

UNIVERSIDAD AUTÓNOMA DE SAN LUIS POTOSÍ
FACULTADES DE CIENCIAS QUÍMICAS, INGENIERÍA, MEDICINA
Y CIENCIAS SOCIALES Y HUMANIDADES
PROGRAMA MULTIDISCIPLINARIO DE POSGRADO EN CIENCIAS AMBIENTALES
AND
TH KÖLN - UNIVERSITY OF APPLIED SCIENCES
INSTITUTE FOR TECHNOLOGY AND RESOURCES MANAGEMENT IN THE TROPICS AND SUBTROPICS

**QUANTIFICATION OF THE ECOSYSTEM FUNCTION PEST CONTROL: ASSESSING
PREDATION RATES OF ARTIFICIAL CATERPILLARS BY BIRDS IN SECONDARY FOREST
FRAGMENTS WITHIN A PERI-URBAN AREA IN SOUTHEASTERN BRAZIL**

THESIS TO OBTAIN THE DEGREE OF
MAESTRÍA EN CIENCIAS AMBIENTALES
DEGREE AWARDED BY UNIVERSIDAD AUTÓNOMA DE SAN LUIS POTOSÍ
AND
MASTER OF SCIENCE
NATURAL RESOURCES MANAGEMENT AND DEVELOPMENT
DEGREE AWARDED BY TH KÖLN – UNIVERSITY OF APPLIED SCIENCES

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Abstract

Urbanization processes are one of the main factors for habitat loss and fragmentation, driving global biodiversity loss and species extinction. The neotropical Atlantic forest in Brazil is considered a global key biodiversity hotspot and used to be one of the most extensive forests of the Americas. Due to substantial deforestation over centuries, its landscape was transformed into a mosaic of small forest fragments surrounded by a predominantly agricultural matrix. Urban expansion and rural urbanization have created peri-urban zones, which still can harbor natural habitat remnants, contributing to biological diversity and thus providing essential ecosystem services to urban and rural areas. The maintenance of such ecosystem services requires an understanding of the ecological processes in the ecosystem. A prerequisite for such an in-depth insight is the quantification of the underlying ecosystem functions. The ecosystem function pest control, a trophic interaction between insectivorous birds and herbivorous arthropods, was quantified in an empirical study using artificial caterpillars as prey models. This technique allows the identification of predator groups and the assessment of their predation rates. A total of 888 plasticine caterpillars were distributed at eight sites in secondary forest fragments surrounding the university campus of the federal university of São Carlos (UFScar) in peri-urban Sorocaba, southeastern Brazil. In sixteen point counts, 72 insect-eating birds, belonging to 19 species, were identified as possible artificial caterpillar attackers. Local habitat variables were measured to describe the forest vegetation structure and the landscape context. The study aimed to assess which structural components of the forest fragments, together with the recorded bird community variables (abundance, richness, α -diversity), best explain the estimated predation rates by birds. The mean predation rate for birds was $8.25 \pm 6.3 \%$ for a reference period of eight days, representing the first quantification of the ecosystem function pest control for the study area. The three treatments of caterpillar placement heights (ground, stem: 0.5 - 1.0 m, leaf: 1.5 - 2.0 m) were the best and only estimator to explain bird predation rates. The little dense understory and ground vegetation might have facilitated the accessibility of artificial caterpillars, especially for carnivorous arthropods and birds. The detected contrast in their foraging and predation patterns suggests that arthropods and birds complement each other in their function of pest control. Bird predation rates were found to be negatively related to the vegetation structure. Thus, more open habitats, with less understory and low tree density, but high canopy cover and including dead trees were correlated with the highest predation rates and also exhibited more specialized forest-dependent bird species. This study confirms the importance of the maintenance of forest fragments in peri-urban areas, even if they are small, to preserve forest-associated birds, to contribute to the biological diversity on a broader scale, and to prevent the loss of ecosystem functions and services, mitigating some of the adverse effects of

urbanization. Further investigation of the effect among the three treatments of caterpillar placement on the predation rates is encouraged, including comparative studies among different habitat types. For future studies, it is recommended to model the avian community variables with the vegetation structure measures to predict habitat preferences of insectivorous birds. Therefore, the sampling of more units and on a bigger scale, including over a more extended period, is necessary to improve the robustness of the results, which could provide the basis for a monetary analysis of the ecosystem service pest control by birds.

Keywords: artificial caterpillars, pest control, forest fragments, Brazilian Atlantic forest, peri-urban areas, biodiversity conservation

Resumen

Los procesos de urbanización son uno de los principales factores de pérdida y fragmentación del hábitat, lo que provoca la pérdida de biodiversidad global y la extinción de especies. El bosque atlántico neotropical en Brasil, antaño uno de los bosques más extensos de América, se considera un hotspot clave de biodiversidad global. Debido a la extensa deforestación durante siglos, su paisaje fue transformado en un mosaico de pequeños fragmentos de bosque rodeados predominantemente por una matriz agrícola. La expansión urbana y la urbanización rural han creado zonas periurbanas, que aún pueden albergar remanentes de hábitats naturales; estos contribuyen a la diversidad biológica y proporcionan servicios ecosistémicos esenciales a las áreas urbanas y rurales. El mantenimiento de los servicios ecosistémicos requiere la comprensión de los procesos ecológicos en el ecosistema. Un requisito previo para una comprensión profunda es la cuantificación de las funciones ecosistémicas subyacentes. La función ecosistémica de control de plagas es una interacción trófica entre aves insectívoras y artrópodos herbívoros, y se cuantificó experimentalmente mediante orugas artificiales como modelos de presa. Esta técnica permite la identificación de grupos de depredadores y la evaluación de las tasas de depredación. Un total de 888 orugas de plastilina fueron distribuidas en ocho puntos en fragmentos de bosque secundario que rodean el campus universitario de la universidad federal de São Carlos (UFScar) en la periurbana de Sorocaba, sureste de Brasil. En dieciséis puntos de conteo, se identificaron 72 aves insectívoras, pertenecientes a 19 especies, como posibles depredadoras de orugas artificiales. Se midieron las variables del hábitat local para describir la estructura de la vegetación forestal y el contexto del paisaje. El estudio tuvo como objetivo evaluar cuáles componentes estructurales de los fragmentos de bosque, junto con las variables de la comunidad de aves registradas (abundancia,

riqueza, diversidad α), explican mejor las tasas estimadas de depredación por aves. La tasa media de depredación de aves fue de $8,25 \pm 6,3$ % durante ocho días, lo que representa la primera cuantificación para el área de estudio. Los tres tratamientos de altura de colocación de las orugas (suelo, tallo: 0,5 - 1,0 m, hoja: 1,5 - 2,0 m) fueron el mejor y único estimador para explicar las tasas de depredación de aves. El sotobosque y la vegetación del suelo, ambos poco densos, podrían haber facilitado la accesibilidad de artrópodos carnívoros y aves a las presas artificiales. El contraste detectado en sus patrones de alimentación y depredación sugiere que los artrópodos y las aves pueden complementarse entre sí en su función de control de plagas. Se encontró que la tasa de orugas artificiales por aves está relacionada negativamente con la estructura de la vegetación. Por lo tanto, los hábitats más abiertos, con menos sotobosque y menor densidad de árboles, pero con una alta cobertura de dosel y árboles muertos presentaron las tasas de depredación más altas, y especies de aves más especializadas y dependientes del bosque. Este estudio confirma la importancia del mantenimiento de fragmentos de bosque en áreas periurbanas, aunque sean pequeñas, ya que podrían preservar las aves asociadas al bosque, enriquecer a la diversidad biológica en una escala más amplia y prevenir la pérdida de funciones y servicios de los ecosistemas, mitigando algunos de los efectos adversos de la urbanización. Se sugiere una mayor investigación del efecto entre los tres tratamientos de altura de colocación de las orugas sobre la tasa de depredación de aves, lo que podría incluir estudios comparativos entre diferentes tipos de hábitats. Se recomienda para estudios futuros, modelar las variables de la comunidad de aves con las medidas de la estructura de la vegetación para predecir las preferencias de hábitat de las aves insectívoras. Por lo tanto, es necesario, aumentar el muestreo a más unidades y a una mayor escala, incluso durante un período más prolongado, para mejorar la solidez de los resultados, cuáles podrían proporcionar la base para un análisis monetario del servicio ecosistémico de control de plagas por aves.

Palabras clave: *orugas artificiales, control de plagas, fragmentos de bosque, bosque atlántico brasileño, áreas periurbanas, conservación de la biodiversidad*

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3 Abbreviations and formula symbols

Symbols	Definition
$\frac{A(\text{polygon})}{\pi * r^2} * 100$	A = Area; π = pi; r = radius.
AIC	Akaike Information Criterion
AICc	Akaike Information Criterion with a correction for small samples
$AICc = AIC + \frac{2k(k+1)}{n-k-1}$	k = number of parameters; n = number of observations.
BIC	Bayesian Information Criterion
df	Degrees of freedom
FLONA	National Forest of Ipanema
$\varphi\mu^p$	Tweedie-variance formula, where: φ = is a positive dispersion parameter; μ = the mean; $p \notin (0, 1)$ = a real-valued index parameter.
$H' = -\sum p_i \ln p_i$	H' = Shannon-Wiener-Index; p_i = the relative abundance of the i th species compared with all species identified in a sample; \ln = natural logarithm.
LM	Linear Model
LM-PCA	Linear Model – Principal Component Analysis
logLik	Log-Likelihood
ND	Null Deviation
PCA	Principal Component Analysis
Q-Q plot	Quantile-Quantile plot
R^2 / R^2 adjusted	Coefficient of determination/ adjusted coefficient of determination
RD	Residual Deviance
RSE	Residual Standard Error
SD	Standard Deviation
T, M, G	Top, Middle, Ground: three treatments of caterpillar placement
Tweedie-GLM-PCA	Tweedie - Generalized linear Model - Principal Component Analysis
τ	tau: Kendall rank correlation coefficient
UFScar	Universidade Federal de São Carlos
$Var(Y_{ji}) = a\mu_i^b$	Variance function of Taylor's Universal Power Law, where: Y = a population count; a and b = positive constants; μ = the mean.

4 Introduction

4.1 Forest fragmentation as a driving force of global biodiversity loss

On the whole planet, old-growth forests are declining drastically, which is mainly attributed to the rapid demographic and economic growth of the human population, which in turn, are leading to increasing and accelerated agricultural, infrastructure, and fossil fuel developments. In consequence, altered landscapes are developing and expanding, generating fragmented patches of forest mingled with different anthropogenic land-uses (Boulinier et al., 2001; Bregman et al., 2014; Laurance, 2014; Riitters et al., 2000; Wade et al., 2003).

Forest fragmentation is the dismembering of former continuous forest into smaller patches that are separated by a transformed land cover (Haddad et al., 2015; Laurance, 2014; Rolstad, 1991). The causes can be of anthropogenic or natural origin but mainly fall back on logging activities, once a new region is explored (Tabarelli et al., 2004; Wade et al., 2003). The main results of forest fragmentation are the reduction of forest area, the increase in isolation among fragments, and the creation of forest edges (Pardini et al., 2009; Sekercioglu & Sodhi, 2007). The partial clearing of the forest causes local habitat loss, also impacting habitat connectivity. There are two main types of connectivity: the structural connectivity, which refers to physical measures among habitat patches, e.g., inter-patch distances (Mühlner et al., 2010). The functional connectivity expresses how species respond to landscape structure and the landscape matrix, e.g., through movement patterns among fragments (Mühlner et al., 2010). Habitat fragments become more isolated and exposed to human land uses, triggering a succession of ecological processes, as well as threatening biodiversity (Haddad et al., 2015; Riitters et al., 2000; Wade et al., 2003). Forest fragments can be classified according to their patch-size into fine- or coarse-grained patterns. Fine-grained fragmentation is defined as the subdivision of habitat into patches smaller than the territory of one organism. Coarse-grained fragmentation corresponds to a habitat subdivision into patches bigger than an individual territory. Many forest landscapes are hierarchically organized mosaic patterns. They consist of locally fine-grained patches, that regionally are grouped into clusters, and on a landscape-scale can function as one coarse-grained patch, containing metapopulation structures (Rolstad, 1991).

The loss and disruption of natural habitats are considered the main factors in species extinction. Especially biodiversity hotspots, like neotropical forests, are affected negatively (Laurance, 2014; Raedig & Lautenbach, 2009; Tabarelli et al., 2004). Compared to other forest types, tropical forests have lost the largest area and have been transformed mainly into agricultural or pastoral lands

(Ramirez-Reyes et al., 2018). In Brazil, large-scale agriculture, driven by globalization and industrial processes, is one of the main drivers for forest disruption and degradation, followed by other industrial activities, like mining, fossil fuel, and developing infrastructure, such as road constructions (Freitas et al., 2010; Laurance, 2014). One example of substantial forest destruction is the Brazilian Atlantic forest, which used to be of great extension, and nowadays is composed of a highly fragmented landscape with small and isolated forest patches (Raedig & Lautenbach, 2009; Ribeiro et al., 2009; Tabarelli et al., 2005; Zanella et al., 2012).

4.1.1 Biodiversity, ecosystem functions, and services

Forest loss and fragmentation can trigger a decrease in species diversity and thus in their ecosystem functions (Barbaro et al., 2014; Bregman et al., 2014; Coelho et al., 2016; Dos Anjos et al., 2019), as well as alter species interactions, e.g., in between plants and animals (De la Vega et al., 2012). The biological or systemic properties, as well as processes of ecosystems, are defined as ecosystem functions (Costanza et al., 1997). Functional diversity refers to those components of biodiversity that influence the functioning or operating of ecosystems, like its stability, productivity, and nutrient balance (Tilman, 2001). Biodiversity is a broader term, which includes not only all species living in a site, but also the spatial and temporal variations of their genotypes and phenotypes among ecosystems (Tilman, 2001). Hence, functional diversity is a subset of biodiversity and can be measured by species traits (Tilman, 2001), like their position in food webs, feeding guilds, or forest-dependency. Haddad et al. (2015) found that habitat fragmentation reduces biodiversity by 13 to 75 % and, therefore, is affecting essential ecosystem functions. Those effects are often found highest in small, isolated fragments (Haddad et al., 2015; Zanella et al., 2012). A decrease in biodiversity, e.g., due to agricultural expansion, urbanization, and forest fragmentation, not only goes along with reductions in ecosystem functions but also can affect ecosystem services negatively (Dobson et al., 2006; Ferreira et al., 2019; Mitchell et al., 2014), or rarely positively (Mitchell et al., 2015).

Ecosystem services are natural outputs of ecosystems and derive from those ecological functions that directly or indirectly benefit humans (Marco Ferrante et al., 2019; Mertz et al., 2007). On a global and local scale, they are essential to maintain the health and functionality of ecosystems and ensure human welfare (Bereczki et al., 2014; Costanza et al., 1997; A. Howe et al., 2009).

According to the Millennium Ecosystem Assessment (2005), ecosystem services can be categorized as:

- provisioning (e.g., food, water, fiber, fuel),
- regulating (e.g., regulation of climate, water, pests),
- cultural (e.g., spiritual, and aesthetic goods, recreation, like bird watching, or education),
- and supporting (e.g., pollination, seed dispersal, primary production, and soil formation) (Wenny et al., 2011).

The global consumption of arthropods by insectivorous birds was estimated at 400 to 500 metric tons per year (Nyffeler et al., 2018). At the lower range, this would correspond to an energy consumption of approximately 2.7×10^{18} J per year, or about 0.15 % of the global terrestrial net primary production (Nyffeler et al., 2018). The economic benefit from ecosystem services can be calculated as a monetary value and is a strong argument in favor of biodiversity conservation strategies for decision-makers (Costanza et al., 1997; Dobson et al., 2006; A. G. Howe et al., 2015; Maas et al., 2015; Wenny et al., 2011). Therefore, it is essential to assess and value the relative importance of an ecosystem's components (Mertz et al., 2007). Ferreira et al. (2019) found a decline of 73.2 % in the total value of ecosystem services, from US\$ 13.7 million to US\$ 3.7 million, due to tree cover losses (1989 – 2014), triggered by urbanization processes in the northeast region of Brazil. The value of the ecosystem service pest control by birds could be estimated by the avoided costs for pesticides, which is based on the quantification of its ecosystem function (Costanza et al., 1997; Wenny et al., 2011). For example, in a study carried out in Costa Rica, birds reduced the infestation of the coffee berry borer beetle (*Hypothenemus hampei*) by almost 50 %. This ecological service of pest control prevented damages between US\$ 75 and US\$ 310 ha-year⁻¹, a benefit per plantation equaling the average annual income of a Costa Rican citizen (Karp et al., 2013).

There is a scientific debate about the extent to which biodiversity is a necessary prerequisite for the maintenance of ecosystem functions and services (Richmond et al., 2005). The arguments were reviewed by Mertz et al. (2007); it is recognized that biodiversity is a structural feature of ecosystems that provides goods, or contributes to ecosystem services (McDonald et al., 2013; Millennium Ecosystem Assessment, 2005). Although many researchers favor the dependency of ecosystem functioning on biodiversity, experimental evidence is challenging to provide. It is difficult to find criteria and indicators that measure ecosystem functions and biodiversity meaningfully and on a multidimensional scale (De Coster et al., 2015; Mertz et al., 2007; Wenny et al., 2011). Furthermore, the interactions are highly complex and require adequate monitoring through long-

term studies (Mertz et al., 2007). Consequently, the economic value of biodiversity and ecosystem services is often underestimated. Yet, the contribution of biological diversity to ecosystems' resilience and stability is a significant argument in the debate. If an ecosystem experiences environmental change, sufficient levels of biodiversity increase the odds that at least some species will adapt to the new conditions and contribute to the ecological functions performed by species that won't tolerate these changes (Clavel et al., 2011; Loreau, 2000; Mertz et al., 2007). Thus, experimental proof is necessary to assess the role of biodiversity in the maintenance of the ecosystem function pest control.

4.1.2 The Brazilian Atlantic forest and its anthropogenic transformation

The neotropical Atlantic forest in Brazil used to be one of the largest forests of the Americas. Due to its wide latitudinal distribution from the northeast to the southwest of the country, it expands over tropical and subtropical regions. The inclusion of several coastal and mountain ranges leads to diverse habitats, favoring high biodiversity and species endemism (Dos Anjos et al., 2011; Morawetz & Raedig, 2007; Raedig & Lautenbach, 2009; Ribeiro et al., 2009; Uezu et al., 2005; Vale et al., 2018). With more than 8000 endemic plant species, and over 650 vertebrates (Tabarelli et al., 2010), like 223 endemic bird species (Vale et al., 2018), the biome is considered a global key biodiversity hotspot (Tabarelli et al., 2010). Hence, the Brazilian Atlantic forest is an equally important center of plant diversity as the Amazon, the Andes, and the Central American region (Raedig, 2010). Forest degradation processes already started in the sixteenth century with the first European colonization wave, accompanied by the exploitation of natural resources, like wood, crops, and minerals (Nehren et al., 2017; Tabarelli et al., 2005, 2010). Especially during the last three centuries, large areas have been deforested for agricultural, cattle, and timber production. These landscape alterations left behind a mosaic of probably by now many times greater than the 245,173 recorded forest fragments (Ribeiro et al., 2009), surrounded predominantly by an agrarian landscape (Casas et al., 2016; Freitas et al., 2010; Haddad et al., 2015). Other threats, like hunting, wild plant collections, and invasion of exotic species, are further degrading the ecosystems and threatening their animal and plant species (Tabarelli et al., 2005). Thus, 112 bird species are threatened by global extinction (Tabarelli et al., 2010). Additionally, massive urban growth has been intruding on the forest remnants (Enedino et al., 2018), leaving 83.4 % of these with a size smaller than 50 ha (Ribeiro et al., 2009). For example, the metropolitan area of São Paulo exhibits annual deforestation rates of almost 3 % (Tabarelli et al., 2010). The expansion of cities fragments the remaining natural habitats and increases the distance between forest patches. The increasing gap among the

fragments also enhances the isolation of remaining species populations and limits their gene flow. One result is the down-breaking of large regional populations to local sub-populations (McDonald et al., 2013). It was estimated by Ribeiro et al. (2009) that today only 11.4 to 16.0 % of the original Atlantic forest vegetation remains, or in other words, more than 80 % of the forest has been lost. Many fragments (= 45 %) are close to forest edges (< 100 m), and thus also to the adjacent landscape, which substantially impacts forest ecological processes (Ribeiro et al., 2009).

Small forest remnants should be given special attention for conservation strategies since they still can harbor outstanding flora and fauna, function as a refuge for animals within a cleared landscape and are essential to connect larger fragments. (Barbosa et al., 2017; Baum et al., 2004; Decocq et al., 2016; Klein et al., 2014; Zanella et al., 2012). Surprisingly, 40 % of the earth's surface is covered by forest fragments with less than 1 to 50 ha, but little is known about their contribution to provide ecosystem services (Decocq et al., 2016).

Despite the massive impacts on the Brazilian Atlantic forest, it is still one of the most important forest habitats, harboring 1-8 % of the world's total species, like 688 bird species, and many other species, some of which are still to discover (Piratelli et al., 2008; Ribeiro et al., 2009). Yet, current conservation reserves are not sufficient to mitigate the on-going degradation process. Therefore, holistic management plans for the entire remnants of the Atlantic forest are necessary (Raedig & Lautenbach, 2009; Ribeiro et al., 2009).

4.1.3 Secondary forests and their interactions with the matrix

Secondary forests grow back on abandoned, cleared landscapes, like former pastureland, which once were covered by natural forests (Casas et al., 2016). This process is called succession since the full recovery of the forest happens in subsequent stages and extends over several years. The habitat structure of secondary forests is, therefore, varying and depends on local and historical factors (Casas et al., 2016). They provide an attractive habitat for many forest-specialists that had disappeared when the forest was logged and lead to recolonization processes of, e.g., insectivorous birds (Banks-Leite et al., 2010; Laurance et al., 2011). How fast plants and animals can move back also depends on the composition of the surrounding landscape or so-called "matrix" and its property to connect isolated habitat fragments, as well as its permeability (Coelho et al., 2016; Laurance et al., 2011; Zanella et al., 2012). The response of animals to forest fragmentation depends on species-specific habitat requirements and their tolerance toward the matrix (Laurance et al., 2011). Döbert et al. (2014) identified four major matrix-context effects that influence population, or community dynamics: the alteration of movement or dispersal patterns, changes in the

availability of alternative resources, the modification of species interactions, and the alteration of edge dynamics in habitat fragments. These factors can influence ecological processes across a wide range of scales (Döbert et al., 2014) and culminate in species extinction (Barbosa et al., 2017).

Even though secondary forests can provide habitat to species, they show different ecological dynamics than old-growth forests (Laurance, 2014). The fragment size is one limiting habitat characteristic, as smaller fragments often cannot provide sufficient vital resources (Laurance et al., 2011; Philippsen et al., 2010). They are often associated with declining species abundance and richness of, for example, tree seedlings, insectivorous birds, or larger mammals (Laurance et al., 2011). The smaller the forest remnant, the more dominant become edge effects that are defined as ecological changes caused by abrupt landcover changes, for example, on forest edges. These changes determine, among others, the forest microclimate, tree mortality, and the presence of fauna, as well as the rate of species loss. However, species that are favored by the environmental conditions of disturbed habitats, such as forest gaps, can even increase in their abundances and reduce extinction rates (Laurance et al., 2011; Vogel et al., 2011), as it was observed for many frog and spider or pioneer plant species (Laurance et al., 2011). Therefore, the same landscape context can be perceived differently by various species regarding their forest dependency (Coelho et al., 2016). Nearby edges accumulate fragments' edge effects, leading to more severe changes in forest climate, as well as plant and animal communities (Laurance et al., 2011). Pardini et al. (2009) found that the total number of forest specialists decreased at edges, compared to the interior. In contrast, forest generalists gradually increased from the interior towards the edge of forest remnants (Pardini et al., 2009). Secondary forests that are growing back on forest gaps or adjacent to edges can remedy harmful edge effects by decreasing the habitat's permeability through regrowing vegetation (Laurance et al., 2011). Since forest fragments interact with the surrounding landscape, this can alter the ecological processes of flora and fauna. For example, the matrix can buffer adverse edge effects or benefit ecological functions, like seed dispersal or pest control (Banks-Leite et al., 2010; Lampila et al., 2005; Laurance et al., 2011; Rolstad, 1991; Tabarelli et al., 2004). More than 70 % of the global forests are within 1 km of an edge towards an anthropogenic landscape, agricultural or urban, which puts those ecosystems at an even higher risk of degradation (Haddad et al., 2015).

Forest fragments are complex and hyperdynamic habitats since they are determined not only by local but also landscape characteristics. Therefore, they are, in general, more vulnerable to threats, like extreme events, than continuous forests, which are considered more resilient ecosystems (Laurance et al., 2011). Since secondary forest undergo different ecological dynamics, their capacity to substitute primary forest habitats is limited (Banks-Leite et al., 2010). Ferraz et al. (2017) studied

how the landscape context influences the provisioning of ecosystem services by forest fragments in the Brazilian Atlantic forest. They found that secondary forests could not substitute for the quality of ecosystem services of old-growth forests. For securing ecosystem services of old-growth forests, it was recommended to increase forest cover, but mainly conserve the old-growth remnants, or enhance forest quality of forest fragments (Ferraz et al., 2014).

Landscape connectivity is defined as the capacity of the landscape to facilitate biological flows among habitat patches, such as forest fragments. For example, the ecosystem service pest control depends on the movement of predators among habitats (Mitchell et al., 2013). The distance between the patches determines the degree of isolation of a habitat fragment, and the probability of extinction or recolonization events (Zanella et al., 2012). Therefore, it is essential to maintain natural vegetation remnants and secondary forest fragments that can function as stepping stones or larger corridors between isolated patches and improve the connectivity of the landscape (Baum et al., 2004; Gómez, 2005; Vogel et al., 2011; Zanella et al., 2012). Landscape connectivity influences biodiversity and ecosystem functions. Yet, it has not been fully understood how changes in landscape connectivity are affecting ecosystem services provision, and which services are impacted the most (Mitchell et al., 2013).

4.2 Urbanization and peri-urban areas in Latin America

The world population has been growing at accelerated rates, giving rise to projections of 9.7 billion people by 2050 (United Nations et al., 2019). This demographic development will have significant impacts on the planet, primarily affecting the environment and its resources, but also triggering social movements, like urban migration processes (Lessi et al., 2016). Hence, it is predicted that 68 % of the world's population will be urban by 2050 (Bhakti et al., 2020; United Nations, 2018). These developments will occur in many countries in Latin America, one of the world's most urbanized regions (United Nations, 2018), where urban growth is predicted to increase, but often without adequate urban planning (Bhakti et al., 2020; United Nations, 2018). In Brazil, the southeastern region is especially affected by urban developments (Manhães & Loures-Ribeiro, 2005).

Urbanization is considered one of the primary and direct drivers of habitat destruction and fragmentation, leading to biodiversity loss and species extinction in the whole world (Bellocq et al., 2017; Bhakti et al., 2020; Marzluff & Rodewald, 2008; Rodrigues et al., 2018). Urban processes develop gradually from urban, over suburban to rural areas, where they often conflict with

agricultural or nature conservation activities (Lourenço & Toledo, 2019). Unlike Europe or North America, urban development in South America is an on-going process (Bellocq et al., 2017). Since the 1970s, rapid and unplanned urban growth has created new urban forms. At the edge of the cities, urban expansion and rural urbanization have led to urban-rural fringes or peri-urban zones. There are many different definitions of peri-urban areas that have changed over time, and according to the scientific background of the authors (MacGregor-Fors, 2010; Simon, 2008). This study uses a definition from the ecological point of view, that refers to a peri-urban area as the geographical transition zone from suburban to adjacent rural areas and therefore exhibits characteristics of both land-use classes: urban infrastructure and natural habitats (Clergeau et al., 2001; MacGregor-Fors, 2010; Ravetz et al., 2013; Simon, 2008). Ravetz et al. (2013) even distinguish between "inner peri-urban" and "outer peri-urban" fringe, which demonstrates the two different sites of urban and rural pressure. Since this type of area is the result of urbanization processes, it can be temporal with often unclear, irregular, and dynamic boundaries. Peri-urban areas are characterized by complex social, economic, political, and environmental interactions, determining the well-being and health of its inhabitants and ecosystems (Simon, 2008). This complexity is also reflected in animal communities, e.g., avian communities have been used to study the effects of urbanization on biodiversity (Clergeau et al., 2001; Filloy et al., 2019; MacGregor-Fors, 2010; A. J. Piratelli et al., 2017). Peri-urban areas usually present an intermediate level of disturbances, a higher amount of natural vegetation, and less population density than in urban areas and in this case, have shown higher levels of biodiversity (Bhakti et al., 2020; Ravetz et al., 2013; Rodrigues et al., 2018). Several aspects of urban habitats have been found positively related to high bird diversities, like the size of green spaces, the age of native vegetation remnants, as well as high heterogeneity and connectivity of habitats. Urban bird conservation projects were very successful when supported by the residents (Piratelli et al., 2017).

Ravetz et al. (2013) assume that peri-urban zones will become the most common type of living and working areas in the twenty-first century. The proximity to the urban market makes these areas especially attractive for agriculture and livestock production. On the other side, industrial farming systems impact the health of rural and urban populations, as well as ecosystems, by, e.g., inadequate usage of agrochemicals (pesticides and fertilizers), water, and natural resources. Environmental consequences include pollution of water, soil, and air through gas emissions, eutrophication of water bodies, soil degradation, heavy traffic, and improper solid waste management (Simon, 2008).

4.2.1 Effects of urbanization on ecosystem services of forest fragments and birds

Urban centers, or cities, often coincide with areas that otherwise would present the highest levels of species richness and endemism (McDonald et al., 2013). This phenomenon is most likely related to a correlation between human population density and biological productivity, which is highest in coastal areas or in the tropics. Both sites are known as biodiversity hotspots (McDonald et al., 2013). Urban regions rely heavily on the ecosystem services of their ecological hinterland (Seto et al., 2013). Peri-urban areas are transition zones that often experience land-use changes due to urban expansion on one side. However, on the other hand, they still contain natural habitat remnants with high biodiversity. These areas potentially can buffer the environmental impacts of the cities, as well as maintain essential ecosystem services in rural areas (Lee et al., 2015). For example, agroecosystems in peri-urban areas can provide ecosystem goods and services that benefit the urban population, such as climate regulation, groundwater recharge, prevention of soil erosion, and habitat for animals and plants (Lee et al., 2015). Whereas, agricultural expansion can result in forest fragmentation, impacting forest-dependent ecosystem services (Mitchell et al., 2014). Even small forest fragments can provide crucial ecosystem services, like pest control, pollination, quality enhancement of water and nutrient cycles, global carbon sinks, which can benefit agricultural fields through spillover effects (Decocq et al., 2016; Lee et al., 2015). Mitchell et al. (2014) found that forest fragments provide multiple services to surrounding agroecosystems. In their study, the highest level of pest control was recorded close to the forest remnants. Yet, the strength of the ecosystem service was dependent on the degree of fragment isolation within the landscape (Mitchell et al., 2014). Natural pest control can be provided by birds, but also by arthropods and mammals. They all contribute to reducing pest infestations in crops, along with lowering costs for pesticides or fertilizers, by enhancing the plants' health (Klein et al., 2014; Mitchell et al., 2014; A. J. Piratelli et al., 2019). Nearly one-third of all birds use agricultural landscapes (Sekercioglu, 2012). Through adequate spatial planning of peri-urban areas, agroecosystem services, such as pest control can be optimized for agrarian land (Lee et al., 2015; Piratelli et al., 2019).

Urbanization processes include many changes, of, e.g., land-use and land cover, species introduction, soil modification, and climate variabilities, among others (Lessi et al., 2016; Marzluff & Rodewald, 2008; Rodrigues et al., 2018). These transformations can directly affect the composition and structure of animal populations, as well as communities (Gómez, 2005; Marzluff & Rodewald, 2008). Indirectly, a populations' viability is influenced by its reproduction, survival, immigration, and emigration rates. A population's decreased viability can trigger extinction or colonization mechanisms and alter community compositions, which in turn, determine competition or predation rates of populations (Marzluff & Rodewald, 2008). Habitat loss was predicted to first

affect species at higher trophic levels, since they usually require larger territories, making them more susceptible to extinction. From there, the effects will accelerate and substantially move to lower trophic levels (Dobson et al., 2006). At the landscape scale, birds' functional diversity is considered a primary driver of bird insectivory. Forest fragmentations and edge effects influence this ecosystem function (Barbaro et al., 2014). Bird insectivory was found to increase at forest edges (Barbaro et al., 2014; González-Gómez et al., 2006), through enhanced functional evenness. The evenness is a measure of the regularity of species communities. Hence it is assumed that species at forest edges are more similar and complement their function through different birdlife traits, like body mass, diet, and foraging method (Barbaro et al., 2014). Insectivorous birds might forage more at forest edges due to higher visibility and accessibility of prey, which represents a rare example of a positive edge effect (Barbaro et al., 2014).

Birds can be divided according to an urban-gradient: the urban invaders (Marzluff & Rodewald, 2008), or 'urban exploiters' according to Blair (1996), are rare in natural areas and reach highest densities in modified habitats (Blair, 1996). Suburban adapters can also adapt to disturbed habitats but still rely on the resources of natural vegetation, e.g., forest fragments in peri-urban areas. Urban avoiders are very sensitive to disturbances and concentrate on natural habitats (Marzluff & Rodewald, 2008). Yet, it is often difficult to quantify an urbanization gradient; therefore, Fischer et al. (2015) proposed an adaptation of the terminology, based on the relative importance of natural and developed areas to population dynamics. They distinguished between urban avoiders, which are dependent on natural habitats, urban utilizers, which depend on natural and developed areas, and urban dwellers, which are independent of natural habitats (Fischer et al., 2015). These guilds can vary according to their migration behavior and ability to recolonize, persist, or become extinguished, as well as the type and intensity of the disturbance in space and time (Devictor et al., 2007; Marzluff & Rodewald, 2008). The combination of the amount of land cover type and its spatial distribution is one crucial factor in determining the number of bird species within an urban landscape (Marzluff & Rodewald, 2008). Peri-urban areas often present the highest species richness due to diversified landscape patterns. The more urban the territory, the more likely it becomes to find urban invaders and adapters, which may outweigh the extinction of avoiders so that species richness could be maintained or even increase (Marzluff & Rodewald, 2008). The number of species declines as soon as extinction exceeds colonization rates. Species composition also determines their interaction, e.g., the occurrence of competition or predation pressure, and again contributes to the persistence or disappearance of birds in urban areas (Marzluff & Rodewald, 2008). Urbanization processes are affecting birds negatively or positively and on different functional levels and traits, which eventually alter and might destabilize communities (Bellocq et al., 2017; Bhakti et al., 2020;

Devictor et al., 2007; Lourenço & Toledo, 2019; Rodrigues et al., 2018; Xu et al., 2018). For example, the noise level has a strong negative, and the availability of green areas a positive effect (Rodrigues et al., 2018). Bird traits have been identified that are correlated to their adaptability to urbanization. They encompass the fields of evolutionary history, morphology, physiology, reproduction, and social and feeding behavior (Philippsen et al., 2010; Piratelli et al., 2017). One phenomenon that has been studied in this context is the functional homogenization, the replacement of many specialist species by a few generalists, resulting in the spatial similarity of their functions (Bellocq et al., 2017; Clavel et al., 2011; De Coster et al., 2015; Devictor et al., 2007; Lourenço & Toledo, 2019; Mangel et al., 2017; Rodrigues et al., 2018). This phenomenon, together with the taxonomic similarity of such generalist communities (taxonomic homogenization), makes up the biotic homogenization, e.g., through the replacement of many native species by an introduced exotic species (Clavel et al., 2011; Devictor et al., 2008; McKinney & Lockwood, 1999). Due to increasing urban developments in the whole world, strategies to maintain high levels of biodiversity and the associated heterogeneous functions and services for human well-being need to be developed and integrated into urban planning management (Bhakti et al., 2020; Marzluff & Rodewald, 2008). Since bird communities are linked to specific land-use types, urban planners should consider preserving an adequate amount of different habitat types to foster bird diversity and their functional diversity (Bhakti et al., 2020; Piratelli et al., 2017).

4.3 Natural pest control by birds in the Brazilian Atlantic forest

For this study, the ecosystem function pest control by birds is defined as a stabilizing effect that birds exert on insect populations, which avoids the explosive increase of insect populations or pest outbreaks (Capinera, 2010). Garfinkel and Johnson (2015) showed that birds rather respond to insect outbreaks than control pest abundance at non-irruptive densities. More than 50 % of all birds are predominantly insectivorous, and 75 % eat insects occasionally (Wenny et al., 2011). This feeding preference might be related to the fact that insects constitute the largest terrestrial food source, regarding biomass and diversity. Insect-eating birds are defined as species with a strictly insectivorous diet, as well as omnivorous birds that consume large amounts of arthropods in addition to other food types (Nyffeler et al., 2018). Forest-associated birds account for 75 % of the global annual arthropod consumption, or more than 300 million tons per year (Nyffeler et al., 2018). They especially consume large numbers of caterpillars, and other arthropods, during the breeding season, to feed their nestlings. Prey consumption in tropical forests was found to be the highest, compared to different biomes, with about $197,000 \times 10^6$ kg per year for the whole tropical area

(Nyffeler et al., 2018). Bird species that use agricultural habitats contribute about 7 % or 28 million tons to the annual consumption of arthropod prey (Nyffeler et al., 2018). Insect-eating birds, therefore, have an important regulatory function within ecosystems (Capinera, 2010) and provide an essential ecosystem service for agriculture (Garfinkel & Johnson, 2015). Insectivorous birds consume a large variety of arthropod taxa, but mostly from the orders Lepidoptera, Coleoptera, Orthoptera, Diptera, Hemiptera, Hymenoptera, and Araneae (Nyffeler et al., 2018). Simplified agricultural systems contain less insectivorous bird species and are more prone to pest outbreaks and to host less specialized bird communities. The usage of pesticides additionally affects insectivores by reducing potential prey (Sekercioglu, 2012).

Habitat fragmentation affects forest birds' density, distribution, and richness, depending on the patch size and landscape context (Lampila et al., 2005; Rolstad, 1991). The bird fauna of the Brazilian Atlantic forest is exceptionally diverse and hosts high levels of endemism (Vale et al., 2018). An updated list of the Atlantic forest birds was compiled by Vale et al. (2018), who identified 223 endemic bird species. About one third (= 31 %) is considered threatened or extinct. The typical bird of the ecoregion was described as a small forest-dependent insectivore (Vale et al., 2018).

Birds are one of the best-known animal groups and are ideal for studying the effects of habitat fragmentation on ecosystem services, many of which result from their foraging behavior (Wenny et al., 2011). They are relatively easy to observe, habitat-dependent, exhibit many ecological functions, and are sensitive to environmental changes (Devictor et al., 2007; Ramírez-Albores & Pérez Suárez, 2018; Rolstad, 1991; Xu et al., 2018). As mobile organisms, they connect different ecosystems and transfer energy within and between habitats by consuming resources. Therefore, birds contribute to the resilience of ecosystems (Figueroa-Sandoval et al., 2019; Wenny et al., 2011). Insectivorous birds are highly sensitive to habitat changes due to their specific habitat and diet requirements (Morante-Filho et al., 2015). Hence, they are good indicators for the conservation status of forest fragments (Casas et al., 2016; Peh et al., 2014; A. Piratelli et al., 2008; Xu et al., 2018), as well as revegetation practices (Gould & Mackey, 2015).

Predator-prey interactions between insectivorous birds and herbivory insects can trigger cascading effects across food webs. These relations can increase or decrease plant fitness as an indirect effect and ultimately also affect the benefits for society (De la Vega et al., 2012; González-Gómez et al., 2006; Wenny et al., 2011). Species interactions can be altered by forest fragmentation, which can be examined, e.g., with exclusion experiments from insectivorous birds to assess the plant's reproductive success (De la Vega et al., 2012). Integrated Pest Management is an environmentally friendly alternative to avoid pest control in agricultural systems with pesticides. It combines many

practices and tactics, considering economical, ecological, and social criteria. One tactic is the biological control or natural pest reduction, which has been used successfully with insect predators, e.g., in sugarcane plantations in Brazil (Parra, 2014). Yet, there are still challenges to widely implement this approach, due to cultural habits and the large scale operation of many farms in Brazil (Parra, 2014). Birds can be integrated into the agricultural system as natural predators, e.g., for insect or rodent pests. This can be done, e.g., with installing nest boxes, perches for foraging, or other landscape structures (natural hedgerows, tall trees, forest remnants) that fulfill the natural predators' habitat requirements (Garfinkel & Johnson, 2015; Wenny et al., 2011).

4.3.1 Birds in urban areas: research in university campuses in Latin America

Many ornithological surveys in Latin America have focused on university campuses and their surroundings as a study area. Bird inventories were conducted among others, in Brazil, e.g., in the state of Paraná (Philippsen et al., 2010; Vogel et al., 2011) and the state of Minas Gerais (Manhães & Loures-Ribeiro, 2005), in Mexico (Castro-Torreblanca, 2014; Ramírez-Albores & Pérez Suárez, 2018), Colombia (Gómez, 2005), and Costa Rica (Stiles, 1990). Many Latinamerican universities are primarily in urban- or peri-urban areas, and their campuses often still host natural vegetation (Vogel et al., 2011), like secondary forest fragments (Gómez, 2005). Therefore, the investigations pay special attention to the effects of urbanization (see Gómez, 2005; Stiles, 1990) and forest fragmentation (see Ramírez-Albores & Pérez Suárez, 2018) on local bird communities. Urbanization is usually associated with the decline of species numbers (Stiles, 1990), yet the field observations show the great potential of adaptation that bird communities possess (Castro-Torreblanca, 2014). The species numbers that were recorded on the campuses ranged in Brazil from 74 (Philippsen et al., 2010), over 121 (Manhães & Loures-Ribeiro, 2005), to 125 (Vogel et al., 2011). Similar numbers were recorded in Mexico, with 76 (Castro-Torreblanca, 2014) and in Colombia with 128 species (Gómez, 2005). The highest abundances were reported again in Mexico (= 141) (Ramírez-Albores & Pérez Suárez, 2018), and Costa Rica (= 188) (Stiles, 1990). Some researches could even demonstrate seasonal fluctuations in species numbers by comparing data from long-term surveys (Castro-Torreblanca, 2014; Philippsen et al., 2010; Stiles, 1990). All studies identified Passeriformes as the most abundant order and Tyrannidae as one of the most abundant families. Migratory birds were mentioned in some cases to have increased the species richness temporarily (Gómez, 2005; Stiles, 1990; Vogel et al., 2011). Insectivores and omnivores were recorded as the predominant feeding guilds. Only a few studies detected specialized species, like wood-creepers, or large frugivores,

which most likely is attributed to the impacts of habitat fragmentation in urban environments (Vogel et al., 2011).

In summary, the campuses were frequented by more generalistic birds, with ample feeding habits, that could cope with a disturbed habitat. In Mexico, even exotic or introduced species, like the monk parakeet (*Myiopsitta monachus*) and the Eurasian collared dove (*Streptopelia decaocto*), were present (Ramírez-Albores & Pérez Suárez, 2018). Vogel et al. (2011) found more than half of the recorded species being related to forest habitats (forest-dependent and semi-dependent species), highlighting the importance of the remaining forest fragments. All studies affirmed the importance of conserving natural vegetation on university campuses to counteract habitat fragmentation and biodiversity loss. Even if vegetation patches are small, they provide essential food and nesting resources for local populations and resting sites for migratory birds and act as biological corridors within the landscape (Gómez, 2005; Guzmán Wolfhard & Raedig, 2019; Ramírez-Albores & Pérez Suárez, 2018; Vogel et al., 2011).

4.4 Biodiversity conservation in fragmented habitats

In parallel to the human-induced transformation of natural habitats and landscapes, the approach of biodiversity conservation has also changed correspondingly. Since biodiversity will depend mostly on species that can adapt to anthropogenically modified landscapes, traditional conservation strategies of the 20th century to only preserve natural reserves are not sufficient anymore (Döbert et al., 2014). In the Brazilian Atlantic forest, strictly protected areas cover less than 2 % of the biome, and most of them are too small to guarantee the long-term persistence of species (Tabarelli et al., 2005, 2010). Only 13.2 % of all forest remnants are protected (Tabarelli et al., 2010). Yet, most species will keep on living in habitat mosaics of semi-natural vegetation fragments and agricultural or urban patches. Over time, the conservation value of these habitats can significantly decline for many species (Sekercioglu & Sodhi, 2007). The provision of forest ecosystem services is related to the understanding of current and historical anthropogenic disturbances and the conservation value of modified landscapes (Tabarelli et al., 2010). Organisms of fragmented landscapes are exposed to processes occurring at local (within patch), at the fragment, and the surrounding landscape (matrix) scale. Therefore, it is not sufficient to consider local fragments as a detached conservation unit, but also include the landscape context, considering the interconnectedness and nestedness of species and habitat interactions (Döbert et al., 2014; Sekercioglu & Sodhi, 2007). For example, small forest fragments are usually associated with declining species populations. Whether this is due to the small area size, the predominance of

adverse edge effects, or the isolation degree within the matrix, can't be assessed separately. The effects can vary in their strength due to synergistic interactions between processes at all levels, according to spatial and temporal progressions (Döbert et al., 2014). Another factor that needs to be considered is the idiosyncrasy of the targeted species since they respond differently in their sensitivity to habitat changes, their dependency on specific habitat characteristics, and their ability to adapt or use other habitat types (Sekercioglu & Sodhi, 2007). In tropical forests, rare bird species, that often are specialists, e.g., scavengers or seed dispersers, frequently disappear first. Birds that are less specialized and have small area requirements are usually less vulnerable to extinction (Sekercioglu & Sodhi, 2007). Migratory birds, for example, have a high range of mobility and dispersion and a higher ability to colonize fragments. Species' ecological traits, like diet, body size, mobility, and habitat dependency, are often correlated with fragmentation sensitivity (Sekercioglu, 2012). Therefore, the understanding of species behavior towards habitat fragmentation is critical for biodiversity conservation (Sekercioglu & Sodhi, 2007). The same idea can be transferred to species populations and communities and their composition of various guilds (Döbert et al., 2014). Pardini et al. (2009) found distinct responses of different taxa, between shade-tolerant forest specialists, that showed a negative response and shade-intolerant generalists that responded positively towards habitat modification. Nevertheless, since the fragmentation and associated loss of primary habitats threatens the majority of bird species, anthropogenic fragmentation needs to be limited, and the effects of existing fragmentation mitigated (Döbert et al., 2014; Tabarelli et al., 2010).

The patch-matrix interface is a critical starting point for conservation efforts. Negative impacts can be reduced by implementing, for example, buffer zones around forest patches. Hence, the land-use of the matrix has a high potential for long-term biodiversity conservation (Barbosa et al., 2017; Vale et al., 2018). For example, the preservation of small fragments, forest corridors, or single trees (stepping stones) can enhance the connectivity of the landscape, especially when the matrix is permeable (Barbosa et al., 2017; Guzmán Wolfhard & Raedig, 2019; Tabarelli et al., 2005; Uezu et al., 2008). A matrix of, e.g., *Eucalyptus*, which is not native to Brazil, was found to favor many insectivorous species in small patches due to higher permeability, helping them to find resources in other areas in the Atlantic forest in southeastern Brazil (Barbosa et al., 2017). Homogeneous agricultural regions, like pasture or sugar cane, are less favorable for the movement of forest-dependent birds (Uezu et al., 2008). Many forest-associated bird species depend on high vegetation structure and cover. Ecologically managed tree monocultures with a rich understory, like traditional cocoa plantations, are, therefore, of high conservation value (Fonseca et al., 2009; Pardini et al., 2009). The conservation value of agroforest systems was also evaluated by Uezu et al. (2008). These

systems can act as stepping stones, facilitating species movements between forest fragments. Secondary forests in the Atlantic forest were found to harbor large numbers of forest specialists, due to a dense understory, offering diverse food resources (Pardini et al., 2009). A great challenge in biodiversity conservation is how to prioritize areas of conservation management. One argument is that cleared landscapes can't sustain vital populations due to resource limitations, and very complex landscapes might have sufficient biodiversity to cope with environmental changes. Therefore, it was suggested to focus on conservation investments on habitats of intermediate structural complexity (Döbert et al., 2014).

Conservation actions should be based on natural boundaries, like biological corridors, rather than political boundaries of municipalities or states, requiring the collaboration between governments (Tabarelli et al., 2005). For bird conservation in the Brazilian Atlantic forest, the preservation of remaining vegetation fragments and the expansion of protected areas is essential for conserving many endemic species (Vale et al., 2018). Large areas are private property, which need to be recognized as indispensable for biodiversity conservation of the region (Campos-Silva & Piratelli, 2020; Guzmán Wolfhard & Raedig, 2019). For the prevention of further deforestation and massive species loss, a holistic conservation strategy is required, integrating public policies and regulations and incentives of forest protection and reforestation, creating a network of sustainably managed landscapes throughout the biome (Tabarelli et al., 2005). In specific, it was suggested by Tabarelli et al. (2010) to extend the size of protected areas and reduce the isolation of their communities, to enhance the functional and structural connectivity among forest patches, followed by lowering edge effects, regenerating forest remnants, and increasing the permeability of the matrix. The plantation of interrelated vegetation forms, like live fences or mixed arrangements of forest species, like agroforest woodlots (Piratelli et al., 2019), as well as agricultural crops, may be less expensive than creating biological corridors, and thus are good alternatives to manage landscape connectivity (Figuerola-Sandoval et al., 2019; Uezu et al., 2008). The great benefit of agroforest woodlots is that they provide an additional income source for local human communities and function as stepping stones for native forest species, especially when they are close to larger patches (Uezu et al., 2008).

4.5 Quantifying the ecosystem function pest control by birds

An effective land use management for the maintenance of ecosystem functions requires their quantification and understanding of the underlying processes, including various trophic levels (bird – insect-plant) (Marco Ferrante et al., 2014; Mitchell et al., 2014; Wenny et al., 2011). Predation is

one of the most critical ecological interactions that determines an ecosystem's structure and stability (Lövei & Ferrante, 2017). There has been a growing interest in research about estimating predation rates of birds with a technique that uses artificial caterpillars as preys (A. Howe et al., 2009; Koh & Menge, 2006; Loiselle & Farji-Brener, 2002; Lövei & Ferrante, 2017; Low et al., 2014; S. M. Roels et al., 2018). They are usually made from plasticine or modeling-clay to mimic lepidopteran larvae and are placed in the field during an experiment (Marco Ferrante et al., 2014; A. Howe et al., 2009; Leles et al., 2017; S. M. Roels et al., 2018). The assessment of predation events under field conditions is difficult since they often happen very fast and without any trace of the predator or prey (A. Howe et al., 2009; Lövei & Ferrante, 2017). In comparison to natural caterpillars, the artificial models lack many biological traits, above all their mobility and chemical cues, which all play an essential role during natural predation events. Yet, the dummy caterpillars allow the quantification of attacks and identification of predator groups, which is suitable for assessing relative predation rates and comparative studies (Lövei & Ferrante, 2017). The technique is not standardized, regarding size, shape, color, placement, exposure time, and data reporting (Lövei & Ferrante, 2017), which makes it challenging to compare predation rates. However, the high flexibility of the procedure, the straightforward handling, and inexpensive material make the usage of sentinel prey adaptable to almost all global ecosystems, where caterpillar predation naturally occurs (A. Howe et al., 2009). Roels et al. (2018) suggested conducting a pilot study in the ecosystem of interest to estimate an appropriate exposure time that maximizes the sampling efficiency. Other techniques to assess predation events include experiments with live preys, field observations, prey labeling (Lövei & Ferrante, 2017), or excremental analysis (Augusto Piratelli & Pereira, 2002). Yet, they all present more considerable effort, know-how, and costs, which again undermines the advantages of predation quantification with artificial prey, which also doesn't harm any animals. Lövei and Ferrante (2017) reviewed 101 articles about experiments with real and fake invertebrates. Studies that used artificial prey found positive as well as negative effects of habitat complexity on predation rates, as well as a positive relation with forest fragmentation that was increasing towards the edge. Predation was found to be higher on trees that suffered herbivory, which might be related to plant volatiles, that are attracting more predators (Mäntylä et al., 2008; K. Sam et al., 2015). Other studies examined the influence of posture (S. M. Roels et al., 2018; Suzuki & Sakurai, 2015), color (M. Ferrante et al., 2017; Remmel & Tammaru, 2009; Solis-Gabriel et al., 2017; Zvereva et al., 2019), material (Katerina Sam et al., 2015), and protection by leaf-rolling (Tvardikova & Novotny, 2012) on the artificial caterpillars.

The predation of invertebrates was found to be higher in temperate than in tropical or cultivated areas, whereas vertebrate predation was higher in tropical than temperate or cultivated zones

(Lövei & Ferrante, 2017). Roslin et al. (2017) conducted a global experiment on six continents with artificial caterpillars to examine geographical gradients of predation strength in the understory. Increasing predation rates were found towards the Equator and towards lower elevations, but only for arthropod predators. For birds and mammals, no global pattern was detected (Roslin et al., 2017). These findings suggest that different predator groups perform the ecosystem function in the understory differently when assessed on a worldwide scale. Hence, it is assumed that other variables at local levels might be decisive. Zvereva et al. (2019) tested for the effect of different colorations of caterpillar prey on a geographical pattern of predation rates. Evidence was found that arthropod predation increased towards lower latitudes, confirming the findings of Roslin et al. (2017). Interestingly, bird predation showed an opposite pattern and intensified towards higher latitudes. Similar to Roslin et al. (2017), it is assumed that prey selection by coloration varies geographically and according to the predator type (Zvereva et al., 2019). Ferrante et al. (2014) found a relation between predation rates and an urbanization gradient of forests in Denmark, from rural, over suburban to urban areas. Chewing insects exerted the highest predation pressure in the original rural forest, compared to suburban and urban fragments. Mammals preyed most in suburban areas, and for birds, predation was not evaluated due to low attack marks.

4.6 The vegetation structure and landscape composition influence suitable bird habitats

Multiple within-site factors influence the presence of bird species. The structural heterogeneity of vegetation is one of the most important factors in determining the diversity and habitat preferences of birds (Gómez, 2005; Gould & Mackey, 2015; Manhães & Loures-Ribeiro, 2005; Philippsen et al., 2010; Ramírez-Albores & Pérez Suárez, 2018). Fragmentation leads to habitat loss, which in turn can decrease vegetation heterogeneity significantly when structurally rich forests are transformed into monocultures. Hence, less heterogeneity of plants also reduces natural filters against environmental impacts on ecosystems (Dos Anjos et al., 2019). Sensitive species, like many specialized insectivorous birds (Sekerçioğlu, 2012), are therefore more susceptible to extinction in forest fragments (Dos Anjos et al., 2019). The structural heterogeneity of, e.g., agroecosystems, is one of the critical factors for the provision of ecosystem services, influencing the abundance of pests and natural enemies: Generalistic predators, like most birds, benefit from heterogeneous vegetation, while pests prefer homogeneous structures (Macfadyen et al., 2015). Vegetation structure indicators, like canopy cover, diameter at breast height, plant height, and plant abundance, are useful measurements to identify habitat attributes that influence bird abundance and richness (Gould and Mackey, 2015). Canopy cover and tree richness have been associated

positively with bird species diversity, whereas plant species diversity per se showed little effect (Roels et al., 2019). Bird abundance and composition vary according to different degrees of changes in the vegetation structure (Casas et al., 2016; Davis, 2004; Jacobs et al., 2012) and vegetation type (Gould & Mackey, 2015).

Casas et al. (2016) examined the influence of vegetation structure on bird diversity, guilds, and species composition in different successional stages of the Brazilian Atlantic rain forest. The guilds were based on preferences in diet and foraging strata: ground, understory, intermediate, and canopy. Eleven structural variables were chosen to describe vertical vegetation structure, tree density, and habitat complexity; among them, tree individuals per m², mean height (m), and standing dead trees on one square meter. Higher richness and diversity were found in advanced forests, where the vegetation structure was more pronounced, compared to initial and intermediate successional stages. Interestingly, bird diversity and species composition were similar in the intermediate and advanced stages. This highlights the importance of conservation of successional forests, especially when they are near old-growth forests (Casas et al., 2016).

The landscape composition determines the intactness of ecological functions and is a relevant dimension to be considered for biodiversity conservation (Zanella et al., 2012). Barbosa et al. (2017) found that especially the landscape composition is a good predictor for the presence of birds in small forest fragments. For example, the proximity to woodland and the distance to grazed pasture explained bird species distribution in tropical reforestation sites (Roels et al., 2019). Another relevant variable is the percentage of forest cover of a forest fragment and its surrounding (Dos Anjos et al., 2019; Gould & Mackey, 2015). Martensen et al. (2012) tested how habitat area (forest cover) and configuration (connectivity and fragment size) affected the richness and abundance of understory bird species in Atlantic forest fragments in southeastern Brazil. Below an assumed threshold of less than 30 % of the remaining forest cover, fragmentation effects should intensify. The richness for highly sensitive species increased, where forest cover was higher, especially when the amount was between 30 and 50 %. This finding suggested a higher threshold of forest cover (30-50 %) for rapid species decline than assumed before (Martensen et al., 2012). The size of forest fragments in The Brazilian Atlantic forest was found to affect large canopy frugivorous birds particularly, due to their bigger area requirements to satisfy their high energy demand, as well as the spatial and temporal variation of food availability (Uezu et al., 2005).

4.7 Modeling caterpillar predation rates by birds

In the reviewed studies, predation rates were usually indicated as the proportion of attacked caterpillars per time unit, which often was 24 h (A. Howe et al., 2009; Lövei & Ferrante, 2017;

Richards & Coley, 2007; Roels et al., 2018). Other studies used the sum of attacked caterpillars as the response variable (Maas et al., 2015). Thus, no standard methods for data collection and analysis exist. Apart from bird community variables (abundance, richness, and diversity), the explanatory variables that have been examined the most were associated with the vegetation type (Garfinkel & Johnson, 2015; A. G. Howe et al., 2015; Low et al., 2016; Moreno & Ferro, 2012; Posa et al., 2007; Roels et al., 2018; Ruiz-Guerra et al., 2012; Seifert et al., 2016; Solis-Gabriel et al., 2017; Tvardikova & Novotny, 2012), the vegetation structure (Marco Ferrante et al., 2019; Gray & Lewis, 2014; Koh & Menge, 2006; Leles et al., 2017; Lemessa et al., 2015; Loiselle & Farji-Brener, 2002; Muiruri et al., 2016; Poch & Simonetti, 2013; Richards & Coley, 2007), as well as the proximity to natural forests (Maas et al., 2015; Milligan et al., 2016; Roels et al., 2018), and edge effects (Berezki et al., 2014; Marco Ferrante et al., 2017; Koh & Menge, 2006). Predation rates were modeled most frequently with General linear mixed models (GLMM) with a binomial distribution and logit link function (Berezki et al., 2014; Marco Ferrante et al., 2017, 2019; Garfinkel & Johnson, 2015; Gray & Lewis, 2014; A. G. Howe et al., 2015; Lemessa et al., 2015; Milligan et al., 2016; Muiruri et al., 2016; Posa et al., 2007; Roslin et al., 2017; Seifert et al., 2016; Solis-Gabriel et al., 2017). These models are mixed since they contain fixed and random components, and therefore can account for the violation of the independence of the data (Zuur et al., 2009). Generalized linear models (GLM) were also used, primarily assuming a binomial distribution (Marco Ferrante et al., 2014, 2017; Koh & Menge, 2006; Low et al., 2016; Molleman et al., 2016; Roels et al., 2018), or a normal distribution (Leles et al., 2017). Few studies applied simple linear regression models (LM) (Fáveri et al., 2008; Maas et al., 2015). Model selection was mainly based on the for small samples corrected Akaike information criterion AICc (for more details, please see 6.7.3.3 in methods) (M. Ferrante et al., 2017; Marco Ferrante et al., 2017; Leles et al., 2017; Maas et al., 2015; Milligan et al., 2016). There is no standard model that fits all data sets and research questions, therefore, the comparison of different models of choice is required. The AIC helps to identify the most suitable model by comparing their quality, using the relative amount of information loss as a criterion (Cavanaugh, 1997; Dormann, 2013).

This study addresses the role of forest remnants in the Brazilian Atlantic forest for the conservation of birds, their ecological function pest control, and the contribution to the preservation of avian ecosystem services. The investigation focuses on the so far under-researched small forest fragments (< 50 ha). The study area contains many fine-grained remnants, which gain in conservation importance through their integration into the bigger regional cluster of the National Forest of Ipanema (FLONA). Suitable methods are necessary that can quantify ecosystem functions representatively. Therefore, the assessment of bird predation rates with artificial caterpillars will

be carried out for the first time on a university campus in a peri-urban area in southeastern Brazil. Urbanization processes will keep transforming natural forests into mosaics of fragmented habitats and urban landscapes, like in the case of peri-urban regions. These habitats will increasingly define the composition of bird communities. The study wants to account for the lack of researches in the Neotropics and peri-urban forest fragments in the Atlantic forest biome. There is a need to improve knowledge about which factors of habitat and community interactions define the success of predation events on a local and landscape scale. Since the vegetation structure is an essential ecosystem component, which defines the diversity and habitat preferences of birds, this study aims to assess which structural components of forest fragment vegetation influence the regulation of caterpillar populations by birds. It is expected that the results will show a pattern of specific variables that are most likely related to high predation rates. In particular, high predation rates are associated with sites where insectivorous birds are most abundant, and the vegetation structure is more heterogeneous.

5 Main objectives and research questions

This thesis seeks to quantify the ecosystem function pest control by insect-eating birds in secondary forest fragments, by using artificial caterpillars. The structural characteristics of a forest affect the habitat preferences of different bird species. Thus, it will be assessed which structural components of the forest fragment vegetation, together with the recorded bird community variables (abundance, richness, α -diversity), best explain the estimated caterpillar predation rates by insectivorous birds.

The relation between predation rates, bird community traits, and vegetation structure is discussed, and it is concluded what the results would mean for future bird conservation projects, regarding the vegetation structure and landscape composition of the forest fragments in the peri-urban study area.

Research questions

Characterization of the bird community

- How many diet groups of bird species can be identified, and what are their proportions?
- Which of the recorded bird species are possible artificial caterpillar attackers?
- What are the relative abundances of the recorded insect-eating bird species, and which ones have been recorded the most?
- How does abundance, richness, and diversity (Shannon-Wiener-Index) of insect-eating bird species vary between the eight sampling locations?

Characterization of the forest habitat

- What do the structural forest variables canopy cover, canopy height, dead trees, tree density, and understory profile look like at each sampling location?
- What do the landscape variables percentage of forest cover and distance to urban campus look like at each sampling location?

Attacked caterpillars and predation rates

- How many artificial caterpillars have been exposed, recovered, and attacked?
- How many predator groups can be identified for the attacked caterpillars, and what are their proportions?
- What do relative predation rates of the predator groups look like for the three different caterpillar placement treatments (Leaf: 1.5 – 2.0 m / stem: 0.5 – 1.0 m / ground)?
- What are the predation rates for insect-eating birds at each sampling point?
- How are caterpillar predation rates, bird abundances, richness, and forest vegetation structure correlated?

Explaining predation rates

- Which model of the habitat variables, together with the bird community variables, explain the estimated caterpillar predation rates best?

6 Methods

6.1 Study area

The study was conducted on the UFScar (Universidade Federal de São Carlos) campus Sorocaba (23°34'55.43"S, 47°31'27.02"W, elevation: 635-670 m a.s.l. (Kortz et al., 2014)) in the state of São Paulo, southeastern Brazil (fig.1). The area forms part of the Atlantic rainforest biome, one of the most threatened biodiversity hotspots in the world. The administrative region of Sorocaba is considered one of the places with the highest remaining vegetation cover in the state of São Paulo (Kortz et al., 2014). The region's biogeography is characterized by the coincidence of seasonal semideciduous forest and the Brazilian Cerrado (tropical savanna) (Kortz et al., 2014). Thus the area contains species of both ecoregions, which makes it highly relevant for biodiversity conservation (Tauhyl & Guimarães, 2012). The study area is determined by an average annual temperature of 22 °C and annual mean precipitation of 1310 mm (Tauhyl & Guimarães, 2012). According to Köppen, the climate classification lies between humid subtropical with dry winter and temperate (Cwb) summer and hot (Cwa) summer (Alvares et al., 2013; Kortz et al., 2014; Tauhyl & Guimarães, 2012). The relief merges two contrasting morphological units: the crystalline Atlantic Plateau and the mainly sedimentary Peripheral Depression of São Paulo (Villela et al., 2013). Hence, the broader landscape is characterized by alternating rough, steep hill landforms towards the south, and smooth, broad hill landforms northwards (Villela et al., 2013). The local study area terrain is, therefore, hilly with varying steepness that locally reaches up to 45 %. The soil is classified after the Brazilian system as Dystrophic Red Latosol (Oxisol) with a moderate horizon and heavy clay (Kortz et al., 2014; Tavares Filho et al., 2010).

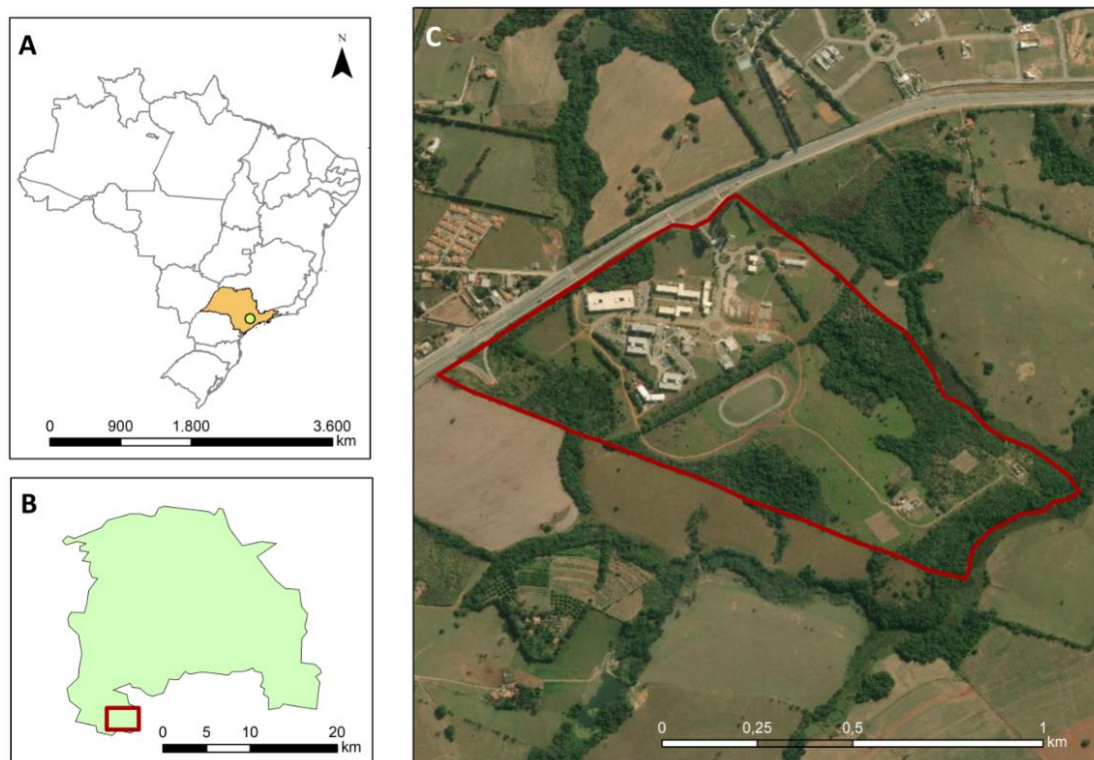


Figure 1 Location of the study area at three different scales.

A) Location of the state of São Paulo (orange) and the city of Sorocaba (green) in Brazil. B) Location of the UFScar university campus (red rectangle) in the city of Sorocaba. C) Boundary of the UFScar university campus with the forest fragments. Credits: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/ Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS user community.

The campus lies in the southwestern outskirts of the city, in a peri-urban matrix. The typical biogeographical transition zones between the Atlantic forest and Cerrado consists of a mosaic (Bhakti et al., 2020), which is here composed of the urban infrastructure of the university campus, secondary forest fragments, and adjacent monocultural fields of predominantly grassland. It comprises a total area of approximately 70 ha (Google Earth Pro, 2020; see fig.1).

The forest remnants are mostly located at the lower slopes towards the border of the campus. During the fieldwork in 2020, the forest patches were perceived as very small and narrow patches, but still different in their shapes. The terrain was mostly plain, with slight slopes towards the outer rim of the study area. Except for two creeks in the first fragment, no waterbodies were detected. In general, the secondary forestage was between 10 and 20 years, belonging to the initial and intermediate successional stages, and the tree stands were widely distributed. They are the result of a reforestation project with the idea of renaturalizing the former pasture, which historically had been used intensively as cattle grazing ground. A total of eight sampling locations were visited (sampling points) in the secondary forest fragments (fig. 2 & 3).

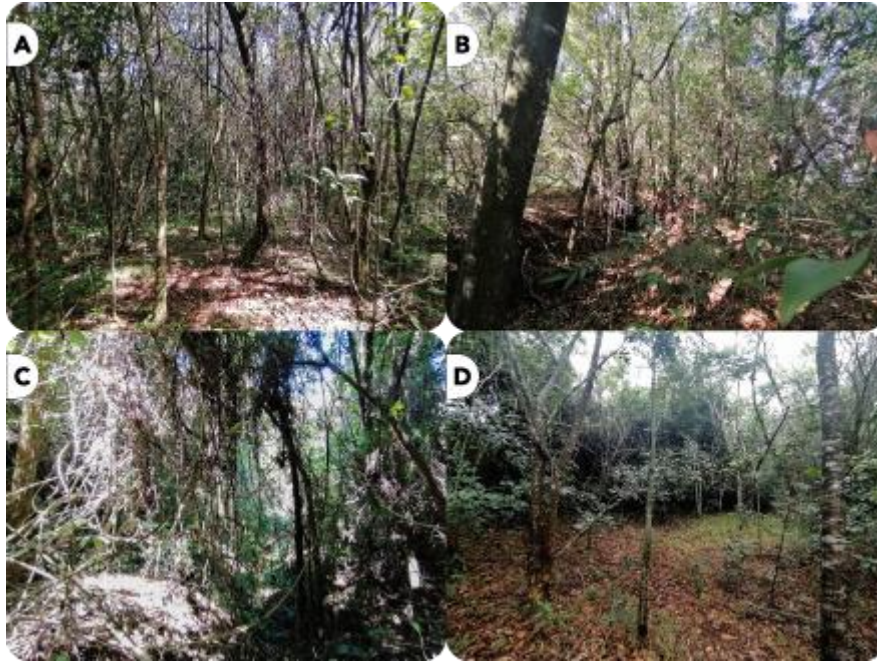


Figure 2 Pictures of the secondary forest fragments at the sampling locations one to four.

A) Point one (CU1). B) Point two (CU2). C) Point three (CU3). D) Point four (CU4).

Currently, the forest fragments are unmanaged and undisturbed and hold great potential as a refuge for many species in the otherwise cleared, forest-less landscape. Kortz et al. (2014) identified the floristic families with the greatest richness on the campus: Fabaceae, Myrtaceae, Euphorbiaceae, Lauraceae, and Melastomataceae. He recorded species that typically occur in the seasonal semideciduous forest, for example, *Aspidosperma olivaceum* Müll.Arg. and *Guarea kunthiana* A.Juss. Typical species of the Cerrado in São Paulo state included *Caryocar brasiliense* Cambess., *Schefflera vinosa* (Cham. & Schltdl.) Frodin & Fiaschi, *Miconia albicans* (Sw.) Triana and *Styrax ferrugineus* Nees & Mart., among others (Kortz et al., 2014).

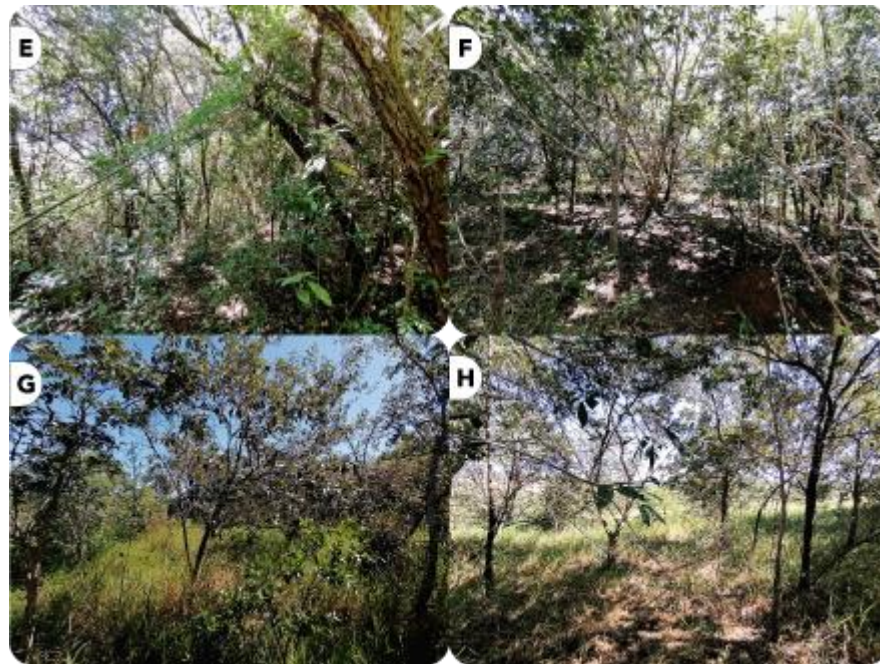


Figure 3 Pictures of the secondary forest fragments at the sampling locations five to eight.

E) Point five (CU5). F) Point six (CU6). G) Point seven (CU7). H) Point eight (CU8).

6.2 Overview graphics of the methods

In the following, the methods are displayed in two overview schemes, which describe the work steps for the preparation and execution of the fieldwork (see fig. 4), as well as the preparation and statistical analysis of the data (see fig. 5).

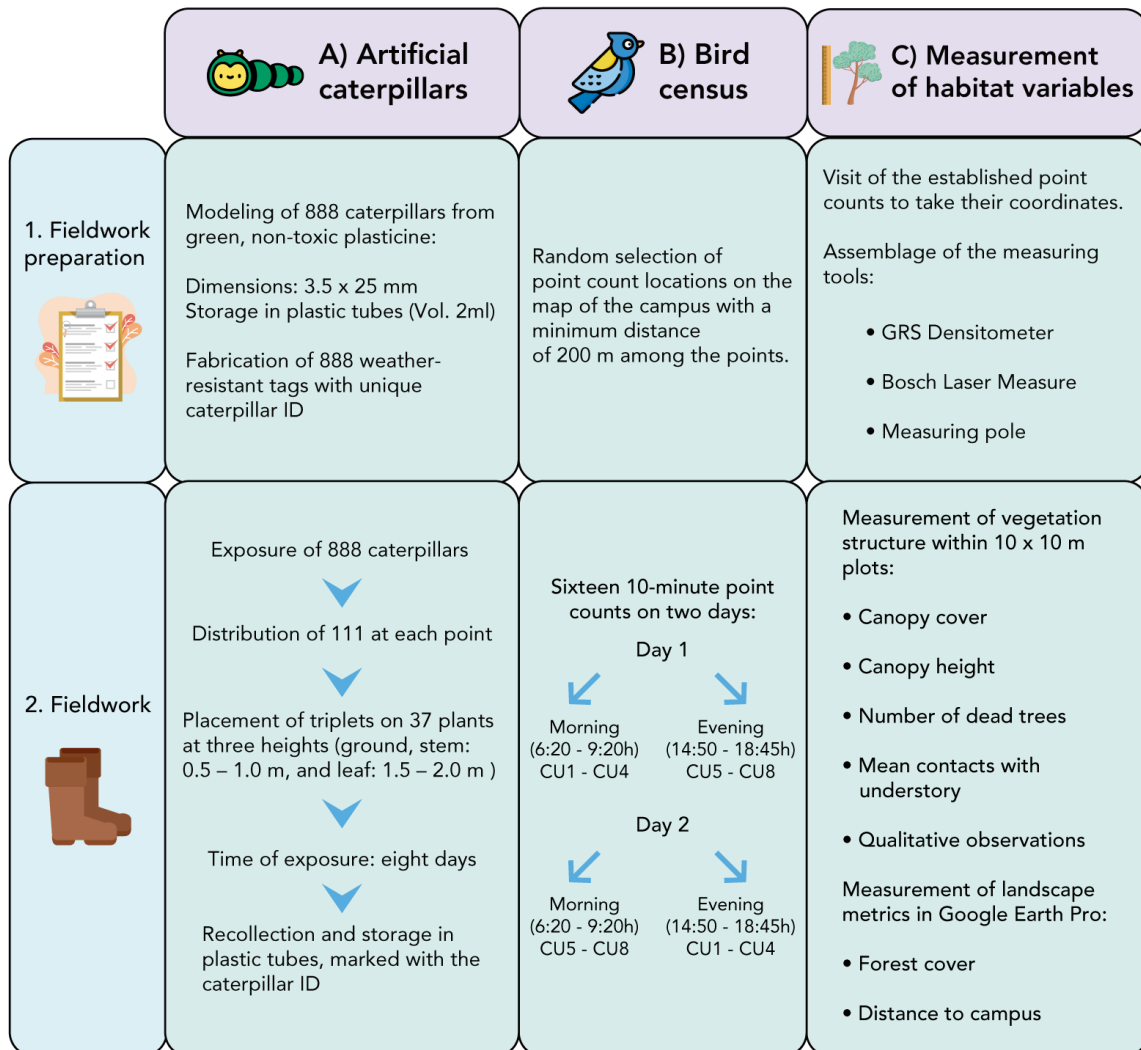


Figure 4 Overview graphic of the methods for preparing and carrying out the fieldwork. The work steps are shown for the three categories of data collection: the artificial caterpillar experiments, the bird census and the measurement of the habitat variables.

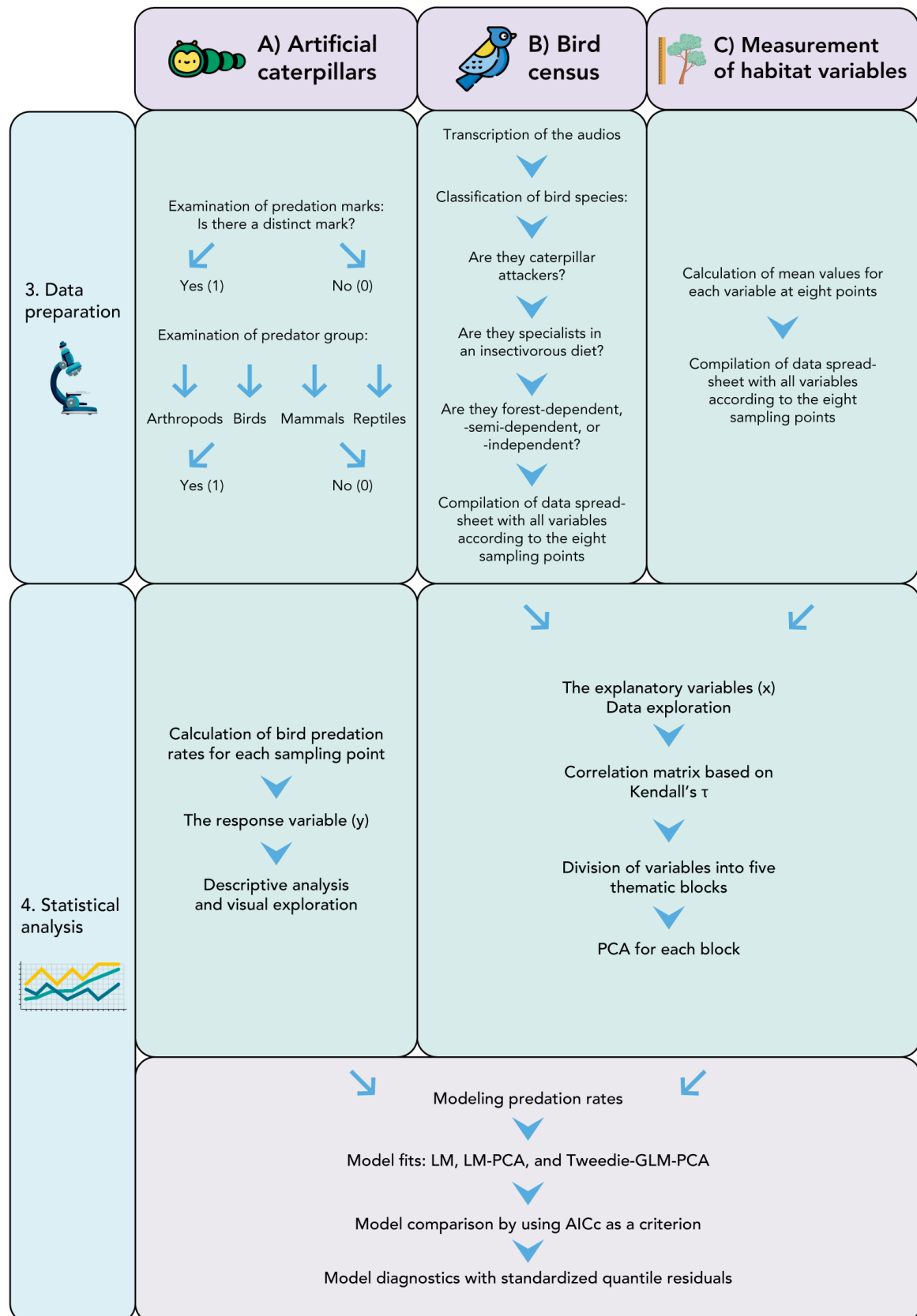


Figure 5 Overview graphic of the methods for preparing and carrying out the data analysis. The work steps are shown for the three categories of data collection: the artificial caterpillar experiments, the bird census and the measurement of the habitat variables.

6.3 Experimental design

Eight sampling locations, which are referred to as sampling points, were selected randomly in the forest fragments and with a minimum distance of 200 m to each other, to meet the independence criterion for bird counts (Bibby et al., 1992).

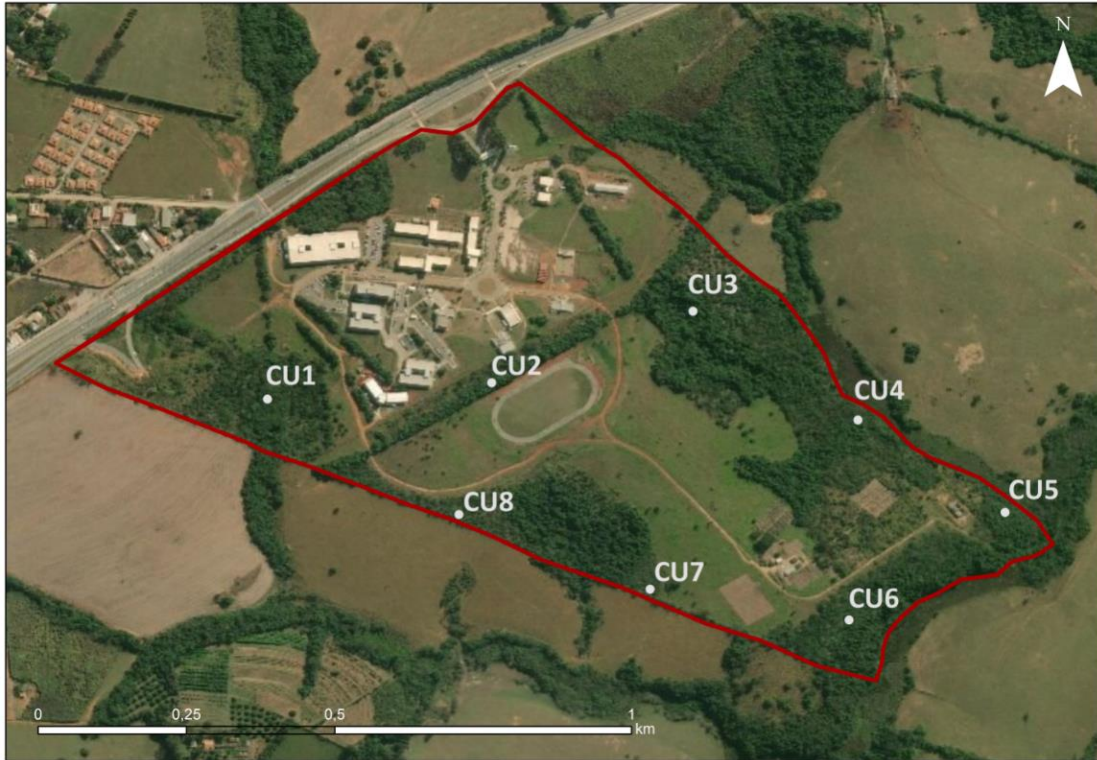


Figure 6 Locations of the eight sampling points (CU1 - CU8) within the secondary forest fragments on the UFscar university campus.

Credits: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/ Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS user community.

At each point, a circle of 25 m radius was determined (see fig. 7). It was the reference for the point count of birds, as well as the boundary for distributing the artificial caterpillars. The center of the point also marked the intersection point of two ten m-transects, creating a 10 x 10 m plot (see fig. 7). This plot sampling method is typical for quantitative forest studies in Brazil (Cielo-Filho et al., 2011), and was used to measure the vegetation structure. For measuring the canopy cover, four additional diagonal transects, surrounding the intersected main transects, were considered (Stumpf, 1993) (see fig. 7). All experiments were conducted during the 13th of March and 17th of April 2020, which is late summer, early autumn, in southeastern Brazil.

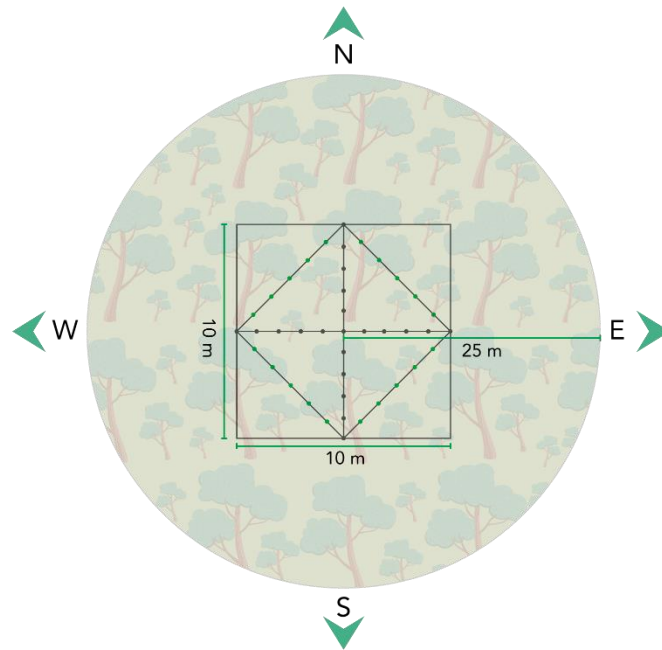


Figure 7 Scheme of the structure of one sampling point. The outer circle represents the boundary of the point count. The square indicates the 10 x 10 m plot and contains the six transects. The shown dimensions are not true to scale.

6.4 Artificial caterpillar experiments

A total of 888 artificial caterpillars, in the following referred to only 'caterpillars', were modeled from nontoxic green plasticine (Modeling Clay from Acrilex) (Howe et al., 2015; see fig. 9 A). The color was chosen to mimic the cryptical coloration of Lepidoptera larvae (Ferrante et al., 2017), and to represent not species-specific, herbivorous caterpillars (Low et al., 2014; Nell et al., 2018; Roels et al., 2018). They were shaped manually into approximately 3.5 x 25 mm roles on a flat stone surface to ensure a smooth surface (Howe et al., 2009) and stored in plastic tubes (Vol. 2 ml; Eppendorf type) for transportation (see fig. 9 A). In the field, 111 caterpillars were distributed at each sampling point within a radius of 25 m (point count circle) and were marked with tags, showing a unique ID for each caterpillar. The caterpillars were attached with non-toxic glue (Pritt white glue, 110 g) and placed on 37 plants in groups of three (see fig. 8): one on the leaf (T= top, height≈ 1.5 – 2.0 m), the stem (M= middle, height≈ 0.5 – 1.0 m) and the ground (G= ground, height≈ 0 m) with a minimum distance of 1m to the next plant (Howe et al., 2015; Leles et al., 2017; Roels et al., 2018;

see fig. 9 B-D). These treatments (T, M, G) were applied to address the different foraging behaviors of insect-eating birds and to achieve a more authentic outcome.

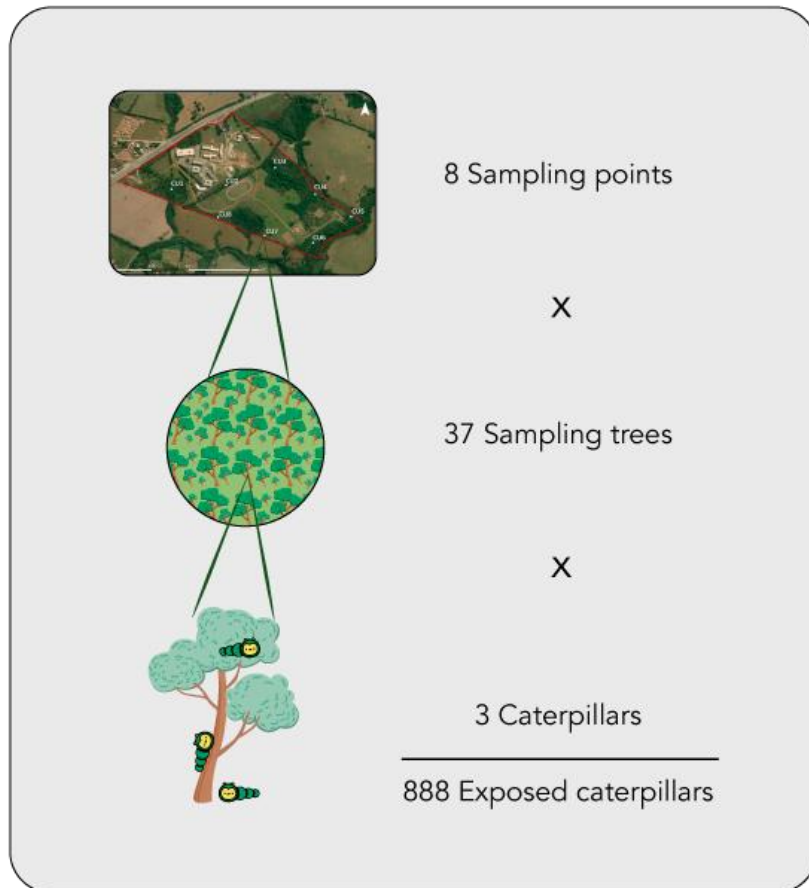


Figure 8 The caterpillar placement criteria on three scales. Within each of the eight sampling points, 37 sampling trees were selected with a minimum distance of 1 m among the plants. On each tree, three caterpillars were placed at three heights: on the leaf (1.5 – 2.0 m), the stem (0.5 – 1.0 m), and the ground. A total of 888 caterpillars were exposed. Credits: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/ Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS user community.



Figure 9 The three treatments of caterpillar placement.

A) One artificial caterpillar in a plastic tube. B) Caterpillar on the leaf (T= top, height≈ 1.5 – 2.0 m), C) the stem (M= middle, height≈ 0.5 – 1.0 m), D) and on the ground (G= ground, height≈ 0 m).

After eight days in the field, the caterpillars were recollected. They were stored in plastic tubes, labeled with the corresponding caterpillar ID, and transported to the laboratory for further analysis (Howe et al., 2015; see fig. 10). In the first step, it was assessed if the recovered caterpillars presented a predation mark, other than from impressions caused by handling the caterpillars in the field. In the case of a predation mark, at least one photo was taken. In the second step, these caterpillars were assigned a broad predator group, by comparing them with the representative images of Low et al. (2014) and the "Guide to bite marks" from Tvardikova ("n.d."), recommended in Leles et al. (2017). It was expected to find at least predation marks of arthropods, birds, and mammals (Howe et al., 2009). Each caterpillar was assigned only one predator group, always prioritizing bird marks, if several marks were found on the same exemplar. The absence and presence of a predation mark were coded as 0 and 1 for all identified predator groups.

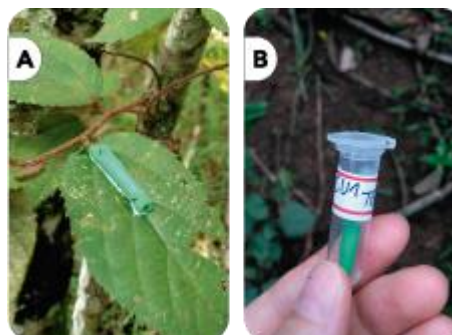


Figure 10 Caterpillar recovery in the field.

A) Caterpillar with beak marks at both ends. B) Recovered caterpillar in plastic tube, labeled with the corresponding caterpillar ID.

6.5 Bird census

During two consecutive days, sixteen 10-minute point counts were conducted at the eight sampling points (see fig. 6). On the first day, the sites 1 to 4 were visited during the morning (6:20 – 9:20 a.m.) and 5 to 8 during the evening (2:50 – 6:45 p.m.). On the second day, points 5 to 8 were visited in the morning and points 1 to 4 in the evening. For 10 minutes, all species audibly or visually identified within a 25 m radius were counted. This method is based on the catch per unit effort principle, which relies on the standardized effort of observation (here 10 min.) to avoid data bias and make studies comparable (Bibby et al., 1992). Overflying individuals were not considered. Every point count was recorded with a microphone (Zoom H4nPro Handy Recorder) for subsequent species identification. The transcription and evaluation of the audio files were realized by the local avifauna expert Prof. Dr. Augusto Piratelli, who was also present during the point counts in the field. The abundance of species was estimated as the total number of contacts (audible or visual observations) at each sampling point. The estimation can be done due to the same sampling effort at each site (two times 10 minutes), accounting for the small number of records (sixteen point counts). If the same species appeared several times during one counting, it was recorded only once, since it is not assured that these were different individuals. The recorded bird species that most likely predated the caterpillars were identified by their diet class and foraging stratum, according to Wilman et al. (2014), and based on the study of Casas et al. (2016). A diet of min 40 % invertebrates defined potential caterpillar attackers, as well as a foraging behavior within at least one of the following strata: ground-, understory-, or mid-high- strata. All other species were excluded from the dataset for further analysis. As species specialized in an insectivorous diet, a minimum of 70 % of invertebrate feeding (Wilman et al., 2014) was set as a criterion. For classifying the insect-eating bird species according to their forest dependency, different studies were compared (Campos-Silva & Piratelli, 2020; Coelho et al., 2016; Da Silva, 1995; Giraudo et al., 2008; Stotz et al., 1996), and three categories were identified: forest-dependent, -semi-dependent, and -independent. Since the study was interested in forest-associated bird species, forest-dependent and semi-dependent species were combined, and forest-independent birds went under the name of species of open-habitats. The Shannon-Wiener-Index was calculated as a measure of α -diversity of the bird community, for each sampling site. The Shannon index was calculated as

$H' = -\sum p_i \ln p_i$, where p_i is the relative abundance of the i th species compared with all species identified in a sample (Ruiz-Guerra et al., 2012). The index considers the number of species (richness), and the evenness of their abundance (number of individuals), or similarity of different species in a sample. Therefore, the index increases, the more species are in an ecosystem, or the greater becomes the evenness of its individuals (Ruiz-Guerra et al., 2012).

6.6 Measurement of habitat variables

6.6.1 Vegetation structure metrics

After placing the caterpillars in the field, and before measuring the environmental variables, two to three days passed, to let disturbances of the natural system settle. All variables were measured within the 10 x 10 m sampling plots (fig. 7).

For measuring the canopy cover, a line-point transect sampling method was applied as described by Stumpf (1993). The two intersecting and four surrounding transects were walked by one-meter-steps, that set a point (total of 41 points per plot), where the canopy was recorded as absent or present (0-1), using a vertical GRS Densitometer (Stumpf, 1993). The quantitative data was complemented by photos of the canopy and a rough sketch of shadow and light at each point.

The canopy height was estimated as the mean height of the tallest trees in the plot. Direct measurements with, e.g., a laser rangefinder, were not possible because trees could not be captured in their whole length, standing within the forest with a dense canopy. The estimation was conducted in four steps: first, standing below the tree, the distance to the highest visible point of the canopy was measured with a laser measurement device (Bosch Laser Measure). Second, the length from the device to the ground was measured equally. Third, the missing distance to the top of the canopy was estimated visually. The total canopy height of one tree was the sum of all values. The procedure was repeated for the highest individuals within the plot. Fourth, the mean value of the estimated canopy heights was built for each sampling site.

The number of dead trees was counted in each plot. For obtaining the tree density, all trees were counted within 100 m² (10 x 10 m plot), considering only individuals of minimum 1.50 m height. For a density profile of the understory, the number of contacts (frequency) of the vegetation with a measuring pole at several fixed levels (0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.25 m) was recorded. The recording was done while walking the two cross-intersected transects (2 x 10 m) within the plot (see fig. 7), holding the measuring pole upfront.

Qualitative observations were made additionally at each sampling point to characterize the habitat. Notes were taken regarding the topography, presence of water bodies, perceived canopy height, number of vegetation strata, litterfall, the density of ground vegetation, estimated forest age, perception of forest density, and dominant trees

6.6.2 Landscape metrics

The local vegetation variables were complemented by two landscape metrics to characterize the habitat: the percentage of forest cover within a radius of 100 m and the minimal distance to the campus. The latter represents the proximity to anthropogenic disturbances, like noise. Both were obtained by using the ruler tool in Google Earth Pro (2020) on an image taken on the 28th of April 2020, shortly after the field research was completed. The method to estimate the percentage of forest cover was inspired by Duhl et al. (2012): circles of an approximate radius of 100 m were laid around each sampling point, and its total area was calculated as $\pi * r^2$. Within each circle, the biggest coherent forest patches, single trees were not included, were traced, creating polygons of the forest cover (fig.11). The percentages were calculated for each site, dividing the polygon's area

by the total area of the circle and multiplying with 100: $\frac{A(\text{polygon})}{\pi * r^2} * 100$

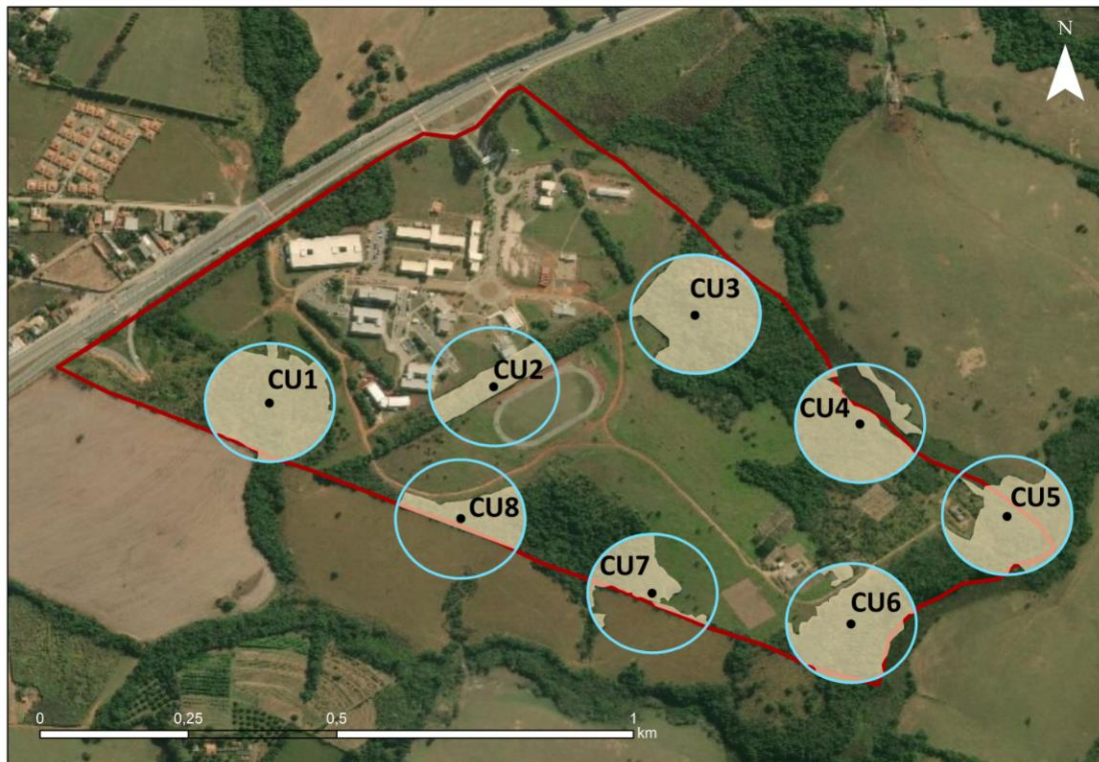


Figure 11 Representation of the landscape variable ‘forest cover’.

The blue circles determine a radius of 100 m around the sampling points. The beige polygons within the circles delimit the area of the forest cover. Credits: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/ Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS user community.

The campus' outline was traced and was taken as a reference for determining the distance to the university. With the ruler tool, the minimal distance from the points' centers to the campus' border was measured in m (fig.12).

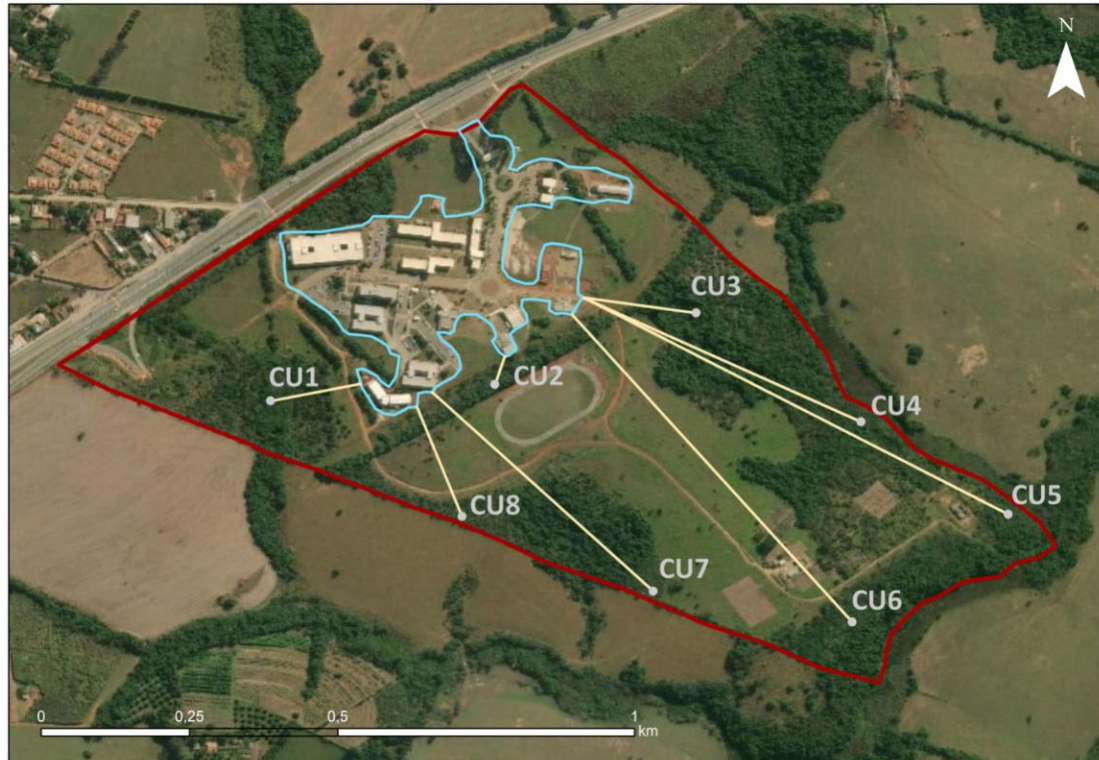


Figure 12 Representation of the landscape variable 'distance to the campus'. The blue polygon delimits the urban structures of the campus. The beige lines measure the minimal distance to the blue polygon. Credits: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/ Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS user community.

6.7 Explaining predation rates

6.7.1 Exploring the response variable 'predation rates'

The predation rates are the calculated proportions of predated caterpillars per sampling site (Leles et al., 2017). For further analysis, they refer to only the ones predated by birds. They were calculated as the sum of predated caterpillars (attacks), divided by the number of recovered caterpillars at each sampling point: $\frac{\text{Sum(attacks) at point } i}{\text{Sum(caterpillars) at point } i}$. The rates refer to a time unit of eight days, the whole time, the caterpillars were exposed in the field. The small sample size results from the study area, which allowed to sample only eight locations (see fig. 6). Therefore, eight replicates of predation rates were obtained and compose the response variable (dependent variable y) that

is to be explained. This general restriction is affecting all further analysis. It results from the adapted experimental design, which is attributed to the unforeseen change of the study area due to limitations of COVID-19 in Brazil in 2020. Initially, the experiments with artificial caterpillars were planned in the FLONA and on two farms in the surrounding rural area. Yet, the national park closed, and the farms could not be visited anymore, which is why the study was carried out alternatively in the forest fragments on the university campus. All statistical analysis was performed with RStudio (v4.0.2) (RStudio Team, 2020), and $\alpha < 0.05$ was used as a significance threshold for all hypothesis tests.

First, the data was explored with simple descriptive statistics, showing the mean, median, and range (min. and max.), as well as the 1st and 3rd quantiles with the "summary" function in the package {base}, and the standard deviation with "describe {Hmisc}". The data's skewness was assessed by comparing the distances between the median and the quantiles: with a symmetrical distribution, the 1st quantile deviates from the median as far as from the 3rd (Dormann, 2013). For a visual exploration of the predation rates, the data was plotted, with a density histogram and empirical density distribution, as well as with a boxplot and scatterplot (Dormann, 2013). To test for normality, a Jarque Bera Test was applied, with the null hypothesis that the data is normally distributed (Thadewald & Büning, 2007). A Kruskal-Wallis test was conducted to test if predation rates differ between the three caterpillar treatments (T,M,G) (Roels et al., 2018), using "kruskal.test {stats}" in R.

6.7.2 Exploring the explanatory bird and habitat variables

6.7.2.1 Correlations based on Kendall's τ

Correlation between all variables was tested using the Kendall rank correlation coefficient with the null hypothesis of independence between variables. The coefficient's value ranges between -1 (perfect negative correlation) and 1 (perfect positive correlation), with zero being the absence of correlation (Abdi, 2007; van Doorn et al., 2018). The output for each pair of variables was tested for its significance with the p-value based function "cor.mtest {corrplot}". The result was summarized in a correlation matrix and graphically displayed as a correlogram with "corrplot {arm}".

6.7.2.2 Division of variables into five thematic blocks

The explanatory variables were grouped into five blocks, according to their thematic context. The classification was done to summarize information and structure the data for more accessible analysis (table. 1).

Table 1 Division of the explanatory variables into five thematic blocks.

Block	Variables
1	Caterpillar placement treatments: T, M, G
2	Numerical description of the recorded bird species: abundance, richness, and diversity (Shannon-Wiener-Index)
3	Classification of the recorded bird species: specialists, generalists, forest and open area species
4	Vegetation structure: canopy cover, canopy height, dead trees, tree density, mean understory contacts
5	Landscape variables: forest cover and minimal distance to campus

6.7.2.3 Principal component analysis (PCA)

The principal component analysis (PCA) is a technique in multivariate analysis to represent correlated variables in an organized and uncorrelated way. The analysis is based on a correlation matrix that here was calculated with Kendall's τ in the previous step, and decomposes its Eigenvalues, which refer to the total variance explained by each variable. The PCA was conducted for each block of variables separately. Herefore, all variables are plotted, and a line that covers the most extensive dispersion of the value points is determined. This line is called the principal component, and each additional one is constructed orthogonally on the previous one. By rotating the initial coordinate system, the variables are projected into the orthogonal space, which makes them uncorrelated. The great advantage of using the principal components for further analysis is that they solve the collinearity problem and reduces the information to the essential part (Dormann, 2013; Wold et al., 1987). In R, the PCA was conducted using "princomp {stats}". Afterward, the Eigenvalues, as well as the cumulative explained variance, were plotted for each component. Only the components with the highest percentage of explained variance were taken into the models.

6.7.3 Modeling predation rates

6.7.3.1 Model fits: LM, LM-PCA, and Tweedie-GLM-PCA

Three candidate regression models were run to explain the dependent variable predation rates (y) for each variable block separately. A linear model (LM) with all variables was fitted with "step(lm {stats})", assuming a normally distributed y . This model was also the basis for model comparison and selection. The second linear model was conducted using only the relevant principal component from the PCA as the explanatory variable (LM-PCA). The corresponding principal component was selected by its proportion of explained variance. The last model consisted of a generalized linear model (GLM), applying "glm {stats}" with the principal component and assuming a Tweedie distribution (Tweedie-GLM-PCA).

6.7.3.2 The Tweedie distribution and the estimation of its parameter Tweedie Power

The Tweedie distributions are a family of probability distributions that belong to the exponential dispersion models. Therefore, they are often used for generalized linear models (GLMs) (Candy, 2004; Dunn & Smyth, 2005; Swallow et al., 2019). The Tweedie model is used as an alternative in this study to more common models. Since it is not a standard distribution, it is presented in more detail in this sub-chapter. The mean-variance relationship characterizes this distribution class. Unlike many other distributions, this relation does not need to be specified in advance, already making assumptions about a concrete distribution, but will be fitted with the model. This characteristic makes the Tweedie family very flexible in its application. They contain many standard distributions as special cases, e.g., Normal, Poisson, Gamma (Dunn & Smyth, 2005; Swallow et al., 2019). Apart from the mentioned distributions, the other Tweedie models don't have explicit forms of density functions (Dunn & Smyth, 2005).

Mathematically the Tweedie distribution is defined by the mean μ and the variance $\varphi\mu^p$, where φ is a positive dispersion parameter and $p \notin (0, 1)$ a real-valued index parameter. This index parameter is also called the Tweedie Power, controlling the shape of the distribution (Dunstan et al., 2013; Swallow et al., 2019). It was estimated with the "tweedie.profile {tweedie}", using maximum likelihood as criteria (Dunstan et al., 2013).

The power mean-variance relationship of the Tweedie distribution describes the variance function of Taylor's Universal Power Law: $Var(Y_{ji}) = a\mu_i^b$. This relation has been observed in ecology and describes the spatial clustering of species. The mean and variance of population abundances submitted to perturbations is expected to reach a "statistical equilibrium" over time (Jørgensen et

al., 2011). Therefore, the Tweedie distribution is often used in ecological and environmental sciences (Swallow et al., 2019), e.g., for species distribution modeling of fish and marine megafauna (Candy, 2004; Dunstan et al., 2013; J. D. Mitchell et al., 2018; Virgili et al., 2018). It especially applies to studies with data with a strong mean-variance relationship, like presence-absence data of, e.g., few sightings or rare species (Virgili et al., 2018), or count data (Dunstan et al., 2013).

6.7.3.3 Model comparison by using AICc as a criterion

The AICc is the corrected Akaike information criterion (AIC) for small samples. It is used to compare the minimized information loss of candidate models and is a basis for model selection. Therefore, the model with the lowest AICc is selected (Cavanaugh, 1997; Dormann, 2013). The AICc was calculated for each candidate model. For the models with the best fit, the linear regression line was plotted against the observed values of the caterpillar predation rates. The formula is an extension of the regular AIC: $AICc = AIC + \frac{2k(k+1)}{n-k-1}$, with k = number of parameters, and n = number of observations. For large n , AICc converges to AIC (Spiess, 2020).

6.7.3.4 Model diagnostics with standardized quantile residuals

Residuals are the differences between observed and predicted values and are commonly used for model diagnosis (Dormann, 2013; Scudilio & Pereira, 2017). A Quantile-quantile plot (Q-Q plot) is a visual way to compare two probability distributions by plotting their quantiles. Here, this was done to assess the normality of the residuals (Zuur et al., 2009). The standardized quantile residuals were compared to the standard normal distribution $N(0,1)$. If the quantiles lie approximately on the 45 ° line ($y=x$), the distributions are similar. First, the residuals were estimated with "plotSimulatedResiduals {DHARMA}" and then plotted with "plotQQunif {DHARMA}". This diagnosis procedure was realized only for the models with the lowest AICc value.

7 Results

7.1 Characterization of the bird community

In sixteen point counts of the secondary forest fragments, 106 birds, belonging to 30 species were recorded (see table 2). Following the classification of Wilman et al. (2014), five diet groups were detected: Frugivores, Granivores, Insectivores, Nectarivores, and Omnivores. Strictly insectivorous birds were the largest group, with a proportion of 44 % (47/106) (fig. 13).

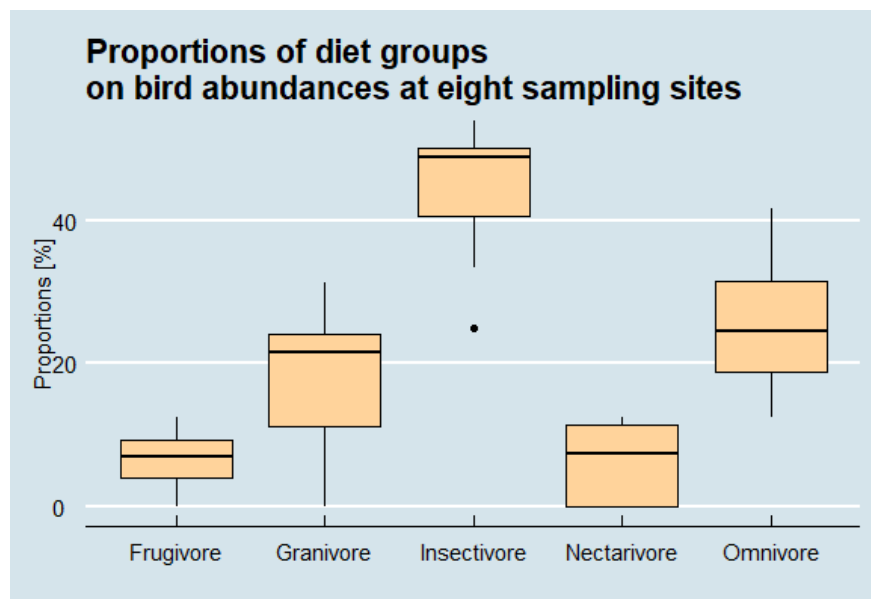


Figure 13 Proportions of five diet groups on bird abundances at eight sampling sites.

The boxplots show the median (black horizontal line), the lower $q_n(0.25)$ and upper $q_n(0.75)$ quartiles (lower and upper box limits), as well as the lowest and the largest data point (black vertical lines) excluding any outliers (black dot).

Most species ($14/72 = 74\%$) were identified as mainly forest-semi-dependent and forest-dependent species, based on Campos-Silva & Piratelli (2020), Coelho et al. (2016), Da Silva (1995), Giraudo et al. (2008), and Stotz et al. (1996) (table 2).

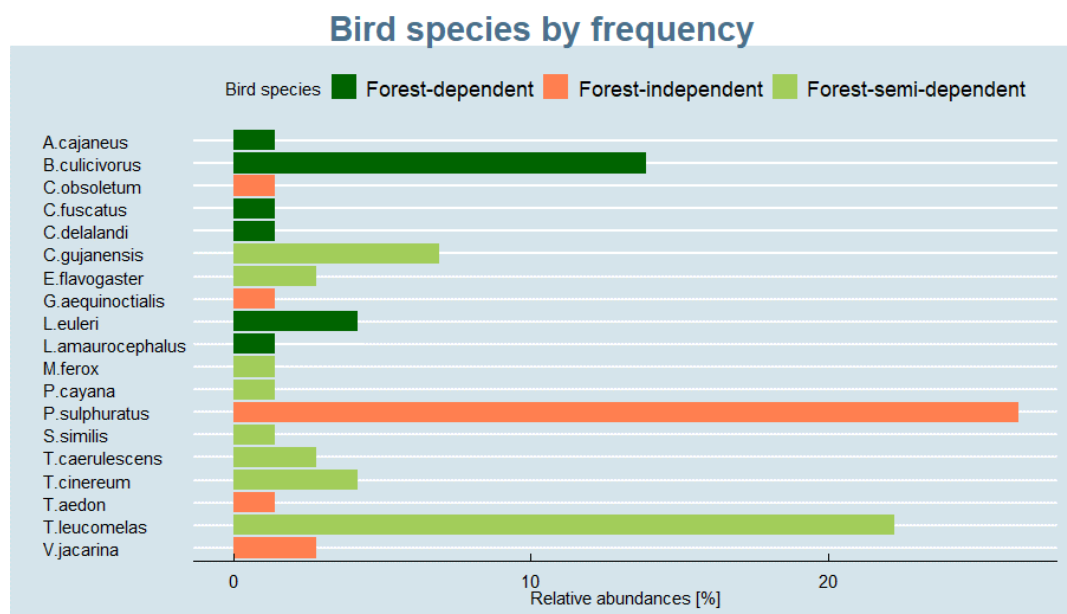
Table 2 Birds species recorded in sixteen point counts in the sampled secondary forest fragments on the UFScar campus in Sorocaba, São Paulo, Brazil.

Diet groups: N= Nectarivore, O= Omnivore, I= Insectivore, F= Frugivore, G= Granivore. Forest dependency: 1= independent, 2= semi-dependent, 3= dependent.

Scientific name	Common name	Total abundance	Diet group	% of invertebrates on diet	Foraging strata	Caterpillar attackers	Forest dependency
<i>Amazilia lactea</i>	Sapphire-spangled Emerald	1	N	10	understory/ midhigh/ canopy/ aerial	No	
<i>Anthracothorax nigricollis</i>	Black-throated Mango	1	N	10	canopy/ midhigh/ aerial/ understory	No	
<i>Aramides cajaneus</i>	Grey-necked Wood-rail	1	O	50	water-aroundsurf/ ground	Yes	3
<i>Basileuterus culicivorus</i>	Golden-crowned Warbler	10	I	80	understory/ midhigh	Yes	3
<i>Camptostoma obsoletum</i>	Southern Beardless-tyrannulet	1	I	70	midhigh/ canopy	Yes	1
<i>Cnemotriccus fuscatus</i>	Fuscous Flycatcher	1	I	100	ground/ understory/ midhigh	Yes	3
<i>Corythopsis delalandi</i>	Southern Antpipit	1	I	90	ground/ understory	Yes	3
<i>Cyclarhis gujanensis</i>	Rufous-browed Peppershrike	5	I	100	understory/ midhigh/ canopy	Yes	2
<i>Elaenia flavogaster</i>	Yellow-bellied Elaenia	2	O	50	midhigh/ canopy/ understory/ aerial	Yes	2
<i>Euphonia chlorotica</i>	Purple-throated Euphonia	1	F	0	canopy/ midhigh	No	
<i>Geothlypis aequinoctialis</i>	Masked Yellowthroat	1	I	100	understory	Yes	1
<i>Lathrotriccus euleri</i>	Euler's Flycatcher	3	I	100	understory	Yes	3
<i>Leptopogon amauro-cephalus</i>	Sepia-capped Flycatcher	1	I	80	understory/ midhigh	Yes	3
<i>Leptotila verreauxi</i>	White-tipped Dove	13	G	20	ground	No	
<i>Myiarchus ferox</i>	Short-crested Flycatcher	1	O	50	understory/ midhigh	Yes	2
<i>Patagioenas picazuro</i>	Picazuro Pigeon	6	G	10	ground/ understory/	No	

					midhigh/ canopy		
<i>Penelope supercilialis</i>	Rusty-margined Guan	1	F	10	ground/ midhigh/ canopy	No	
<i>Phaethornis pretrei</i>	Planalto Hermit	4	N	10	undertsory	No	
<i>Piaya cayana</i>	Squirrel Cuckoo	1	I	100	canopy/ midhigh	Yes	2
<i>Pitangus sulphuratus</i>	Great Kiskadee	19	O	40	ground/ understory/ midhigh	Yes	1
<i>Saltator similis</i>	Green-winged Saltator	1	I	60	understory/ midhigh	Yes	2
<i>Tangara cayana</i>	Burnished-buff Tanager	4	F	10	midhigh/ understory/ canopy	No	
<i>Thamnophilus caerulescens</i>	Variable Antshrike	2	I	80	understory/ midhigh	Yes	2
<i>Tangara sayaca</i>	Sayaca Tanager	1	O	10	canopy/ midhigh/ ground	No	
<i>Todirostrum cinereum</i>	Common Tody-flycatcher	3	I	90	understory/ midhigh/ canopy	Yes	2
<i>Troglodytes aedon</i>	House Wren	1	I	80	understory	Yes	1
<i>Turdus leucomelas</i>	Pale-breasted Thrush	16	I	70	ground/ understory/ midhigh	Yes	2
<i>Volatinia jacarina</i>	Blue-black Grassquit	2	O	40	ground	Yes	1
<i>Zenaida auriculata</i>	Eared Dove	1	G	0	midhigh/ ground/ understory/ canopy	No	
<i>Zonotrichia capensis</i>	Rufous-collared Sparrow	1	G	30	ground	No	

The three most abundant species were *Pitangus sulphuratus* (= 19; 26 %), *Turdus leucomelas* (= 16; 22 %), and *Basileuterus culicivorus* (= 10; 14 %) (see table 2 & fig. 14). As Insect-eating birds, 72 individuals belonging to 19 species were identified. These species also include omnivores (see 6.5 in methods) and are considered possible caterpillar attackers. Five species were identified as residents of open habitats: *Camptostoma obsoletum*, *Geothlypis aequinoctialis*, *Pitangus sulphuratus*, *Troglodytes aedon*, and *Volatinia jacarina* (fig 14). The majority (= 13/19= 68 %) of the insectivorous bird species were identified as specialists (≥ 70 % invertebrates) in an insectivorous diet and about one third (32 %) as generalists (< 70 % invertebrates) (see table 2).



Data source:
Own survey and presentation

Figure 14 Recorded insectivorous bird species by frequency.

Relative abundances of insect-eating bird species on n= 72 and in percentage. Representation of the species classification according to their forest dependency into three groups: forest-dependent, -independent, and -semi-dependent birds. For complete species names, please see table 2.

Insect-eating bird abundance and richness showed a similar pattern of pronounced variation between the eight sampling sites, with a maximum at point five (abundance= 14, richness= 7) and a minimum at point three (abundance= 5, richness= 4). Point one (abundance= 14, richness= 6) and five stands out due to its rather high abundances, but in proportion few recorded species (see table 3 & fig. 15). The mean value with SD of the "Shannon-Wiener-Index," was 1.55 ± 0.24 . Point two and five presented the highest diversity (= 1.85 and 1.81) since the richness was here the highest (= 7) (table 3).

Table 3 Results of the bird community variables at the eight sampling points.

Points	Abundance	Richness	Shannon-Wiener-Index
CU1	13	6	1.63
CU2	11	7	1.85
CU3	5	4	1.33
CU4	10	6	1.7
CU5	14	7	1.81
CU6	7	4	1.28
CU7	6	4	1.24
CU8	6	5	1.56

Abundance, richness and diversity at eight sampling sites



Data source:

Own survey and presentation

Figure 15 Abundance, richness and diversity at eight sampling sites. Representation of the variation of the three variables among the eight sampling points.

7.2 Characterization of the forest habitat

Table 4 Results of the vegetation structure and landscape variables at the eight sampling points.

Points	Canopy cover [%]	Canopy height [m]	Tree density on 100 m ²	Number of dead trees	Mean contacts with understory	Forest cover [%]	Minimal distance to campus [m]
CU1	87.8	6.74	26	2	13.14	89	142
CU2	90.2	7.5	26	3	15.68	26	49.7
CU3	92.7	8.27	14	1	15.71	88	176
CU4	87.8	6.94	16	0	12.82	71	478
CU5	85.4	8.4	58	1	25.29	70	753
CU6	80.5	9.92	18	2	12.93	76	674
CU7	56.1	5.2	33	0	19.93	35	479
CU8	73.2	5.03	20	0	12.25	33	197

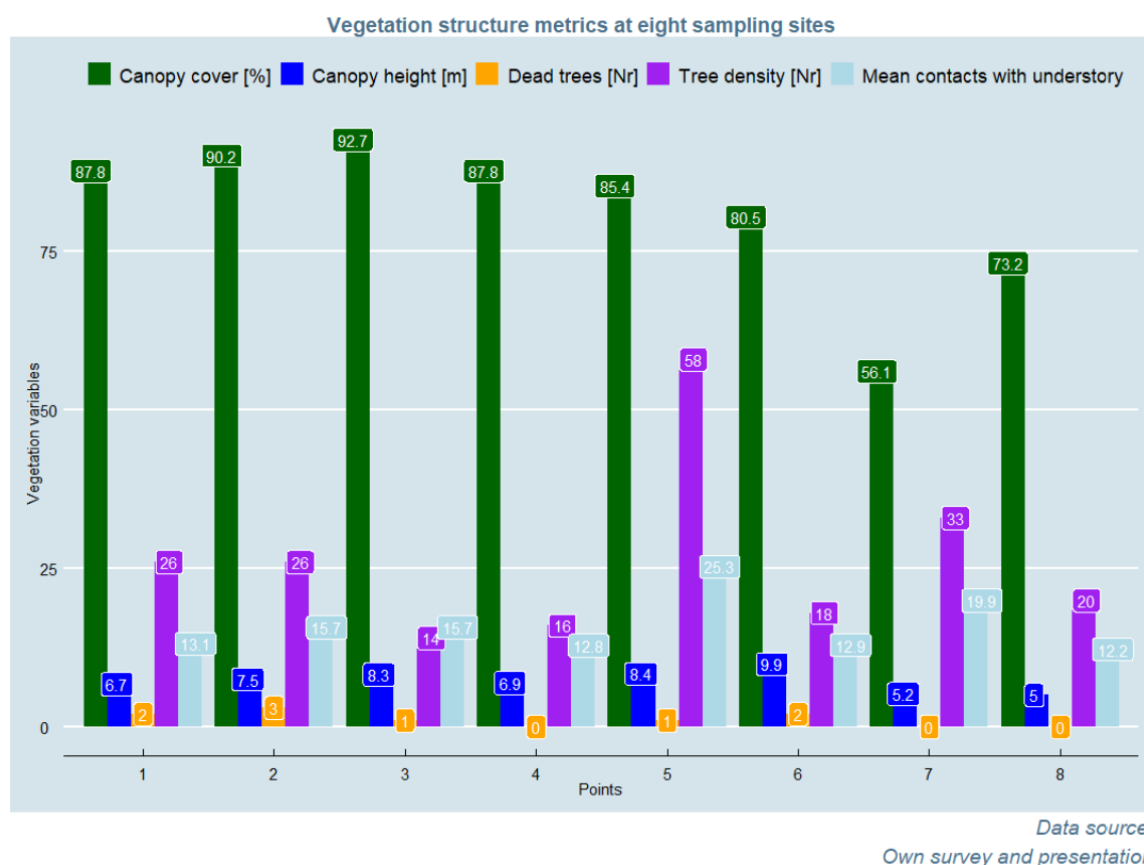


Figure 16 Vegetation structure metrics at eight sampling sites. Representation of the variation of the five vegetation structure variables among the eight sampling points.

The mean canopy cover with SD was 82 ± 12.0 %, which coincides with the quantitative field observations of a general dense canopy (see table 4). Yet, there is an exceptional minimum (= 56 %) at point seven (fig. 16), where the vegetation structure resembled a uniformly planted orchard. The mean canopy height lies at 7.3 ± 1.65 m (see table 4). The smallest trees were found at points seven and eight (≈ 5 m), where the canopy was primary uniform and had a maximum of 2 distinct strata. At those two points, no old trees were found (see fig. 16). Dead trees (1.1 ± 1.14) were very scarce or non-existing. The tree density was perceived in general as medium to little, which also confirms the average of 26 ± 14.2 trees. Yet, the variation between points was very high. Point five presented the densest vegetation with 58 trees, whereas for point three, only 14 trees were counted (see fig. 16). The mean contacts with the understory, as a measure of understory density, was in generally low (16 ± 4.5). At point five, the underwood (0.5 – 3.25 m) was the thickest, while this variable was relatively low for the other points (see fig. 16).

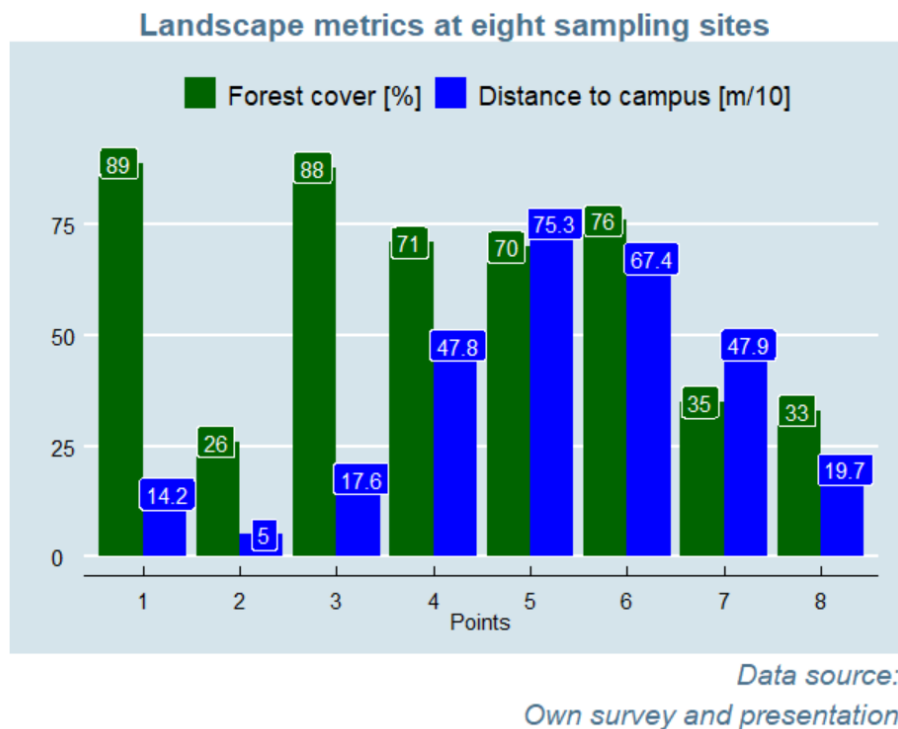


Figure 17 Landscape metrics at eight sampling sites. Representation of the variation of the two landscape variables among the eight sampling points.

The percentage of forest cover within a radius of 100 m around the sampling points was, on average, with SD, $61 \% \pm 25.7$ for the study area (table 4). The mean value indicates the main habitat characteristic of the forest remnants: they are small patches, and their ecological processes underly the heavy influences of the open matrix, primarily through edge effects. The fragment two was the narrowest (= 26 %) and closest to the university campus (= 50 m) (see fig. 17). The two most extensive forest patches at point one (= 89 %) and three (= 88 %) are among the closest to the university campus (= 142 m and 176 m) (fig. 17), and most likely also experience the most anthropogenic disturbances, like noise, air pollution, walkers, etc.

7.3 Attacked caterpillars and predation rates

From the 888 caterpillars that were exposed in the field, 854 (= 96 %) could be recovered. Thirty-four caterpillars were lost; they possibly got dragged away by a predator, or their position could not be localized again. More than one third, 34.7 % (296/854), of the recovered caterpillars were attacked and attributed to four predator groups (see fig. 19): 75 % (221/296) of the attacks were predated by arthropods, mainly by ants. Birds were the second most frequent predator group, with

23 % (69/296). Only 1.3 % (4/296) of the caterpillars had teeth marks from mammals, and reptiles presented the lowest predation rate, with 0.7 % (2/296) (fig. 18).

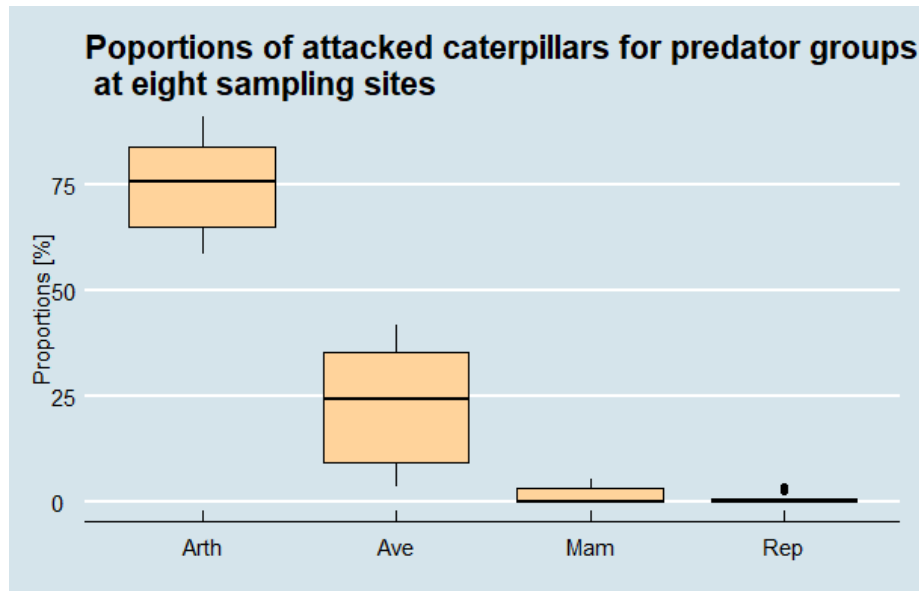


Figure 18 Proportion of attacked caterpillars for four predator groups at eight sampling sites.

Arth= arthropods, Ave= birds, Mam= mammals, Rep= reptiles.



Figure 19 Examples of bite marks for four predator groups.

A) Arthropod predation. B) Bird predation. C) Mammal predation. D) Reptile predation.

Arthropods and birds showed an opposite pattern of attacks regarding the three placement treatments of the caterpillars. Arthropods attacked most of the caterpillars that were placed on the ground, whereas birds primarily attacked at higher levels, as on the leaves (see fig. 20). These results should match the general foraging patterns of both animal groups. However, the three treatments did not differ significantly in either the group of arthropods or birds (Kruskal -Wallis test: $\chi^2 = 2$, $df = 2$, $p\text{-value} > 0.05$).

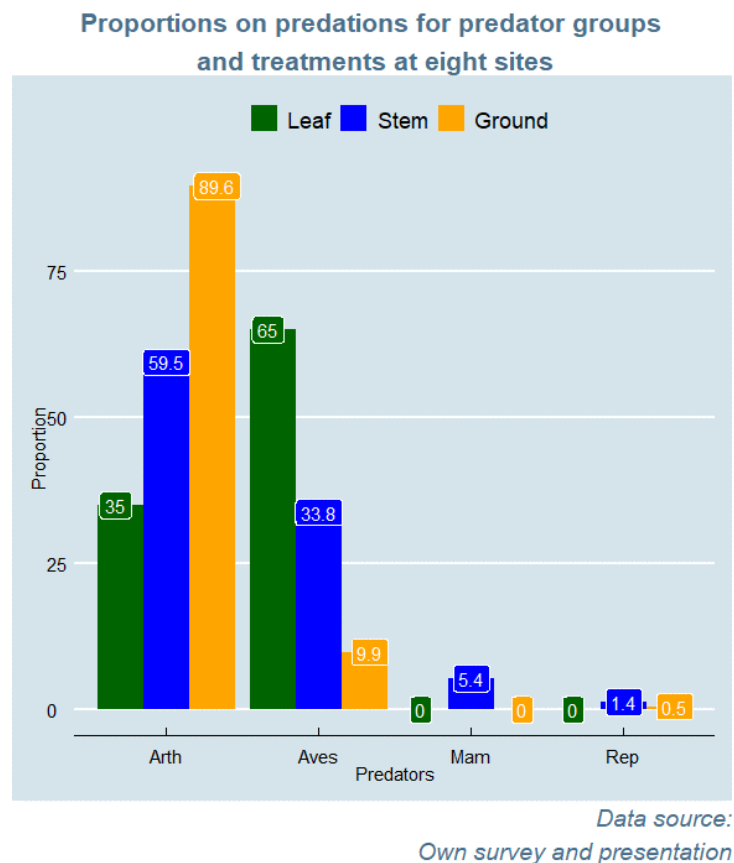


Figure 20 Proportions on predations for predator groups and treatments at eight sites. Representation of variations of predation events among the four predator groups and the three treatments of caterpillar placement. Arth= arthropods, Aves= birds, Mam= mammals, Rep= reptiles.

The predation rates for insect-eating birds ranged between 1.0 and 19 % (see fig. 21: scatterplot) among the eight sampling sites, and on average were 8.25 ± 6.3 %. The highest level of predation was recorded at the sampling site four, where the canopy height, tree density was low, and the understory little dense (see fig. 16). The lowest level of predation was detected at point five, which

contradicts the assumed positive relations between bird abundances, vegetation structure, and predation rates, since the highest abundance (= 14) of forest bird species and insectivorous specialists (= 10) were recorded here (table 3), together with the highest level of the tree (= 58) and understory density (= 25.29) (table 4).

The predation rates of insect-eating birds compose the response variable y . The mean ($= 8.25 \pm 6.32 \%$) is higher than the median ($= 7.5$), and its distance from the 1st quantile ($= 4.0$) is slightly bigger than to the 3rd quantile ($= 3.75$), indicating a right-skewed distribution (see fig. 21: histogram & boxplot). Data clustering can be observed at the tails (see fig. 21: histogram). The data underlies an assumed normal distribution, which was confirmed with a Jarque-Bera test ($X\text{-squared} = 0.64334$, $df = 2$, $p\text{-value} > 0.05$) that did not find significance to reject the null hypothesis of normality.

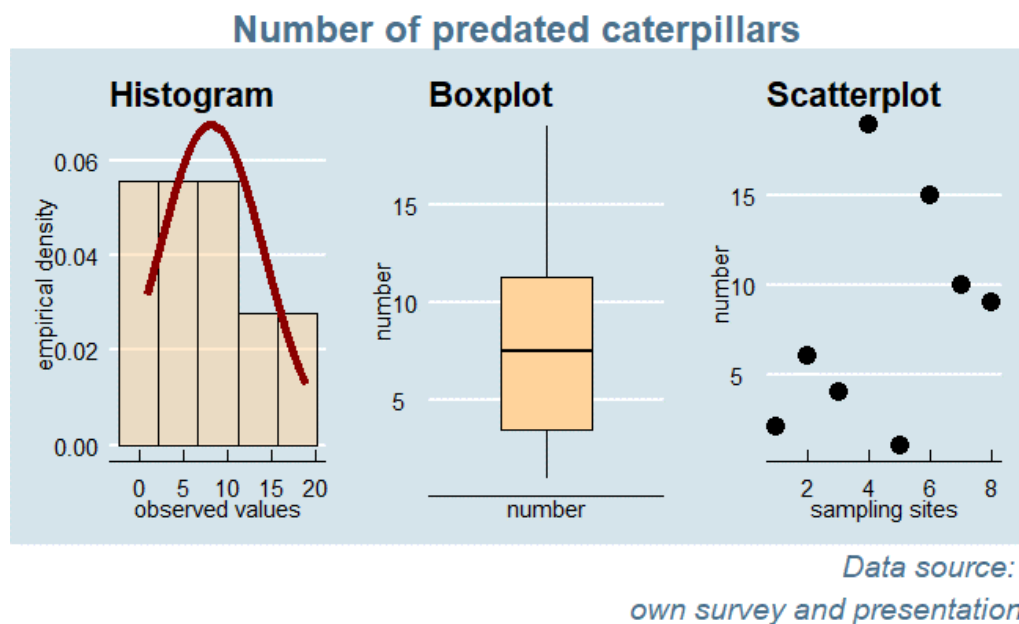


Figure 21 Number of predated caterpillars.

Three representations of the number of the attacked caterpillars by birds. Left: empirical density histogram, which shows the proportions of five interval classes on the empirical sample size ($n = 296$), as well as its density distribution, which displays the probability of observing a value within an interval. Center: boxplot of the eight predation values, which show the median (black horizontal line). Right: scatterplot of the eight predation values according to the sampling sites.

7.4 Correlations between bird predation rates, bird community variables, and forest vegetation structure

The correlation between all variables was calculated based on the Kendall rank correlation coefficient (Kendall's τ), tested for significance, and displayed in a correlogram.

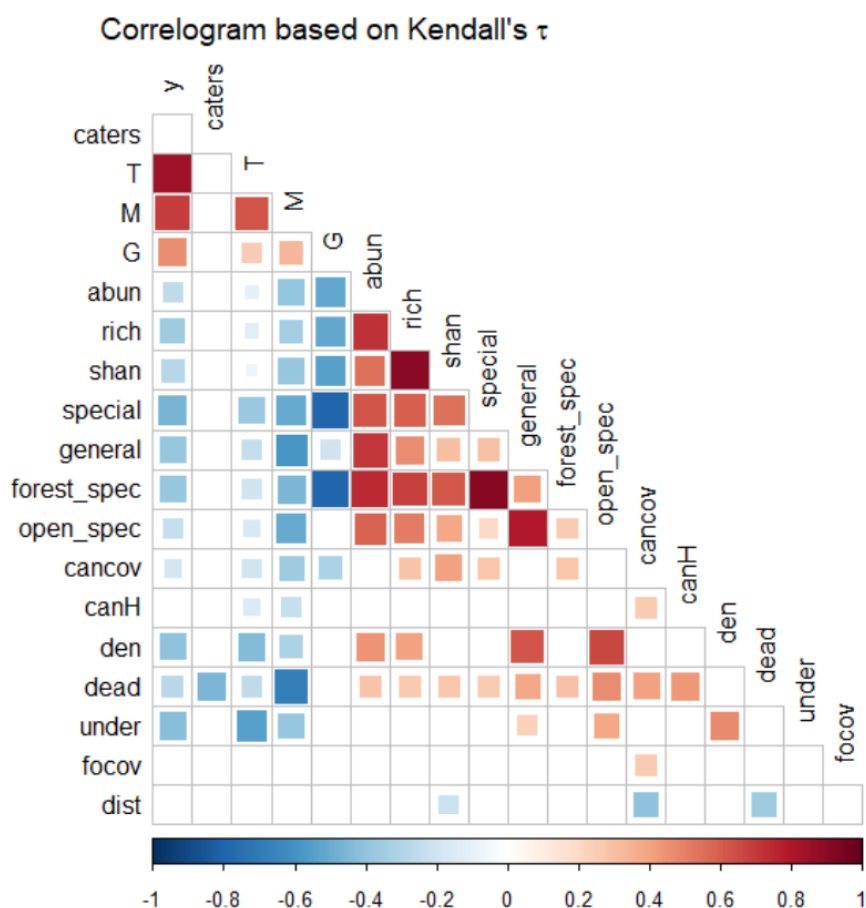


Figure 22 Correlogram based on Kendall's τ .

Representation of the significant ($p < 0.05$) correlations among pairs of variables. Positive correlations are displayed in red and negative correlations in blue. Strong correlations have values close to 1 or -1. Y= bird predation rates, caters= number of recovered caterpillars, T= caterpillar placement on the leaf, M= caterpillar placement on the stem, G= caterpillar placement on the ground, abun= bird abundances, rich= bird richness, shan= bird diversity (Shannon-Wiener-Index), special= birds with a specialized diet in invertebrates, general= birds with a more generalistic diet, forest_spec= forest-dependent and -semi-dependent species, open_spec= forest-independent species, cancov= canopy cover, canH= canopy height, den= tree density, dead= number of dead trees, under= mean contacts with understory vegetation, focov= forest cover, dist= distance to campus. Source: own survey and representation.

There was no statistical evidence of a positive correlation between predation rates (y) and bird abundances ($\tau = -0.26$, $p\text{-value} < 0.05$) or richness ($\tau = -0.36$, $p\text{-value} < 0.05$).

For bird abundance and richness, a positive correlation with tree density ($\tau = 0.44$ and 0.4 , $p\text{-values} < 0.05$) and the number of dead trees ($\tau = 0.28$ and 0.26 , $p\text{-values} < 0.05$) was detected. Richness also correlated positively with canopy cover ($\tau = 0.28$, $p\text{-value} < 0.05$). Forest-associated species were positively related to specialists with an insectivorous diet ($\tau = 0.92$, $p\text{-value} < 0.05$), and species of open-habitats with birds of a generalistic diet ($\tau = 0.79$, $p\text{-value} < 0.05$). Tree density was positively related to bird abundance and richness, especially regarding generalistic species of open-habitats ($\tau = 0.62$ and 0.67 , $p\text{-values} < 0.05$). The latter functional group showed also a positive relation with the mean contacts with the understory ($\tau = 0.23$ and 0.39 , $p\text{-values} < 0.05$). Whereas, specialized forest-species, were positively associated with canopy cover ($\tau = 0.28$ and 0.28 , $p\text{-values} < 0.05$). The number of dead trees, was positively correlated with both functional groups.

As for the predation rates, powerful and positive correlations were revealed for all three treatments, which reflect the different heights of caterpillar placement ($\tau = 0.85$, 0.69 , and 0.46 , $p\text{-values} < 0.05$). The treatments are attributed to the foraging behaviors of insect-eating birds, that in this case, explored all layers of leaves, stem, and ground, and supports the caterpillar placement method for achieving a most authentic caterpillar distribution. The negative relationships between predation rates and the vegetation structure variables (canopy cover, tree density, number of dead trees, and mean understory contacts), as well as bird abundance, richness, and diversity were not anticipated. The landscape variables forest cover did not play a significant role. The distance to the university campus was only negatively correlated with bird diversity ($\tau = -0.21$, $p\text{-value} < 0.05$). There is evidence that the fewer trees and less dense the vegetation at a sampling site, the more caterpillars were attacked (see fig. 22).

7.5 Explaining predation rates

Fifteen candidate models (three models for five variable blocks) were fitted and compared to find the one that best explained the response variable predation rates (y) (see 6.7.3.1 in methods). The parameter p (Tweedie Power) of the Tweedie distribution was estimated with the log-likelihood criterion to be 2.05 ($L_{\max} = 12.8$) (see fig. 23). Only the first block of caterpillar placement treatments (T, M, G) explained the variance in y (see fig. 24 and see appendix). All models (LM, LM-PCA, and Tweedie-PCA) turned out to be significant ($p < 0.05$), with relatively high R^2 ($> 76\%$) and low AICcs (< -26.6) compared to the other blocks (see appendix). According to the AICc, the linear

model with the principal component (LM-PCA) is the best fit model (RSE= 0.01; df= 6; R^2 / R^2 adjusted = 0.95; AICc = -35.7; logLik= 23.9). Closely followed by the simple linear model (LM) with the highest R^2 and R^2 adjusted (RSE= 0.00; df= 4; R^2 / R^2 adjusted = 1.00; AICc = -34.8; logLik= 37.4) (fig. 24). The Tweedie-GLM-PCA did best in modeling the other blocks (ND= 6.76; df= 7; RD= 2.24; df= 6; R^2 / R^2 adjusted = 0.75; AICc = -26.6; logLik= 16.5) (see appendix).

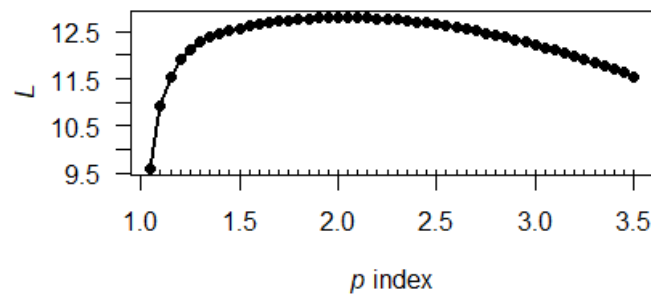


Figure 23 Estimation of the Tweedie Power (p).
Parameter estimation through the maximization of the
Log-likelihood . $p = 2.05$ ($L_{max} = 12.8$).

	LM-Basic model 1	LM-PCA model 1	Tweedie-GLM-PCA model 1
<i>Predictors</i>	<i>Estimates</i>	<i>Estimates</i>	<i>Estimates</i>
(Intercept)	0.00	0.08 ***	-2.80 ***
T	0.01 ***		
M	0.01 **		
G	0.01 ***		
PC1[, 1]		0.01 ***	0.18 **
Observations	8	8	8
R^2 / R^2 adjusted	0.998 / 0.997	0.953 / 0.945	0.757
AIC	-34.772	-35.707	-26.607

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Figure 24 Summary of the three fitted candidate models for the first variable block.
Predictors: T= caterpillar placement on the leaf, M= caterpillar placement on the stem, G= caterpillar placement on the ground, PC1[,1]= first principal component.

Within this variable block, the first principal component of the PCA (PC1[,1]) was selected to enter the second and third model since it alone accounted for more than 80% of the explained variance in the data (fig. 25)

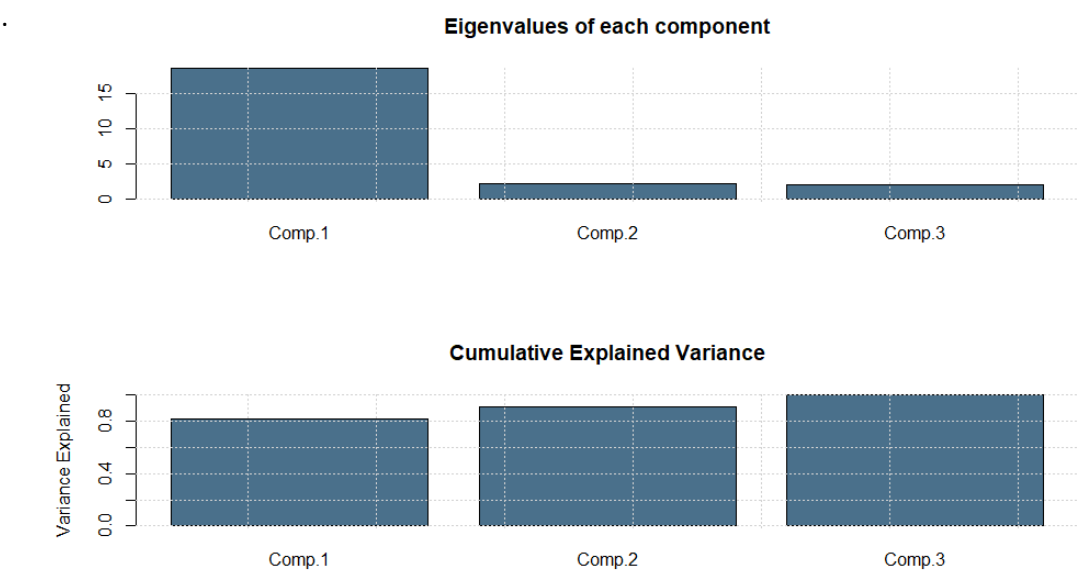


Figure 25 Representation of the Eigenvalues and cumulative explained variance of three principal components of the first variable block.
Comp= principal component.

The fitted linear regression line (LM-PCA) fits the observed data points of the caterpillar predation rates very well (fig. 26).



Figure 26 Linear model with the first principal component of the first variable block.
X-axis= values of the first principal component, Y-axis= bird predation rates.

The winner model was validated with a Q-Q plot of the residuals that compares the expected quantiles from a standard normal distribution with the observed ones. The plot of the residuals is approximately linear and supports the assumption that the residuals are normally distributed (see fig. 27). The same finding was supported by the Kolmogorov–Smirnov test (KS test), which did not find statistical evidence to reject the null hypothesis of normality. The Dispersion test examined the null hypotheses of equidispersion against the alternative of over- or underdispersion. No evidence was found to reject the null. No significant p-value was found for extreme observations or outliers (fig. 27). For all tests, the deviation was not significant (Deviation n.s.), indicating no misspecification of the variance, e.g., through multicollinearity, or a wrongly assumed functional relationship between the variables (Dormann, 2013).

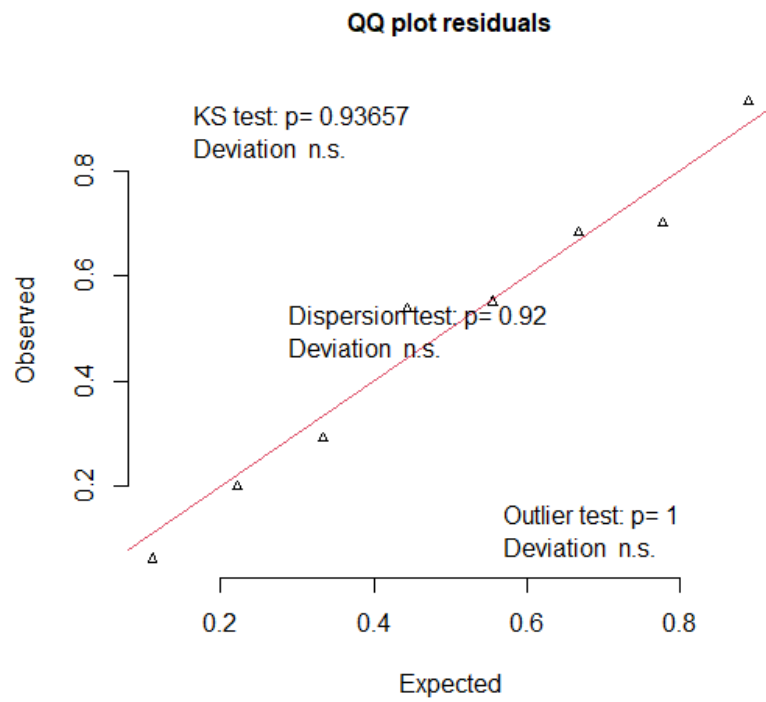


Figure 27 Q-Q plot of the residuals of the LM-PCA model.
KS test= Kolmogorov–Smirnov test, Deviation n.s.= not significant.

The fitted Tweedie-GLM-PCA model is simulated for 1000 values to display the distribution graphically (fig. 28). The model is also validated with a Q-Q plot of the residuals and showed no evidence of the residuals not being normally distributed (fig. 29).

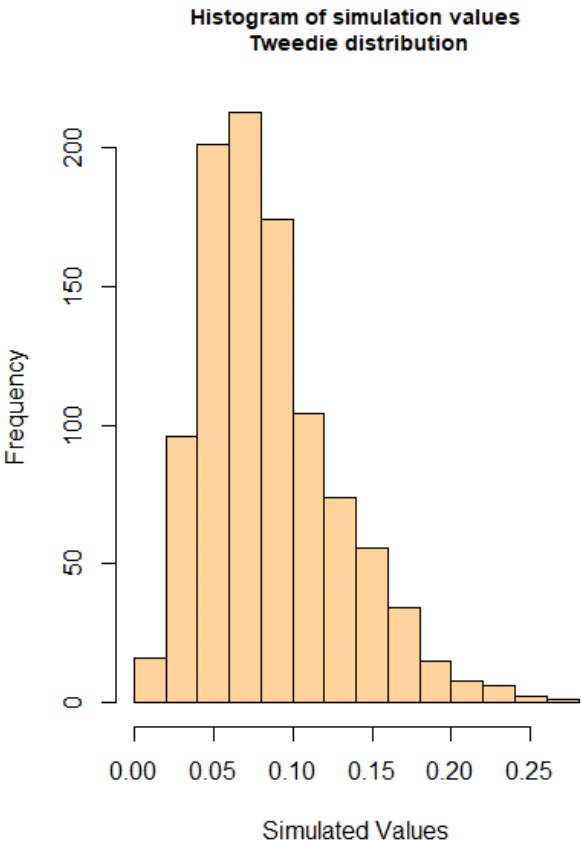


Figure 28 Histogram of the simulated values of the Tweedie distribution. The Tweedie-GLM-PCA model is simulated for 1000 values.

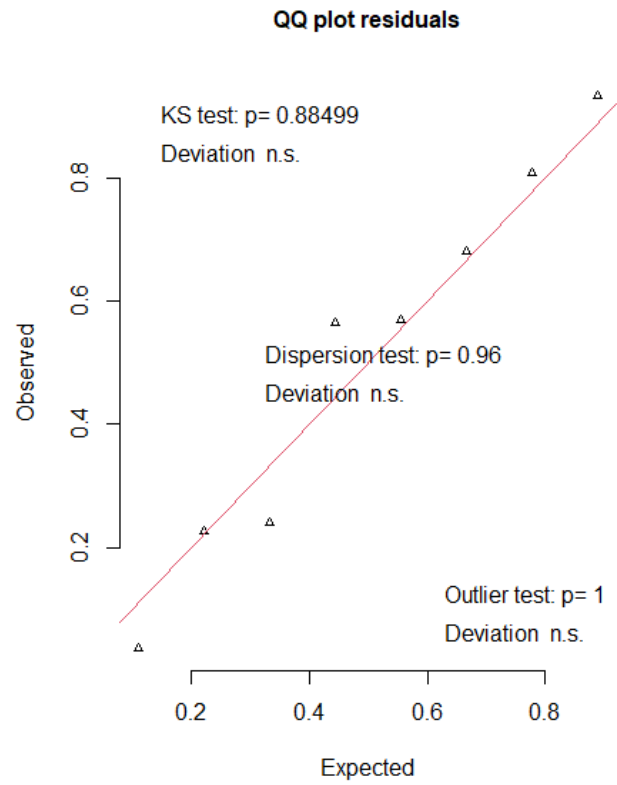


Figure 29 Q-Q plot of the residuals of the Tweedie-GLM-PCA model.
KS test= Kolmogorov–Smirnov test, Deviation n.s.= not significant.

Both models, the LM-PCA and the Tweedie-GLM-PCA, fit the observed predation rates well when plotted against the eight sampling points. Yet, the regression line of the first model looks better adjusted to the points, as the AICc also supported (see fig. 30).

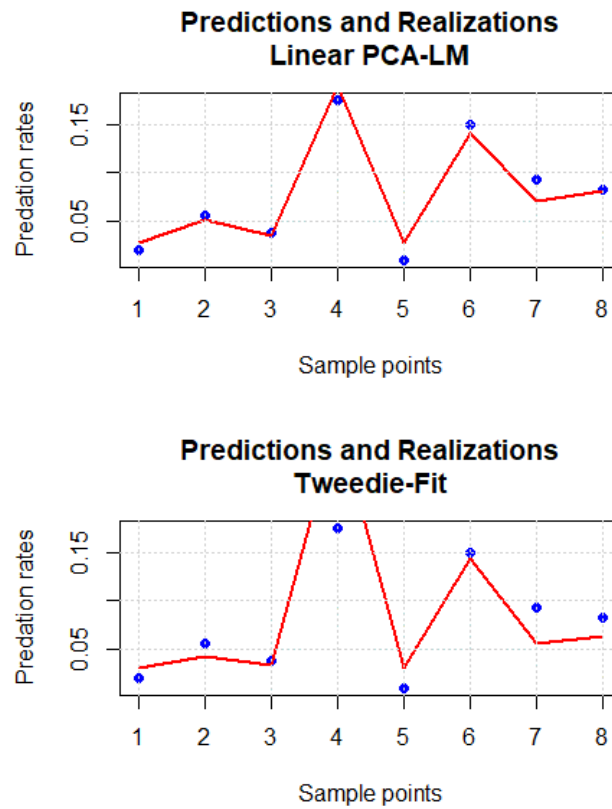


Figure 30 Representation of the predictions and realizations of the LM-PCA and Tweedie-GLM-PCA models. The red regression lines approach the blue predation rates at the eight sampling points.

8 Discussion

8.1 The pro and con of recording the bird community and habitat variables

During sixteen point counts in April 2020, 72 birds, out of 19 species, were identified as insect-eating and thus as possible caterpillar attackers. Their majority is semi-dependent or dependent on forest habitats. Both groups are essential for performing the ecosystem function pest control (Coelho et al., 2016). Vogel et al. (2011) pointed out the importance of forest remnants on university campuses in Brazil for the conservation of forest associated bird species. Even though the landscape of the UFScar university campus is highly fragmented, and the forest patches are small (< 50 ha) (a size defined by Ribeiro et al. (2009)), they are yet well connected at a local scale. One reason is the short distances among the patches (< 200 m), which result from the fragments' shape, framing the campus (see fig. 6). Small gaps are bridged with tree rows and patches, that function as stepping stones and facilitate the movement of birds. As it was already reported by Coelho et al. (2016) and Uezu et al. (2005), well-connected forest patches favor the functional group of insectivorous forest birds. Yet, the classification of the ecological trait "forest dependency" was not straightforward, since many authors published differing classification schemes for neotropical bird species of Brazil (Campos-Silva & Piratelli, 2020; Coelho et al., 2016; Da Silva, 1995; Giraudo et al., 2008; Stotz et al., 1996). The first problem was that some of the here recorded species did not appear in the lists of other authors, except for Stotz et al. (1996), who presented a complete species compilation. The second complication resulted from the inconsistency in the presentation of the data. Whereas Da Silva (1995) used a numerical representation of three categories of the forest-dependency (1= independent, 2= semi-dependent, 3= dependent), Coelho et al. (2016) presented only two quantitative groups (dependent or independent). Campos Silva & Piratelli (2020) ranked the dependency according to its strength (low, intermediate, high). The list of Stotz et al. (1996) does not allow to extract the forest-dependency directly. Still, it shows the most common habitat types, which then needed to be translated into categories according to own established criteria. The difference in forest dependency classifications might be the result of variations in the studies' focuses, the study locations, and the period (1995 – 2020). Most importantly, many authors mentioned having included their observations and knowledge into the classification. Therefore, the final categorization might be influenced by somewhat subjective criteria. Yet, it would be constructive for foreign researches, who are not familiar with the ecological guilds of neotropical birds, to have an updated standard work for species classification, as well as for the dominant foraging guilds and foraging strata of these species.

The two most common diet groups of all recorded bird species were insectivores and omnivores. These feeding guilds have been observed several times in urban-influenced habitats similar to the study area, like secondary forests on university campuses in southern Brazil (Campos-Silva & Piratelli, 2020; Gómez, 2005; Manhães & Loures-Ribeiro, 2005; Philippsen et al., 2010; Vogel et al., 2011), and forest fragments of the Brazilian Atlantic forest (Coelho et al., 2016; Sekercioglu, 2012), especially for small fragments (2-12 ha) (Uezu et al., 2008). Large birds, like big insectivores or frugivores, are typical for intact ecosystems of the Atlantic forest. However, they were not recorded on the campus in Sorocaba, which can be an example of the anthropogenic landscape transformation, and is a typical finding for small secondary forests in this biome (Coelho et al., 2016; Vogel et al., 2011). For example, *Corythopsis delalandi*, *Leptopogon amaurocephalus*, and *Lathrotriccus euleri* were identified as potential caterpillar attackers on the UFScar campus and are typical species of the seasonal semi-deciduous forest in the Brazilian Atlantic forest (Dos Anjos et al., 2011). In another study, these species were found to be less vulnerable to population declines in fragmented forests and to tolerate better anthropogenic transformed landscapes (Dos Anjos et al., 2011). Other insect-feeding species that were also recorded by Gómez (2005) on a university campus in Colombia, and by Manhães & Loures-Ribeiro (2005) on campus in Minas Gerais, are typical species of small forest fragments and edges: *Todirostrum cinereum*, *Pitangus sulphuratus*, *Camptostoma obsoletum* (Tyrannidae), *Troglodytes aedon* (Troglodytidae), *Basileuterus culicivorus* (Parulidae), *Piaya cayana* (Cuculidae), *Thamnophilus caerulescens* (Formicariidae), *Turdus leucomelas* (Muscicapidae), *Cyclarhis gujanensis* (Vireonidae), and *Saltator similis* (Emberizidae).

Apart from insectivorous birds, Gómez (2005) and Manhães & Loures-Ribeiro (2005) also reported species of other the feeding guilds that were also recorded in this study. These species are considered generalists of a vast distribution and can adapt to small habitat fragments in peri-urban areas: e.g., granivorous species, like *Zenaida auriculata*, *Leptotila verreauxi* (Columbidae), *Volatinia jacarina* (Emberizidae), and *Zonotrichia capensis* (Emberizidae); omnivorous species, like *Elaenia flavogaster*, *Myiarchus ferox*, and *Pitangus sulphuratus* (Tyrannidae); as well as nectarivores *Phaethornis pretrei* (Trochilidae), and frugivores *Tangara cayana* (Emberizidae).

The three most abundant insect-eating species on the UFScar campus were *Pitangus sulphuratus* (26%), *Turdus leucomelas* (22%), and *Basileuterus culicivorus* (14%). Giraudo et al. (2008) compared bird assemblages between small (< 100 ha) and large (> 6000 ha) forest remnants in the Atlantic forest of Argentina. *Pitangus sulphuratus* and *Turdus leucomelas* were both more abundant in small fragments with a corresponding mean and standard deviation of 1.9 ± 1.4 and 1.5 ± 0.6 . In Sorocaba, *Pitangus sulphuratus* had a mean abundance of 2.4 per fragment, which is higher than the mean recorded by Giraudo et al. (2008), but yet within the reported range. *Turdus leucomelas* occurred

on average exactly twice (mean= 2.0) in each fragment of the UFScar, and thus also coincides with the upper limit of the mean recorded in Argentina. Interestingly, *Basileuterus culicivorus* was recorded more (mean= 2.8 ± 1.6) in large fragments, but on average, only differed 0.2 compared to the small fragments (mean= 2.6 ± 1.3) (Giraud et al., 2008). In Sorocaba, the corresponding mean was 1.3, exactly matching the lower limit for small fragments in Argentina.

However, the bird census for this study was conducted during early autumn in southeastern Brazil. At this time of the year, the reproductive stage of most birds already finished, and individuals usually don't sing much anymore (Philippsen et al., 2010). Hence, not all species that were actually on campus could likely be recorded, and species abundances are most likely underestimated (Boulinier et al., 2001). Migratory species had also already left, but during summer can increase insectivorous predator diversity, which would enhance predation rates (Bael et al., 2008; Vogel et al., 2011). Two bird inventories were realized on the UFScar university campus during 2007 and 2016 (unpublished data). A total of 1232 birds, belonging to 130 species was recorded: 683 birds, belonging to 106 species in 2007, and 549 birds, comprising 108 species in 2016. Although the method was a different one, the numbers show a massive difference in species richness compared to the 30 species of this study (see table 2). Regarding insect-eating birds, a total abundance of 599 birds and total richness of 63 was recorded for both years: in 2007, it was 330 birds, belonging to 51 species, and in 2016, 269 birds and 53 species. The proportion of insectivorous birds was about 49 % ($63/130$) in both years (2007 and 2016), whereas in this study (2020), it was 63 % ($19/30$). Since the classification of insectivorous birds differed among the studies, the numbers are not comparative directly. Yet, the ratio of insectivorous and other diet groups is about the same ($63/67 = 0.94$ in 2007 and 2016, and $19/21 = 0.91$ in 2020). Therefore, the community composition of this study was a good estimate regarding the dietary groups. Nevertheless, species richness and abundance are far less probably due to seasonal limitations in the study.

The point counts as a sampling unit for birds and habitat variables, enabled fast and effective fieldwork. Yet, it is recommended for future studies to measure vegetation structure variables more than once within the fragments to get more reliable results. One possibility could be to sample four plots, each with a size of 10 x 10 m, or at randomly selected distances from the point count locations to achieve a broader sampling range of the area (Jacobs et al., 2012).

The eight sampling points represented a similar vegetation structure (Manhães & Loures-Ribeiro, 2005) since the distances among them were short (about 200 m). Therefore, it was challenging to detect the effects of the vegetation structure on the predation rates. Again, the sampling of more points and on a bigger scale (> 1 km of distance between points) might improve the power of the

data. For example, Bereczki et al. (2014) sampled 40 points, where artificial caterpillars were placed, and vegetation structure was measured, which is five times more sampling effort compared to this study (eight points). Another interesting approach would be to sample different forest types and compare them, as it has been realized in other studies for tropical areas (Leles et al., 2017; Moreno & Ferro, 2012; Roels et al., 2018). Initially, a comparative study was planned for the FLONA in the state of São Paulo and the surrounding agricultural land. This study design would have enabled a comparison of the ecosystem function pest control according to the vegetation structure among forest and cultivated land, as well as its application to agroecosystems. In a similar analysis, the landscape context could be considered as well, by choosing adequate variables, like the shortest distance of agricultural fields to the most significant forest fragment or to pasture land (Maas et al., 2015; Milligan et al., 2016; Roels et al., 2018).

8.2 The pro and con of assessing predation rates

One main finding of this study was that the three treatments of caterpillar placement (T, M, G) were the best estimator to explain predation rates, assuming a linear model and using only the first principal component (LM-PCA). All three treatment variables were positively correlated with the response variable. The relationship with predation rates will be discussed later in more detail. To recent knowledge, the placement method, as it was applied in this study, has not been published yet. Only Posa et al. (2007) tested for different heights of placing the artificial caterpillars (ground, 1–1.5 m, and > 3 m). However, they also did not find a significant difference in predation among the three heights. At least in this study, this might be due to the small sample size (< 5), which can lead to an inaccurate p-value (Ostertagová et al., 2014). Furthermore, there are no standardized minimum separations between caterpillars to ensure the independence of the observations (Lövei & Ferrante, 2017). Yet, the Kruskal-Wallis test assumes that the data is independent; therefore, the result might also not be valid (Ostertagová et al., 2014).

Three quarters (75% (221/296)) of all attacks were attributed to arthropods, which lets them stand out among all predator groups. Even though they were not investigated in more detail for this study, this finding suggests that they are critical predators, which should be examined in further studies, similar to K. Sam et al. (2015) and Katerina Sam et al. (2015). Nevertheless, while looking at the bite marks in the laboratory, it was recognized that the main arthropod predators were ground-active insects, which was reported by many other studies too (Fáveri et al., 2008; Ferrante et al., 2014; Howe et al., 2009; Low et al., 2016; Maas et al., 2015), and they were primarily ants (Leles et al., 2017). This study encourages future researches to include arthropods as predators in their analysis

and to sample for their species richness and abundance. One significant challenge of the fieldwork was to relocalize the artificial caterpillars in the field after the exposure time had expired. Since several people worked on distributing them in the fragments, not all sample plants could be recognized again, and the searching was time-consuming. Thus, it is recommended to coarsely mark the sample trees on a map for each sampling plot.

The exposure time of the caterpillars in the field is a non-standardized variable, most likely because predation pressure varies among the ecosystems. One possibility to make the data comparative is to present daily predation rates, which require the daily checking for predation marks in the field, as well as the replacement of attacked caterpillars (Lövei & Ferrante, 2017). For this study, it was decided to not work with daily rates, because the checking also leads to disturbances of the natural system, which could falsify the results by, e.g., scaring away possible predators. On the other hand, not having daily predation rates made it difficult to compare the results with other studies (Fáveri et al., 2008; Howe et al., 2009; Lövei & Ferrante, 2017; Roels et al., 2018). Nonetheless, the main research question of this study was to explain predation rates. Therefore it would be interesting to include the disturbances in the field as an explanatory variable and, for example, compare mean predation rates with and without daily checkings.

8.3 The challenges of modeling small samples

Studies with small sample size have the general problem of low statistical power, the reduced ability to detect an actual effect. Low power can lead to false interpretations and low reproducibility of the results. The same is true for overestimating effects since only large effects can be identified and pass the threshold of significance ($p < 0.05$) (Button et al., 2013). In this study, only eight points could be sampled to meet still the criteria of independence for point counts of birds (min. separation of 200 m) (Bibby et al., 1992). Therefore, it was challenging to find a suitable model that fitted the data. Also, because the statistical analysis of the reviewed literature was often not described sufficiently for repetition, or the applied model was not specified.

There is evidence of skewness of the data for predation rates towards the right (mean 8.25 ± 6.32 > median 7.5). This characteristic indicates that there are effects that were not accounted for but are influencing the results. Hence, it is recommended for follow-up studies to sample more than eight points, and on a larger area, for example, with many locations quite distant from each other, like one kilometer. Another possibility would be to combine the caterpillar experiments with exclusion experiments like it was realized by Ruiz-Guerra et al. (2019). Herefore, part of the

branches of a tree get covered with a net, through which arthropods could pass, but neither birds nor bats (Classen et al., 2014; De la Vega et al., 2012). This way, the abundance of real arthropods could be estimated, as well as the leaf damage in both contexts, with and without the presence of predators. Finally, the strength of the ecosystem function pest control by birds and bats can be quantified. It is also recommended to include other variables into the analysis, to account for other potentially influential variables; like tree diversity or richness, which were proven to indirectly enhance predation rates (Nell et al., 2018; Poch & Simonetti, 2013), tree stand age (Fonseca et al., 2009), or leave damage (insect herbivory) which attracts birds and arthropods (Mäntylä et al., 2008; K. Sam et al., 2015).

The typical approach of model comparison and selection has its difficulties: (1) the definition of suitable models, (2) to address the uniqueness of each count data set and its specific fitting problems, and (3) different selection criteria (AIC, BIC, Log-likelihood, etc.) can lead to other choices. These problems can be addressed with the Tweedie model that can adapt automatically to the specific underlying distributions of the data (Bonat et al., 2018). The data of the predation rates presented a vast difference between the mean of 8.25 and the variance of 39.9, probably due to the very small sample size. This characteristic made it complicated to adopt a model that already requires the specification of the mean-variance relationship (Dunn & Smyth, 2005; Swallow et al., 2019). For example, the Poisson distribution is the only choice for count data to conduct a GLM (Bonat et al., 2018). Yet, this was not possible due to the specified mean-variance ratio of Poisson, which is one, determining that the variance equals the mean. Therefore, the Tweedie model is a promising model regarding the flexibility of the mean-variance ratio. The log-likelihood of the model fit confirmed this for the variable blocks 2 to 5 (see table 1). Yet, the Tweedie model also uses more parameters, which is why regarding the AICc, it doesn't stand out (see the formula in 6.7.3.3 in methods). The study aimed to explain predation rates, which was achieved only by the block one, the caterpillar placement treatments. Following the AICc criterion, the linear model with the first principal component (LM-PCA) for the three treatments was the best fitting model (AICcs: -35.70717 (LM-PCA) < -34.77201 (LM) < -26.60710 (Tweedie-GLM-PCA)).

8.4 Comparing predation rates and the influence of vegetation structure

The overall attack rate of the recovered caterpillars after eight days of exposure was 34.7 %. As already mentioned, this value can not be compared directly to other studies, since the experiments vary in, e.g., the making of the caterpillars, their exposure time, and in placement criteria (Lövei & Ferrante, 2017). For example, Leles et al. (2017) assessed a mean predation rate of 20.9 % in a tropical forest in China after four days of exposure. Overall attack rates, based on daily attacks

(Lövei & Ferrante, 2017), were estimated, e.g., by Fáveri et al. (2008). They recorded 6.3 %, for tropical forest fragments of 10 ha in Brazil, and 4.2 % for 1 ha fragments. In both cases, the caterpillars were placed above the ground. Studies in the neotropics reported even higher rates, like Koh & Menge (2006), who found 45 % (68 /150) of artificial caterpillars attacked within 48 h in forest fragments in Panama. Also, in Panama, Roels et al. (2018) reported 43.6 % of overall attacks in different vegetation forms but also had an exposure time of ten days. The study that came closest to the habitat type on the UFScar campus was conducted by Moreno & Ferro (2012) in a semideciduous forest in Brazil. They recorded a mean predation rate of 10.4 % after four days of exposure, which is about one-third of the here presented attack rate after eight days of exposure. Unfortunately, this study didn't show specific predation rates for birds. Compared to the values reported for other experiments in the tropics, the here presented overall attack rate seems to be similar, with a tendency towards the upper limit. In comparison to a study in the temperate zones, there is a tendency that the predation rate is higher, yet a direct comparison is also not suitable. Bereczki et al. (2014) recorded a mean predation rate of artificial caterpillars in an oak forest in Hungary of 27.5% (SD = 13.77, n = 40), after six days in the field. This relation would match the general pattern of Roslin et al. (2017), who found increasing predation rates towards the Equator.

The mean attack rate with SD for birds was 8.25 ± 6.3 %. During the dry season in a tropical moist forest in Mexico, the mean bird predation was found 2.2 times higher in a fragmented forest (32 ± 0.02 %) than in continuous forest (15 ± 0.02 %), the exposure time was not mentioned (Ruiz-Guerra et al., 2012). The mean predation rate for birds based on daily attacks (Lövei & Ferrante, 2017) was estimated for a fragmented temperate forest in Chile by González-Gómez et al. (2006). For forest seedlings, a bird predation rate of 13.0 % was recorded, which for adult trees was 11.0 %. In both habitats, the caterpillars were placed above the ground. There is a tendency that the mean bird predation rate on the UFScar campus is lower than the reported values for tropical and temperate zones. Unfortunately, no values have been reported for neotropical forests in Brazil. The comparison to other studies is challenging due to differences in biome, habitat, exposure time, and method. It is recommended to repeat the experiment in the closest bigger fragment, e.g., in the FLONA, to obtain a direct reference for the study area.

A contrasting attack pattern was found for the caterpillar treatments (T, M, G) for arthropods and birds: arthropods predated most at ground level, where birds attacked the least. Whereas birds predated most caterpillars on leaves, arthropods attacked here with the lowest success. This pattern could be partly explained by the presence of only a few specialized bird species on the ground and stem foraging strata. Most birds forage in the understory and mid-high strata and are visual foragers (Barbaro et al., 2014). In contrast, arthropods, which here were primary ants, occur

and forage primarily on the ground and in the understory (Leles et al., 2017). They rely more on chemical cues while foraging and, therefore, can also find concealed caterpillars in the foliage (K. Sam et al., 2015). This finding coincides with Lövei & Ferrante (2017), who also found invertebrate attacks most frequent at ground level, and Loiselle & Farji-Brener (2002) found bird predation only in the canopy layer. Consequently, the question arises if the two animal groups complement each other in performing the ecosystem service pest control. One mechanism that maintains ecosystem function under variable environmental conditions is the complementary response of different species (Richmond et al., 2005). The biomass of a community can measure ecosystem function, and therefore also reflect responses to disturbances (Richmond et al., 2005). One possible argument would be that the larger arthropod biomass could compensate for the body size of other predators. This theory is suggested for further investigation, e.g., to estimate the arthropod biomass, together with that of birds of different communities, and assess their relations. Roels et al. (2018) found that birds and arthropods can perform the ecosystem function pest control simultaneously in the same habitat. This finding leads to the premise that this is not a competitive but complementary interaction (Clavel et al., 2011). These relations are known even to increase an ecosystem's productivity and resilience (Clavel et al., 2011; Loreau, 2000). A complimentary elevation gradient was also found, with decreasing ant population and increasing bird population with elevation in Papua New Guinea (K. Sam et al., 2015; Tvardikova & Novotny, 2012). Roslin et al. (2017) identified a latitudinal and elevation pattern for arthropods, and a contrasting geographical pattern was found by Zvereva et al. (2019), regarding prey selection by colors for birds and arthropods. Classen et al. (2014) could demonstrate the complementation of pollination and pest control services in coffee production systems through a pollinator and vertebrate (birds and bats) exclusion experiment. Pollinators and vertebrates increased coffee productivity complementarily by affecting different fruit parameters regarding their quantity and quality (Classen et al., 2014). These relationships give way to the assumption that also within the same ecological function, arthropods and birds can complement each other in their function as pest controllers, which in the future should be tested further.

One characteristic of the study area was the small size of the forest fragments, so that fragmentation processes, like edge effects, are more dominant. Edge effects can penetrate up to 200 m into the forest (Banks-Leite et al., 2010; Dos Anjos et al., 2011); accordingly, the fragments on the UFScar campus would be all edge. Thus, the bird community assemblage consists of species that can cope with these habitat attributes (Vogel et al., 2011), like the small patch size and peri-urban landscape context (Lampila et al., 2005; Rolstad, 1991). Birds that can use urban structures, like buildings, can even benefit from a transformed anthropogenic habitat (Gómez, 2005; Stiles,

1990). As already discussed before, the species recorded on the campus, are typical species of small forest fragments and edges, most of them being more generalistic species of a vast distribution.

There is a debate about if generalistic species can perform ecosystem functions, like pest control, as well as specialists (Clavel et al., 2011; De Coster et al., 2015; Richmond et al., 2005). In fragmented landscapes, rare-specialized species are often substituted by abundant-generalists, which are more adapted to open and clearcut areas (biotic homogenization) (Devictor et al., 2007; McKinney & Lockwood, 1999; Morante-Filho et al., 2015; Piratelli et al., 2008). This might be, due to the observation, that generalists are more tolerant of suboptimal environmental conditions, but as the conditions become more optimal, more specialists will thrive (Richmond et al., 2005). The result of environmental changes would be a more similar community and the reduction in functional diversity (functional homogenization) (Clavel et al., 2011). There is a general assumption that generalists could never outperform specialists due to the higher costs associated with generalists, being able to accommodate multiple prey types or variable environments (Richmond et al., 2005). In other words, generalists perform ecological functions less efficiently than specialists (Clavel et al., 2011). However, if the cost of generalization is less than the cost of coping with the environmental fluctuations, generalist species may contribute to a more efficient ecosystem functioning over a broad set of ecological conditions (Richmond et al., 2005).

A positive relation was found between generalistic species and forest-independent species, whereas specialists correlated positively with forest-dependent and semi-dependent species. Expanding this relation by considering the vegetation structure, a positive correlation of generalistic forest-independent species with tree density, dead trees, and mean understory contacts was detected. That is, the denser the forest and the understory, which is typical for young fragments, the more generalists are found. The tree density was also associated with less specialized and forest-independent species in Campos-Silva & Piratelli (2020). Since dense forests were linked to initial stages of ecological succession, they might not provide the same quantity of resources as older and more structural forests (Campos-Silva & Piratelli, 2020). Another attribute of forest structure is the number of standing dead trees, which was also a significant variable for both functional groups. Campos-Silva & Piratelli (2020) also found a positive relationship between the number of dead trees and bird richness and diversity. Coelho et al. (2016) also detected a positive correlation among dead trees and canopy cover, which are attributes that often are associated with older fragments and specialized forest-dependent birds. The results of this study also showed a positive relation between specialized forest-dependent species and canopy cover, as well as the number of dead trees. In contrast to the present study, Campos-Silva & Piratelli (2020) showed that the canopy cover drove the abundance of low forest-dependent birds, like the Great Kiskadee

(*Pitangus sulphuratus*). These results suggest that the two functional bird groups of varying forest dependency can respond differently to vegetation structure, which is essential to understand for conservation purposes (Coelho et al., 2016). Since most of the fragments are younger, in the initial to the intermediate successional stage, more generalistic birds were found that might not perform the ecosystem service as well as rare specialists.

Positive correlations characterized the relationship between vegetation structure and insect-eating bird community variables. First, a positive relation was detected between tree density, dead trees, both are forest structure attributes (Campos-Silva & Piratelli, 2020), and bird abundance and richness. Second, canopy cover was positively correlated with richness and diversity (Shannon-Wiener-Index), as well as dead trees with diversity. Therefore, the more forest structure, the more birds were recorded, which was also found for insectivorous birds by Bereczki et al. (2014). Compared to the study of Campos Silva and Piratelli (2020), the same positive correlation between standing dead trees and species richness, as well as diversity, was found. In contrary to the results presented here, they found a negative relationship between tree density (number of trees) and bird richness (Campos-Silva & Piratelli, 2020). Since these relations seem to be rather complex, it is recommended to look deeper into the associations between vegetation structure and bird community variables (abundance, richness, diversity). For example, by modeling the community variables, and find the explanatory variables that best describe them. However, it needs to be considered, that single species can respond differently to habitat fragmentation and, e.g., edge effects than their functional group (Banks-Leite et al., 2010; Dos Anjos et al., 2011)

There was no correlation between forest cover and abundance or richness. The same result was also reported by Morante-Filho et al. (2015) for the Brazilian Atlantic forest. Yet, they found an effect of forest cover, when the species were classified into forest-specialists and -generalists. A similar classification into forest-species and species of open area habitat was realized for this study. Yet, these functional groups didn't show any correlation with forest cover. Since there are species that are more sensitive to forest cover loss than others, the sensitive species could have been replaced by more tolerant species. Therefore, the total abundance and richness might not change drastically with the forest cover (Morante-Filho et al., 2015). For the future, it would be interesting to include the level of sensitivity of bird species into the analysis and compare the community composition to a more intact, continuous forest.

The correlation between predation rates and vegetation structure was found to be negative. Consequently, open habitats presented the highest predation rates. This finding would also coincide with the result that older fragments, with less understory and tree density, but high canopy

cover and dead trees, present more forest-dependent birds, specialized in an insect-diet. The open stand of trees, with less understory, increases the visibility of prey, especially for birds that are visible foragers (Leles et al., 2017). The same result was found in a study in Brazil, where predation rates of artificial caterpillars were tested in different vegetation forms of varying structural complexity (campo sujo, campo cerrado, cerrado sensu stricto and semideciduous forest) (Moreno & Ferro, 2012). Here the highest mean predation rate was found in the campo sujo (= 16.7 %), which had the simplest and most open vegetation structure (less richness and tree density). The semi-deciduous forest presented the second-highest predation rate with 10.4 % (Moreno & Ferro, 2012). It was assumed that this is associated with the higher visibility and chemical detectability of the caterpillars, which were more exposed to their predators in open habitats (Moreno & Ferro, 2012). This phenomenon also occurs naturally, where real caterpillars suffer less from attacks if they are foraging within plant parts and structures that conceal them (Price et al., 1980).

Nevertheless, the vegetation structure did not explain predation rates with the measured habitat variables. Other variables should be taken into account, e.g., a direct measure of understory density, tree diversity, or fragment age. A restriction of this study was the structural similarity due to the relative proximity of the sampling points. Thus, more points at more distinctly different locations should be sampled to detect the actual effects of the vegetation structure on predation rates. Additionally, other landscape variables could complement the analysis, like the proximity to other patches (connectivity), neighborhood dominance of surrounding land-use types, and patch size (Ferraz et al., 2014).

The relation between predation rates and bird community variables (abundance, richness, diversity) was negatively correlated. This result is contrary to the assumed positive relationship that what based on the outcome of many other studies (Bereczki et al., 2014; Howe et al., 2009; Maas et al., 2015; Nell et al., 2018; Roels et al., 2018). Species and communities differ in their response to disturbance (Clavel et al., 2011), and abundance and richness can mask bird community patterns (Morante-Filho et al., 2015) of their pest controlling function. Richmond et al. (2005) even assumed that certain key species might be more essential to maintain ecosystem functioning than species richness. Thus, it is proposed that the abundance and richness as a whole didn't determine the predation success here, but instead the presence of specific species (Banks-Leite et al., 2010; Dos Anjos et al., 2011), which was not tested in this study. It would be interesting to relate bite marks to species and their specific function, which is a great challenge yet to be addressed (Low et al., 2014). At this point, the small sampling size should be considered, which might have been not enough to accurately detect the relation between predation rates and bird abundances and richness. Additionally, the end of the reproductive phase of birds at this time of the year (early

autumn) contributed not to have identified all species on the campus. Furthermore, species vary in their detectability, and only the noisiest species might have been recorded (Bibby et al., 1992; Dos Anjos et al., 2011). Future studies are encouraged to test for seasonal patterns of the bird community, indirectly affecting predation rates, as well as variations during day and night time (Seifert et al., 2016).

The α -diversity (Shannon-Wiener-Index) is an indirect measure of functional diversity (Tilman, 2001) and was negatively related to predation rates. This finding contributes to the discussion, whether biological diversity is necessary to maintain ecosystem functions and services (Mertz et al., 2007), or if the interaction between species or the presence of specific species might be more important than their diversity per se (Richmond et al., 2005). Yet, this study didn't account for all levels of diversity and was conducted in only one season. Hence to make a general assumption, more data is necessary, also contemplating experiments during more seasons.

The positive effect of the three caterpillar treatments on predation rates was the strongest and only one that explained the variance in the response variable. This result strongly supports the placement method of three different heights (ground, stem (0.5 – 1.0 m), and leaves (1.5 – 2.0 m)). The treatment is an excellent criterion to estimate bird predation rates in the study area, consisting of fragmented secondary forest in the Atlantic forest biome. Until now, a straightforward ecological explanation is not known. Since the understory and ground vegetation of the study site, in general, was not very dense, the artificial prey might have been more accessible to potential predators on all heights, especially arthropods and birds. Mammals and reptiles had very low attack rates and almost only predated caterpillars on the stem (0.5 – 1.0 m). This again might speak for the good visibility of the prey due to little dense understory. Thus, the three treatments should be investigated more in future studies, also in other habitats with different vegetation structures to get comparable data and further explore their effects.

9 Conclusions

In the secondary forest fragments on the UFScar university campus in Sorocaba, 72 insect-eating birds, belonging to 19 species, were identified as possible artificial caterpillar attackers. Due to seasonal limitations, species abundances and richness were most likely underestimated (Boulinier et al., 2001), since the reproductive phase already finished, and migratory birds had left. By conducting artificial caterpillar experiments, an overall attack rate of 34.7 % was assessed for eight

days. The mean predation rate for birds was $8.25 \pm 6.3 \%$, which is lower than reported values for tropical and temperate zones. The main result of the study was that the three treatments of caterpillar placement were the best and only estimator to explain the estimated predation rates of birds. The little dense understory and ground vegetation might have facilitated the accessibility of artificial prey for potential predators, especially for arthropods and birds. A contrasting attack pattern of attacks was detected among the caterpillar treatments for arthropods and birds. This finding might be attributed to the specific foraging behavior of the animal groups since most birds forage in the understory and search visually (Barbaro et al., 2014) and arthropods, occur and feed primarily on the ground (Leles et al., 2017). It is assumed that arthropods and birds can complement each other in their function of pest control, which should be examined with further empirical studies. Most of the sampled fragments were of an early successional stage with a denser understory. Hence, more generalistic birds were recorded that might not perform the ecosystem service as well as rare specialists (Clavel et al., 2011; De Coster et al., 2015; Richmond et al., 2005). The correlation between predation rates and vegetation structure attributes was found negative. Consequently, more open habitats presented the highest predation rates. This finding coincides with other results that older fragments, with less understory and tree density, but high canopy cover and dead trees, exhibit more specialized forest-dependent birds. The open stand of trees and less understory increases the visibility of prey (Leles et al., 2017). Contrary to previous expectations, the vegetation structure did not explain predation rates, and bird community variables (abundance, richness, diversity) were negatively correlated. It is hypothesized that the bird community variables didn't determine the predation success, but instead the presence of specific species (Banks-Leite et al., 2010; Dos Anjos et al., 2011). For further testing, bite marks would need to be related to species and their specific function (Low et al., 2014).

A limiting factor of the study was the similar vegetation structure of the eight sampling points (Manhães & Loures-Ribeiro, 2005), due to their relative proximity. It is recommended for future studies to improve statistical power by sampling more units and on a bigger scale. Furthermore, to avoid the underestimation of the avifauna, seasonal patterns, as well as variations between day and night, should be recorded. The temporal abundance of natural caterpillars in the forest fragments was not evaluated in this study. Yet, it is an important aspect that can explain seasonal diet preferences of insectivorous birds for caterpillars, e.g., for feeding their nestlings, and thus also the strength of their predation pressure (Nyffeler et al., 2018). For explaining bird predation rates, other variables can be included into the analysis, to also prevent skewness of the data; like tree diversity or richness (Nell et al., 2018; Poch & Simonetti, 2013), a direct measure of understory density, tree stand age (Fonseca et al., 2009), or leave damage (insect herbivory) (Mäntylä et al.,

2008; K. Sam et al., 2015). At the landscape scale, variables, like fragment size, their connectivity, and land-use types of the surrounding landscape, could be included. Follow-up studies are encouraged to look deeper into the associations between vegetation structure and bird community variables (abundance, richness, diversity), e.g., by statistical modeling and the identification of the most relevant explanatory variables. The effect of the three treatments should be investigated in more detail, including experiments in other habitat types with different vegetation structure to conduct a comparative analysis.

Urbanization processes are the main factors for habitat loss and fragmentation, driving global biodiversity loss and species extinction (Bellocq et al., 2017; Bhakti et al., 2020; Marzluff & Rodewald, 2008; Rodrigues et al., 2018). On the community level, this can lead to biotic and functional homogenization (Clavel et al., 2011). As for the ecosystem function and service pest control by birds, this would most likely mean a shift towards communities dominated by generalistic species with similar functions that might not outperform specialized species in their efficiency (De Coster et al., 2015; Richmond et al., 2005; Sekercioglu, 2012). Therefore, the understanding of the underlying ecological processes of trophic interactions, like predation, in anthropogenically transformed habitats is essential for biodiversity conservation. This study postulates for the maintenance of forest remnants in peri-urban areas, like on university campuses, because they are necessary for the preservation of forest associated bird species, contributing to the biological diversity on a broader scale (Gómez, 2005). Even if vegetation patches are small (Ribeiro et al., 2009), they can act as stepping stones, enhancing habitat connectivity between larger patches, and facilitate the species' movement to reach alternative resources (Uezu et al., 2005). The same effect can be achieved through the implementation of live-fences, such as hedgerows, e.g., in traditional agricultural systems (Figueroa-Sandoval et al., 2019). Small forest fragments also increase the structural heterogeneity of the habitat, offering a broader range of resources for resident and migratory birds, which can attenuate some of the adverse effects of urbanization (Castro-Torreblanca, 2014; Gómez, 2005; Ramírez-Albores & Pérez Suárez, 2018). Yet, the preservation of large forest fragments should be a priority, since they meet more demanding habitat requirements of specialized species (Uezu et al., 2005). Especially for peri-urban areas, forest remnants hold great potential as a refuge for surrounding urban and rural agricultural areas (Ramírez-Albores & Pérez Suárez, 2018). The latter benefits from insectivorous birds spilling over to agroecosystems, contributing to the regulation of pest outbreaks and stabilizing yields (Decocq et al., 2016; Lee et al., 2015; Sekercioglu, 2012). In the long run, the monetary value of this ecosystem service by birds might even outweigh the costs of agrochemicals, like pesticides and fertilizers (Karp et al., 2013; Klein et al., 2014). The economic valuation of ecosystem services was not part of this study but

could provide the basis for a corresponding analysis (Costanza et al., 1997; Wenny et al., 2011). Thus, the results of this study could contribute to preventing the loss of biodiversity and ecosystem services by, e.g., providing the basis for the implementation of compensation payments for pest control services (Ferreira et al., 2019; Mertz et al., 2007). The engagement of relevant stakeholders, especially local communities, is a crucial strategy for the success of conservation measures (Mertz et al., 2007). For example, in Mexico, the payment of ecosystem services to landowners could slow down forest fragmentation at regional and national levels (Ramirez-Reyes et al., 2018). To further explore the benefits and limitations of avian pest control service, this study reinforces the urgent need for detailed field studies, which compare the ecosystem function pest control by birds between continuous forests, forest fragments, and traditional agroecosystems, ideally in landscapes that vary in their vegetation structure and composition (Sekercioglu, 2012).

Ecological urban planning is a promising approach that integrates all of the discussed aspects to maintain avian biodiversity, promote their ecosystem functions, and benefit society through ecosystem services (Bhakti et al., 2020; Marzluff & Rodewald, 2008; Piratelli et al., 2017). The protection of small vegetation reserves, like forest patches, or parks can provide habitat for urban avoiders and enhance the quality of the matrix by increasing its permeability. The heterogeneity of the landscape can be increased by planning explicitly for a mix of open and closed vegetation structures, which can meet the requirements for a greater variety of birds. Already existing natural areas should be restored when degraded, or adapted to the needs of specific species, e.g., through cavity building for woodpeckers or nest boxes for small insectivores. Another critical approach to gain the support and involvement of local communities is to launch awareness campaigns and participative citizen science projects to build up people's identification with their immediate environment and the related problems (Marzluff & Rodewald, 2008; Piratelli et al., 2017). Since birds provide a great variety of ecological functions, they possess critical positions in food webs, linking different ecosystems and various species (Wenny et al., 2011). Therefore, conservation measures that target birds will also most likely benefit other animals and plants, promote biodiversity as a whole, and ultimately ensure the well-being and health of humans.

10 References

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11 Appendix

Data table of all variables used in the statistical analysis.

y	attacks	caters	points	T	M	G	abun	rich	shan	special	general	forest_spec	open_spec	cancov	canH	den	dead	under	focov	dist
2	2	104	CU1	0	1	1	13	6	1.63	9	4	10	3	87.8	6.74	26	2	13.14	89	142
6	6	107	CU2	2	1	3	11	7	1.85	7	4	5	6	90.2	7.5	26	3	15.68	26	49.7
4	4	108	CU3	0	2	2	5	4	1.33	4	1	4	1	92.7	8.27	14	1	15.71	88	176
19	20	108	CU4	10	9	1	10	6	1.7	8	2	8	2	87.8	6.94	16	0	12.82	71	478
1	1	110	CU5	0	1	0	14	7	1.81	9	5	10	4	85.4	8.4	58	1	25.29	70	753
15	15	100	CU6	9	3	3	7	4	1.28	3	4	4	3	80.5	9.92	18	2	12.93	76	674
10	11	108	CU7	2	4	5	6	4	1.24	3	3	3	3	56.1	5.2	33	0	19.93	35	479
9	10	109	CU8	3	4	3	6	5	1.56	3	3	4	2	73.2	5.03	20	0	12.25	33	197

Data table of all recorded bird species at the eight sampling sites.

Species	CU1	CU2	CU3	CU4	CU5	CU6	CU7	CU8	Total
<i>Amazilia lactea</i>	0	0	0	0	0	0	0	1	1
<i>Anthracothorax nigricollis</i>	0	0	0	0	0	0	1	0	1
<i>Aramides cajaneus</i>	0	0	0	0	0	1	0	0	1
<i>Basileuterus culicivorus</i>	3	1	2	1	3	0	0	0	10
<i>Camptostoma obsoletum</i>	0	1	0	0	0	0	0	0	1
<i>Cnemotriccus fuscatus</i>	0	0	0	1	0	0	0	0	1
<i>Corythopsis delalandi</i>	1	0	0	0	0	0	0	0	1
<i>Cyclarhis gujanensis</i>	1	0	0	0	1	2	1	0	5
<i>Elaenia flavogaster</i>	1	0	0	0	0	0	0	1	2
<i>Euphonia chlorotica</i>	0	0	0	0	0	0	0	1	1
<i>Geothlypis aequinoctialis</i>	0	0	0	0	0	0	0	1	1
<i>Lathrotriccus euleri</i>	0	1	0	2	0	0	0	0	3
<i>Leptopogon amaurocephalus</i>	0	0	0	0	1	0	0	0	1
<i>Leptotila verreauxi</i>	2	0	0	4	3	2	2	0	13
<i>Myiarchus ferox</i>	0	0	0	0	1	0	0	0	1
<i>Patagioenas picazuro</i>	2	0	1	0	2	1	0	0	6
<i>Penelope supercilialis</i>	1	0	0	0	0	0	0	0	1
<i>Phaethornis pretrei</i>	1	0	1	0	2	0	0	0	4
<i>Piaya cayana</i>	0	0	0	1	0	0	0	0	1
<i>Pitangus sulphuratus</i>	3	2	1	2	4	3	3	1	19
<i>Saltator similis</i>	0	0	0	0	0	0	0	1	1
<i>Tangara cayana</i>	0	1	1	1	0	1	0	0	4
<i>Thamnophilus caerulescens</i>	0	0	1	0	0	1	0	0	2
<i>Tangara sayaca</i>	0	0	0	0	0	1	0	0	1
<i>Todirostrum cinereum</i>	0	0	0	0	2	0	1	0	3
<i>Troglodytes musculus</i>	0	1	0	0	0	0	0	0	1
<i>Turdus leucomelas</i>	4	3	1	3	2	0	1	2	16
<i>Volatinia jacarina</i>	0	2	0	0	0	0	0	0	2
<i>Zenaida auriculata</i>	0	0	0	1	0	0	0	0	1
<i>Zonotrichia capensis</i>	0	1	0	0	0	0	0	0	1
Total	19	13	8	16	21	12	9	8	106

Statistical summary of the three fitted candidate models for the second variable block.

	LM-Basic model 2	LM-PCA model 2	Tweedie-GLM-PCA model 2
<i>Predictors</i>	<i>Estimates</i>	<i>Estimates</i>	<i>Estimates</i>
(Intercept)	0.08 **	0.08 *	-2.62 ***
PC2[, 1]		-0.01	-0.15
Observations	8	8	8
R ² / R ² adjusted	0.000 / 0.000	0.148 / 0.006	0.274
AIC	-16.927	-12.611	-19.139

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Statistical summary of the three fitted candidate models for the third variable block.

	LM-Basic model 3	LM-PCA model 3	Tweedie-GLM-PCA model 3
<i>Predictors</i>	<i>Estimates</i>	<i>Estimates</i>	<i>Estimates</i>
(Intercept)	0.08 **	0.08 *	-2.60 ***
PC3[, 1]		-0.01	-0.10
Observations	8	8	8
R ² / R ² adjusted	0.000 / 0.000	0.130 / -0.016	0.188
AIC	-16.927	-12.437	-18.442

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Statistical summary of the three fitted candidate models for the fourth variable block.

	LM-Basic model 4	LM-PCA model 4	Tweedie-GLM-PCA model 4
<i>Predictors</i>	<i>Estimates</i>	<i>Estimates</i>	<i>Estimates</i>
(Intercept)	0.28	0.08 *	0.01
cancov	-0.00		
canH	0.02		
dead	-0.03		
under	-0.01		
PC4[, 1]		0.00	-0.00
PC4[, 2]		-0.00	-0.00
Observations	8	8	8
R ² / R ² adjusted	0.632 / 0.142	0.385 / 0.140	0.660
AIC	64.670	-5.889	-18.619

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Statistical summary of the three fitted candidate models for the variable block.

	LM-Basic model 5	LM-PCA model 5	Tweedie-GLM-PCA model 5
<i>Predictors</i>	<i>Estimates</i>	<i>Estimates</i>	<i>Estimates</i>
(Intercept)	0.08 **	0.08 *	0.01
PC5[, 1]		0.00	0.00
Observations	8	8	8
R ² / R ² adjusted	0.000 / 0.000	0.101 / -0.049	0.177
AIC	-16.927	-12.176	-18.356
* <i>p</i> <0.05 ** <i>p</i> <0.01 *** <i>p</i> <0.001			

