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Joana Nascimento de Mattos

EFEITOS DA DISPONIBILIDADE DE MELATO NAS INTERAÇÕES ECOLÓGICAS, RIQUEZA E DIVERSIDADE DE AVES NO SUL DO BRASIL

Florianópolis
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Joana Nascimento de Mattos

Efeitos da disponibilidade de melato nas interações ecológicas, riqueza e diversidade de aves no sul do Brasil

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Orientador: Dr. Eduardo Luís Hettwer Giehl
Coorientador: Dr. Guilherme Renzo Rocha Brito

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Prof.(a) Dr.(a) Malva Isabel Medina Hernández
Universidade Federal de Santa Catarina

Prof. Dr. Marco Aurelio Pizo
Universidade Estadual Paulista

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Dedico esse trabalho aos meus
pais, que sempre acreditaram
em mim mesmo quando não
fui capaz de fazê-lo, e também
a todas as mulheres que seguem
na luta por uma ciência mais justa

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quando eu não conseguia me mexer
foram mulheres
que vieram me banhar os pés
até eu voltar a ter forças
para me levantar
foram mulheres
que me nutriram
para eu voltar a viver
- irmãs

"Meu corpo minha casa" - Rupi Kaur (2020)

RESUMO

O melato é uma solução de carboidrato secretada por cochonilhas enquanto se alimentam do floema das plantas hospedeiras. O consumo de melato é uma interação estabelecida entre aves e cochonilhas em que o melato pode vir a ser a principal fonte de carboidratos consumidos pelas aves. Aqui descrevemos quais espécies de aves consomem melato produzido por cochonilhas (Hemiptera, Coccoidea) hospedeiras de *Mimosa scabrella.* Avaliamos a relação entre a disponibilidade de melato e a riqueza e diversidade de aves, e analisamos a contribuição de cada espécie para a diversidade beta (SCBD) em comunidades de aves no sul do Brasil. Localizamos 15 árvores focais e instalamos parcelas circulares (raio = 10 m) ao redor delas. Em cada parcela, contamos a densidade de árvores da espécie hospedeira e ainda a presença de melato em quatro zonas de altura em cada árvore destas como um indicador da disponibilidade de melato. Em seguida, observamos, identificamos e contamos as aves visitantes e de forma concomitante aos registros de consumo direto de melato ou dos insetos possivelmente atraídos pelo melato. Com um esforço amostral de 12 h/parcela (=180 h) Registramos 947 visitas de 39 espécies de aves, das quais 23 se alimentaram de melato e 16 de insetos. Alguns destes registros incluem novas espécies entre aquelas que utilizam esse recurso. No entanto, a riqueza de consumidores de melato diminuiu com o aumento da disponibilidade de melato e da densidade da árvore hospedeira. *Leucochloris albicollis* e S*etophaga pitiayumi* foram as espécies mais comuns e tiveram baixos valores de SCBD. Isso sugere que tais espécies são oportunistas que dominam o melato como fonte de alimento, especialmente sob alta densidade de árvores hospedeiras. Como a baixa disponibilidade de recursos provavelmente não atrai as espécies mais especialistas e dominantes, a diversidade alfa e beta pode aumentar nessas condições. Por fim, mesmo que diversas aves consumam melato e algumas sejam dominantes, as diferenças locais no nível de disponibilidade parecem permitir que mais espécies acessem esse recurso.

Palavras-chave: interações ecológicas; forrageio de melato; disponibilidade de recurso; partição de nicho; defesa de recurso.

ABSTRACT

Honeydew is a carbohydrate solution secreted by scale insects while feeding on the phloem of host plants. Honeydew foraging is an interaction established between birds and scale insects, where honeydew can be the main carbohydrate source for many bird species. Here we describe bird communities feeding on honeydew produced by scale insects (Hemiptera, Coccoidea) hosted by *Mimosa scabrella* trees, and assess how honeydew availability relates to bird richness and diversity, and evaluate the contributions of single species to beta diversity (SCBD) among bird communities in southern Brazil. We located 15 focal trees and installed circular plots (radius = 10 m) around them. In each plot, we counted host-tree density and honeydew presence in four height zones of each tree as an indicator of honeydew availability. We then observed, identified, and counted bird visitors and recorded whether they fed directly on honeydew or on insects possibly attracted by honeydew for 12 h/plot (=180 h). We recorded 947 visits by 39 bird species, of which 23 fed on honeydew and 16 on insects. Some records represent new honeydew foraging interactions. However, the richness of honeydew consumers decreased with increasing honeydew availability and host-tree density. *Leucochloris albicollis* and *Setophaga pitiayumi* were the most common species and had low SCBD values. This suggests that such species are specialists dominating honeydew as a food source, especially under high host-tree density. Given that low resource availability likely does not attract more specialist and dominant species, alpha and beta diversity can increase under such conditions. Finally, although a wide range of birds consume honeydew and some act as dominant species, local differences in availability seem to enable resource partitioning among species.

Keywords: ecological interactions; honeydew foraging; resource availability; niche partitioning, resource defense.

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SUMÁRIO

1. INTRODUÇÃO GERAL

Em estudos de ecologia, busca-se compreender os padrões e processos que estruturam a diversidade, abundância e composição das comunidades. Nesse contexto, as interações ecológicas desempenham um papel importante na influência de vários aspectos da biodiversidade em diversos níveis organizacionais (GUIMARÃES, 2020). Essas interações entre indivíduos promovem conexões entre populações de diferentes espécies, impactando assim a estabilidade e organização da comunidade, e por fim moldando a estrutura de diversidade destas (MACARTHUR, 1967). Por isso, pesquisas sobre nichos ecológicos têm crescido nas últimas décadas, buscando compreender a relação entre biodiversidade, o uso de recursos e interações dentro de uma comunidade (HOOPER et al, 2005; NORTHFIELD et al, 2005). Esses estudos têm explorado como a disponibilidade de recursos pode ser um fator crucial que influencia a riqueza de espécies dentro de comunidades locais. Especificamente, tem sido observado que um aumento na disponibilidade de recursos está associado a um aumento correspondente na riqueza de espécies (CARRARA; VASQUEZ, 2010). No entanto, quando múltiplas espécies dentro de uma comunidade compartilham o mesmo recurso, variações na quantidade de recursos e nas interações entre as espécies consumidoras tornam-se fundamentais na estruturação tanto da riqueza de espécies quanto da composição entre os consumidores, impactando subsequentemente os padrões de diversidade na comunidade local (AKATOV; PEREVOZOV, 2011).

Comunidades podem exibir diversos tipos de interações e relações entre indivíduos ou populações, resultando em uma comunidade complexa de múltiplas camadas (MELLO, 2019). Esses padrões podem ser gerados através de interações entre animais e plantas, proporcionando fontes diretas ou indiretas de uma ampla gama de recursos que são utilizados por muitas espécies consumidoras ou criar micro-hábitats que atendem às necessidades de outras plantas e animais (DEL-CLARO; TOREZAN-SILINGARDI, 2012). Um exemplo desse tipo de sistema ocorre quando cochonilhas se alimentam do floema de árvores hospedeiras, produzindo o melato (*honeydew*) que atrai aves e insetos, os quais por sua vez podem servir como fonte de alimento para as aves, proporcionando o desenvolvimento de uma rede de múltiplos recursos alimentares para uma variedade de espécies. No entanto, para obter uma compreensão abrangente desse sistema, é crucial avaliar as espécies envolvidas, a natureza de suas conexões e interações, e como a disponibilidade desses recursos pode afetar seu consumo e as interações formadas.

1.1 Cochonilhas e a produção de melato no sul do Brasil

Em diversos ecossistemas, as cochonilhas produtoras de melato (Hemiptera, Coccoidea), apesar de sua biomassa relativamente reduzida, desempenham papéis ecológicos de significância e têm potencial para atuar como espécies-chave nesses ecosistemas (BEGGS et al. 2005; GAMPER et al. 2011). O melato, uma solução rica em açúcar, é produzido e secretado por indivíduos pertencentes a seis famílias de hemípteros (Coccoidea), comumente denominados cochonilhas (*scale insects*). Essas cochonilhas alimentam-se do floema de plantas hospedeiras, que é rico em nitrogênio para a síntese de proteínas, e liberam o melato sob forma de gotas através de um filamento anal longo localizado no caule das plantas (MARTINS-MANSANI, 2021). É reconhecido que pelo menos seis famílias de cochonilhas são fontes de melato em várias regiões do mundo (CHAMORRO et al. 2013). A família Stigmacoccidae é particularmente notável como a principal produtora de melato na América do Sul, com duas espécies predominantes no Brasil, *Stigmacoccus asper* e *Stigmacoccus paranaenses* (HODGSON et al. 2007; GAMPER et al. 2011; CHAMORRO et al. 2013). Na região sul do Brasil, a produção de melato por cochonilhas ocorre predominantemente em interação com árvores de bracatinga (*Mimosa scabrella* Benth, Fabaceae; CAMPOS et al. 2003; Figura 1), sendo *S. paranaenses* a principal espécie produtora de melato nessa planta (WOLFF et al. 2015).

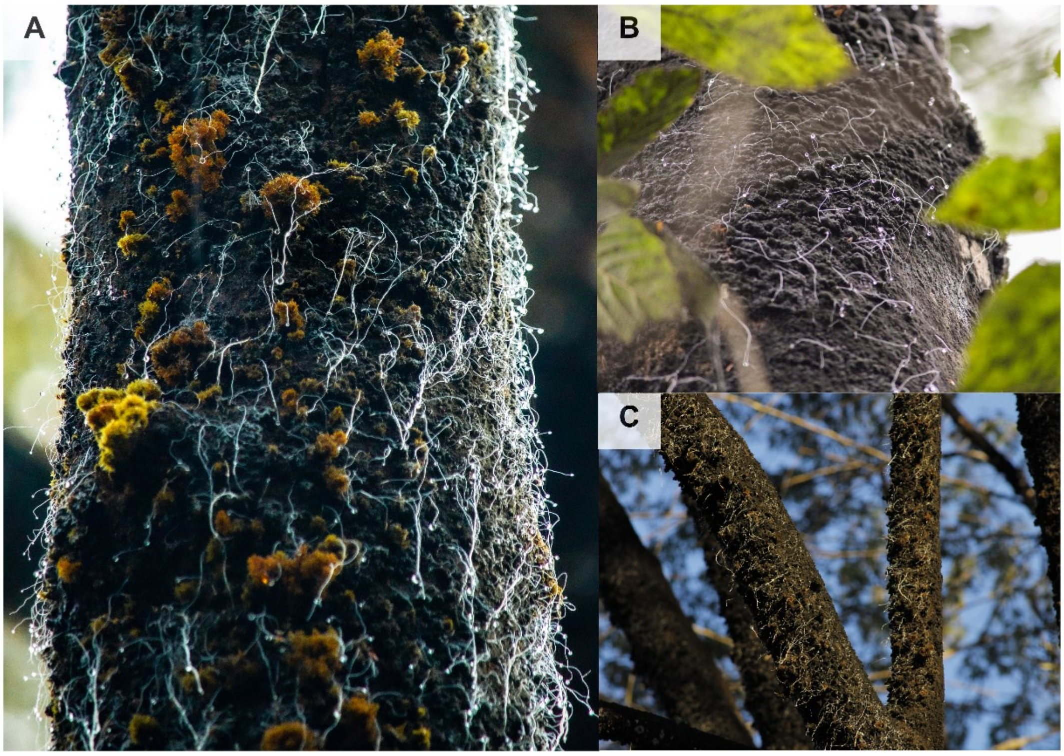

Figura 1: Caules de *Mimosa scabrella* mostrando os filamentos de cochonilhas com gotas de melato nas extremidades. Foto de (A) João Garbers, (B) Ariane Ferreira e (C) Joana Mattos.

A bracatinga é uma espécie nativa dos climas mais frios do Brasil (CARPANEZZI et al; 1988), pioneira de ciclo curto, essencialmente heliófita, e exclusiva da vegetação secundária da Floresta Ombrófila Mista (MAZUCHOWSKI, 2012). A espécie ocorre naturalmente e de forma mais expressiva nos planaltos paranaenses, em praticamente todo o planalto de Santa Catarina e em parte do Rio Grande do Sul (HATSCHBACH e KLEIN, 1962). O melato de bracatinga é conhecido mundialmente devido a sua interação com abelhas (eg. *Apis mellifera*), que utilizam bianualmente o melato pelas cochonilhas para a produção de mel (Rio Grande do Sul, Wolff et al. 2015; Santa Catarina, Mariano-da-Silva et al. 2011). O mel de melato é sucesso no mercado internacional e 90% da produção catarinense é exportada para a Europa, e é no estado de Santa Catarina que se concentra 80% de toda a produção nacional do produto (CERON, 2019). Porém, o conhecimento sobre o forrageio de melato por outras espécies no sul do Brasil ainda é limitado.

1.1.1 O uso de melato pelas aves

O forrageio de melato por aves tem sido documentada como uma interação aparentemente importante com cochonilhas (Hemiptera, Coccoidea) (TEIXEIRA et al. 2013; LARA et al. 2011; GAMPER; KOPTUR, 2010). No entanto, o entendimento dessa interação e os fatores que poderiam influenciar seu consumo pelas aves ainda é pouco explorado. Espécies de aves como *Setophaga pitiayumi* (Vieillot, 1817), *Stilpnia peruviana* (Desmarest, 1806), *Stephanophorus diadematus* (Temminck, 1823), *Tachyphonus coronatus* (Vieillot, 1822), e *Zonotrichia capensis* (Müller, 1776), foram registradas utilizando o melato no caule de uma árvore de bracatinga (*Mimosa scabrella*) no norte do estado de Santa Catarina (SICK, 1988). Em alguns ecossistemas, o uso de melato também tem sido observado em insetos como formigas, vespas e abelhas (MOLLER; TILLEY, 1989; DIDHAM, 1993), e aves insetívoras podem ser beneficiadas indiretamente pela disponibilidade de melato consumindo essas espécies que também se alimentam de melato, intensificando as conexões tróficas (GRANT; BEGGS, 1989). Porém, sendo um recurso muito energético e possivelmente escasso em algumas épocas do ano, árvores ou partes da floresta com produção de melato podem ser ativamente defendidas, assim como ocorre quando aves protegem flores produtoras de néctar (FEINSINGER, 1976; MAC NALLY; TIMEWELL, 2005) e frutos (MALE; ROBERTS, 2006; PRATT, 1984).

Embora a relação entre espécies e disponibilidade de recursos frequentemente resulte em maior riqueza e diversidade, outras interações, como a competição intra ou interespecífica, podem levar a resultados diferentes, potencialmente resultando em menos espécies (AKATOV;

PEREVOZOV, 2011). Comunidades com um alto nível de dominância tendem a exibir uma menor riqueza de espécies locais em comparação com aquelas com baixa dominância (AKATOV; PEREVOZOV, 2011). Por exemplo, no México 21 espécies de aves foram registradas consumindo melato, e verificaram algumas competindo pelo recurso e utilizando comportamentos para defendê-lo. Conforme a abundância de insetos produtores de melato aumentava, os comportamentos de defesa também aumentavam (GAMPER; KOPTUR, 2010). Essas defesas agressivas por parte de espécies mais especialistas podem impactar a presença de outras espécies, levando a buscar alimento em outras áreas, o que consequentemente influencia a riqueza, composição e a diversidade da comunidade (GAMPER; KOPTUR, 2010).

Um método que pode auxiliar na compreensão do papel de cada espécie nas interações ao consumir o mesmo recurso em uma comunidade é a quantificação da Contribuição das Espécies para a Diversidade Beta (SCBD, do inglês "Species Contribution to Beta Diversity"). As SCBDs representam a importância relativa de cada espécie na influência dos padrões de diversidade beta, propostas por Legendre e De Cáceres (2013). Os traços biológicos das espécies podem influenciar suas contribuições para a diversidade beta, já que certas características podem afetar a ocupação e a abundância de outras (HEINO; GRONROOS, 2014). A variação no grau de ocupação também pode influenciar os valores de SCBD, uma vez que espécies que apresentam uma maior variação na ocupação nos locais podem ter contribuições maiores para a diversidade beta (da Silva et al. 2018). Essas informações ajudam a elucidar os padrões de diversidade beta e identificar os traços-chave das espécies que são relevantes dentro do contexto específico do estudo (HEINO; GRONROOS, 2014; LEGENDRE; DE CÁCERES, 2013).

Entretanto, também é importante reconhecer que a disponibilidade de melato, as interações e ocupação das espécies não aparentam serem os únicos fatores que influenciam o consumo de melato pelas aves. A "Hipótese da Convergência" (GREENBERG et al. 1993) esclarece a distribuição geográfica única e desigual da busca de melato por aves em todo o mundo. Essa hipótese sugere que condições climáticas regionais comuns levaram à ocorrência limitada da busca de melato por aves. Habitats como florestas temperadas e climas amenos contribuem para a presença reduzida de formigas, que são conhecidas consumidoras de melato, promovendo assim um maior uso de melato por aves. Além disso, a temperatura pode afetar diretamente a atividade das cochonilhas, influenciando consequentemente a produção e concentração de melato (GAZE; CLOUD, 1993). Analisar essas interações complexas pode proporcionar informações importantes sobre os fatores que moldam os padrões de consumo de melato pelas comunidades de aves.

Diante da lacuna de informações acerca da utilização do melado pelas aves e da aparente relevância desse recurso como fonte alimentar, a análise da complexa rede de interações gerada por esse consumo ganha destaque ao fornecer informações cruciais sobre os elementos que configuram os padrões de consumo de melato por aves. A obtenção de dados relacionados às características biológicas das espécies consumidoras e à disponibilidade do recurso nos locais de estudo assume um papel fundamental para compreender os fatores que influenciam o consumo, a ocupação, a diversidade e a composição das aves que recorrem a essa fonte alimentar.

1.2.OBJETIVO GERAL

Buscamos registrar as espécies de aves consumidoras de melato e insetos nas árvores hospedeiras de *Mimosa scabrella* no Planalto sul do Brasil, a fim de caracterizar essa comunidade e avaliar o possível papel desse recurso para a avifauna. Além disso, investigamos como a disponibilidade do melato, as condições ambientais de temperatura e as interações entre as espécies podem influenciar o consumo de melato pelas aves. No primeiro capítulo, baseado na premissa que melato é um recurso altamente disputado, esperamos observar interações competitivas entre as espécies, prevendo que os beija-flores ocupem uma hierarquia de dominância mais elevada. Também é nossa expectativa que as espécies nectarívoras desempenhem um papel central como principais consumidoras desse recurso. No segundo capítulo, esperamos encontrar uma maior riqueza de espécies se alimentando de melato em áreas com maior disponibilidade de melato. Também formulados duas hipóteses alternativas como mecanismos diferentes: (1) locais com alta disponibilidade de recurso podem possuir uma menor riqueza de consumidores na presença de espécies mais especializadas, que acabam defendendo mais os recursos e (2) locais com menor disponibilidade de recurso, que não atrai espécies especialistas, podem apresentar maior diversidade de consumidores, resultando assim em poucas interações competitivas.

1.2.1. Objetivos Específicos

Capítulo 1: Avian use of honeydew: effects of ecological interactions and species dominance among bird communities in southern Brazil

(1) Registrar as espécies de aves consumidoras de melato e insetos em árvores de *Mimosa scabrella* no Planalto do sul do Brasil;

(2) Caracterizar a comunidade de aves consumidoras de melato e insetos que ocorrem em árvores de *Mimosa scabrella*, e os seguinte parâmetros de cada espécie: dieta, massa corporal, número e porcentagem total de visitas e o tempo total e média da duração de cada evento de forrageio;

(3) Avaliar a contribuição de cada espécie para a diversidade beta (Species Contribution to Beta-diversity) e sua relação com o número de visitas de forrageio de melato.

Capítulo 2: Influence of temperature and honeydew availability on alpha and beta diversity of bird communities in subtropical Brazil

(1) Avaliar a relação da disponibilidade de melato com a riqueza de espécies de aves consumidoras de melato e insetos;

(2) Analisar se o consumo de melato difere em função da temperatura do dia da coleta e da semana anterior;

(3) Avaliar se existe uma relação entre disponibilidade de melato e outras variáveis ambientais com componentes de diversidade beta (troca de espécies e diferença de riqueza).

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2. CAPÍTULO 1: AVIAN USE OF HONEYDEW: EFFECTS OF ECOLOGICAL INTERACTIONS AND SPECIES DOMINANCE AMONG BIRD COMMUNITIES IN SOUTHERN BRAZIL

Joana Nascimento de Mattos[1,2]; Eduardo L. H. Giehl[1,2]; Guilherme Renzo Rocha Brito[1]

[1]Department of Ecology and Zoology/Federal University of Santa Catarina, Brazil

[2]Graduate Program in Ecology/Federal University of Santa Catarina, Brazil

Abstract: Honeydew is a carbohydrate solution secreted by scale insects while feeding on the phloem of host plants. Honeydew foraging is an interaction established between birds and scale insects, where honeydew can be the main carbohydrate source for some birds. Here we registered birds feeding on honeydew produced by scales hosted by the tree *Mimosa scabrella,* and characterized the guild within some biological traits. We also analyzed each species contribution to beta diversity (SCBD) through their frequency of visits. We located 15 focal host-trees and placed circular plots (radius = 10 m) around them. In each plot, we counted host-tree density and honeydew presence in four height zones of each one as a proxy for honeydew availability. We then observed, identified and counted bird visitors and registered whether birds fed on honeydew or insects for 12 h/plot (=180 h). We recorded 947 visits by 39 bird species – 23 feeding on honeydew and 16 on insects –, some being new records of honeydew foraging interactions. Six frugivorous and nectarivorous species made 48% of all foraging trips, 23 insectivores (34,5% of all visits), eight omnivores (13,8% of all visits), and two plant and seed (4,4% of all visits). It is noteworthy that almost all species had not been previously observed foraging on any type of sugary excretion. Interactions ranged from affiliative to agonistic. Out of the 23 agonistic behaviors, 60.9% (n=14) were interspecific and 39.2% (n=9) intraspecific. *Leucochloris albicollis* was the most aggressive and dominant species, being chased only by conspecifics. We found a correlation between species visitation frequency and their contributions to beta diversity, with the most registered species presenting the lowest SCBD-values, which means they contribute little to community compositional differences in space or time. This study has significantly contributed to confirming and clarifying honeydew consumption by bird communities in southern Brazil and highlights the importance of this resource in structuring communities with high levels of diversity.

Keywords: ecological interactions, honeydew foraging, resource defense, niche partitioning.

INTRODUCTION

Ecological interactions play an important role in influencing various facets of biodiversity across a wide range of organization levels (GUIMARÃES, 2020). These interactions among individuals foster connections between populations of different species, thereby affecting community stability and organization, and ultimately shaping community structure and diversity (MCARTHUR, 1955; THOMPSON, 2005). Some communities exhibit intricate structures with diverse types of interactions or relationships among individuals or populations, giving rise to a complex multilayer community (MELLO, 2019). A notable example of such a system occurs when scale insects feed on the phloem of host-trees, producing honeydew that attracts birds and insects, which in turn may serve as a food source for birds, creating a network of multiple feeding resources for a diverse array of species. However, to gain a comprehensive understanding of this system, it is crucial to assess the species involved, the nature of their connections, and how these interactions might influence resource utilization. This evaluation should encompass not only trophic relationships (PRICE, 2002) but also aspects of life histories, biology, and behavior of all the species involved (DEL CLARO, 2004).

Honeydew is a sugar-rich solution, produced and secreted by various hemipterans from six families known as scale insects (Coccoidea). These scale insects feed on the phloem of host plants, which provides them with nitrogen for protein production, and they excrete honeydew in the form of droplets on plant stems (LATTA et al; 2001). Honeydew foraging has been observed as an interaction between birds and scale insects, and it may serve as a primary source of carbohydrates for a diverse range of species (GRANT; BEGGS, 1989), leading to the establishment of direct and indirect relationships. However, our understanding of honeydew utilization by birds in Brazil remains limited. Some species, such as *Setophaga pitiayumi*, *Stilpnia peruviana*, *Stephanophorus diadematus*, *Tachyphonus coronatus*, and *Zonotrichia capensis*, were recorded using honeydew on the stems of *Mimosa scabrella* trees in the northern region of Santa Catarina state (SICK, 1988), with no further investigations on the phenomenon. Given its high carbohydrate content, honeydew can be considered a valuable food resource, likely to be partitioned by numerous consumers (LARA et al, 2001), and it may play a central role in the diet of nectarivorous and frugivorous birds, particularly during periods when floral resources and fruits are scarce (FEINSINGER, 1976; MACNALLY; TIMEWELL, 2005; GAMPER; KOPTUR, 2010). Consequently, birds, similar to their protection of nectar-producing flowers (FEINSINGER, 1976; MACNALLY; TIMEWELL, 2005), could actively defend honeydew.

Competition for resources plays a pivotal role in driving population dynamics and shaping ecological communities (SEABLOOM et al, 2003). Specifically, competition for food resources is a major driver of these processes (HUTCHINSON, 1959; MACARTHUR; LEVINS, 1967; CONNELL, 1983; SCHOENER, 1983; AINLEY et al, 2004). The degree of competition for consumption appears to influence the coexistence of species, and niche shifts may arise as a consequence to facilitate the coexistence of species utilizing the same resources (HUTCHINSON, 1959). For instance, it has been proposed that bird species can coexist while utilizing the same food type by foraging at different heights within the same tree (LARA et al; 2011). This spatial segregation has been supported by other studies (LARA et al, 2011) that observed hummingbirds foraging on honeydew at different heights, thus reducing aggressive behaviors. However, behavioral dominance represents another mechanism by which bird communities utilizing the same food resource may be structured (LARA et al; 2011). For example, in Mexico, 21 bird species were observed consuming honeydew, with some displaying aggressive behaviors to defend the resource (GAMPER; KOPTUR, 2010), a phenomenon also observed in hummingbird communities sharing ephemeral floral resources (LARA et al; 2011). Such instances of aggressive defense by more specialized or opportunistic species might impact the presence of other species, compelling them to forage in alternative areas, consequently influencing community composition and diversity (GAMPER; KOPTUR, 2010).

Interaction patterns play a significant role in shaping evolutionary and ecological processes (KAISER-BUNBURY et al, 2017; KONDOH, 2003; LOEUILLE, 2010). Understanding the emergent relationships and their impact on community composition and diversity requires an assessment of species characteristics, behaviors, occupancy, and biological traits (DEL CLARO, 2004). One method that can aid in this understanding is the quantification of Species Contribution to Beta Diversity (SCBD). Such contribution measure was proposed by Legendre and De Cáceres (2013) to represent the relative importance of each species in influencing beta diversity patterns. Species` biological traits may influence their contributions to beta diversity, as it could affect occupancy and abundance (HEINO; GRONROOS, 2014). This information helps elucidate the biological processes and patterns underlying beta diversity and identify key species and traits that are relevant within the specific context of the study (HEINO; GRONROOS, 2014; LEGENDRE; DE CÁCERES, 2013).

In view of the apparent significance of honeydew as a food resource for bird communities and the limited understanding of its use and interactions, we initiated this study to investigate the bird community's interactions with scale insects linked to *Mimosa scabrella* trees in southern Brazil. Our objective is to elucidate the importance of this interaction in the ecosystem. Based on the premise that honeydew is a highly-disputed resource, we expected to observe behavioral dominance among consuming birds, with possibily higher levels of dominance by hummingbirds. Additionally, we expected nectarivorous species, particularly the resident ones, to be the most frequent consumers of honeydew.

MATERIALS AND METHODS

Study site

The study was conducted in the highlands of southern Brazil, specifically in the state of Santa Catarina. The research areas encompassed both the São Joaquim National Park (28.19˚S, 49.53˚W) and private areas within the Urubici city region. This region comprises one of the highest elevated zones in southern Brazil. The predominant ecoregions in the highlands include high-altitude grasslands and mixed rainforest, known as Araucaria forest. The coldest month, July, experiences an average minimum temperature of 0.2 °C, while the hottest month, January, has an average maximum temperature of 23°C. The lowest recorded temperature was −9.0 °C, while the highest recorded temperature reached 31.4 °C. Winter in the region is characterized by frequent frosts, with occasional occurrences of snow (INMEP, 2023).

Study organisms

Mimosa scabrella

Mimosa scabrella Benth (Fabaceae) or "bracatinga" is a native tree species found in the coldest climates of Brazil (CARPANEZZI et al. 1988) and is exclusive to mixed rainforests (Araucaria forest). *M. scabrella* is a pioneer species with a short life cycle and is primarily adapted to open, sunlit conditions (MAZUCHOWSKI, 2012), thus being common on secondary vegetation such as areas affected by fires, nearby roadsides, and at forest edges. Besides, these trees play a significant role in carbon storage, making them environmentally important (MAZUCHOWSKI, 2012). Because of such features, it is often recommended for the restoration of degraded habitats. *M. scabrella* is also the main host tree for some scale insects that produce honeydew (CAMPOS et al. 2003).

Scale insects and honeydew

Honeydew is a sugary solution produced and excreted by individuals of six families of hemipterans known as scale insects (Coccoidea). Scales feed on the phloem sap of host plants, which is rich in nitrogen and essential for protein production. They secrete honeydew in the form of droplets on plant stems (LATTA et al. 2001). In the case of the bracatinga tree (*M. scabrella*), the main scale insect species involved in the interaction is *Stigmacoccus paranaenses* (HODGSON, 2007). This species has been documented in southern Brazil, including the States of Paraná, Santa Catarina, and Rio Grande do Sul, and has been found on several plant species such as *Inga* spp., *Schizolobium excelsum* (Fabaceae), and *Mimosa scabrella* (Mimosaceae; WOLFF et al. 2015). While honeydew can be a significant carbohydrate source for a wide range of species (GRANT; BEGGS, 1989), including birds and other insects, giving rise to a myriad of direct and indirect ecological relationships.

Sampling method and data collection

Plot selections

To assess the use of honeydew by birds, we placed 15 circular plots (r = 10 m), each centered at a focal *Mimosa scabrella* tree. We selected focal trees where we had different host-tree densities (low, medium and high density). We then counted the number of adult *M. scabrella* trees inside each plot to refine our density estimate. The focal tree height and the CBH (circumference at breast height) of each *M. scabrella* individual was also registered. This sampling design was chosen focusing on later a study in which honeydew foraging under varying resource amounts will be assessed.

For a more thorough estimate of honeydew availability in each plot, we developed a visual division of the tree into four zones. In the central area (trunk), we divided the trunk in three zones: “zone 1” (lowest part – 0-33.3% of the trunk), “zone 2” (middle part – 33.4-66.7% of the trunk) and “zone 3” (high part – 66.8100% of the trunk). The “zone 4” encompassed the peripheral area (all the branches of the tree). Then, in each zone, we assessed presence or absence of honeydew

Bird sampling

To quantify honeydew use by birds, we observed bird visits to focal trees and bird behavior during such events throughout the year of 2022. Observations were made during the first and last three hours of the day depending on the time of sunrise and sunset on each sampling day (following TEIXEIRA; AZEVEDO, 2013), resulting in a total of 12 hours per plot (equivalent to 180 hours of total observations). Data were collected throughout the year, in different seasons, and with varying temperatures to provide a baseline description of the bird community that uses honeydew directly, or indirectly, consuming insects attracted by honeydew itself. For each visit to the focal-tree, we recorded the bird species, number of individuals, time of arrival and departure, and whether birds were foraging on honeydew or insects. We were unable to recognize and account for individual birds, thus the same individual may have made multiple visits. We also classified the species into migratory and residents based on SOMENZARI et al. (2018). Species description into foraging guilds and body mass were classified based on WILMAN et al. (2014).

In order to examine spatial variations in honeydew consumption, we considered the same four zones used to estimate honeydew availability. During each visit, we recorded the specific zone where each species was engaged in foraging behavior. All direct visual observations were conducted from a distance of 10 meters away from the focal tree, with the aid of binoculars (Solognac 10x42mm) and photographic records (Canon EOS T7 75-300mm). Furthermore, we registered both inter and intraspecific interactions, as well as agonistic interactions, which provided valuable insights into resource defense.

Bird guild characterization and data analysis

We first listed all species that visited focal trees after honeydew or insects. Then we made a literature review to look for previous records of honeydew foraging from the identified species. We also assessed the foraging guilds and body mass of each species, to search for links between such traits and the type of resource. We then characterized the bird guild that consumed honeydew and insects with the following parameters: diet, body mass, the number and total percentage of visits, and the total and average duration of each foraging event. To check for potential dominance of food sources, we used the estimated overall number of visits carried out by each bird species and the spatial differences in the list of bird species. The last information was used to prepare two matrices of species presence–absence, sorting out honeydew and insect consumers. Each presence–absence matrix was standardized using the Hellinger method and both were then used to compute Species Contribution to Beta Diversity, based on the Podani family of indices (SCBD; LEGENDRE; DE CÁCERES, 2013, LEGENDRE, 2014). This method was used in order to understand how species characteristics and frequency of visits could affect species composition and consumption. SCBD-values range from 0 to 1, and an increasing SCBD indicates the species has a higher contribution to community differentiation in space, thus increasing beta diversity. In turn, species showing low

SCBD-values tend to be widespread in space, lowering beta diversity. After, to investigate the relationship between the contribution of each species of honeydew consumers to beta diversity and the frequency of visits, we fit beta regression as our modeling method. We considered the number of visits as an explanatory variable, as well as their quadratic term, and the SCBD-values previously calculated as the response variable. Beta regression is typically used to model variables that show values between 0 and 1, and naturally incorporates features such as heteroskedasticity or skewness, which are typically observed in response data taking values from 0 to 1. We computed SCBDs with the “adespatial” package (DRAY et al. 2022), and the beta regression models with the “betareg” package (Cribari-Neto & Zeileis, 2010), both in R (R CORE TEAM, 2023).

RESULTS

We found 39 bird species visiting *Mimosa scabrella* trees, belonging to 13 bird families. Out of these species, 23 foraged on honeydew (Table 1) and 16 on insects (Table 2). Thraupidae was the richest family (11 species), followed by Tyrannidae (6 spp.), and Trochilidae and Parulidae (4 spp.). Only four species were classified as partially migratory, with the remaining 35 species considered permanent residents. In terms of foraging guilds, six frugivorous and nectarivorous species made 48% of all foraging trips, 23 insectivores (34.5% of all visits), eight omnivores (13.8% of all visits), and two plant and seed consumers (4.4% of all visits). The highest tree zones (zone 3 and 4) were visited by almost all species, either foraging on honeydew or insects, while the lowest zones were mainly used by honeydew consumers (Figure 1). It is noteworthy that almost all species had not been previously observed foraging on any type of sugary excretion. Among the 23 species identified as honeydew consumers in this study, 15 species were not previously documented as such.

Table 1: List of honeydew and insect consumers on *Mimosa scabrella* trees. Consumption: H = Honeydew, I = insects; Diet based on Wilman et al. (2014): I = invertebrate, O = omnivores, F/N = frugivores / nectarivores, P/S = plants / seeds; Body mass in grams based on Wilman et al. (2014); Record: NR = New record (Species previously registered were referenced). Species with one asterisk (*) are considered Partially Migratory species based on Somenzari et al. (2018). Species with two asterisks (**) are considered Near Threatened species by IUCN Red List of Threatened Species.

Species	Consumption	Diet	Body mass	Record
Trochilidae				
White-throated Hummingbird (*Leucochloris albicollis)*	H	F/N	6.3	Sick 1988
Glittering-bellied Emerald *(Chlorostilbon lucidus)*	H	F/N	3.5	Teixeira *et al.* 2013
Violet-capped Woodnymph *(Thalurania glaucopis)*	H	F/N	4.8	NR
Violet-crowned Plovercrest *(Stephanoxis loddigesii)*	H	F/N	4.0	NR
Picidae				
Mottled Piculet (*Picumnus nebulosus)***	I	I	11.6	NR
White-browed Woodpecker (*Piculus aurulentus)***	I	I	74.99	NR
Psittacidae				
Maroon-bellied Parakeet (*Pyrrhura frontalis)*	H/I	P/S	72	Rosário 1996
Dendrocolaptidae				
Scalloped Woodcreeper *(Lepidocolaptes falcinellus)*	I	I	27.92	NR
Olivaceous Woodcreeper *(Sittasomus griseicapillus)*	I	I	13.12	NR
White-throated Woodcreeper *(Xiphocolaptes albicollis)*	I	I	118	NR
Furnariidae				
Sharp-billed Treehunter *(Heliobletus contaminatus)*	I	I	14.0	NR
Striolated Tit-Spinetail *(Leptasthenura striolata)*	I	I	10.5	NR
Araucaria Tit-Spinetail *(Leptasthenura setaria)***	I	I	11.0	NR
Rhynchocyclidae		O	69.44	NR
Mottle-cheeked Tyrannulet *(Phylloscartes ventralis)**	H	I	8.3	NR
Tyrannidae				

Elaenia sp.	I	I		NR
Small-billed Elaenia *(Elaenia parvirostris)**	I	I	13.8	NR
Olivaceous Elaenia (*Elaenia mesoleuca)*	H/I	I	17.6	NR
White-crested Tyrannulet *(Serpophaga subcristata)*	I	I	6.6	NR
Bran-colored Flycatcher *(Myiophobus fasciatus)**	I	I	9.9	NR
Tropical Kingbird *(Tyrannus melancholicus)**	I	I	37.4	NR
Variegated Flycatcher *(Empidonomus varius)**	I	I	27.1	NR
Corvidae				
Azure Jay *(Cyanocorax caeruleus)***	I	O	272	NR
Turdidae				
Rufous-bellied Thrush *(Turdus rufiventris)*	I			
Passerellidae				
Rufous-collared Sparrow *(Zonotrichia capensis)*	H	P/S	20.31	Sick 1988
Icteridae				
Golden-winged Cacique *(Cacicus chrysopterus)*	I	O	36.16	NR
Parulidae				
Tropical Parula *(Setophaga pitiayumi)*	H	I	6.82	Sick 1988
White-browed Warbler *(Myiothlypis leucoblephara)*	H	I	15.1	NR
Golden-crowned Warbler *(Basileuterus culicivorus)*	H	I	10.5	Capelão *et al.* 2018
Neotropical River Warbler (*Myiothlypis rivularis)*	H	I	13.5	NR
Thraupidae				
Gray-throated Warbling-Finch *(Microspingus cabanisi)*	H	O	19.2	NR

Chestnut-backed Tanager *(Stilpnia preciosa)*	H	F/N	22.8	NR
Diademed Tanager *(Stephanophorus diadematus)*	H	O	35.4	NR
Bay-chested Warbling-Finch *(Castanozoster thoracicus)*	H	O	11.0	NR
Ruby-crowned Tanager *(Tachyphonus coronatus)*	H	I	29.3	Sick 1988, Teixeira *et al.* 2013, Capelão *et al.* 2018
Blue-black Grassquit *(Volatinia jacarina)*	H	O	11.0	NR
Thick-billed Saltator *(Saltator maxillosus)*	H	I		NR
Chestnut-headed Tanager *(Thlypopsis pyrrhocoma)*	H	I	15.6	NR
Azure-shouldered Tanager *(Thraupis cyanoptera)***	H	F/N	43.3	Capelão *et al.* 2018
Fawn-breasted Tanager *(Pipraeidea melanonota)*	H	O	21.0	NR

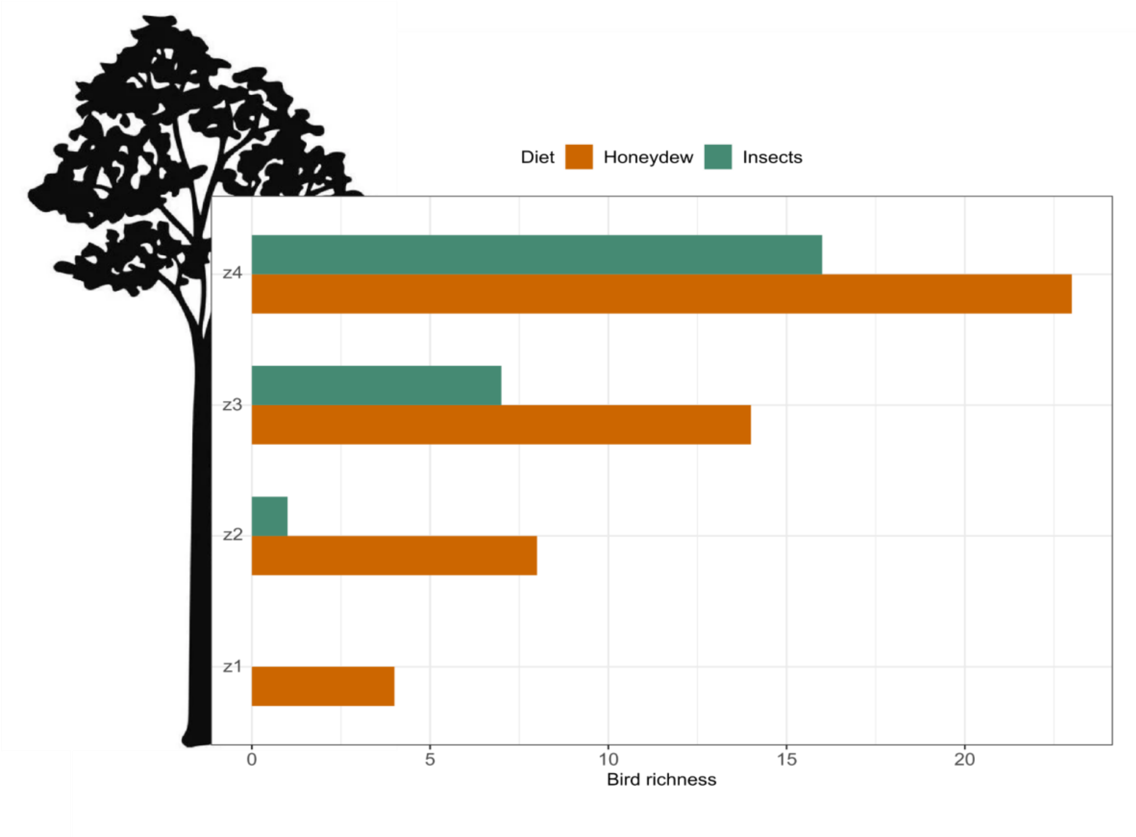

Figure 1: Barplot of the bird richness of honeydew and insect consumers, separated within the four tree zones. All zones were mainly dominated by honeydew consumers.

We recorded 955 foraging events on *Mimosa scabrella* trees. *Leucochloris albicollis* had the highest number of visits (n=326 trips), followed by the *Setophaga pitiyumi*, (n=167 trips), and *Microspingus cabanisi* (n=83 trips) – all three foraging on honeydew only (Table 3). Some species or individuals visited the trees at the same time. Interactions ranged from affiliative to agonistic. Out of the 23 agonistic behaviors, 60.9% (n=14) were interspecific and 39.2% (n=9) intraspecific (Figure 2). Among the most active consumers of honeydew, *L. albicollis* was the most aggressive and dominant species, being chased only by individuals of the same species. This species also displayed one of the shortest durations of time spent foraging on honeydew (60 seconds per visit) but had the longest total foraging time (8 hours and 46 minutes), highlighting its high level of dominance (34.25% of all visits).

Table 2: Birds consuming honeydew and insects on *Mimosa scabrella* trees. N° visits = total number of visits to honeydew; Consumption, H=honeydew, I=insects; Visits (%) = percentage of visits; Total time foraging on honeydew = total time foraging on honeydew in hours; Mean length of foraging visits = mean length of foraging visits in seconds.

Species	Consumption	N° visits	Visits (%)	Total time foraging on HD (h)	Mean lenght of foraging visits (s)
White-throated Hummingbird *(Leucochloris albicollis)*	H	326	34.25	08:46	60
Tropical Parula *(Setophaga pitiayumi)*	H	167	17.55	06:49	120
Gray-throated Warbling-Finch *(Microspingus cabanisi)*	H	83	8.72	04:35	180
Glittering-bellied Emerald *(Chlorostilbon lucidus)*	H	66	6.94	01:13	60
Chestnut-backed Tanager *(Stilpnia preciosa)*	H	47	4.94	01:49	120
Rufous-collared Sparrow *(Zonotrichia capensis)*	H	39	4.10	03:09	240
Elaenia sp.	I	33	3.48	01.33	120
Diademed Tanager *(Stephanophorus diadematus)*	H	26	2.74	01:43	180
White-browed Warbler *(Myiothlypis leucoblephara)*	H	18	1.90	00:31	60
Golden-crowned Warbler *(Basileuterus culicivorus)*	H	15	1.58	00:25	70
Violet-crowned Plovercrest *(Stephanoxis loddigesii)*	H	12	1.27	00:13	50
Bay-chested Warbling-Finch *(Castanozoster thoracicus)*	H	10	1.06	00:19	60
Ruby-crowned Tanager *(Tachyphonus coronatus)*	H	9	0.95	00:15	60
Small-billed Elaenia *(Elaenia parvirostris)*	I	9	0.95	00:14	55
Neotropical River Warbler *(Myiothlypis rivularis)*	H	9	0.95	00:14	55
Scalloped Woodcreeper *(Lepidocolaptes falcinellus)*	I	7	0.74	00:13	60
Sharp-billed Treehunter *(Heliobletus contaminatus)*	I	7	0.74	00:23	180
Bran-colored Flycatcher *(Myiophobus fasciatus)*	I	7	0.74	00:12	60
Violet-capped Woodnymph *(Thalurania glaucopis)*	H	4	0.43	00:04	50
Olivaceous Elaenia *(Elaenia mesoleuca)*	H/I	10	1.05	00:15	60
White-crested Tyrannulet *(Serpophaga subcristata)*	I	6	0.64	01:09	660
Blue-black Grassquit *(Volatinia jacarina)*	H	4	0.43	00:06	60
Striolated Tit-Spinetail *(Leptasthenura striolata)*	I	4	0.43	00:06	60
Araucaria Tit-Spinetail *(Leptasthenura setaria)*	I	4	0.43	00:11	120
Olivaceous Woodcreepe *(Sittasomus griseicapillus)*	I	4	0.43	00:08	120
Mottle-cheeked Tyrannulet *(Phylloscartes ventralis)*	H	3	0.32	00:09	180

Thick-billed Saltator *(Saltator maxillosus)*	H	3	0.32	00:07	120
Golden-winged Cacique *(Cacicus chrysopterus)*	H	3	0.32	00:10	180
Tropical Kingbird (*Tyrannus melancholicus)*	I	3	0.32	00:07	120
Azure Jay *(Cyanocorax caeruleus)*	I	3	0.32	00:05	60
Mottled Piculet *(Picumnus nebulosus)*	I	3	0.32	00:02	55
Chestnut-headed Tanager *(Thlypopsis pyrrhocoma)*	H	2	0.22	00:05	120
Maroon-bellied Parakeet *(Pyrrhura frontalis)*	H/I	2	0.22	00:16	480
White-browed Woodpecker (*Piculus aurulentus)*	I	2	0.22	00:04	120
Azure-shouldered Tanager *(Thraupis cyanoptera)*	H	1	0.11	00:01	45
Variegated Flycatcher *(Empidonomus varius)*	I	1	0.11	00:01	60
White-throated Woodcreeper *(Xiphocolaptes albicollis)*	I	1	0.11	00:01	50
Rufous-bellied Thrush (*Turdus rufiventris)*	I	1	0.11	00:13	780
Fawn-breasted Tanager (*Pipraeidea melanonota)*	H	1	0.11	00:03	180

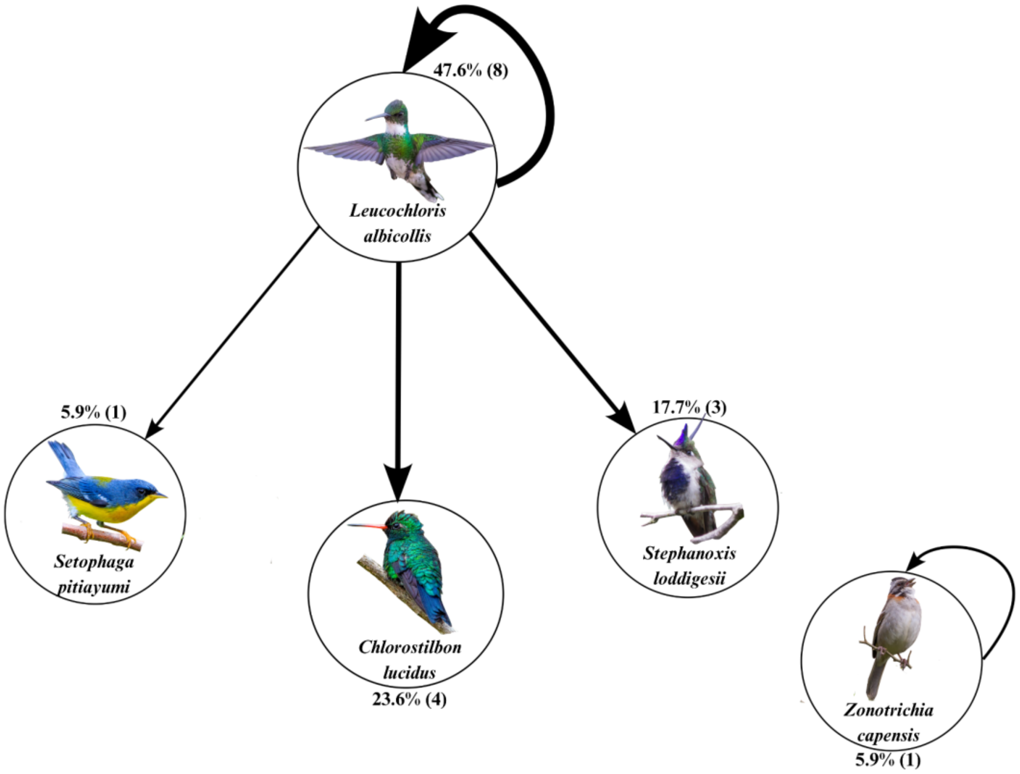

Figure 2: Diagrammatic representation of interactions among birds utilizing honeydew on *Mimosa scabrella*. Arrows indicate aggressive/agonistic interaction by the source species against the species to which the arrows point (interspecific chasing); curved arrows indicate intraspecific competition. Percentage of total chases and number of actual chases are provided. Trees were dominated by *Leucochloris albicollis*, with intraspecific

agonistic behaviors, with the two other species of hummingbirds (*Chlorostilbon lucidus* and *Stephanoxis loddigesii*) being the most frequent targets of interspecific defensive chases.

We found the most frequent species had the lowest SCBD-values (Table 3 and 4), which means their contribution to the community in space and time is the smallest. Rare species also showed low values. The SCBD-values were significantly related to number of visits, and its quadratic term (Betareg visits^1, Z = -6.704, P= >0.001; visits^2, Z = -7.460, P= >0.001; model pseudo-R^2 = 0.409). Notably, species with a moderate frequency of visits exhibited the highest SCBD-values (Figure 3), thus contributing to bird community differentiation and increasing beta diversity. Specifically, *L. albicollis* and *S. pitiayumi* had the lowest SCBD indices while also being the most frequently observed species. This suggests that these species may be specialists, exerting dominance over honeydew, using it as a primary food source, and consequently engaging in more agonistic behaviors that likely repeal other species.

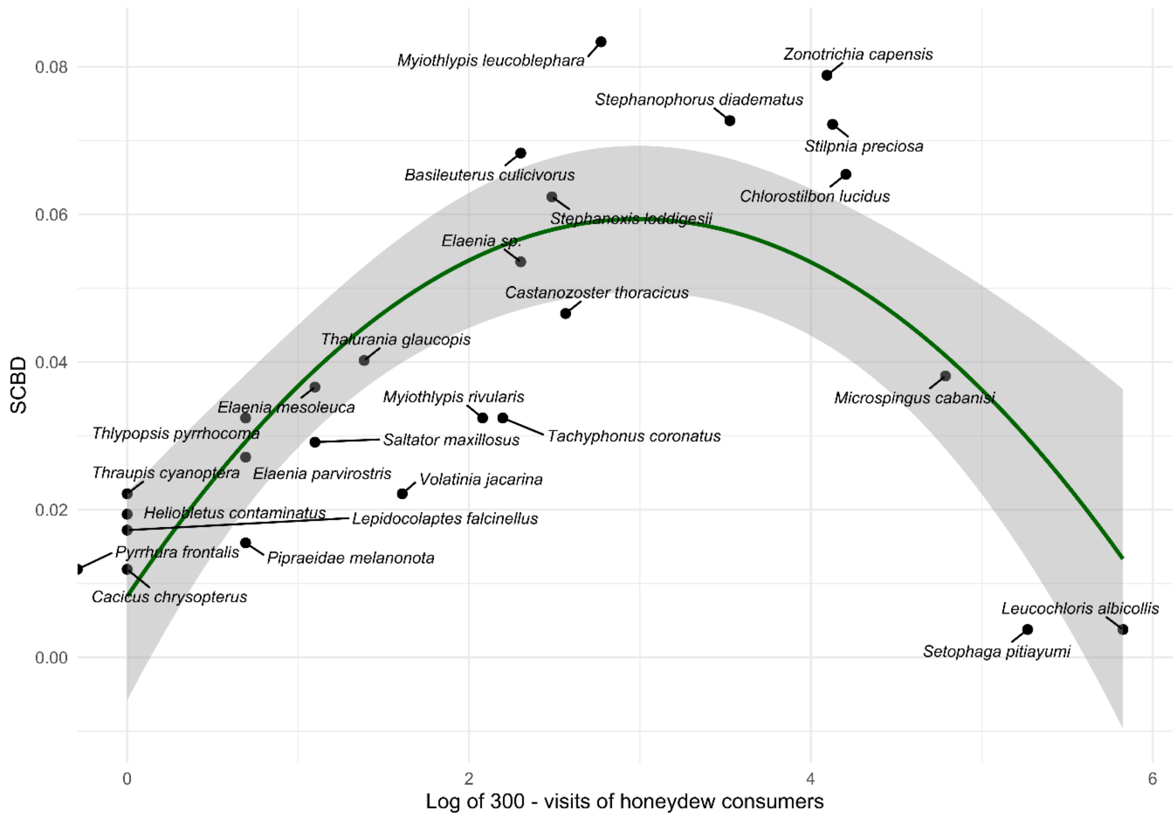

Figure 3: Scatter plot representing the relationship between the visitation frequency of honeydew-consuming species with SCBD values. Each point in the graph represents a different species. The x-axis was adjusted using the logarithm of 326 (higher number of visits registered) for a better visualization, as there was a large variation in these values (Betareg visits^1, Z = -6.704, P= >0.001; visits^2, Z = -7.460, P= >0.001; model pseudo-R^2 = 0.409).

DISCUSSION

Our results revealed frequent visits from local birds to *Mimosa scabrella* trees for direct and indirect honeydew foraging. These results indicate that honeydew excretion serves as a significant energy source for the bird community, as evidenced by the documented presence of 23 honeydew-consuming species, totaling 850 visits during the 180-hour observation period. Honeydew consumption was observed across various species from distinct families, including not only nectarivores, but also insectivores and omnivores that rely primarily on food sources other than nectar or sugary excretions. Remarkably, 15 out of the 23 registered honeydew consumers were previously unknown to feed on honeydew. For example, *Setophaga pitiayumi*, recognized as an insectivore, had the second highest visitation frequency (167), underscoring the importance of the resource even for non-nectarivorous species.

Species often select food types and adapt their foraging behavior to maximize fitness while minimizing energy expenditure – the Optimal Foraging Theory (EMNLEN, 1966; MACARTHUR; PIANKA, 1966). Honeydew is a sugary excretion of phloem-feeding insects and a valuable carbohydrate-rich food source (GAMPER, 2009). Compared to other food types, honeydew is more easily metabolized, and its foraging costs are lower than other resources such as invertebrates, especially those that are difficult to locate and capture (MURPHY; KELLY, 2003). Given that honeydew is a nutrient-rich resource that is easily metabolized and has low foraging costs, it seems an advantageous option and its use may fit the OFT. The high number of species supports this and the visits recorded, especially among species whose primary food source is not nectar or other sugary excretions. In particular, a group of about five *Pyrrhura frontalis* individuals was observed foraging on honeydew during the winter. While Psittacidae species are typically considered frugivorous based on their behavior and morphology (SICK, 1997), when fruits and flowers are scarce, they turn to alternative food sources that are rich in carbohydrates and easily metabolized.

Feeding on insects that concentrate around their own food sources can be a similarly optimal strategy. Insects, including ants and bees, also use honeydew as a food source (MOLLER, 2012), and birds consuming insects may indirectly benefit from honeydew availability. Scale insects commonly infest the trunks and branches of trees, with honeydew being a conspicuous presence in these areas. Birds observed foraging on foliage with a more aggressive and abrupt foraging behavior were likely targeting arthropods, indicating a direct relationship with insects rather than an indirect association with honeydew. While it cannot be definitively concluded that insect consumers foraging in lower zones are specifically targeting insects that feed on honeydew, it is worth noting that areas infested with scale insects consistently showed signs of insect infestation. Therefore, bird species observed foraging on insects in these infested areas might also be consuming insects that rely on honeydew as a food source.

While honeydew foraging is important to every individual or single species, we also observed multiple species foraging honeydew on the same tree. This suggests that there may be a hierarchical arrangement of species or resource partitioning in either space or time to mitigate competition, thereby enabling numerous species to exploit the resource concurrently (VILA; RODRIGUEZ, 1992). This observation provides evidence of resource partitioning among coexisting species, an anticipated outcome of past or ongoing competition (PAINE, 1981), allowing species coexistence and promoting biodiversity (TILMAN, 1982). In the realm of foraging behavior, species often resort to forming groups as a common strategy to mitigate the risk of predation (COUZIN, 2002). Extensive research has revealed that as group size increases, there is a noticeable reduction in individual time devoted to anti-predator vigilance, coupled with a concurrent enhancement in the average feeding rate (CARACO et al. 1980; ELGAR, 1989). Morphological variations have also been associated with distinct resource use strategies among coexisting species, leading to adaptations in feeding behaviors (SCHOENER, 1974). Previous studies have reported dominance and spatial segregation among hummingbirds (ANTUNES, 2003; LARA et al. 2011). Larger individuals appear to assert dominance in areas with abundant resources and high tree areas (LARA at el. 2011; CAMFIELD, 2006), whereas smaller species tend to forage on lower tree areas to minimize aggressive interactions (LARA et al. 2011). Here we found evidence of a dominance hierarchy involving *Leucochloris albicollis*, which is the largest hummingbird species among those observed. This species had the highest visitation frequency (326 visits, accounting for 34.25% of all visits) and was primarily observed foraging at canopy supporting branches (tallest tree zones). Notably, agonistic behavior was common between this species and all other hummingbird species, with *L. albicollis* being excluded only by individuals of the same species. Despite the evidence of spatial segregation, this species displayed exclusionary behavior towards others, reinforcing its high degree of dominance.

Our findings suggest a correlation between species visitation frequency and their contributions to community compositional differences in space or time, thus affecting beta diversity. While the most frequently recorded species exhibited a higher number of visits and lower contribution to beta diversity, species with moderate visitation frequencies displayed higher contributions. Notably, *Leucochloris albicollis* and *Setophaga pitiayumi* were widespread species with low SCBD values. This suggests their specialization in exploiting honeydew as a food source, potentially leading to decreased alpha and beta diversity in the presence of such species. On the other hand, more generalist species seemed to have moderate visitation frequencies and higher contribution to beta diversity, allowing for coexistence of multiple species within the same niche dimension, thus promoting increased alpha and beta diversity. Nonetheless, the quantity of honeydew appears to play a role in explaining bird community alpha and beta diversity among honeydew consumers, which will be further explored in an upcoming study.

We draw attention to *Setophaga pityaumi*, which exhibited the second-highest number of visits while foraging on honeydew (n= 167 visits). Species from the Parulidae family are traditionally considered insectivores (SICK, 1997), making it intriguing to observe their frequent visits and underlining the significance of the honeydew resource beyond nectarivorous and frugivorous species. While Sick (1988) had previously documented *S. pitiayumi* foraging on honeydew in *M. scabrella* trees, our study provides further confirmation of its utilization and niche adaptation for this species.

CONCLUSIONS

With this study, we bring confirmation and clarification of many patterns and processes related to honeydew consumption, as well as new registers of species involved in this underexplored ecological relationship. Surprisingly, we discovered evidence of more species utilizing honeydew than initially predicted, including probable instances of indirect consumption through insect feeding. Our findings highlight the importance of this resource because of its effects over the structure of highly diverse bird communities. Moreover, our study has deepened our understanding of the interactions among consuming species, emphasizing the resource's significance, particularly during periods of resource scarcity. Additionally, the observed niche partitioning, facilitated by differentiated use of honeydew and insects, along with spatial variations in resource utilization, points to a mechanism promoting coexistence among species in the community.

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3. CAPÍTULO 2: INFLUENCE OF TEMPERATURE AND HONEYDEW AVAILABILITY ON ALPHA AND BETA DIVERSITY OF BIRD COMMUNITIES IN SUBTROPICAL BRAZIL

Joana Nascimento de Mattos[1,2]; Eduardo L. H. Giehl[1,2]; Guilherme Renzo Rocha Brito[1]

[1]Department of Ecology and Zoology/Federal University of Santa Catarina, Brazil

[2]Graduate Program in Ecology/Federal University of Santa Catarina, Brazil

Abstract: It has been observed that an increase in resource availability is associated with a corresponding rise in species richness. However, when multiple species within a community share the same resource niche, variations in resource quantity and interactions become paramount in shaping both species richness and composition. Honeydew foraging by birds has been documented as a significant interaction with scale insects. The consumption of honeydew may serve as a primary carbohydrate source for a diverse range of wildlife, however, understanding of this interaction and the factors that could influence its consumption remains limited. This study aims to investigate the impact of temperature and honeydew availability on both alpha and beta diversity of bird communities in subtropical Brazil. We located 15 focal host-trees and placed circular plots (radius = 10 m) around them. In each plot, we counted host-tree density and honeydew presence in four height zones of each one as a proxy for honeydew availability. We then observed, identified and counted bird visitors and registered whether birds fed on honeydew or insects for 12 h/plot (=180 h). We recorded 947 visits by 39 bird species – 23 feeding on honeydew and 16 on insects. We found that honeydew availability has an influence in bird richness, but areas rich in resources can attract dominant species, and the interactions and dominance tend to be the most important influence in bird richness and honeydew availability. We also found that temperature and observation shift can influence the consumption by honeydew and insect consumers, affecting scale insect activity and other insects interacting with honeydew, and the observation shift can also help to explain the environment changes affecting temperature and consumption.

Keywords: honeydew foraging, resource availability, habitat resources.

INTRODUCTION

In recent decades, research on ecological niches has significantly expanded, with ecologists focusing on exploring the intricate relationship between biodiversity and resource utilization across various communities (NORTHFIELD et al. 2010). These studies have encompassed a diverse array of community types and trophic levels, with resource availability emerging as a pivotal factor influencing species richness within local communities. Specifically, it has been observed that an increase in resource availability is associated with a corresponding rise in species richness (CARRARA; VASQUEZ, 2010). In resource-rich areas, a greater number of species can coexist, benefiting from the ample resource supply (CARRARA; VASQUEZ, 2010). However, when multiple species within a community share the same resource niche, variations in resource quantity and interactions become paramount in shaping both species richness and composition among consumers, subsequently impacting the patterns of diversity in the local community (AKATOV; PEREVOZOV, 2011).

Honeydew foraging by birds has been documented as a significant interaction with scale insects (Hemiptera, Coccoidea) (TEIXEIRA et al. 2013; LARA et al. 2011; GAMPER; KOPTUR, 2010). Scale insects have high phloem nutrient demands, leading to the excretion of large quantities of honeydew, a sugary waste rich in carbohydrates and amino acids. This excretion occurs through small droplets at the end of a long anal filament (MARTINS-MANSANI, 2021). In certain ecosystems, honeydew utilization has been observed among ants, wasps, and bees (MOLLER; TILLEY, 1989; DIDHAM, 1993). The consumption of honeydew may serve as a primary carbohydrate source for a diverse range of wildlife, enhancing trophic connections (GRANT; BEGGS, 1989). Nevertheless, our understanding of this interaction and the factors that could influence its consumption remains limited.

Indeed, while the relationship between species and resource availability often leads to increased richness and diversity, other interactions such as intra or interspecific competition can yield different outcomes, potentially resulting in fewer species . Notably, communities with a high dominance level tend to exhibit lower local species richness compared to those with low dominance (AKATOV; PEREVOZOV, 2011). Given that honeydew serves as a primary carbohydrate source for numerous species, it may be subject to active defense, as evidenced in previous studies (LARA et al. 2011, see chapter 1). Understanding the intricate relationship between honeydew quantity, species richness, and other ecological characteristics is essential in comprehending this interaction.

However, it is important to recognize that honeydew availability is not the sole determinant influencing honeydew consumption. The "Convergence Hypothesis" (GREENBERG et al. 1993), elucidates the unique and uneven geographical distribution of avian honeydew foraging worldwide. If confirmed, this hypothesis could suggest that common regional climatic conditions have led to the limited occurrence of honeydew foraging by birds. Habitats such as temperate forests and mild climates contribute to the reduced presence of ants, which are known honeydew consumers, thereby promoting greater use of honeydew by birds. Additionally, temperature can directly affect scale insect activity, consequently influencing honeydew production and concentration (GAZE; CLOUD, 1993). Examining these complex interactions can provide valuable insights into the factors shaping honeydew consumption patterns among avian communities.

In response to the perceived significance of honeydew for bird communities and the limited research on its potential effects, we undertook this study to investigate the impact of temperature and honeydew availability on both alpha and beta diversity of bird communities in subtropical Brazil. Our primary hypothesis is that a) alpha diversity (species richness) would increase with rising honeydew availability. However, we also proposed two alternative hypotheses to explore different mechanisms: b) areas with high resource availability might exhibit lower consumer richness in the presence of more specialist species, owing to behavioral defenses, and c) areas with low resource availability, which do not attract specialist species, might experience higher consumer richness, leading to fewer competitive interactions. Furthermore, we also look for climatic variables that potentially influence honeydew consumption by birds and discuss the relevance of the "Convergence hypothesis" within the context of our study. Through these investigations, we aim to shed light on the intricate relationships between honeydew availability, species richness, and ecological interactions within avian communities.

MATERIAL AND METHODS

Study site

The study was conducted in the highlands of southern Brazil, specifically in the state of Santa Catarina. The research areas included both the São Joaquim National Park (28.19˚S, 49.53˚W) and privately owned regions within the Urubici area. This region comprises one of the highest elevated zones in southern Brazil, characterized by diverse ecoregions such as high-altitude grasslands and mixed rainforests known as Araucaria forest. The climate in this area varies significantly throughout the year. The coldest month, July, experiences an average minimum temperature of 0.2°C, while the hottest month, January, reaches an average maximum temperature of 25°C. The temperature extremes can be quite remarkable, with the lowest recorded temperature being −9.0°C and the highest reaching 31.4°C. Winter in the region is marked by frequent frosts, and there are occasional occurrences of snow (INMEP, 2023).

Study organisms

Mimosa scabrella

Mimosa scabrella Benth (Fabaceae) or "bracatinga" is a native tree species found in the coldest climates of Brazil (CARPANEZZI et al. 1988) and is exclusive to mixed rainforests (Araucaria forest). *M. scabrella* is a pioneer species with a short life cycle and is primarily adapted to open, sunlit conditions (MAZUCHOWSKI, 2012), thus being common on secondary vegetation such as areas affected by fires, nearby roadsides, and at forest edges. Besides, these trees play a significant role in carbon storage, making them environmentally important (MAZUCHOWSKI, 2012). Because of such features, it is often recommended for the restoration of degraded habitats. *M. scabrella* trees are also the main host for some scale insects that produce honeydew (CAMPOS et al. 2003).

Scale insects and honeydew

Honeydew is a sugary solution produced and excreted by individuals of six families of hemipterans known as scale insects (Coccoidea). Scales feed on the phloem sap of host plants, which is rich in nitrogen and essential for protein production. They secrete honeydew in the form of droplets on plant stems (LATTA et al. 2001). In the case of the bracatinga tree (*M. scabrella*), the main scale insect species involved in the interaction is *Stigmacoccus paranaenses* (HODGSON, 2007). This species has been documented in southern Brazil, including the States of Paraná, Santa Catarina, and Rio Grande do Sul, and has been found on several plant species such as *Inga* spp., *Schizolobium excelsum* (Fabaceae), and *Mimosa scabrella* (Mimosaceae; WOLFF et al. 2015). While honeydew can be a significant carbohydrate source for a wide range of species (GRANT; BEGGS, 1989), including birds and other insects, giving rise to a myriad of direct and indirect ecological relationships.

Avian use of honeydew

Honeydew foraging has been documented as an important interaction between birds and scale insects (TEIXEIRA; AZEVEDO, 2013). A few species have already been recorded using honeydew from bracatinga trees in the northern region of Santa Catarina State (SICK, 1988), including *Setophaga pitiayumi* (Vieillot, 1817), *Stilpnia peruviana* (Desmarest, 1806), *Stephanophorus diadematus* (Temminck, 1823), *Tachyphonus coronatus* (Vieillot, 1822), and *Zonotrichia capensis* (Müller, 1776). However, honeydew is a highly energetic resource that may be both a key resource and limited at certain times of the year. Thus, either honeydew-producing trees or forest patches can be actively defended, similar to the defensive behavior observed in birds protecting nectar-producing flowers (FEINSINGER, 1976, MACNALLY; TIMEWELL, 2005). It is worth stressing that the factors influencing honeydew consumption by birds are still poorly understood and warrant further study.

Sampling method and data collection

Plot selection

To compare foraging behavior of birds in forest patches with varying honeydew availability, we established 15 circular plots under distinct *M. scabrella* density. The plots were, at first, visually fit into four density levels: isolated, low, medium, and high density. Each plot was centered at a focal adult *M. scabrella* tree. Next, to refine our density estimate, we counted all *M. scabrella* adults found at a maximum radius of 10 meters. To provide a more comprehensive assessment of honeydew availability within each plot, we implemented a visual division of the bracatinga tree in four height zones. Starting with the central area or trunk, we divided it into three zones: "zone 1" representing the lowest part of the trunk (0-33.3% of the trunk), "zone 2" corresponding to the middle part (33.4-66.7% of the trunk), and "zone 3" encompassing the upper part (66.8-100% of the trunk). In addition, we designated "zone 4" including the upper branches sustaining the canopy of the tree. Within each of these zones, we recorded the presence or absence of honeydew. Moreover, we collected information regarding the height of the focal individuals and the circumference at breast height (CBH) for each tree in the plot. These measurements helped us assess the vertical distribution of honeydew and its association with tree characteristics such as height and trunk circumference.

Bird sampling

To quantify the use of honeydew by birds, we conducted focal observations on the selected focal trees throughout the year of 2022. The observation protocol followed the guidelines proposed by Teixeira and Azevedo (2013). Observations were conducted during the first and last three hours of daylight, aligning with the specific sunrise and sunset times for each day of fieldwork. Data collection was carried out across different seasons of the year and under varying temperature conditions. During each observation session, we recorded the following information for each bird visit to the honeydew source (i.e., when a bird probed an anal tube or consumed an insect): species identity, number of individuals, time of arrival and departure, and whether the individual fed on honeydew or an insect. It is important to note that the birds were not individually banded, so multiple visits may have been made by the same individual bird over the course of the observation period.

To examine spatial variations in honeydew consumption, we utilized the previously established visual division of the tree into four zones. During each observation, we recorded the specific zone where each bird species was feeding. These observations were conducted from a distance of 10 meters away from the focal tree, with the aid of utilizing binoculars (Solognac 10x42mm) and photographic records documentation (Canon EOS T7 75-300mm). Furthermore, we recorded both inter- and intraspecific interactions among the observed bird species. By documenting agonistic interactions, we were able to describe the conditions under which the honeydew resource was defended by certain individuals or species. These interactions shed light on the dynamics of resource utilization and potential competition among the birds.

Factors that may influence honeydew consumption by birds

In addition to honeydew amount, we collected temperature data (ºC) from the "Bom Jardim da Serra – Morro da Igreja" Surface Observation Weather Station, located at latitude -23.852022º and longitude -48.164817º, with an altitude of 1676 meters (available at and retrieved from: https://mapas.inmet.gov.br/). We retrieved the mean minimum temperature during the three-hour observation period on the observation date (T_{min}), as well as the mean minimum temperature for the preceding week ($T_{min\_7\_days}$). We used temperature to assess whether it influenced honeydew consumption, although we were unable to clarify if visits were affected directly because of low temperature reducing bird activity or indirectly, by lowering honeydew production.

Data analysis

To check for potentially collinear variables, we first carried out bivariate graphical exploratory analyses coupled using Spearman correlations. First, we checked for an association between *M. scabrella* density and honeydew availability (by summing honeydew presence by height zones). Because our analysis revealed a strong correlation between tree density and honeydew availability, we decided to use only honeydew availability in the following analyses, given its direct relevance to our research objectives. Second, we assessed the correlation between temperature on the observation date (T_{min}) and the temperature of the preceding week

($T_{min\_7\_days}$). Because both information showed little/no correlation, we kept both for further analyzes.

To investigate the relationship between bird species richness and potential explanatory variables, we fit generalized linear mixed models (GLMMs). Such models were constructed separately for bird species either feeding directly on honeydew or those feeding on insects, and total bird richness. We considered honeydew availability, shift of the day (morning vs. afternoon), temperature (T_{min} and $T_{min\_7\_days}$), and Pielou's evenness index (J) as potential explanatory variables (fixed effects). We also added quadratic versions of the mean temperatures to account for potential nonlinear relationships following preliminary graphical analyses. The 15 plots were treated as random effects to accommodate potential variability linked to specific plot characteristics and repeated plot sampling. In total, data were collected four times in each plot, resulting in 60 fieldwork instances (4 samplings/15 plots = 60), with each sampling day presenting distinct environmental variables. Because species richness is a discrete numerical variable, we chose between appropriate distributions (e.g. Poisson, negative binomial). After evaluating the assumptions of normality and homoscedasticity of the residuals using the DHARMa package (HARTIG, 2022), we determined that the negative binomial distribution and a logarithmic link function better fit the species richness data. Afterwards, we simplified the initial model based on the statistical significance of the variables, retaining only the most influential predictors. The GLMMs were fitted using the glmmTMB package (BROOKS et al., 2017).

To investigate the potential factors influencing differences in bird species composition and beta diversity, we used the following approach. First, we calculated Sorensen dissimilarity based on species presence-absence data to understand overall compositional differences and thus beta diversity. Dissimilarities contrasted both plots in space and along time. We further decomposed beta diversity into richness differences and replacement components (LEGENDRE; DE CÁCERES, 2013). Such a decomposition results in three dissimilarity matrices: total dissimilarity plus both components. The two components were calculated using the Podani family of indices, which decomposes the Sorensen dissimilarity (as implemented in the adespatial package; LEGENDRE, 2014). Next, we run two distance-based redundancy analysis (db-RDA), with each dissimilarity matrix in turn as a response to a set of potential explanatory variables (the same used to model species richness). To determine the subset of variables that best explained each of the beta diversity components, we conducted a permutational multivariate analysis of variance (Permanova) followed by model reduction using both significance and R^2. To account for repeated measures and the overall sampling design, we restricted permutations to be allowed only within plots and for entire plots at a time, with the goal of reducing false-positives. The db-RDAs and Permanovas were computed using the vegan package (OKSANEN et al., 2022). By applying these analytical techniques, we aimed to identify the key factors driving the observed differences in bird species composition and both components of beta diversity.

All the mentioned analyses and packages were used in the R program (R CORE TEAM 2022).

RESULTS

We recorded 39 bird species visiting *Mimosa scabrella* trees, totaling a remarkable number of 955 foraging events. Among these species, 23 fed exclusively on honeydew and 16 on insects only. We observed that bird richness had an inverse relationship with honeydew volume: it was higher in plots under low host-tree density and honeydew availability (low density: 73 spp; medium density: 51 spp; high density: 43 spp; Figure 1). Furthermore, we observed a slight variation in bird richness and the number of visits depending on the shift of the day, both being higher during the morning than at the afternoon (Figure 2). Additionally, we found that bird richness tended to be higher on colder days, at least in the range of temperatures assessed during samplings (Figure 3).

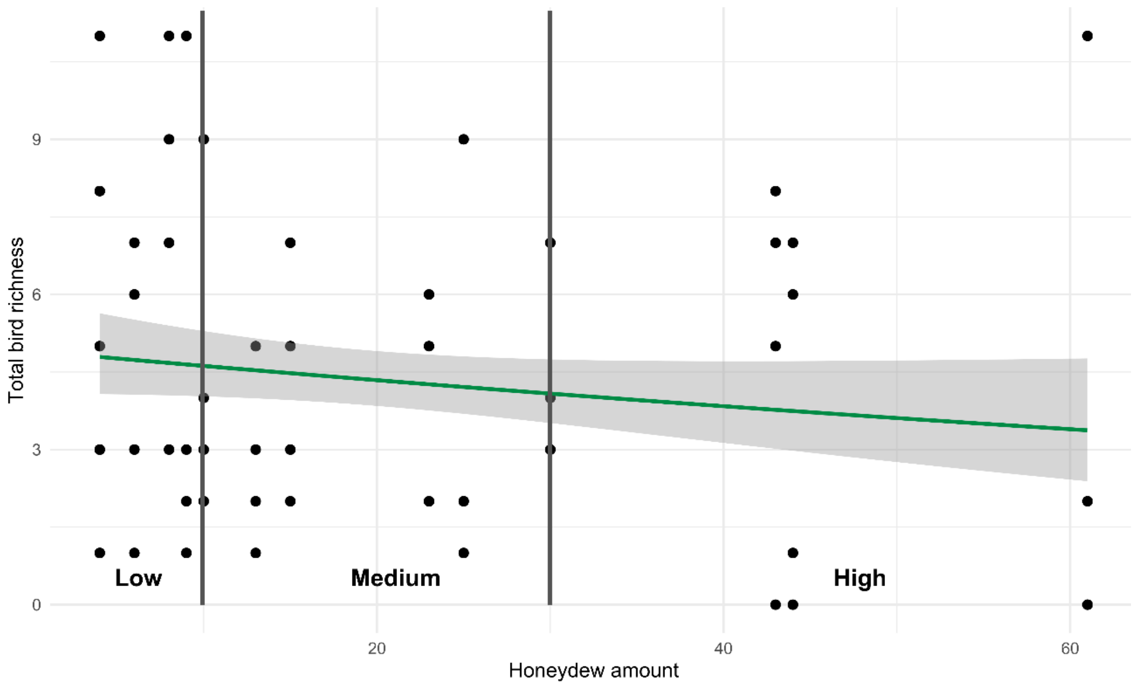

Figure 1: Scatterplot of the relationship between honeydew amount (quantified by the presence of absence of honeydew in trunk zone in each tree of the plots) and the total bird richness (honeydew and insects consumers),

in *Mimosa scabrella* trees, in southern Brazil. We also highlighted the different host-tree densities that were divided by low, medium and high density (GLMM, Z= -2. 602, P= 0.00927).

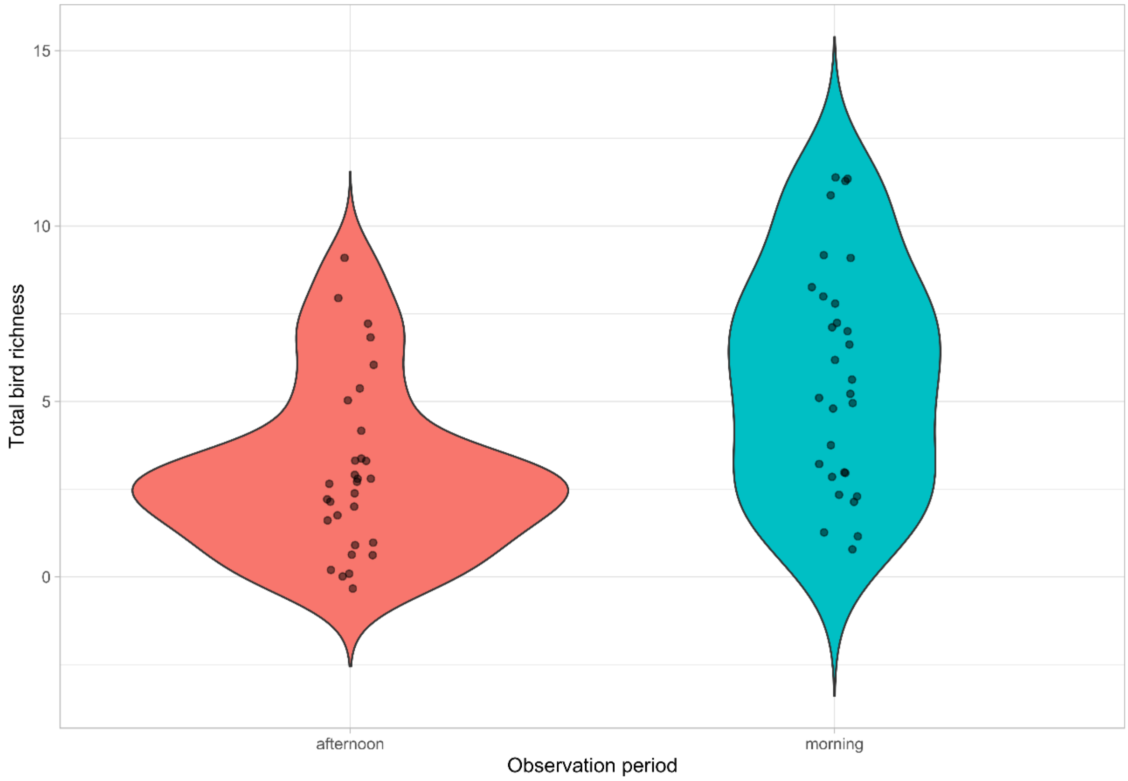

Figure 2: Violin plot representing the differences in total bird richness of honeydew and insects consumers in *Mimosa scabrella* trees, during the morning (blue) and afternoon (pink) period. It is possible to see there is a slight difference, with richness being higher during the morning period, compared with the afternoon (GLMM, Z= 2.874, P= 0.00406). The points represent each observation, showing that during the afternoon, most observations had a low richness, being concentrated in the larger width part of the plot, while observations during the morning showed a normal distribution.

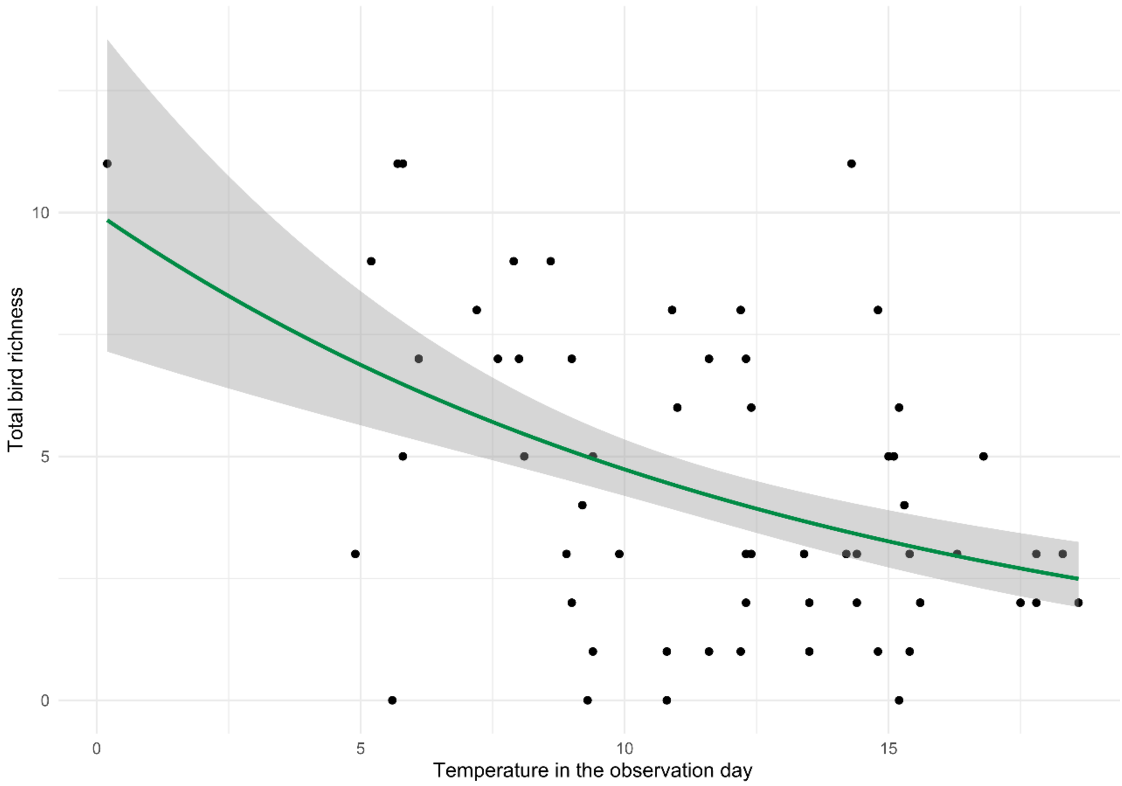

Figure 3: Scatterplot representing the relationship between the mean temperature of the observation day and the total bird richness (honeydew as insect consumers) in *Mimosa scabrella* trees, in southern Brazil (GLMM, Z= -2.440, P= 0. 1470).

Alpha diversity

Contrary to our expectation, we found bird species richness of honeydew consumers per plot to increase with decreasing honeydew availability (GLMM, Z = -2.375, P = 0.0175; Figure 4). Bird richness further increased at colder days (Z = -2.027, P = 0.0427) and during morning shifts (Z = -2.146, P = 0.0319). Bird richness of insect consumers also exhibited the highest values in plots characterized by lower host-tree density and honeydew availability (low density: 60 spp; medium density: 42 spp; high density: 35 spp), however this variable did not show a significant influence. The richness of insect consumers was significantly influenced by the temperature on the observation day (GLMM, Z = -2.558, P = 0.0106) and the afternoon shift (GLMM, Z = -2.782, P = 0.0054; Figure 5).

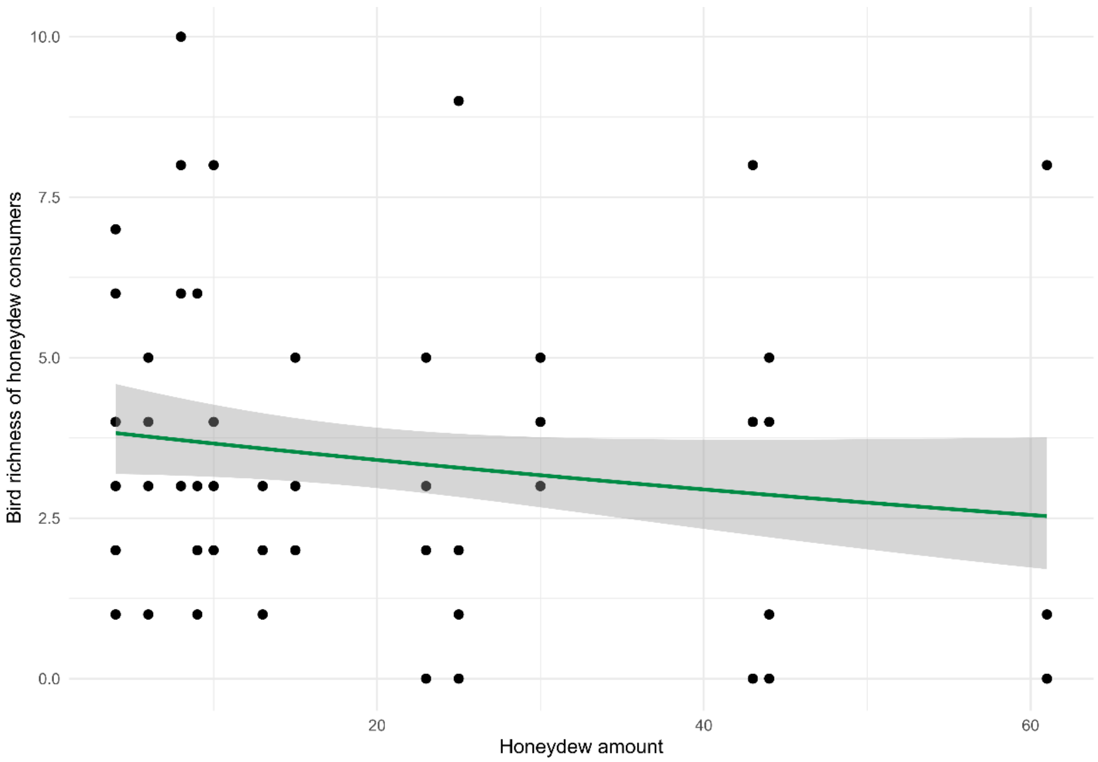

Figure 4: Scatter plot representing the relationship between honeydew amount and bird richness of honeydew consumers in *Mimosa scabrella* trees, in southern Brazil (GLMM, Z= -2.375, P= 0.0175).

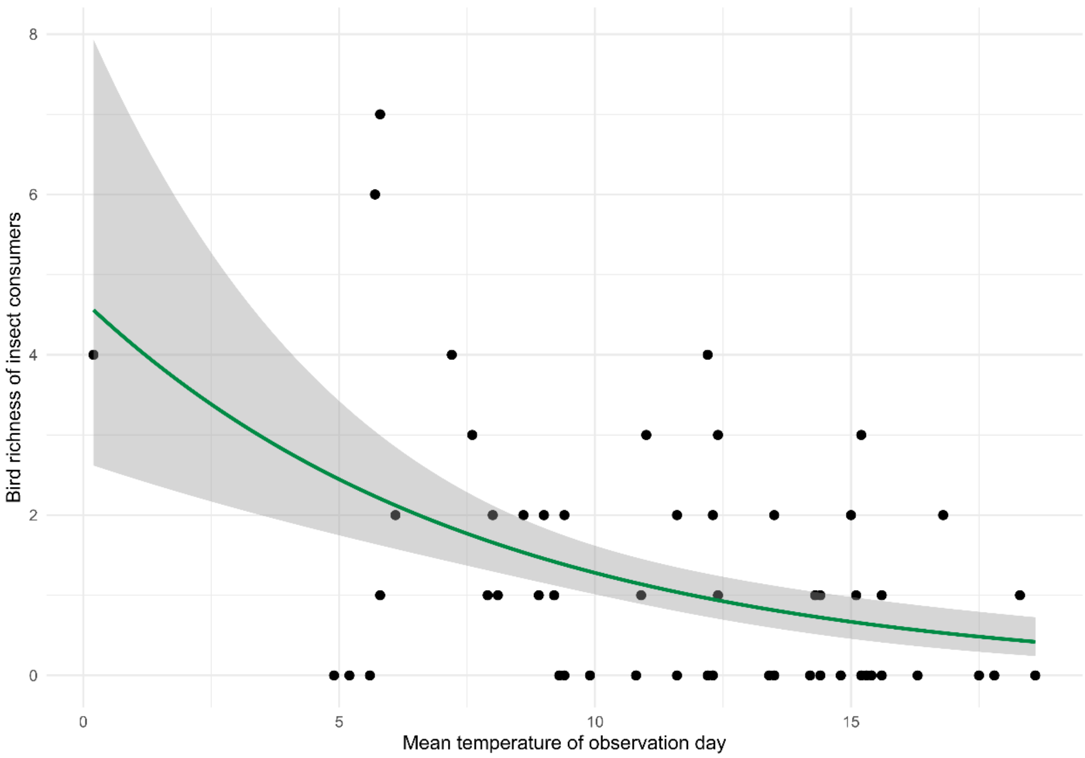

Figure 5: Scatter plot representing the relationship between the mean temperature of observation day and bird richness of insect consumers in *Mimosa scabrella* trees, in southern Brazil (GLMM, Z= -2.558, P= 0.0106).

Beta diversity and its components

When considering birds feeding exclusively on honeydew, we found distinct relationships between beta diversity components and drivers. First, the species replacement component of beta diversity was correlated only with honeydew availability ($R^2 = 0.148$, $P < 0.001$; Figure 6), indicating that bird species were sorted differently depending on the amount of the resource. Second, the species richness difference component of beta diversity was correlated with the shift of the day ($R^2 = 0.062$, $P = 0.031$) and the temperature on the observation day ($R^2 = 0.125$, $P = 0.002$; Figure 6), suggesting temporal factors played a role in shaping compositional differences by means of species "gains" or "losses".

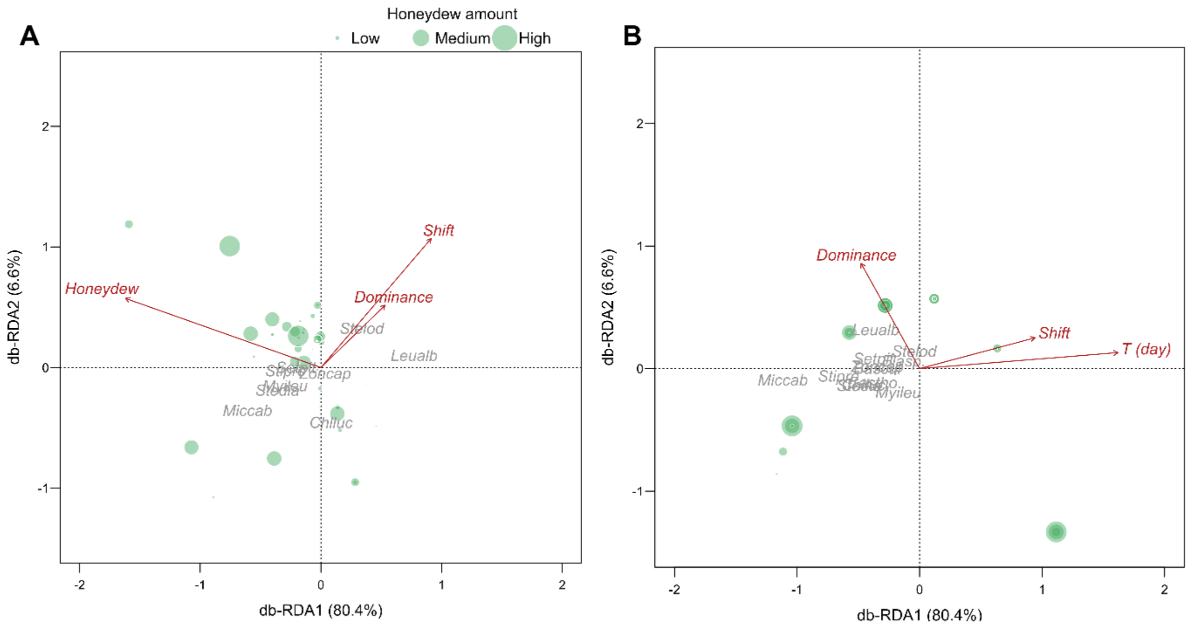

Figure 6: Distance-based redundancy analysis (db-RDA) representing the influence of the variables on the different beta diversity components of honeydew consumers in *Mimosa scabrella* trees, in southern Brazil. (A) Represents species replacement. (B) Represents richness difference. The replacement component was only correlated with honeydew availability (PERMANOVA, $R^2=0.148$, $P<0.001$), and richness difference with the shift of the day (PERMANOVA, $R^2=0.062$, $P=0.031$) and temperature of the observation day (PERMANOVA, $R^2=0.125$, $P=0.002$). The other variables that did not show significance were only added to the plots for a better visualization.

Beta diversity components of insect consumers were influenced by different variables. The species replacement component showed a correlation with the shift of the day ($R^2 = 0.054$, $P < 0.001$; Figure 7), suggesting a temporal partitioning of consumption of insects attracted to honeydew. Conversely, the beta diversity component related to richness differences correlated with the temperature on the observation day ($R^2 = 0.143$, $P = 0.009$) and species dominance based on the number of visits of the more frequent species ($R^2 = 0.065$, $P = 0.040$; Figure 7). This indicates that temperature and the presence of dominant species can act on the size of the list of species able to be the pool of species that use honeydew directly or indirectly.

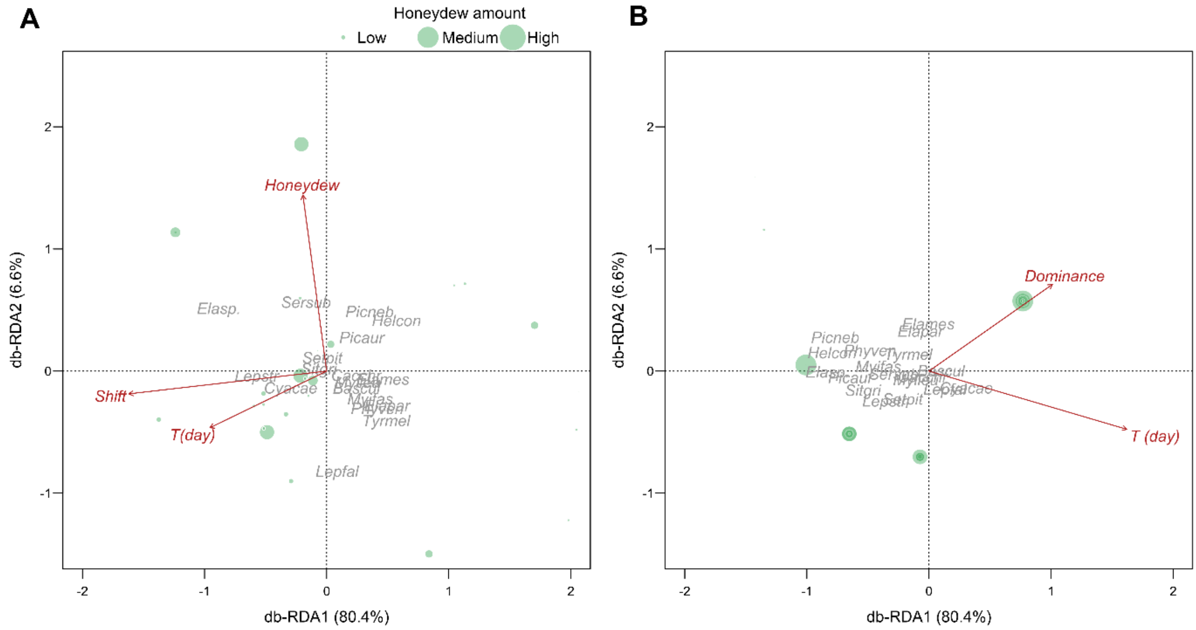

Figure 7: Distance-based redundancy analysis (db-RDA) representing the influence of the variables on the different beta diversity components of insect consumers in *Mimosa scabrella* trees, in southern Brazil. (A) Represents species replacement. (B) Represents richness difference. The replacement component was only correlated with the shift of the day (PERMANOVA, R^2=0.054, P<0.001), and richness difference with the temperature of the observation day (PERMANOVA, R^2=0.143, P=0.009), and species dominance (PERMANOVA, R^2=0.065, P=0.040). The other variables that did not show significance were only added to the plots for a better visualization.

DISCUSSION

Our main hypothesis that increasing resource availability would result in higher species richness of honeydew-consuming birds was contradicted by our findings. Surprisingly, bird richness was found to be highest in areas with low honeydew availability, peaking in sites where only one or two host-trees were present, and to be lowest under high-density sites with more than 15 host-trees. These results suggest changes in resource quantity may selectively influence the occurrence of species in each location, but not in the way we expected.

Effects of dominance on species richness and honeydew availability

Although more resources could in theory allow more species to coexist, the alternative in which sites rich in resources can attract dominant species seems to prevail here. The relationship between dominance and species richness in ecological communities has been extensively studied within the context of niche theory (AKATOV; PEREVOZOV, 2011). Communities with high dominance generally exhibit lower local species richness compared to those with low dominance (AKATOV; PEREVOZOV, 2011). Although most such studies define dominance as a result of species with the greatest relative abundances, here we suggest that a higher visit frequency can result in resource dominance as well. Consequently, it is reasonable to assume that as the visit frequency of a dominant species increases within a community, fewer resources remain available for competing species. Therefore, it is likely that resource quantity plays a role in determining the occurrence of dominant species in specific areas (AKATOV; PEREVOZOV, 2011).

Our study revealed a clear dominance hierarchy among hummingbirds, with the White-throated Hummingbird (*Leucochloris albicollis*) emerging as the most dominant species. This species accounted for 326 out of the 955 foraging visits recorded in the study, representing 34.25% of all visits (see, Chapter 1). This hummingbird species chased and excluded other species, especially of other hummingbirds, and also showed agonistic interaction and exclusion among conspecifics (see, Chapter 1). Despite being a widespread species across sites, visits by *L. albicollis* peaked at sites with high availability of honeydew, where species richness was lower. We suggest that at such sites the higher resource abundance attracts specialist species and, as the energy gain is more rewarding, it becomes worthwhile to invest energy to defend the resources from competitors, unlike in low-density sites. This finding may thus help to explain why species richness increased as honeydew availability decreased, because it is associated with reduced attractiveness to dominant specialist species.

Revising the Avian Convergence Hypothesis

Birds are not the only group known to consume honeydew in significant quantities. Honeybees, bumblebees, wasps, and ants (GAZE; CLOUT, 1983; MOLLER et al., 1996; BEGGS, 2013) also consume the resource. By acting as competitors, these insects may then affect honeydew consumption by birds, an issue that has in part been addressed by the Avian Convergence Hypothesis. The original formulation of the Avian Convergence Hypothesis highlighted the importance of resource heterogeneity: honeydew feeding by birds would be prominent in temperate evergreen forests characterized by long, relatively cool growing seasons (GREENBERG et al. 1993). Such temperate conditions likely reduce ant activity but maintain plant photosynthetic activity, thus supporting honeydew production throughout much of the year, therefore keeping resources undisputed to birds. Ants have a well-known mutualistic relationship with honeydew-producing insects, providing protection against predators and parasites in exchange for access to honeydew (SABATA; GIBB, 2016). Following such expectation, here we observed few ants feeding on honeydew, likely because we studied one of the coldest regions of Brazil, which might lead to low ant abundances, to low ant activity or, at least, low honeydew consumption (KLUNK, 2018).

Wasps, in turn, are recognized for both high honeydew feeding frequency and dominance where honeydew is present, as demonstrated in numerous studies (BEGGS, 2013; MOLLER; TILLEY, 1989). In New Zealand's beech forests, birds feeding on honeydew were found to compete primarily with *Vespula* wasps, leading to a decline in the available honeydew and going below levels necessary for sustaining bird populations (GARDNER; BEGGS, Gardner and Beggs, 2012). *Vespula* wasps have feeding behaviors that allow them to consume honeydew at a faster rate compared to most generalist birds (BEGGS, 2013). In our study, we observed a noticeable pattern whereby areas with high bird richness exhibited extremely low presence of wasps and bees, whereas areas with low bird richness showed a high abundance of these insects. Many bird species foraging on honeydew in our study are non-nectarivores and lack specialized behaviors to forage on honeydew, except for hummingbirds that can hover while foraging. Consequently, at sites with a high density of bees and wasps, birds that require landing on tree trunks and branches for foraging may be unable to do so because of either limited space, the presence of competing insects, or both. This situation might also help to explain the frequent occurrence of hummingbirds in all sampling sites and times, but further data and analyses are necessary to test this assumption.

Other factors that may affect honeydew consumption by birds

Honeydew is a highly seasonal resource, reaching its peak during the winter and being absent during the austral summer (MARTINS-MANSANI, 2021). Weather plays a significant role in honeydew concentration and the productivity of scale insects, which are responsible for honeydew production. Lower temperatures tend to result in higher scale insect density and increased honeydew production (SABATA; GIBB, 2016). Moreover, honeydew can be depleted in the summer or as temperatures increase throughout the day, given that air humidity decreases and the heat causes honeydew droplets to evaporate (CAPELÃO, 2018). The combination of both processes lead to more honeydew available on colder days, leading to a correlation between cold days and species richness of honeydew feeding birds, which was corroborated here. Initially, we considered the morning period as a variable in our analysis, as this was when data collection was standardized and coincided with the peak activity of the birds (ARAÚJO et al; 2020). However, we now understand that during the first hour of the day, temperatures are lower, leading to higher concentrations of honeydew. As the day progresses, honeydew droplets evaporate, making the morning shift a more favorable time for honeydew foraging.

Temperature also influenced the richness of insectivorous bird species. Because insects are ectothermic organisms and are often more active at warm temperatures (ABRAM et al; 2017), insectivorous birds could have been taking advantage of shifts during colder temperatures, when insects may become lethargic and easier to catch. Although we did not register whether birds foraging in lower tree heights targeted insects that feed on honeydew, we observed that scale insect groupings were associated with visits from other insects. Therefore, insectivorous bird species in these infested areas could have been indirectly attracted and regulated by honeydew availability.

One question that arises is the potential impact of climate change on honeydew production. Research indicates that elevated temperatures, particularly exceeding 29°C, can negatively affect the physiological functions, size, and foraging behavior of sap-sucking insects (SABATA; GIBB, 2016). Considering the projected increase in global temperatures by the end of this century, there is concern that these higher temperatures could lead to a decline in honeydew availability. Such a decline in honeydew resources could have adverse effects on the trophic ecology and ecological interactions of species that depend on this resource (SABATA; GIBB, 2016). The implications of climate change for honeydew-dependent species and their associated ecological dynamics merit further investigation and consideration.

Beta diversity and species composition

Beta diversity can result from the allocation of species along environmental gradients, including resource gradients (KRAFT et al; 2011; WANG; ZHANG, 2012, RICKLES, 2004). In the context of honeydew consumers, the replacement component of beta diversity was found to correlate exclusively with honeydew availability, accounting for 14% of the variation in species composition across sites. This suggests honeydew availability can directly affect species composition, at least to some extent, with additional variation likely related to other abiotic factors and biotic filters (e.g., abiotic environment on species interactions mediated by resource availability, habitat structure, and other ecological processes; GRAHAM; WEINSTEIN, 2018).

Our study shows that dominance hierarchy and biotic interactions among birds and beyond have the potential to influence bird communities under different honeydew availability. For instance, the co-occurrence of hummingbirds alongside bees and wasps may be due to their specific foraging behaviors and morphological adaptations that are well-suited for consuming honeydew. However, it is important to recognize that species categorized as non-nectivores may also have unexplored dependencies on honeydew, and these interactions and adaptations could alter consumption dynamics. Further work is needed to elucidate the nature of these interactions and their implications for non-nectarivore species. Thus, investigating how species traits or behaviors contribute to variation in species composition under varying resource quantity remains an open venue to reach a better understanding of the dynamics of interactions and their implications for beta diversity (GRAHAM; WEINSTEIN, 2018).

The richness difference component of honeydew consumers exhibited a stronger association with temperature, accounting for 12% of the observed changes in species richness across sites. Similarly, the same variable was found to be correlated with richness differences among insect consumers, explaining 14% of the variation in species richness, reinforcing a pattern of finding more bird species on colder days for both honeydew and insect consumers. This relationship could be attributed to the influence of temperature on scale insect abundance and insect activity levels. However, it is important to further investigate the potential influence of temperature on honeydew production, especially over time.

CONCLUSIONS

In conclusion, we found that honeydew availability has an influence in bird richness, just no in the way we predicted. Although more resources could in theory allow more species to coexist, the alternative in which sites rich in resources can attract dominant species seems to prevail, and the interactions and dominance tend to be the most important influence in bird richness and honeydew availability. We also found that temperature and observation shift can influence the consumption by honeydew and insect consumers, affecting scale insect activity and other insects interacting with honeydew, and the observation shift can also help to explain the environment changes affecting temperature and consumption. More analyzes need to be developed in order to better understand the relationship between bees and wasps and bird consumers.

In short, we consider our beta diversity analyzes to be exploratory in nature. To gain a comprehensive understanding of the factors driving compositional variation among locations, it is crucial to incorporate additional measurements, including the assessment of functional traits of species, availability of other resources, and characteristics of the habitat structure. These factors and their potential dynamics over time can play a significant role in shaping the observed variation in species composition. By examining these additional mechanisms, we can obtain a more comprehensive understanding of the underlying processes driving beta diversity patterns.

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4. CONCLUSÕES GERAIS

Com este trabalho, ressaltamos a importância do melato para a comunidade de aves, e como as interações competitivas têm o poder de moldar comunidades, afetando sua riqueza e composição. No primeiro capítulo, os resultados indicam o uso de melato por 23 espécies de aves, sendo que 15 ainda não haviam sido registradas neste tipo de recurso. As evidências de interações competitivas ao defender o melato ressaltam ainda mais a sua importância, principalmente em épocas que outros recursos são mais escassos. A relação encontrada entre a frequência de visitas das espécies e suas contribuições para a diversidade beta mostram como traços biológicos podem afetar a ocupação de outras espécies. O capítulo traz novos dados para estudos na área de ornitologia que podem auxiliar no desenvolvimento de outros trabalhos.

No segundo capítulo, verificamos que a disponibilidade de melato possui uma influência na riqueza das espécies, mas que as interações competitivas aparentam ser a principal influência, trazendo essa conexão entre os dois capítulos apresentados. Por mais que, na teoria, mais recursos poderiam atrair mais espécies, a dominância pelas espécies mais especialistas parece ser a principal influência a estruturar a diversidade, sendo as espécies aparentemente mais atraídas por áreas com maior disponibilidade de recursos, aumentando as interações competitivas, e consequentemente diminuindo a riqueza. Por isso, trazemos no estudo a importância de se analisar os traços biológicos que podem afetar nas interações e nas contribuições da diversidade beta, já que algumas características podem afetar a ocorrência e abundância de outras espécies envolvidas no consumo. Explorar essas variáveis pode ajudar a identificar os traços-chave das espécies que são mais relevantes e possam influenciar mais contextualmente o estudo.

Em relação às análises de diversidade beta, consideramos de natureza mais exploratória. Para uma compreensão mais abrangente dos fatores que podem influenciar as variações na composição das espécies, é fundamental incorporar medidas adicionais. Isso inclui avaliar as características funcionais das espécies, a disponibilidade de outros recursos e as características estruturais do habitat. Além disso, em relação às outras variáveis analisadas, observamos que tanto a temperatura quanto o período de observação exercem influência sobre o consumo de melato e os insetos consumidores. Essa influência afeta não apenas a atividade das cochonilhas, mas também outros insetos que interagem com o recurso. A consideração do período de observação também contribui para a explicação das mudanças ambientais que impactam a temperatura e o consumo. No entanto, é importante ressaltar que análises mais aprofundadas também são necessárias para melhor compreensão da relação entre abelhas, vespas e os consumidores de aves.

Uma questão importante é o impacto potencial das mudanças climáticas na produção de melato e consequente influência nas comunidades dependentes e que utilizam o recurso. Pesquisas indicam que temperaturas elevadas, especialmente acima de 29°C, podem afetar negativamente as funções fisiológicas, o tamanho e o comportamento de alimentação de insetos sugadores de floema. Considerando o aumento projetado das temperaturas globais até o final deste século, preocupa-se que essas temperaturas mais altas possam resultar em uma diminuição na disponibilidade de melato. Uma diminuição nos recursos de melato poderia ter efeitos adversos na ecologia trófica e nas interações ecológicas das espécies que dependem desse recurso. Portanto, as implicações das mudanças climáticas para as espécies dependentes de melato e suas dinâmicas ecológicas associadas merecem investigações e considerações mais aprofundadas.