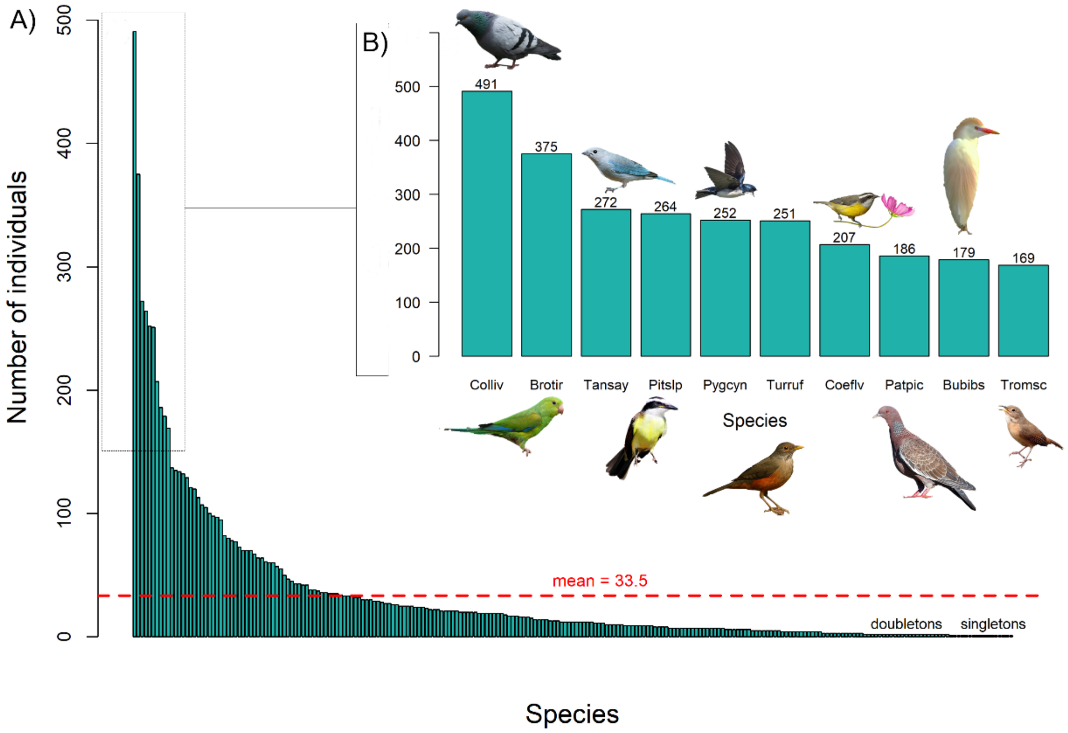

Figure 3 Bar plots of abundance of bird species recorded in UGs of São Paulo megacity, Southeast Brazil; a) total bird assemblage, and b) zoom showing the ten most abundant species. Bird pictures were extracted from first author files. Acronymous: Colliv, *Columba livia* (Rock Pigeon); Brotir, *Brotogeris tirica* (Plain Parakeet); Tansay, *Tangara sayaca* (Sayaca Tanager); Pitslp, *Pitangus sulphuratus* (Great Kiskadee); Pygcyn, *Pygochelidon cyanoleuca* (Blue-and-white Swallow); Turruf, *Turdus rufiventris* (Rufous-bellied Thrush); Coeflv, *Coereba flaveola* (Bananaquit); Patpic, *Patagioenas picazuro* (Picazuro Pigeon); Bubibs, *Bubulcus ibis* (Cattle Egret); and Tromsc, *Troglodytes musculus* (House Wren).

The FD measures per site varied according to the bird guilds. The largest amplitude of FRic was found in frugivores-nectarivores (min = 0.13 to max = 0.99; mean = 0.40; SD = 0.29), followed by the total bird assemblage, migrant, insectivorous, and resident birds (Table 2). Insectivores performed major variation in FEve, (0.54 - 0.94; mean = 0.82; SD = 0.09), and the total bird assemblage showed larger range of FDiv (min = 0.37 to 0.86; mean = 0.74; SD = 0.10) (Table 2).

Table 2 Functional diversity (FD) from each bird guilds recorded in UGs of São Paulo megacity, Southeast Brazil.

Bird guilds	**FRic**				**FEve**				**FDiv**			
	min	*max*	*mean*	*sd*	*min*	*max*	*mean*	*sd*	*min*	*max*	*mean*	*sd*
Bird assemblage	0.04	0.88	0.18	0.19	0.56	0.93	0.74	0.10	**0.37**	**0.86**	0.74	0.10
Residents	**0.04**	**0.53**	0.18	0.13	0.58	0.95	0.76	0.10	0.68	0.89	0.80	0.05
Migrants	**0.12**	**0.93**	0.40	0.24	0.61	0.99	0.84	0.11	0.55	0.99	0.70	0.12
Insectivores	0.07	0.71	0.25	0.18	**0.54**	**0.94**	0.82	0.09	0.58	0.97	0.72	0.09
Frugiv-Nectarivores	**0.13**	**0.99**	0.40	0.29	0.61	0.92	0.79	0.09	0.67	0.89	0.78	0.07

FD metrics: FRic: functional richness; FEve, functional evenness; and FDiv, functional divergence. **In bold**, the major amplitudes of FD by each bird guilds.

Size area was the main environmental variable to influence bird's FRic according to our best-ranked models. Size area had a positive relation with FRic of residents (wAICc = 0.437) and migrants (wAICc = 0.270), reflecting on the total bird assemblage (wAICc = 0.273) (Figure 4a-c, Table 3). Other best-rank models showed positive interaction between size area and shrub cover for FRic of insectivores (wAICc = 0.362) and frugivores-nectarivores (wAICc = 0.631) (Fig. 4d-g, Table 3). On the other hand, FRic of resident birds decreased with the tree cover (wAICc = 0.437, Fig. 4h, Table 3), and the number of cats negatively influenced FRic of residents (wAIC = 0.437), and insectivores (wAICc = 0.362), also reflecting on the total bird assemblage (wAICc = 0.273) (Figure 4i-k, Table 3).

Table 3 GLM models showing the relation between biotic and abitic variables and FD indices from each bird guilds (and entire assemblage) in São Paulo megacity, Brazil.

FD index of bird guilds	**Intercept**	**Best ranked AICc models [interaction power]**	**df**	**logLik**	**AICc**	**ΔAIC**	**ω**
FRic							
Total bird assemblage	**0.0494**	**~ size [0.07] + cats [-0.04]**	**4**	**25.2**	**40.4**	**0.00**	**0.273**
	0.0257	~ size [0.07]	3	23.6	40.0	0.36	0.228
	0.0188	~ cats[-0.04] + size [0.05] + srb.cov [0.01]	5	26.5	39.9	0.54	0.209
	[-0.004]	~ cats[-0.04] + size [0.05] + srb.cov [0.01]	4	24.7	39.4	0.95	0.169

	0.075	~ cats[-0.04] + size [0.06] + wind [-0.003]	5	26.0	38.8	1.62	0.121
Resident	**0.13800**	**~ cats[-0.030] + size[0.042] + srb.cov[0.007] + tree.cov[-0.010]**	**6**	**44.08**	**-71.2**	**0.00**	**0.437**
	0.14890	~ cats[-0.031] + size[0.048] + tree.cov[-0.009]	5	42.15	-71.0	0.24	0.387
	0.14890	~ cats[-0.037] + size[0.046]	4	39.75	-69.4	1.83	0.176
Migrant	**0.19150**	**~ size[0.065]**	**3**	**11,546**	**-15.9**	**0.00**	**0.261**
	0.11770	~ size[0.065] + water[0.004] + wind[-0.008]	5	14,476	-15.6	0.27	0.228
	0.23990	~ size[0.059] + wind[-0.006]	4	12,671	-15.2	0.65	0.188
	0.06229	~ size[0.062] + tree.cov[0.019]	4	12,629	-15.2	0.74	0.181
	0.09418	~ size[0.070] + water[0.002]	4	12,387	-14.7	1.22	0.142
Insectivorous	**0.06933**	**~ cats[-0.040] + size[0.037] + srb.cov[0.028]**	**5**	**33,640**	**-53.9**	**0.00**	**0.362**
	0.12300	~ cats[-0.033] + size[0.038] + srb.cov[0.029] + tree.cov[-0.009]	6	35,049	-53.2	0.79	0.244
	0.07432	~ size[0.043] + srb.cov[0.031] + tree.cov[-0.014] + water[0.001]	6	34,931	-52.9	1.03	0.217
	0.12230	~ size[0.040] + srb.cov[0.030] + tree.cov[-0.012]	5	32,931	-52.5	1.42	0.178
Frugivorous	**0.10940**	**~ cats[-0.084] + size[0.051] + srb.cov[0.039]**	**5**	**13,929**	**-14.5**	**0.0**	**0.520**
	0.17620	~ cats[-0.093] + size[0.052] + srb.cov[0.032] + wind[-0.006]	6	14,985	-13.0	1.5	0.246
	0.06281	~ size[0.056] + srb.cov[0.039]	4	11,513	-12.9	1.6	0.233
FEve							
Total Bird assemblage	**0.7781**	**~ veic[-0.005]**	**3**	**25,326**	**-43.5**	**0.00**	**0.689**
	0.7742	~ veic [0.0006] + wind[-0.007]	4	25,985	-41.9	1.59	0.311
Resident	**0.8609**	**~srb.cov[-0.013] + wind[-0.005]**	**4**	**25,094**	**-40.1**	**0.00**	**0.197**
	0.7696	*null*	2	22,204	-39.8	0.25	0.174
	0.8301	~size[-0.015] + wind[-0.004]	4	24,840	-39.6	0.51	0.153
	0.7903	~ wind[-0.003]	3	23,119	-39.0	1.05	0.117
	0.7932	~ size[-0.011]	3	23,086	-39.0	1.11	0.113
	0.8008	~srb.cov [-0.007]	3	22,828	-38.5	1.63	0.087
	0.7521	~dogs[0.018]	3	22,777	-38.4	1.73	0.083
	0.8597	~srb.cov[-0.013] + veic[0.0006] + wind[-0.008]	5	25,773	-38.2	1.87	0.077
Migrant	**0.7444**	***null***	**2**	**-1,143**	**6.9**	**0.00**	**0.165**
	0.6354	~ srb.cov[0.025]	3	-0.032	7.3	0.41	0.135
	0.8043	~ pedest[-0.004]	3	-0.120	7.4	0.58	0.123
	0.3319	~ cats[0.119] + srb.cov[0.036 + water[0.006]	5	2,510	8.3	1.46	0.080
	0.7908	~ dogs[-0.048]	3	-0.569	8.3	1.48	0.079
	0.6950	~ size[0.023]	3	-0.599	8.4	1.54	0.076
	0.7137	~ cats[0.067]	3	-0.637	8.5	1.62	0.074
	0.4768	~ srb.cov[0.030] + water[0.004]	4	0.798	8.5	1.65	0.072
	0.5431	~ srb.cob[0.034] + wind[0.009]	4	0.715	8.7	1.82	0.067
	0.5921	~ cats[0.077] + srb.cov[0.027]	4	0.700	8.7	1.85	0.066
	0.6533	~ water[0.003]	3	-0.793	8.8	1.93	0.063
Insectivorous	**0.8038**	**~ dogs[0.026]**	**3**	**27,717**	**-48.2**	**0.00**	**0.240**
	0.8541	~ size[-0.011]	3	27,309	-47.4	0.81	0.160
	0.8294	*null*	2	25,960	-47.3	0.88	0.154
	0.7914	~ cats[0.026] + dogs[0.027]	4	28,618	-47.1	1.10	0.138
	0.8164	~ dogs[0.028] + wind[-0.002]	4	28,423	-46.7	1.49	0.114
	0.8782	~ size[-0.014] + wind [-0.003]	4	28,341	-46.6	1.66	0.105

	0.8253	~ dogs[0.020] + size[-0.007]	4	28,184	-46.3	1.97	0.090
Frugivorous	**0.8337**	**~ dogs[-0.092]**	**3**	**9,914**	**-12.6**	**0.00**	**0.56**
	0.8036	~ dogs[-0.096] + veic[0.001]	4	11,126	-12.1	0.48	0.44
FDiv							
Total bird assemblage	**0.7094**	**~ dogs[0.03]**	**3**	**23.6**	**[-40.1]**	**0.00**	
	0.7392	*null*	2	21.9	-39.3	0.75	0.204
	0.6719	~ dogs[0.04] + size [0.012]	4	24.6	-39.2	0.84	0.195
	0.6246	~ dogs[0.03] + tree.cov [0.01]	4	24.6	-39.1	0.96	0.184
	0.7252	~ dogs[0.03] + pedest [-0.001]	4	24.1	-38.3	1.80	0.121
Resident	**0.8517**	**~ pedest[-0.001] + size[-0.010] + veic[-0.0004]**	**5**	**47,403**	**-81.5**	**0.00**	**0.329**
	0.8552	~ pedest[-0.001] + size[-0.010] + wind[-0.002]	5	47,275	-81.2	0.26	0.290
	0.8403	~ cats[0.015] + pedest[-0.0012] + size[-0.009] + veic[-0.0004]	6	48,825	-80.7	0.76	0.225
	0.8440	~ cats[0.014] + pedest [-0.0013] + size[-0.009] + wind[-0.002]	6	48,467	-80.0	1.48	0.157
Migrant	**0.6137**	***null***	**2**	**3,262**	**-2.0**	**0.00**	**0.117**
	0.6692	~ pedest[-0.004]	3	4,536	-1.9	0.08	0.112
	0.5172	~ srb.cov[0.022]	3	4,529	-1.9	0.09	0.111
	0.6454	~ pedest[-0.005] + veic[0.001]	4	5,813	-1.5	0.43	0.094
	0.4217	~ srb.cov[0.032] + wind[0.009]	4	5,720	-1.3	0.62	0.086
	0.6400	~ pedest[-0.005] + wind[0.007]	4	5,423	-0.7	1.21	0.064
	0.3611	~ cats[0.080] + srb.cov[0.035] + wind[0.010]	5	6,971	-0.6	1.34	0.060
	0.4928	~ pedest[-0.003] + srb.cov[0.025] + wind[0.011]	5	6,914	-0.5	1.46	0.056
	0.4814	~ cats[0.064] + srb.cov[0.024]	4	5,263	-0.4	1.53	0.054
	0.4673	~ srb.cov[0.026] + veic[0.001]	4	5,223	-0.3	1.61	0.052
	0.5886	~ cats[0.055]	3	3,753	-0.3	1.65	0.051
	0.5747	~ size[0.018]	3	3,752	-0.3	1.65	0.051
	0.5843	~ pedest[-0.002] + srb.cov[0.016]	4	5,136	-0.2	1.79	0.048
	0.5472	~ pedest[-0.004] + srb.cov[0.018] + veic[0.001]	5	6,679	0.0	1.93	0.044
Insectivorous	**0.6986**	***null***	**2**	**26,448**	**-45.7**	**0.00**	**0.250**
	0.7252	~ pedest[0.001]	3	24,670	-44.8	0.93	0.157
	0.6368	~ pedest[0.001] + tree.cov[0.009]	4	27,239	-44.4	1.32	0.129
	0.7621	~ srb.cov[-0.008]	3	25,766	-44.3	1.36	0.126
	0.6844	~ cats[0.026] + pedest[0.002]	4	27,217	-44.3	1.37	0.126
	0.6873	~ srb.cov[-0.010] + tree.cov[0.012]	4	27,086	-44.1	1.63	0.111
	0.8016	~ dogs[-0.024] + srb.cov[-0.012]	4	26,983	-43.9	1.83	0.100
Frugivorous	**0.8085**	**~ dogs[-0.088]**	**3**	**11,373**	**-15.5**	**0.00**	**0.410**
	0.7802	~ dogs[-0.093] + wind[0.005]	4	12,292	-14.5	1.07	0.240
	0.8600	~ dogs[-0.104] + size[-0.017]	4	12,061	-14.0	1.53	0.191
	0.7465	~ dogs[-0.092] + water[0.002]	4	11,883	-13.7	1.89	0.160

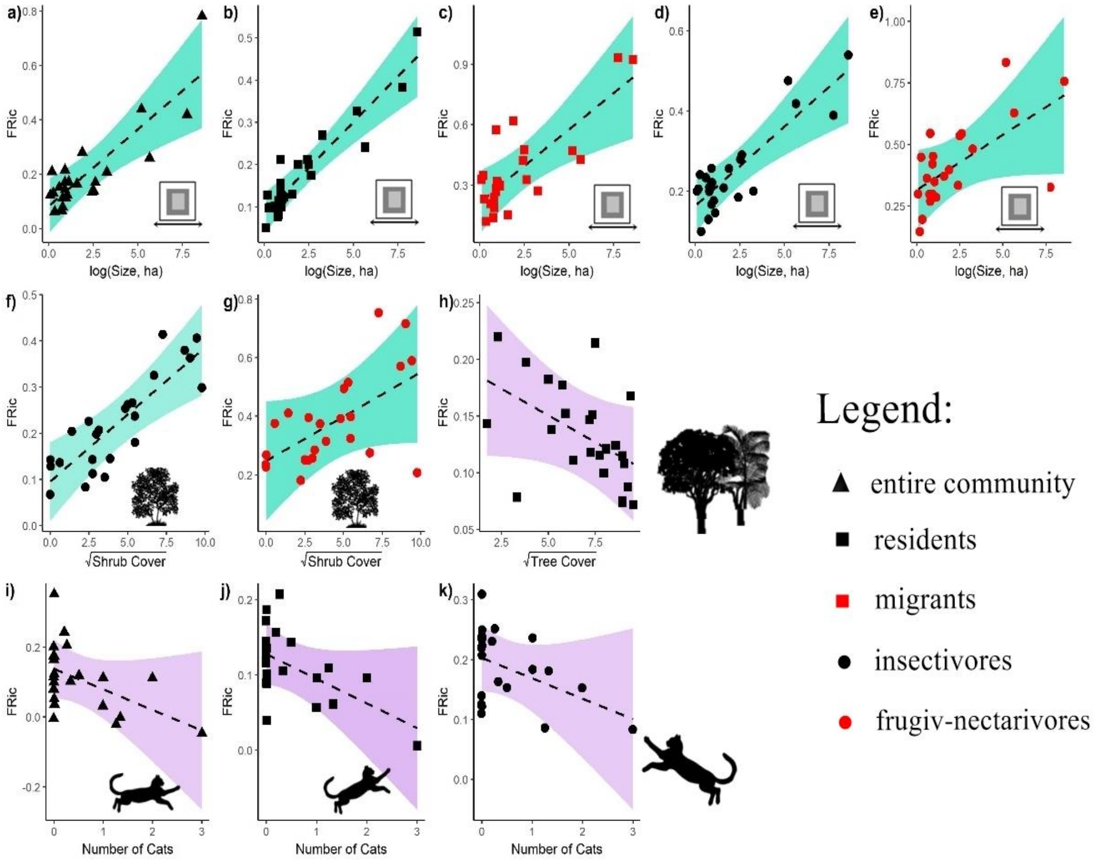

Figure 4 Relationship between environmental variables and functional richness (FRic) of bird guilds recorded in urban greenspaces of São Paulo megacity. Legend: dashed line represents the fitted line; purple and lightseablue areas are the confidence intervals at 95%, representing negative and positive effects, respectively. Bird guilds: triangles, entire bird community; black-squares, residents; red-squares, migrants; black-circles, insectivores; and red-circles, frugivores-nectarivores.

The increase of glass windows reduced the FEve of the entire bird assemblage (wAICc = 0.689) and resident birds (wAICc = 0.197) (Fig. 5a,b, Table 3). The number of dogs reduced both FEve (wAICc = 0.571) and FDiv (wAICc = 0.506) of frugivores-nectarivores (Fig. 5c,d, Table 3), but increased FDiv of the entire bird assemblage (wAICc = 0.297) (Fig. 5e, Table 3). The number of vehicles and pedestrians, and size area reduced FDiv of resident birds (wAICc = 0.329) (Figure 5 f-h, Table 3).

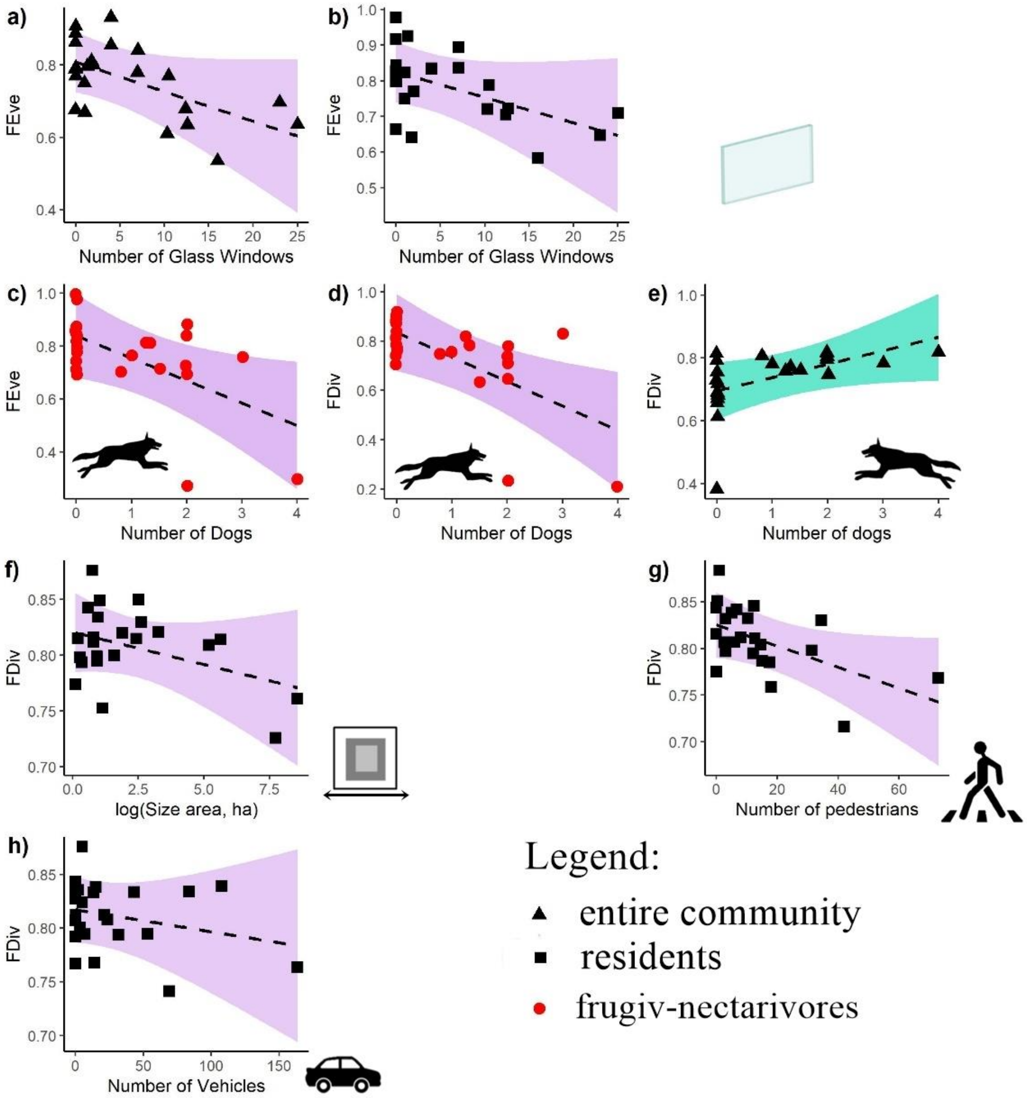

Figure 5 Relationship between environmental variables and functional diversity metrics (FEve, functional evenness and FDiv, functional divergence) of bird guilds recorded in urban greenspaces of São Paulo megacity. Legend: The black dashed line represents the fitted line; purple and lightseablue areas are the confidence intervals at 95%, which respectively represent negative and positive associations with studied variables. Bird guilds: triangles, entire bird community; black squares, residents; and red circles, frugivores-nectarivores.

Discussion

Our results confirmed our first prediction that size area of the UGs was the most important variable to drive high FRic for all bird guilds. Our second prediction was also confirmed by shrub cover selectively increasing FRic of insectivores and frugivores-nectarivores, although also increased non-selectively resident's FRic. The third prediction was partially confirmed by the number of cats negatively impacting FRic of specialist (insectivores), and the negative effects on FRic of residents and the entire assemblage suggest that cats can impact both specialist and non-specialist functional groups, and by tree cover decreasing resident's FRic. As also predicted, some biotic-abiotic variables acted on species and/or trait abundance. This was confirmed by increasing (1) the number of glass panes negatively influenced the regularity of trait abundance (FEve) of residents and the entire bird assemblage; (2) the number of dogs reduced FEve and FDiv of specialist birds (frugivores-nectarivores); (3) the number of pedestrians and vehicles reduced FDiv of residents. However, part of our second prediction was rejected as herbaceous cover and proximity of water have not influenced FRic of migrant birds. We also found contrasting results to our predictions, such as FDiv of resident birds has increased with increased in the number of dogs and reduced with increased size area.

Size area was the main positive predictor of high bird's FRic in the UGs of São Paulo megacity. Our study increases evidences that FRic agrees with the strong positive species-area relation in cities across the world (Beninde et al., 2015; Carbó-Ramírez & Zuria, 2011; Fernández-Juricic & Jokimäki, 2001; Leveau, 2019; Peris & Montelongo, 2014; Shanahan et al., 2011; Schütz & Schulze, 2015)). As the area increases, the amount of available energy, resources, and environmental heterogeneity also increases, arising in rich communities (Macarthur & Wilson, 1967). High species richness fill a higher volume of traits occupied by a community (Cornwell et al., 2006), leading to a strong positive

FRic-area relationship as seen here and in previous studies (Ding et al., 2013; Karadimou et al., 2016; Schütz & Schulze, 2015). Our findings show that increase in size area has strong positive influence on FRic of all bird guilds (i.e., frugivores-nectarivores, insectivores, residents, and migrants) and on the entire avian assemblage; i.e. the available resources are more efficiently exploited (Mason et al., 2005) by distinct functional bird guilds in larger UGs than in smaller ones. We stress the value of larger UGs in sustaining high functional niche space for varied bird guilds and likely their ecosystem functions. There are also evidences that large-sized areas are important for FRic of frugivores in native fragments of the Atlantic Forest (Bovo et al., 2018).

Shrub cover was a positive bird FRic modulator. UGs with high shrub cover increased FRic for insectivorous and frugivorous-nectarivorous birds. These findings support our prediction that the increased shrub cover selectively drive functional traits of specific bird guilds. Shrub plants provide additional foraging resources, escape refuges, and nesting sites for urban birds (Ikin et al., 2013; Melles et al., 2003; Savard et al., 2000) improving functional niche space for functional traits related to insectivores and frugivores-nectarivores, as also seen in an undergoing Atlantic Forest restoration habitat (Melo et al., 2020). Large-sized area and high shrub cover in UGs may perform as interesting tools for management of functional niche space for insectivorous and frugivorous-nectarivorous birds and likely their ecosystem services (i.e., insect control, seed dispersal, and pollination). Tree-lined streets can also increase habitat suitability and permeability (Fernández-Juricic, 2000a; Suri et al., 2017), and have been recommended for mitigating the negative impacts of urbanization on bird’s FD (Pena et al., 2017).

Domestic dogs were negatively related to FEve of frugivores-nectarivores in UGs, and improve the FDiv of frugivores-nectarivores, reflecting in positive FDiv of the bird assemblage. Number of dogs has a bimodal effect over FD of frugivores-nectarivores.

Due to the prey-predator effects, dogs may reduce occurrence and diversity of birds in urban habitats (Lim & Sodhi, 2004; Shwartz et al., 2008), mainly those moderately abundant and rare species (MacGregor-Fors & Schondube, 2011). We expand this effect to the most abundant frugivores-nectarivores (e.g., *Coereba flaveola*, *Eupetomena macroura*, and *Turdus amaurochalinus*) associated to shrub cover, the lowest strata. They may be more vulnerable to dogs and dog walkers (Kark et al. 2007) or by the negative interference caused by the mutual suitable habitats for both dogs and birds (MacGregor-Fors & Ortega-Álvarez, 2011). This explains FEve's declines we recorded, which could be translated in decline of pollination and seed-dispersal provided by the most abundant birds. However, dogs also represent a threat for cats (Chang & Lee, 2016; Kark et al., 2007) and may indirectly reduce the chances of birds being captured by felines, mainly those which forages at the lower vegetation strata (Daniels & Kirkpatrick, 2006), as frugivores-nectarivores and others (e.g., insectivorous - *Troglodytes musculus;* omnivorous - *Turdus rufiventris;* granivores - *Columbina talpacoti* and *Zenaida auriculata*). This should have increased the occurrence of species with unique functional traits, increasing the FDiv of frugivores-nectarivores and also for the entire bird assemblage. We provided insights that reduction of street-cat population likely may increment ecosystem services provided by birds with some diet specialization in detriment of those generalist species.

The number of cats was related to a severe decline in FRic of insectivores (and for the entire bird assemblage), and the interaction between the number of cats and shrub cover reduced FRic of resident birds. To our knowledge, the present study is the first to associate the number of cats to the loss of FRic of birds in UGs. A pet census estimated that 23.9 M of cats live in Brazil (IBGE, 2015), and urban parks and squares of São Paulo megacity are places where humans illegally abandoned domestic cats (*pers. obs.*).

Although, we only recorded occasional bird predation by domestic cats, these pets have been assigned as one of the main causes of avian mortality in urbanized areas (Loss et al., 2015). Our findings highlighted the possible impact of free-ranging cats on the functional space occupied by insectivores and also for the entire bird assemblage. Insectivorous (52%), omnivorous (16%), and granivorous (12%) summed ~80% of the species. These birds forage at the low stratums (from the ground to understory) (Wilman et al., 2014), and probably are more susceptible to cat predation. We also stress the interaction between shrub cover and free-ranging cats on the resident's FRic. Representatives of the most frequent resident families (e.g. Columbidae, Turdidae, Tyrannidae, Coerebidae, Passeridae, and Thraupidae) also forage from the ground to low height trees and shrubs. There are evidences that feral cats may suppress the ground and shrub bird nesters in urbanized areas (Churcher & Lawton, 1987; Lim & Sodhi, 2004). Specialized bird species have a great amount of unique traits important to fill substantial volume of functional niche space (dos Anjos et al., 2019). We support that cat predation causes losses of specific insectivores and ground/shrub foraging guilds, resulting in severe decline of bird's FRic.

Our data also revealed that, as tree cover increased, FRic of resident birds has also decreased, in an opposite pattern described for species richness of resident and migrant guilds in São Paulo's greenspaces (Barbosa et al., 2020). Previous studies have attributed such results to the impacts of low diversity of native trees, exotic tree dominance (Campos-Silva & Piratelli, 2020; Lessi et al., 2016; MacGregor-Fors, 2008; Reis et al., 2012) and low environmental heterogeneity found in urban (public and private) greenspaces (Morelli et al., 2018). A large-scale study performed in European countries found that parks and cemeteries occupied predominantly by one type of habitat (> 65% of area) were less heterogeneous and shelter low bird species richness (Morelli et al., 2018). Although we are aware of the differences between temperate and tropical birds (Murgui & Hedblom, 2017), most of our UGs showed high tree coverage (> 50% to 90%). It likely reduced the environmental heterogeneity of our UGs, implying in loss of functional space for the resident birds and FRic declines.

Bird-window collisions are among the main causes of bird mortality in urban ecosystems (Loss et al., 2014, 2015), affecting from small hummingbirds to large raptors (Basilio et al., 2020). In this study, the mean increase of glass panes was negatively associated with FEve of both resident and the entire bird assemblage, confirming our prediction that glass-windows is related to the loss in the regularity of trait abundance. There are evidences that bird-window strikes are often recorded near UGs in Neotropical cities (Agudelo-Álvarez et al., 2010; Cupul-Magaña, 2015; Delgado-V. & Correa-H, 2013). Forty percent of the 25 sampled UGs showed a higher glass-windows interference than the mean value (5.85). Although we did not directly count bird-window collisions, our findings suggest that these accidents are dramatically influencing bird populations in our study sites. As insectivores and omnivores (which perform substantial arthropod predation and seed dispersal) together comprises 68% of the bird assemblage, their likely declines related to bird-window collisions have potential for decrease the regularity of insect control and plant diversity maintenance in UGs.

Resident's FDiv decreased with the number of vehicles, number of pedestrians, and increase in area of UGs. Our findings suggested that UGs massively used by humans and surrounded by streets and avenues with heavy traffic, could have limited resident avian species with unique trait values, reflecting a shorter niche differentiation. Some of the studied urban parks (e.g., Trianon, Ibirapuera, Bosque Maia, and others), provide relative habitat heterogeneity or vegetation complexity, yet have high impact of human visitation and traffic car from neighborhood avenues. Indeed, bird diversity has decreased with car and pedestrian traffics, as in earlier Neotropical urban bird studies (MacGregor-Fors & Schondube, 2011; Ortega-Álvarez & MacGregor-Fors, 2009; Silva et al., 2015). This impact may be more intense in smaller than in larger sites, because small UGs do not pose suitable size areas for birds to avoid the human presence, vehicle traffic, and noise (Barbosa et al., 2020; Chang & Lee, 2016; Fernández-Juricic & Jokimäki, 2001). This reduces the liability of birds with unique traits to live within these small "urban green islands", thus explained the low FDiv of resident birds. On the other side, FDiv declined as increased in the size area. As the largest UGs shelter great bird diversity (i.e. Cantareira and Itaberaba state parks; Tietê ecological park), FDiv of the assemblage should have significantly decreased because of high overlap effect of species niche and intensified resource competition (Chang & Lee, 2016). However, whether functional traits of more abundant species are placed next to the center in tropical communities, FDiv decreases in function of a high similarity of functional traits (Chang & Lee, 2016; Cornwell et al., 2006). We also observed high abundance of insectivores living in UGs, as in other Brazilian urban bird communities (e.g. Barbosa et al., 2020; Lees & Moura, 2017). Likely, the trait redundancy should have masqueraded some relationship between biotic-abiotic variables and FEve and FDiv of insectivores, as seen in (Melo et al., Chapter 1). Future investigations should analyze their foraging strata guilds (e.g., air, ground, understory, mid-story, and canopy insectivores) to search for new insights for these abundant bird guilds, as in a previous study (Melo et al., 2020). On the other hand, the absence of correlation between environmental variables and FEve and FDiv of migratory birds can reflect their low abundance variation across sites. For example, a simple couple of migrant passerines (*Myiodynastes maculatus*) require large (2.5 to 5.4 ha) home-ranges (Vitório et al., 2019), usually the maximum area that small UGs in São Paulo may provide. This stress the role of large sized areas for migratory birds.

Conclusions

We found high avian diversity in small- to large UGs of São Paulo megacity, which is an excellent opportunity to develop avian conservation and improve ecosystem services in most populous South American city. However, our study highlighted that small sized UGs has restrict conditions to preserve bird functional diversity linked to (1) few habitat heterogeneity (2) absence of shrub layer; (3) high impact of traffic, and massive presence of (4) glass windows, (5) pedestrians, and (6) domestic animals. We also stress that dog and cat abandons may cause declines in bird ecological functions (insect control, seed dispersal, and pollination) central for sustaining biodiversity in UGs.

We recommend that urban planners and managers should priories large sized areas with high shrub cover. We are aware that large green areas have severe restrictions in heavily urbanized cityscapes; urban planners should invest time and resources to increment shrub cover and mitigates the negative impact on birds caused by glass windows, traffic vehicles, human presences, and domestic animals. In most of the UGs we studied, these actions are feasible and important tools to improve bird diversity and likely a better provisioning of ecosystem services provided by specific bird guilds. Urban public policies should destinate economic resources from public and private to creates more effectives (1) domestic animal castration-adoption programs and environmental education; (2) restriction in glass use as material of construction and/or adoption of preventive bird-collision measures in already existent glass-windows (Basilio et al., 2020; Ribeiro & Piratelli, 2020); (3) study the physical characteristics of native shrub and wood plant species as a simultaneous acoustic barrier to mitigates urban noise pollution and increment resources for birds; and (4) create preserved zones to protect specific habitats of UGs where the access of domestic animals and humans should be restricted.

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Capítulo 3

Feathered neighbors: vegetation cover and red clay roofs drive bird taxonomic and functional diversity in housing areas of São Paulo megacity, Brazil

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Abstract

Urbanization creates the most irreversible and human-dominated form of land use, often resulting in species losses and functional homogenization of bird communities. Due to the increased rates of urbanization and biodiversity crisis across the world here we investigate whether housing areas in a Neotropical megacity may increase bird species occurrence and ecosystem functions in high densely habited areas. Using three local scales (radius of 50, 100, and 200 m), we tested how bird species richness, functional groups and indexes of functional diversity may be influenced by the percentages of normalized difference vegetation index (NDVI, a proxy of primary productivity) and red clay roofs (RCR, a potential urban nesting site) in São Paulo megacity, Brazil. We recorded 40 bird species, and most nest on trees, and few and high abundant (native and exotic) birds may use roofs and other urban structures as nest sites. The GLM models showed that species richness increased with high NDVI and low RCR. Functional richness increased with synchronized increases of NDVI and RCR covers. High NDVI and RCR maintained high functional evenness, and lesser NDVI and RCR increased functional divergence. Moreover, these bird indices were sensitive at distinct local scales, translated into different responses depending on the functional groups. Our findings suggest that a best configuration between high NDVI (> 0.5) and high RCR cover at smaller scale is recommended to improve bird conservation in Neotropical cities. This stress that urban planners should focus attention on house's roofs and other urban attributes in highly habited areas, which should be managed to reduce negative impacts of invasive species on native birds and increase suitable habitats for more diverse avian assemblages.

Keywords: Anthropogenic Structures. Functional Groups. Nest Opportunities. Primary Productivity. RLQ Analyses. Urban Birds.

Introduction

Urbanization is a continuous process that creates the most irreversible and human-dominated form of land use (Seto et al., 2012). The urbanization changes land cover, hydrological systems, biogeochemistry, climate, and biodiversity – including birds, a well-studied group on the urban ecology perspective (Grimm et al., 2008; Marzluff, 2017; Murgui and Hedblom, 2017). These changes are very rapid and most aimed to attend the human's primary needs (Fontana et al., 2011; McKinney, 2006). As the human population grows at high rates (Grimm et al., 2008; United Nations, 2018), rural and pristine sites are often replaced by buildings, roads, and other human-made structures (MacGregor-Fors and Schondube, 2011; Shanahan et al., 2013), and few, disconnect, and small-sized remnants of natural and semi-natural areas persist (Faggi and Caula, 2017; Fontana et al., 2011). This process creates a complex environmental mosaic composed of built areas and greenspaces, varying in size, form and level of human-interference, and -occupation (MacGregor-Fors and Schondube, 2011; McKinney, 2006). Gardens, road strips, and street trees often assume an important role in maintaining habitat and resources for birds and their ecosystem functions (Carbó-Ramírez and Zuria, 2011; Fernández-Juricic, 2000; Juri and Chani, 2009; Pena et al., 2017), like pollination, propagules dispersal, insect and rodent control, and nutrient cycles (Nyffeler et al., 2018; Sekercioğlu, 2006).

Functional diversity is a critical facet of biodiversity and has been linked to ecosystem functioning (Díaz and Cabido, 2001). The knowledge of the relationships between urban characteristics and species and their functional traits may help urban planners, decision-makers, and conservationists to take most parsimonious decisions for preserves not only more diverse specie's, but also the ecosystem functions they provide (Cadotte and Tucker, 2018; Oliveira Hagen et al., 2017). Ecologists have measured urban environment characteristics by remote sensor spatial tools to understand how birds are spatially spread across cityscapes (Bino et al., 2008; Leveau et al., 2020, 2018). The use of the normalized difference vegetation index (NDVI), has been growing, acting as an indicator of primary productivity, and predicting the potential of urban habitats to preserve ecological relationships (Bae et al., 2018; Bino et al., 2008; Leveau et al., 2018; Pettorelli et al., 2005).

Urbanization reduces the availability of vegetation cover, creating massive native local extinction of birds (Beninde et al., 2015; Fernández-Juricic et al., 2001; Leveau and Leveau, 2004; Sol et al., 2017; van Rensburg et al., 2009), and benefit few native and exotic/introduced species, which increase abundances and thrive in cities (Bonier et al., 2007; Fischer et al., 2015; Møller et al., 2015). Urban filters strongly select some pre-adapted avian functional traits (Croci et al., 2008; Hensley et al., 2019) which find new opportunities for feeding and or nesting (James Reynolds et al., 2019; Mainwaring, 2015; Sol et al., 2011), compared to immediate rural-nature surrounding habitats (Clergeau et al., 2001, 1998; Leveau and Leveau, 2004). Habitat simplification in urbanized sites also represents a limiting factor for a large number of native bird species-specialists on diet/foraging strata to persist within the cities (Aronson et al., 2014; Sol et al., 2014; Melo et al., Chapter 1). A global review found that urbanization benefit only omnivorous and granivorous species across the world (Chace and Walsh, 2006). However, when individually analyzed Neotropical cities favor omnivorous and insectivorous species (Ortega-Álvarez and MacGregor-Fors, 2011). Those functional groups deserve special attention for urban ecologists due to their value for ecosystem functioning (Díaz and Cabido, 2001; Sekercioğlu et al., 2004) within the cities (Oliveira Hagen et al., 2017), beyond specialists, which provide unique ecosystem services (Casas et al., 2016; Galetti et al., 2013; Sekercioğlu et al., 2004).

As the urban fringe increases (Cincotta et al., 2000; Seto et al., 2012), natural resources become scarce (Emlen, 1974; Hill and Neto, 1991; Mainwaring, 2015) and birds found abundant and heterogeneous anthropogenic materials and urban structures that may be used as foraging, roosting, and nesting sites (Batisteli et al., 2019b; Emlen, 1974; James Reynolds et al., 2019; Mainwaring, 2015; Pellissier et al., 2012; Pike et al., 2017). Neotropical region meets higher rates of urbanization (United Nations, 2018) and greater bird diversity (Myers et al., 2000), but little attention has been given to how birds breed in urbanized sites, and the most published data are dispersed as grey literature. In Neotropical cities, there are cases of hummingbirds breeding over electric cables (Escobar-Ibáñez and MacGregor-Fors, 2015), woodcreepers and wrens in varied types of artificial holes (del Hoyo et al., 2019; Pizo, 2018), tyrants on power transformers and pole lamps (Sandoval and Barrantes, 2009), raptors on tall telecommunication towers (Maurício et al., 2013), swifts in chimneys (Sick, 1997), and passerines and non-passerines using buildings (Batisteli et al., 2019a; Hill and Neto, 1991; Sick, 1997; Sigrist, 2009; Stewart, 1974). Thus, the potential of anthropogenic structures as buildings, house roofs, bridges, and metal pipes to provide crevices/hole for cavity-nesters (Emlen, 1974; James Reynolds et al., 2019; Mainwaring, 2015; Pellissier et al., 2012), and high-rise buildings to mimic cliff habitats for cliff-nester birds (Evans et al., 2011; Fisk, 1978; Symes et al., 2017) have been few explored in Neotropical cities. Only cliff-nesters, which reproduces on rooftops and other urban structures, have been studied in South American cities (Branco et al., 2008; Chávez-Villavicencio, 2014; Vermeer et al., 1988), and cavity-nesters, that nest under roofs, roof eaves, and others (Emlen, 1974; Pellissier et al., 2012) are barely known. Roofs give support for many birds in temperate regions (Emlen, 1974; Mainwaring, 2015; Pellissier et al., 2012), and the large roof availability in most populous South American cities also should offer central nest-sites for urban birds. Many different roof types may be found in Brazilian cities, and red clay tiles is an inherited from European architecture and very popular in cities of southeastern Brazil, where some native and exotic birds may roost and breed (del Hoyo et al., 2019; Matarazzo-Neuberger, 1992; Saiki et al., 2009; Sick, 1997; Simões, 2010).

In this study, we evaluated how bird species traits interact with house characteristics. This knowledge is important as many specie's traits may be strongly associated with urban characteristics, affecting species persistence and ecological functions provided by birds in urban ecosystems (Leveau et al., 2020; Pauw and Louw, 2012; Pena et al., 2017; Sekercioglu, 2012), driving distinct management and conservation strategies (Chace and Walsh, 2006; Chávez-Zichinelli et al., 2010; Pike et al., 2017). We tested how the balance between primary productivity of housing areas (proxy by the mean NDVI values) and red clay roofs (RCR - as a nest site broadly available in Brazilian cities) influence the presence of species traits, relative abundance, and FD indices of birds living in a Neotropical megacity. Based on previous studies (Bino et al., 2008; Leveau et al., 2020, 2018), we predict that (1) high mean NDVI, that is, high primary productivity and low urban infrastructures (including RCR values) may increase habitat and resources availability in ecosystems and support high species diversity and functional richness due to high occupancy of diverse functional groups (i.e., frugivores-nectarivores, insectivores, scavengers, carnivores, lighter to medium biomass, and tree nesters); (2) both high NDVI and RCR values should significantly increase bird's abundance (Abu) and functional evenness (FEve) – associated to high dominance of synanthropic bird groups (i.e., roofs-, chimneys-, and pole lamp nesters, aerial and ground foragers, and heavier biomass); (3) low rates of RCR cover and NDVI values should reduce the dominance of fewer abundant functional traits (buildings-, tree/pole lamps-, chimney-, and roof nesters, omnivores/insectivores, aerial foragers, large- and medium sized species, reducing FEve and increasing FDiv of birds in housing areas.

Methods

Study area

We conduct the study in urban dwellers areas of São Paulo (23°32’56”S, 46°38’20”W, 12.2 M inhabitants, 7,400 people per km²) and Guarulhos (23°27’46”S, 46°31’58”W, 1.3 M inhabitants, 3,800 people per km²) municipalities, which encompass a set of 39 municipalities called São Paulo metropolitan region (hereafter São Paulo megacity), in southeastern Brazil (23.54°W, 46.63°S; Figure 1). São Paulo megacity is the most populous urban area of the southern hemisphere (~22 M inhabitants), creating a large territory (2100 km²) densely urbanized across the Atlantic Forest biome - one of the biodiversity hotspots of the world (Cincotta et al., 2000; IBGE, 2020; Myers et al., 2000). São Paulo and Guarulhos municipalities harbor 60% of the human population of the São Paulo megacity and represent the main South American financial center (IBGE, 2020).

The regional climate is humid subtropical with mild, dry winters, and rainy summers with moderately high temperatures (Alvares et al., 2013). The native vegetation includes dense rain forest, a typology of Atlantic Forest Biome (Veloso et al., 1991). São Paulo and Guarulhos territories originally were floodplains of “Várzea do Tiete”, fields, and native forests. Since the 1940s, the region has faced intense urbanization process and rapid population growth, leading to the removal of massive portions of native vegetation (Braga et al., 2006; Instituto Florestal, 2020). Currently, the region is highly-dense habited (housing areas) with urban infrastructure as builds (and their roofs), roads and streets, light and telecommunication structures (e.g., pole lamps, cables, towers), traffic cars, and citizens (IBGE, 2020). This caused the suppression of large native forest patches, which today are found around cities (> 1000 ha, i.e., Serra do Mar and Serra da Cantareira state parks). These sites conserve an important pool of Atlantic Forest bird diversity (Schunck et al., 2019; Tonetti et al., 2017) globally recognized as important bird areas – IBAs by BirdLife International (Bencke et al., 2006).

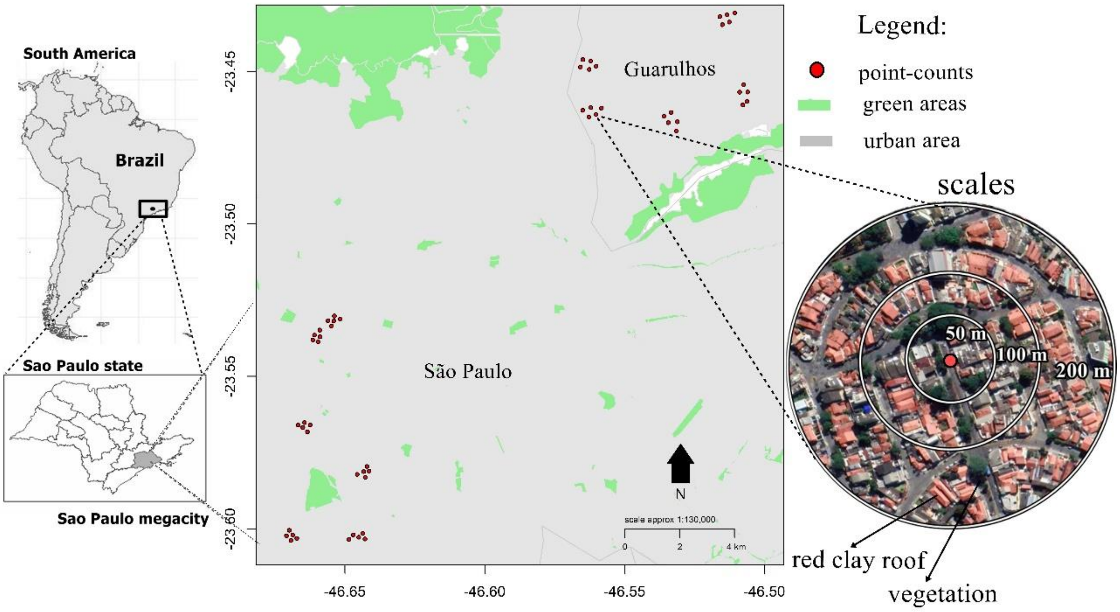

Figure 1 Distribution of 11 blocks with 55 point-count sites scattered across housing areas of São Paulo megacity, Southeast Brazil. Legend: red circles, point counts; green patches, urban green areas; gray, urban area of municipalities of São Paulo and Guarulhos; and scales, buffer zones (radius: 50, 100 and 200 m) where we take measures (%, m²) of the covers of red clay roof and vegetation.

Environmental data

We measured NDVI and Red clay roof cover from three buffer zones (50, 100 and 200 m) (Table 1). For each variable, we used ARC Gis tools and Google Earth images to build buffer zones from the center of each 55 sampled point-count sites settled across housing areas in the São Paulo megacity.

Table 1 Percentage of red clay roof (RCR) and NDVI measured in three buffer zones from point-counts in housing areas of São Paulo megacity, Southeast Brazil. The selection of the variables and measurement methods were based on the effect on birds in previous studies (Leveau et al., 2020; McClure et al., 2015). To our knowledge, the influence of RCR cover on urban birds is here first time evaluated.

Category	Buffer zone	Acronym	Method
NDVI	50 m	NDVI 50	The NDVI values were generated using the satellite images of the study areas obtained from the Landsat satellite 8 of 15th November of 2017 obtained from the Earth Explorer website (https://earthexplorer.usgs.gov/). Using bands 4 (red) and 5 (near-infrared) from these images and the following equation from the NDVI values: "NDVI = (Band 5 – Band 4) / (Band 5 + Band 4)". This step was made in the ArcGis Software Version 10.2.1. Next, NDVI values were generated for each buffer of the 50, 100, and 200m of the fixed-point. This procedure was performed using the option "Extract by mask", where only the NDVI raster values were left for each buffer. Next, the mean NDVI for each buffer was calculated using the option "Zonal Statistics", with the value in the option "Statistic type" of "mean" (to calculate the NDVI with the averages). This step was made in the ArcGis Software Version 10.2.1.
	100 m	NDVI 100	
	200 m	NDVI 200	
RCF	50 m	RCR 50	The values of the RCRs were obtained using public satellite images from Google Earth (Google, 2020). We performed a digital image classification to recognize spectral patterns of RCR pixels from these images, converted in ".tiff". For this, we used the tool "Image Classification", and through it we used the tool "Training Sample Manager". Using the "Draw Polygon" option, we created distinctive regions of interest including areas of Red clay roofs. These polygons served as the basis for the supervised classification of RCRs. All these steps were made using the ArcGis Software Version 10.2.1. We use the Kappa statistic to validate the accuracy of the digital image classification. For this we used 70 ground truth points that were located in areas of RCRs. As a reference, the Kappa statistic ranges from 0 to 1, and 1.0 indicating a perfect agreement of the digital image classification (van Vliet et al., 2011). The Kappa value of the brick areas was n = 1.0, classified as a perfect agreement for the RCRs in the digital image classification. Next
	100 m	RCR 100	
	200 m	RCR 200	

			we checked the area of the RCRs in m^2 for each point-count separated in buffers of 50, 100, and 200m respectively.

Bird data

Birds were surveyed in eleven blocks of housing areas scattered across São Paulo and Guarulhos municipalities, in southeastern Brazil. Each housing block was sampled by five fixed point-counts, adding 55 point-count sites (Suppl. Mat. 1). For attending independence of sampling, a minimum distance of 200 m between each point-count (Ralph et al., 1993) and 1 km distant to each other housing block was observed. We recorded the number of contacts of specimens heard and/or seen (8x42 mm binoculars) in each point count sampling, along 10 minutes- 50 m limited radius (Bibby et al., 1993). We counted birds flying over only when foraging (*e.g.* aerial insectivores; Hirundinidae and Apodidae). To avoid bird count bias, (1) only the first author performed all bird counts; (2) all point-count sites were equally surveyed three times in a randomized order, and never revisited in the same month; (3) we conducted bird surveys from September to March (2017-2018), when birds are more conspicuous due to the reproductive season (Sick, 1997) and more completeness with the arrival of migratory species (Somenzari et al., 2018); and (4) we performed surveys at the first three hours of the day on sunlight enough to perform bird counts and avoided rainy, windy, and foggy days.

Bird functional traits

We classified bird species based on functional traits most common used to describes their ecological roles within the avian community (diet type, foraging strata, biomass, Petchey and Gaston, 2006; Wilman et al., 2014), and nest sites, due to the persistence capability of the avian species in ecosystems (James Reynolds et al., 2019; Tomasevic and Marzluff, 2017) (Table 2).

Table 2 Bird functional traits used in the functional diversity analyses performed in São Paulo megacity, Southeast Brazil.

Functional group	**Trait classification**
Diet [1]	six categories: 1) plant/seed, 2) frugivores-nectarivores, 3) omnivores, 4) insectivores, 5) carnivores, and 6) scavengers
Foraging strata [1]	four categories: 1) ground, 2) canopy, 3) mixed, and 4) aerial
Nest site [2]	six categories: 1) buildings, 2) roofs, 3) chimney, 4) artificial hole, 5) tree/post, and 6) trees - includes shrubs
Biomass (g) [1]	four classes: (1) 0-49g, lighter; (2) 50-99g, lighter-medium; (3) 100-199g, medium; and (4) >200g, heavier

Sources: 1, Wilman et al. (2014); 2, James Reynolds et al. (2019); Sick (1997); Sigrist (2009); Tomasevic and Marzluff (2017).

Other classifications were here used only to characterize the bird assemblage. Migrants (Somenzari et al., 2018): migrant species (MGT), have populations that regularly and seasonally move away from their breeding sites and return in every breeding season; partially migratory (MPR) are species in which only part of their populations has migratory behavior, while the other individuals are sedentary; and resident (RE) species occupy the same area all year round, including nomadic birds. Distribution range: Atlantic Forest endemic, species restrict to the biome (Vale et al., 2018); wide-distributed, species occurs in more than one biome (Sick, 1997); exotic, non-native birds introduced by humans (Sick, 1997); and allochthonous, native birds introduced by anthropic actions in a region without historic occurrence (Schunck, 2008). Bird conservation status was based on regional (São Paulo, 2018) and global (IUCN, 2019) red lists. We considered the following categories: threatened, taxa classified as vulnerable, endangered, or critically endangered; near-threatened, species close to being at high risk of extinction in the near future; and least-concern, species unlikely to become extinct in near future. Nomenclature follows that of the Brazilian Ornithological Records Committee (Piacentini et al., 2015).

Bird indices

We used bird species richness (BSR) and abundance (Abu) as taxonomical indices. To the first, we considered the total accumulated of the number of species observed in each site (Gotelli and Colwell, 2011), while to the second, we used the maximum number of contacts from each species observed in one of the three samplings (Sandström et al., 2006), avoiding thus oversampling caused by repeated sampling in each point-count.

To calculates FD indices, we followed the protocol proposed by Laliberté and Legendre (2010). Functional distance between each bird species pair was calculated according to their trait values using Gower's distance (Gower, 1966; Podani, 1999). A functional distance matrix was then submitted to principal coordinate analysis (PCoA) to obtain a subset of PCoA axes for use as new "traits". For this, we used the *pcoa* function of the *ape* package (Paradis and Schliep, 2018). Finally, FD indices were calculated using the new "traits" data and relative abundance data. Bird indices such as BSR, Abu and five functional diversity (FD) indices were calculated for each site, using the *dbFD* function of the *FD* package (Laliberté et al., 2014; Laliberté and Legendre, 2010). However, to describe bird community, we used only three FD indices. Functional richness (FRic) is the volume of multidimensional space occupied in the community within the functional space (Villéger et al., 2008). High values of FRic occurs when the available resources are more efficiently used by organisms (Mason et al. 2005). As functional richness (FRic) and bird species richness (BSR) are monotonically related (Mason et al., 2005; Petchey and Gaston, 2006), we used both indices because they provide a better comprehension of how unique functional traits are associated with changes in species in the community (Oliveira et al., 2020). Functional evenness (FEve) is the evenness of abundance distribution in the functional trait space (Mouillot et al., 2005; Villéger et al., 2008). The FEve values decrease either when abundance is less evenly distributed among species or when functional distances among species are less regular (Villéger et al., 2008). Functional divergence (FDiv) reflects the divergence in the distribution of abundance in the trait volume and represents niche differentiation in a biological assemblage and increases with the number of species that have unique functional trait values (Villéger et al., 2008).

Statistical analysis

All analyses were conducted in the R program version 3.5.2 (R Core Team, 2018). Prior to analysis, the data were checked for normality using Shapiro-Wilk test and evaluated for heteroscedasticity and presence of extreme outliers by plotting residuals. Next, Moran's I test was calculated to explain the absence of spatial autocorrelation for all bird indices (Moran's I: 0.02, *p-value*: >0.1) here utilized. We also examined by the presence of multicollinearity problems in our environmental variables using the *vif* function of the *usdm* package (Naimi et al., 2014). Due to the high variance inflation factor (VIF > 5), RCR 100 was excluded, resting five uncorrelated and suitable variables to perform our analyses (Suppl. Mat. 1).

To test the relation between bird indices (i.e., BSR and Abu; and FRic, FEve, and FDiv) and environmental characteristics of housing areas (mean NDVIs 50, 100, and 200, and RCR 50 and 200), we fitted generalized linear models (GLMs) with Gaussian distribution because all dependent variables were continuous. For each bird indices, we used *glm* function of the *stats* package (R Core Team, 2018) to build a global model including all environmental variables and possible combinations (i.e., NDVI100: RCR 100, and others). We also included a null model representing the absence of effect of predictor variables for thus evaluate if the models were better than would be expected by chance. We then computed the Akaike's Information Criterion (AIC) corrected for small sample size (AICc, Burnham and Anderson, 2002) and the difference in AICc between each model and the model with the lowest AICc (ΔAICc). Models with ΔAICc < 2.0 were selected as "better" because they provide substantial support and equally plausible (Burnham and Anderson, 2002). Finally, the best model results were plotted using *visreg2d* function of the *visreg* package (Breheny and Burchett, 2017).

To investigate the relationships between bird species' traits/functional groups and urban environmental variables (NDVI and RCR categories), we used three matrices: species abundance data (L), environmental variables (R), and species traits (Q) in a fourth-corner analysis (Brown et al., 2014). The fourth-corner model is good to reveal how species traits and environmental variables are associated. It provides coefficient values that quantify strength and direction (positive, neutral or negative) of associations. For this, we used *traitglm* function of the package *mvabund* with a negative binomial distribution (Wang et al., 2012), considering the least absolute shrinkage and selection operator (LASSO) penalty via the *glm1path* method. It was used to remove all interactions that failed to improve model fit, obtaining thus the most parsimonious model. The same analysis was repeated without specifying a trait matrix (Q) to fits a multivariate species distribution model, obtaining then a different environmental response for each species.

Results

Avifauna characterization

A total of 2,428 contacts from 40 bird species were recorded (Suppl. Mat. 2, Figure 2), representatives of 20 families and eight orders. The most recorded birds were Rock Dove (*Columbia livia*, 15.3% of contacts), Plain Parakeet (*Brotogeris tirica*, 11.8%), Blue-and-white Swallow (*Pygochelidon cyanoleuca*, 8.4%), House Sparrow (*Passer domesticus*, 7.8%), and Sayaca Tanager (*Tangara sayaca*, 7.6%). Exotic birds were represented by Rock Dove, House Sparrow, and Common Waxbill (*Estrilda astrild*, 0.5%) (Sick, 1997), and allochthonous were Red-shouldered Macaw (*Diopsittaca nobilis*, 2.2%), Yellow-chevroned Parakeet (*B. chiriri*, 0.1%), and Turquoise-fronted Parrot (*Amazona aestiva*, 0.5%) (Schunck, 2008). The latter is a regional near-threatened bird (São Paulo, 2018). Thirty-two species have wide geographic distribution (Sick, 1997), and Plain Parakeet is the unique Atlantic Forest endemic bird (Vale et al., 2018) restrict to part of Serra do Mar ecoregion (Cracraft, 1985). Sick's Swift (*Chaetura meridionalis*, 2.8%) and Tropical Kingbird (*Tyrannus melancholicus*, 1.6%) are migrant and partial migratory birds, respectively (Somenzari et al., 2018) (see Suppl. Mat. 2, Figure 2).

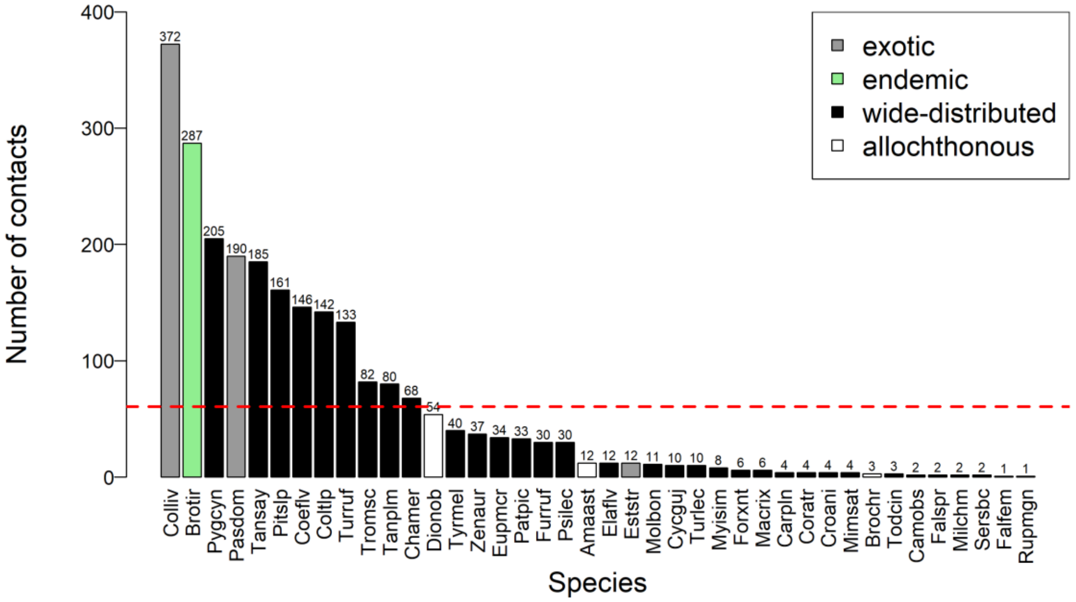

Figure 2 Bar plots showing (decrescent order) the number of contacts of the bird species recorded in São Paulo megacity's housing areas, Southeast Brazil. Legend: geographic distribution: gray, exotic; green, Atlantic Forest endemic; black, native *widely distributed*; and white, allochthonous. Red dashed line, represents the mean number of contacts (60.7) in this study.

Most of bird species (n = 29, 72.5%, i.e. mainly Tyrannidae, Thraupidae, and Turdidae) depends on trees as nest site. However, the more abundant birds (e.g., Plain Parakeet, House Sparrow, White-eyed Parakeet - *Psittacara leucophthalmus*, and others) have the potential to nest under house's roofs constructed with red clay tiles, followed by those that use buildings (i.e., Rock Dove and Blue-and-white Swallow), artificial holes (House Wren, *Troglodytes musculus*), and chimneys (Sick's Swift). The richest diet groups were insectivores (12 spp.), plant/seedeaters (10), and omnivores (8), followed by frugivores-nectarivores (5), carnivores (3), and scavengers (2). Most species (26) foraged in mixed strata, with few on the ground (8), canopy (4), and aerials (2). Lighter-weighted birds were the richest group (0-49 g, 21 spp.), with fewer heavier (> 200 g, 8 spp.), lighter-medium (50-99 g, 6 spp.) and medium (100-199 g, 5 spp.) species (Suppl. Mat. 2).

Bird relationship with NDVI/RCR

Our best rank-models showed strong relation between bird taxonomical/FD indices and mean NDVI and RCR interactions, at distinct buffer scales (Table 3). Bird species richness increased with high mean NDVI 100 and reduced RCR 200 cover (wAICc = 0.340 Figure 3a, Table 3). Functional richness (FRic) increased with synchronized increases of NDVI 50 and RCR 50 (wAICc = 0.387, Figure 3b, Table 3), with FRic increasing more slowly than BSR and on a smaller scale than that latter. High NDVI 200 m and RCR 200 maintained high FEve (wAICc = 0.606, Figure 3c, Table 3), and lesser RCR 200 and NDVI 100 increased bird's FDiv values (wAICc = 0.398, Figure 3d, Table 3). Bird's abundance models were not distinct from the null model and were excluded from our dataset.

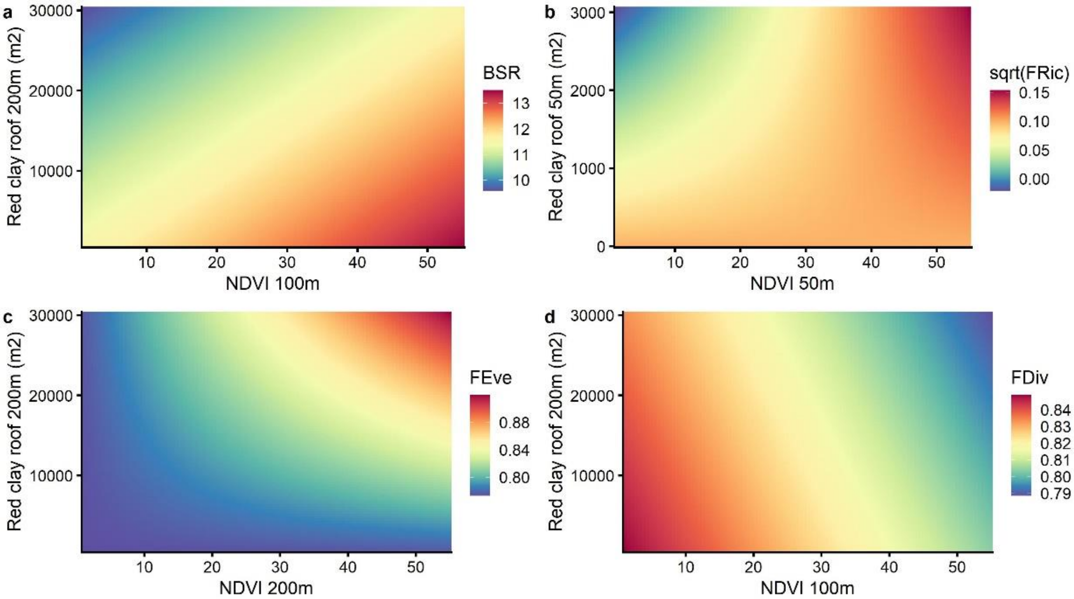

Figure 3 Relationship between environmental characteristics (NDVI and RCR from distinct buffered zones: 50, 100, and 200 m) and bird indices recorded in housing areas of São Paulo megacity, southeastern Brazil. a) BSR, bird species richness; b) FRic, functional richness; c) FEve, functional evenness; and e) FDiv, functional divergence. Hot and cold colors represent higher and lower values, respectively.

Table 3 GLM models showing the relationships between covers of red clay roof and NDVI and bird taxonomic and functional diversity indices in the housing areas of São Paulo megacity, Southeast Brazil.

Response variable	**Model**	**df**	**AICc**	**ΔAIC**	**wAIC**
BSR ~	**ndvi100 + rcr200**	4	228.6	0	0.340
	ndvi100 + rcr200 + ndvi50:rcr50	5	228.8	0.2	0.310
	ndvi100	3	230	1.4	0.167
	ndvi100 + ndvi200 + rcr200 + ndvi50:rcr50	6	231	2.4	0.103
	null	2	232.9	4.3	0.040
	ndvi50 + ndvi100 + ndvi200 + rcr200 + ndvi50:rcr50	7	233.4	4.8	0.030
	ndvi50 + ndvi100 + ndvi200 + rcr50 + rcr200 + ndvi50:rcr50	8	236.1	7.5	0.008
	ndvi50 + ndvi100 + ndvi200 + rcr50 + rcr200 + ndvi100:rcr50 + ndvi50:rcr50	9	238.9	10.4	0.002
	ndvi50 + ndvi100 + ndvi200 + rcr50 + rcr200 + ndvi200:rcr200 + ndvi100:rcr50 + ndvi50:rcr50	10	241.9	13.4	0
FRic ~	**ndvi50:rcr50**	**4**	**-315**	**0**	**0.387**
	null	2	-313.9	1.1	0.225
	rcr50 + ndvi200:rcr200 + ndvi50:rcr50	5	-313.3	1.7	0.169
	ndvi200 + rcr50 + ndvi200:rcr200 + ndvi50:rcr50	6	-313.1	1.8	0.153

	ndvi50 + ndvi200 + rcr50 + ndvi200:rcr200 + ndvi50:rcr50	7	-310.7	4.3	0.046
	ndvi50 + ndvi100 + ndvi200 + rcr50 + ndvi200:rcr200 + ndvi50:rcr50	8	-308.4	6.5	0.015
	ndvi50 + ndvi100 + ndvi200 + rcr50 + rcr200 + ndvi200:rcr200 + ndvi50:rcr50	9	-305.8	9.2	0.004
	ndvi50 + ndvi100 + ndvi200 + rcr50 + rcr200 + ndvi200:rcr200 + ndvi100:rcr50 + ndvi50:rcr50	10	-302.9	12.1	0.001
FEve ~	**ndvi200 + rcr200**	**4**	**-119.1**	**0**	**0.606**
	ndvi50 + rcr200 + ndvi200:rcr200	5	-117.4	1.7	0.256
	ndvi50 + rcr50 + rcr200 + ndvi200:rcr200	6	-115.1	3.9	0.085
	ndvi50 + rcr50 + rcr200 + ndvi200:rcr200 + ndvi50:rcr50	7	-113.1	6	0.03
	null	2	-111.3	7.8	0.012
	ndvi50 + rcr50 + rcr200 + ndvi200:rcr200 + ndvi100:rcr50 + ndvi50:rcr50	8	-110.4	8.7	0.008
	ndvi50 + ndvi100 + rcr50 + rcr200 + ndvi200:rcr200 + ndvi100:rcr50 + ndvi50:rcr50	9	-107.6	11.5	0.002
	ndvi50 + ndvi100 + ndvi200 + rcr50 + rcr200 + ndvi200:rcr200 + ndvi100:rcr50 + ndvi50:rcr50	10	-104.7	14.4	0
FDiv ~	**ndvi100 + rcr200**	**5**	**-212.4**	**0**	**0.398**
	null	2	-211.7	0.7	0.281
	ndvi100 + ndvi200:rcr200	4	-210.3	2	0.143
	ndvi50 + ndvi100 + rcr200 + ndvi200:rcr200	6	-210.1	2.3	0.125
	ndvi50 + ndvi100 + rcr200 + ndvi200:rcr200 + ndvi50:rcr50	7	-207.4	4.9	0.034
	ndvi50 + ndvi100 + rcr200 + ndvi200:rcr200 + ndvi100:rcr50 + ndvi50:rcr50	8	-205.5	6.9	0.013
	ndvi50 + ndvi100 + rcr50 + rcr200 + ndvi200:rcr200 + ndvi100:rcr50 + ndvi50:rcr50	9	-203.7	8.7	0.005
	ndvi50 + ndvi100 + ndvi200 + rcr50 + rcr200 + ndvi200:rcr200 + ndvi100:rcr50 + ndvi50:rcr50	10	-200.7	11.7	0.001

Legend: taxonomical = BSR, bird species richness; and functional indices = FRic, functional richness; FEve, functional evenness, and FDiv, functional divergence. Abundance null model was the most significant between other models and wasn't shown in this table.

We also found strong associations between birds (species and functional groups) and housing environmental characteristics (mean NDVI and RCR cover) measured over distinct buffer zones (Figure 4 a-b). Species and functional groups showed had local scale sensitivity, revealing that some functional groups and taxa were central to drive changes on the abovementioned bird indices. High NDVI 100 and low RCR 200 allowed the presence of a greater number of species. The species as Southern Caracara, Bananaquit, Ruddy-ground Dove, Palm Tanager, Sayaca Tanager, Rufous-bellied Thrush – *Turdus rufiventris*, Tropical Kingbird were benefited high NDVI, whereas lesser RCR 100 cover had positive associations with Sick’s Swift, Swallow Hummingbird, Rufous Hornero, House Sparrow, and House Wren (Figure 4b).

The increased coverage of NDVI 50 and RCR 50 supported diverse functional groups in the functional niche space. For example, roof-nesters (Plain Parakeet and House Sparrow), chimney-nesters (Sick’s Swift), aerial insectivores (Blue-and-White Swallow), frugivore-nectarivore (Bananaquit and Palm Tanager), and lighter-medium to medium biomass birds (Rufous-bellied Thrush and Smoothed-bill Ani – *Crotophaga ani*). The increase in NDVI 50 and RCR 50 also converged for the presence of ground foragers (Common Waxbill, Rufous Hornero, and Rock Dove), and insectivorous (Common Tody-Flycatcher – *Todirostrum cinereum*), and Picazuro Pigeon and Turquoise-fronted Parrot (Figure 4a-b).

High values of NDVI 200 and RCR 200 were related to great bird’s trait abundance. Large biomass birds (>200 g, e.g., Rock Dove, Southern Caracara - *Caracara plancus*) were positively related to RCR 200, and negatively influenced by NDVI 100 (i.e., Picazuro Pigeon - *Patagioenas picazuro*). A similar and weak relation was observed for birds that nest on trees and pole lamps (e.g., Great Kiskadee). Roof nesters, carnivores, and aerial foragers (e.g., Blue-and-white Swallow and Sick’s Swift) had a strong and negative relations with NDVI 100. Both scavenger (Southern Caracara) and insectivorous (Sick’s Swift, Smooth-billed Ani, Yellow-bellied Elaenia - *Elaenia flavogaster*, and Rufous Hornero) groups increased, respectively, with NDVI 100 and 200, and with RCR 200. Plant-seed (Picazuro Pigeon and Ruddy Ground-Dove) strongly decreased with NDVI 200, like birds that nest at buildings (Blue-and-white Swallow) and canopy foragers (Red-shouldered Macaw and Yellow-bellied Elaenia) decreased with RCR 200. This latter also was negatively related to omnivorous and lighter-medium (50-99 g) weight birds. Birds that nest under roofs (i.e. Plain Parakeet and House Sparrow, respectively) also increased with RCR 200 (Figure 4,ab).

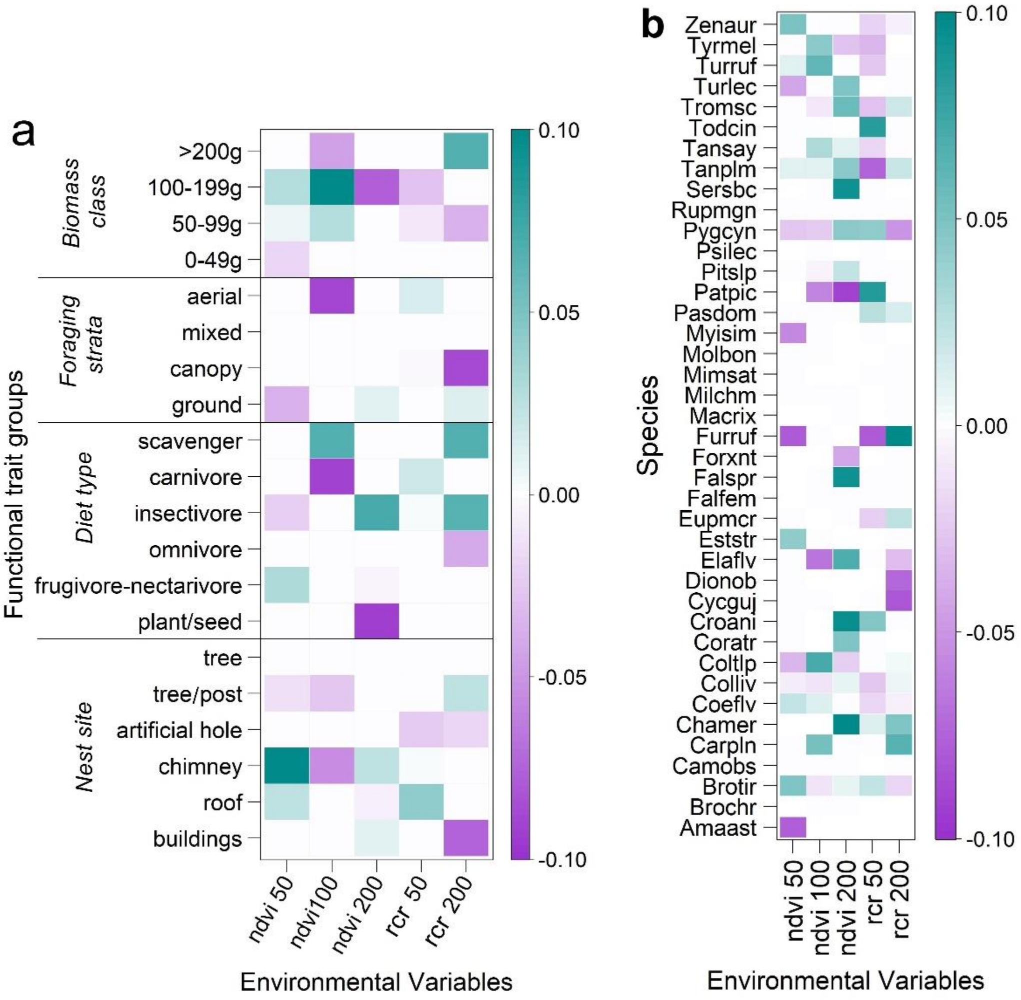

Figure 4 The relationship among the environmental variables and a) bird functional traits and b) species identity. Colors represent the strength of the interactions (shading) and their direction (green, positive and purple, negative). The scaled bar represents the values of fourth-corner coefficients. Legend: NDVI, primary productivity, and RCR, red clay roof measured at varied buffer zones (50, 100, and 200 m) from each point-count (Suppl. Mat. 1). Species acronyms are available in Suppl. Mat. 2.

Discussion

We confirmed our predictions (1) high mean NDVI 100 values and low RCR 200 cover have significantly increased BSR; (2) a synergic high mean NDVI (50 and 200) and RCR (50 and 200) significantly increased bird's FEve, and (3) a mutual low NDVI 100 and RCR 200 cover increased bird's FDiv. Contrary to our expectations, high mean NDVI 50 and RCR 50 increased bird's FRic. Our findings agree with previously described patterns of positive relationships between mean NDVI and bird taxonomical/FD indices, such as BSR, Abu, and FRic (Bino et al., 2008; Coetzee and Chown, 2016; Leveau et al., 2020, 2018) (Bino et al., 2008; Leveau et al., 2018) and reveals new insights on how bird functionality (here represented by FDiv) behaves in housing areas. Species and functional groups responded to distinct local scales, indicating diverse environmental sensitivities. The NDVI values had few ranges of variation (0-0.55), and the highest NDVI values (>0.5) support high BSR and FRic, and significantly decreased from NDVI <0.5. These results support that an NDVI threshold below 5 has strong effects in reducing BSR in urban areas (Leveau et al., 2018).

Confirming our predictions, BSR significantly increased with the interaction between high mean NDVI 100 values and RCR 200 cover. A high NDVI is a proxy of a greater amount of primary productivity which represents more availability of resources for birds (Pettorelli et al., 2005; Radeloff et al., 2019), and several studies found positive correlations between increased NDVI and high BSR and FRic in both urban and non-urban ecosystems (Bino et al., 2008; Coetzee and Chown, 2016; Leveau et al., 2018; Silva et al., 2015). Contrary to expected, we found that FRic increased only with a mutual high mean of NDVI 50 and RCR 50 values. This means that the juxtaposition between RCRs and vegetation cover in a minimal spatial scale (50 m), may improve the provision of niche and resources for bird species with unique functional traits, a distinct pattern found to BSR. However, few point-counts sites had this environmental condition required to shelter birds with unique functional traits, thus FRic increases more slowly than BSR. Our results agree that habitat simplification from urbanization converges bird species with similar functional traits (Coetzee and Chown, 2016; Croci et al., 2008; Devictor et al., 2007; Pagani-Núñez et al., 2019). The higher aggregation of high RCR and vegetation cover allowed the presence of birds having more diversified traits. These environmental conditions meet urban bird species (1) primarily dependents on vegetation for feeding, shelter, and nesting (i.e., frugivorous-nectarivorous, lighter to medium weighted body, and plant-seedeater) and those (2) weakly associated with vegetation resources in urbanized sites (i.e., insectivorous, and scavengers) which may feed on anthropogenic sources (Leveau and Leveau, 2005) and nest sites from other urban structures. There are reports of Rufous Hornero nesting on pole lamps and buildings (Marreis and Sander, 2006), Great Kiskadee on pole lamps and energy transformers (Sandoval and Barrantes, 2009), Southern Caracara over tall telecommunication towers (Maurício et al., 2013), and House Wren in a broad other human-made crevices and cavities (del Hoyo et al., 2019). In our study, House Wren nested in wall cavities, nest boxes, and pole lamps.

Although some studies investigated how roof nesters are influenced within the cities (e.g., Leveau and Leveau, 2005; Pellissier et al., 2012), to our knowledge this is the first study to evaluates the relationships between the availability of roof types and trait abundance of roof nesters. We found high FEve positively correlated with a matched high mean NDVI 200 and RCR 200 cover even without significant changes in bird’s Abu in function of sampled environmental variables. This indicates that (1) FEve and FRic changes are related to the same environmental conditions; however, the first over a larger local scale than this later; (2) FEve is more sensitive than Abu; and (3) non-significant shifts in the abundance may also drive changes in the use of vegetation and roof as resources by birds. Only roof nesters as House Sparrow (Pellissier et al., 2012) and Plain Parakeet (Simões, 2010) were positively correlated with increase in RCR cover. Others roof nesters as White-eyed Parakeet and Red-Shouldered Macaw (Saiki et al., 2009; Sigrist, 2009) were neutral or negatively correlated with high RCR cover, respectively. This likely reflects different dynamics of roof nest occupation by those species. In our study site, abundant colonies of House Sparrow and couples of Plain Parakeet utilize RCR as breeding sites (*pers. obs.*). On the other side, populations of White-eyed Parakeet and Red-shouldered are expanding (Tonetti et al., 2017, *pers. obs.*), which still found large niche vague in housing areas of Guarulhos – most peripherical region. We reported for the first time, an Atlantic Forest endemic bird - Plain Parakeet (Vale et al., 2018), leading advantages in urban ecosystems probably influenced by the roof nest availability. Other bird's functional groups (chimney and tree-lamp post nesters, aerial and ground foragers, and large bodied species) also positively responded to both high RCR and NDVIs, contributing to high FEve in the housing areas. These last functional groups were also related to other urban structures cooccurring with RCR cover. Aerial insectivorous could be benefited in the most urbanized sites (Cruz and Piratelli, 2011; Sacco et al., 2015) likely using (1) open aerial space next to house's roofs and trees for capturing flight insects (Matarazzo-Neuberger, 1992) and by the (2) use of house's chimneys and human edifications as nesting site (Argel-de-Oliveira, 1995; del Hoyo et al., 2019; Matarazzo-Neuberger, 1992; Sick, 1997). Similarly, RCR cover may have buffered the effect that tree-post/power transformer and building density have on tree/lamp pole nesters and ground forager/large biomass birds. These birds also may be benefited by the greater availability of organic waste and anthropogenic food resources in urban settlements (Argel-de-Oliveira et al., 1998; Leveau and Leveau, 2005; Matarazzo-Neuberger, 1995; Sacco et al., 2015).

Contrary to a previous study (Coetzee and Chown, 2016), we found that bird's FDiv increased with both low NDVI 100 and RCR 200 cover. The high FDiv represent that most abundant species had extreme functional trait values compared to the functional trait space occupied by the community. Conflicting to FEve relations found in this study, a mutual reducing NDVI and RCR cover maintained a high abundance of birds with unique traits; i.e., a high abundance of birds could be maintained under a limited environmental condition in housing areas. The spatial arrangement between builds and some vegetation heterogeneity, also including urban greenspaces, could provide differential habitats for urban birds (Leveau et al., 2015; Oliveira Hagen et al., 2017; Pellissier et al., 2012) converging in augmented niche differentiation between species's assemblages. We recommend that further studies should test the isolated effects of anthropogenic food (i.e., organic wastes, processed foods, bird feeders, pet foods, and other sources) (Argel-de-Oliveira et al., 1998; Leveau and Leveau, 2005; Pena et al., 2017) on urban bird communities.

Conclusions

Our study provides important comprehension of how interactions between vegetation cover and urban infrastructures could affect bird species and FD's facets in housing areas. We showed that functional bird traits and diversity metrics respond to environmental changes at different local scales, suggesting the need to apply distinct management strategies for improving bird conservation in Neotropical urban spaces. A high NDVI and RCR covers (and other urban resources) benefited large native bird populations (including until same Plain Parakeet, an Atlantic Forest endemism), but also supported a high abundance of exotic species (Rock Dove and House Sparrow). Whether urban planners and decision-makers objectives are increasing in species and ecosystem functions within the urbanized areas (Oliveira Hagen et al., 2017; Sol et al., 2014), the best configuration between high NDVI (> 0.5) (Leveau et al., 2018) and high RCR cover at a smaller scale is recommended to improve bird conservation in Neotropical cities. This stresses that urban planners, engineers, and architects should focus attention on house's roofs and other urban attributes in highly habited areas, which should be managed to (1) reduce negative impacts of invasive species on native birds and increase suitable habitats for more diverse local avian assemblages (García-Arroyo et al., 2020; MacGregor-Fors et al., 2017, 2010). To achieve this goal, the increase of street-tree diversity plantings (da Silva et al., 2020; Pena et al., 2017; Sacco et al., 2015) is central, including large trees (Morelli et al., 2017) with varied reproductive phenology (Gagetti et al., 2016). Massive use of "green roofs" and “vertical gardens” in Neotropical cities, which are very scarce in the region (Escobar-Ibáñez and MacGregor-Fors, 2017), could also provide additional habitat and resources for birds, as related in other regions of the world (Deng and Jim, 2017; Lundholm, 2015; Wang et al., 2017; Washburn et al., 2016). These strategies likely would maximize biodiversity gains (Williams et al., 2014), climate regulation, carbon sequestration, public health, and citizen well-being (Alho, 2012; Fuller et al., 2007; Hystad et al., 2014; Tratalos et al., 2007) even in the largest Neotropical cities.

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Considerações finais

O presente estudo demonstrou de diferentes formas como a urbanização da maior metrópole da América do Sul impacta negativamente as comunidades de aves e diversidade funcional da Mata Atlântica. O presente estudo ainda aponta quais as características ambientais influenciam a manutenção de comunidades mais diversas, tanto taxonomicamente e/ou funcionalmente, fornecendo assim medidas específicas de manejo para os dois ambientes mais comumente encontrados em cidades (parques urbanos e áreas densamente habitadas), a fim de aumentar a ocorrência de funções ecossistêmicas nestes habitats.

De modo geral, este estudo ressalta a importância de preservar grandes áreas protegidas de floresta nativa (LNF) no entorno imediato de uma megacidade Neotropical para reduzir a enorme perda de espécies e, presumivelmente, aumentar o fornecimento de bens e serviços ecossistêmicos (e.g., controle de insetos, dispersão de sementes, polinização, ciclagem de nutrients e outros) em áreas verdes urbanas, mas não em áreas densamente habitadas/residenciais. Esta massiva perda de espécies e diversidade funcional das aves em áreas verdes urbanas e, principalmente em áreas densamente habitadas, está relacionada com a simplificação dos habitats urbanos quando comparados com os grandes fragmentos de floresta nativa. Neste sentido, a quantidade e altura das edificações, poluição luminosa (aqui representada pelos postes de lampadas) e presença de aves invasoras foram fortes indutores da dominância de poucas espécies e homogeneização funcional dentro dos habitats urbanizados. Além disso, urbanização reduz drasticamente o tamanho das áreas verdes e aumenta as distâncias entre estas e áreas fontes, geralmente localizadas nos limites da cidade. Estes dois fatores impactaram negativamente o número de espécies e riqueza funcional das comunidades de aves que vivem em habitats urbanos (áreas verdes e áreas densamente habitadas) quando comparado com as áreas fontes.

Por outro lado, este estudo demonstrou que, tanto em escala local como regional, o aumento das coberturas de herbáceas e arbustos foram responsáveis por aumentar a co-ocorrência de espécies de aves com características funcionais únicas (maior FRic) em grandes áreas de florestas nativas e em áreas verdes urbanas. Provavelmente, isto ocorreu devido ao incremento da largura de nicho (Laliberté & Legendre, 2010; Mason et al., 2005) aumentando o número de espécies funcionalmente distintas (Melo et al., 2020), enquanto que cobertura de árvores, em escala regional, aumentou a regularidade da abundância dos traços funcionais no espaço de nicho funcional, melhorando a eficiência do uso dos recursos (Mason et al., 2013; Villéger et al., 2008). Entretanto, o aumento da cobertura arbórea em pequenas áreas verdes impactou o espaço funcional das aves residentes, provavelmente pela redução da heterogeneidade ambiental - a qual as espécies respondem positivamente.

Por fim, o aumento da produtividade primária (vegetação) junto a disponibilidade de telhados de barro (RCR), onde as espécies utilizam como sítio de nidificação, também foi importante para que áreas densamente habitadas mantivessem maior número de espécies e riqueza funcional. Outras características presentes nas cidades como chaminés, transformadores de energia elétrica, postes de eletricidade, antenas de telecomunicação e muros fornecem cavidades articiais e locais de forrageamento para as aves. Assim, uma melhor distribuição espacial destas características urbanas com aumento da vegetação pode incrementar a ocorrência de espécies de aves e de suas funções ecossistêmicas em áreas densamente habitadas.

Supplementary Materials:

Click on the links below to access supplementary materials of each chapter.

1. *Chapter 1*

    Online Resource 1 https://drive.google.com/file/d/1Ps8RypzlVR6RWo_q3WpH_eW56wZKBRGL/view?usp=sharing

    Online Resource 2 https://drive.google.com/file/d/1_Hb4OyxioT7Z6KaRu5Q6mFv9zw_saejj/view?usp=sharing

2. *Chapter 2*

    Suppl. Mat. 1
    https://drive.google.com/file/d/1-O57At3jI7ZRdnfjNc5biqh6u3ANKAvX/view?usp=sharing

    Suppl. Mat. 2
    https://drive.google.com/file/d/1aifVINUrKcm5JOJ1nRXaiPvjpdA4H7Dp/view?usp=sharing

    Suppl. Mat. 3
    https://drive.google.com/file/d/12fiPctpdsbd_9TenfZkAowklpL0ij5dB/view?usp=sharing

3. *Chapter 3*

    Suppl. Mat. 1:
    https://drive.google.com/file/d/17XGfDfxoqZu_MiOmhDQEoUZ-tySUvLGh/view?usp=sharing

    Suppl. Mat. 2:
    https://drive.google.com/file/d/16NA5OTkMDFiMMrWv5M9U2lkA3XU5nfjl/view?usp=sharing