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Influência de modelos de expansão urbana na avifauna e nos processos ecológicos de consumo de frutos e controle top-down de artrópodes por aves

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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais da Universidade Federal de São Carlos como parte dos requisitos necessários para a obtenção do título de Doutor em Ciências, área de concentração em Ecologia e Recursos Naturais.

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Dedico esta tese aos meus familiares... que me apoiaram desde
sempre na minha jornada rumo a ecologia

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"Se vi mais longe foi por estar de pé sobre ombros de gigantes" (Isaac Newton)

Resumo

As cidades estão crescendo de forma rápida e heterogênea por meio de diversos modelos de expansão. Esses modelos são definidos como os padrões específicos de expansão dos espaços urbanos. Como cada modelo realiza mudanças físicas e sociais singulares ao longo da paisagem, tal característica precisa ser ponderada no planejamento urbano, a fim de equilibrar o crescimento urbano e a conservação da biodiversidade. O objetivo da tese foi o de compreender como modelos de expansão urbana do tipo compactado (i.e., *land-sparing*) e espalhado (i.e., *land-sharing*) afetam a paisagem do ecossistema urbano, e como, consequentemente, influenciam a sua biodiversidade, e por sua vez em suas funções ecológicas. Para isso utilizamos as aves como modelo biológico. No primeiro capítulo foi avaliado como esses modelos de expansão urbana afetam os tamanhos dos espaços verdes e cinzas ao longo de um gradiente de urbanização, e como, consequentemente, afeta a diversidade de aves em uma área conurbada existente entre dois municípios (i.e., Sorocaba e Votorantim) no Brasil. Os resultados mostram que existem diferenças de tamanhos dos espaços verdes e cinzas entre os modelos de expansão urbana, com maiores valores de espaços verdes para o modelo compactado, possuindo inclusive maiores valores de diversidade funcional das aves. Esse resultado pode embasar medidas voltadas à conservação de áreas verdes de tamanhos maiores, uma vez que foi detectada relação positiva entre a área de florestas nativas e área de árvores isoladas e diversidade de aves. Além disso, o resultado pode embasar o direcionamento do crescimento das cidades para o modelo compactado ao invés de espalhado, pois foi registrado maior diversidade funcional de aves no primeiro modelo. O segundo capítulo busca entender como esses dois modelos de expansão urbana afetam a diversidade de aves frugívoras e também o seu consumo de frutos. Os resultados mostram que (1) há maiores valores de diversidade funcional das aves para o modelo compactado ao invés do espalhado, (2) há relação

positiva entre diversidade funcional de aves e extensão de áreas verdes, e há (3) relação positiva entre diversidade funcional de aves e consumo de frutos. Esses resultados podem embasar medidas voltadas ao direcionamento do crescimento das cidades para o modelo compactado ao invés de espalhado, uma vez que foi detectada maior diversidade funcional de aves, e em também medidas protetivas voltadas à conservação de áreas verdes urbanas mais extensas. Uma vez que o consumo de frutos está relacionado a processos ecológicos como a dispersão de sementes e estrutura da dinâmica de redes entre plantas e frugívoros, que consequentemente, afetam a distribuição e nível populacional de plantas, esses resultados podem auxiliar também no bem-estar das pessoas que vivem nas cidades, uma vez que plantas desempenham diversos tipos de serviços ecossistêmicos. O terceiro capítulo busca entender como esses dois modelos de expansão urbana afetam a diversidade de aves insetívoras e também o seu papel no controle predador-presa de artrópodes. Os resultados mostram que (1) há maiores valores de diversidade funcional das aves insetívoras para o modelo compactado ao invés do espalhado, (2) há relação positiva entre diversidade funcional de aves insetívoras e extensão de áreas verdes, e há (3) relação positiva entre diversidade funcional de aves insetívoras e controle predador-presa de artrópodes. Esses resultados podem embasar medidas direcionadas ao crescimento das cidades para o modelo compactado ao invés de espalhado, uma vez que foi detectada maior diversidade funcional de aves insetívoras, e também em medidas protetivas voltada à conservação de extensão de áreas verdes urbanas mais extensas. O controle predador-presa de artrópodes por aves está relacionado à manutenção da estrutura da dinâmica da relação aves-artrópodes, fator que afeta a distribuição e nível populacional de artrópodes. Esse resultado pode ser utilizado para subsidiar a conservação de aves insetívoras e os ecossistemas como um todo, e também no bem-estar das pessoas que vivem nesses locais, uma vez que existem artrópodes que desempenham diversos tipos de serviços e desserviços ecossistêmicos ao longo da paisagem urbana.

Palavras-chaves: *Land-sharing*, *land-sparing*, crescimento urbano, Aves Latino-Americanas, aves consumidoras de frutos, aves consumidoras de insetos

Abstract

Cityscapes are growing fast and heterogeneously through of diverse urban sprawl models. Urban sprawl models are defined as the specific patterns of the urban spaces' growth. Since each model performs unique physical and social landscape changes, this needs to be evaluated in urban planning, aiming balance the urban development and biological conservation. The main objective of the thesis was to understand how compacted (i.e., land-sparing) and sprawled (i.e., land-sharing) urban sprawl models affect the urban landscape, and how, consequently, influence its biodiversity, and in turn their ecological functions. For this we used the birds as the biological model. In the first chapter was evaluated how these urban sprawl models affect the sizes of the green and gray spaces along an urbanization gradient, and how, consequently, they affect birds' diversity in a conurbation area existing between two cities (i.e., Sorocaba and Votorantim) in Brazil. The results show that there is a difference in the sizes of the green and gray spaces between the urban sprawl models, with larger green spaces in the compacted model, and higher birds' diversity in the compacted model. This result can support strategies aimed at the conservation of larger green spaces, since a positive relationship was detected between both native forests, trees and birds' diversity. In addition, this result can support the urban growth leaded to the compacted model instead of spread, since higher birds' functional diversity was registered in the first model. The second chapter aims to understand how these urban sprawl models affect the frugivorous birds' diversity and also the fruit consumption by birds. The results show that (1) there are higher frugivorous birds' functional diversity in the compacted model instead of the sprawled, (2) there is a positive relationship between frugivorous birds' functional diversity and the size of green spaces, and there is (3) a positive relationship between frugivorous birds' functional diversity and fruit consumption by birds. These results can support strategies leading the cities growth for the compacted model instead of sprawled, since higher frugivorous birds' functional diversity was detected, and also in conservation actions aimed at conserving of larger urban green spaces. Fruit consumption is related to ecological processes, e.g., seed dispersal and the structure of plants-frugivores networks dynamics, which consequently affect the plants' distribution and population. Therefore, these results can also help in the well-being of the people who live in the cities, since plants perform ecosystem services. The third chapter aims to understand how these urban sprawl models affect the insectivorous birds' diversity and their ecological function related to the top-down control of arthropods. The results show that (1) there is higher insectivorous birds' functional diversity in the compacted model than in the sprawled, (2) there is a positive relationship between insectivorous birds' functional diversity and green spaces' size, and also that there is (3) a positive relationship between insectivorous birds' functional diversity and top-down control of arthropods. These results can support strategies aimed at cities growth related to the compacted model instead of spread, since greater insectivorous birds' functional diversity was detected, and also in conservation efforts leaded in larger urban green spaces. The top-down control of arthropods by birds is related to the maintenance of the bird-arthropod dynamics' structure, a factor that consequently, affects the arthropods' distribution and population. Arthropods perform many ecosystem services and disservices along the urban landscape. Therefore, these results can influence the insectivorous birds' conservation, and also the well-being of the people who live in the cityscapes.

Keywords: Land-sharing, land-sparing, urban development, Neotropical cityscapes, fruit-eating birds, insect-eating birds

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1 Introdução geral

1.1 A expansão urbana e a avifauna

Atualmente mais da metade da população humana reside em paisagens urbanas (Nations, 2019), e as cidades estão crescendo de forma rápida e heterogênea, criando padrões irregulares ao longo de toda a paisagem (Ramalho & Hobbs, 2012). A urbanização é um massivo e rápido modificador da paisagem (Leveau et al., 2020), e um causador global de ameaças às espécies (Grimm et al., 2008; MacGregor-Fors et al., 2020). Esse processo aciona consequências imediatas e de longo prazo à biota global, reduzindo principalmente a diversidade de espécies (Carvajal-Castro et al., 2019; Zurita et al., 2017), afetando diversos níveis de organização da biota (Blair, 2004).

O crescimento das cidades, causado pelo processo de expansão urbana, surge a partir das demandas humanas por recursos sociais, e.g., moradias e áreas de industrialização (Mehriar et al., 2020; Nassar et al., 2014), e pode ser definido como um processo multidimensional de expansão da periferia de uma cidade (Heirman & Coppens, 2013). A expansão urbana causa mudanças físicas ao longo da paisagem, e ocorre de diferentes maneiras, decorrentes de características sociais, políticas, financeiras e ambientais (Rubiera-Morollón & Garrido-Yserte, 2020). Essas formas de expansão urbana, também conhecidas como modelos de expansão, são definidas como padrões específicos dos assentamentos urbanos novos, e que podem influenciar de formas distintas as comunidades biológicas (McDonald et al., 2020). Pesquisas têm focado em buscar as melhores formas de direcionar o desenvolvimento urbano, sob os pontos de vista socioeconômicos e ambientais (Bibri et al., 2020; Bontje, 2001; Mehriar et al., 2020; Wolff et al., 2018). Tais estudos têm analisado os custos e benefícios do desenvolvimento urbano de acordo com dois tipos de modelos de expansão urbana, i.e., cidades compactadas vs. cidades espalhadas (Bibri et al., 2020). O modelo compactado visa condensar os espaços urbanos e suas estruturas em pontos adensados (Mehriar et al., 2020). Por outro lado, o modelo espalhado é um formato dispersado, com espalhamento das infraestruturas urbanas (Dieleman & Wegener, 2004). Com relação a propósitos ambientais, benefícios à biodiversidade são esperados em cidades compactadas, por meio da conservação de habitats naturais e redução de emissão de CO_2 (Liu et al., 2014). O modelo *espalhado* têm efeitos negativos socioeconômicos e ambientais, como longas jornadas para áreas de trabalho e de compras, alto consumo de energia, poluição, acidentes, demanda de maiores áreas a serem utilizadas para usos específicos da terra, menor qualidade do transporte público em áreas mais distantes (Dieleman & Wegener, 2004).

Emprestando conhecimentos dos agroecossistemas, pesquisas têm analisado os efeitos de modelos *land-sharing* e *land-sparing* de utilização dos usos da terra em áreas urbanas, a fim de fornecer um equilíbrio entre recursos essenciais aos seres humanos e conservação da biodiversidade ao longo da paisagem urbana (Dennis et al., 2019; Geschke et al., 2018; Suhonen et al., 2022). O modelo *land-sharing* é definido como um método de manejo do uso da terra que integra áreas de conservação e de produção (Fischer et al., 2014). No contexto urbano, esse método consiste de áreas de baixa densidade de áreas construídas, por exemplo, áreas residenciais, combinados com espaços verdes no formato de pequenos jardins e parques, sem grandes áreas contínuas de florestas e parques antigos (Lin & Fuller, 2013). Por outro lado, o método *land-sparing* integra a divisão de usos da terra entre conservação e produção, e dentro do contexto urbano, consiste de áreas com alta concentração de espaços construídos, e.g., prédios residenciais, compartilhado com grandes espaços verdes contínuos (Lin & Fuller, 2013). Como previamente visto em agroecossistemas

(Balmford et al., 2019; Cannon et al., 2019; Edwards et al., 2015; Edwards et al., 2021; Feniuk et al., 2019; Hasan et al., 2020), pesquisas realizadas nas cidades têm demonstrado que o modelo *land-sparing* direciona a melhores resultados para a biodiversidade. Isso porque atua na conservação biológica de diversos taxa, e.g., mamíferos (Caryl et al., 2016), aves (Suhonen et al., 2022), insetos (Soga et al., 2014), plantas (Collas et al., 2017), além da manutenção da estrutura de comunidades ecológicas (interação predador-presa; Jokimäki et al., 2020), e também na preservação de espécies raras e únicas (Suhonen et al., 2022).

As paisagens das cidades são geralmente denotadas como um grande mosaico (MacGregor-Fors & Schondube, 2011), contendo diferentes espaços urbanos, principalmente dominado por estruturas antropogênicas (Barbosa et al., 2020; Schneider et al., 2010), mas também possuindo manchas de vegetação, como florestas urbanas, parques, jardins (Campos-Silva & Piratelli, 2021; de Toledo et al., 2012; Palmer et al., 2008), e corpos d'água (Barbosa et al., 2020), os quais podem manter representativos componentes da biodiversidade nativa, como comunidades de aves. De forma simplificada, os espaços urbanos podem ser divididos em espaços cinzas e verdes, dependendo principalmente da composição de estruturas construídas não-naturais e infraestruturas naturais presentes na paisagem (Tischer et al., 2017; Wesener et al., 2017). Espaços cinzas urbanos são constituídos principalmente por estruturas construídas não-naturais e superfícies impermeáveis, os quais podem ser subdivididas de acordo com o tipo de uso, o principal tipo de infraestrutura presente, e a densidade de pessoas (e.g., áreas industriais, comerciais e residenciais; Chormanski et al., 2008; Suligowski et al., 2021). Os espaços verdes urbanos são paisagens que possuem principalmente componentes de origem de plantas e que podem ser subdivididas em classes de acordo com certas características da vegetação presente, e também de acordo com o tipo de uso pelas pessoas (e.g., florestas nativas, jardins, praças, parques) e são vitais para o bem estar das pessoas (Horwood, 2011; Jabbar et al., 2021; Zou & Wang, 2021). Cada tipo de espaço verde urbano desempenha um papel específico na conservação biológica e na manutenção das funções ecológicas desempenhadas pelas espécies (Campos-Silva & Piratelli, 2021; Lepczyk et al., 2017). Função ecológica é definida como a soma de todas as interações de uma espécie, o qual determina a sua influência ou contribuição tanto para os processos ecossistêmicos, como para os padrões das interações intraespecíficas, comportamento, e dinâmica social características de uma espécie (Akçakaya et al., 2020). Fatores socioeconômicos e geográficos são críticos para os padrões da biodiversidade ao longo da paisagem urbana; bairros mais distantes do centro da cidade e com maiores rendimentos financeiros podem ter mais áreas verdes e zonas amigáveis a biodiversidade (Wood & Esaian, 2020). Por outro lado, áreas mais próximas do centro e com menor rendimento financeiro oferece poucas oportunidades para a manutenção da biodiversidade nativa (Melles, 2005). Tem sido demonstrado que os tipos de espaços verdes urbanos e suas extensões influenciam na biodiversidade de diferentes maneiras (Lepczyk et al., 2017; Melo et al., 2021; Shahabuddin et al., 2021). Dessa forma, identificar como os modelos de expansão urbana interferem nos padrões de conformação dos espaços cinzas e verdes devem ser um tópico central a ser investigado para a conservação biológica nas cidades.

As aves são um dos organismos mais representativos dos ecossistemas globalmente (Lees et al., 2022; Sherry et al., 2020; Whelan et al., 2015), podendo ser até mesmo encontrados em paisagens onde é predominante a presença de infraestruturas cinzas, como as cidades (Aronson et al., 2014; Croci et al., 2008). No entanto, não são todas as espécies de aves que conseguem se ajustar às mudanças de uso da terra inerentes ao processo de urbanização (Aronson et al., 2014). Esse processo atua diretamente na seleção não-aleatória de traços funcionais das espécies ao longo das paisagens urbanas (Aronson et al., 2014; Croci et al., 2008). Uma vez que cada espécie desempenha uma função ecológica única no ambiente, decorrente de seus específicos traços funcionais (Tobias et al., 2022), é necessário conhecer como os padrões de urbanização afetam a seleção de espécies já que impactam diretamente em suas funções ecológicas e consequentemente nos serviços ecossistêmicos ao longo das paisagens.

Aves frugívoras são espécies chaves nos ecossistemas, direcionando padrões e processos ecológicos em diversos níveis de organização, e.g., interações tróficas e espaciais de redes de dispersão de sementes (Carreira et al., 2020; Emer et al., 2018; Rumeu et al., 2020), e que podem ser afetados por mudanças antropogênicas decorrentes do uso da terra (Fontúrbel & Medel, 2017). Muitos frugívoros são organismos especialistas no estrato de forrageamento, no habitat e no tipo de alimentação (Sekercioğlu et al., 2016; Todeschini et al., 2020); sendo muito sensíveis a mudanças nas paisagens que impactam diretamente seus recursos, incluindo a fragmentação e perdas de habitats naturais (Fuzessy et al., 2022). Grandes frugívoros geralmente são os mais negativamente afetados, desaparecendo de fragmentos pequenos (Bovo et al., 2018; Donoso et al., 2020). Esse fato interfere diretamente nos ecossistemas, e.g., causando a diminuição de sementes direcionadas pela defaunação, acionando mudanças funcionais e estruturais ao longo das paisagens (Donoso et al., 2020). Os resultados relacionados à defaunação decorrentes da perda de frugívoros podem ser muito pronunciados em áreas altamente antropizadas, como em áreas urbanas, onde a perda de espécies é mais severa.

Outro grupo de aves que desempenha importante papel ecológico são as aves insetívoras, que regulam massivamente populações de artrópodes (Nyffeler et al., 2018). Estimativas predizem que em torno de 400-500 milhões de toneladas de artrópodes são removidos globalmente por ano pela aves (Nyffeler et al., 2018); muita dessa contribuição, mediada pelo controle predador-presa, afeta positivamente a economia e o bem-estar humano (Mäntylä et al., 2011; Whelan et al., 2015). Impactos econômicos decorrentes da remoção de artrópodes são especialmente registrados em áreas de agriculturas e lavouras (Kellermann et al., 2008; Maas et al., 2015; Tela et al., 2021). Entretanto, apesar dessa importância ser amplamente conhecida em agroecossistemas, é quase desconhecido o papel ecológico desempenhado pelas aves insetívoras e como elas moldam as populações de artrópodes nos ecossistemas urbanos, e como elas são afetadas pelas mudanças de usos da terra nas cidades (Seress et al., 2018; Stemmelen et al., 2020; Turrini et al., 2016). Áreas urbanas também possuem espaços verdes (e.g., jardins urbanos (Tresch et al., 2019), lavouras urbanas (Duchemin et al., 2008) e árvores de ruas (McPherson et al., 2016)), os quais fornecem serviços ecossistêmicos, como bem-estar e provisão de alimento. Estratégias de manejo direcionadas para a preservação de estruturas biológicas que incrementam seu papel, como o controle predador-presa devem estar nos objetivos de medidas de políticas públicas.

Muitas cidades ao redor do mundo estão buscando planejar seu desenvolvimento a fim de promover o crescimento sustentável e minimizar os efeitos negativos às comunidades biológicas inerentes ao crescimento urbano (Nilon et al., 2017). No entanto, o rápido crescimento urbano e desordenado nos Neotrópicos causa profundas perdas de habitas nativos, e.g., florestas, favorecendo o surgimento de estruturas do tipo cinza (Piratelli et al. 2017). Uma vez que a estrutura da vegetação define as características ecológicas das aves (Campos-Silva & Piratelli, 2021), os processos de urbanização nas regiões neotropicais podem ocasionar efeitos em cascata, afetando a composição das comunidades e, consequentemente, suas funções ecológicas e os serviços ecossistêmicos. Dessa forma, analisar o papel dos modelos de expansão urbana no direcionamento das comunidades biológicas se faz necessário a fim de fornecer estratégias para o crescimento sustentável das cidades.

1.2 Capítulos da tese

No primeiro capítulo eu avaliei como o gradiente de urbanização e modelos de expansão urbana do tipo compactado (i.e., *land-sparing*) e espalhado (i.e., *land-sharing*) afetam a comunidade de aves e as extensões de espaços verdes e cinza. Além disso, avaliei como as extensões dos espaços verdes e cinzas afetam a diversidade funcional de aves. No segundo capítulo busquei entender como os modelos de expansão urbana do tipo compactado (i.e., *land-sparing*) e espalhado (i.e., *land-sharing*) afetam os tamanhos dos espaços verdes urbanos e também a diversidade funcional de aves frugívoras e o consumo de frutos. Além disso, avaliei como a diversidade funcional de aves frugívoras influencia no consumo de frutos por aves. No terceiro capítulo avaliei como modelos de expansão urbana do tipo compactado (i.e., *land-sparing*) e espalhado (i.e., *land-sharing*) afetam os tamanhos de espaços verdes e consequentemente a diversidade funcional de aves insetívoras e a função ecológica de controle predador-presa de artrópodes por aves. Além disso, avaliei como a diversidade funcional de aves insetívoras influencia no controle predador-presa de artrópodes por aves.

Nesses três capítulos busquei entender como modelos de expansão urbana atuam na conformação dos espaços verdes e cinzas, na biodiversidade e por sua vez em suas funções ecológicas. Isso pode ser utilizado como ferramentas de políticas públicas voltadas ao crescimento sustentável das cidades, embasado na conservação biológica e desenvolvimento urbano.

1.3 Área de estudo

Esse estudo foi realizado na área conurbada dos municípios de Sorocaba e Votorantim, no Estado de São Paulo, sudeste do Brasil (632 m acima do nível do mar).

Sorocaba possui território de cerca de 450 km² e ~ 670 mil habitantes, com uma densidade de cerca de mil habitantes por quilômetro quadrado, com crescimento populacional a uma taxa de 1.75% (IBGE, 2022a). Votorantim tem ~184 km² e ~ 124500 habitantes, com uma densidade populacional de 591,04 habitantes por quilometro quadrado (IBGE, 2022b). A maioria da população de Sorocaba (98%) vive em áreas urbanas (IBGE, 2022a), o qual representa 66% do município, com a vegetação restante consistindo de fragmentos de Floresta Atlântica e Cerrado, principalmente (~ 60%) menor que um hectare (de Mello et al., 2016). O clima nos dois municípios é subtropical com invernos secos (temperaturas abaixo de 18ºC) e verões quentes (cerca de 22ºC), com precipitação média anual de 1,311 mm e temperatura anual média de 22,1ºC (Alvares et al., 2013). A estação seca se estende de abril a setembro, e a estação chuvosa de outubro a março (INMET, 2022).

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Capítulo 1

Compacting cities and conserving large green spaces reduce the negative effects of the urbanization on birds diversity

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Research Paper

Compacting cities and conserving large green spaces reduce the negative effects of the urbanization on birds diversity

Highlights

- Urban sprawl sparing model has higher functional diversity of birds than the sharing model;
- Urban sprawl sparing model has larger areas of urban green spaces than sharing model;
- The amount of urban green spaces has a positive relation to functional diversity of birds;
- The amount of gray infrastructures has a negative effect on functional diversity of birds.

Abstract

1. More than half of the human population lives in urban settlements, and the cityscapes are growing fast, heterogeneously, and sometimes disorderly. The urban sprawl occurs by different models, causing physical and social environmental changes, and may have diverse effects on biological communities. However, these consequences remain poorly known, particularly in Neotropical cities.
2. In this paper, we tested the effects of land-sharing vs sparing urban sprawl models in a gradient of urbanization, composed by the following sites: rural, urban sprawl models and urban core, related to (1) size of the urban green and gray spaces and (2) birds taxonomic and functional diversity. We hypothesize that there are differences across this gradient related to (a) the amount of green and gray spaces; and (b) functional diversity of birds. We also hypothesize that (c) the size of the green and gray spaces affects functional diversity of birds, and that (d) the rural settlements harbor larger and smaller areas of green and gray spaces, respectively, increasing birds taxonomic and functional diversity. We predict that the land-sparing urban model (a) will have larger areas of green spaces and (b) higher functional diversity of birds than the land-sharing and the urban core. In addition, (c) the sizes of green and gray urban spaces areas are positively and negatively related to functional diversity of birds, respectively.
3. We confirmed our hypotheses that there are differences across the gradient of urbanization related to functional diversity of birds, and differences between land-sharing and land-sparing models, with better results to the sparing model. We also confirmed our hypotheses that green and gray spaces affect functional diversity of

birds, with green and gray affecting positively and negatively functional diversity of birds, respectively.

4. Our results can provide important tools for planning the growth of cities, aimed at the selection of urban sprawl models that balance the urban development, engaged with the conservation of larger green spaces that benefit the specialized bird species.

Keywords: Avifauna**,** ecological functions, Latin American birds, urban growth, Neotropical cityscapes

1. Introduction

More than half of the human population lives in urban settlements (Lepczyk et al., 2017; Nations, 2019), and the cityscapes are growing fast and heterogeneous, creating irregular spatial patterns (Ramalho & Hobbs, 2012). Urbanization has been assigned as one of the main rapid ways of landscape changing (Leveau et al., 2020) and a global causes of species endangerment (Grimm et al., 2008; MacGregor-Fors et al., 2020), triggering immediate and long-term consequences for the global biota, mostly reducing species diversity (Carvajal-Castro et al., 2019; Zurita et al., 2017) and affecting several levels of biotic organization (Blair, 2004).

Urban landscapes are often typified by a mosaic of different spaces (MacGregor-Fors & Schondube, 2011), mostly dominated by anthropogenic structures (Barbosa et al., 2020; Schneider et al., 2010), but also including patches of mixed vegetation as parks, gardens, and remnants of native plant life (Campos-Silva & Piratelli, 2021; de Toledo et al., 2012; Palmer et al., 2008; Shwartz et al., 2008) and water bodies (Barbosa et al., 2020), which may support representative components of native bird communities. Socioeconomic and geographical issues are also critical for determining patterns of urban biodiversity; neighborhoods far from the city center and/or with greater economy incoming, usually have more green areas and biodiversity-friendly zones. On the other hand, more central and/or lower-incoming neighborhoods offer few opportunities to sustain native biodiversity (Melles, 2005).

Urban sprawl can be defined as a multidimensional process of expansion of the periphery of a city (Heirman & Coppens, 2013), arising from the internal demand for social resources (e.g. housing and industrialization areas (Mehriar et al., 2020; Nassar et al., 2014). Urban sprawl causes physical changes in the environment, with the development of human-made structures in different forms according to social, political and environmental characteristics (Rubiera-Morollón & Garrido-Yserte, 2020). These forms, also called models (Rubiera-Morollón & Garrido-Yserte, 2020), may have distinct effects on biological communities (McDonald et al., 2020). One of the approaches in urban ecology has been the concern on how best to drive urban development, both from a socioeconomic and environmental point of view (Bibri et al., 2020; Bontje, 2001; Mehriar et al., 2020; Wolff et al., 2018). These studies have been analyzed the benefits and costs of urban development according to two sprawl models, i.e., compacted and sprawled (Bibri et al., 2020). The first model, i.e., compacted, aims to centralize urban areas and their structures at core zones (Mehriar et al., 2020). On the other hand, the second model, i.e. sprawled, is characterized by a widespread growth of urban structures (Dieleman & Wegener, 2004). From the environmental point of view, there would be a more favorable condition for biodiversity in compacted cities through the conservation of natural areas and reduction of CO_2 release (Liu et al., 2019). From socioeconomic and environmental standpoints, the sprawled model as arises in long journeys to the shopping and work areas, higher energy consumption, pollution, accidents, extreme land use areas, and low public transportation along sparsely inhabited areas (Dieleman & Wegener, 2004). Correspondingly, and related to the urban context, the compacted and the sprawled urban sprawl models can be related to land-sparing and land-sharing, respectively (Dennis et al., 2019; Geschke et al., 2018; Suhonen et al., 2022). Land-sharing is defined as a land use management method that *integrate* both the conservation and the production land uses (Fischer et al., 2014) and, in a urban context, consists of low-density built-up areas (e.g., private housing settlements) combined with green spaces in the shape of gardens and small parks, although without large continuous forest areas or older parks (Lin & Fuller, 2013). On the other hand, land-sparing integrate the *division* of conservation and production land uses (Fischer et al., 2014), and in a urban context, consists of high-density built-up areas (e.g. residence buildings) with large, continuous green areas divided (Lin & Fuller, 2013).

Several cities have been planning their development, in order to mitigate the negative impacts on biological communities, and to promote a sustainable growth (Nilon et al., 2017). However, urban sprawl has occurred quickly and often in a disorderly fashion in the Neotropical region, causing loss of native vegetation, and priorizing gray structures (Piratelli et al. 2017). The amount of green structures shape the ecological characteristics of birds (Campos-Silva & Piratelli, 2021). Native species with narrow ecological requirements may be replaced by generalist and - often - abundant species, with effects on species biological traits (Croci et al., 2008), and on several dimensions of their ecological niche. This cascade of events ultimately leads to losses in their ecological functions.

In this paper, we test the effects of a gradient of urbanization, from countryside to core area, and two models of urban sprawl, i.e., land-sharing *vs.* sparing on (1) the amount of urban green and gray spaces; and (2) bird taxonomic and functional diversity. We hypothesize that there would be differences along this gradient related to (a) size of the green and gray spaces; and (b) bird taxonomic and functional diversity. We also hypothesize that (c) the size of the green and gray spaces affects bird functional diversity. We predict that (a) the rural settlements harbor larger areas of green spaces and smaller areas of gray spaces, increasing the taxonomic and functional diversity of birds; (b) the land-sparing model will have larger areas of green spaces and bird functional diversity than land-sharing and urban core area; (c) the sizes of green and gray urban spaces are positively and negatively related to bird functional diversity, respectively. These results may help to fill a gap in the knowledge, particularly regarding Neotropical urban birds, thus supporting policymaking aimed at conserving biodiversity in urban landscapes. As far as we know, this is the first study aiming to identify the impacts of different urban sprawl models on bird communities in the Neotropical region.

2 Methods

2.1 Study area

We carried out the study in the conurbated area of the cities of Sorocaba and Votorantim, in the state of São Paulo, southeastern Brazil (632 m a.s.l., Fig. 1). Sorocaba encompasses about 450 km² and has ~ 670,000 inhabitants, for a density of over one-thousand inhabitants per square kilometer, with the annual population growth rate of 1.75% (IBGE, 2022a). Votorantim has ~184 km² and ~ 124,500 inhabitants, for a density of over 591.04 inhabitants per square kilometer (IBGE, 2022b). Most inhabitants in Sorocaba (98%) live in urban areas (IBGE, 2022a), which represent 66% of the city, with the remaining native vegetation consisting of patches of Atlantic Forest and Brazilian Savanna, mostly (~ 60%) smaller than one hectare (de Mello et al., 2016). The climate in this two cities is subtropical with dry winters (temperatures below 18ºC) and hot summers (over 22ºC), an average annual precipitation of 1,311 mm, and an average annual temperature of 22.1ºC (Alvares et al., 2013). The dry season extends from April to September and the rainy season, from October to March (INMET, 2022).

2.2 Gradient of urbanization and land-sharing *vs.* sparing urban sprawl modelling

To test the hypothesis, we first achieved data from the local urban sprawl settlements (Fig. 1). Next, an analysis of the symmetrical difference of Sorocaba and Votorantim urban polygons were proceed to define the areas of urban expansion, based on satellite images from 2000 and 2019 obtained by Landsat 7 and Landsat 8, respectively, and using spatial analyst methodology (Martines et al., 2015). Then, their centroids were generated, based on geometric figures from the symmetrical difference between the urban spots (Martines et al., 2015). Moreover, the density values from the point cloud of the urban areas were calculated using the Kernel density estimator, or core estimator, based on the difference between the images (i.e., 2000 and 2019; Barbosa et al., 2014). Next, a gradient of values was created based on the Kernel estimator, from the highest to the lowest values of urban sprawl. Two classes of urban sprawl values were used as treatments, namely *Land-Sharing* and *Land-Sparing Models*. These models were created using the values of the Kernel Estimator, which were transformed through the "option to group raster values into classes" ("Symbology"). Next, we performed the following operation: Classes = 3, Classification = Natural Breaks (Jenks optimization method). For graphical illustration of the map, two colors were applied, one for each expansion model. The *Land Sparing Urban Sprawl Model* describes a cloud of urban sprawl dots with larger urban areas than *Land-Sharing*. Area and density of urban sprawl settlements were used to define the characteristics of these two urban sprawl models.

The following study sites were adopted from the least to the most urbanized sites to define the urbanization gradient, (1) rural; (2) areas of urban expansion, regardless of the model and (3) urban core. Two non-urban sprawl sites were selected, here named (1) rural and (2) urban core. "Sites" was here used as the two urban sprawl models (land-sharing and land-sparing) and the two non- urban sprawl areas (i.e., rural and urban core). Rural site was defined as non-urban areas found on the fringe of urban settlements, and were settled until 1 km far from the outermost limit of urban sprawl sites, outside any urban polygon, whether expansion or not. Urban core was defined as consolidated urban settlements that were not subject to any urban sprawl. For each site, 40 sampled points were randomly selected, where data were collected for both landscape and birds (Online Resource 1; Fig. 1).

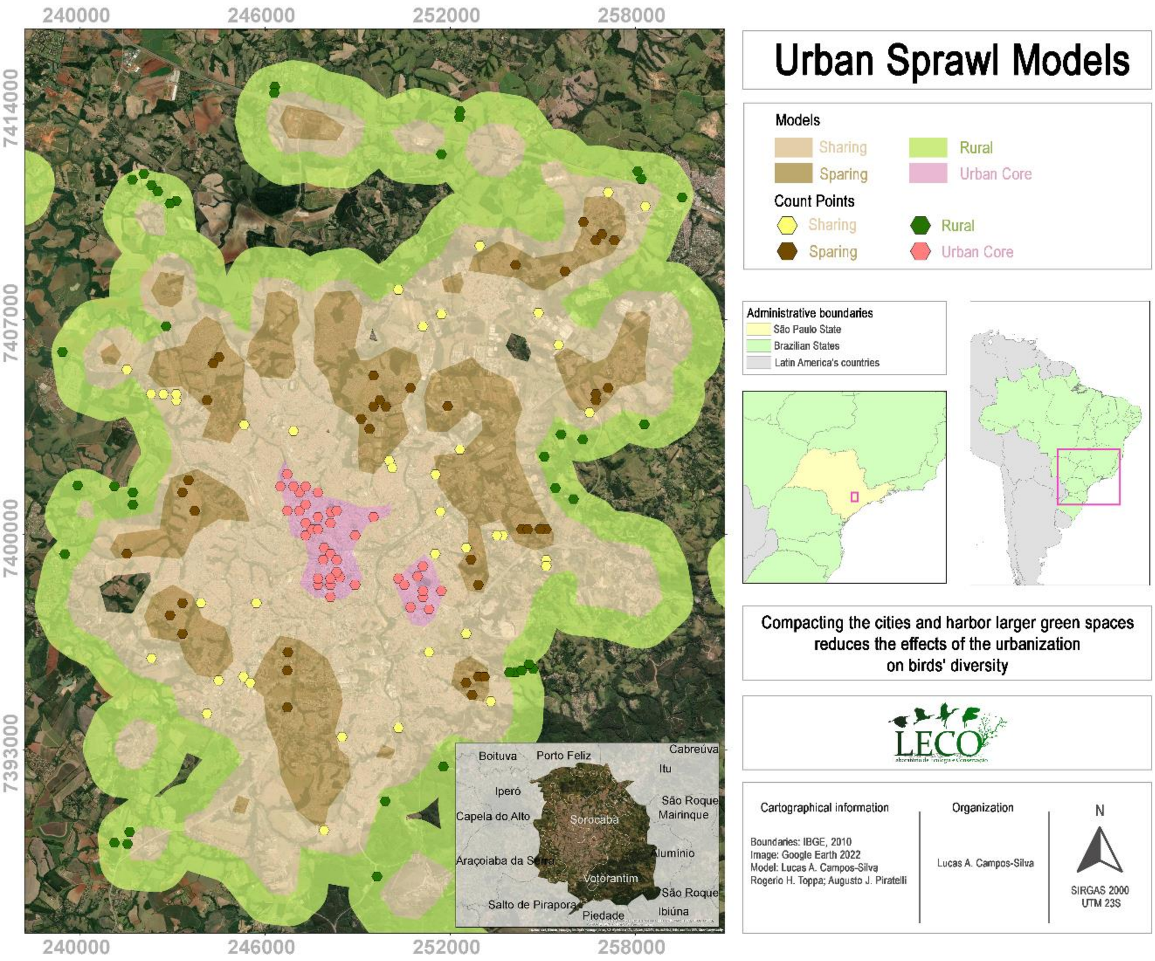


Figure 1 – Land-sharing/sparing urban sprawl areas and the two non- urban sprawl areas studied in Sorocaba and Votorantim, Brazil.

2.3 Mapping urban green and gray spaces

To test the hypothesis that both the (1) land-sharing/-sparing urban sprawl modelling and gradient of urbanization affect green and gray spaces sizes, and that (2) area occupied by each land use class influence the functional diversity of birds, we estimate their sizes from the sampling points. For this, we defined a 100 meters-radius for each sampling point, where we the respective polygons of green and gray spaces were achieved. We defined this radius to check how the specific amount for each type of gray or green space locally influences the avifauna of these environments. We manually delimited green and gray spaces polygons through the Geographic Information System, using Google Earth images as a basis for each sampling point (Fig. 2, Online Resource 2). A scale of 1:1.000 was used for the delimitation of these polygons, followed by a land use mapping validation for all created polygons. The Google Street View was used to identify the green spaces classes when the date of image capture was as close as possible to the sampling bird data.

We selected 15 urban space types, named here as green and gray urban spaces. Green spaces are landscapes having mostly components of plant origin (e.g., native forests, field/pasture, grassy areas). Gray spaces are features of the landscape that mostly have human-made structures (Table 1). Human occupation patterns were also considered when separating each urban space class. For example, in “non-gated community residences” the houses have smaller lot sizes compared to residences within gated communities.

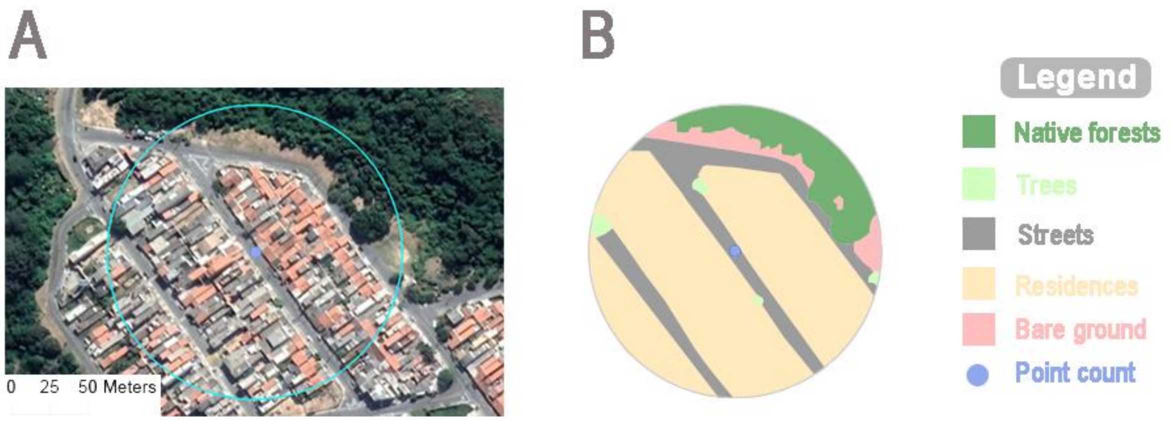
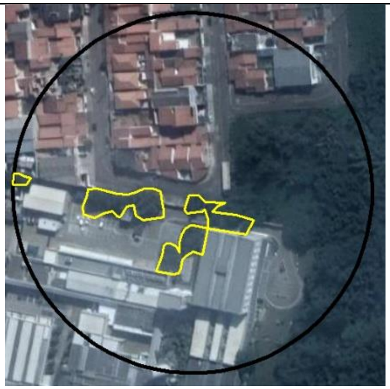


Figure 2 – Example of urban green and gray spaces polygons at one of the sampling points. A) Satellite image of an area with bird sampling points; B) Green and gray spaces polygons constructed from the satellite image.

Table 1 – Types of urban green and gray spaces, and their descriptions. The yellow polygons delimit the type of urban space. Images are from Google Earth.

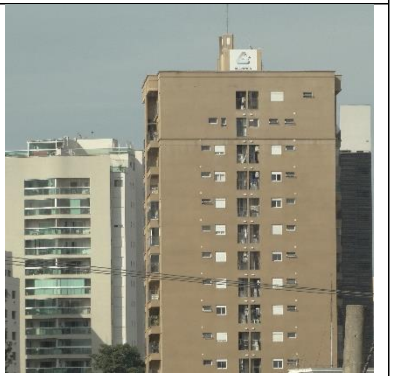
Color of infrastructure	**Land use**	**Meaning**	**Spatial sample**	**Ground sample**
Green	Native forest	Areas of urban native forests, including understory and other structures of forested areas.		
Green	Trees	Isolated trees, without any understory, and generally associated with streets and sidewalks.		

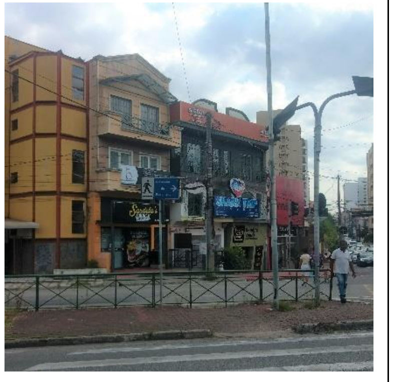
Green	Anthropic fields	Areas of non-managed fields and pastures, including mostly covered by *Brachiaria* grasses. May contain dry trees or shrubs.		
Green	Lawn	Grassed areas with regular human management, usually with not exceeding ~ 15 cm in height.		

Green	Forestry	*Eucalyptus* plantation areas		
Green	Agriculture	Herbaceous monoculture areas		

Green	Green Fence	A line of trees or shrubs delimiting houses and other gray structures. In general, composed by only one plant species.		
	Vacant lots	Areas that are generally small and are replaced over time by houses or other gray structures. When still vacant, they usually have grasses and herbs associated with small gray structures.		

Gray	Non-gated community residences	Individualized houses without walls surrounding a group of houses and no ordinance limiting the people access. These generally have smaller lot sizes when compared to gated community homes.		
Gray	Gated Community	Individual houses that have a wall surrounding a set of houses and that have an ordinance that limits the access of people. These generally have larger lot sizes when compared to		

		Non-Gated Community Residences.		
Gray	Buildings	Commercial or residential buildings		
Gray	Industry	Places that produce and distribute various manufactured products		

Gray	Commerce	Places that resell miscellaneous items of human origin. In general, land use identification is only possible through land validation since its roof structure does not have a specific pattern.		
Gray	Streets	Paved areas that interconnect different types of gray land use. They are generally used for crossing vehicles and people. We consider paved parking areas as street areas as well.		

Gray	Bare ground	Region where the soil is exposed. There is no gray or green infrastructure above this soil.		

2.4 Bird surveys

We carried out bird censuses from September to March in 2019, 2020, and 2021, by 10-minutes count points with 50-meters radius, 200 meters far from each other to reduce overestimation of species abundance (Vielliard et al. 2010). The sampling points for birds were the same where the landscape features were sampled, totaling 160 sampling points (i.e., 40 by study site; Fig. 1). Each point was twice sampled in the first four hours from sunrise, using the highest value for the respective sampling point for bird's richness and abundance. Thus, a total of 320 sampling points were carried out in the study. All individuals were counted, even if they were in flocks. Aerial insectivores, shorebirds, waterfowl, raptors, and nocturnal and crepuscular species were not included (Pennington & Blair, 2011; Bibby et al. 2000). All individuals perching, nesting, feeding, and flying five meters over the canopy were included. Species having high abundance, frequency, and relationship with gray infrastructures, e.g., Rock Dove (*Columba livia*), House Sparrow (*Passer domesticus*), and Eared Dove (*Zenaida auriculata*), were not included.

2.5 Taxonomic and bird diversity indices

Functional divergence was used as proxy for functional diversity of birds recorded in these study areas. Functional divergence is the degree to which abundance distribution in niche space maximizes divergence in functional traits in a community (Mason et al., 2005). This index reveals how far the higher species abundances are from the center of the functional space (Mouchet et al., 2010), indicating levels of niche differentiation (Cannon et al., 2019). The higher the functional divergence, the more abundant species are in the extremes of the functional traits range in a biological community (Fig. 3; Mason et al., 2005).

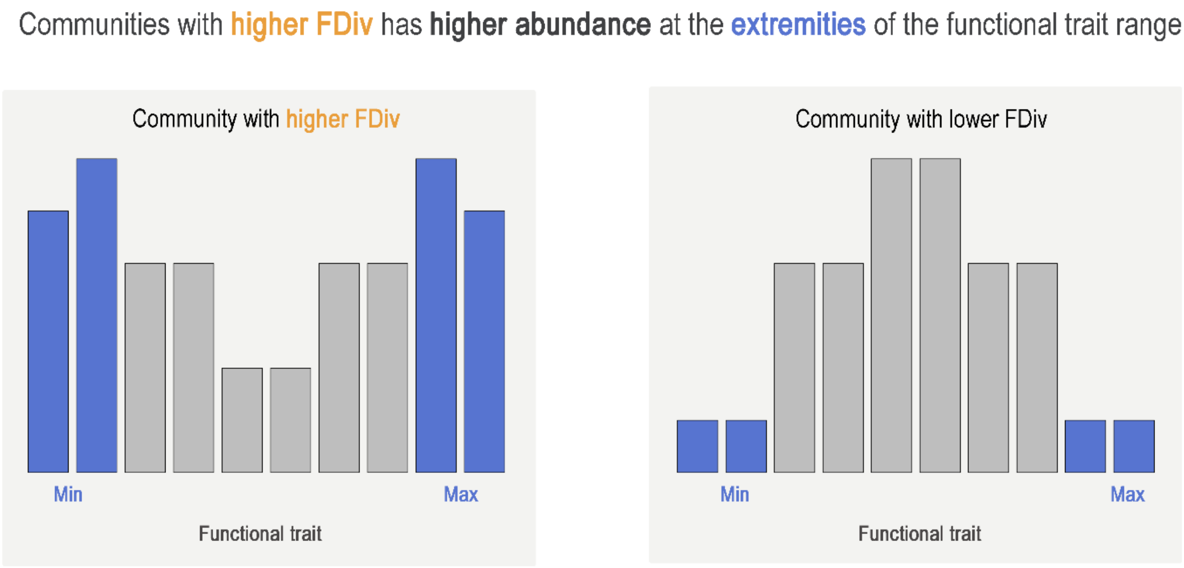


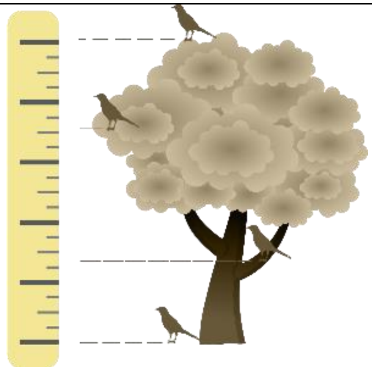
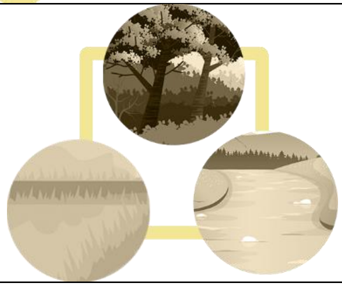
Figure 3 - Visual representation of communities that have higher (right side) and lower (left side) functional divergence. The vertical and horizontal axes represent abundance and niche space, respectively.

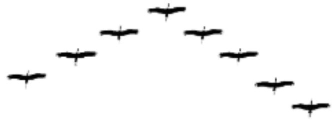
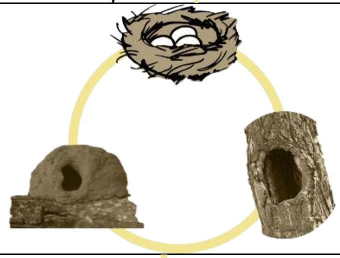
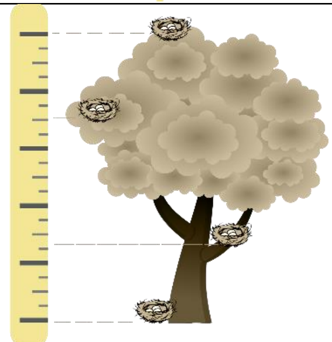
To estimate the functional diversity, nine ecological and five morphometric traits were selected, which could indicate a close relationship between the specialized frugivorous birds and the green infrastructures of these urban sprawl areas. The traits selected were: *Ecological traits* – (1) Diet, (2) Foraging stratum, (3) Habitat, (4) Distribution, (5) Migratory status, (6) Nest Substrate, (7) Nest descriptions, (8) Cavity Dependence, (9) Nest Strata; *Morphometric Traits* – (1) Body Length, (2) Bill Length, (3) Gape Width, (4) Wing Length, and (5) Body Mass (Table 2).

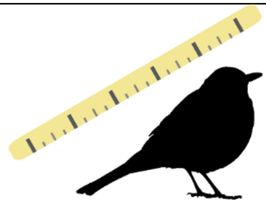
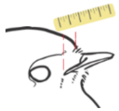
Diet and foraging stratum reflect how specialized are species niches in exploring feeding resources, and the main stratum they forage (Todeschini et al., 2020). These traits can also accurately indicate their ecological functions in the environment (Whelan et al., 2015). The habitat can reveal the relationship between birds and the environment, where they find resources to live (Morelli et al., 2019). Distribution is related to bird species dispersal and can indicate how restrict is a species in its spatial distribution (Vale et al., 2018), (Sick, 1997). Migratory traits reveal the recurrent and regular movement of individuals across their breeding and non-breeding sites (Somenzari et al., 2018; Webster et al., 2002). These traits can indicate their presence, and seasonal ecological functions. Nest substrate is a key-factor in nest-site selection (de Meireles et al., 2018). Nest-site is a component of habitat selection (Swaisgood et al., 2018), and this can define the range of a bird species distribution. Nest descriptions refer to the type of the nest (Simon & Pacheco, 2005). Many urban adapters have closed nests, while urban avoiders, open cup nests (Croci et al., 2008); these patterns are related to the infrastructures that birds found in the urban and not urban habitats. Cavity dependence describe the reliance of birds in nesting in cavity substrate, which may also limit species range (Bonaparte et al., 2020). Nest strata indicate the height that bird use to nest and may imply in the specificity with the vertical stratum.

Body length, size, and mass are related with many aspects that a species play in the environment (Thornton & Fletcher, 2014), dispersal ability (Ottaviani et al., 2006) and susceptibility to disturbance and extinction risk (Fritz et al., 2009). Likewise, body mass is related to the magnitude of the ecological functions played by a species in the environment (Brown et al., 1978), and is also related with the energy flow in the ecosystems (Sibly et al., 2013). Bill length is commonly related with specialization and ecological function (Lederer, 1975; Maglianesi et al., 2014), and gape width (i.e., bill width) is associated to feeding specialization and ecological functions (Bender et al., 2018). Wing length is related to species' dispersal ability (Sheard et al., 2020). Gape width, body mass, and wing length are traits related to plant-frugivore networks structures and seed dispersal dynamics (Bender et al., 2018; Bonfim et al., 2021; Li et al., 2018). Functional diversity is defined as an index that indicate how complex is it an environment which can shelter more specialist birds abundances (e.g., larger-bodied, larger winged-length and larger-gaped width species).

Table 2 – Functional traits and their definitions.

Type	Functional traits	Symbol	Range	Categories	Definition	Reference
Ecological	**Diet**		4	Invertebrate, FruiNect, Omnivore, PlantSeed	The predominant diet items consumed by bird species (e.g., nectar, fruits, seeds, plants, and invertebrates)	Wilman et al. (2014)
	Foraging stratum		5	Ground, Understory, Midhigh, Canopy, Mixed	The predominant foraging strata level used by the species, e.g., ground, underground, middle, canopy, aerials, water below the surface, water around the surface.	Wilman et al. (2014)
	Habitat		3	Mixed, Non-Forest, Forest	The predominant habitat used by each species, i.e., forest, non-forest, water and mixture of habitats.	Tobias et al. (2022)
	Distribution		3	Endemic, non-endemic, Exotic	Bird species' distribution	Vale et al. (2018); Sick (1997)

	Migratory		2	Resident, partially migratory	Reflects the recurrent and seasonal movement of individuals among their breeding and non-breeding sites	Somenzari et al. (2018)
	Nest Substrate		4	Palm leaves, Tree branch, Tree hollow, Tree hollow/Rufous Hornero's nest	Nest-site habitat selection	Simon & Pacheco (2005)
	Nest descriptions		3	Cavity, Closed, Cup	Refers to the type of the nest	Simon & Pacheco (2005)
	Cavity Dependence		2	Exploiter, Non-Cavity Dependent	Describe the dependence of the bird in nesting in cavity substrate	Bonaparte et al. (2020)
	Nest Strata		4	Ground, understory, mid-story, canopy and brood parasite	The nesting strata level	WIKIAVES, 2022; Sick, 1997

Morphometric	**Body Length**		5	120-139, 140-159, 160-189, 190-219, >220	Class of the average body length (cm) of each species	Rodrigues et al. (2019)
	Bill Length		5	10-11, 12-13, 14-15, 19-20, >21	Class of the average bill length size (mm) of each species	Rodrigues et al. (2019)
	Gape width		5	5-5.9, 8-99, 10-11, 12-139, >14	Class of the average bill width size (mm) of each species	Rodrigues et al. (2019)
	Wing Length		5	40-59, 60-79, 80-99, 100-119, >120	Class of the average wing length size (mm) of each species	Rodrigues et al. (2019)
	Body Mass		7	0-9, 10-19, 20-29, 30-39, 40-49, 50-99, >100	Class of the average weight (g) of each species	Rodrigues et al. (2019)

2.6 Relationship between gradient of urbanization, urban sprawl modelling, and functional diversity of birds

Some steps were incorporated for the creating models to predict the relationship between response variable (i.e., functional diversity of birds) and the explanatory (i.e., study sites). First, we checked for spatial autocorrelation for the response variables, using the "Moran.I" function of the "ape" package (Paradis & Schliep, 2019). We detected spatial autocorrelation in the functional diversity ($p < 0.00$), which was added in the models as random effect (Online resource 3). The type of the distribution's values was tested for the response values and included into the respective models. To check these distributions, we used the "fitDist" function from "fitdistrplus" package (Delignette-Muller & Dutang, 2015). The machine learning model selected to make this relationship was the "Generalized additive model for location, scale, and shape (GAMLSS)", through the "gamlss" function, from the "gamlss" package (Rigby and Stasinopoulos, 2005). This model allows to include a wide range of distributions of the response variable, and non-parametric smoothing functions, random effects, or other additive terms into the predictor variables (Rigby & Stasinopoulos, 2005). Sizes of urban green and gray spaces were also added in the model as random effects (Online resource 4). To avoid the insertion of predictor variables with high correlation levels, we performed a correlation check through the "vifstep" function of the "usdm" package (Naimi et al., 2014). This function calculates variance inflation factor (VIF) for a set of variables and exclude the highly correlated variables from the set through a stepwise procedure. Only variables with $VIF < 3$ were considered in the predictive model. The mathematical formula for the predict model is described in the online resource 5.

2.7 Relationship between functional diversity of birds and green and gray spaces sizes

To evaluate the relationship between the response variable (i.e., functional diversity of birds) and explanatory variables (i.e., green and gray space sizes), the mean sampled area of each urban green and gray spaces was used. In order to create models to predict the relationships between responses variable and the explanatory the same first two steps adopted in section 2.6, were here adopted. The machine learning model selected to make this relationship was the GAMLSS, through the "gamlss" function, from the "gamlss" package (Rigby and Stasinopoulos, 2005). Both the spatial autocorrelation and the study sites (i.e., rural, land-sharing, land-sparing, and urban core) were also added in the models as random effect (Online resource 5). The stepGAICAC function was used to select the model variables. This function fits a selection model using the Generalized Akaike Information Criterion (GAIC; Rigby and Stasinopoulos, 2005). After returning the selected variables, we implement the final model through the "gamlss" function containing only the variables selected by the previous step. The "term-plots" function, from the gamlss package, was used for visual analysis of the results. The mathematical formula for this best predictive model is described in the Online Resource 6.

2.8 Patterns of urban green and gray spaces between study sites

To identify possible differences in green and gray spaces patterns between the gradient of urbanization, which could influence the functional diversity of birds, we made four lines of descriptive analysis from the landscape perspective (Table 3). The first analysis aims to identify possible differences between the urban sprawl models (i.e., land-sharing and land-sparing) related to the of urban sprawl polygons sizes. The other analyzes focus to identify differences in the green and gray spaces characteristics (e.g., spaces sizes) among the studied sites. Since dwelling settlements represent a significant portion of the cityscape (Bagan & Yamagata, 2014; Hu et al., 2021), they were analyzed, in two types, named (1) non-gated communities and (2) gated communities.

To avoid possible biases, only urban green and gray space types that had a minimum of six polygons and six samples per site were included, removing outliers for each test. To check for statistical differences for each descriptive analysis, we performed t-student and ANOVA tests for parametric values from the "t.test" and "lm" functions, respectively from the "stats" package (R Core Team, 2022). For non-parametric values Mann-Whitney and Kruskal-Wallis tests were used via functions "wilcox.test" and "kruskal.test", from the "stats" package (R Core Team, 2022). Normal distribution was checked using the "shapiro.test" function (R Core Team, 2022). All these analyzes were done in the R language

Table 3 – Descriptive analyses, hypotheses and predictions related to patterns of urban green and gray spaces between study sites.

Descriptive analysis line	Relationship	Step description	Hypotheses	Predictions
Urban sprawl polygons	Number of urban sprawl polygons by model	The urban sprawl polygons were classified in: <10 hectares; 10-20 hectares; 21-30 hectares, 31-40 hectares, >40 hectares	There are differences between the models by polygon size classes	Sharing model will have higher number of polygons in smaller classes than sparing model
Green and gray space around the gradient of urbanization	Amount of green and gray space types per site	We compared the amount of green and gray space types by site	Each study site will have different amount of green and gray space types	Sharing model will have higher amount of gray space types than sparing model
	Amount of green and gray spaces polygons per site	The Amount of green and gray spaces polygons was compared by site	The number of green and gray spaces polygons will be different for each site	Sharing model will have higher amount of both green and gray spaces polygons than sparing model
	Mean sampled area of each green and gray space type by site	A comparison was made between the average sample area for each use of the between the sites	Each site will present different area values for each land use	Since sharing model tends to have more fragmented green spaces than sparing model, we expect greater urban green spaces for the land-sparing site than land-sharing

3 Results

3.1 Birds biodiversity

A total of 41 birds species were recorded, representing 7 orders, and 16 families (Online Resource 7). We recorded a reduction of bird species along of gradient of urbanization (rural – N = 40; urban sprawl model / land-sharing N = 38 and land-sparing N = 34; urban core N = 23; Fig. 5). The most frequent bird species in the rural site were House Wren (*Troglodytes aedon*), Sayaca Tanager (*Tangara sayaca*), Rufous-collared Sparrow (*Zonotrichia capensis*), Picazuro Pigeon (*Patagioenas picazuro*) and Blue-black Grassquit (*Volatinia jacarina*), respectively. The most frequent bird species in the land-sharing were Sayaca Tanager, House Wren, Bananaquit (*Coereba flaveola*), Ruddy Ground-dove (*Columbina talpacoti*), and Chalk-browed Mockingbird (*Mimus saturninus*), respectively. The most frequent birds species in the land-sparing were Sayaca Tanager, Ruddy Ground-dove, House Wren, Chalk-browed Mockingbird and Rufous Hornero (*Furnarius rufus*). The most frequent birds species in the urban core were Sayaca Tanager, Pale-breasted Thrush (*Turdus leucomelas*), Ruddy Ground-dove, Bananaquit and House Wren, respectively (Fig. 4, Online resource 8).

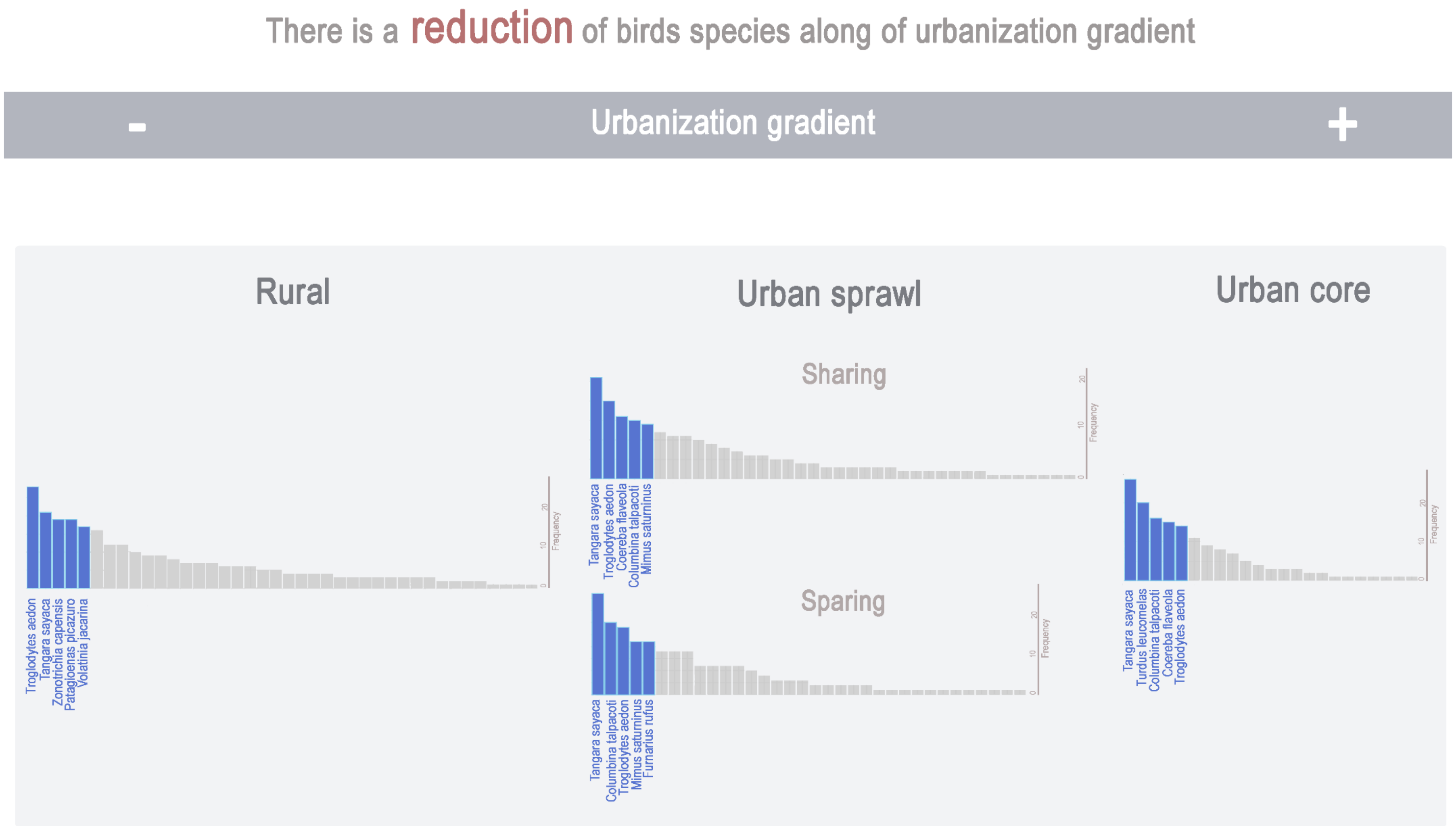


Figure 4 – Frequencies of bird species along a gradient of urbanization (left to right) in Sorocaba and Votorantim, Brazil. The highlight in blue indicates the top five frequent species.

The land-sparing model had higher bird abundance in the extremities of the morphological traits range related to body size, bill width and bill length compared to the others urban sites (i.e., land-sharing and urban core; Fig. 5). The land-sparing model had higher abundances proportion of ecological traits related to FruiNect/PlantSeed—diet, exploiter— cavity dependence and understory— nest stratum, than other urban settlements others urban sites (i.e., land-sharing and urban core; Fig. 6).

Sparing model has higher abundance in traits related to FruiNect/-PlantSeed -Diet, Exploiter Cavity-Dependence and understory nest stratum

Click in this link to see the image in high definition.

Figure 6 – Abundances proportion of birds by ecological traits in gradient of urbanization (left to right) in Sorocaba and Votorantim, Brazil. The highlight in blue indicates abundances of traits related to FruiNect/PlantSeed—diet, exploiter—cavity dependence and understory— nest stratum in land-sparing model. Cavity dependence – ND: Non dependent of cavities. Nest Strata – C: Canopy - U: understory - M: mid-story - G: ground – BP: brood parasite.

3.2 Relationship between functional diversity of birds and gradient of urbanization

We recorded differences related to functional diversity of birds between all the sites, excepted by the pair rural-land-sparing and sharing-urban core, with a reduction of functional diversity along of gradient of urbanization. We registered that land-sparing have higher functional diversity in comparative with other urban sites (i.e., land-sharing and urban core; see the p values results in the Online resource 9; Fig. 7).

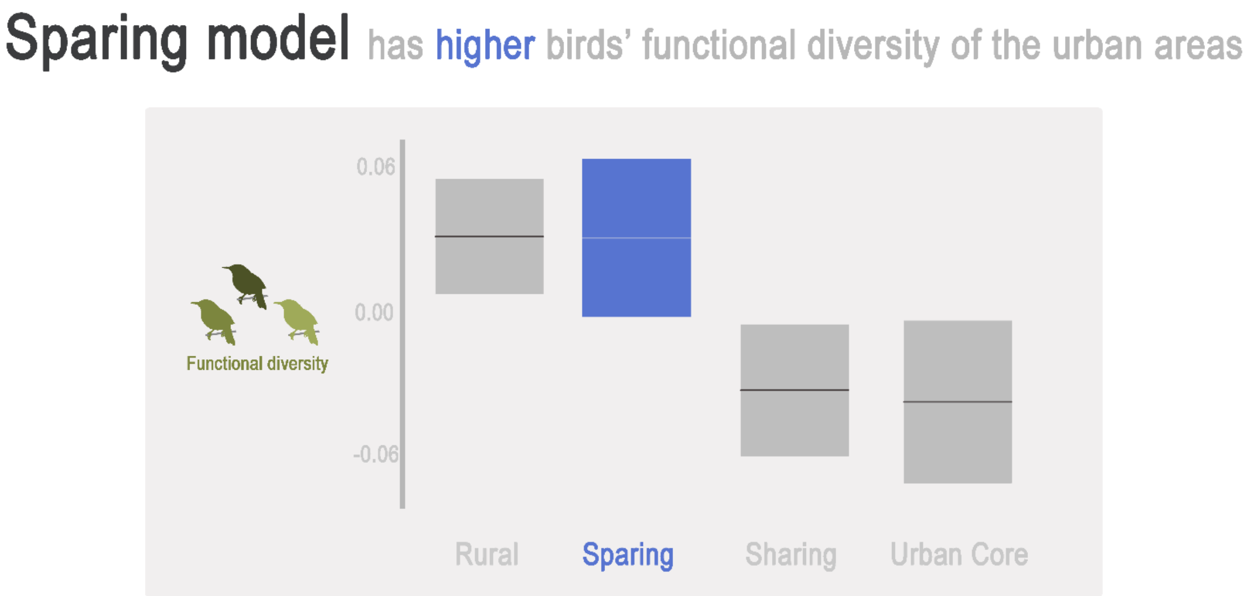


Figure 7 – Relationship between functional diversity along of urbanization gradient in (Left to right) Sorocaba and Votorantim, Brazil. The highlight in dark blue indicates the boxplot with the values indicating the model with the highest value of functional diversity

3.3 Relationship between functional diversity of birds and green and gray space sizes

Three green and four gray spaces affected the functional diversity (Fig. 9 and 10, Online resource 10). Native forest ($p < 0.00$, $t = -3.30$), trees ($p < 0.00$, $t = -3.00$), and vacant lots ($p < 0.0$, $t = 2.50$) were positively related to functional diversity (Fig. 8). Streets ($p < 0.000$, $t = 4.36$), buildings ($p < 0.00$, -3.00), Industry ($p < 0.000$, $t = -35.00$) and OGI (p <

0.000, t = -5.00) were negatively related to the functional diversity (Fig. 9). Agriculture, bare ground, commerce, and silviculture did not affect the functional diversity (p = 0.50, t = 0.72; p < 0.70, t = 0.40; p < 0.40, t = 1.00; p < 0.08, t = 2.00, respectively).

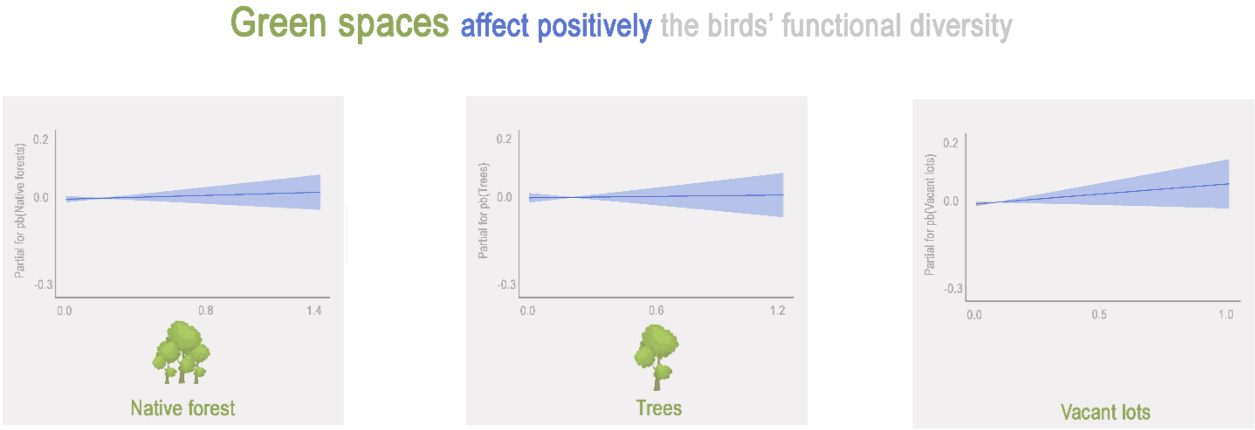


Figure 8 – Relationship between functional diversity and green spaces along a gradient of urbanization (left to right) in Sorocaba and Votorantim, Brazil.

Figure 9 – Relationship between functional diversity and gray spaces along a gradient of urbanization (left to right) in Sorocaba and Votorantim, Brazil. OGI – Other grey infrastructures.

3.4 Landscape features – Amount of urban sprawl polygons

As predicted, we found a higher amount of urban sprawl polygons in smaller areas classes in land-sharing than land-sparing (Fig. 10A, C). However, we recorded that in classes with larger areas of urban sprawl polygons the higher values were in the sparing model (Fig. 10B, D)

Figure 10 – Number of polygons of urban sprawl areas by urban sprawl model. A) Urban sprawl polygons in the land-sharing model; B) Urban sprawl polygons in the land-sparing model; C) Amount of urban sprawl polygons smaller than 10 hectares classified by model; D) Number of urban sprawl polygons classified by size classes greater than 10 hectares.

3.5 Characterization of the sites by urban green and gray spaces

We found that the sparing model had, in overall, higher values of mean sampled area in green spaces, especially related to complex infrastructures (e.g., forests), compared to the sharing model (Online Resource 10, 11, 12, 13). Related to gray spaces, this difference was not very clear, with highlights in gated communities that showed higher values for the sparing model than sharing model (Online Resource 10, 11, 12, 13).

We found that the urban core generally had little mean sampled area and by polygon values for complex green infrastructure, e.g., forests, and higher values for gray-type infrastructure (Online Resource 10, 11, 12, 13). The rural site, in turn, had a smaller area of gray-type structures and higher values for green infrastructure, including having unique land uses such as forestry, agriculture and hedges (Online Resource 10, 11, 12, 13).

4 Discussion

We confirmed our hypotheses related to functional diversity of birds of which (1) there are differences of values along the gradient of urbanization between the study sites, (2) there are differences of values between land-sharing and land-sparing models and (3) that green and gray spaces affect functional diversity of birds. We confirmed our prediction (1) that along the gradient of urbanization there is a reduction of functional diversity of birds. Also, (2) we confirmed our prediction that the land-sparing has greater functional diversity of birds compared to land-sharing model. We have also (3) confirmed that land-sparing had larger areas of urban green spaces, trees excepted, than sharing model. We also confirmed that (4) urban green spaces sizes affect positively the functional diversity of birds, and (5) that gray spaces sizes affect negatively the functional diversity of birds. Our results can provide important tools for planning the growth of cities.

The sparing model preserves larger green spaces, e.g., native forests, consequently, maintaining key ecological resources that may support better functional diversity of birds, through the reduction of environmental factors related to the larger size of these spaces (Magnago et al., 2015; Püttker et al., 2020; Schwartz, et al., 2017; Zambrano et al., 2020). This is supported by the positive relationship between the functional diversity of birds and green spaces that we found. Larger green spaces may show lesser negative effects, as edged effects, related to urbanization. Fragmentation and edge effects cause secondary impacts into the key resources along the habitats, as native forests (e.g., reduction of tree abundance due to wind, fall, tree mortality and removal of standing dead trees; (Laurance et al., 2007; Magnago et al., 2015; Schwartz, et al., 2017)). This catalyze negative effects on birds biodiversity, mainly for habitat- and diet specialists (Magnago et al., 2015; Püttker et al., 2020; Schwartz, et al., 2017; Zambrano et al., 2020).

Contrasting result related to functional diversity of birds was found in the sharing model. This can be explained by the fact that this model has greater amount of urban sprawl fragments (i.e., polygons) of the smaller size classes, and greater amount of urban gray space types, as we recorded, two characteristics which may have increased the spatial heterogeneity of gray infrastructures. Such intrinsic factors may have contributed in the species richness, as we recorded, mainly related to species that can use gray infrastructure resources. However, these same inherent gray features may influence the cityscape composition, notably the green spaces, driving negatively the functional diversity, through reducing of the urban green spaces' sizes, as recorded. This fact may lead in a reduction of key resources, required for the maintenance of specialized avifauna, especially species dependent on native forest structures to nest and feed, as standing dead trees, understory, flowers and fruits (Campos-Silva & Piratelli, 2021; Moreira-Arce et al., 2021; Rodrigues & Araujo, 2011). Furthermore, the green spaces in this model may have a higher anthropic influence, due to increase of human density, consequence of the decrease in the green spaces' size. Escape distance is influenced by the increase in the pedestrian density (Melo et al., 2021; Mikula, 2014; Piratelli et al., 2015), thereby affecting bird foraging behavior.

Contrary to our expectations, the rural site showed no difference with the sparing model related to functional diversity. However, we noted that there was a marked reduction in functional diversity along the gradient of urbanization (excepted by the sparing model). Our outcomes, related to a reduction of both functional diversity and species along this gradient is similar to found in another researches in cityscapes (Croci et al., 2008; Máthé & Batáry, 2015; Schneiberg et al., 2020; Xie et al., 2019). However, we highlight our outcome related to higher functional diversity in the sparing model, as registered in the rural areas. As in rural areas, this model maintained larger green space, which may have contributed to an increase in functional diversity, once it maintains important key resources. Urban sprawl sites are essentially new urban settlements and can maintain more structures of the native green landscapes, such as fields and native forests, in association with gray infrastructures than urban core, for example. The maintenance of native green characteristics associated with some gray structures may have helped to increase this birds index. This is supported by the positive relationship recorded between green spaces (e.g., native forests, trees) and functional diversity, which may contribute in the maintenance of specialized avifauna. Fact that corroborates with this thought, is that we detected higher abundance proportion in the extremities of the morphological traits range related to body size, bill width and bill length in sparing model than in the others urban sites (i.e., land-sharing and urban core). This found is important because these traits are linked to ecological drivers (e.g., plant-frugivore interaction structures and seed dispersal dynamics (Baños-Villalba et al., 2017; Donoso et al., 2020; Moran & Catterall, 2010; Muñoz et al., 2016; Rehm et al., 2019) and top-down control of arthropods (Hespenheide, 1971; Janes, 1994; Lederer, 1975; Sherry & McDade, 1982; Sherry et al., 2020). Therefore, sparing models may shelter key resources that maintain specialist birds, affecting consequently, the ecological functions along the cityscape as well.

As we had predicted, the urban green sizes influenced positively the functional indices. Native forests within the urban settlements influences the composition of the avifauna, because they have structures as trees, shrubs and other local green infrastructures that benefit feeding-, habitat- and nesting-resources available to birds (Blewett & Marzluff, 2005; Campos-Silva & Piratelli, 2021; Fröhlich & Ciach, 2020; Rigacci et al., 2021; Rodrigues & Araujo, 2011; Shahabuddin et al., 2021). This pattern may have shaped the abundance and functional diversity along this gradient of urbanization, mainly related to birds that depend on local key resources shelter in larger native forests

(Magnago et al., 2015; Püttker et al., 2020; Schwartz, et al., 2017; Zambrano et al., 2020). Our outcome related to native forest is important, because we found that in both sharing model and urban this green space was found in small, isolated fragments. This fact may have contributed to lower functional diversity of birds, affecting mostly the forest-dependent species. As the native forest, we recorded that tree green space positively affected the functional diversity. Trees are green infrastructures that can provide key resources to birds, as food (e.g., flowers, fruits, and arthropods; Silva et al., 2020; Somme et al., 2016; Teodosio-Faustino et al., 2021), and suitable sites for shelter and nesting areas (Beisiegel, 2006; Sulaiman et al., 2013). We highlight this fact because we found more area occupied by isolated trees in sharing model, instead of the sparing model. Once have been showed that are positive consequences into the biodiversity when we merge some characteristic of sharing and sparing model (Grass et al., 2019). Our found corroborate with this, because we found a positive relationship between this important element of this type of green space and functional diversity. Vacant lots have been found as a positive catalyzer of functional diversity. It has been reported that small green spaces, as vacant lots, can contribute to bird biodiversity, mainly in open-habitats(Grass et al., 2019).

Residential lands, excepted by buildings, were not included in the analysis due to the high correlation with the other landscape variables. However, the green spaces configuration may be related to the intrinsic consequences of the social use of gray-type landscape structures, as the residential lands. Residential lands notoriously cause changes to the landscape around them (Mockrin et al., 2017; Pejchar et al., 2015). Here we observed two types of residential land uses not related to buildings, which are very often found in these study areas, (1) common house settlements and (2) gated communities. We highlight these two residential land uses, because we recorded differences sizes patterns related to gated community residential between the urban sprawl models. We saw that land-sparing has higher frequency and extension of gated communities than the sharing model. This fact possibly helped shaping the green spaces, especially the native forests. The presence of gated communities in the cityscape help in the conservation of green spaces, mainly the forested areas (Campos-Silva & Piratelli, 2021). This occurs because, during the implementation of the gated communities, it is mandatory by local legislation the protection of some spaces designed to the biological conservation (Campos-Silva & Piratelli, 2021). Once is known that gated communities contain aspects of the green spaces that are important in biological conservation (Campos-Silva & Piratelli, 2021), this fact may have helped in the spatial configuration of the green urban spaces that we observed, and consequently benefited the functional diversity of birds.

5 Conclusion

Our results indicate that the sparing model should be priories, as it may support higher functional diversity of birds. We recommend the direction of the development of the cities towards this model, because it may improve the conservation of important green spaces as native forests, and open habitats (e.g., lawn and vacant lots), which positively influence the biodiversity of the urban birds, delivering ecosystem functions and services.

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8 Online Resource

Online resource 1 - Randomizing the sampled points

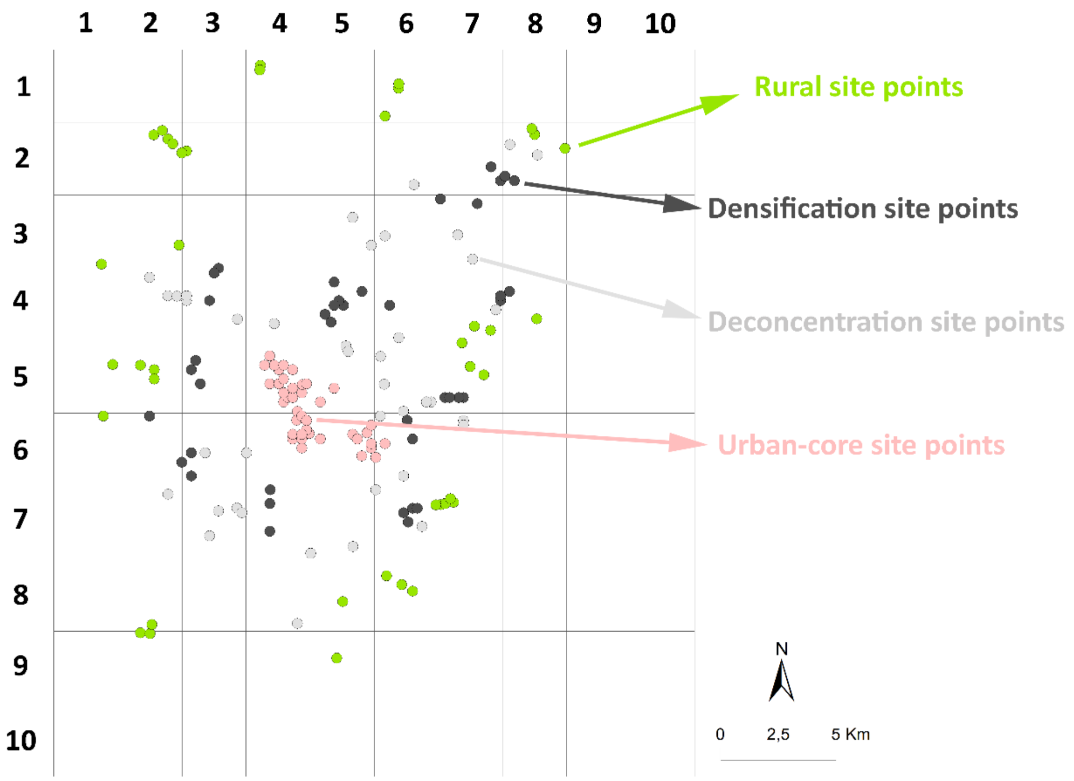
To avoid possible biases resulting from the distance between the sampling points, we divided all the study area into four quadrants and selected 10 random sampled points by study site in each quadrant. Each one of these four quadrants had smaller quadrants. Each intersection of the smaller quadrant was at least 200m of the nearest intersection. We randomly select the sampled points within these intersections using the “Random Points” option in the GIS Software, selecting the intersections of these smaller quadrants as the selected areas. To select the random sampled points for the urban sprawl sites, we took care to take into account intersections that had within urban sprawl polygons. To the urban core site, we selected intersections that had urban polygons, but that were not urban sprawl polygons, which were generally limited to the urban core. The sampled points of the rural sites were selected through intersections that were not in any type of urban polygon, whether expansion or not.

Online Resource 2 – Construction of urban green and gray spaces polygon

For each sampling point we delimited a 100m buffer which we manually constructed each urban green space polygon. To configure as an image base, we used the most recent images available from Google Earth. For each buffer we cut a satellite image and from it we delimited the urban green space polygons manually using GIS Software editing tools (Fig. 3). For the construction of the polygons, we used the scale of 1:1.000. Ground validation was performed for all constructed polygons. Google Street View was used to help identify the urban green spaces, using it only when the date of image capture was as close as possible to the sampling of birds' data.

Online Resource 3 – Creating the random effects variable related to spatial autocorrelation

In order to insert the spatial autocorrelation effect in the predictive models, we placed all the points in a 10 by 10-hectare grid as shown in the figure below.



We named each quadrant as a respective text value in order to make it a categorical variable. For each predictive model we enter the respective sample point value related to its specific quadrant as shown in the table below.

Quadrant name	Points	Lat	Lon
11	qc_rural_1	7389969	241110
11	qc_rural_5	7389932	241535
14	qc_rural_4	7388871	249623
21	qc_rural_8	7390321	241605
23	qc_land_sharing_1	7390370	247911
24	qc_rural_3	7391320	249883
25	qd_rural_8	7392439	251774
25	qd_rural_9	7392058	252437
25	qd_rural_10	7391769	252910
31	qc_land_sharing_6	7395969	242310
32	qc_land_sharing_2	7395378	245296
32	qc_land_sharing_4	7394170	244111
32	qc_land_sharing_5	7395170	245511
32	qc_land_sharing_7	7395246	244489
33	qc_land_sparing_2	7396172	246734
33	qc_land_sparing_3	7394369	246710
33	qc_land_sparing_9	7395570	246710
34	qc_land_sharing_3	7393702	250321
34	qc_land_sharing_8	7393410	248488
35	qd_rural_6	7395512	253913
35	qd_land_sharing_5	7394569	253310
35	qd_land_sharing_9	7396170	251310
35	qd_land_sparing_5	7395169	252510
35	qd_land_sparing_6	7395369	252910
35	qd_land_sparing_7	7395369	253110
35	qd_land_sparing_10	7394769	252710
36	qd_rural_1	7395625	254681
36	qd_rural_2	7395524	254123

36	qd_rural_5	7395570	254315
36	qd_rural_7	7395780	254548
40	qc_rural_6	7399364	239505
41	qc_land_sparing_5	7399370	241510
41	qc_land_sparing_7	7397369	242911
42	qc_land_sparing_4	7396769	243311
42	qc_land_sparing_6	7397769	243310
42	qc_land_sharing_9	7397769	243910
43	urban_core_3	7397969	248110
43	urban_core_5	7398369	247710
43	urban_core_8	7398570	247711
43	urban_core_9	7398370	248111
43	urban_core_10	7398607	248417
43	urban_core_15	7398769	248310
43	urban_core_17	7399179	247878
43	urban_core_18	7399370	248110
43	urban_core_29	7399169	248310
43	urban_core_40	7398569	248110
43	qc_land_sharing_10	7397769	245710
44	urban_core_1	7397634	250709
44	urban_core_4	7397970	251111
44	urban_core_6	7398170	251110
44	urban_core_11	7398569	250310
44	urban_core_12	7398370	250510
44	urban_core_14	7398640	250935
44	urban_core_16	7398970	251110
44	urban_core_22	7398369	248910
45	urban_core_2	7397569	251310
45	urban_core_7	7398169	251710
45	qd_land_sharing_6	7396769	252510

45	qd_land_sharing_7	7399369	251510
45	qd_land_sparing_8	7398369	252910
45	qd_land_sparing_9	7399188	252670
46	qd_land_sharing_3	7399170	255110
46	qd_land_sharing_4	7398970	255110
50	qc_rural_9	7401603	239918
51	qc_rural_2	7401370	241710
51	qc_rural_7	7400969	241711
51	qc_rural_10	7401570	241111
52	qc_land_sparing_1	7400770	243711
52	qc_land_sparing_8	7401370	243310
52	qc_land_sparing_10	7401769	243511
53	urban_core_13	7399566	247912
53	urban_core_20	7399970	247310
53	urban_core_21	7400169	247510
53	urban_core_23	7400169	247711
53	urban_core_24	7400369	247311
53	urban_core_25	7400369	248111
53	urban_core_27	7400570	247710
53	urban_core_28	7400732	248123
53	urban_core_30	7400769	246711
53	urban_core_31	7400770	247111
53	urban_core_32	7400969	247310
53	urban_core_33	7400770	248310
53	urban_core_34	7401369	247110
53	urban_core_35	7401569	246911
53	urban_core_36	7401370	247710
53	urban_core_37	7401564	246488
53	urban_core_38	7401570	247311
53	urban_core_39	7401970	246711

54	urban_core_19	7399969	248910
54	urban_core_26	7400569	249510
54	qa_land_sharing_2	7402404	250017
54	qa_land_sharing_8	7402169	250115
55	qb_land_sharing_8	7401957	251522
55	qd_land_sharing_1	7399969	253710
55	qd_land_sharing_2	7399970	253510
55	qd_land_sharing_8	7399569	252511
55	qd_land_sharing_10	7400744	251676
56	qb_rural_7	7402537	255045
56	qd_rural_3	7401507	255407
56	qd_rural_4	7401153	255991
56	qd_land_sparing_1	7400169	255110
56	qd_land_sparing_2	7400169	254910
56	qd_land_sparing_3	7400169	254310
56	qd_land_sparing_4	7400169	254510
61	qa_land_sharing_1	7404581	242301
61	qa_land_sharing_3	7404564	242697
61	qa_land_sharing_7	7405369	241510
62	qa_land_sparing_4	7405764	244500
62	qa_land_sparing_7	7405569	244311
62	qa_land_sparing_9	7404369	244110
62	qa_land_sharing_4	7403570	245310
62	qa_land_sharing_5	7404369	243110
62	qa_land_sharing_6	7404570	243110
63	qa_land_sharing_10	7403370	246910
64	qa_land_sparing_1	7404169	249911
64	qa_land_sparing_2	7405169	249510
64	qa_land_sparing_3	7403769	249110
64	qa_land_sparing_5	7404769	250710

64	qa_land_sparing_6	7403433	249376
64	qa_land_sparing_8	7404369	249710
64	qa_land_sparing_10	7404169	249510
65	qb_land_sparing_9	7404169	251911
65	qb_land_sharing_2	7402770	252310
66	qb_land_sparing_1	7404369	256710
66	qb_land_sparing_3	7404567	256714
66	qb_rural_1	7403258	255585
66	qb_rural_9	7403086	256290
66	qb_land_sharing_3	7403969	256510
67	qb_land_sparing_2	7404769	257110
67	qb_rural_3	7403582	258286
70	qa_rural_6	7405946	239425
71	qa_rural_1	7406779	242784
74	qa_land_sharing_9	7407970	250310
74	qb_land_sharing_10	7406769	251110
75	qb_land_sharing_1	7407169	251710
76	qb_land_sparing_4	7408769	254110
76	qb_land_sparing_10	7408569	255710
76	qb_land_sharing_4	7406169	255511
76	qb_land_sharing_9	7407214	254858
81	qa_rural_3	7411551	241691
81	qa_rural_4	7411369	242310
81	qa_rural_7	7411745	242061
81	qa_rural_8	7410769	242910
81	qa_rural_9	7411169	242511
82	qa_rural_5	7410859	243115
85	qb_land_sharing_5	7409395	252959
86	qb_land_sparing_5	7409569	256710
86	qb_land_sparing_8	7410169	256310

87	qb_land_sparing_6	7409569	257310
87	qb_land_sparing_7	7409769	256910
87	qb_rural_2	7410969	259511
87	qb_rural_5	7411566	258191
87	qb_rural_6	7411821	258069
87	qb_land_sharing_6	7411138	257117
87	qb_land_sharing_7	7410684	258317
93	qa_rural_2	7414569	246310
93	qa_rural_10	7414363	246283
95	qb_rural_4	7413576	252294
95	qb_rural_8	7413769	252311
95	qb_rural_10	7412369	251710

Online Resource 4 – Mean sampled area and respective class of urban green and gray types for each count point.

The data may be accessed by the following link:

https://1drv.ms/u/s!AtGlvSBmoPEorjqNqvEfDDW3eLCj?e=A2bS8D

Online Resource 5 - Mathematical formula for the predict model of the relationship between gradient of urbanization and urban sprawl modelling and functional diversity of birds and table containing description of the values contained in the mathematical formula

FunctionalDiversity = StudySites, random = Spatial Autocorrelation, random = Agriculture, random = BareGround, random = Buildings, random = Commerce, random = Industry, random = Field, random = NativeForest, random = GreenFence, random = IndustrialSheds, random = Lawn, random = VacantLots, random = OGI, random = Silviculture, random = Streets, random = Trees

Value	Description
FunctionalDiversity	Functional diversity of birds in the respective count point
StudySites	Type of the study site in the respective count point
random = Spatial Autocorrelation	Spatial autocorrelation for the response variable in the respective count point
random = Agriculture	Size class of agriculture in the respective count point
random = BareGround	Size class of bare ground in the respective count point
random = Buildings	Size class of building in the respective count point
random = Commerce	Size class of commerce in the respective count point
random = Industry	Size class of industry in the respective count point
random = Field	Size class of anthropic field in the respective count point
random = NativeForest	Size class of native forest in the respective count point
random = GreenFence	Size class of green fence in the respective count point
random = IndustrialSheds	Size class of industrial sheds in the respective count point
random = Lawn	Size class of lawn in the respective count point
random = VacantLots	Size class of vacant lots in the respective count point
random = OGI	Size class of other gray infrastructures in the respective count point
random = Silviculture	Size class of silviculture in the respective count point
random = Streets	Size class of streets in the respective count point
random = Trees	Size class of trees in the respective count point

Online Resource 6 - Mathematical formula for the predict model of the relationship between functional diversity of birds and green and gray spaces sizes and table containing description of the values contained in the mathematical formula. For all the explanatory variables, excepted by the silviculture, we used the additive terms “pb()”, which are the current version of P-splines (Rigby and Stasinopoulos, 2005).

FunctionalDiversity = pb(Agriculture), pb(BareGround), pb(Buildings), pb(Commerce), pb(Industry), pb(NativeForest), pb(VacantLots), pb(OGI), Silviculture, pb(Streets), pb(Trees), random = Spatial Autocorrelation, random = StudySites, family=GA

Value	Description
FunctionalDiversity	Functional diversity of birds in the respective count point
pb(Agriculture)	Size of the agriculture area in the respective count point
pb(BareGround)	Size of the bare ground area in the respective count point
pb(Buildings)	Size of the building area in the respective count point
pb(Commerce)	Size of the commerce area in the respective count point
pb(Industry)	Size of the industry area in the respective count point
pb(NativeForest)	Size of the native forest area in the respective count point
pb(VacantLots)	Size of the vacant lots area in the respective count point
pb(OGI)	Size of the other gray infrastructures area in the respective count point
Silviculture	Size of the silviculture area in the respective count point
pb(Streets)	Size of the streets area in the respective count point
pb(Trees)	Size of the trees area in the respective count point
random = Spatial Autocorrelation	Spatial autocorrelation for the response variable in the respective count point
random = StudySites	Type of the study site in the respective count point
family=GA	GA distributional family from the FunctionalDiversity response variable

Online Resource 7 – Species of birds recorded in land sharing-sparing urban sprawl modelling in neotropical cities of Sorocaba and Votorantim, São Paulo, Brazil.

Id	Order	Family name	Common name	Scientific name
1	COLUMBIFORMES	Columbidae	Picazuro Pigeon	*Patagioenas picazuro*
2			White-tipped Dove	*Leptotila verreauxi*
3			Ruddy Ground-dove	*Columbina talpacoti*
4	CAPRIMULGIFORMES	Trochilidae	Planalto Hermit	*Phaethornis pretrei*
5			Swallow-tailed Hummingbird	*Eupetomena macroura*
6			Sapphire-spangled Emerald	*Amazilia lactea*
7	CUCULIFORMES	Cuculidae	Smooth-billed Ani	*Crotophaga ani*
8	CHARADRIIFORMES	Charadriidae	Southern Lapwing	*Vanellus chilensis*

9	PICIFORMES	Picidae	Ochre-collared Piculet	*Picumnus temminckii*
10			Green-barred Woodpecker	*Colaptes melanochloros*
11			Campo Flicker	*Colaptes campestris*
12			White-spotted Woodpecker	*Veniliornis spilogaster*
13	PSITTACIFORMES	Psittacidae	Plain Parakeet	*Brotogeris tirica*
14			Blue-winged Parrotlet	*Forpus xanthopterygius*
15			White-eyed Parakeet	*Psittacara leucophthalmus*
16	PASSERIFORMES	Furnariidae	Rufous Hornero	*Furnarius rufus*
17		Tyrannidae	Common Tody-flycatcher	*Todirostrum cinereum*
18			Yellow-bellied Elaenia	*Elaenia flavogaster*
19			White-crested Tyrannulet	*Serpophaga subcristata*
20			Cattle Tyrant	*Machetornis rixosa*
21			Northern Streaked Flycatcher	*Myiodynastes maculatus*
22			Social Flycatcher	*Myiozetetes similis*
23			Variegated Flycatcher	*Empidonomus varius*
24			Tropical Kingbird	*Tyrannus melancholicus*
25			Masked Water-tyrant	*Fluvicola nengeta*
26		Troglodytidae	House Wren	*Troglodytes aedon*
27		Mimidae	Chalk-browed Mockingbird	*Mimus saturninus*
28		Turdidae	Pale-breasted Thrush	*Turdus leucomelas*
29		Estrildidae	Common Waxbill	*Estrilda astrild*
30		Fringillidae	Purple-throated Euphonia	*Euphonia chlorotica*
31		Passerellidae	Grassland Sparrow	*Ammodramus humeralis*
32			Rufous-collared Sparrow	*Zonotrichia capensis*
33		Icteridae	Shiny Cowbird	*Molothrus bonariensis*
34		Thraupidae	Bananaquit	*Coereba flaveola*
35			Blue-black Grassquit	*Volatinia jacarina*
36			Lined Seedeater	*Sporophila lineola*
37			Double-collared Seedeater	*Sporophila caerulescens*
38			Saffron Finch	*Sicalis flaveola*
39			Sayaca Tanager	*Tangara sayaca*
40			Palm Tanager	*Tangara palmarum*
41			Burnished-buff Tanager	*Tangara cayana*

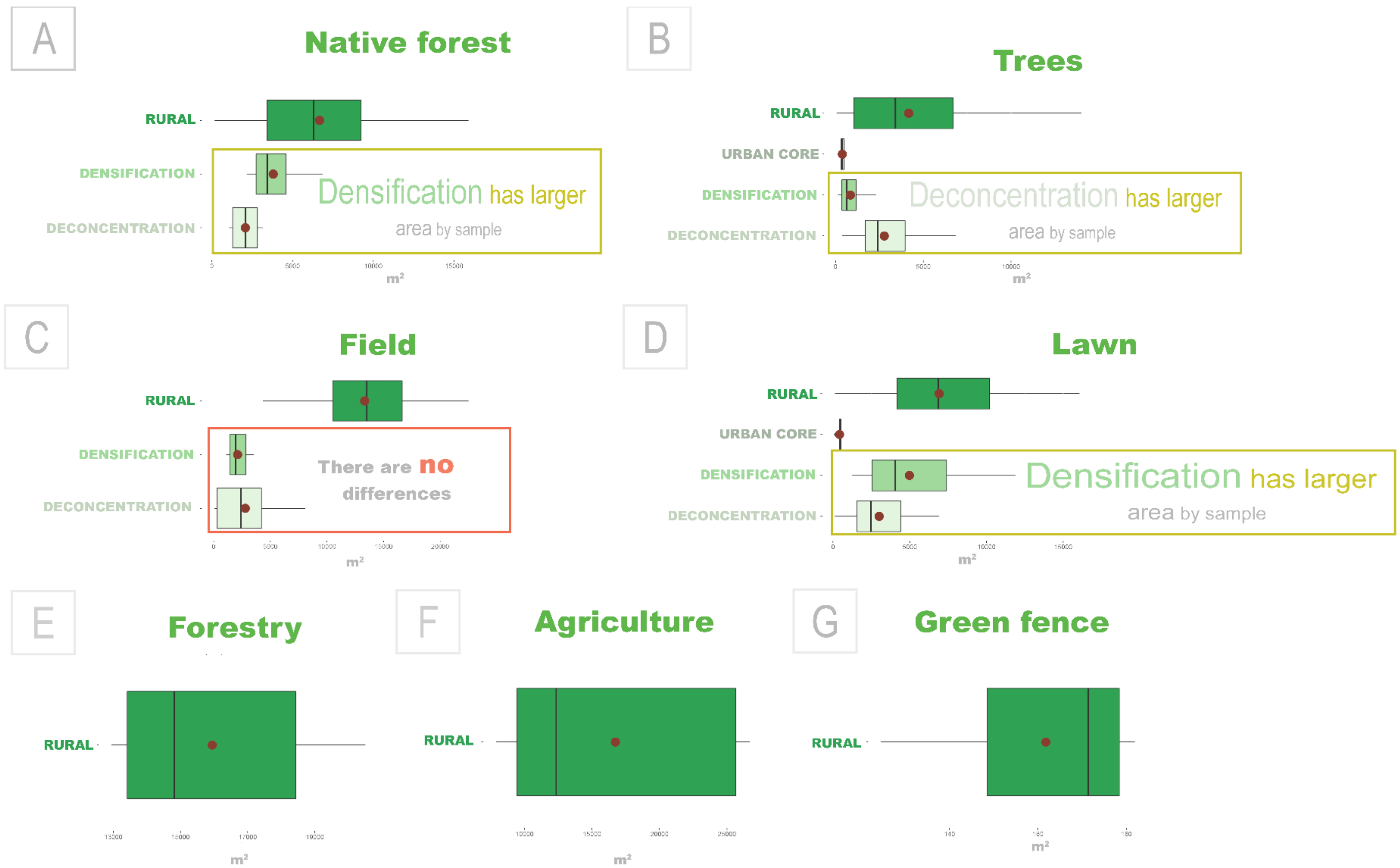
Online Resource 8 – Birds species' frequency in Sorocaba and Votorantim, Brazil.

The data may be accessed by the following link:

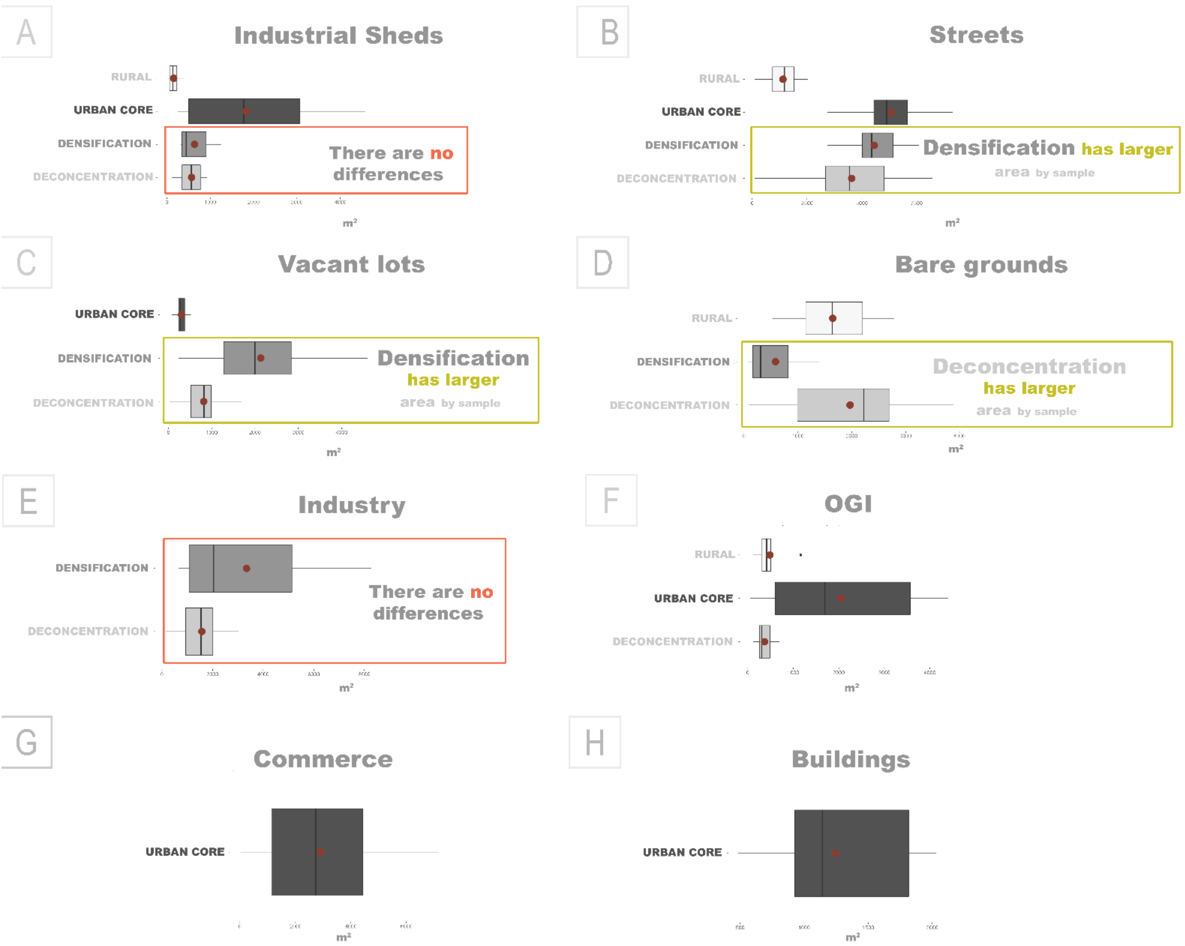
https://1drv.ms/u/s!AtGlvSBmoPEorjqNqvEfDDW3eLCj?e=A2bS8D

Online Resource 9 – Results of multiple comparisons of mean of the functional diversity of birds between study sites along an urban gradient in Sorocaba and Votorantim, Brazil.

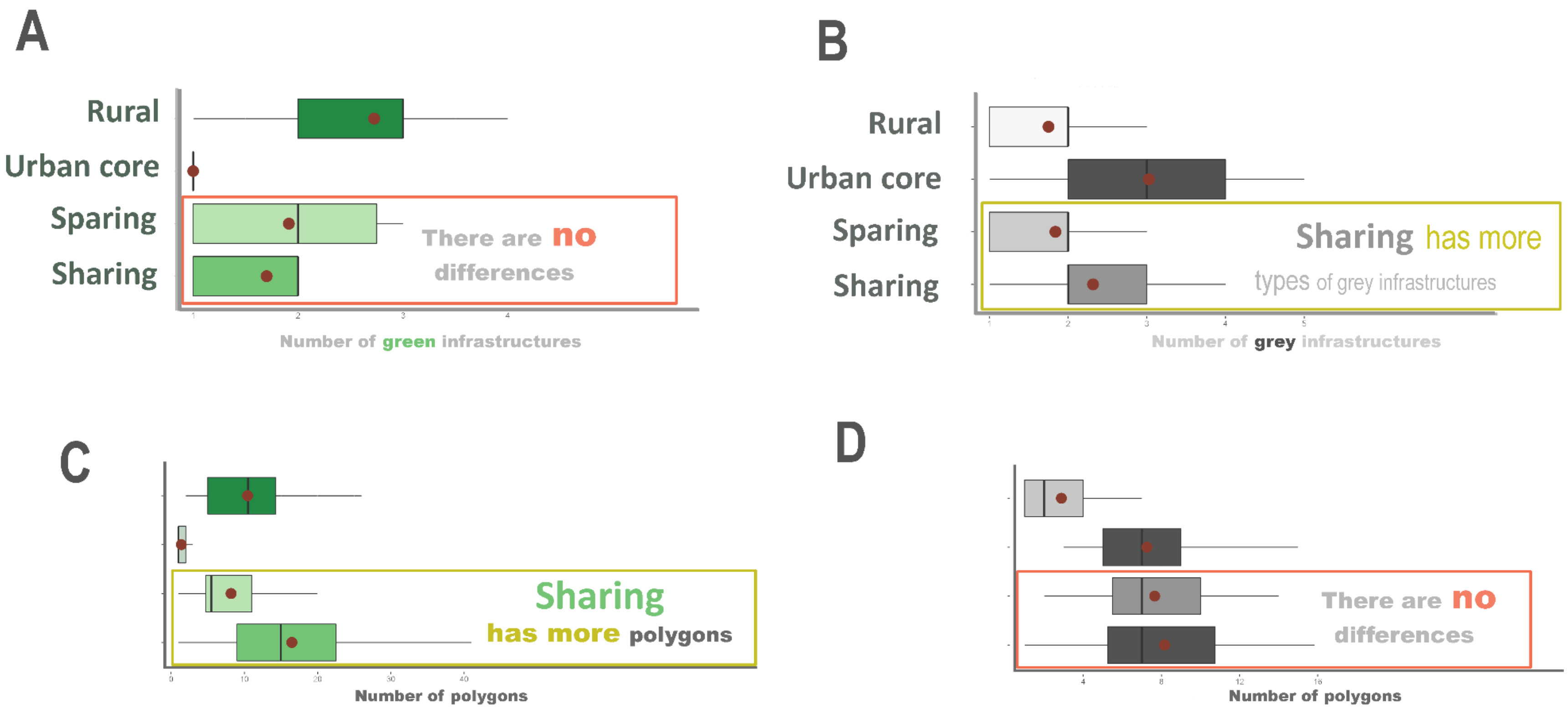
```
$contrasts
 contrast              estimate     SE  df z.ratio p.value
 rural - sharing       0.045981 0.0155 Inf   2.967  0.0159
 rural - sparing       0.000372 0.0168 Inf   0.022  1.0000
 rural - urban_core    0.049369 0.0170 Inf   2.898  0.0196
 sharing - sparing    -0.045610 0.0174 Inf  -2.614  0.0443
 sharing - urban_core  0.003388 0.0177 Inf   0.192  0.9975
 sparing - urban_core  0.048998 0.0188 Inf   2.603  0.0457

P value adjustment: tukey method for comparing a family of 4 estimates
```



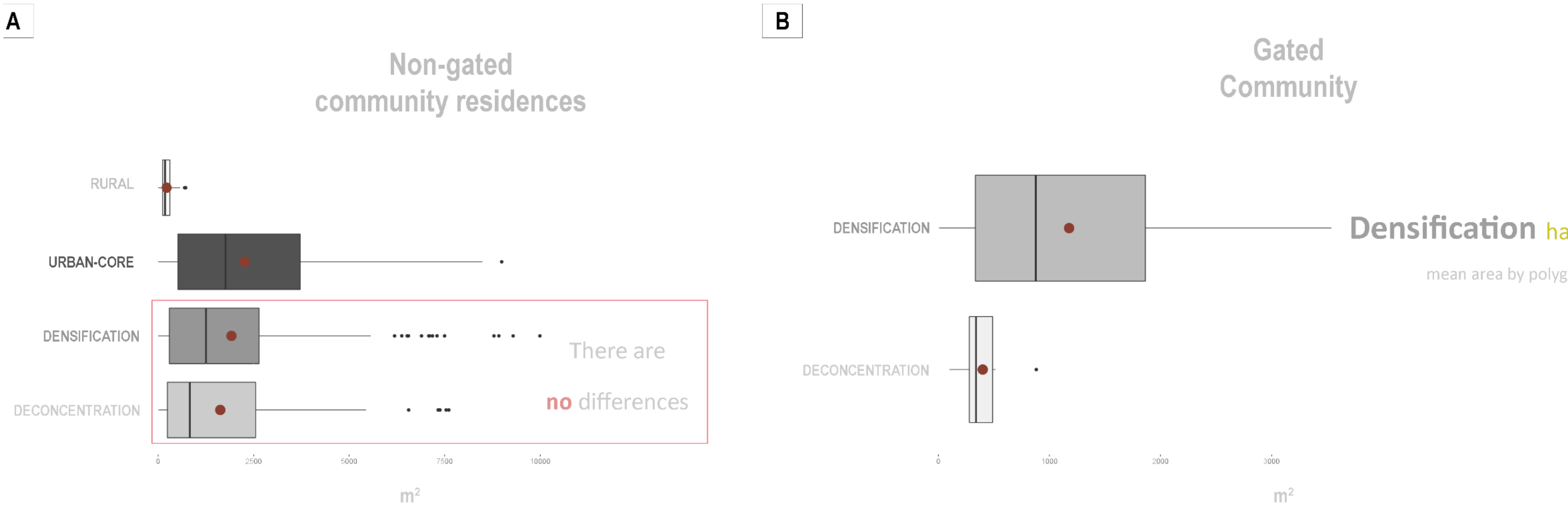
Online Resource 10 – Mean sampled area for land uses separated by sites for green infrastructures. The highlighted boxes indicate the existence of relationship or not between the urban sprawl models for the respective land use. A) Native forest; B) Trees; C) Field; D) Lawn; E) Forestry; F) Agriculture; G) Green fence.



Online Resource 11 – Mean sampled area of gray land uses by sites. The highlighted boxes indicate the existence of relationship or not between the urban expansion models for the respective land use. A) Industrial sheds; B) Streets; C) Vacant lots; D) Bare ground; E) Industry; F) OGI; G) Commerce; H) Buildings



Online Resource 12 – Relationship between the studied sites and infrastructures by color in three lines of descriptive analysis. A) Number of infrastructures by study sites to green infrastructures; B) Number of infrastructures by study sites to gray infrastructures; C) Number of polygons of green infrastructure between the study sites; D) Number of polygons of gray infrastructure between the study sites. The highlighted boxes indicate the existence of either relationship or not between the urban sprawl models.



Online Resource 13 – Mean area by polygon for residential land uses. A) Non-gated community residences; B) Gated communities.

Universidade Federal de São Carlos

Centro de Ciências Biológicas e da Saúde

Programa de Pós-Graduação em Ecologia e Recursos Naturais

Laboratório de Ecologia e Conservação - LECO

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Capítulo 2

Compacting urban sprawl reduces the negative effects of urbanization on frugivorous birds and fruit consumption

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2022

Research Paper

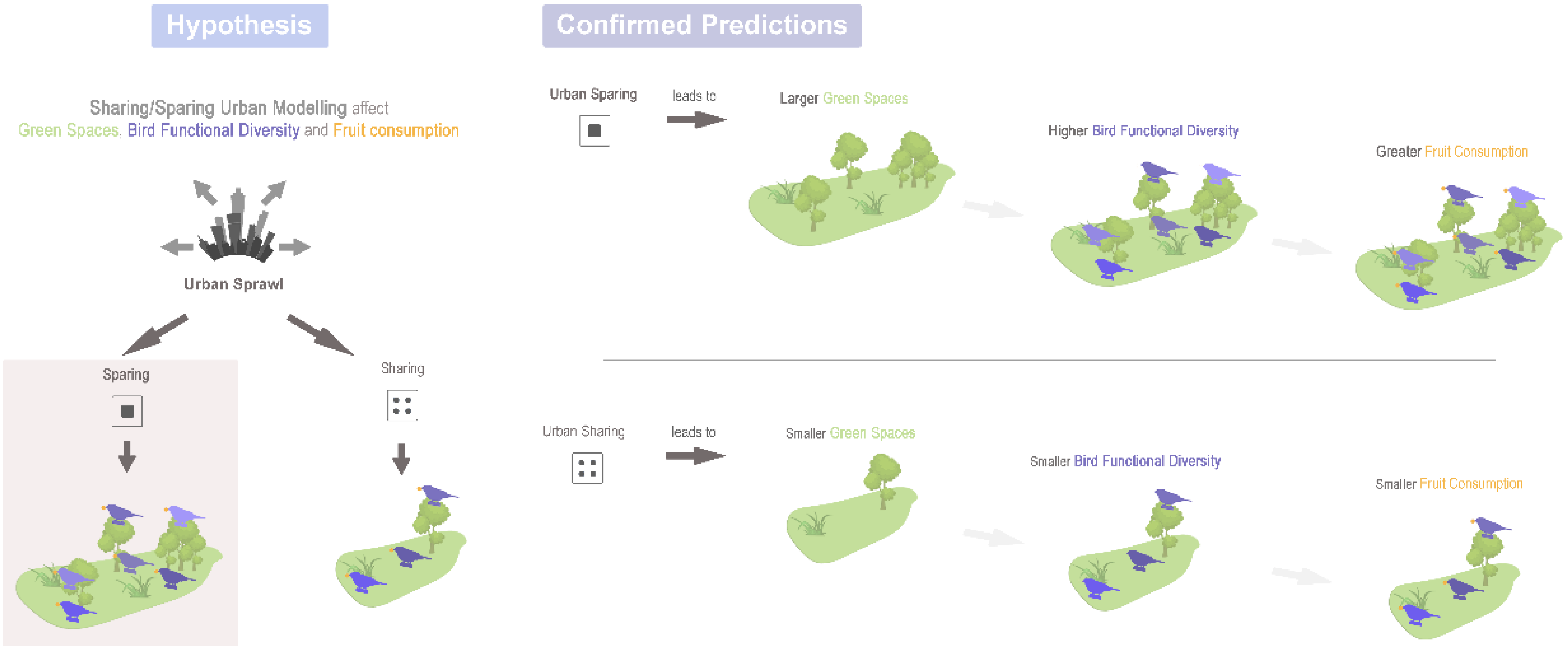
Compacting urban sprawl reduces the negative effects of urbanization on frugivorous birds and fruit consumption

Highlights

- The land-sparing urban sprawl model harbors larger areas of urban green spaces, e.g., native forests and lawns, than the land-sharing model.
- The land-sparing urban sprawl model supports higher bird taxonomic and functional diversity and fruit consumption by birds than the land-sharing model.
- Fruit consumption is positively related to the functional diversity of fruit-eating birds.

Click in this link to see the image in high definition.

Graphical abstract



Abstract

1. Cityscapes are growing fast and heterogeneously through of diverse urban sprawl models. Urban sprawl models are the specific expansion patterns of urban settlements. Since each model performs unique physical and social landscape changes, this needs to be weighed in urban planning, to balance urban growth and conservation. Urban land sharing/sparing modelling may affect the biodiversity of specialized groups like frugivorous, triggering cascading effects in the structure and dynamic of frugivores-plant interactions. However, this is barely understood in cities of Neotropical region.
2. We tested whether land sharing *vs*. sparing models affect bird taxonomic and functional diversity, and fruit consumption by frugivorous species in a Neotropical urban settlement. We predict that the sparing model may have larger green spaces, thus favoring bird taxonomic and functional diversity, and fruit consumption by birds.
3. Confirming our predictions, the sparing model has (1) larger green spaces areas, as native forests and lawn; (2) higher taxonomic and functional bird diversity; and (3) higher fruit consumption. We also confirmed that (4) functional diversity is positively related to the fruit consumption.
4. The sparing model can shelter larger areas of green lands, as native forests, thus supporting habitat— and fruit-eating —specialist birds. Our results provide insights for establishing policymaking aimed at the selection of urban sprawl models to balance the urban development, engaged with the conservation of larger green spaces. This would benefit particularly specialized frugivores, thus supporting the ecological functions they perform (e.g., seed dispersal).

Keywords: Land-sharing, land-sparing, Neotropical cityscapes, urban development, fruit-eating birds, Latin American birds

1 Introduction

More than half of the human population lives in urban settlements (United Nations, 2019), and the cityscapes are growing fast and heterogeneous, creating irregular spatial patterns (Ramalho & Hobbs, 2012). Urbanization has been assigned as one of the main rapid ways of landscape changing (Leveau et al., 2020) and a global causes of species endangerment (Grimm et al., 2008; MacGregor-Fors et al., 2020), triggering immediate and long-term consequences for the global biota, mostly reducing species diversity (Carvajal-Castro et al., 2019; Zurita et al., 2017) and affecting several levels of biotic organization (Blair, 2004).

The growth of cities caused by the urban sprawl arises from the human demands for social resources, e.g. housing and industrialization areas (Mehriar et al., 2020; Nassar et al., 2014), and can be defined as a multidimensional process of expansion of the periphery of a city (Heirman & Coppens, 2013). Urban sprawl causes physical changes in the environment, as the development of human-made structures, and occurs by different ways according to social, political, financial, and environmental characteristics (Rubiera-Morollón & Garrido-Yserte, 2020). These forms, also called models (Rubiera-Morollón & Garrido-Yserte, 2020), may have distinct effects on biological communities (McDonald et al., 2020). Previous studies have focused on better ways to drive the urban development, from both the socioeconomic and environmental views (Bibri et al., 2020; Bontje, 2001; Mehriar et al., 2020; Wolff et al., 2018). These studies have analyzed the benefits and costs of urban development according to two sprawl models, i.e., compacted *vs.* sprawled cities (Bibri et al., 2020). The first model (i.e., compacted) aims to assemble urban settlements and their structures in core points (Mehriar et al., 2020). On the other hand, the sprawled model is a dispersed format, with sprawling urban buildings (Dieleman & Wegener, 2004). For environmental porpoises, biodiversity benefits are expected in compacted cities through the conservation of natural areas and reduction of CO_2 release (Liu et al., 2014). The sprawling model has negative socioeconomic and environmental effects, such as long journeys to the shopping and work areas, higher energy consumption, pollution, accidents, extreme consumption of land use areas, and low public transportation quality in sparsely populated areas (Dieleman & Wegener, 2004).

Lending theoretical knowledge from the agricultural ecosystems, research in urban ecosystems has been analyzing the effects of the land-sharing and land-sparing models in urban settlements, to provide a balance between essential resources to the human beings and the biodiversity conservation (Dennis et al., 2019; Geschke et al., 2018; Suhonen et al., 2022). Land-sharing is defined as a land use management method that *integrate* both the conservation and the production land uses (Fischer et al., 2014) and, in a urban context, consists of low-density built-up areas (e.g., private housing settlements) combined with green spaces in the shape of gardens and small parks, although without large continuous forest areas or older parks (Lin & Fuller, 2013). On the other hand, land-sparing integrate the *division* of conservation and production land uses (Fischer et al., 2014), and in a urban context, consists of high-density built-up areas (e.g. residence buildings) with large, continuous green areas divided (Lin & Fuller, 2013). As previous seen in agroecosystems (Balmford et al., 2019; Cannon et al., 2019; Edwards et al., 2021; Feniuk et al., 2019; Hasan et al., 2020), research in urban settlements have revealed that land-sparing model may have better results for the conservation of many biological taxa (e.g., mammals (Caryl et al., 2016), birds (Suhonen et al., 2022), insects (Soga et al., 2014), plants (Collas et al., 2017)), structure of ecological communities (predator-prey; Jokimäki et al., 2020), and central to shelter rare and unique species (Suhonen et al., 2022).

Urban landscapes are often typified by a mosaic of different urban spaces (MacGregor-Fors & Schondube, 2011), mostly dominated by anthropogenic structures (Barbosa et al., 2020; Schneider et al., 2010), but also including mixed vegetation patches as parks, gardens and remnants of native plant life (Campos-Silva & Piratelli, 2021; de Toledo et al., 2012; Palmer et al., 2008) and water bodies (Barbosa et al., 2020) which may support representative components of native bird communities. In a simple way, urban spaces can be divided into urban grey and green spaces, depending mainly of the composition of non-natural built-up and natural infrastructures present in the landscape (Tischer et al., 2017; Wesener et al., 2017). Urban grey spaces are landscapes constituted mainly by non-natural built-up structures and impervious surfaces, which can be subdivided according to (1) the type of use, (2) the mainly type of infrastructures present, and (3) the people density (e.g., industrial, commercial, and residential areas) (Chormanski et al., 2008; Suligowski et al., 2021). Green spaces are components of the green infrastructure, and can be subdivided into uses or classes according to certain characteristics of the present vegetation, and use by the citizens (e. g. native forests, gardens, squares, parks) and are vital for citizens' wellbeing (Horwood, 2011; Jabbar et al., 2021; Zou & Wang, 2021). Each type of urban green space plays a specific role on biodiversity conservation and their ecological functions (Campos-Silva & Piratelli, 2021; Lepczyk et al., 2017). Socioeconomic and geographical factors are critical for urban biodiversity patterns; neighborhoods far from the city center and/or with greater economy incoming would have more green areas and biodiversity-friendly zones. On the other hand, more central and/or lower-incoming areas deliver few opportunities to sustain native biodiversity (Melles, 2005). It has been thoroughly demonstrated that the types of urban green spaces and their sizes impact the biodiversity by different ways (Lepczyk et al., 2017; Melo et al., 2021; Shahabuddin et al., 2021); thus diagnosing how urban sprawl models interfere in the land use patterns are a central topic to be investigated for conservation in urban settlements.

Frugivores are key species in the ecosystems, driving ecological patterns and process at several levels of organization (e. g. trophic and spatial networks of seed dispersal interactions) (Carreira et al., 2020; Emer et al., 2018; Rumeu et al., 2020), and they have been affected by anthropogenic land uses (Fuzessy et al., 2022; Fontúrbel & Medel, 2017). Many frugivores are stratum-, habitat- and feed-specialist organisms (Şekercioğlu et al., 2016; Todeschini et al., 2020); being sensitive to changes in the structures of landscapes that impact these resources, including fragmentation and loss of natural habitats (Fuzessy et al., 2022). Larger frugivores have been found to be the most negatively affected, disappearing in small patches. This have severe impacts to the ecosystems, as the seed downsizing driven by the defaunation, triggering functional and structural changes in the landscapes (Donoso et al., 2020). The outcomes related with the defaunation may be very pronounced in high human-made sites, like in the urban settlements, where species losses are more severe.

Several cities are attempting to plan their development, in order to mitigate the negative effects on biological communities and promoting sustainable growth (Nilon et al., 2017). However, urban sprawl has been rapid and often disordered in the Neotropics, causing loss of native vegetation, and favoring gray structures (Piratelli et al. 2017). Vegetation structure defines the ecological characteristics of birds (Campos-Silva & Piratelli, 2021), and native species with restrictive ecological requirements may be replaced by generalist and - often - abundant species, with effects on the species biological traits (Croci et al., 2008); thus, on the use of different dimensions of their ecological niche.

In this paper, we test the effects of land-sharing vs sparing urban sprawl modelling on (1) size of urban green spaces; (2) taxonomic and functional diversities; (3) fruit consumption by birds. We hypothesize that there are differences in (a) green spaces areas; (b) both bird taxonomic and functional diversity, (c) fruit consumption by birds; and (d) green spaces areas affect bird functional diversity. We predict that (a) land-sparing urban sprawl may shelter larger areas of green land uses, increasing bird taxonomic and functional diversity and fruit consumption. We also predict that (b) green spaces areas are positively related with bird functional diversity, and (c) fruit consumption is positively related to the functional diversity (Fig. 1). These results may help to fill a gap in the knowledge regarding Neotropical urban birds, thus supporting policymaking aimed at conserving biodiversity in urban landscapes and the development of the cities. As far as we know, this is the first study that aims to detect the impacts of different urban sprawl models on frugivores and this role in the Neotropical region.

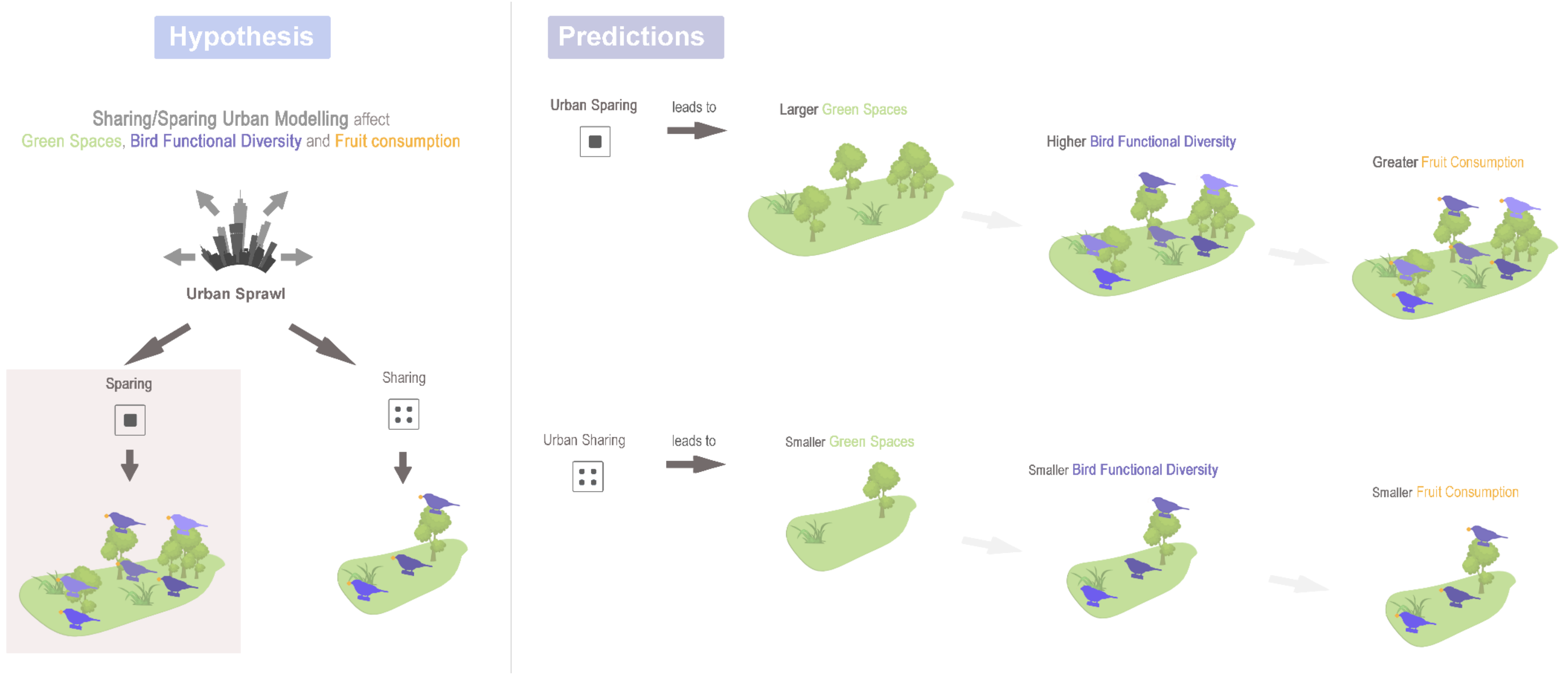


Figure 1 – Conceptual diagram of hypothesized and predicted modelling of urban sprawl of land sharing-sparing and their consequences in urban green spaces, functional diversity and fruit consumption by birds.

2 Methods

2.1 Study area and models of urban sprawl

This study was carried in the same cities and urban sprawl sites were the same as adopted in the section “2.1 Study area” and “2.2 Gradient of urbanization and land-sharing vs. sparing urban sprawl modelling” in chapter 1. For each type of urban sprawl model, 20 sampling points were randomly selected for data collection related to (1) green spaces, (2) birds, and (3) fruit consumption (Online Resource 1; Fig. 2).

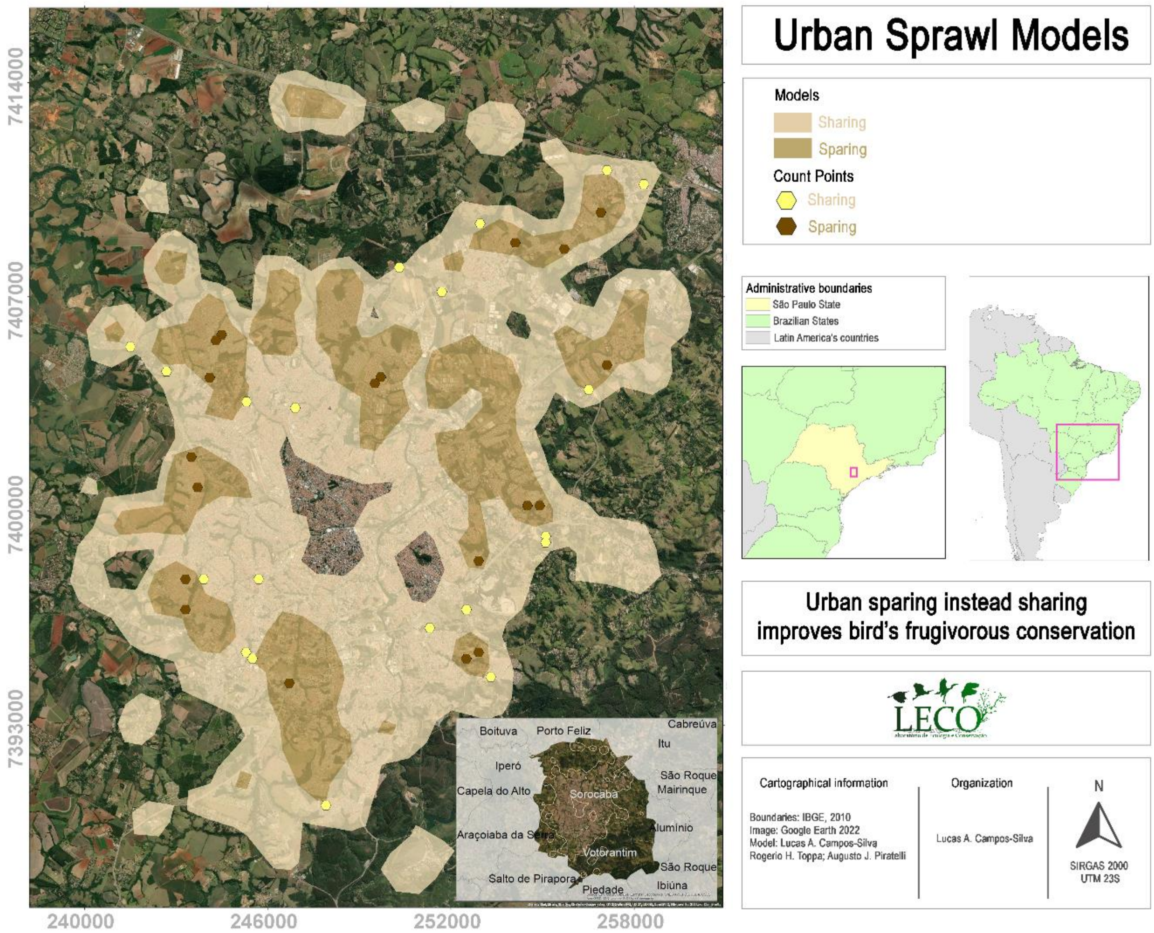


Figure 2 – Land-sharing/-sparing urban sprawl areas studied in Sorocaba and Votorantim, Brazil.

2.2 Mapping urban greens spaces

To test the hypothesis that (1) land-sharing/sparing urban sprawl modelling affect urban green spaces sizes, and (2) green space size influences the functional diversity of birds, the sizes of urban green spaces were estimated from the sampling points. Green spaces are components of the green infrastructure, and can be subdivided into uses or classes having mostly components of plant origin (e.g., native forests, anthropic fields, lawn areas). To achieve this goal, a radius of 100 meters for each sampling point was designed, where specific green spaces polygons were defined. We selected this radius to detect the impact of each type of green spaces on avifauna and fruit consumption. We selected four urban green spaces types (Fig. 3). We manually delimited the green urban spaces as the same way adopted in the section "2.3 Mapping urban green and gray spaces" in chapter 1.

Figure 3 – Urban green spaces, and their descriptions. The yellow polygons delimit the type of urban green space. Images are from Google Earth.

2.3 Bird surveys

We carried out bird censuses from September to March in 2019, 2020, and 2021, by 10-minutes count points with 50-meters radius, 200 meters far from each other to reduce overestimation of species abundance (Vielliard et al. 2010). The sampling points for birds were the same where the landscape features were sampled, totaling 40 sampling points (i.e., 20 by urban sprawl model; Fig. 1). We twice sampled each point in the first four hours of the daylight, using the highest value for the respective sampling point for bird's richness and abundance. Thus, a total of 80 sampling points were carried out in the study. All individuals were counted, even if they were in flocks. We collected bird data, excluding aerial insectivores, shorebirds, waterfowl, raptors, and nocturnal and crepuscular species, because counts points are not effective to detect these birds (Pennington & Blair, 2011; Bibby et al. 2000). All individuals perching, nesting, feeding, and flying five meters over the canopy were included.

In order to relate avifauna and its role in fruit consumption, we considered as 'frugivores' only species that have at least 30% of their diet composed of fruits (Wilman et al., 2014) and were considered as herbivore by the AVONET dataset (Tobias et al., 2022). Bird species with high outliers' abundances were excluded from the analyses. Bird taxonomy followed Version 6 of the Handbook of the Birds of the World and BirdLife International (2022). To avoid bias, all birds field data were collected by the first author (L. A. Campos-Silva).

2.4 Fruit consumption

To estimate the fruit consumption by birds we used 1.5 cm modeling clay (plasticine) artificial fruits in red and black (Duan et al., 2015; Gagetti et al., 2016) These colors were adopted because they are assumed to be among the colors preferred by birds (Gagetti et al., 2016). The fruits were mainly arranged on tree branches (Fig. 3A) and were settled in the same sites where the avifauna sampling points were carried out (Fig. 2). Twenty artificial fruits of each color were settled at each point count, totaling 1600 fruits, being 800 of each color (Fig. 3B). The fruits were left at each point for seven consecutive days, within a radius of 50m from the center of the point count. We mostly selected street trees to conduct the experiment, between a height of 0.70 m to 2 m from the ground level (Fig. 3C). The fruits were placed in pairs, one red and one black at 10 cm from each fruit (Fig. 3C). All the birds' species analyzed were considered as potential consumers of fruits, and that fit the criteria.

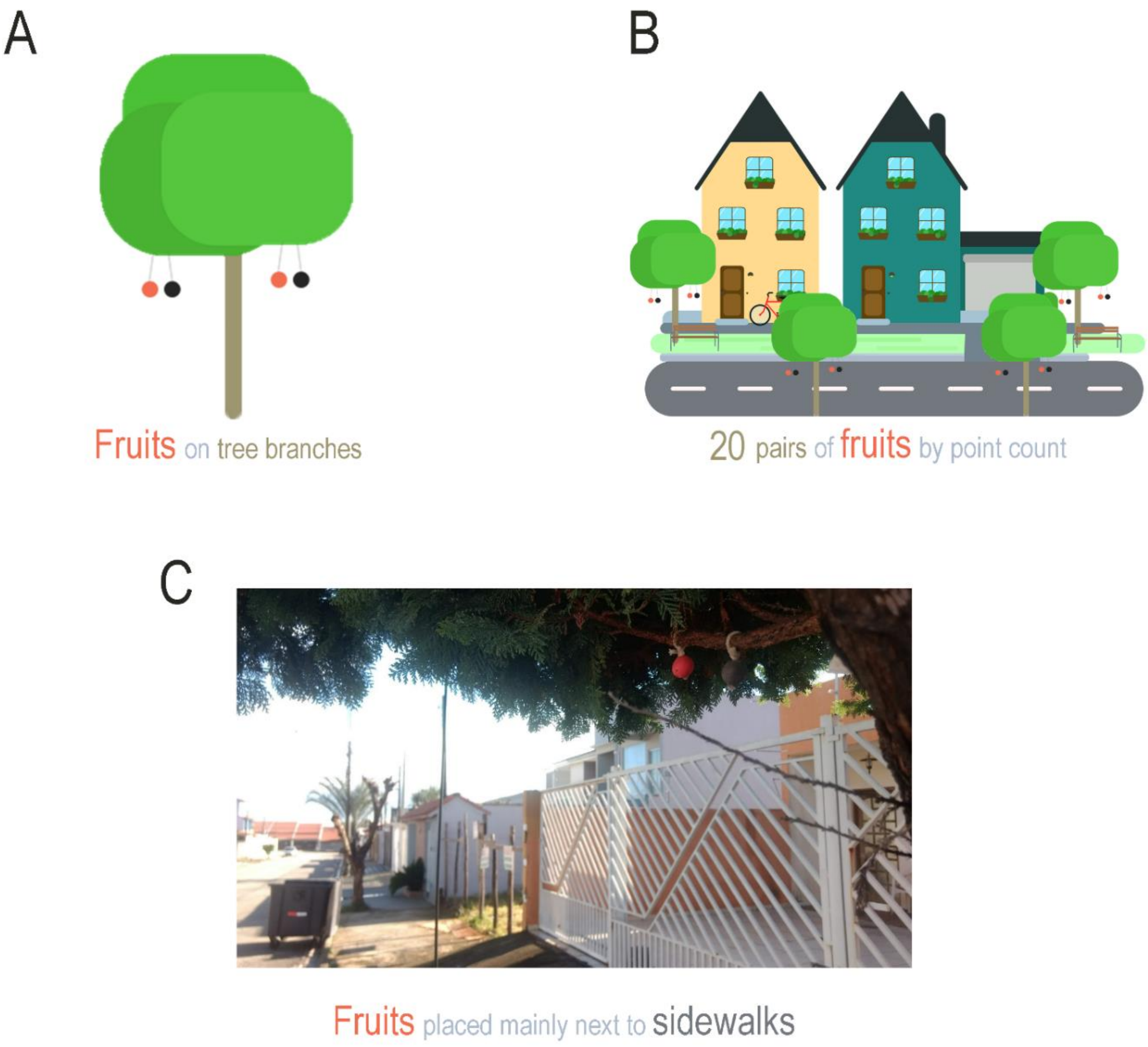


Figure 3 - Experimental study design of fruit consumption by birds in land-sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil

The artificial fruits were left in the field for seven days and were inspected only in the last day. They were assigned as consumed by birds when presenting pecking marks based on theoretical references (Alves-Costa & Lopes, 2001; Davis et al., 2010; Gagetti et al., 2016). Pecking by birds leaves patterns of specifics marks on artificial fruits, which may vary in size and shape depending on specific characteristics (e.g., bird species, strength angle of incidence, and part of the beak that touches the fruits; Fig. 4).

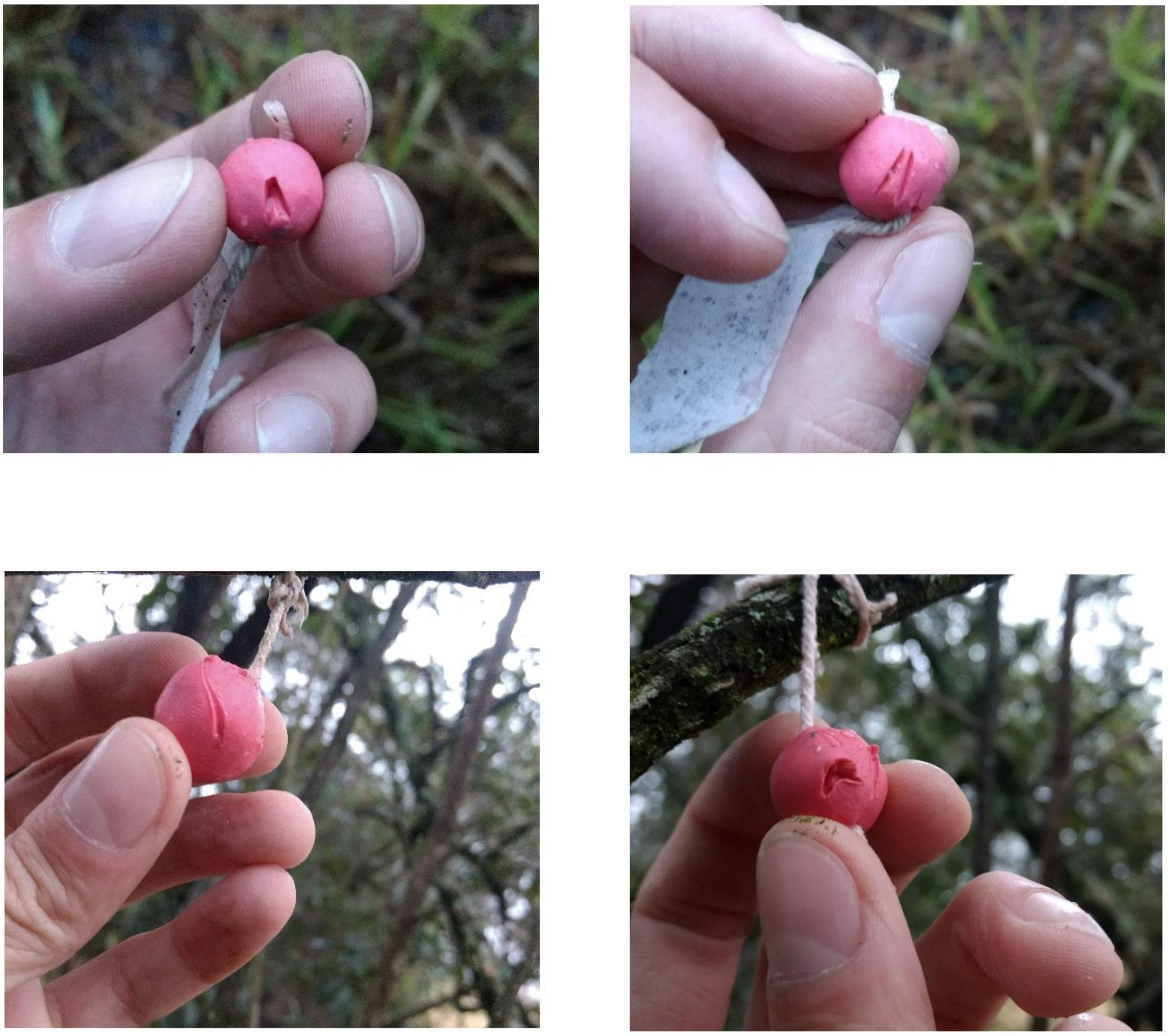


Figure 4 – Examples of bird pecking marks on artificial fruits (Photos: Lucas Andrei Campos-Silva).

2.5 Taxonomic and bird diversity indices

Functional divergence was used as proxy for functional diversity of frugivorous birds recorded in these urban sprawl areas as the same way adopted in the section “2.5 Taxonomic and bird diversity indices” in chapter 1. Also, we used the same eight ecological and five morphometric traits as in the section “2.5 Taxonomic and bird diversity indices” in chapter 1.

Diet and foraging stratum reflect how specialized are species niches in exploring feeding resources, and the main stratum they forage (Todeschini et al., 2020). These traits can also accurately indicate their ecological functions in the environment (Whelan et al., 2015). The habitat can reveal the relationship between birds and the environment, where they find resources to live (Morelli et al., 2019). Migratory traits reflect the recurrent and regular movement of individuals across their breeding and non-breeding sites (Somenzari et al., 2018; Webster et al., 2002). This trait can indicate their presence, and thus their seasonal ecological function. Nest substrate is a key-factor in nest-site selection (de Meireles et al., 2018). Nest-site is a component of habitat selection (Swaisgood et al., 2018), and this can define the range of a bird species distribution. Nest descriptions refer to the type of the nest (Simon & Pacheco, 2005). Many urban adapters have closed nests, while urban avoiders, open cup nests (Croci et al., 2008); these patterns are related to the infrastructures that birds found in the urban and not urban habitats. Cavity dependence describes the reliance of birds in nesting in cavity substrate, which may also limit species range (Bonaparte et al., 2020). Nest strata usually indicate the height that the birds use to nest and may imply in the specificity with the vertical stratum.

Body length, size, and mass are related with many aspects that a species play in the environment (Thornton & Fletcher, 2014), dispersal ability (Ottaviani et al., 2006) and susceptibility to disturbance and extinction risk (Fritz et al., 2009). Likewise, body mass is related to the magnitude of the ecological functions played by a species in the environment (Brown et al., 1978), and is also related with the energy flow in the ecosystems (Sibly et al., 2013). Bill length is commonly related with specialization and ecological function (Lederer, 1975; Maglianesi et al., 2014), and gape width (i.e., bill width) is associated to feeding specialization and ecological functions (Bender et al., 2018). Wing length is related to species' dispersal ability (Sheard et al., 2020). Gape width, body mass, and wing length are traits related to plant-frugivore networks structures and seed dispersal dynamics (Bender et al., 2018; Bonfim et al., 2021; Li et al., 2018). We adopted here the functional diversity as an index that indicate how complex is it an environment that can harbors abundances of more specialist frugivorous birds (e.g., larger-bodied, larger winged-length and larger-gaped width species).

2.6 Relationship between urban sprawl models and fruit consumption

The number of fruits with attempted consumption by birds were used as a proxy for *fruit consumption.* Thus, from now on in the text, we will only adopt the term *fruit consumption* indicating fruits with attempted consumption. The relationship between fruit consumption and urban sprawl model was tested separated by the colors of the consumed fruits (i.e., black and red). Some steps were incorporated for creating models to predict the relationships between response variable (fruit consumption) and the explanatory (urban sprawl models) ones. First, only data from sites where at least 70% of the fruits were found (i.e., neither removed nor damaged) were used. Fruits that were intentionally dented by human action were assigned as "*damaged*". We tested for spatial autocorrelation for the response variables using the "Moran.I" function of the "ape" package (Paradis, 2019). No spatial autocorrelation was detected for any of these response variables (red fruits – p = 0.65; black fruits – p =0.10). Ultimately, the type of the distribution's values was tested for the response values and included into the respective models. To check these distributions, we used the "fitDist" function from "fitdistrplus" package (Delignette-Muller & Dutang, 2015). The machine learning model selected to make this relationship was the "Generalized additive model for location, scale, and shape (GAMLSS)", through the "gamlss" function, from the "gamlss" package (Rigby and

Stasinopoulos, 2005). This model allows to include a wide range of distributions of the response variable, and non-parametric smoothing functions, random effects, or other additive terms into the predictor variables (Rigby & Stasinopoulos, 2005). Sizes of urban green spaces were also added in the models as random effect (Online resource 2).

The mathematical formulas for each predict model are described as follows (the following terms' meanings are in online resource 3):

FrRed = Model, random = NativeForest, random = Field, random = Lawn, random = Trees, family = BCPE (eqn 1)

FrBlack = Model, random = NativeForest, random = Field, random = Lawn, random = Trees, family = BCPEo (eqn 2)

2.7 Relationship between urban sprawl models and functional and taxonomic diversity

The functional divergency was used as a proxy for functional diversity, and species richness/abundance for taxonomic diversity. In order to create models to predict the relationships between the response variables (i.e., taxonomic and functional diversity) and the explanatory (urban sprawl models) the same first three steps and the last, related to distribution of response variable, adopted in section 2.7, were here adopted. No spatial autocorrelation was detected for any of these response variables (functional diversity - p = 0.77; richness – p = 0.72; abundance – p = 0.47). Lastly, the type of the distribution of the response variables was checked using the "fitDist" function from "fitdistrplus" package (Delignette-Muller & Dutang, 2015). The machine learning model chose to make this relationship was also the GAMLSS. Sizes of urban green spaces were also added in the models as random effect.

The mathematical formulas for each predict model are describe as follows (the following terms' meanings are in online resource 6):

FunctionalDiversity = Model, random = NativeForest, random = Field, random = Lawn, random = Trees, family = BCPE

(eqn 1)

Richness = Model, random = NativeForest, random = Field, random = Lawn, random = Trees, family = BCPEo

(eqn 2)

Abundance = Model, random = NativeForest, random = Field, random = Lawn, random = Trees, family = BCPE

(eqn 3)

2.8 Relationship between urban green spaces areas and functional diversity

To evaluate the relationship between functional diversity and green space sizes, the mean sampled area of each urban green space (i.e., native forest, fields, lawn, and trees) was used. In order to create models to predict the relationships between responses variable (i.e., functional diversity) and the explanatory (i.e., urban green spaces) the same first three steps and the last, related to distribution of response variable, adopted in section 2.7, were here adopted. No spatial autocorrelation was detected for the functional diversity (p = 0.53). The machine learning model chose to make this relationship was the “Linear Mixed-Effects Models-Lmer””, through the “lmer” function, from the “lme4” package (Bates et al., 2015). The urban sprawl model types were added in the models, as random effect. The mathematical formula is described below (the following terms’ meanings are in online resource 5:

*FunctionalDiversity = NativeForest * Field, random * Lawn * Trees, random = Model, family = Gaussian*

(eqn 1)

2.9 Relationship between size of urban green spaces and urban sprawl model

The *mean sampled area* was used as a proxy of *size* in order to test whether there are differences of urban green space sizes between each urban sprawl model. *Mean* was selected as a metric because it tends to penalize sampling points that have a greater number of polygons of the same type of urban green space, since it tends to be smaller with the increase in the number of polygons. Land-sharing is a model that has in its essence the sharing of urban grey and green spaces, and therefore tend to have more fragments/polygons, whether green or gray spaces. This can result in urban green spaces smaller than sparing model.

We used 40 sampling points by model to this for this effect (see online resource 6 to check how these points were sampled). To avoid biases, we followed these steps before performing the statistical analysis: (1) only urban green spaces with a minimum of six polygons and six samples per model were included; (2) the outliers were removed for each test; (3) normalized distribution was identified for each land use values using the "shapiro.test" function. Finally, to check for statistical differences, t-student tests were performed for parametric values by the "t.test", from the "stats" package; for non-parametric values Mann-Whitney test was used by the function "wilcox.test", from the "stats" package (R Core Team, 2022). All these analyzes were performed in the R language, via the R Studio Development Interface (R Core Team, 2022).

3 Results

3.1. Bird biodiversity

A total of 14 frugivorous species were recorded, representing three orders, and six families (Online Resource 7). The most frequent birds in the land-sparing models were Sayaca Tanager, Chalk-browed Mockingbird, Pale-breasted Thrush, White-eyed Parakeet (*Psittacara leucophthalmus*), and Picazuro Pigeon, with two species in the top frequency heavier than 200gr (White-eyed Parakeet and Picazuro Pigeon; Fig. 5). The most frequent species in the land-sharing models were Sayaca Tanager, Great Kiskadee, Chalk-browed Mockingbird, Bananaquit, Pale-breasted Thrush and Picazuro Pigeon. Only Picazuro Pigeon is heavier than 200 gr (Fig. 5).

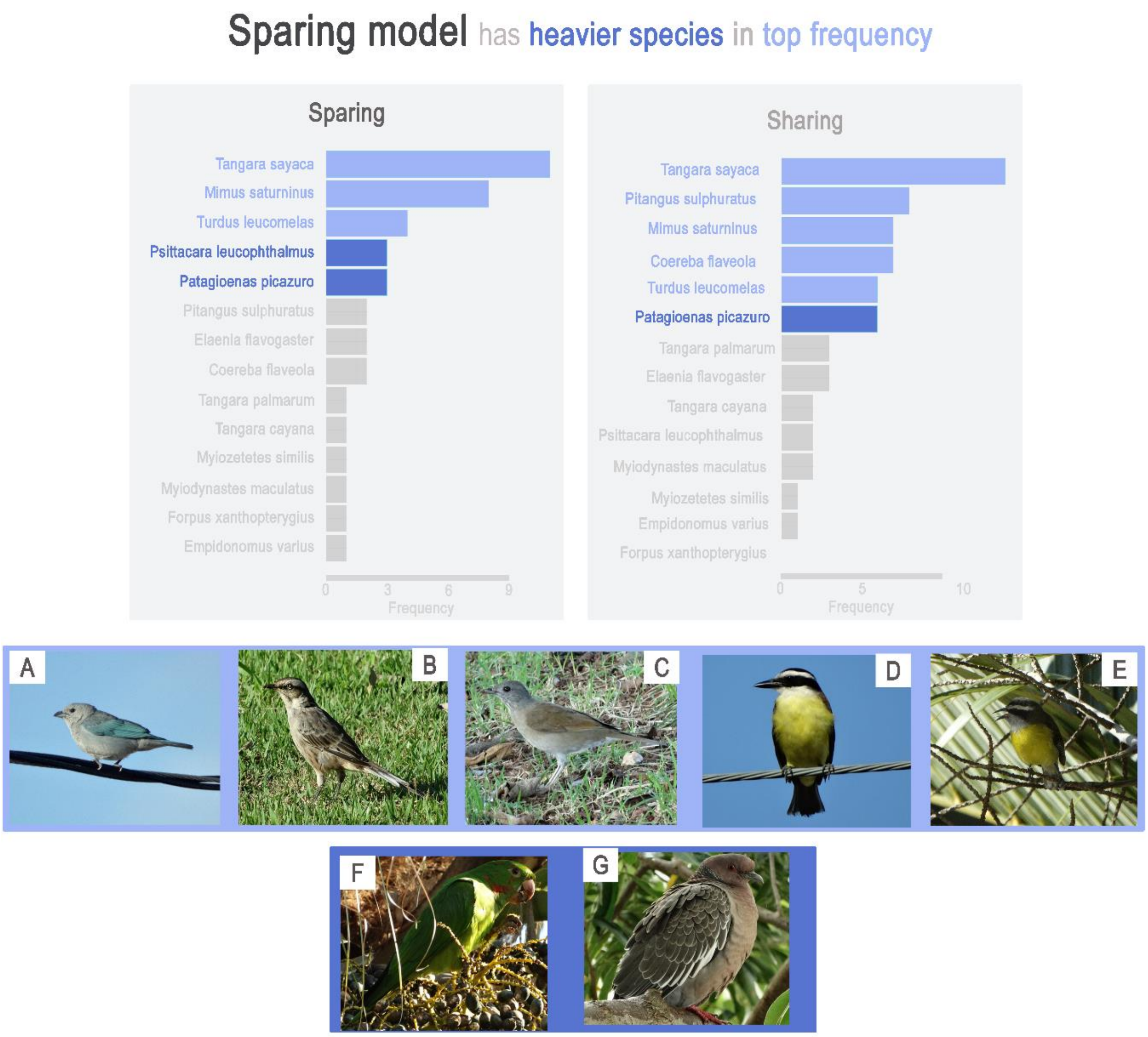


Figure 5 – Frequency of frugivorous birds across two models of urban sprawl (land-sparing and land-sharing) in Sorocaba and Votorantim, Brazil. The highlight in blue indicates the most frequent species. The dark blue indicates the species heavier than 200 gr. A) Sayaca Tanager; B) Chalk-browed Mockingbird; C) Pale-breasted Thrush; D) Great Kiskadee; E) Bananaquit; F) White-eyed Parakeet; G) Picazuro Pigeon. Photos: A-D, F and G by Lucas Andrei Campos-Silva; E by Thais Rodrigues Marinaci.

The land-sparing model had higher bird abundance in upper extremes of the traits range, related to plant-frugivore interactions structures and seed dispersal dynamics (e. g., gape width, body mass, and wing length) than sharing (Fig. 6). The land-sparing model had higher proportion of the abundances of traits related to the canopy and nest cavity-dependents than land-sharing (Fig.7).

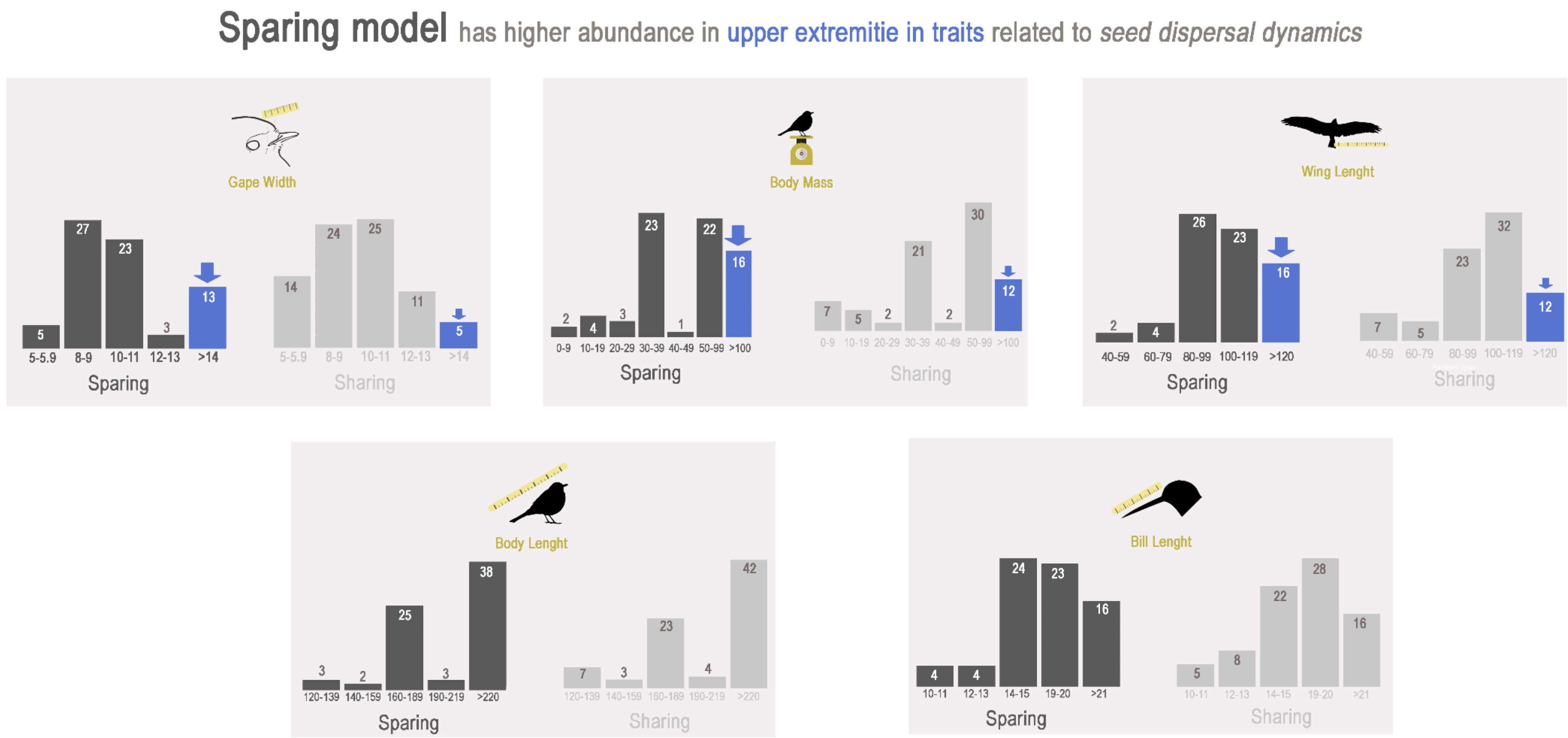


Figure 6 – Abundance of frugivorous birds by morphological traits in land-sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil. The highlight in blue indicates abundances in the upper extremes of functional traits range, related to plant-frugivore interaction structures and seed dispersal dynamics.

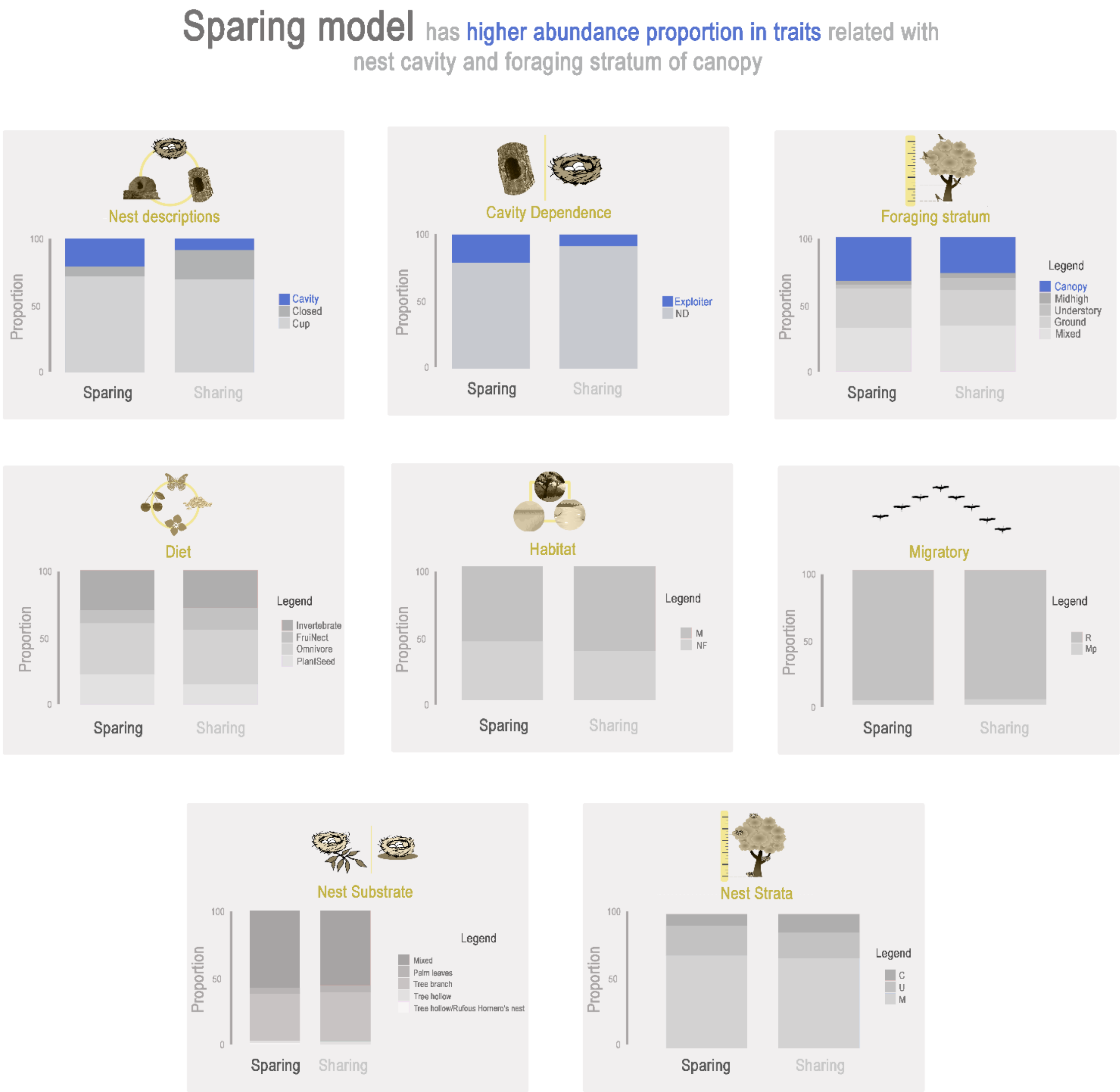


Figure 7 – Proportion of abundances of frugivorous birds by ecological traits in land-sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil. The highlight in blue indicates abundances of traits related to canopy foraging stratum and nest cavity-dependence. Cavity dependence – ND: Non dependent of cavities. Nest Strata – C: Canopy - U: understory - M: mid-story.

3.2 Fruit Consumption

A total of 220 (14%) of the fruits were consumed by birds, being 112 reds and 108 black; this suggests that both colors were attractive to the birds. An amount of 269 (16%) fruits were damaged, removed or not found. Seventy percent of the total fruits were not attacked by birds (Fig. 8).

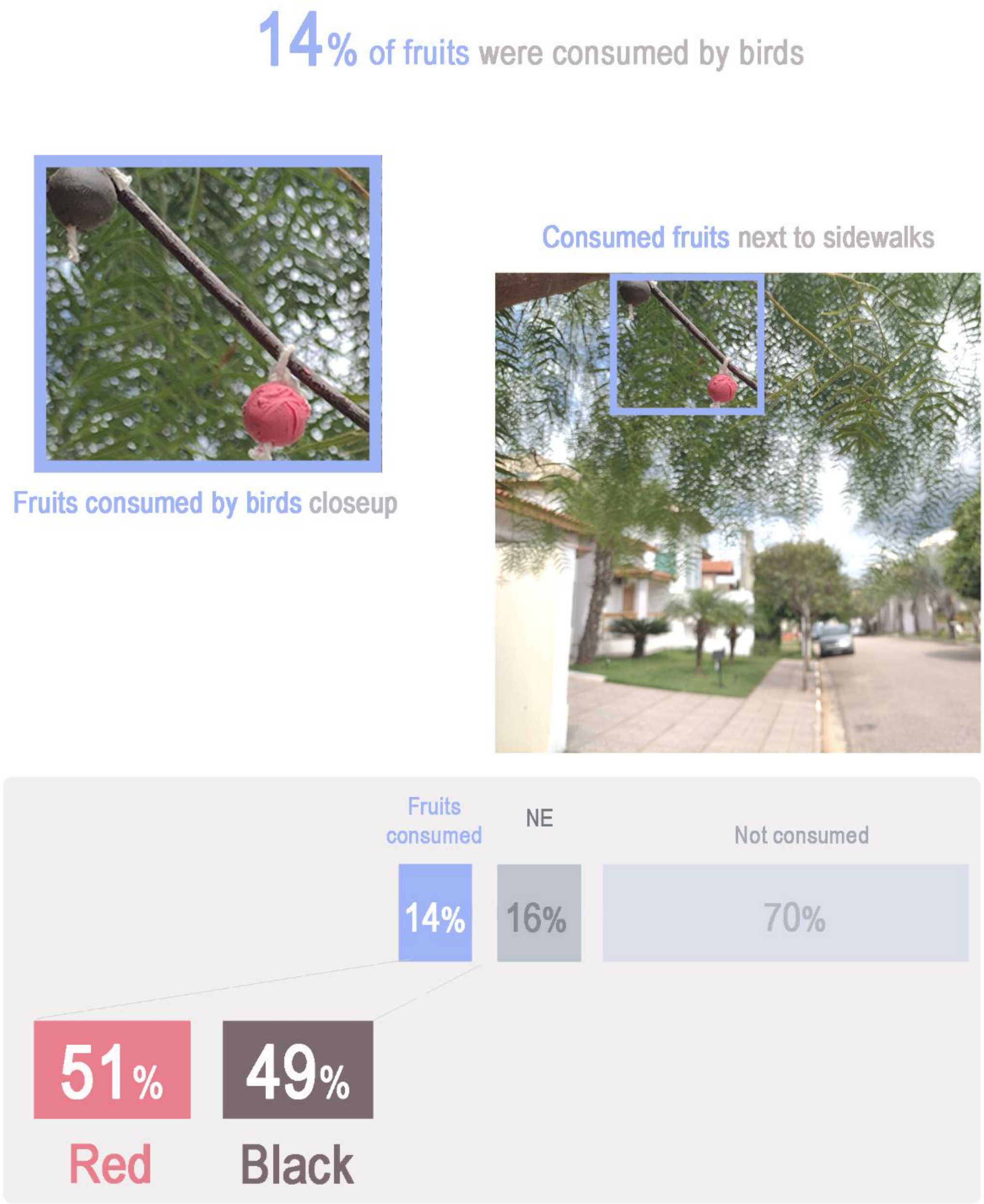


Figure 8 – Descripted results of fruit consumption by birds in land-sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil.

3.3 Relationship between urban sprawl, birds taxonomic and functional diversity, and fruit consumption

Estimates of fruit consumption of both colors were higher in the sparing than the sharing model (red fruits - t = 379.30, p < 0.000; black fruits - t = 168.00, p < 0.000, Fig. 9). A positive relationship between functional diversity and fruit predation was observed in both urban sprawl areas (t = 33.25, p < 0.001, Fig. 10). The land-sparing model had higher values for functional diversity, richness and abundances of the frugivorous birds (t = 134.20, p < 0.000; t = 25.85, p < 0.000; t = 224.31, p < 0.000, Fig. 11, respectively).

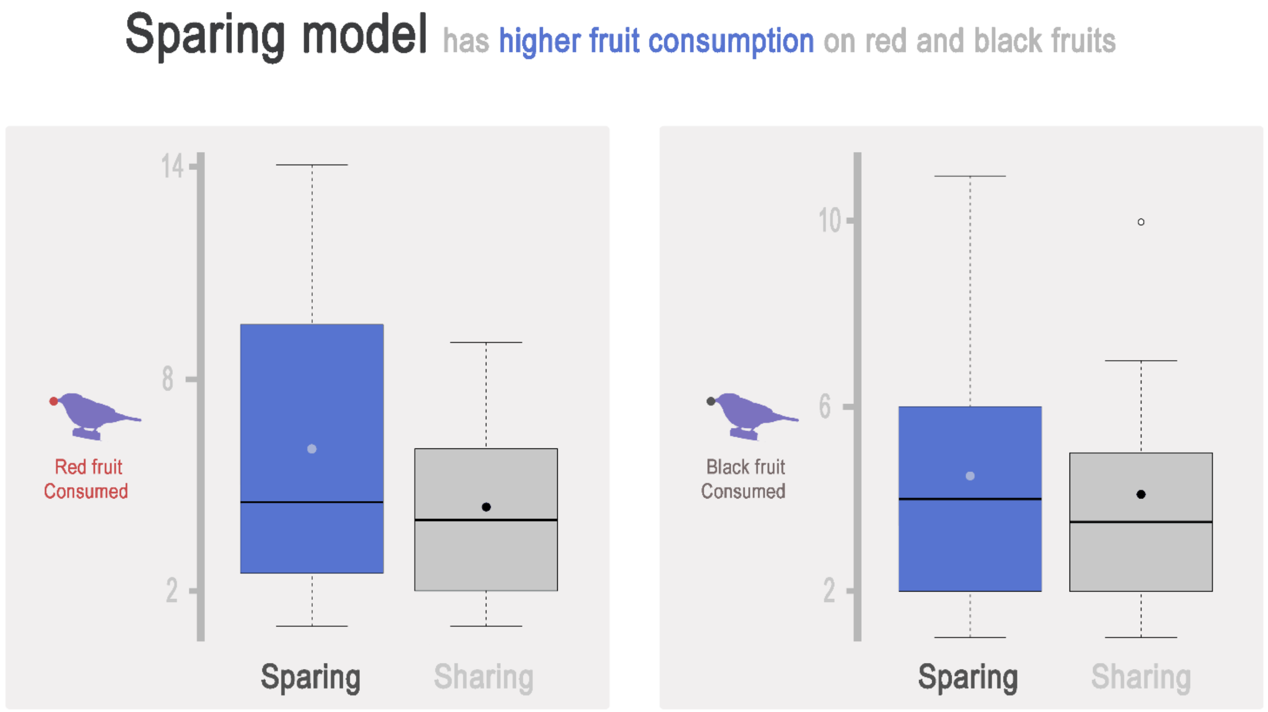


Figure 9 – Relationship between consumption of red and black fruits by birds in land-sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil. The circles in the center of the box plots indicate the mean values.

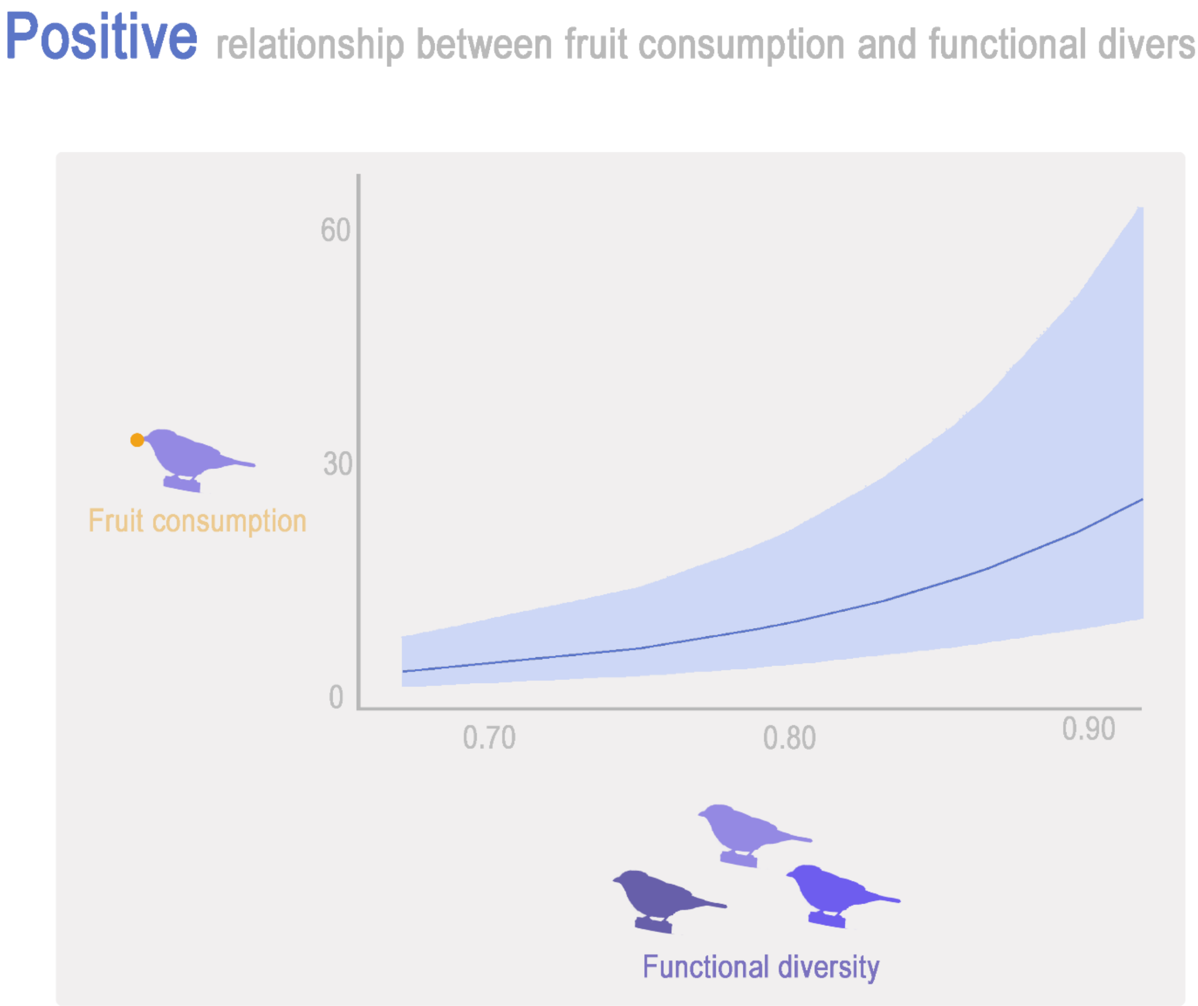


Figure 10 – Relationship between the functional diversity and fruit consumption by frugivorous birds in land-sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil.

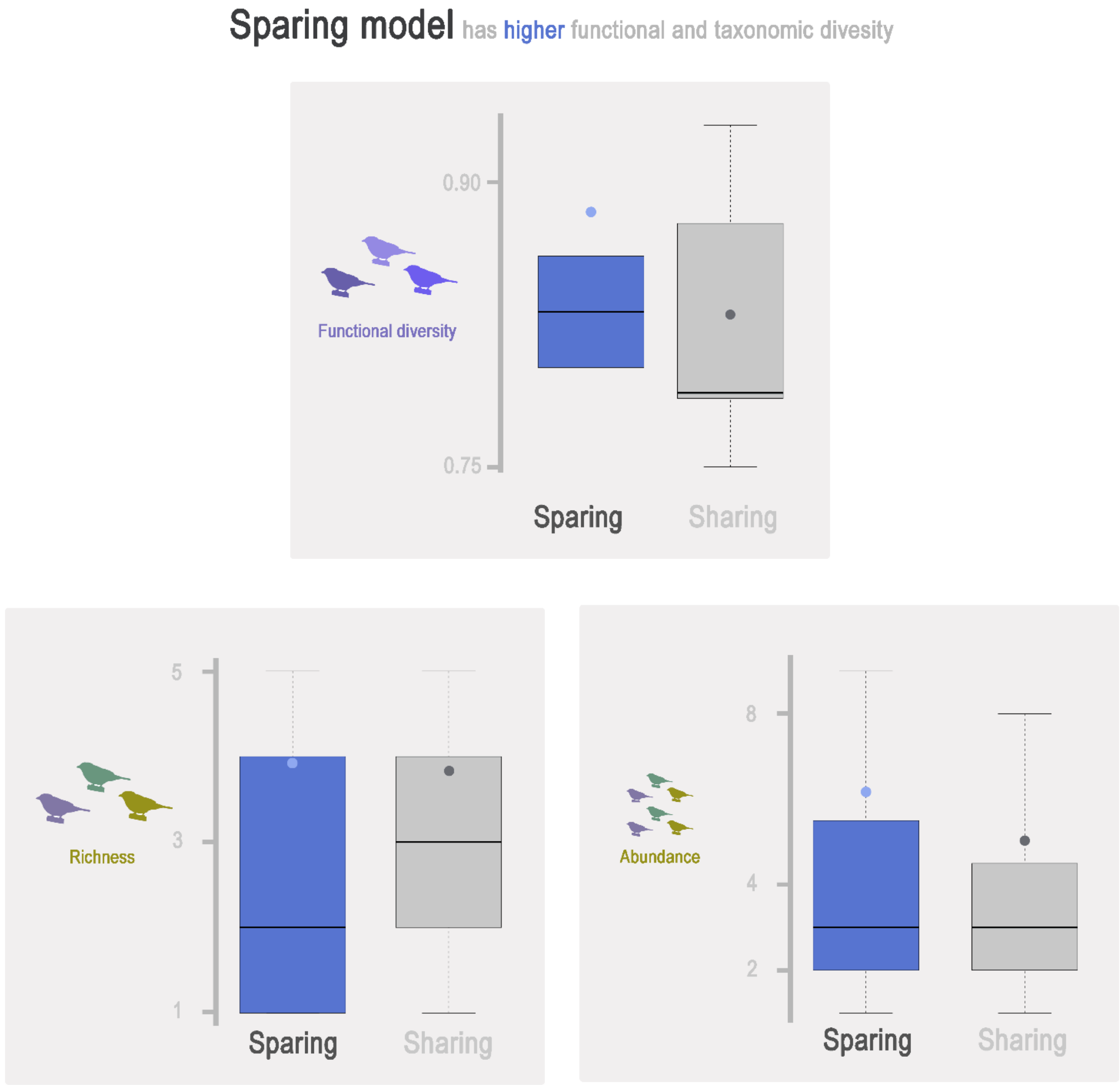


Figure 11 – Relationship between functional diversity and taxonomic indices of birds in land-sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil. The blue dots indicate the mean values predicted by the respective models.

3.4 Patterns of green spaces sizes in land-sharing and land-sparing urban modeling

Sites of land sparing presented higher values of mean sampled area of native forests, and lawns ($t = -3.15$, $p < 0.006$, and $w = 134$, $p < 0.04$, respectively; Fig 12). Land-sharing sites had more values of mean sampled trees (w = 840, p < 0.000, Fig. 15). No difference was observed for fields comparing these models (W = 56, p = 0.92).

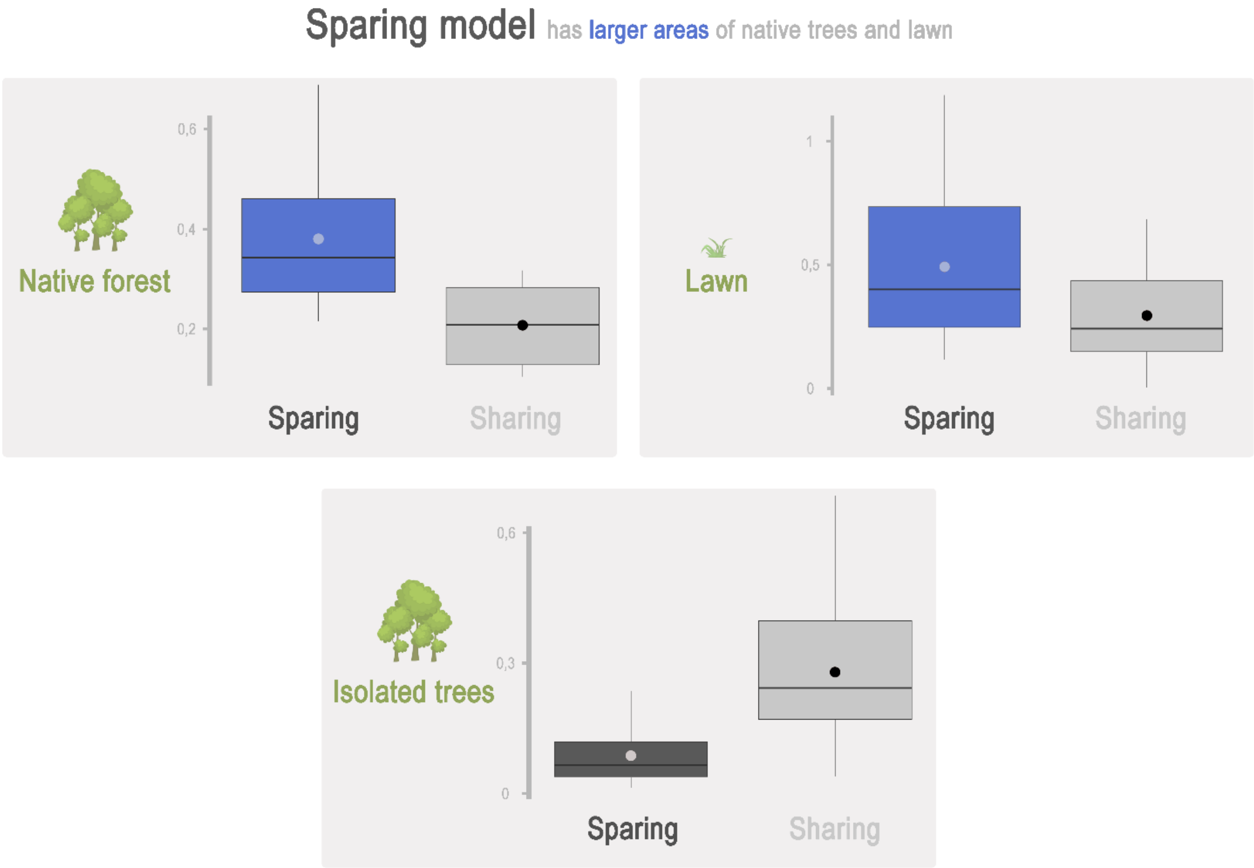


Figure 12 – Mean sampled areas of green urban spaces by land-sharing/-sparing urban sprawl models in Sorocaba and Votorantim, Brazil. The vertical axis values are in hectares.

3.5 Relationship between urban green spaces and functional diversity

The area occupied by isolated trees had a positive relationship with the functional diversity (t = 2.60, p = 0.04). The interaction between trees and lawn performs a positive relationship to the functional diversity (t = 0.01, p < 0.0001; Fig. 13). Native forests, lawn, and fields have not affected the functional diversity of frugivorous birds (see the online resource 8).

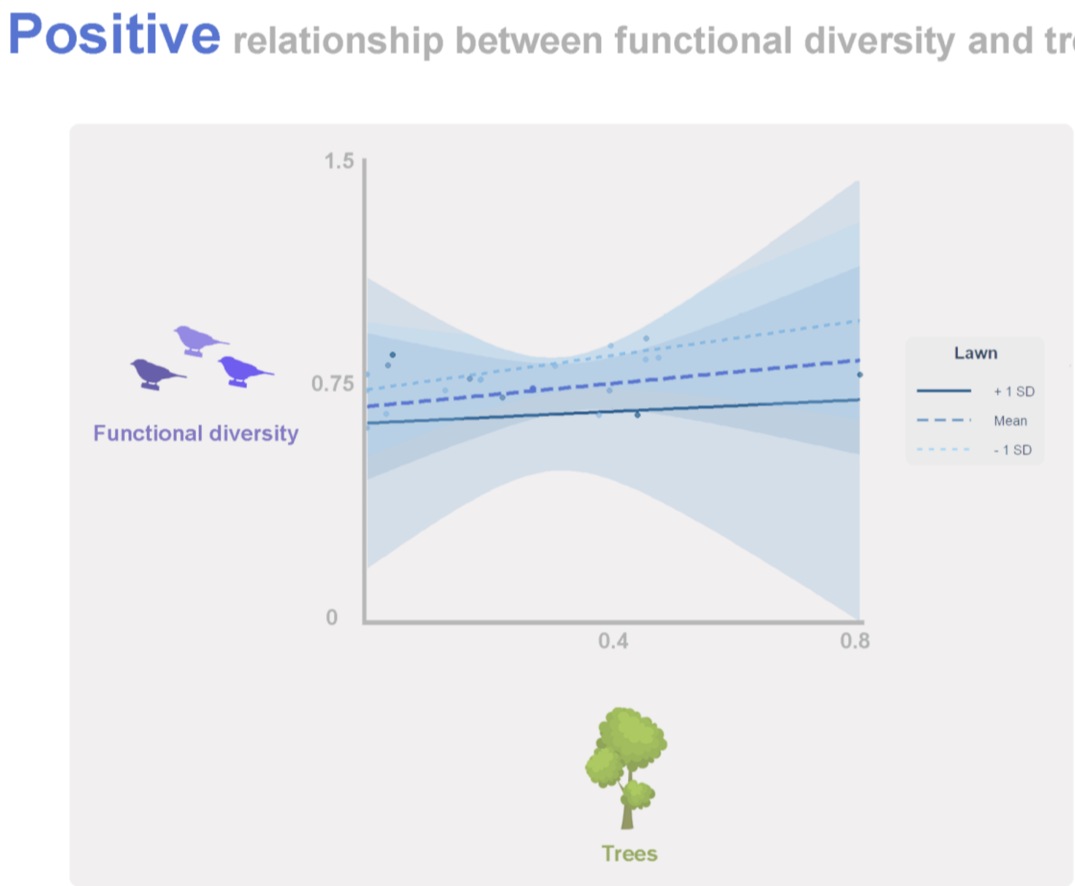


Figure 13 – Relationship between functional diversity and trees in land sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil. This graph contains the interaction between trees and lawn.

4 Discussion

We confirmed our hypotheses that the land sharing/sparing urban sprawl modelling affect differently (1) the size of urban green spaces, (2) both the taxonomical and functional diversity, and (3) fruit consumption by birds. We confirmed our predictions that the land-sparing have (1) greater values for both taxonomic and functional diversity, and (2) fruit consumption by birds. We have also confirmed our predictions that (3) land-sparing have larger areas of urban green spaces; isolated trees excepted. We also confirmed that (4) urban green spaces areas have positively affected the functional diversity, and (5) functional diversity is positively related to fruit consumption.

The land-sparing urban sprawl model allowed greater fruit consumption by birds; this can lead to critical results, for both the human population and biodiversity. Fruit consumption can affect the spatiotemporal distribution of plant populations, mediated by both seed dispersal and predation (Carvalho et al., 2020; Li et al., 2019, 2020). Plants delivery many ecosystem services in urban settlements, as carbon sink, provisioning, regulating, and cultural (Livesley et al., 2016; Stroud et al., 2022). This result can be used by city planners to delineate new urban settlements that offer all the basic resources to human beings, and that minimize the negative impacts on biodiversity, thus maximizing the ecological functions and ecosystems services. Frugivorous birds are central mobile links for plant species in urban settlements (Andrade et al., 2011), and they can be severely affected by changes in the landscape characteristics (Bonfim et al., 2021; Schneiberg et al., 2020).

We recorded higher bird taxonomic diversity in land sparing than in land sharing model. This result follows the same patterns previously found in urban settlements (Caryl et al., 2016; Collas et al., 2017; Edwards et al., 2021; Jokimäki et al., 2020) and in agroecosystems (Cannon et al., 2019). Urbanization is a massive homogenizing force that filter some traits, positively selecting urban adapters and restricting avoiders species (McKinney, 2006). Many Neotropical bird species are potential seed dispersers (D'Avila et al., 2010; Francisco & Galetti, 2002; Pizo, 2004), thus environmental characteristics that increase taxonomical diversity (e.g., richness and abundance), should positively affect the ecosystem functions they perform (Biggs et al., 2020). Therefore, we highlight our positive results found in the land-sparing model, delivering knowledge to balance conservation of more diverse biodiversity and human needs.

Land-sparing model support higher functional diversity and abundance in upper extremes of the traits range, related to the structure of plant-frugivore networks and seed dispersal dynamics (e.g., gape width, body mass, and wing length). These findings can also be used as a strategy for biodiversity conservation in urban settlements, once upper extremes of the range of these functional traits are linked to ecological drivers (Donoso et al., 2020). Gape width of birds' beak influence the size of the fruits they consume, hence shaping the composition and diversity of plants (Moran & Catterall, 2010; Rehm et al., 2019), affecting the plant species dispersion in the landscapes. Larger-gaped birds can swallow and disperse larger seeds, impacting the distribution of larger plants (Rehm et al., 2019). Larger body-sized and winged frugivorous birds are key species that may favor greater seed removal, disperse seeds across longer distances, and increase seed mass recruitment (Muñoz et al., 2016), playing an important role by shaping the structure and functioning of landscapes (Baños-Villalba et al., 2017; Donoso et al., 2020). Furthermore, we highlight our outcomes related with the higher abundance of traits related to cavity-dependent species in the sparing model. These findings can indicate that the sparing model shelter essential reproductive resources for nesting cavity dependent birds as tree cavities (Schaaf et al., 2021). Many frugivorous birds, mainly the medium- and large-bodied species, depend on cavities to reproduce (Guix et al., 1999; Perrella & Guida, 2019; Zulian et al., 2021), factors which may affect their abundance and ecological functions. Therefore, these outcomes may offer foundation for city managers to choose an urban sprawl model, as the sparing model, for delivering landscapes features that can shelter specialized biodiversity, positively triggering cascade effects; in this case, mainly related to bird-plant interactions.

We recorded few of the most frequent species having body mass higher than 200g. This result was expected, as urbanization filters traits as body mass, causing notorious downsizing. Small vertebrates have been highlighted as key elements in sustaining habitat structure and ecosystems functions (Carreira et al., 2020) in degraded habitats. However, environmental factors that promote the improvement of taxonomic diversity function of medium- and large sized frugivorous birds also need to be promoted to deliver a more robust contribution to fruit removal (Muñoz et al., 2016). Therefore, we highlight our outcomes related to the sparing model, which shelters heavier species in the top frequency than in the sharing model. Urbanization homogenizes the interactions of plant-frugivore bird networks (Schneiberg et al., 2020), leading to the erosion of some functional traits (Croci et al., 2008), and causing downsizing in bird species. Thus, selecting an urban sprawl model that leads to increase in the richness, abundance, and specialized functional traits of frugivorous must be prioritized for catalyzing positive cascade effects in the landscapes.

We observe that the fruit consumption is positively related to the functional diversity of frugivorous birds. Fruit consumption drives both the spatial distribution and the size of plant population (Carvalho et al., 2020; Li et al., 2019, 2020), thus triggering ecological cascade effects through landscapes. Therefore, selecting urban sprawl models that conserve ecological aspects of fruit consumption, must be included in the goals for conservation in urban settlements. Thereby, we emphasize our outcomes related to the greater functional diversity in the sparing model.

We recorded that land-sparing has larger areas of native forests and lawns. It is recognized that size of the vegetation structure of forested areas influences the biodiversity of frugivorous birds (Bonfim et al., 2021; Bovo et al., 2018; Campos-Silva & Piratelli, 2021; Emer et al., 2018; Schneiberg et al., 2020). The outcomes related to smaller spaces of native forest areas and lawn was expected. This occurs because the sharing model has in its essentials the division of urban settlements and green spaces, in smaller areas. This could affect the bird fauna as well, changing both the functional and taxonomic indices as here recorded. Therefore, selecting urban sprawl model that shelter larger areas and high habitat complexity must be in plan actions, because it has direct effects on urban biodiversity, mostly on specialized frugivorous birds.

We recorded that isolated trees have positively influenced the functional diversity of birds. Unlike the other kind of infrastructures that represent types of urban green spaces, as native forests and lawns, larger areas of isolated trees were found in the land-sharing model. Many researches have shown that the combination of landscape features of land-sharing/sparing models is beneficial to the biodiversity (Grass et al., 2019), and our data support the positive insights of joining the features of these models, which can improve the specialized biodiversity, as frugivorous birds. Trees are notorious urban green structures that reduce the negative effects of urbanization on birds (Pena et al., 2017), and that drive the composition of functional traits of organisms (Campos-Silva & Piratelli, 2021). Furthermore, trees can act as natural corridors, connecting urban green spaces, as fragmented native forests (Matsuba et al., 2016). As the functional diversity of birds positively affects the fruit consumption, and thus potential seed dispersal, our result can subside important basis for management of green infrastructures in the cities.

5 Conclusions

We successfully prove our hypothesis that land-sharing *vs* land-sparing urban sprawl modelling affect the (1) fruit consumption, (2) both the functional and taxonomic diversity of frugivorous birds and, (3) size of urban green spaces, with better results for the sparing model. These findings have important implications for urban planning. This outcome provides insights for supporting policymaking aimed at the selection of urban sprawl models that balance the urban development, engaged with the conservation of larger green spaces that benefit specialized frugivorous, thus supporting the ecological functions they perform (e.g., seed dispersal).

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8 Online Resource

Online resource 1 - Randomizing the sampled points

To avoid possible biases resulting from the distance between the counts points, we divided all the study area into four quadrants and selected 5 random sampled points by each urban sprawl model. Each of these four quadrants had smaller quadrants. Each intersection of the smaller quadrant was at least 200m of the nearest intersection. We randomly select the sampled points within these intersections using the “Random Points” option in the GIS Software, selecting the intersections of these smaller quadrants as the selected areas. To select the random sampled points for each urban sprawl sites, we took care to take into account intersections that had within urban sprawl polygons.

Online Resource 2 – Mean sampled area and respective class of urban green types for each count point.

Point counts	Model	Field (hectares)	Field class	Forests (hectares)	Forests class	Lawn (hectares)	Lawn class	Trees (hectares)	Trees class
QB_L_Sparing_7	Sparing	0	0	0.216	0.200-0.299	0.744	0.700-0.799	0.573	0.500-0.599
QD_L_Sparing_4	Sparing	0	0	0	0	0.268	0.200-0.299	0.279	0.200-0.299
QC_L_Sparing_10	Sparing	0	0	0	0	0.425	0.400-0.499	0.035	>0-0.049
QD_L_Sparing_5	Sparing	0	0	0	0	0.105	0.100-0.199	0.071	0.050-0.099
QC_L_Sharing_1	Sharing	0	0	0	0	0.092	0.050-0.099	0.085	0.050-0.099
QA_L_Sparing_4	Sparing	0	0	0	0	0	0	0.016	>0-0.049
QA_L_Sparing_8	Sparing	0	0	0	0	0	0	0.005	>0-0.049
QD_L_Sharing_3	Sharing	0	0	0.991	0.900-0.999	0.19	0.100-0.199	0	0
QD_L_Sharing_4	Sharing	0.255	0.200-0.299	0.317	0.300-0.399	0.536	0.500-0.599	0.685	0.600-0.699
QB_L_Sharing_6	Sharing	0	0	0.533	0.500-0.599	0.885	0.800-0.899	0	0
QB_L_Sparing_10	Sparing	0	0	0.254	0.200-0.299	0.965	0.900-0.999	0.227	0.200-0.299
QC_L_Sharing_10	Sharing	0	0	0.26	0.200-0.299	0	0	0.107	0.100-0.199
QB_L_Sparing_4	Sparing	0	0	0	0	0	0	0.157	0.100-0.199
QC_L_Sparing_6	Sparing	0	0	0	0	0	0	0.902	>0.900
QD_L_Sparing_2	Sparing	0	0	0.688	0.600-0.699	0.488	0.400-0.499	0	0
QC_L_Sparing_4	Sparing	0	0	0.555	0.500-0.599	0.359	0.300-0.399	0.789	0.700-0.799
QA_L_Sharing_7	Sharing	0.943	0.900-0.999	0	0	0	0	0	0
QA_L_Sharing_3	Sharing	0	0	0	0	0.156	0.100-0.199	0.455	0.400-0.499
QA_L_Sparing_9	Sparing	0.109	0.100-0.199	0.17	0.100-0.199	0	0	0.397	0.300-0.399
QB_L_Sharing_3	Sharing	0	0	0	0	0.893	0.800-0.899	0.042	>0-0.049
QA_L_Sparing_10	Sparing	0	0	0	0	0	0	0.475	0.400-0.499
QA_L_Sharing_9	Sharing	1.84	>1.500	0	0	0	0	0.454	0.400-0.499
QD_L_Sparing_8	Sparing	0	0	0.28	0.200-0.299	0.39	0.300-0.399	0.035	>0-0.049
QC_L_Sparing_1	Sparing	0	0	0.06	>0-0.099	0	0	0.307	0.300-0.399
QA_L_Sharing_4	Sharing	0	0	0.13	0.100-0.199	0	0	0	0

QB_L_Sparing_2	Sparing	0	0	0.438	0.400-0.499	1.191	1.00-1.499	0.803	0.800-0.899
QD_L_Sharing_5	Sharing	0	0	0	0	0	0	0	0
QD_L_Sharing_6	Sharing	0.279	0.200-0.299	0	0	0.372	0.300-0.399	0.168	0.100-0.199
QA_L_Sharing_10	Sharing	0	0	0	0	0	0	0.186	0.100-0.199
QD_L_Sparing_6	Sparing	0.114	0.100-0.199	0	0	0	0	0.185	0.100-0.199
QB_L_Sharing_1	Sharing	0	0	0.506	0.500-0.599	0.175	0.100-0.199	0.271	0.200-0.299
QA_L_Sparing_7	Sparing	0.155	0.100-0.199	0.402	0.400-0.499	0	0	0	0
QC_L_Sharing_2	Sharing	0	0	0.208	0.200-0.299	0.011	>0-0.049	0.128	0.100-0.199
QC_L_Sharing_5	Sharing	0.866	0.800-0.899	0	0	0.151	0.100-0.199	0.395	0.300-0.399
QC_L_Sparing_3	Sparing	0	0	1.1	>1.00	0.481	0.400-0.499	0.221	0.200-0.299
QB_L_Sharing_5	Sharing	1.654	>1.500	0	0	0	0	0.032	>0-0.049
QB_L_Sharing_7	Sharing	0	0	0	0	1.683	1.500-1.999	0.441	0.400-0.499
QC_L_Sharing_9	Sharing	0.809	0.800-0.899	0.702	0.700-0.799	0	0	0.378	0.300-0.399
QD_L_Sharing_9	Sharing	0.56	0.500-0.599	0	0	0.07	0.050-0.099	0	0

Online Resource 3 - Description of the values contained in the mathematical formulas for the relationship between fruit consumption and land-sharing vs land-sparing urban sprawl modelling.

Value	**Description**
FrRed	Amount of consumed black fruits by birds
FrBlack	Amount of predated black fruits by birds
Model	Land sharing or land sparing urban sprawl model
random = NativeForest	Size class of native forest in the respective count point
random = Field	Size class of field in the respect count point
random = Lawn	Size class of lawn in the respect count point
random = Trees	Size class of trees in the respect count point
family = BCPE	BCPE distributional family from the FrRed response variable
family =BCPEo	BCPEo distributional family from the FrBlack response variable

Online Resource 4 - Description of the values included in the mathematical formulas for the relationship between taxonomic and functional diversity and land-sharing *vs.* land-sparing urban sprawl modelling.

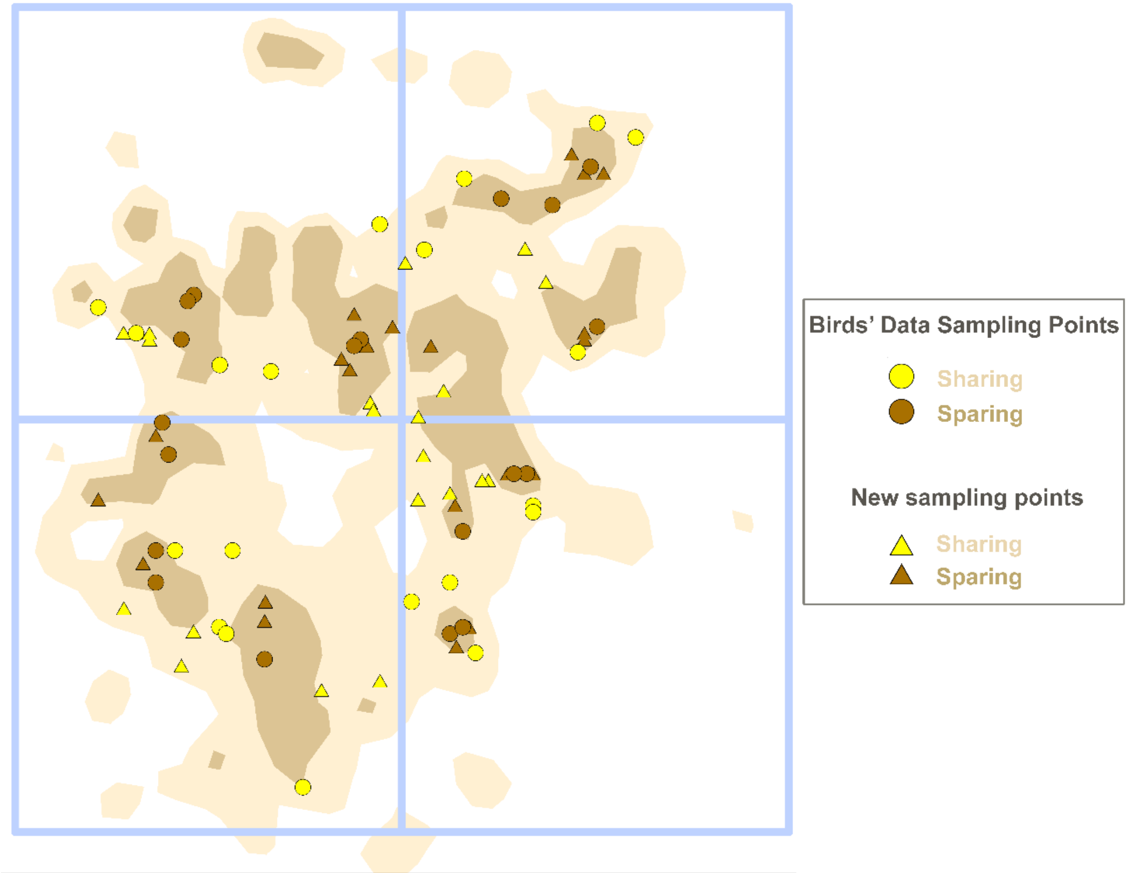
Value	Description
FunctionalDiversity	Functional diversity of the frugivorous birds
Richness	Richness of the frugivorous birds
Abundance	Abundance of the frugivorous birds
Model	Land sharing or land sparing urban sprawl model
random = NativeForest	Size class of native forest in the respective count point
random = Field	Size class of field in the respect count point
random = Lawn	Size class of lawn in the respect count point
random = Trees	Size class of trees that was present in the respect count point
family = BCPE	BCPE distributional family from both the *FunctionalDiversity* and *Abundance* response variables
family = *BCPEo*	The exponential distributional family from the *Richness* response variable

Online Resource 5 - Description of the values included in the mathematical formulas for the relationship between urban green spaces areas and functional diversity.

Value	Description
FunctionalDiversity	Functional diversity of the frugivorous birds
NativeForest	Value of the mean sampled area of native forest in hectares in the respective site
Field	Value of the mean sampled area of anthropic field in hectares in the respective site
Lawn	Value of the mean sampled area of lawn in hectares in the respective site
Trees	Value of the mean sampled area of trees in hectares in the respective site
random = Model	Land sharing or land sparing urban sprawl model
family = Gaussian	Gaussian distributional family used to FunctionalDiversity response variable

Online Resource 6 – Selecting the sampling points for the analyses between urban green spaces and urban sprawl modelling

Since the relationship between green spaces areas and urban sprawl models comprise only two landscape variables, we added another 40 sampling points, being 20 by urban sprawl model, in order to reinforce the statistical tests. We randomly plotted them in quadrants as the same way described in the "*Online resource 1 - Randomizing the sampled points*", being five by quadrant. From these 80 sampling points we obtained the areas of the urban green spaces' polygons. The image bellow illustrates all these sampling points.



Online Resource 7 – Frugivorous birds recorded in land sharing-sparing urban sprawl modelling in neotropical cities of Sorocaba and Votorantim, São Paulo, Brazil.

ID	Scientific name	Order	Family name	Common name
1	*Patagioenas picazuro*	Columbiformes	Columbidae	Picazuro Pigeon
2	*Forpus xanthopterygius*	Psittaciformes	Psittacidae	Blue-winged Parrotlet
3	*Psittacara leucophthalmus*			White-eyed Parakeet
4	*Elaenia flavogaster*			Yellow-bellied Elaenia
5	*Pitangus sulphuratus*			Great Kiskadee
6	*Myiodynastes maculatus*		Tyrannidae	Northern Streaked Flycatcher
7	*Myiozetetes similis*			Social Flycatcher
8	*Empidonomus varius*			Variegated Flycatcher
9	*Mimus saturninus*	Passeriformes	Mimidae	Chalk-browed Mockingbird
10	*Turdus leucomelas*		Turdidae	Pale-breasted Thrush
11	*Coereba flaveola*			Bananaquit
12	*Tangara sayaca*		Thraupidae	Sayaca Tanager
13	*Tangara palmarum*			Palm Tanager
14	*Tangara cayana*			Burnished-buff Tanager

Online Resource 8 – P values of the relationship between functional diversity of frugivorous birds and urban green spaces in land sharing-sparing urban sprawl modelling in neotropical cities of Sorocaba and Votorantim, São Paulo, Brazil.

FIXED EFFECTS:

	Est.	S.E.	t val.	d.f.	p
(Intercept)	0.76	0.04	18.91	8.00	0.00
Field	-0.08	0.04	-1.73	8.00	0.12
Forests	0.06	0.35	0.18	8.00	0.86
Lawn	0.15	0.08	1.87	8.00	0.10
Trees	0.30	0.13	2.29	8.00	0.05
Field:Forests	-0.39	2.11	-0.18	8.00	0.86
Field:Lawn	-0.74	0.90	-0.83	8.00	0.43
Forests:Lawn	-0.28	0.55	-0.51	8.00	0.63
Field:Trees	0.11	0.13	0.87	8.00	0.41
Forests:Trees	-0.78	1.19	-0.65	8.00	0.53
Lawn:Trees	-0.62	0.20	-3.03	8.00	0.02
Field:Forests:Trees	0.97	5.78	0.17	8.00	0.87
Field:Lawn:Trees	0.50	2.78	0.18	8.00	0.86
Forests:Lawn:Trees	1.46	1.23	1.18	8.00	0.27

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Programa de Pós-Graduação em Ecologia e Recursos Naturais

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Capítulo 3

Compacting urban sprawl reduces the negative effects of urbanization on top-down control of arthropods by birds

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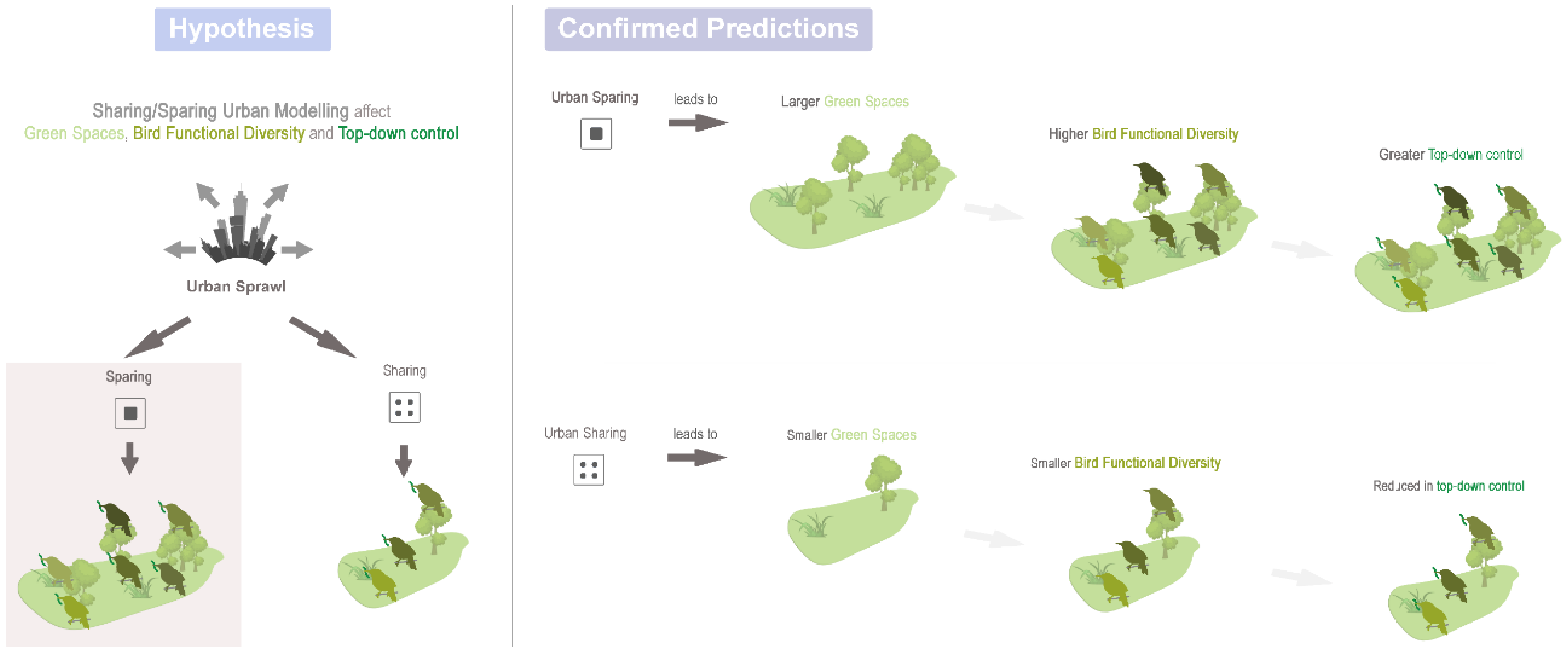
Research Paper

Compacting urban sprawl reduces the negative effects of urbanization on top-down control of arthropods by birds

Highlights

- The land-sparing urban sprawl model shelters larger areas of urban green spaces, e.g., native forests and lawns, than the land-sharing model.
- The land-sparing urban sprawl model supports higher top-down control of arthropods by birds and insectivorous functional diversity of birds, than land-sharing model.
- The land-sharing urban sprawl model has higher taxonomic diversity of insectivorous birds than the land-sparing model.
- Functional diversity of insectivorous birds is positively related to the top-down control of arthropods by birds.

Graphical abstract



Abstract

1. Cityscapes are growing fast and heterogeneously across the world, through different urban sprawl models, which can be described as specific shapes of development. Each model performs unique social and physical landscape changes, resulting in distinct balances between human development and biodiversity conservation. Sprawled and compact ways of urban growth, as urban land-sharing/sparing modelling may impact the biodiversity of specialized groups, e.g., insectivorous, triggering cascading effects in the structure and dynamic of top-down arthropod control. However, this is poorly understood in cities of Neotropical regions.
2. We tested whether land-sharing *vs*. land-sparing models affect bird taxonomic and functional diversity of insectivorous birds, and the top-down control of arthropods by birds in Neotropical urban settlements. We predict that the sparing model may have larger green spaces, thus favoring bird taxonomic and functional diversity, and ultimately, the top-down control by birds.
3. Confirming our predictions, the sparing model has (1) larger green areas, as native forests and lawns; (2) higher functional bird diversity; and (3) higher top-down control of arthropods. Contrary to our predictions, (4) higher taxonomic diversity were detected in land-sharing model. We also confirmed that (5) functional diversity of insectivorous birds is positively related to the top-down-control of arthropods.
4. The sparing model can shelter larger areas of green spaces, as native forests, thus supporting habitat- and feeding specialized insectivorous birds.
5. Our results provide insights for the establishing of policies aimed at the selection of urban sprawl models to balance urban development, aimed at conserving larger green spaces. This would benefit specialized insectivorous, thus supporting the ecological function they perform (i.e., top-down-control of arthropods).

Keywords: Land-sharing, land-sparing, Neotropical cityscapes, urban development, insect-eating birds, Latin American birds

1 Introduction

Urbanization is a massive landscape modifier (Leveau et al., 2020) and a global prompter of species endangerment (Grimm et al., 2008; MacGregor-Fors et al., 2020), triggering direct and long-term consequences for the global biota, typically reducing species diversity (Carvajal-Castro et al., 2019; Zurita et al., 2017) and affecting many levels of biotic organization (Blair, 2004). The growing of the cities, caused by the urban sprawl, ascends from the human demands for social resources, e.g., housing and industrialization zones (Mehriar et al., 2020; Nassar et al., 2014), and can be defined as a multidimensional process of growth of the border of a city (Heirman & Coppens, 2013). Urban sprawl causes physical changes in the landscape, e.g., the development of human-made structures, and occurs by different forms according to social, political, financial, and environmental features (Rubiera-Morollón & Garrido-Yserte, 2020). These forms, also called models (Rubiera-Morollón & Garrido-Yserte, 2020), may affect differently the biological communities (McDonald et al., 2020). Previous studies have focused on better models to lead the urban growth, from both the socioeconomic and environmental views (Bibri et al., 2020; Bontje, 2001; Mehriar et al., 2020; Wolff et al., 2018). These approaches have analyzed the balance between the benefits and costs of urban growth related to two sprawl models, i.e., compacted *vs.* sprawled cities (Bibri et al., 2020). The first model seek to agglutinate urban settlements and their structures in dense areas (Mehriar et al., 2020). On the other hand, the sprawled model is a dispersed format, with scattering of urban buildings (Dieleman & Wegener, 2004). For ecological purposes, biodiversity benefits are expected in compacted cities through the conservation of larger areas of natural habitats and reduction of CO_2 release (Liu et al., 2014). The sprawling model has negative socioeconomic and environmental effects, e.g., long journeys to the shopping and work sites, higher energy consumption, pollution, accidents, severe use of land use areas, and low public transportation quality in sparsely populated areas (Dieleman & Wegener, 2004).

Similarly to agroecosystems, current research has been analyzing the effects of the land-sharing and land-sparing models in urban settlements, to provide a balance between the basic human needs and the biological conservation (Dennis et al., 2019; Geschke et al., 2018; Suhonen et al., 2022). Land-sharing is defined as a land use management method that *integrate* both the conservation and production (Fischer et al., 2014) and, in a urban context, consists of low-density built-up settlements, e.g., private housing, combined with green spaces, e.g., gardens and small parks, without large continuous forest or older parks (Lin & Fuller, 2013). On the other hand, land-sparing integrate the *division* of conservation and production land uses (Fischer et al., 2014) in a urban framework, comprising high-density built-up settlements, e.g., residence buildings, associated to large and continuous green spaces (Lin & Fuller, 2013). As in agroecosystems (Balmford et al., 2019; Cannon et al., 2019; Edwards et al., 2021; Feniuk et al., 2019; Hasan et al., 2020), research in urban settlements have revealed that land-sparing model may have better results for the conservation of many biological taxa (e.g., mammals (Caryl et al., 2016), birds (Suhonen et al., 2022), insects (Soga et al., 2014), and plants (Collas et al., 2017)), structure of ecological communities (predator-prey (Jokimäki et al., 2020)), and central to shelter rare and unique species (Suhonen et al., 2022).

Cityscapes are composed by a mosaic of different types of urban spaces (MacGregor-Fors & Schondube, 2011), dominated mostly by anthropogenic structures (Barbosa et al., 2020; Schneider et al., 2010), associated to vegetation patches, e.g., parks, gardens and remnants of native plant life (Campos-Silva & Piratelli, 2021; de Toledo et al., 2012; Palmer et al., 2008) , and water bodies (Barbosa et al., 2020), which may shelter representative components of native bird communities. Urban spaces can be split into grey and green structures, related to composition of non-natural built-up and natural infrastructures present in the landscape, respectively (Tischer et al., 2017; Wesener et al., 2017). Gray spaces are components of urban landscapes mostly composed by non-natural structures and impervious surface. They can be subdivided according to (1) the type of use, (2) the main type of infrastructures, and (3) the human density, e.g., industrial, commercial, and residential areas (Chormanski et al., 2008; Suligowski et al., 2021). Urban green spaces are components of urban landscapes mostly having components of plant origin, which can be subdivided according to vegetation characteristics , and having a direct human uses (e. g., native forests, gardens, squares, parks) (Horwood, 2011; Jabbar et al., 2021; Zou & Wang, 2021). Each class of urban green space performs a specific role in biodiversity conservation and their ecological functions (Campos-Silva & Piratelli, 2021; Lepczyk et al., 2017). Socioeconomic and geographical factors are critical for urban biodiversity patterns, e.g., neighborhoods far from the city center and/or with greater economy incoming, would have more green areas and biodiversity-friendly zones (Melles, 2005). On the other hand, central and/or lower-incoming areas deliver few opportunities to sustain native biodiversity (Melles, 2005). Likewise, it has been thoroughly demonstrated that the types of urban green spaces and their sizes impact the biodiversity in different ways (Lepczyk et al., 2017; Melo et al., 2021; Shahabuddin et al., 2021). Therefore, identifying how urban sprawl models affect the patterns of green spaces must be a central topic to be investigated in urban settlements.

Insectivores are key species in the top-down controls of arthropods, delivering important ecosystems services, as pest control (García et al., 2021; Nyffeler et al., 2018; Sekercioglu, 2006). Many of insectivorous are stratum-, habitat- and feed-specialist organisms (Sekercioglu et al., 2002; Sherry et al., 2020). Land uses changes triggered by anthropogenic actions, including fragmentation and loss of natural habitats, cause negative impacts on the insectivorous birds (Sekercioglu et al., 2002; Sreekar et al., 2015; Stratford & Stouffer, 2015; Trollope et al., 2009), including reduction in taxonomic diversity attributes (e.g., richness and abundance) (Ibarra et al., 2017; Sekercioglu et al., 2002; Sreekar et al., 2015; Stratford & Stouffer, 2015; Trollope et al., 2009), and functional diversity (Ibarra et al., 2017; Tscharntke et al., 2008). Insectivores that depend on cavities to nest are one of the most affected negatively affected (Ibarra et al., 2017), disappearing in small patches, connected to the reduction of their limitation resources (i.e., cavities; Cornelius et al., 2008). Likewise, understory and ground insectivores are negatively affected by anthropogenic land uses, mainly fragmentation and isolation of native patches, becoming either rare or locally extinct in small-isolated fragments (Stouffer, 2020; Stouffer et al., 2011) (Sekercioglu et al., 2002). This can severely impact ecosystems, causing disruption to ecological functions (e.g., loss of natural pest control by trophic cascades, arising in pest outbreaks, and crop losses; Şekercioğlu et al., 2004).

Insectivorous birds massively regulate arthropods' population (Nyffeler et al., 2018). Estimates predict that 400-500 million tons of arthropods are removed across the world annually (Nyffeler et al., 2018) by birds. Many of this contribution, mediated by the top-down control, affect positively the humans' economy and well-being (Mäntylä et al., 2011; Whelan et al., 2015), as extensively reported in farmlands (Kellermann et al., 2008; Maas et al., 2015; Tela et al., 2021). However, these processes are barely known in urban ecosystems (Seress et al., 2018; Stemmelen et al., 2020; Turrini et al., 2016). Urban landscapes have green spaces, e.g., gardens (Tresch et al., 2019), crops (Duchemin et al., 2008) and tree-lined streets (McPherson et al., 2016), that deliver ecosystems services as well-being and food production. Therefore, public policies aimed at urban biological conservation should include the management of green areas, to maintain top-down control of arthropods by birds. Many cities across the world are planning their urban development, in order to mitigate the negative effects on biological communities and promoting sustainable growth (Nilon et al., 2017). However, urban sprawl has been rapid and often disordered in the Neotropics, causing severe losses of native vegetation, and favoring gray structures (Piratelli et al. 2017), which may affect the insectivorous birds and the top-down effects. Different models of urban sprawl can exert distinct effects on this ecological dynamic, but this is poorly known in cities in Neotropical regions.

In this paper, we test the effects of land-sharing *vs*. sparing urban sprawl modelling on (1) size of urban green spaces; (2) taxonomic and functional diversities of insectivorous birds; (3) the top-down control of arthropods by birds. We hypothesize that there are differences in (a) size of green spaces; (b) both taxonomic and functional diversity, (c) top-down control of arthropods by birds; and (d) range of green spaces size affect bird functional diversity. We predict that (a) land-sparing may shelter larger areas of green land uses, increasing bird taxonomic and functional diversity and top-down control of arthropods by birds; (b) range of green spaces are positively related with bird functional diversity; (c) top-down control is positively related to bird functional diversity (Fig. 1).

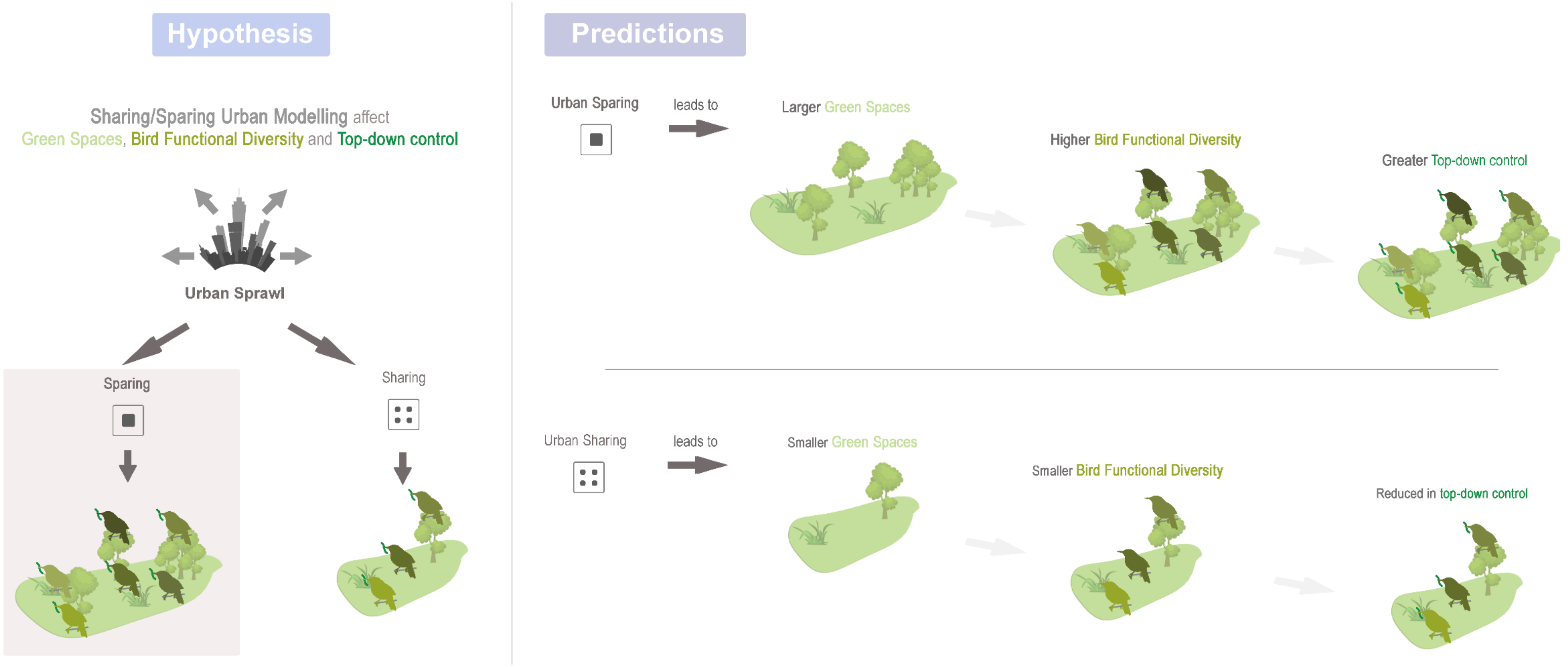


Figure 1 – Conceptual diagram of hypothesized and predicted modelling of urban sprawl of land-sharing/-sparing and their consequences in urban green spaces, insectivorous birds' functional diversity and top-down control of arthropods by birds.

2 Methods

2.1 Study area and models of urban sprawl

This study was carried out in the same urban sprawl sites and sampling points as adopted in the section "2.1 Study area and models of urban sprawl" in chapter 2.

2.2 Mapping urban green spaces

The urban green spaces analyzed and mapped are the same as adopted in the section "2.2 Mapping urban greens spaces" in chapter 2.

2.3 Bird surveys

The birds' data were sampled as the same way as adopted in the section "2.3 Bird surveys" in chapter 2, except that we considered in all the analyzes only birds that have 30% of their diet composed by arthropods (Wilman et al., 2014).

2.4 Top-down control of arthropods by birds

To estimate the top-down control of arthropods by birds we used 3.0 cm modeling clay (plasticine) green dummy caterpillars. The green color was used because it is related to bird preferences in insect consumption, since predators can perceived these dummy caterpillars as palatable and undefended prey (Howe et al., 2009). The dummy caterpillars were settled in the following vegetation strata: (1) leaves, (2) branches, (3) on the ground. All the dummy caterpillars were settled in the same sites where the avifauna sampling points were carried out (Fig. 2). Fifteen caterpillars were settled by stratum at each point count, totaling 1800 caterpillars, being 600 by stratum (Fig. 2). The dummy caterpillars were left at each point for seven consecutive days, within a radius of 50m from the center of the point count. We mostly selected street trees to conduct the experiment, and to set dummy caterpillars on branches and leaves varying from 0.7 to 2m in height. (Fig. 2). All the bird species analyzed were considered as potential consumers of dummy caterpillars, and that fit the aforementioned criteria.

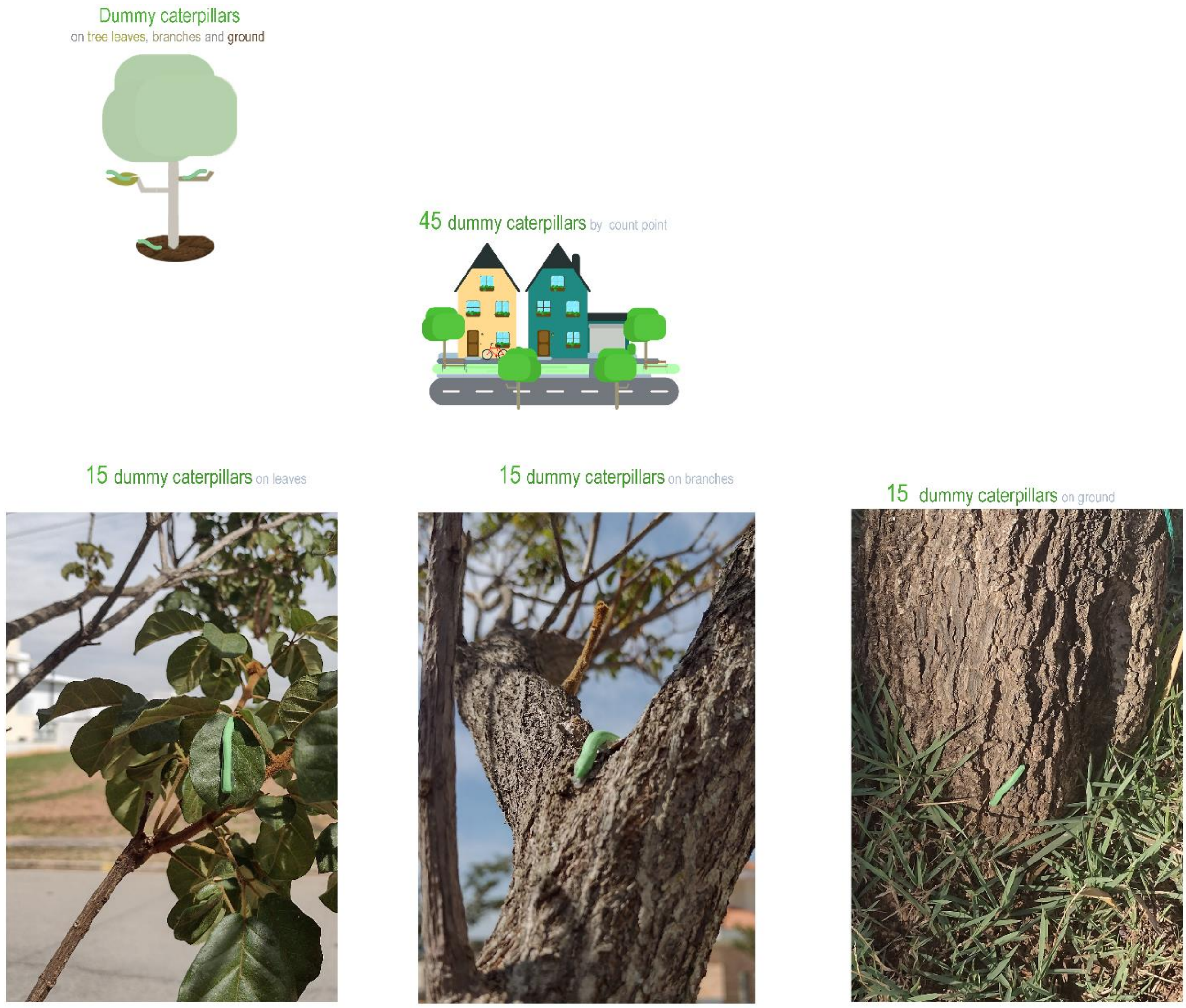


Figure 2 - Experimental study design of top-down control of arthropods by birds in land-sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil.

The experiment was left in the field for seven days and were inspected only on the last day. The caterpillars were assigned as consumed by birds when presenting pecking marks based on theoretical references (Ferrante et al., 2017; Howe et al., 2009; Meyer et al., 2017; Roslin et al., 2017).

Pecking by birds leaves specifics marks on dummy caterpillars, which may vary in size and shape depending on bird species, strength pecking angle of incidence, and part of the beak that touches the dummy caterpillars; Fig. 3).

Figure 3 – Examples of bird pecking marks on dummy caterpillars (Photos: Lucas Andrei Campos-Silva).

2.5 Taxonomic and bird diversity indices

We used the functional divergence as proxy for the *insectivorous birds' functional diversity* as the same way adopted in the section "2.5 Taxonomic and bird diversity indices" in chapter 1. Also, we used the same eight ecological and five morphometric traits as in the section "2.5 Taxonomic and bird diversity indices" in chapter 1.

2.6 Relationship between top-down control of arthropods by birds and urban sprawl models

The number of dummy caterpillars pecked by birds was assumed as a proxy for the *top-down control of arthropods by birds*. The relationship between the top-down control and the urban sprawl models were tested considering (1) all pecked caterpillars and (2) the stratum where they were consumed. Some steps were adopted to construct models to predict the relationships between responses variable (i.e., arthropod predation by birds) and the explanatory (i.e., urban sprawl models). Only data from sites where at least 70% of the dummy caterpillars were found (i.e., neither removed nor damaged) were included. Caterpillars having marks of other organisms (e. g. arthropods, mammals) was considered in the analysis if they had clear bird-pecking marks too. We do not consider dummy caterpillars that were intentionally dented by human action, which here were characterized as "*damaged*". Spatial autocorrelation for the response variables was tested using the “Moran.I” function of the “ape” package (Paradis & Schliep, 2019). No spatial autocorrelation was detected for any of these response variables (total dummy caterpillars - $p = 0.40$; dummy caterpillars on leaves – $p = 0.66$; and dummy caterpillars on branches – $p = 1.00$). At last, we tested the type of the distribution’s values from the response’s values and, Inserted then in the respective models. To check these distributions, the “fitDist” function from “fitdistrplus” package (Delignette-Muller & Dutang, 2015) was used.

The machine learning model chosen to make this relationship was the “Generalized additive model for location, scale, and shape (GAMLSS)”, through the “gamlss” function, from the “gamlss” package (Rigby & Stasinopoulos, 2005). This model allows the incorporation of a wide range of distributions, including those of the response variables. This model also allows to incorporate either non-parametric smoothing functions, random effects, or other additive terms into the predictor variables (Rigby & Stasinopoulos, 2005). We also have added into the models, as random effect, the urban green space sizes from each point-count. Since the random effects can only be inserted into the model in categorical values, we plotted them into classes of hectares (see Online resource 4 from chapter 2 to see all these respective classes). Once that we have registered only six dummy caterpillars consumed on the ground strata, we had not considered them into the model related to the urban sprawl model.

The mathematical formulas for each predict model are described as follows (terms meanings are in Online resource 1):

ConCatAll = Model, random = NativeForest, random = Field, random = Lawn, random = Trees, family = BCPEo

(eqn 1)

ConCatLeav = Model, random = NativeForest, random = Field, random = Lawn, random = Trees, family = BCPEo

(eqn 2)

ConCatBranc = Model, random = NativeForest, random = Field, random = Lawn, random = Trees, family = BCPEo

(eqn 3)

2.7. Relationship between both functional and taxonomic diversity and urban sprawl models

The functional divergency was used as a proxy for functional diversity, and both species richness and abundance for taxonomic diversity. In order to construct models to predict the relationships between the response variables (i.e., taxonomic and functional diversity) and the explanatory (i.e., urban sprawl models) we developed the same steps adopted in the section “2.6” from this study to avoid bias. No spatial autocorrelation was detected for any of these response variables (functional diversity - p = 0.13; richness – p = 0.60; abundance – p = 1.00).

The machine learning model chosen to make this relationship was also the GAMLSS. We also have added into the models, as random effect, the respective values urban green spaces sizes (see Online resource 4 from chapter 2 to see all these respective classes).

The mathematical formulas for each predict model are described as follows (terms meanings are in Online resource 2):

FunctionalDiversity = Model, random = NativeForest, random = Field, random = Lawn, random = Trees, family = BCPEo

(eqn 1)

Richness = Model, random = NativeForest, random = Field, random = Lawn, random = Trees, family = BCPEo

(eqn 2)

Abundance = Model, random = NativeForest, random = Field, random = Lawn, random = Trees, family = BCPEo

(eqn 3)

2.8. Relationship between top-down control of arthropods by birds and birds' functional diversity

We used the number of dummy caterpillars consumed in all the strata as a proxy for top-down control of arthropods and the functional divergency as a proxy for functional diversity. In order to construct models to predict the relationships between the response variables (i.e., top-down control of arthropods) and the explanatory (i.e., functional diversity) we developed the same steps adopted in "2.6" from this study to avoid bias. No spatial autocorrelation was detected for the top-down control of arthropods ($p = 0.60$).

The machine learning model chose to make this relationship was the "Linear Mixed-Effects Models", through the "lmer" function, from the "lme4" package (Bates et al., 2015). We also have added into the models, as random effect, the both land-sharing/-sparing modelling, and values of urban green spaces sizes from each point-count (see Online resource 4 from chapter 2 to see all these respective classes).

The mathematical formula for the model is described as follows (terms meanings are in Online resource 3):

Log (Insectivory) = FunctionalDiversity, random = Model, random = NativeForest, random = Field, random = Lawn, random = Trees

(eqn 1)

2.9. Relationship between insectivorous birds' functional diversity and urban green spaces sizes

To evaluate the relationship between insectivorous birds' functional diversity and the extension of the green land uses, we used the mean sampled area in hectares of each green spaces studied (i.e., native forest, fields, lawn and trees). In order to construct models to predict the relationships between responses variable (i.e., functional diversity) and the explanatory (i.e., urban green spaces) we incorporated the last steps adopted in the section "2.6" from this study. We did not detect spatial autocorrelation for the functional diversity (p = 0.90).

The machine learning model selected to make this relationship was the GAMLSS. We also have added into the models, as random effect, the respective urban sprawl model type. In order to select the best model, we performed a stepwise model selection using a Generalized Akaike Information Criterion (GAIC). We have made this using the "stepGAIC()" function from "gamlss" package (Rigby & Stasinopoulos, 2005).

The mathematical formula for the model is described as follows (terms meanings are in Online resource 4):

$$FunctionalDiversity = NativeForest + Field, random + Lawn + Trees, random = Model, family = BCPEo \quad \text{(eqn 1)}$$

2.10 Relationship between size of urban green spaces and urban sprawl model

We made this step in the same way made in the section "2.10" on chapter 2. All these analyzes were performed in the R language (R Core Team, 2022).

3 Results

3.1 Bird biodiversity

A total of 18 insectivorous bird species were recorded, representing two orders, and eight families (Online Resource 5). The most frequent species in the land-sparing urban sprawl model were Chalk-browed Mockingbird (*Mimus saturninus*), House Wren (*Troglodytes aedon*), Rufous Hornero (*Furnarius rufus*), Pale-breasted Thrush (*Turdus leucomelas*) and Tropical Kingbird (*Tyrannus melancholicus*, Fig. 4). The top frequently species recorded in the land-sharing model were House Wren, Great Kiskadee (*Pitangus sulphuratus*), Tropical Kingbird, Chalk-browed Mockingbird and Bananaquit (*Coereba flaveola*), (Fig. 4).

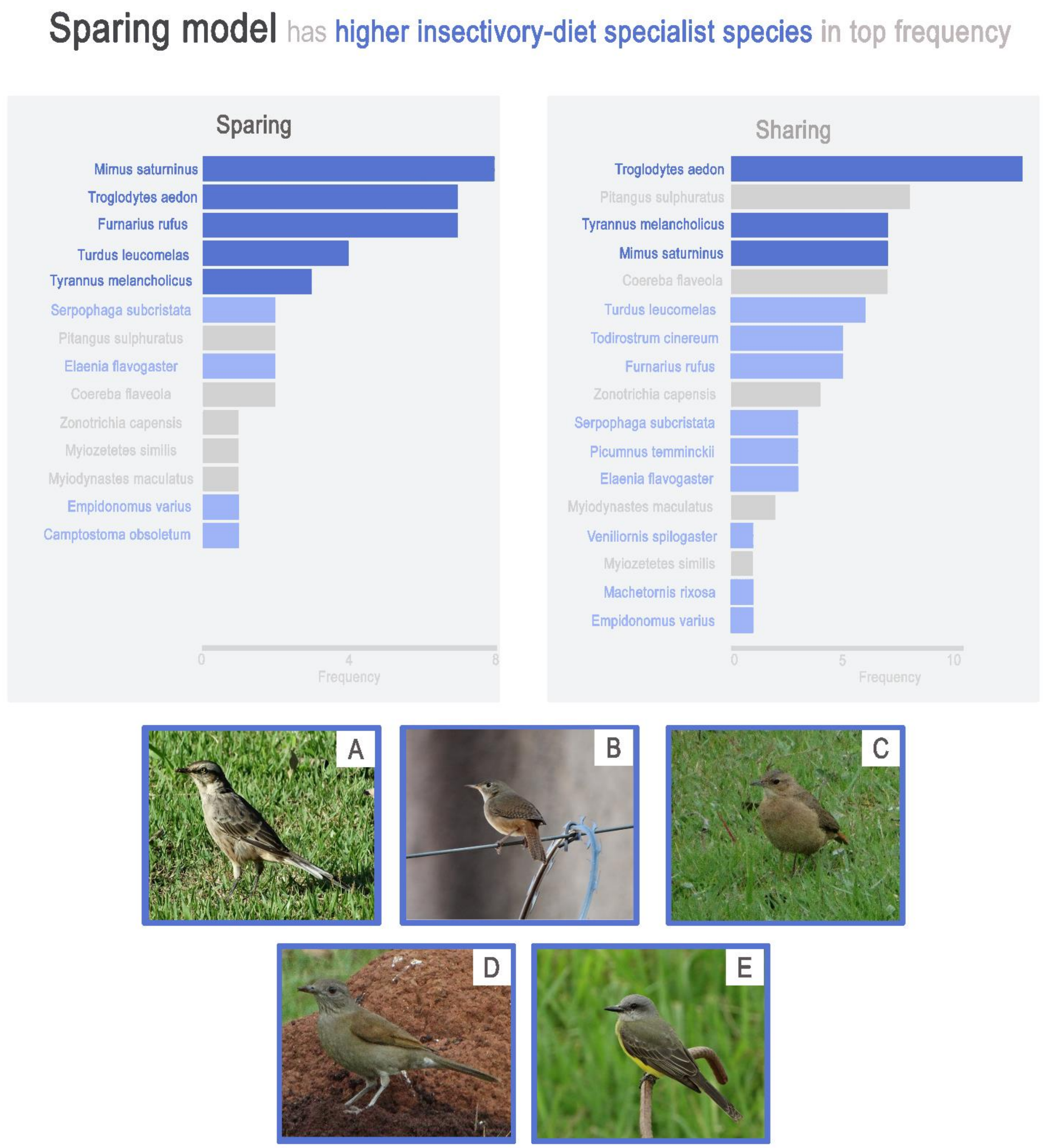


Figure 4 – Frequency of insectivorous birds by model in land-sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil. The dark blue indicates the top species frequency that are specialists related to insectivory-diet. The light blue indicates the other specialist birds related to insectivory-diet that are not in the top species frequency. A) Chalk-browed Mockingbird; B) House Wren; C) Rufous Hornero; D) Pale-breasted Thrush; E) Tropical Kingbird. Photos: Lucas Andrei Campos-Silva

The sparing model had higher abundance in the upper extremes of traits related to bird-arthropod interactions as bill length, body size (e.g., body mass and length), and related to dispersion (Fig. 5). The sparing model had more proportion of abundance in upper extremes of functional traits related to constructor cavity dependence, understory nest strata and invertebrate diet (Fig. 6, Online resource 6).

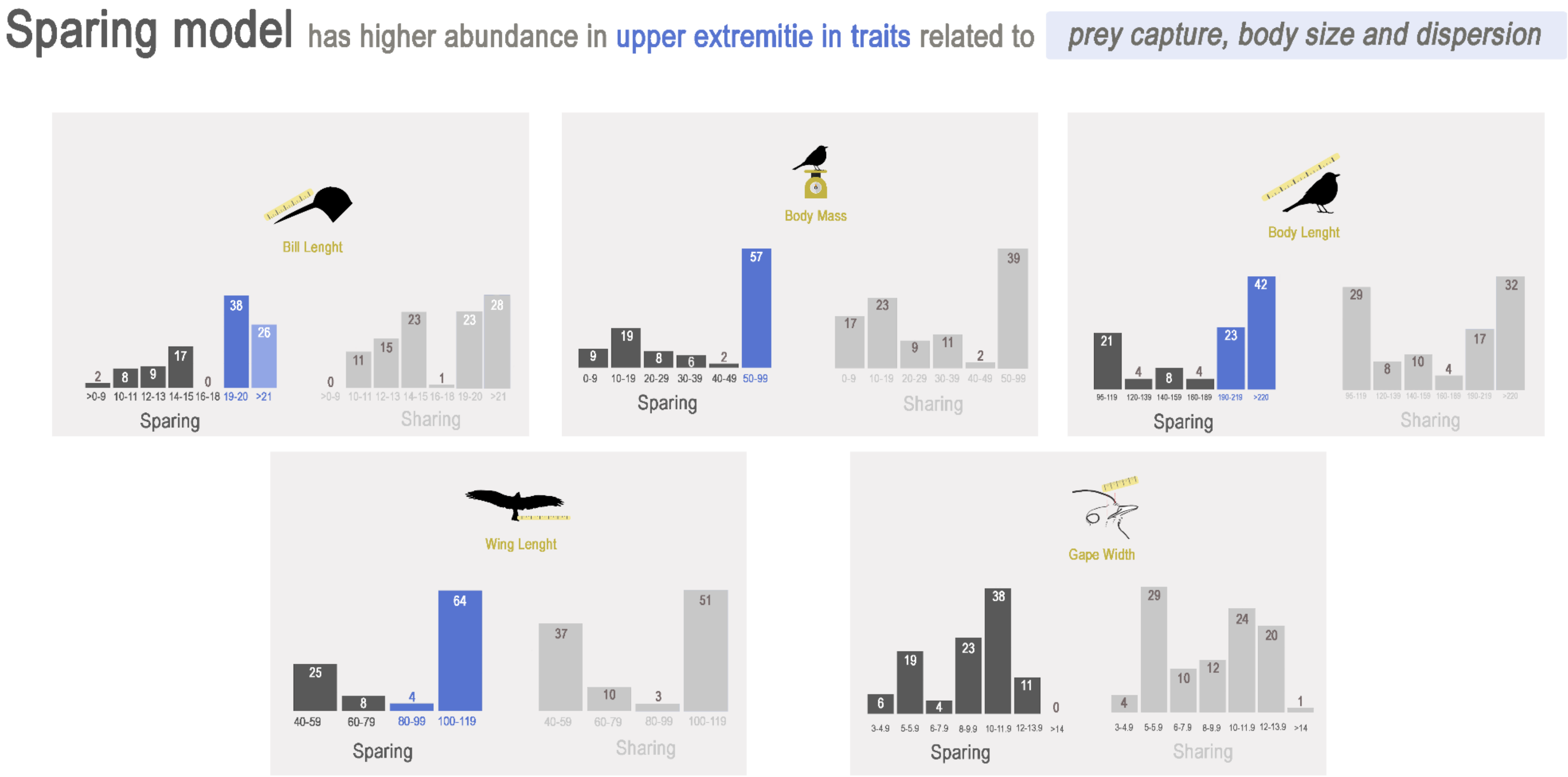


Figure 5 - Abundances proportion of insectivorous birds by morphological traits in land sharing-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil. The vertical and horizontal axes represent abundance proportion and niche space, respectively. The highlight in blue indicates abundances in upper extremities of functional traits related to arthropod-insectivory interactions and dispersion.

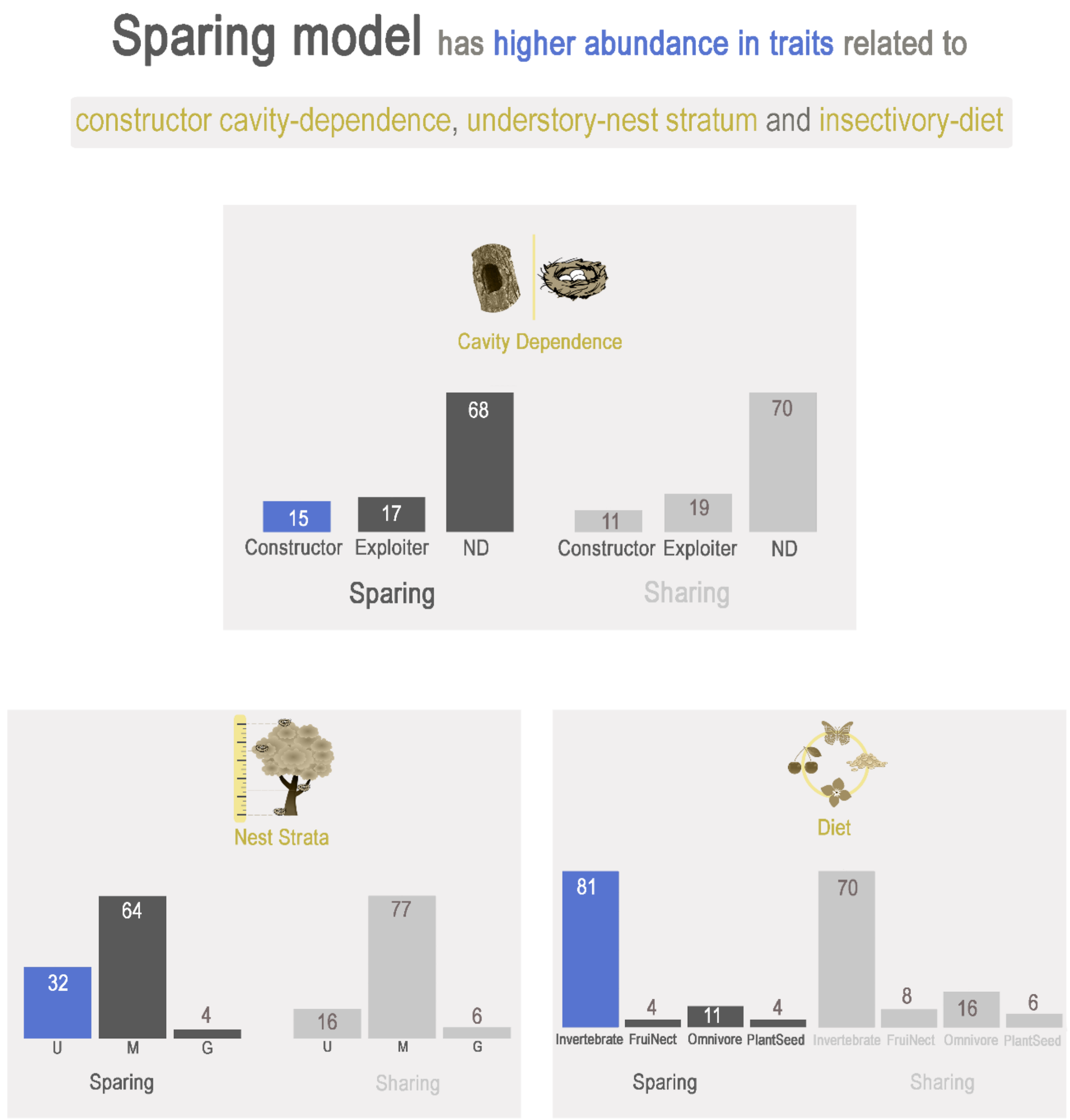


Figure 6 - Abundances proportion of insectivorous birds by ecological traits in land sharing-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil. The vertical and horizontal axes represent abundance proportion and niche space, respectively. The highlight in blue indicates higher abundances proportion in functional traits related to constructor-cavity dependence, understory-nest stratum and invertebrate-diet. Cavity dependence – ND: Non dependent of cavities. Nest Strata – U: understory - M: mid-story - G: ground.

3.2 Top-down control of arthropods by birds

A total of 55 (3%) dummy caterpillars were consumed by birds, being 11 (20%) on leaves, 38 (70%) on trunks and 6 (10%) on the ground. An amount of total of 211 (12.0%) dummy caterpillars were damaged, removed or not found. Eighty-five percent of the total dummy caterpillars were not consumed by insectivorous birds (Fig. 7).

Figure 7 – Descripted results of the consumption of dummy caterpillars by birds in land-sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil. NE: dummy caterpillars damaged, removed or not found.

3.3 Relationship between urban sprawl, birds taxonomic and functional diversity and top-down control of arthropods

We found significative differences between the top-down control of arthropods in all the dummy caterpillars among the two urban sprawl models; the higher number in the sparing model (t = 46.10, p < 0.0001, Fig. 8). We also found a higher number of caterpillars attacked by birds on leaves and branches in the sparing model (t = 140.00, p < 0.0001, Fig. 8, and t = 184.00, p < 0.0001, Fig. 8, respectively). A positive relationship between top-down control of arthropods and functional diversity was observed in these urban sprawl areas (t = 15.00, p < 0.0001, Fig. 9).

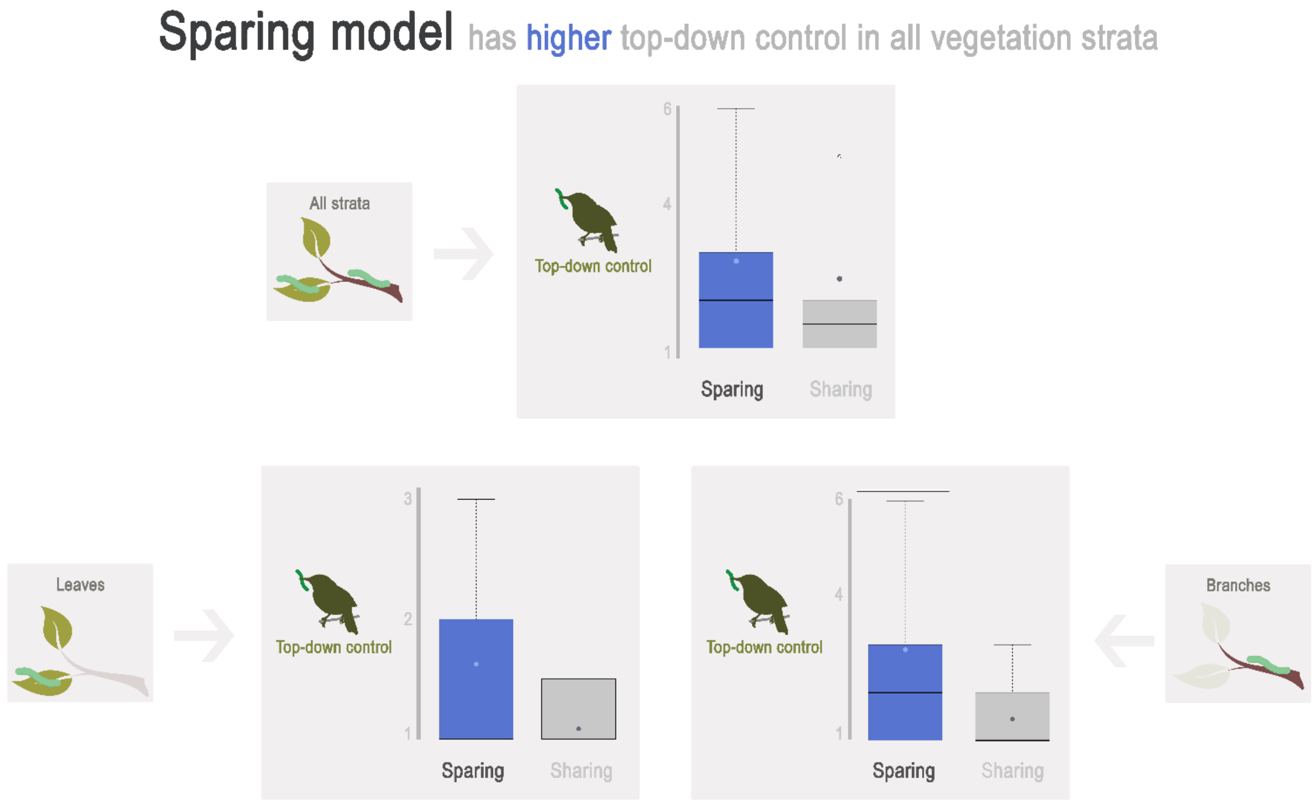


Figure 8 – Relationship between the top-down control of arthropods by model in modelling in land-sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil. The larger dots indicate the mean values predicted by the respective models.

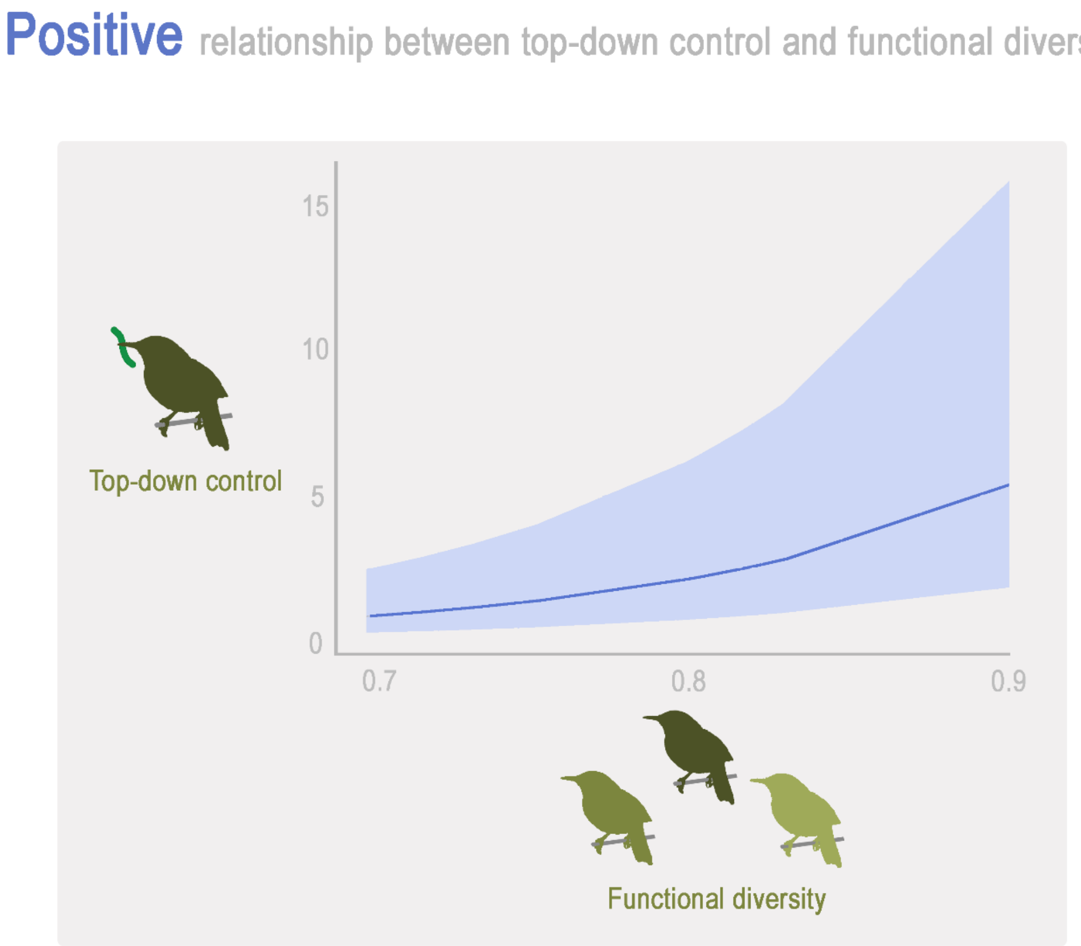


Figure 9 – Relationship between the top-down control of arthropods and insectivorous birds' functional diversity in land-sharing/-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil.

The land sparing model had higher values of insectivorous birds' functional diversity ($t = 7.00$, $p < 0.0001$; Fig. 10). The land sharing model has higher values of both richness and abundances of insectivorous birds ($t = -170.00$, $p < 0.0001$; $t = 182.00$, $p < 0.0001$; Fig. 10).

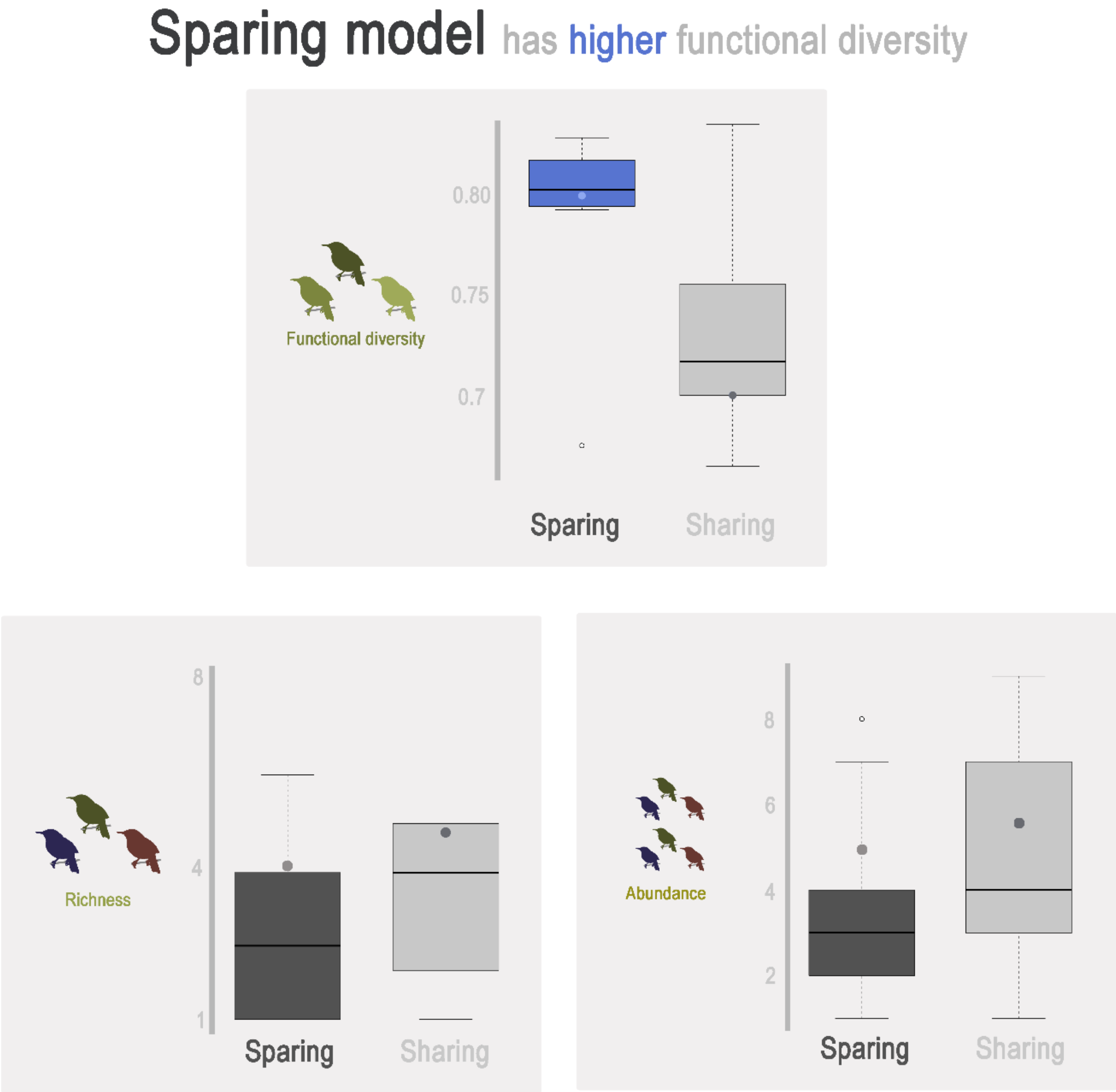


Figure 10 – Relationship between both functional diversity and taxonomic indices of insectivorous birds and land sharing-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil. The larger dots in the boxplots indicate the mean values predicted by the respective models.

3.4 Amount of green spaces in land sharing and land sparing urban modeling

The land-sparing urban model presented higher values of mean sampled area for native forests, and lawn land uses ($t = -3.15$, $p < 0.006$, and $w = 134$, $p < 0.04$, respectively) compared to the land-sharing urban sprawl model (Fig 11). Land-sharing urban sprawl models had more values of mean sampled for trees than land sparing urban sprawl model (w = 840, p < 0.000, Fig. 11). The anthropogenic field was not different into these models (w = 56, p = 0.92).

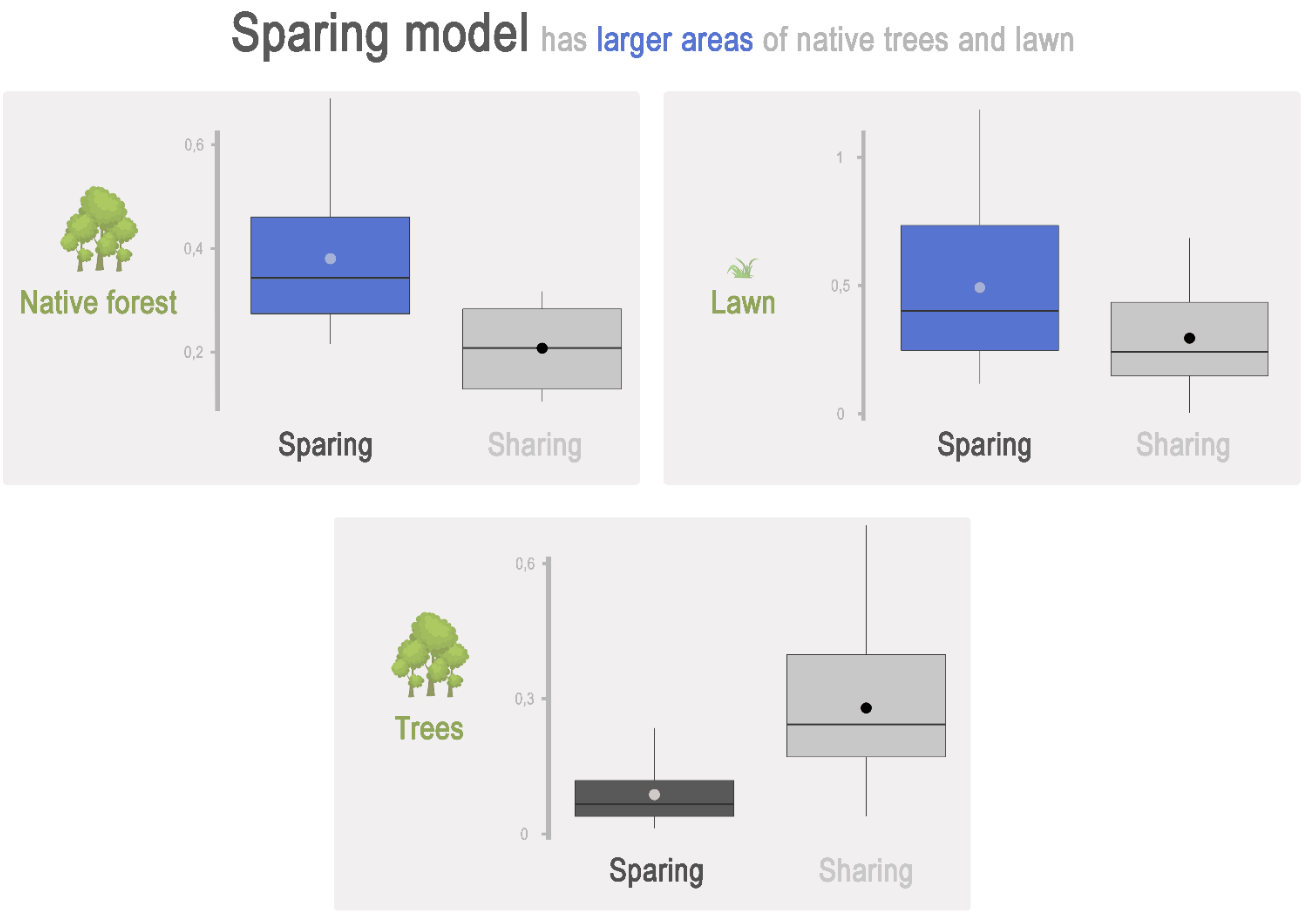


Figure 11 – Mean sampled areas' green urban space by land sharing-sparing urban sprawl in Sorocaba and Votorantim, Brazil. The vertical axis values are in hectares. The larger dots indicate the mean values by the respective models.

3.5 Relationship between functional diversity and urban green spaces sizes

Trees had a positive relationship with the functional diversity (t = 462.00, p < 0.0001, Fig. 12) and anthropogenic fields, a negative relationship with this variable (t = 462.00, p < 0.0001, Fig. 12). Native forests and lawns have not affected the functional diversity of insectivorous birds (see the online resource 7 to check all these statistics values).

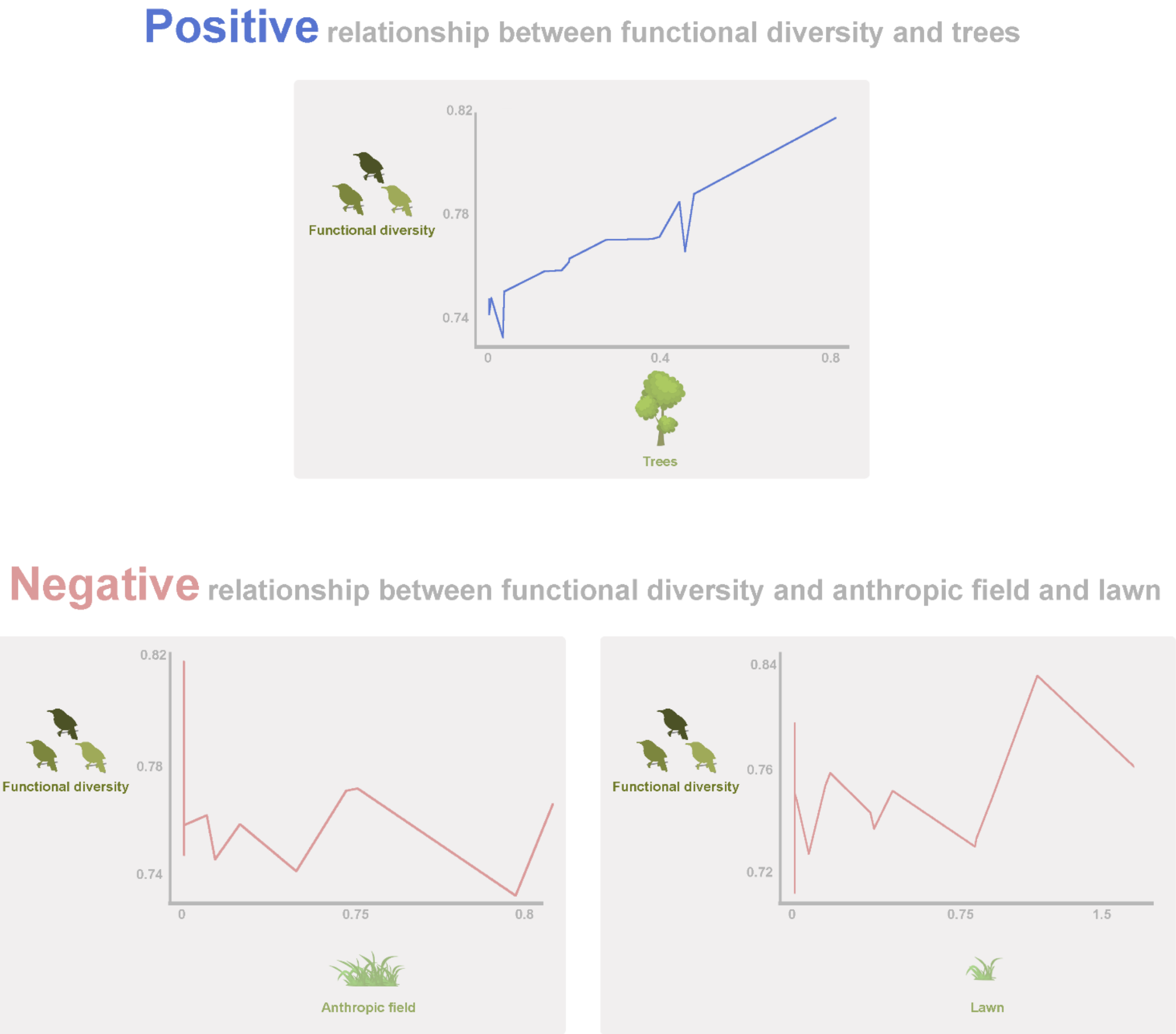


Figure 12 – Relationship between insectivorous birds' functional diversity and urban green spaces birds in land sharing-sparing urban sprawl modelling in neotropical cities of Sorocaba and Votorantim, São Paulo, Brazil. The vertical axis is in hectares.

4 Discussion

We confirmed our hypotheses that the land sharing/sparing urban sprawl modelling affect (1) the amount of urban green spaces, (2) both the taxonomical and functional diversities and (3) the top-down control of arthropods by birds. We also confirmed our predictions that the land-sparing have (a) greater values of functional diversity, and (b) top-down control of arthropods by birds. Contrary to our prediction, we detected that (c) the taxonomic diversity was higher in land-sharing model. We also confirmed our predictions that (d) land-sparing have larger areas of urban green spaces, except to isolated trees, which has higher values in land-sharing model. We also confirmed that (e) the area of urban green spaces has positively affected the functional diversity only for trees, while anthropogenic fields had a negative effect on the functional diversity of insectivorous birds. And ultimately, we confirmed that (f) functional diversity of birds is positively related to top-down control of arthropods. The fact that the land-sparing urban sprawl model had greater bird top-down effects than land-sharing may have critical concerns not only to the urban biodiversity, and also to humans living in urban settlements. The insectivorous birds can drive both the spatial distribution and size of arthropod populations (Roels et al., 2018; Tela et al., 2021), thus affecting the ecological functions of the arthropods and their ecosystems services and disservices as well (Gunnarsson & Hake, 1999; Nyffeler et al., 2018; Roels et al., 2018; Tela et al., 2021). Arthropods offer many services in urban settlements, as regulating and supporting ecosystem services (McIntyre et al., 2001), and also disservices like pest damage to urban trees or crops (McCluney et al., 2017). Insectivorous birds are severely affected by changes in the components of the landscapes (Trollope et al., 2009), once these changes affect the essential resources for them, e.g., food (Egerer et al., 2017; Trigos-Peral et al., 2020; Vergnes et al., 2012) and nest site (Fröhlich & Ciach, 2020; Máthé & Batáry, 2015). Therefore, our results can be used by city planners to delineate new urban settlements that offer all the basic resources to the humans, and furthermore minimize the impacts on insectivorous birds, thus maximizing the ecological functions and ecosystems services they provide, as the pest control.

We detected that the land-sparing model has both greater functional diversity and abundance proportion in the upper extremities of morphological traits related to prey capture adaptation (bill length), body size (body mass and length), than land-sharing. These were expected patterns in sites having greater functional diversity (i.e., in sparing model). Bill length is related to prey capture adaptation (Sherry & McDade, 1982; Sherry et al., 2020), and can shape the composition and diversity of arthropod consumed across landscapes, mediated by the prey selection (Radford & Du Plessis, 2003). Long-billed birds can be able to capture faster moving arthropod preys than short-billed birds (Lederer, 1975), affecting the interaction processes, e.g. competition and distribution of arthropods into the landscape. Body size of insectivorous birds have been related with the size of the consumed preys (Hespenheide, 1971; Janes, 1994); large-bodied insectivorous tends to consume larger-bodied preys (Hespenheide, 1971; Janes, 1994), affecting the arthropods composition along the landscape. Likewise, we highlighted our outcomes in sparing model related to greater proportion of abundance in cavity-dependent nests, in the understory stratum. These two findings can suggest that the sparing model shelter essential reproductive resources to birds that are related to cavity dependence, e. g. tree cavities, and vegetation structure related with understory nesting. Many insectivorous, especially the medium— and large-bodied-species, depend of the cavity to reproduce (Blanc & Martin, 2012), which affect their abundance and, their ecological function along landscapes. Many insectivorous bird species nest in understory vegetation stratum (Visco et al., 2015). Urbanization leads to erosion of the vegetation structures in the understory strata of urban green spaces (Campos-Silva & Piratelli, 2021; Heyman, 2010; Heyman & Gunnarsson, 2011), affecting their nesting sites. Thus, selecting an urban sprawl model that allows the conservation of understory nesting sites may be used by city planners as a strategy to preserve the vegetation complexity of urban green spaces. These outcomes related to the morphological and ecological traits, may offer foundation for city managers to choose an urban sprawl model, like the sparing model, that offer landscapes features that can shelter a bird fauna with more functional diversity, positively triggering cascade effects related to top-down interaction, mediated by the birds-arthropods cascading trophic interactions.

Contrary our expectations, we registered greater taxonomic diversity in land-sharing than land-sparing model. This result related to abundance and richness does not follows the same patterns previously described in urban settlements (Caryl et al., 2016; Collas et al., 2017; Edwards et al., 2021; Jokimäki et al., 2020). One possible explanation is our sampling method, which was delineated to answer our ecological questions. Many of the sampled points were settled next to human-made infrastructures (e. g. residences and sidewalks), and some forest birds, which usually have a delimited territory (Duca et al., 2006; Ribon & Marini, 2016), could not be sampled in this study. So, the higher abundance detected in the sharing model could be probably related to common open-habitat birds' species that were present in this grey infrastructure's settlements. In fact, the top five bird's species recorded in the sharing models are all open-areas species, being two of them not specialist insectivory-diet bird (Great Kiskadee and Bananaquit).

We found that the top-down control of arthropods is positively related to the functional diversity of insectivorous birds. Top-down control of arthropods by birds drives both the spatial distribution and the size population of arthropods (Seress et al., 2018; Stemmelen et al., 2020; Turrini et al., 2016), thus triggering ecological cascade effects through the landscapes. Therefore, selecting urban sprawl models that conserve ecological factors that directly affect top-down control of arthropods, as we reported for the functional diversity, must be a priority for biological conservation in urban settlements.

We also detected that urban land-sparing has larger areas of native forests and lawns. It is recognized that size (Vaccaro et al., 2022) and vegetation structure of forested fragments (Campos-Silva & Piratelli, 2021; Elliot et al., 2022) influence the biodiversity of insectivorous birds in urban landscapes. The outcome related to smaller spaces of native forest areas and lawn was expected in the sharing model. This occurs because this model has in its essentials the division of urban grey and green spaces, both with smaller areas. This fact could affect the insectivorous birds as well, affecting both the functional and taxonomic indices as we recorded, with greater values of the taxonomic in sharing model. However, selecting urban sprawl sparing model must be an urban conservation strategy.

We recorded that trees and both the anthropogenic fields and lawns had positive and negative effects on bird functional diversity, respectively. We demonstrate that insectivorous birds' functional diversity positively drives the top-down interactions, then we can assume that trees may act reducing the negative effects of urbanizing. Greater area of trees triggers a cascading positive effect in the urban landscape, increasing the functional diversity of insectivorous birds, thus catalyzing the top-down interaction of birds and arthropods. Many researches have shown that the combination of landscape features of land-sharing/sparing models is beneficial to the biodiversity (Grass et al., 2019), and our outcome also brings substantial helpful insights of joining the features of these models, which can positively affect the specialist biodiversity, as the insectivorous birds. This because we found that larger areas of trees were detected in the land-sharing model, unlike the other urban green spaces, as native forests and lawn that were greater in sparing model. Trees are central urban green infrastructures that reduce the negative effects of urbanization (Pena et al., 2017), driving the composition of functional traits of birds (Campos-Silva & Piratelli, 2021). Trees can also act as natural corridors, connecting urban green spaces, as fragment forests (Matsuba et al., 2016; Trollope et al., 2009). Therefore, our results can imply in important basis to management leading to the increment of this the green infrastructures in the cities, which can reduce the impact of the urbanization on top-down effects. On the other hand, we have detected that anthropogenic fields and lawns lead to negative effects on insectivorous birds, and thus may affect negatively the top-down interaction. Despite that we detected greater amount of birds that use open-habitats in these urban sprawl settlements, many of them depend of tree vegetation resources to nesting (e. g., tree cavities (Kirwan, 2009; Maurício et al., 2013), tree branches (Daros et al., 2018; Nunes et al., 2020; Ruiz et al., 2017)) and to foraging (upper vegetation stratum like medium and canopy (Gabriel & Pizo, 2005)), which that can affect the insectivorous birds' functional diversity. These open areas, i.e., anthropogenic fields and lawns, have not the same resources as the native fields, and may fails to sustain the functional diversity of this native birds. Therefore, our results can offer basis to the management of these open habitats in order to their improvement and leading to the maintenance of natural resources like scattered shrubs and trees in these anthropogenic habitats.

5 Conclusions

We successfully prove our hypothesis that sprawling vs compacting the urban settlements mediated by land-sharing vs land-sparing modelling affect the (1) top-down control of arthropods by birds, (2) both the taxonomic and functional diversity of insectivorous birds and also, (3) urban green spaces size, with better results to sparing model. These findings have important implications to urban planning. This outcome provides insights for supporting policymaking aimed at the selection of urban sprawl models that balance the urban growth, toward to the conservation of larger green spaces that benefit specialized insectivorous, thus supporting the ecological functions they perform (e.g., top-down control of arthropods).

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8 Online Resources

Online resource 1 - Description of the values contained in the mathematical formulas for the relationship between top-down control of arthropods by birds and land-sharing vs land-sparing urban sprawl modelling.

Value	Description
ConCatAll	Total amount of consumed dummy caterpillars by insectivorous birds
ConCatLeav	Amount of consumed dummy caterpillars by insectivorous birds on leaves
ConCatBranc	Amount of dummy caterpillars consumed by insectivorous birds on branches
Model	Land-sharing or land-sparing urban sprawl model
random = NativeForest	Size class of native forest in the respective count point
random = Field	Size class of field in the respect count point
random = Lawn	Size class of lawn in the respect count point

random = Trees	Size class of trees in the respect count point
family =BCPEo	BCPEo distributional family from the *ConCatAll*, *ConCatLeav* and *ConCatBranc* response variables

Online resource 2 - Description of the values contained in the mathematical formulas for the relationship between top-down control of arthropods by birds and land-sharing vs land-sparing urban sprawl modelling.

Value	Description
FunctionalDiversity	Birds' functional diversity
Richness	Birds' richness
Abundance	Birds' abundance
Model	Land-sharing or land-sparing urban sprawl model
random = NativeForest	Size class of native forest in the respective count point
random = Field	Size class of field in the respect count point
random = Lawn	Size class of lawn in the respect count point
random = Trees	Size class of trees in the respect count point
family =BCPEo	BCPEo distributional family from the *FunctionalDiversity*, *Richness* and *Abundance* response variables

Online resource 3 - Description of the values contained in the mathematical formulas for the relationship between top-down control of arthropods by birds and birds' functional diversity

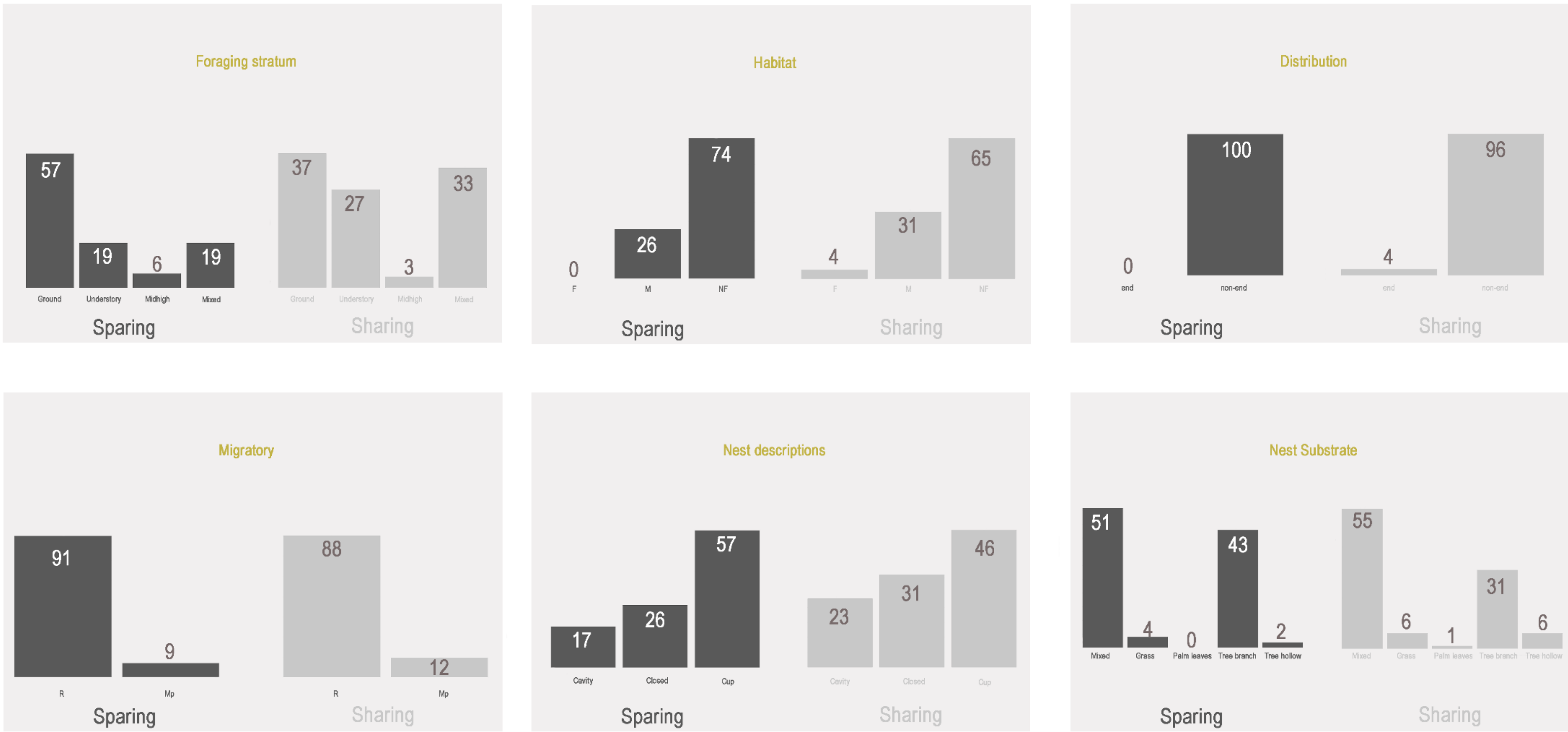
Value	Description
Log (Insectivory)	Number of dummy caterpillars consumed in all the three strata in log
FunctionalDiversity	Insectivorous birds' functional diversity
Model	Land-sharing or land-sparing urban sprawl model
random = NativeForest	Size class of native forest in the respective count point
random = Field	Size class of field in the respect count point
random = Lawn	Size class of lawn in the respect count point
random = Trees	Size class of trees in the respect count point

Online Resource 4 - Description of the values contained in the mathematical formulas for the relationship between insectivorous birds' functional diversity and urban green spaces sizes

Value	Description
FunctionalDiversity	Functional diversity of the insectivorous birds
NativeForest	Value of the mean sampled area of native in hectares that was present in the respective point-count
Field	Value of the mean sampled area of field in hectares that was present in the respect point-count
Lawn	Value of the mean sampled area of lawn in hectares that was present in the respect point-count
Trees	Value of the mean sampled area of trees in hectares that was present in the respect point-count
Model	Land-sharing or land-sparing urban sprawl model that was present in the respect point-count
BCPEo	BCPEo distributional family used to FunctionalDiversity response variable

Online Resource 5 – Insectivorous birds recorded in land sharing-sparing urban sprawl modelling in neotropical cities of Sorocaba and Votorantim, São Paulo, Brazil.

ID	Scientific name	Order	Family name	Common name
1	Picumnus temminckii	PICIFORMES	Picidae	Ochre-collared Piculet
2	Veniliornis spilogaster			White-spotted Woodpecker
3	Furnarius rufus	PASSERIFORMES	Furnariidae	Rufous Hornero
4	Todirostrum cinereum		Tyrannidae	Common Tody-flycatcher
5	Camptostoma obsoletum			Southern Beardless Tyrannulet
6	Elaenia flavogaster			Yellow-bellied Elaenia
7	Serpophaga subcristata			White-crested Tyrannulet
8	Pitangus sulphuratus			Great Kiskadee
9	Machetornis rixosa			Cattle Tyrant
10	Myiodynastes maculatus			Northern Streaked Flycatcher
11	Myiozetetes similis			Social Flycatcher
12	Empidonomus varius			Variegated Flycatcher
13	Tyrannus melancholicus			Tropical Kingbird
14	Troglodytes aedon		Troglodytidae	House Wren
15	Mimus saturninus		Mimidae	Chalk-browed Mockingbird
16	Turdus leucomelas		Turdidae	Pale-breasted Thrush
17	Zonotrichia capensis		Passerellidae	Rufous-collared Sparrow
18	Coereba flaveola		Thraupidae	Bananaquit



Online Resource 6 – Abundances proportion of insectivorous birds by ecological traits in land sharing-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil. The vertical and horizontal axes represent abundance proportion and niche space, respectively. Habitat - F: Forest, M: Mixed, NF: Non-Forest. Distribution – end: Endemic, non-end: non-endemic. Migratory – R: Resident, Mp: partially migratory.

Online Resource 7 – P values of the relationship between functional diversity of insectivorous birds and urban green spaces in land sharing-sparing urban sprawl modelling in Sorocaba and Votorantim, Brazil.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	-0.30	10.00×10^{-05}	-3164	< 0.0001
Field	-0.04	1.20×10^{-04}	-304	< 0.0001
Lawn	-0.02	1.40×10^{-04}	-125	< 0.0001
Trees	0.20	3.00×10^{-04}	561	< 0.0001

Considerações finais

Ao longo desses três capítulos foi confirmado que modelos de expansão urbana, influenciam de forma distinta na conformação dos espaços verdes e cinzas, com melhores resultados para o modelo compactado (i.e., *land-sparing*). Foi detectado que o modelo compactado apresentou, em geral, maiores extensões de importantes espaços verdes, e.g., florestas nativas. Além disso, foi demonstrado que o modelo compactado apresentou também melhores resultados relacionados à diversidade funcional para (1) comunidade geral de aves, (2) aves frugívoras e também para as (3) aves insetívoras. Adicionalmente, foi confirmado no estudo que a extensão de áreas verdes influencia positivamente na diversidade funcional da comunidade geral de aves, nas aves frugívoras e também nas aves insetívoras. Foi observado também que a diversidade funcional de aves frugívoras pode afetar positivamente o consumo de frutos, e que a diversidade funcional de aves insetívoras afeta positivamente o controle predador-presa de artrópodes por aves.

Esses dados podem fornecer ferramentas de políticas públicas voltados à adoção do modelo compactado para a expansão das cidades, uma vez que os resultados encontrados podem contribuir para conservação de áreas verdes maiores e direcionar para maior diversidade funcional de aves frugívoras e insetívoras e seus respectivos papeis ecológicos.