UNIVERSIDADE DE SÃO PAULO
CENTRO DE ENERGIA NUCLEAR NA AGRICULTURA

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Diet and ecosystem services of insectivorous bats assessed with stable isotopes

Piracicaba
2016

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Revised version according to the Resolution CoPGr 6018, 2011

Dissertação apresentada ao Centro de Energia Nuclear na Agricultura da Universidade de São Paulo para obtenção do título de Mestra em Ciências

Área de Concentração: Química na Agricultura e no Ambiente

Orientador: Prof. Dr. Plínio Barbosa de Camargo

Piracicaba

2016

Dados Internacionais de Catalogação na Publicação (CIP)

Seção Técnica de Biblioteca - CENA/USP

Assis, Cecília Kruszynski de

Diet and ecosystem services of insectivorous bats assessed with stable isotopes / Dieta e serviços ecossistêmicos dos morcegos insetívoros avaliados por isótopos estáveis / Cecília Kruszynski de Assis; orientador Plínio Barbosa de Camargo. - - revised version according to the Resolution CoPGr 6018, 2011.- - Piracicaba, 2016.
64 p. : il.

Dissertação (Mestrado – Programa de Pós-Graduação em Ciências. Área de Concentração: Química na Agricultura e no Ambiente) – Centro de Energia Nuclear na Agricultura da Universidade de São Paulo.

1. Carbono 2. Chiroptera 3. Controle de pragas 4. Fauna silvestre 5 Inventário 6. Isótopos estáveis 7. Morcegos 8. Nitrogênio I. Título

CDU 599.4 : (574.4 + 54.027)

I dedicate this dissertation to all the people that believed in me, especially my mom.

ACKNOWLEDGEMENTS

As a friend used to say, this part is the only personal touch you can give to a dissertation. Where you realize that behind your rational scientist side, there is a human being full of hopes and dreams, and sometimes even good ideas. Thankfully, my master study there were a lot of people that helped me, not only finish it, but also made the scientist, in heart and soul, which I am today.

First, I would like to thank my family, because without their strength I would probably have given up my scientific life a long time ago. To my mom, who always pushes me up to be a better person and it is always there for me. To my dad, that always has protected me. I love you both unconditionally.

Thanks to my supervisor, Prof. Plínio Barbosa de Camargo, who accepted my crazy idea to work with bats and always believed that I was able to do this work with competence. To Prof. Luiz Antonio Martinelli and Prof. Marcelo Moreira, for the exchanged ideas along the way. Also, to all the employees and colleagues of the Isotope Ecology Laboratory, at Center of Nuclear Energy in Agriculture that helped me, from processing the biological material to just making coffee at refreshing break times.

To my co-supervisor Prof. Marco Mello, who was open to help with my bat doubts, corrected my text and taught me so much about the academy.

To Prof. Ducati and Evandro Tadeu da Silva, that analyzed some samples when I needed.

To my co-workers, Thais R. Diniz-Reis, Siglea Freitas and Silvia Mardegan, who I owe these last two and a half years. Thank you for putting up with my complaints, my doubts and my wandering. You guys became true friends that I'm very happy to have made. You guys made the days easier. Thank you for all the laughter. In particular, to Thais, who helped more than anyone could ever have. This was a hard work accomplished by us. Thank you for the patience, all the collaborations, the solutions and the questions we resolved together. It was a pleasure.

To all my friends, I do not know why some people come into our lives and make everything better, but I definitely would not be here without them. To Renata Muylaert that lent me all her field material and initiated me in the "bat world". To Neliton Lara, Ayesha Pedrozo, Lucia Martinez, Bruna Merlin, Pamella Brennand, Thais Diniz-Reis, that helped me with field work and made it so much fun.

To Ayesha Pedrozo, who taught me so much about bats. Thank you for the help and patience. To Cristiane "Tita" Millan and Patricia Rogeri, that although entered in this study just in the final line and helped me so much with the final isotope analysis that was essential to the accomplishment of this study. To Anderson Feijó, also in the final line, but that helped me in the writing by giving several tips (I should probably thank Hannah Nunes, since she was a link to literature!). To José Wagner "Xuleta" Ribeiro Junior and Rafael Valadares that motivated me to keep on my academic life (that day was crazy guys, and life changing). To Thiago "Fudnciu" Castro, that helped me with my questions about insects and why there is not a book called "Pests". Lunch has been a fun time over these last few years.

To my "roomies", Pamella Brennand, Jeronymo Dellapicola and Edson Fiedler (even for a brief time), that made me dinner or offered me a beer to calm my problems. That was essential.

To B.C.M.B. that collaborated with so different things, from answering to serious academic questions to nonsense doubts.

To my best friends, Gabriela Helena da Silva, Bruna Merlin and Aline Morgan that have been present in my academic life since the beginning. Although we changed over the years, something about us were made to be, because as we always say, if you have a friend more than seven years, it is for a life time. Thank you for always being there. Count me in for everything as well.

To National Council for Scientific and Technological Development (CNPq) for the financial support to accomplish this project.

For last, but not least, to all the little birds that I did not mentioned here but also are nested in my heart through all my academic years. For you all, I say thank you.

“We cannot solve our problems with the same thinking we used to create them.”

Albert Einstein

ABSTRACT

KRUZYNSKI, C. **Diet and ecosystem services of insectivorous bats assessed with stable isotopes**. 2016. 64 p. Dissertação (Mestrado) - Centro de Energia Nuclear na Agricultura, Universidade de São Paulo, Piracicaba, 2016.

Ecosystem services are natural environmental functions and ecological process that humans benefit from. In the present study, it was highlighted one of the services provided by bats: agricultural pest control. In Brazil, studies with insectivorous bats as potential pest suppressors are still scarce, despite the country being one of the biggest agricultural producers in the world and concentrating a high diversity of those animals. The use of heterogeneous landscapes, formed by native vegetation and crop fields, optimize the investment applied in this search. For that, it was described, for the first time, the bat assemblage in heterogeneous landscape in Piracicaba, at the campus “Luiz de Queiroz” that comprehends urbanized and agricultural areas, which provides many food resources for bats. Further, it was tested if there is difference in isotopic values ($\delta^{13}C$ and $\delta^{15}N$) between bat species related to diet, spatial foraging behavior, sex or taxonomic classification and which specie is a better pest suppressor. Bats were captured by mist nets and stable isotope analysis of carbon and nitrogen ($\delta^{13}C$ e $\delta^{15}N$, respectively) were used to access its food source. Through the analysis of $\delta^{13}C$ and $\delta^{15}N$ of insects, we determined the proportion of plants with photosynthetic cycles of C_3 and C_4 in bats’ diet and its trophic level. It was captured 90 bats of 11 species, three families and four dietary categories, corresponding to 66% of the total local richness estimated. From those, five are insectivorous species. *Molossus molossus* were the most abundant specie, followed by *Artibeus lituratus* and *Glossophaga soricina*. Carbon values showed that insectivores, frugivores and nectarivores consume insects, including pests, in different proportions per specie and diet group. Besides, $\delta^{15}N$ values showed that bat trophic level were very similar, so bats are more generalist than usually assumed. This study points a need to quantify this important ecosystem service provided by bats that can reduce diseases and crop damages.

Keywords: Chiroptera. Agricultural landscape. Carbon. Nitrogen. Pest control.

RESUMO

KRUZYNSKI, C. **Dieta e serviços ecossistêmicos dos morcegos insetívoros avaliados por isótopos estáveis**. 2016. 64 p. Dissertação (Mestrado) - Centro de Energia Nuclear na Agricultura, Universidade de São Paulo, Piracicaba, 2016.

Serviços ecossistêmicos são funções dos ambientes naturais e dos processos ecológicos dos quais humanos se beneficiam. Esses benefícios podem ser acessados por uma perspectiva econômica e ecológica. No presente estudo, nós destacamos um dos serviços ambientais fornecidos por morcegos: controle de pragas agrícolas. No Brasil, os estudos com morcegos insetívoros como potenciais supressores de pragas ainda são escassos, apesar de o país ser um dos maiores produtores agrícolas do mundo e abrigar uma alta diversidade desses animais. O uso de paisagens heterogêneas, formadas por vegetação nativa e lavouras agrícolas, otimiza o investimento aplicado nessa busca. Para tanto, descrevemos, pela primeira vez, a assembleia de morcegos em um ambiente heterogêneo de Piracicaba, o campus “Luiz de Queiroz”, que possui desde áreas urbanizadas a agrícolas, disponibilizando diversos recursos alimentares para os morcegos. Ademais, testamos se há diferenças nos valores isotópicos ($\delta^{13}C$ e $\delta^{15}N$) entre as espécies de morcegos em relação à dieta, comportamento espacial de forrageamento, sexo ou classificação taxonômica para identificar quais grupos são os melhores supressores de pragas agrícolas. Utilizamos redes de neblina para a captura dos morcegos e análises de isótopos estáveis de carbono e nitrogênio ($\delta^{13}C$ e $\delta^{15}N$, respectivamente) para acessar sua fonte de dieta. Por meio das análises, determinamos a proporção de plantas com ciclos fotossintéticos do tipo C_3 e C_4 na dieta dos morcegos, bem como seu nível trófico. Capturamos 90 morcegos de 11 espécies, três famílias e quatro classes de dieta, correspondendo a 66% da riqueza estimada para o local. Destas, cinco são espécies classificadas insetívoras. *Molossus molossus* foi a espécie mais abundante, seguida por *Artibeus lituratus* e *Glossophaga soricina*. Valores de $\delta^{13}C$ mostraram que insetívoros, frugívoros e nectarívoros consomem insetos, inclusive pragas, em diferentes proporções por espécie e grupo de dieta. O grupo mais efetivo no controle de pragas agrícolas foi *M. molossus*, seguido por *A. planirostris*. Os valores de $\delta^{15}N$ mostraram que o nível trófico dos diferentes grupos alimentares de morcegos foi similar, de modo que eles são mais generalistas que previsto na literatura. Nosso estudo aponta a necessidade de quantificação desse importante serviço ecossistêmico promovido por morcegos, que podem reduzir doenças e prejuízos nas lavouras, além de combater vetores de doenças.

Palavras-chave: Chiroptera. Paisagem agrícola. Carbono. Nitrogênio. Controle de pragas.

SUMMARY

1. GENERAL INTRODUCTION

Ecosystem services are the benefits humans obtain from natural environmental functions and ecological processes (MILLENNIUM ECOSYSTEM ASSESSMENT, 2005). Those benefits can be accessed from an ecological or economical perspective (MYERS, 1996). In the present study, it was highlighted one of the environmental services provided by bats: crop pest suppression (KUNZ et al., 2011). Some insectivorous bats prey on a large amount of insects in a single night, consuming up to one and a half times their own body weight (KASSO; BALAKRISHNAN, 2013). In agricultural areas, insectivorous bats are potential crop pest suppressors (MARTIN et al., 2013), which help farmers reduce damage to crops and, therefore, production costs (CLEVELAND et al., 2006). There is no information on the potential service of bats as crop pest suppressors in Brazil. This is essential, as the country is one of the largest agricultural producers in the world (BRASIL, 2015) and harbors very high bat diversity (REIS et al., 2006). In addition, data on the feeding habits of insectivorous bats in Brazil is very scarce, so baseline studies are also urgently needed.

To fulfill that gap, the diet of insectivorous bats has been traditionally assessed through the analysis of insect parts found in feces (BURLES et al., 2008). Although bringing useful information on which groups bats feed on, this method has little effectiveness, as it is very difficult to identify insects from small, chewed body parts. Additionally, this method does not allow researchers to access very important information: the habitat where those prey were consumed. In other words, from that, it is not known if insectivorous bats consume prey in natural (e.g., forests and savannas) or agricultural areas (e.g., sugarcane, eucalyptus, or corn plantations, and pastures). As insectivorous bats move large distances and use several kinds of habitats (JUNG; KALKO, 2010), they are potential insect controllers, including crop pests insects.

One of the most accurate method to identify the original habitat where a prey was consumed is stable isotope analysis of the predator's tissues (LAYMAN et al., 2012). It allows identifying the chemical composition of carbon (C) and nitrogen (N) in the sample, which reflects the items consumed by the predator (RANKAMA, 1956). As different tissues are formed at different times, if the predator changes its diet, tissues of rapid formation will show a different isotopic composition than tissues that take longer to form (DEMOTS et al., 2010). This analysis is based on the variation of the isotopic composition of carbon and nitrogen ($\delta^{13}C$ e $\delta^{15}N$, respectively) in predator tissues. $\delta^{13}C$ values indicate the original environment where the prey was consumed - forest (C_3 plants) or agricultural area (typically C_4 plants) (DENIRO; EPSTEIN, 1978), while $\delta^{15}N$ values indicate the trophic level of predator and prey in each environment (DENIRO; EPSTEIN, 1981). Generally, the enrichment of nitrogen for each trophic level is ~3‰ and ~1‰ for carbon (FRY, 2006), which allows partially reconstructing the food web of the study area. $\delta^{15}N$ analysis may also be used in differentiating crops with and without fertilization (BATEMAN; KELLY; JICKELLS, 2005). As tissues are reconstructed in different periods, they reflect the animals diet from that specific time (DEMOTS et al., 2010). Inert tissues, as hair, are used to acquire information on long term diet (CAUT; ANGULO; COURCHAMP, 2008). The stable isotope analysis is highly suitable for studying bats, even endangered ones, as it requires a small amount of tissue collected *in-situ*. Furthermore, through non-lethal tissue collection, such as hair, it has minimal impact on the bats (VOIGT, 2009).

In order to make the first assessment of the crop pest suppression service delivered by insectivorous bats in Brazil, it was carried out the present study in the campus of University of São Paulo at Piracicaba. The study area was chosen for being very heterogeneous with small patches of native vegetation (semidecidous forest and savanna) at different successional stages, pastures under extensive and intensive management, and crops with different cycles (annuals, perennials, and semi-perennials), forestry production areas, and urban areas (DEMÉTRIO et al., 2000). This diversity of environments leads to a diverse fauna that included species able to live in different habitats (GHELER-COSTA et al., 2002), including bats of different guilds.

The working hypothesis was that insectivorous bats in the area feed mainly on insects that damages crops, which would characterize an important ecosystem service. To test this hypothesis, it was inventoried the bat community of an agricultural heterogeneous landscape and collected tissue samples of bats, insects, and plants in the study area and compared their isotopic values.

Therefore, following this introduction, the second chapter of this dissertation is going to be submitted to Check List with an inventory of the bat fauna of the campus "Luiz de Queiroz", University of São Paulo at Piracicaba (USP), state of São Paulo, southeastern Brazil. Some species were recorded for the first time in the municipality of Piracicaba: *Cynomops planirostris*, *Molossus molossus*, and *M. rufus* (Molossidae), *Sturnira lilium* and *Desmodus rotundus* (Phyllostomidae), *Myotis nigricans* and *Histiotus velatus* (Vespertilionidae,). The other species captured in our study had already been recorded for Piracicaba: *Artibeus lituratus*, *Platyrrhinus lineatus*, and *Glossophaga soricina*

(Phyllostomidae). Vouchers of the species will be deposited in the mammal collection of the Zoological Museum of USP (MUZUSP). Some previously recorded species were not captured by us: *Lasiurus blossevilli* (Vespertilionidae) and *Nyctinomops laticaudatus* (Molossidae).

The third chapter is a manuscript that will be submitted to the Journal of Applied Ecology, which reports on the diet of insectivorous and phytophagous bats in an agricultural landscape. The studied bat species consumed prey with similar isotopic values and seem to be at the same trophic level, consuming insects in various proportions from native vegetation and crops. The insectivore *Molossus molossus* is the most potential pest controller in this area.

Therefore, it was concluded that agricultural landscapes hold common bat species and all of them play important ecosystem services, as pest control. For that, bats should be prioritized in ecological studies in those areas. Also, there was highlighted the need of more studies on diet of bats to base future ecosystem services quantifications.

1.1 INTRODUÇÃO GERAL

Serviços ecossistêmicos são os benefícios que os humanos obtêm de processos e funções ecológicas dos ambientes naturais (MILLENNIUM ECOSYSTEM ASSESSMENT, 2005). Esses benefícios podem ser acessados pela perspectiva ecológica e econômica (MYERS, 1996). No presente estudo, foi destacado um dos serviços ambientais promovidos por morcegos: supressão de pestes agrícolas (KUNZ et al., 2011). Alguns morcegos insetívoros predam uma grande quantidade de insetos por noite, podendo consumir até uma vez e meia seu peso corporal (KASSO; BALAKRISHNAN, 2013). Assim, em áreas agrícolas, morcegos insetívoros podem ser potenciais controladores de pragas agrícolas (MARTIN et al., 2013), ajudando fazendeiros a reduzir danos às lavouras e, portanto, custos de produção (CLEVELAND et al., 2006). Não existem informações sobre o potencial serviço dos morcegos como controladores de praga no Brasil. Informações essenciais, já que o país é um dos maiores produtores agrícolas do mundo (BRASIL, 2015) e abriga uma alta diversidade de morcegos (REIS et al., 2006). Ademais, pouco se conhece sobre os hábitos alimentares dos morcegos insetívoros no Brasil, e estudos de base são necessários urgentemente.

Tradicionalmente, a dieta de morcegos insetívoros tem sido acessada através da análise de partes de insetos encontradas em fezes (BURLES et al., 2008). Esse método tem pouca eficácia, já que é muito difícil identificar insetos por pequenas partes mastigadas.

Além disso, como morcegos insetívoros podem se mover a longas distâncias e usar diferentes tipos de habitats (JUNG; KALKO, 2010), análise fecal pelo microscópio não permite a obtenção de uma informação muito importante: o habitat onde a presa foi consumida. Em outras palavras, não é possível saber que presas os morcegos insetívoros se alimentam em ambientes naturais (por exemplo, florestas e savanas) ou áreas agrícolas (por exemplo, cana-de-açúcar, silvicultura e pastos).

Um dos métodos mais acurados para identificar o habitat original onde as presas foram consumidas é análise dos isótopos estáveis dos tecidos do predador (LAYMAN et al., 2012). Ele permite identificar a composição química do carbono (C) e nitrogênio (N) das amostras, refletindo os itens consumidos pelo predador (RANKAMA, 1956). Como diferentes tecidos são formados em tempos divergentes, se o predador mudar sua dieta, o tecido de formação rápida mostrará uma diferença isotópica na composição do tecido em relação ao tecido de formação lenta (DEMOTS et al., 2010). Essa análise é baseada na variação isotópica da composição de carbono e nitrogênio ($\delta^{13}C$ e $\delta^{15}N$, respectivamente) do tecido do predador: $\delta^{13}C$ indica o ambiente original do qual a presa foi consumida – floresta (Plantas C_3) ou áreas agrícolas (tipicamente plantas C_4) (DENIRO; EPSTEIN, 1978), enquanto $\delta^{15}N$ indica o nível trófico do predador e presas em cada ambiente (DENIRO; EPSTEIN, 1981). Na análise de nitrogênio, existe um enriquecimento de ~3‰ quando subimos um nível trófico (FRY, 2006), permitindo a reconstrução parcial da cadeia trófica da área de estudo. Essa análise também pode ser usada para diferenciar lavouras com e sem fertilização (BATEMAN; KELLY; JICKELLS, 2005). As análises isotópicas são adequadas para o estudo da dieta dos morcegos, pois exige pouca quantidade de tecidos coletados *in-situ.* Além disso, através de coleta não letal de tecidos, como pelo, tem um mínimo impacto nos morcegos (VOIGT, 2009).

Para fazer uma primeira avaliação do serviço de controle de pragas promovido por morcegos no Brasil, o presente estudo foi realizado no Campus da Universidade de São Paulo, em Piracicaba. A área de estudo foi escolhida por compreender uma área heterogênea com pequenas manchas de vegetação nativa em diferentes estágios de sucessão (floresta semidecídua e savana), pasto sob manejo intensivo e extensivo, lavouras com diferentes ciclos (anuais, perenes e semi-perenes), silvicultura e áreas urbanas (DEMÉTRIO et al., 2000). Essa diversidade de ambientes leva a diversidade de fauna que inclui espécies capazes de viver em diferentes habitats (GHELER-COSTA et al., 2002), e também, morcegos de guildas diferentes.

Foi estudado o serviço de controle de pragas dos morcegos insetívoros nessa paisagem heterogênea. A hipótese de trabalho é que os morcegos insetívoros nessa área se alimentam principalmente de insetos que danificam lavouras, caracterizando um importante serviço ecossistêmico. Para testar essa hipótese, foram coletados amostras de morcegos, insetos e plantas, e comparados seus valores isotópicos.

O segundo capítulo dessa dissertação é um manuscrito que será submetido à Revista *Check List*, consistindo num inventário da fauna de morcegos do campus "Luiz de Queiroz", Universidade de São Paulo, em Piracicaba (USP), estado de São Paulo, sudeste do Brasil. Algumas espécies foram registradas pela primeira vez em Piracicaba: *Cynomops planirostris*, *Molossus molossus*, e *M. rufus* (Molossidae), *Sturnira lilium* e *Desmodus rotundus* (Phyllostomidae), *Myotis nigricans* e *Histiotus velatus* (Vespertilionidae,). As outras espécies capturadas no nosso estudo já haviam sido registradas para Piracicaba: *Artibeus lituratus*, *Platyrrhinus lineatus*, e *Glossophaga soricina* (Phyllostomidae). *Vouchers* das espécies serão depositados na coleção zoológica do Museu da USP (MUZUSP). Algumas das espécies registradas anteriormente não foram capturadas por nós: *Lasiurus blossevilli* (Vespertilionidae) and *Nyctinomops laticaudatus* (Molossidae).

O terceiro capítulo é um manuscrito que será submetido à Revista *Applied Ecology*, que relata a dieta dos morcegos insetívoros e fitófagos numa paisagem agrícola. Os morcegos estudados consumiram presas com valores isotópicos similares e parecem se encontrar no mesmo nível trófico, consumindo insetos em várias proporções da vegetação nativa e agrícola.

Portanto, morcegos podem consumir insetos de vegetações distintas, e como eles consomem presas de áreas abertas, em áreas agrícolas, eles consomem pragas em lavouras, promovendo um importante serviço ecossistêmico, de controle de pragas agrícolas.

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2. BATS (MAMMALIA: CHIROPTERA) OF HETEROGENEOUS LANDSCAPE IN PIRACICABA, SOUTHEASTERN BRAZIL[1]

Abstract

Although little is known about the structure of bat communities in urban and peri-urban landscapes in Brazil, those areas might hold key species for the local ecosystem functions. In order to help fulfill this gap, it was sampled bats in the campus of the University of São Paulo at Piracicaba, as it is an area composed by agriculture and urban matrix and patches of native vegetation, which the fauna might use as local refuge. In a total effort of 80,000 h.m² at six different sites, it was captured 90 bats of 11 species, which represents 66% of the estimated richness. The bat fauna of the campus showed to be low richness and evenness, with a predominance of insectivorous and frugivorous species. Three species were dominant: *Molossus molossus* (29%), *Artibeus lituratus* (27%) and *Glossophaga soricina* (23%), and all other eight species compromised the rest 11%. Despite it, the resilient species in those areas might still play important regulating services, as seed dispersal and insect control. For that, bats should be further investigate and prioritize on management plans and in studies at agricultural areas.

Keywords: community, inventory, insectivore, frugivore.

[1] It will be submitted to **Check List** (Porto Alegre).

Resumo

Apesar de pouco se conhecer sobre a estrutura da comunidade de morcegos em paisagens urbanas e peri-urbanas no Brasil, essas áreas podem abrigar espécies chave para o funcionamento do ecossistema nestes locais. Para preencher essa lacuna, foram amostrados os morcegos no Campus da Universidade de São Paulo, Piracicaba, visto que esta é uma área formada por matriz agrícola e urbana e fragmentos de vegetação nativa, podendo ser usada pela fauna para refúgio. Em um esforço total de 80.000 $h.m^2$ em seis diferentes ambientes, foram capturados 90 morcegos de 11 espécies, que representa 66% da riqueza de espécies estimada para o local. A quiropterofauna do *campus* se mostrou empobrecida e com menor equabilidade que outros ambientes antropizados do estado de São Paulo, com predominância de espécies insetívoras e frugívoras. Três espécies foram dominantes: *Molossus molossus* (29%), *Artibeus lituratus* (27%) e *Glossophaga soricina* (23%), enquanto as outras oito restantes compuseram somente 11% da comunidade. Apesar disso, as espécies resilientes nesses ambientes ainda devem exercer importantes serviços ecossistêmicos regulatórios, como controle de insetos e dispersão de sementes. Portanto, os morcegos devem ser investigados e priorizados em planos de manejo e em estudos em paisagens agrícolas.

Palavras-chave: comunidade, inventário, insetívoros, frugívoros.

2.1 Introduction

Most of the current pristine and protected areas have been diminished by agriculture and urban expansion (MEDELLÍN; EQUIHUA; AMIN, 2008). Studies in fragmented areas are important to extend our knowledge on species that resist in human modified sites and that keep playing ecosystem services in anthropic landscapes. In those fragmented areas, bats have a great importance on seed dispersal and insect suppressor, especially by its ability to fly long distances and the adaptation of certain species living in these anthropogenic environments (BREDT, 1998). In the city, the latter role is crucial, since in the last years diseases transmitted by mosquitoes have been a major concerning for public health and bats could be a key tool to reduce the vector population.

Several bat species have been recorded maintaining viable populations in native vegetation fragmented areas (SOUZA et al., 2006), but many species seems unable to adapt, suffering severe population declines (BROSSET et al., 1996). In order to develop effective strategies for keeping bat regulating services, it is needed to better survey its biodiversity in those anthropic landscapes.

Even though the state of São Paulo has a broad history of mastozoological studies, being regarded as one of the most well-known states of Brazil, only a few studies had been conducted in nearby urban areas. Those studies point a range of 17 to 36 species of bats registered in anthropic environments (UIEDA; CHAVES, 2005; CHAVES et al., 2012). The south-central region of São Paulo, in Piracicaba, is a key area for those studies by being composed by a mixed landscape of urban area, agriculture fields and remnants of Atlantic forest (SPAROVEK, 1993). Surveys in those type of sites optimize financial resources on science by obtaining simultaneous data for conservation (bats and forest), economic (agriculture insect pest control) and healthcare interests (disease vector population control). For this reason, the present study aim to describe the bat assemblage in heterogeneous landscape of Piracicaba.

2.2 Material and Methods

2.2.1 Study Area

This study was carried out in the campus of the University of São Paulo, known as Escola Superior de Agricultura "Luiz de Queiroz" (ESALQ), in a peri-urban area of Piracicaba, state of São Paulo, southeastern Brazil (22º42'30"S, 47º38'30"W). The campus has 914.5 ha and harbors heterogeneous landscape composed of small patches of secondary semi-deciduous forest (the largest have 14 and 9.5 ha), extensive and intensive pastures, crops, silviculture, and urban areas (DEMÉTRIO et al., 2000). It also contains two streams, which are tributaries of the Piracicaba River, and form wetlands and artificial reservoirs (Figure 2.1).

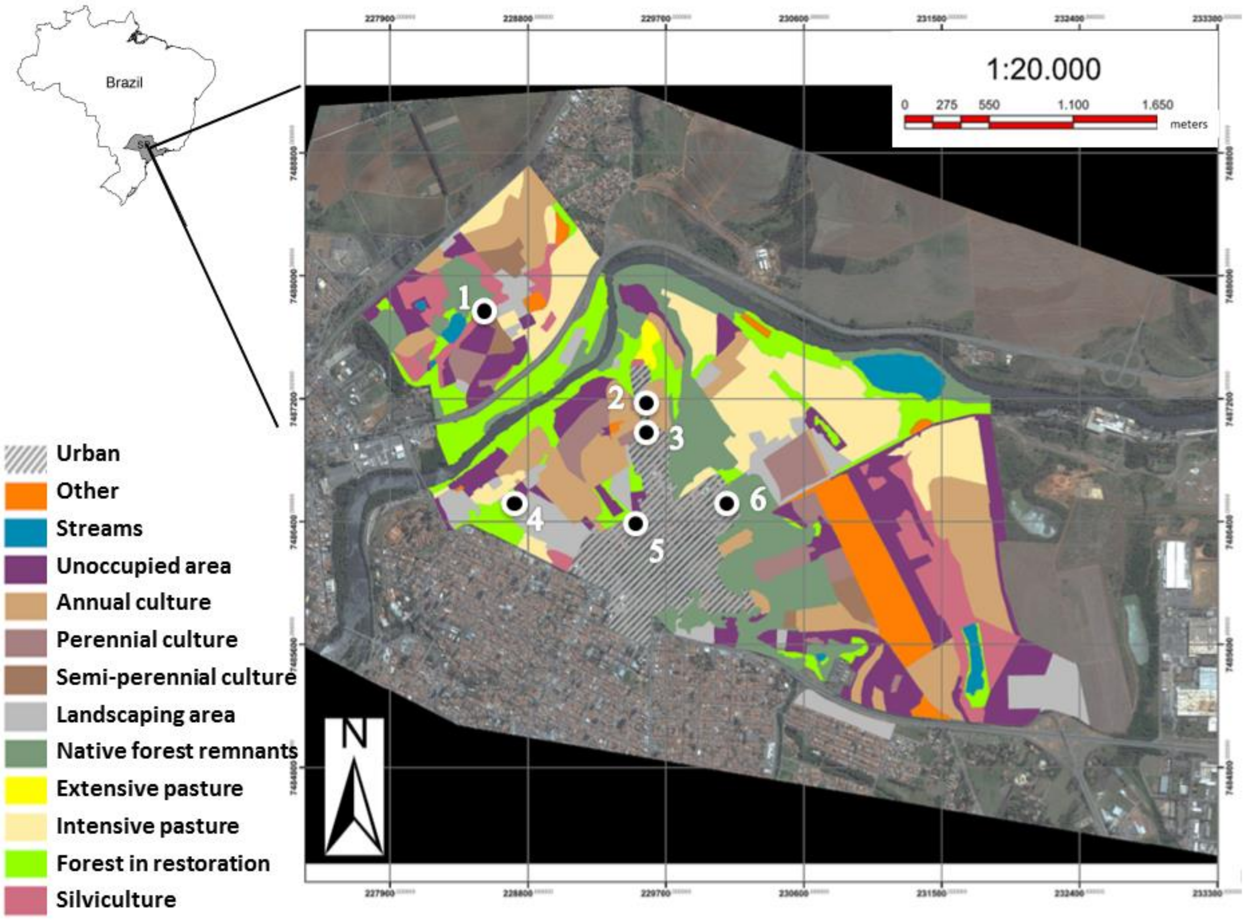

Figure 2.1 - Landscape of the study area (University of Sao Paulo, campus Escola Superior de Agricultura "Luiz de Queiroz") classified by its land use and sample sites (numbered black dots in order of sampling).

2.2.2 Data collection

Bats were sampled for 11 nights from December 2013 to June 2015 at six sites (Figure 2.1). It was set up three to six mist nets each night, which were opened at sunset and closed after six hours. Net size ranged from 10 x 3 m to 12 x 3 m with 2.5 mm mesh (Ecotone Inc., Poland). The nets were placed around the urban area, nearby buildings where we found evidence of bat roosts (such as feces), and on the edges and in trails within forest fragments.

All individuals captured were taxonomically identified and measured (forearm length and weight) and had their sex, age class, and reproductive status determined. Bats were identified to the finest possible taxonomic level using the specialized keys published by Gardner (2007), Vizzoto and Taddei (1973) and Gregorin and Taddei (2002). Also, they were classified by diet as omnivorous, insectivorous, frugivorous, nectarivorous, carnivorous, or sanguivorous (KALKO, 1997). Age classes were estimated based on the degree of ossification of their phalangeal epiphyses (KUNZ; ANTHONY, 1982).

Fieldwork was carried out following the guidelines of the American Society of Mammalogists and received permits from the Brazilian Institute for the Environment and Natural Resources (process number 41352-1) and the Ethics Committee for Animal Experimentation of the Centre for Nuclear Energy in Agriculture (protocol number 2013-18). Three couples of each species captured were collected as vouchers for accurate identification and are being processed for deposit in Brazilian museums (Zoological Museum of the University of São Paulo, Zoological Collection of the Federal University of Minas Gerais, and Mammalogical Collection of the Federal Rural University of Rio de Janeiro).

2.2.3 Data analysis

The structure of the local bat community were described through a species list, species richness index, evenness index, species abundance distribution plot. The total number of bat species in the area was estimated by a rarefaction curve (GOTELLI; COLWELL, 2001) based on first-order Jackknife. The total sampling effort was calculated by multiplying the area of one mist net by the total number of nets used and the total number of hours of sampling (STRAUBE; BIANCONI, 2002). All analyses were ran in the software R (R Development Core Team 2010) using the *vegan* package (OKSANEN et al., 2010).

2.3 Results

In a total sampling effort of 80,017.2 h m^2, it was captured 90 bats of 11 species, three families, and four dietary categories (Table 2.1). According to the Jackknife estimator, we sampled 66% of the local bat richness (16.5 ± 2.62) (Figure 2.2), with an evenness distribution of 0.77.

The most abundant and diverse dietary category was insectivorous bats, represented by five species of two families (45% of the total richness), followed by frugivorous bats with four species (36%) (Figure 2.3). The other two categories were represented by one nectarivorous specie (9%), and one sanguivorous specie (9%). *Molossus molossus* (Molossidae) was the most abundant species (29%), followed by *Artibeus lituratus* (Phyllostomidae, 27%) and *Glossophaga soricina* (Phyllostomidae, 23%), while *Cynomops* cf. *planirostris* was very rare (1%).

Table 2.1 - Body measurements (mean ± standard deviation) and number of individuals of the bat species captured at the campus "Luiz de Queiroz" of the University of São Paulo at Piracicaba (ESALQ) divided by taxonomic level, dietary categories and sex.

Taxonomic classification	**Dietary categories**	**Males**		**Females**	
		Weight (n)	**Forearm**	**Weight (n)**	**Forearm**
Molossidae					
Cynomops cf. planisrostris (Peters, 1865)	insetivore	-	-	7.00 (1)	32.10
Molossus molossus (Pallas, 1766)	insetivore	13.83±2.93 (15)	38.89±1.2	13.00±1.71 (13)	37.79±1.8
Molossus rufus É. Geoffroy, 1805	insetivore	34.00±4.24 (2)	51.40±1.84	22.50 (1)	48.20
Phyllostomidae – Desmodontinae					
Desmodus rotundus (É. Geoffroy St.-Hilaire, 1810)	sanguivore	40.50 (1)	61.50	40.00 (1)	63.20
Phyllostomidae – Glossophaginae					
Glossophaga soricina (Pallas, 1766)	nectarivore	10.17±0.98 (17)	34.51±1.32	10.92±0.8 (6)	35.97±0.51
Phyllostomidae – Sternodermatinae					
Artibeus cf. planirostris (Spix, 1823)	frugivore	-	-	85.00 (1)	69.10
Artibeus lituratus (Olfers, 1818)	frugivore	75.32±5.71 (12)	69.75±3.6	79.89±8.08 (12)	70.93±3.08
Platyrrhinus lineatus (É. Geoffroy St.-Hilaire, 1810)	frugivore	24.50 (1)	47.80	32.25±4.57 (4)	47.97±1.26
Sturnira lilium (É. Geoffroy St.-Hilaire, 1810)	frugivore	26.10 (1)	44.30	20.20 (1)	39.50
Verpertilionidae					
Histiotus velatus (I. Geoffroy St.-Hilaire, 1824)	insetivore	11.50±2.83 (2)	44.40±1.7	-	-
Myotis nigricans (Schinz, 1821)	insetivore	5.00 (1)	31.30	-	-

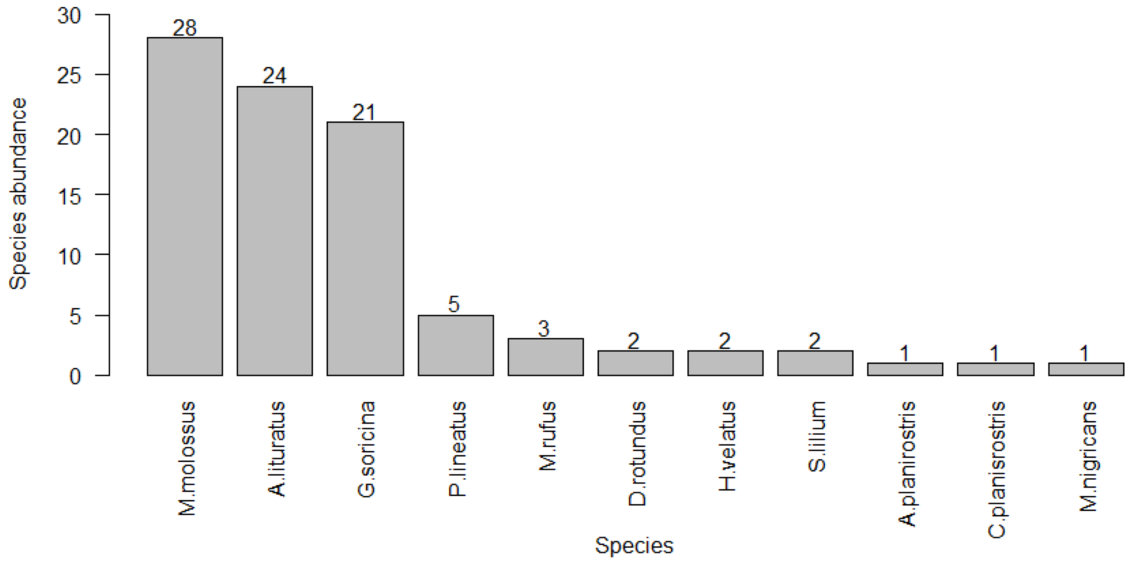

Figure 2.2 - Species abundance diversity in the University of Sao Paulo, campus "Luiz de Queiroz", Piracicaba.

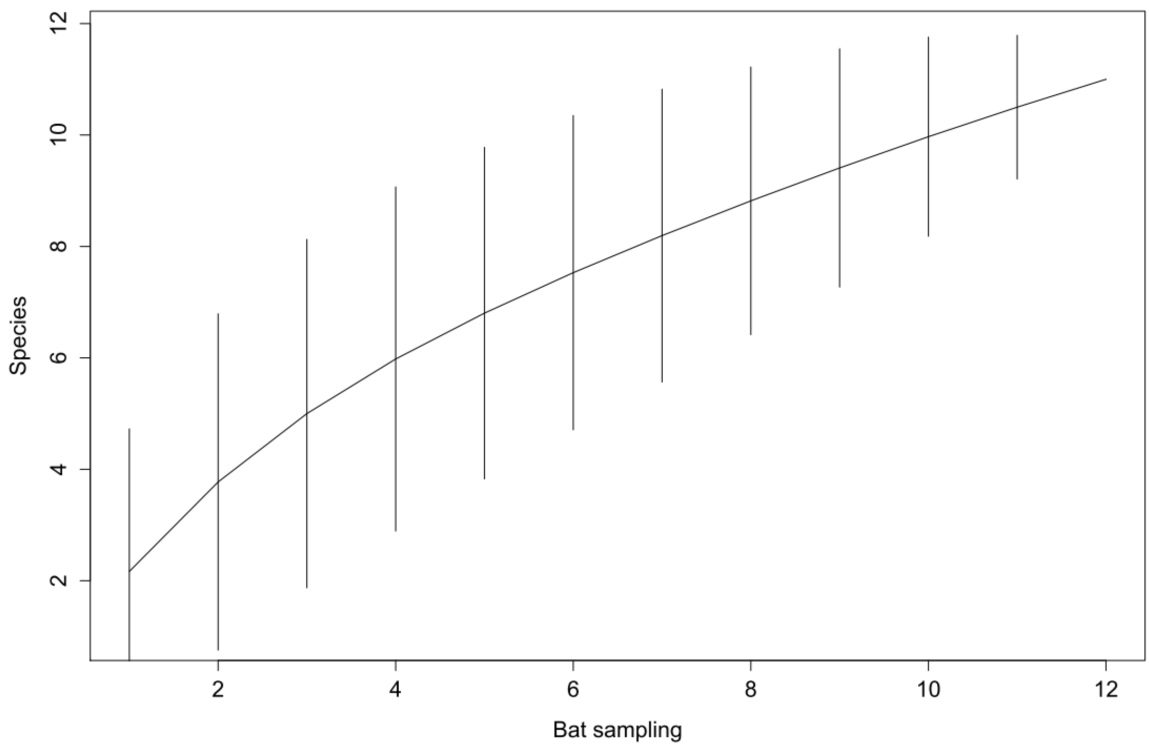

Figure 2.3 - Rarefaction curve showing accumulation of species of bats by sampling days in the University of São Paulo, Piracicaba. Vertical lines are the confidence interval.

2.4 Discussion

This was a punctual inventory made for ESALQ campus. The bat community presented many taxonomic groups within families, species and dietary groups. It also presented low diversity, species evenness and high predominance of insectivorous and frugivorous species.

The higher abundance of those species with dietary behavior may be explained by: (i) availability of shelter and food and (ii) the easiness of insectivores to fly on open tridimensional spaces. The proximity of native vegetation remnants and the large quantity of buildings provide places for roosts as well as constant food-supply. In urban areas these are provided by insects attracted by street lights or trees used in urban planting that they can explore (BREDT; UIEDA; PEDRO, 2012), like primary plants that usually benefits in degraded forests (CORLETT, 2005) such as *Piper* sp., *Cecropia* sp., *Ficus* sp., *Solanum* sp. Yet the increased bats' dislocation along a wider area and their success of insect capture is probably related to the high available area within the urban part of the campus and agricultural fields, that consequently support more individuals of this group (ARAÚJO; BERNARD, 2015).

This bat assemblage is composed by species commonly found within the state of São Paulo (NOGUEIRA et al., 2014), either on more pristine areas, as national or state parks (PASSOS et al., 2003), or anthropic ones, as agricultural and urban landscapes (CHAVES et al., 2012). They are also listed as least concern by the IUCN Red List of Threatened Species (2015). However, some of the captured species have been considerate in needed of taxonomic reviews: *Artibeus planirostris* (BARQUEZ; DIAZ, 2015), *Molossus rufus* (BARQUEZ et al., 2015a), *Glossophaga soricina* (BARQUEZ et al., 2015b), *Histiotus velatus* (GONZALEZ; BARQUEZ, 2008), and *Myotis nigricans* (BARQUEZ et al., 2008). For that, our data may be used by posterior studies on distribution and ecology of the remained species.

Bat surveys in anthropic areas have shown very different richness within the state of São Paulo (MUYLAERT et al., 2014; OPREA et al., 2009; SATO et al., 2015), however the richness recorded here is lower than found in other studies in this state (UIEDA; CHAVES, 2005), even considering that estimated by the curve. A possible explanation for that may be the high level of disturbance in the area, demonstrated by the absence of some very sensitive key species, as some Phyllostominae (MEDELLÍN; EQUIHUA; AMIN, 2008) and by the low richness on other animal groups registered by other studies in the study area, as herpetofauna (MARCHINI; FERRAZ, 2014), birds (ALEXANDRINO et al., 2013) and non-flying mammals (GHELER-COSTA; VERDADE; ALMEIDA, 2002). As the estimated curve did not stabilize, additional bat surveys are needed for a more robust bat assemblage list. Furthermore, it should include a combination of mist netting and complementary methods, as bioacoustics monitoring (SAMPAIO et al., 2003). Additionally, sample sites should also be more diversified, as by water ponds, creeks and wetlands, what may increase the richness index, change the evenness index and the species abundance estimated here.

In conclusion, the heterogeneous landscape of the ESALQ campus harbors a bat assemblage with low richness and low evenness even for anthropic areas. The resilient species may play important regulating services, as insect control and seed dispersal. For that, bats should be further investigate and prioritize on management plans.

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3. WHERE DO BATS GET THEIR FOOD IN AN AGRICULTURAL LANDSCAPE?[2]

Abstract

Pest control by bats is one of the most unknown ecosystem services in Brazil. To fulfill this gap, studies in agricultural landscapes that lost most of their native vegetation can be useful to unveil if this service is still functional there and which bats provide it. In the present study, it was tested whether (i) differences in carbon (C) and nitrogen (N) isotopic composition values ($\delta^{13}C$ and $\delta^{15}N$, respectively) between bat species are related to diet and spatial foraging behavior, sex or taxonomic classification and (ii) some bat species are better at suppressing pests than others. Bats were sampled with mist nests in different habitat types and had their dorsal hair characterized isotopically on ^{13}C e ^{15}N. Insects, fruits and leaves were sampled in order to determine the stable isotope baseline of the resources consumed by bats. The proportion of food items in the diet of different species and guilds was estimated using Bayesian statistics. $\delta^{13}C$ values showed that insectivorous, frugivorous, and nectarivorous bats feed on insects in different proportions for species and dietary group. The insects consumed can feed on crops or on native plants. $\delta^{15}N$ values showed that bats of different dietary group presents similar trophic levels, so bats are more generalists than usually assumed. Therefore, insectivorous bats, and phytophagous bats at a lesser degree, consume insects in both natural and agricultural areas, playing the role of pest suppressers. This study points out to the need of quantification of this important ecosystem service delivered by bats, which can decrease insect-borne diseases, such as dengue and zika, and the reduction of crop damages.

Keywords: Chiroptera, pests, crops, stable isotopes, ecosystem services.

[2] It will be submitted to **Journal of Applied Ecology** (Oxford)

Resumo

Controle de insetos-praga por morcegos é um dos serviços ecossistêmicos menos estudados no Brasil. Para preencher essa lacuna, estudos em paisagens agrícolas que perderam a maior parte da vegetação nativa podem ser úteis para revelar se esse serviço ainda é funcional nessas paisagens e quais morcegos são capazes de exercê-lo. No presente estudo, foi testado se (i) as diferenças nos valores das composições isotópicas de carbono (C) e nitrogênio (N) ($\delta^{13}C$ e $\delta^{15}N$, respectivamente) entre espécies de morcegos são relacionados à dieta, comportamento espacial de forrageamento, sexo ou classificação taxonômica e (ii) algumas espécies de morcegos são melhores supressores de pestes que outras. Os morcegos foram amostrados por meio de redes de neblina em diferentes tipos de vegetação e tiveram seu pelo dorsal caracterizado isotopicamente para ^{13}C e ^{15}N. Insetos, folhas e frutos foram coletados nos mesmos locais e períodos para definir a base das análises isotópicas dos recursos consumidos por morcegos. A proporção de cada fonte na dieta de cada espécie de morcego e guilda foram estimadas por estatística Bayesiana. Valores de $\delta^{13}C$ mostraram que insetívoros, frugívoros e nectarívoros consomem insetos, inclusive pragas, em diferentes proporções por espécie e grupo de dieta. Ademais, valores de $\delta^{15}N$ mostraram que as espécies dos diferentes grupos alimentares possuem nível trófico semelhante, de modo que morcegos são mais generalistas que normalmente assumido. Portanto, morcegos insetívoros, e fitófagos em menor proporção, consumem insetos de ambas as áreas, nativa e agrícola, exercendo o serviço ecossistêmico de controle de pragas agrícolas em ambas. Este estudo aponta a necessidade de quantificação desse importante serviço ecossistêmico promovido por morcegos, que podem reduzir os prejuízos nas lavouras.

Palavras-chave: Chiroptera, pragas, plantações, isótopos estáveis, serviços ecossistêmicos.

3.1 Introduction

Understanding the connection between land use, biodiversity, and ecosystem services is essential for maintaining functional ecosystems in the world (BARKER; MORTIMER; PERRINGS, 2010). Therefore, studies in heterogeneous landscapes formed by anthropic areas and habitat remnants might be useful to understand which ecosystem services are still functional in areas that lost most of their native vegetation (TILMAN et al., 1997). Several of these services such as pollination, seed dispersal and pest control are provided by bats (KUNZ et al., 2011). Those studies might reveal which bat species are resilient to habitat change, and which species play the role of pest suppressers.

When population and biodiversity of bats decrease, loss of those services are estimated to be $22.9 billion per year for the USA agricultural industry (BOYLES et al., 2011). In the state of Texas, USA, insectivorous bats helped reduce the use of pesticides in cotton production (FEDERICO et al., 2008) and saved farmers up to $173 per acre (CLEVELAND et al., 2006). In Brazil, one of the most important food producer worldwide (BRASIL, 2015), there is still a huge lack of knowledge on this bat service, and no estimation have been done yet. However, the contribution as pest suppressor should be even higher as Brazilian insectivorous bat richness is 242% bigger than in the USA (PAGLIA et al., 2012), with 114 species.

To quantify this ecosystem service, bat studies have relied almost exclusively on fecal analysis (BURLES et al., 2008). However, this method does not allow to be tracked the habitat where the insects were consumed, so it is not able to know whether insects are suppressed mainly in natural or anthropic areas. One useful method for this is the analysis of stable isotopes, which assesses the composition of isotopes on animal tissues, and has become an important tool to study diet composition, population structure and movements (FRY, 2006). In this method, the diet composition is determined mainly through the analysis of $\delta^{13}C$ in predator tissues. The consumption of plants with different photosynthetic cycles will reflect on different of ^{13}C values of the insects. So, when the tissue is formed through the ingestion of crop insects (which feed on C_4 plants) it will be richer in ^{13}C compared to tissues formed through the ingestion of forest insects (which feed on C_3 plants) (DENIRO; EPSTEIN, 1978). Likewise, the analysis of $\delta^{15}N$ in predator tissues will determine the trophic level of the individuals, since it accumulates in each item consumed, being plants the most depleted, and top predators the most enriched (DENIRO; EPSTEIN, 1981). The proportion of food sources in the analyzed tissues is estimated with stable isotope Bayesian mixed models, including the isotopic fractionation of each tissue through the food web (STOCK; SEMMENS, 2013).

In the present study, it was assessed the pest suppression service delivered by insectivorous bats in heterogeneous landscape through stable isotope analysis. It was tested whether (i) differences in isotopic values ($\delta^{13}C$ and $\delta^{15}N$) between bat species are related to diet and spatial foraging behavior, sex or taxonomic classification and (ii) some bat species are better at suppressing pests than others. It is expected that the most probable bat group to play this service will be insectivores, as a single individual consume about one and a half time of its body in insects in one night (KUNZ et al., 2011). Although, other groups are also able to consume insects, including nectarivores (HERRERA; HOBSON, 2001) and frugivores (HERRERA et al., 2001). These groups could also help, in a lesser degree, to mitigate agriculture losses. Between insectivores, uncluttered habitat foraging species should consume more crop insects than closed habitat ones, as crop fields are mostly open areas habitat.

3.2 Material and Methods

3.2.1 Study area

Fieldwork was carried out in the campus of Escola Superior de Agricultura Luiz de Queiroz (ESALQ), which belongs to the University of São Paulo at Piracicaba (22º42’30” S 47º38’30” W), state of São Paulo, southeastern Brazil. The study area has heterogeneous landscape composed of urban areas, crops, and forest fragments (see more in chapter 2, item 2.2.1).

3.2.2 Data collection and species identification

Bats were captured as described in chapter 2, item 2.2.2. All captured individuals had dorsal hair samples aseptically cut from the top of their right scapula (about 5 mg) and stored in plastic tubes. Hair is an inert tissue, so it is expected that it revels the predator’s diet from one year ago, approximately (VOIGT et al., 2003). Bats were classified into three dietary categories: insectivore, frugivore, and nectarivore, and further in five guilds: uncluttered space aerial insectivore; highly cluttered space gleaning nectarivore; highly cluttered space gleaning canopy frugivore; highly cluttered space gleaning shrub frugivore; background cluttered space aerial insectivore (following Sampaio et al., 2003). The only captured sanguivorous bat, *Desmodus rotundus*, was removed from the analysis as there is no evidence that this species feeds on insects.

The potential prey of bats was collected in the same area during the sampling period. Insects were sampled in pastures, corn fields, native forests and silviculture areas. Insect traps consisted of an electric lamp placed 30 cm away from the center of a white cloth (3 x 2 m), which was suspended by ropes and had folded bottom. The insects were identified to family by Sinval Silveira Neto, curator of the Entomology Museum of ESALQ, as it is the most common taxonomic level used on trophic studies of bats (KALKA et al., 2008). Each family was classified by its economic importance by literature comparison, considering as pest if they feed and damage C_4 plants (GALLO et al., 2002).

To stablish an isotopic baseline, it also was collected leaves and fruits in the study area (POST, 2002). The fruits collected were the ones usually consumed by bats, such as *Ficus guaranitica*, *Solanum* sp., *Cecropia* sp., *Piper amalago*, and *Piper* sp. (BREDT; UIEDA; PEDRO, 2012). Plants were identified by Gabriel Dalla Colleta by comparison with vouchers deposited in the Herbarium of ESALQ.

3.2.3 Sample preparation and stable isotope analysis

All samples were treated in Isotope Ecology Laboratory, at Center of Nuclear Energy in Agriculture, Piracicaba, São Paulo. Samples of bats, insects, and plants were washed with distilled water to remove dirt, and then oven dried at 60 ºC for 48 h. Insects and leaves were grounded in liquid nitrogen until pulverization. Each sample was weighed from 0.8 to 1.2 mg for animal samples and 2.5 to 2.8 mg for plants into tin capsules (5 x 9 mm) at a precision balance (Sartorius Genius ME, 0.01 mg). Afterwards, it was processed by on-line combustion in an elemental analyzer Carlo Erba (CHN-1110) coupled to a mass spectrometer Finnigan Delta Plus, through the methodology CF-IRMS (Continuous Flow - Isotope Ratio Mass Spectrometers). Stable isotope ratios were calculated as $\delta X(‰) = [(R_{sample} - R_{standard})/R_{standard}] * 1000$, where X represents ^{13}C or ^{15}N, R_{sample} is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio of the sample and $R_{standard}$ the respectively ratio of the standard. The standard reference materials were PeeDee Belemnite for C and atmospheric N_2 for N. Local standard made of sugarcane was inserted every ten samples to calibrate the system and to allow posterior corrections for any drift over time. The acceptable analytical errors were 0.3 and 0.1%, for C and N concentrations, and 0.5 and 0.3‰, for isotopic values of $\delta^{13}C$ and $\delta^{15}N$, respectively.

3.2.4 Data analysis

The average isotopic values of C and N and their standard deviations were calculated for: (i) each bat species, separated by sex and guilds; (ii) each family of insects; and (iii) each plant genus collected. For the bat species that had both sexes captured, we ran a t-test to verify differences related to sex.

To determine the contribution of insects from each type of habitat, differences on $\delta^{13}C$ and $\delta^{15}N$ values of each habitat were compared using one-way ANOVA. In this test, only insects sampled in pasture fields were isotopically different from the other areas. For that reason, insects were grouped by a cluster analysis with Euclidean distances. The cut on the 1.5 high resulted in five separated insect groups (Appendix A). It was added a group 6 with all the fruits we collected for complementary data on frugivorous bats (Table 3.1). Each group was separated in a range of $\delta^{13}C$ and $\delta^{15}N$ different from the others (Table 3.1).

The proportion of incorporated C_3 and C_4 prey into bats' tissues were first calculated by mixing model as follow: C_4 (%) = 100 - ($\delta^{13}C_{sample}$ - $\bar{x}\delta^{13}C\ C_{4vegetation}$) / ($\bar{x}\delta^{13}C\ C_{3vegetation}$ - $\bar{x}\delta^{13}C\ C_{4vegetation}$) using the mean $\delta^{13}C$ values for C_3 and C_4 plants extracted from our vegetation data (Appendix B) (MARTINELLI et al., 2009). Then, it was used Bayesian probability distributions (median, 2.5th and 97.5th percentiles) on stable isotope mixing model, using the package *MixSIAR* GUI 1.0 (STOCK; SEMMENS, 2013) of the R software (R Core Team 2015). Discrimination factors were 3.0±1.6‰ for C and 3.5±0.6‰ for N, as approximated values extracted from literature data for bat tissues (Supplement A). Mixture isotopic model was tested for each dietary categories and species as random effect, first without individual effect and, then, including individual effect (Markov chain Monte Carlo parameters: chain length = 600.000/1.000.000, burn in = 300.000/500.000, thin = 30/500, number of chains = 3). The conversion of models was tested and accepted for Gelman-Rubin, Heidelberger-Welch and Geweke diagnostic tests.

Table 3.1 – Composition of group sources and their range of δ^{13}C and δ^{15}N values. Groups 1-5 are formed by insect orders (in bold) and families collected in University of São Paulo, campus "Luiz de Queiroz", Piracicaba. Group 6 is formed by fruits found in the study area.

Groups	**1**	**2**	**3**	**4**	**5**	**6**
Range of δ^{13}C	-21.5 to -34.2	-10.6 to -23.2	-24.5 to -30.8	-10.0 to -13.9	-34.4	-31.4 to -33.3
Range of δ^{15}N	0.4 to 8.9	3.8 to 12.5	9.0 to 15.0	-3.3 to 2.5	-2.6	2.1 to 6.6
Orders/Families/*Species*	**Coleoptera**	**Diptera**	**Blattaria**	**Coleoptera**	**Lepidoptera**	*Cecropia* sp.
	Coccinellidae	Culicidae	Blattellidae	Scarabaeidae	Tortricidae	*Ficus guaranitica*
	Diptera	No family defined	**Coleoptera**	Cicadellidae		*Piper amalago*
	Chironomidae	**Lepidoptera**	Carabidae	**Lepidoptera**		*Piper* sp.
	Tachinidae	Crambidae	Scarabaeidae	Noctuidae		*Solanum* sp.
	Tephritidae	Geometridae	Tenebrionidae			
	No family defined	Pyralidae	**Dermaptera**			
	Hemiptera (Heteroptera)	**Neuroptera**	Forficulidae			
	Reduviidae	Chrysopidae	**Diptera**			
	Rhopalidae		Culicidae			
	Hymenoptera		Muscidae			
	Pompilidae		Tachinidae			
	Lepidoptera		**Hemiptera (Heteroptera)**			
	Acrolophidae		Miridae			
	Erebidae		**Lepidoptera**			
	Pyralidae		Gelechiidae			
	No family defined		Noctuidae			
	Crambidae		No family defined			
	Gelechiidae		Passalidae			
	Noctuidae		**Neuroptera**			
	Geometridae		Chrysopidae			
	Neuroptera		Hemerobiidae			
	Chrysopidae		**Hymenoptera**			
			Apidae			
			Ichneumonidae			
			Odonata			
			Libellulidae			

3.3 Results

The isotopic distribution of bats based on $\delta^{13}C$ and $\delta^{15}N$ values showed that insectivorous and phytophagous (frugivorous and nectarivorous) bats in the studied heterogeneous landscape fed in different proportions on C_4 and C_3-prey (Figure 3.1). The proportion of incorporated C shows that insectivores consumed a higher amount of C_4-prey (57 – 89%) over phytophagous (36 – 51%). Among insectivores, *Molossus* sp. had the highest percentage of C_4-prey in their diets (89%), followed by *Cynomops* cf. *planirostris* (77%), *Histiotus velatus* (66%), while *Myotis nigricans* had the lowest (57%). Among phytophagous bats, the frugivore *Artibeus* cf. *planirostris* was an outlier, consuming 84% of C_4-prey, while, the others seem to consume less C_4-prey, *Glossophaga soricina* (51%), *A. lituratus* (41%), *Sturnira lilium* (37%) and *Platyrrhinus lineatus* (36%). Bats' $\delta^{15}N$ isotope values had little variance among dietary groups and species. Nectarivores were the group with the most ^{15}N-enriched, while insectivores and frugivores had similar $\delta^{15}N$ values. The biplot dispersion of both isotopic values of bat community suggests that there are no differences between males and females of any species analyzed (Table 3.2) (Appendix C).

The insect assemblage as food source for bats is formed by 11 orders and 31 families, with 19 insects considered agriculture and health pests (Appendix D). Plants $\delta^{13}C$ and $\delta^{15}N$ were different between C_3 and C_4 photosynthetic cycles. Fruits and eucalyptus leaves had ^{13}C-depleted and ^{15}N-enriched (-32.15±0.70 and 5.4±1.7‰, respectively), while corn and grass leaves had ^{13}C-enriched and ^{15}N-depleted (-13.53±1.06 and 0±3.3‰, respectively) (Appendix B). These differences enabled us to establish different baselines for crop fields and forested areas.

The stable isotope mixing models for each dietary categories and species, with and without individual effect, were convergent. In the model without individual effect, the variance in the diet was better explained by dietary categories ($\sigma_{\text{dietary categories}}$ = 0.93 (0.418 – 1.962), σ_{species} = 0.322 (0.02 – 0.869). In the model with individual effect, species better explained by the variance in the diet ($\sigma_{\text{dietary categories}}$ = 0.652 (0.085 – 1.686), σ_{species} = 0.779 (0.477 – 1.313) $\sigma_{\text{individual}}$ = 0.043 (0.002 – 0.142)). They showed that bat community consumed a larger amount of insects from group 3 (26%), formed by insects of a mixture zone of $\delta^{13}C$ and $\delta^{15}N$-enriched values, and a small amount of the group 1 (7.6%), also insects of a mixture zone of $\delta^{13}C$ (with C_3 and C_4 plants) but with $\delta^{15}N$-depleted values (Figure 3.2). Among dietary categories, insectivores consumed more of group 4 (36%), insects of a mixture zone of $\delta^{13}C$ but with low $\delta^{15}N$ values, and 3 (27%). Frugivores had fruits (group 6) as main food resource, as expected, but also consumed insects from group 3 (21%). Nectarivores consumed group 3 (33%) and 6 (22%) (Appendix E).

Among species, *Molossus molossus* and *M. rufus* had very similar sources. Genus *Molossus* had distinguished preference for sources 2, 3 and 4; *A. planirostris* for source 2. Noteworthy, the diets of Vespertillionidae, *C. planirostris* and *G. soricina* diet were not dominated by a single C source (Figure 3.3). The similarity of diet between species is shown by three groups. The first group is formed by *M. molossus*, *M. rufus* and *A. planirostris* with a ^{13}C-depleted isotopic composition (around -15.8‰). The second group was formed by *C. planirostris* and *H. velatus*, with $\delta^{13}C$ intermediary values (around -18.9‰). Finally, the group formed by *M. nigricans*, *G.soricina*, *A. lituratus*, *P. lineatus* and *S. lillium*, had ^{13}C-enriched values (around -24.2‰). These results suggest a higher consumption of pest-insects by the first bat group followed by the second one.

Table 3.2 – Results of test-T for differences between sexes in isotopic values of bat species.

Species	t-value for $\delta^{13}C$	p	t-value for $\delta^{15}N$	p
Artibeus lituratus	0.01	0.98	0.66	0.51
Glossophaga soricina	1.59	0.13	1.75	0.1
Molossus molossus	0.64	0.52	0.97	0.33
Molossus rufus	3.06	0.2	6.77	0.09
Platyrrhinus lineatus	0.83	0.49	0.28	0.8

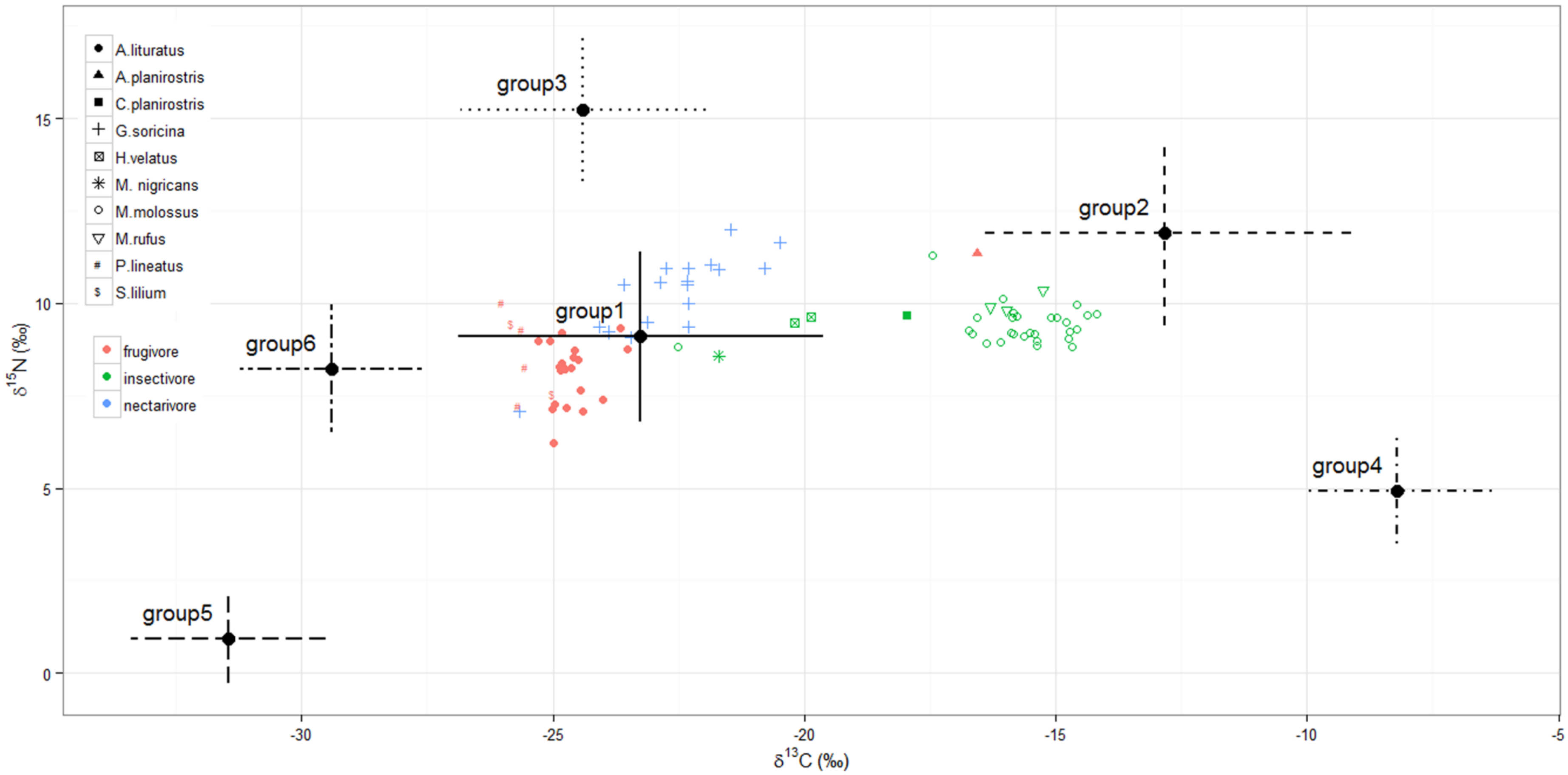

Figure 3.1 - Carbon and nitrogen isotopic values ($\delta^{13}C$ and $\delta^{15}N$, respectively) for bats, insect and plant groups as potential food sources. Bats are classified by dietary categories (color) and species (shape). Insects and plants are separated by isotopic cluster groups (see Appendix E) and have been adjusted by discrimination values (MEAN±SD).

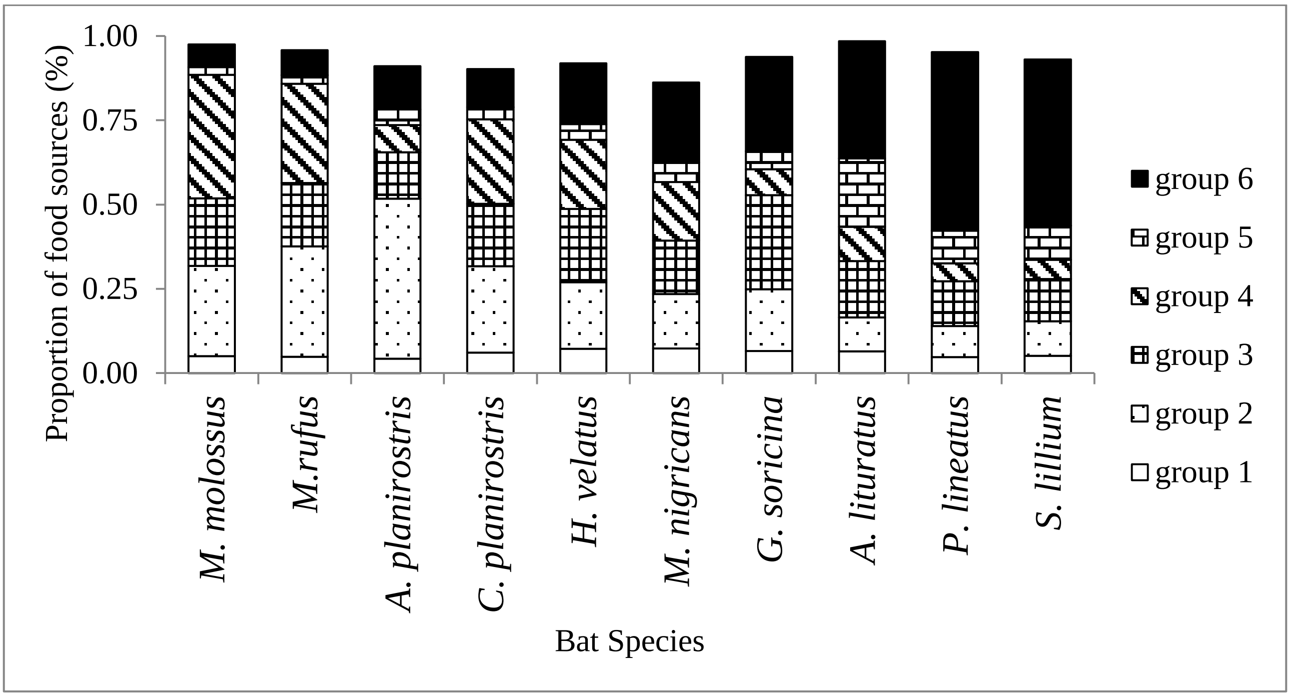

Figure 3.2 - Proportion of group sources (insects and plants – see Table 3.1) in the diet of each bat species according to the mixture model with individual effect.

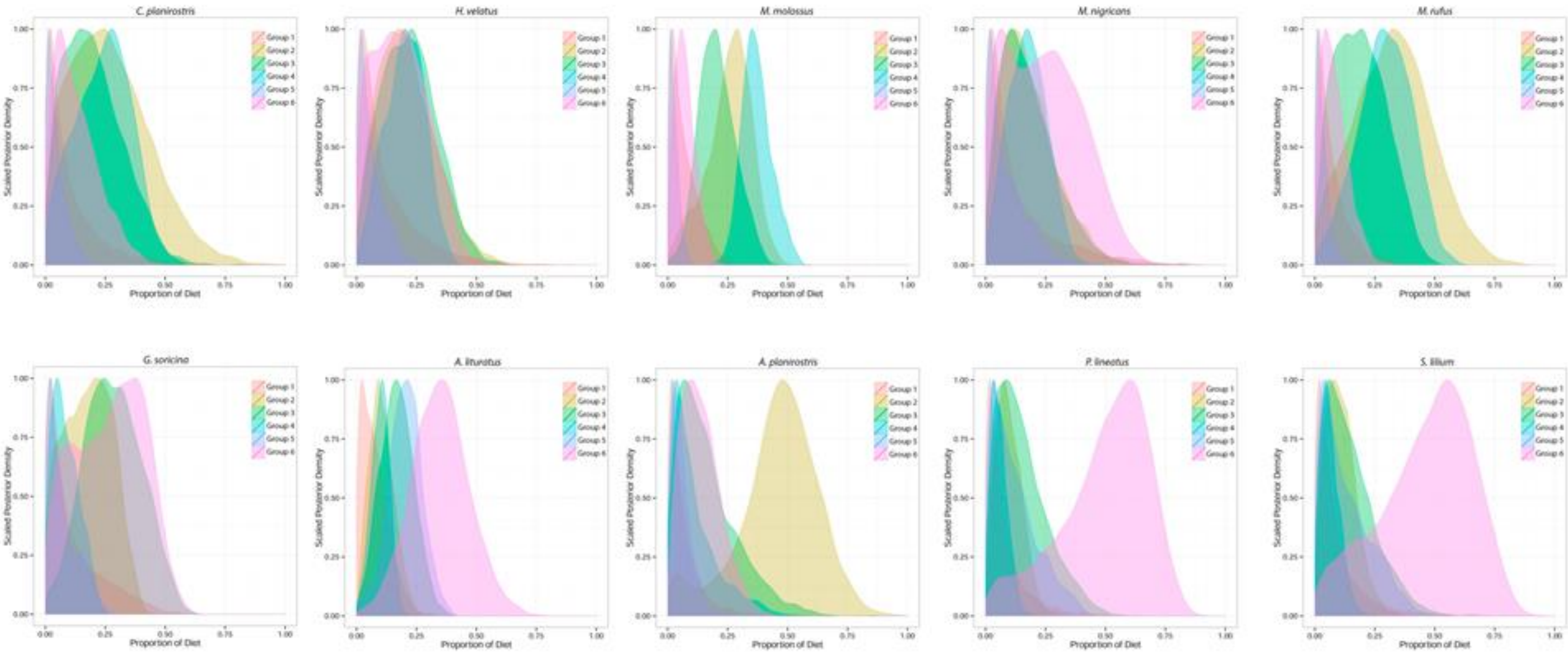

Figure 3.3 - Proportion of each insect and plant group (1 to 6) in the diet of each bat species of campus "Luiz de Queiroz" at University of São Paulo, Piracicaba, estimated by stable isotope mixing models.

3.4 Discussion

In this study, bats consumed insects of several families, including crop pests in natural, urban, and agricultural areas, which show that they play an important ecosystem service in different types of habitat. This finding has important implications for bat conservation, public health and agriculture, as discussed below.

Bats fed on the several pest insect groups that were registered here and were dispersed along the landscape. Even if insects fly all over the different sites in the landscape, hampering the track of its original environment, the stable isotope analysis showed to be useful in separating insects that feed on C_3 or C_4 plants. Since insectivorous bats consume insects in a greater height (KUNZ; RACEY, 1998), they may consume those insects from different areas, acting as pest suppressor in all the environments of the landscape. Still, the accurately estimative of this service demands also information on the trophic levels to be able to determine if bats are consuming directly the pest insects or the predators of these pests. Here, the $\delta^{15}N$ values of bat species, followed the order of nectarivores, insectivores and then frugivores (YORK; BILLINGS, 2009), however they were not enough to determinate different trophic levels (more than 3.5‰, POST, 2002), indicating that bats' diet is more generalists than usually expected by literature.

The data on the overall bat community consumption of more insects from a mixture zone is probably biased due to the inclusion of different dietary categories, from frugivorous to C_4-consuming insectivorous, from species that forage in uncluttered spaces to cluttered ones. The stable isotope mixture model approximates the whole community to the prey group consumed by the most frequent bat group found, here the uncluttered space aerial insectivore *M. molossus*. Although, it shows that all bats do feed on insects, including ones of agricultural and health importance, as discussed more detailed for each group.

Each bat species fed on different proportion of C_3 and C_4 insects, but diet was similar for the most predefined guild. The uncluttered space aerial insectivores, including *M. molossus* and *M. rufus*, were the most agricultural-pest insect controller group. Individuals of those two species, which shared the same roost, presented the most similar food source consumption of most C_4-insects. The same spatial behavior is registered on the *C. planirostris* that had also similar isotopic diet to them. On the other hand, *M. nigricans* and *Histiotus velatus*, consumed aerial insects from a mixture zone of C_3 and C_4 plants, showing a spatial foraging behavior distinct from those bats. Data of *M. nigricans* show that it could be consuming some proportion of fruits, as registered by other study (NOVAES et al.,

2015) and mainly insects from edge space. Fenton and colaborators (1999) also found differences between *Myotis* sp. and *H. velatus* diet, where the first one consumed more coleopterans and the last, more lepidopterans. That variation on insects in the diet is shown in our results. Coleopterans were more abundant in C_4 areas, corn and pasture, and presented ^{13}C-enriched values, while lepidopterans were more abundant in all areas, varying C values through C_3 and C_4. This consumption on C_4-lepidopterans may suppress larval insects and pathogens and mycotoxins in corn plantations (MAINE; BOYLES, 2015), as well as in other cultures (GALLO et al., 2002). As only one individual of *Myotis* was analyzed, more information is needed to extrapolate those findings. Although, those bats may act as biological controllers in these systems if, as opportunistic feeders, they may rapidly exploit local resurgences in pest numbers in C_4-fields (MCCRACKEN et al., 2012).

Insects are also suppressed by phytophagous bats. The results corroborates previous information on the eventual consumption on insects by the highly cluttered space gleaning canopy and shrub frugivore bats (HERRERA; HOBSON, 2001) and contradicts records pointing them as exclusively dependent on fruits (WILLIG; CAMILO; NOBLE, 1993). Between them, the results indicate a possible overlooked insectivory for *Artibeus* cf. *planirostris*, including it as one of the most important suppressor of pest insects in our sample. Although, as only one individual of *A. planirostris* was sampled, it is suggested more studies on foraging behavior of this genus in different types of environment, since they might be consuming more insects than it is noted in the literature.

In the same way, the consumption of a large proportion of insects by the highly cluttered space gleaning nectarivore, *G. soricina*, is probably biased. This species have been registered as CAM flower nectar dependent (VOIGT; SPEAKMAN, 2007; WELCH JUNIOR; HERRERA; SUAREZ, 2008), which could result in ^{13}C-enriched values tissues, but it was not possible to collect samples of those plants in this study. However, the data is still valid, as this bat do consume insects (HERRERA et al., 2001) and some studies point that not only opportunistically (CLARE et al., 2014). This feeding behavior is worth to be further explored as insects could be an alternative food source to nectar flowers in areas with low abundance of them, as the majority of the Brazilian agricultural fields (BENTON; VICKERY; WILSON, 2003).

The data suggests that all bats living in this agricultural landscape can help regulate crop pests across a variety of local and landscape management's regimes. This is mostly done by insectivores that forage in uncluttered habitat, as *Molossus* sp. Moreover, it is important to increase efforts to determine the diet of phytophagous bats in heterogeneous landscapes, to understand its contribution to insect consumption service. This study highlighted the need to quantify the consumption of pests by Neotropical bats, not only to determine the ecosystem service, but also to put and economic value in the conservation of those animals, since producers can be instigated to protect them to save production costs. Therefore, implementation of conservation efforts to protect the remaining bat community in deforested areas, such as agricultural fields, and document bat pest-regulating services is essential to prevent regional extinctions of species and ecosystem services.

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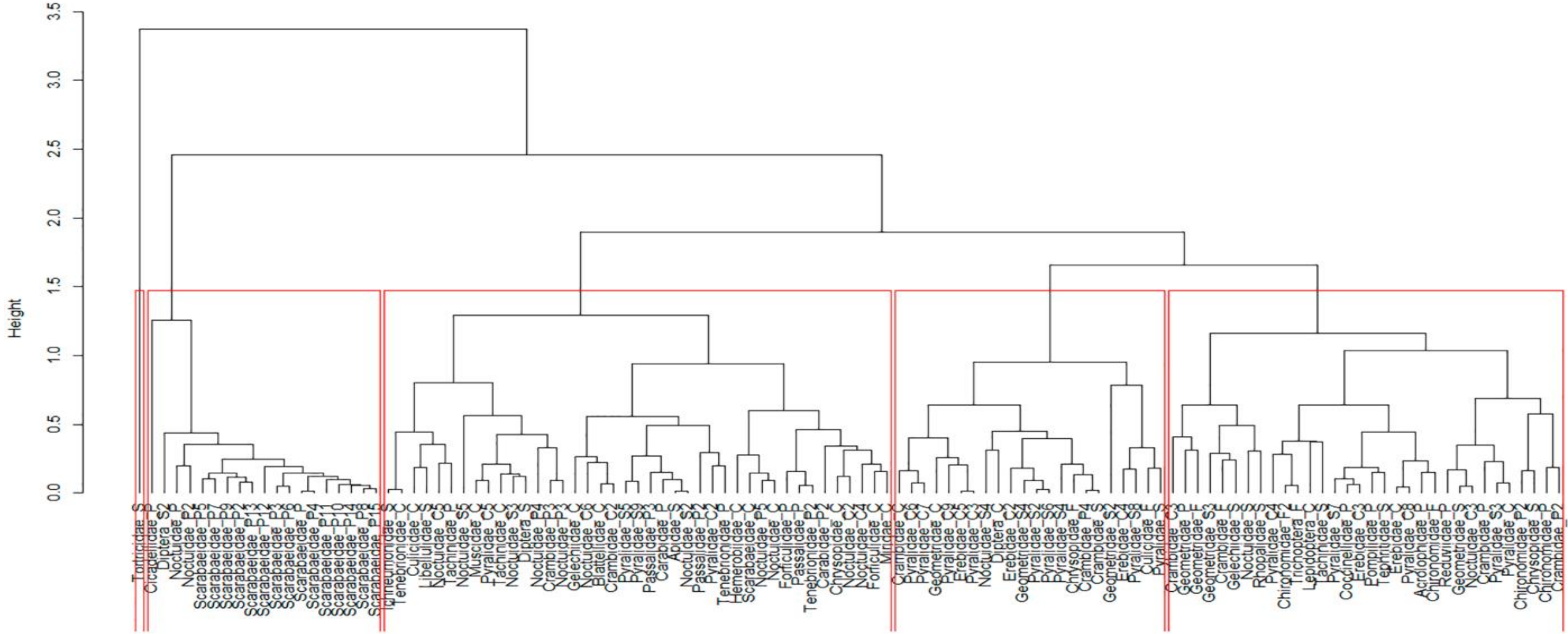
APPENDIX

Appendix A – Insect families collected in University of São Paulo, Piracicaba, as potential food sources for bats, grouped by cluster analysis with Euclidian distances using $\delta^{13}C$ and $\delta^{15}N$ values. Environments are separated and numerated as C (corn), F (forest), P (pasture) and S (silviculture). Each group (1-5) is separated by red lines, starting from the right.



Appendix B – Isotopic values of plants collected in the campus of University of São Paulo, Piracicaba, southeastern Brazil, divided by taxon and tissue.

Plants	Tissue	$\delta^{13}C$	$\delta^{15}N$
Cecropia sp. Loefl.	fruit	-33.3	6.0
Corn	leaf	-14.2	2.4
Eucalyptus	leaf	-31.2	7.6
Ficus guaranitica Chodat	fruit	-31.8	2.8
Grass	leaf	-12.7	-2.4
Piper amalago L.	fruit	-31.9	6.6
Piper sp. L.	fruit	-31.9	4.4
Solanum sp. L.	fruit	-32.4	5.0

Appendix C - Carbon and nitrogen isotopic values (MEAN±SD, ‰) of the University of São Paulo, Piracicaba bat community, divided by taxon (family, subfamily and species) and guild. (n) is the number of sampled individuals; (A) uncluttered space aerial insectivore; (B) highly cluttered space gleaning nectarivore; (C) highly cluttered space gleaning canopy frugivore; (D) highly cluttered space gleaning shrub frugivore; (E) background cluttered space aerial insectivore.

Species	Guilds	Males		Females	
		δ^{13}C±SD (n)	**δ^{15}N+SD**	**δ^{13}C±SD (n)**	**δ^{15}N+SD**
Molossidae					
Cynomops cf. planisrostris (Peters, 1865)	A	-	-	-17.9 (1)	9.6
Molossus molossus (Pallas, 1766)	A	-15.9±1.9 (15)	9.3±0.4	-15.5±0.9 (13)	9.5±0.6
Molossus rufus É. Geoffroy, 1805	A	-16.1±0.2 (2)	9.8	-15.2 (1)	10.3
Phyllostomidae – Glossophaginae					
Glossophaga soricina (Pallas, 1766)	B	-22.3±0.8 (17)	10.5±0.8	-23.3±2.0 (6)	9.4±2.0
Phyllostomidae – Sternodermatinae					
Artibeus cf. planirostris (Spix, 1823)	C	-	-	-16.5 (1)	11.3
Artibeus lituratus (Olfers, 1818)	C	-24.6±0.6 (12)	8.2±0.9	-24.6±0.2 (12)	8.0±0.6
Platyrrhinus lineatus (É. Geoffroy St.-Hilaire, 1810)	C	-25.5 (1)	8.3	-25.7±0.2 (4)	8.8±1.4
Sturnira lilium (É. Geoffroy St.-Hilaire, 1810)	D	-25.8 (1)	9.4	-25.0 (1)	7.5
Verpertilionidae					
Histiotus velatus (I. Geoffroy St.-Hilaire, 1824)	E	-20.0±0.2 (2)	9.5±0.1	-	-
Myotis nigricans (Schinz, 1821)	E	-21.7 (1)	8.5	-	-

Appendix D – Isotopic values of carbon and nitrogen (‰) of insects of the University of São Paulo, Piracicaba, represented by taxon (order and family), site of sampling, cluster group (1-5) and economic relevance. To be continued.

Local	Cluster Group	Importance	Order/family	^{13}C	^{15}N
			Blattaria		
	3	Medical	Blattellidae	-14.08	10.55
			Coleoptera		
	3	Pest	Scarabaeidae	-15.98	6.15
	3	Pest	Tenebrionidae	-19.71	8.07
			Dermaptera		
	3	Predator	Forficulidae	-13.18	5.41
			Diptera		
	3	Medical	Culicidae	-23.27	8.86
	3	Medical	Muscidae	-19.81	11.06
	2	-	No family defined	-25.09	10.67
	3	Predator	Tachinidae	-17.90	10.74
			Hemiptera (Heteroptera)		
	3	Pest	Miridae	-14.26	5.50
			Lepidoptera		
	2	Pest	Crambidae	-24.53	12.39
	3			-14.24	10.31
Corn	1			-34.24	8.22
	1	Pest	Erebidae	-22.89	7.37
	2			-28.46	9.53
	1			-25.36	7.03
	2			-25.01	14.74
	2			-27.65	12.39
	3	Pest	Gelechiidae	-12.42	10.39
	2	Forest Pest	Geometridae	-29.23	11.98
	3	Pest	Noctuidae	-16.44	5.65
	3			-14.13	3.84
	1			-27.40	3.09
	3			-13.03	4.75
	3			-20.01	9.82
	3			-13.90	9.57
	1	Pest	Pyralidae	-26.79	4.67
	3			-12.39	7.52
	2			-27.60	12.42

Appendix D – Continued. Isotopic values of carbon and nitrogen (‰) of insects of the University of São Paulo, Piracicaba, represented by taxon (order and family), site of sampling, cluster group (1-5) and economic relevance.

Local	Cluster Group	Importance	Order/family	^{13}C	^{15}N
Corn	1	Pest	Pyralidae	-23.71	5.91
	3			-19.57	11.40
	2			-25.40	12.35
	2			-25.90	12.25
	1			-23.21	7.39
	2			-27.50	11.60
	1	-	No family defined	-21.57	4.08
			Neuroptera		
	3	Predator	Chrysopidae	-13.75	4.27
	3	Predator	Hemerobiidae	-17.31	6.61
Forest			**Diptera**		
	1	Medical	Chironomidae	-21.70	6.88
	1			-22.02	5.15
	2	Medical	Culicidae	-26.56	15.02
			Lepidoptera		
	1	Pest	Crambidae	-28.84	7.05
	1	Forest Pest	Geometridae		
			Neuroptera	-31.28	8.91
	2	Predator	Chrysopidae	-29.88	10.86
			Trichoptera		
	1	-	No family defined	-22.34	5.25
Pasture			**Coleoptera**		
	3	Predator	Carabidae	-14.64	8.44
	3			-11.71	4.28
	1	Predator	Coccinellidae	-24.97	7.12
	3	Pest	Passalidae	-11.29	6.29
	3			-10.67	8.69
	3			-15.24	9.01
	4	Pest	Scarabaeidae	-11.16	1.07
	4			-10.82	2.22
	4			-10.40	1.39
	4			-11.07	1.04
	4			-10.56	2.54
	4			-10.16	1.52

Appendix D – Continued. Isotopic values of carbon and nitrogen (‰) of insects of the University of São Paulo, Piracicaba, represented by taxon (order and family), site of sampling, cluster group (1-5) and economic relevance.

Local	**Cluster Group**	**Importance**	**Ordem**	^{13}**C**	^{15}**N**
	4	Pest	Scarabaeidae	-10.01	2.27
	4			-11.14	1.44
	4			-11.46	2.32
	4			-11.10	1.63
	4			-11.60	1.71
	4			-12.26	1.29
	4			-10.81	1.91
	4			-10.86	1.42
	4			-11.30	1.36
	3	Pest	Tenebrionidae	-11.23	7.94
	3			-11.67	6.28
			Dermaptera		
	3	Predator	Forficulidae	-12.28	5.86
			Diptera		
	1	Medical	Chironomidae	-26.98	1.09
	1			-23.62	2.17
Pasture	3	Predator	Tachinidae	-21.37	9.44
			Hemiptera (Auchenorryncha)		
	4	Pest	Cicadellidae	-10.93	-3.33
			Hemiptera (Heteroptera)		
	1	Predator	Reduviidae	-27.93	3.58
			Hymenoptera		
	1	Predator	Pompilidae	-25.27	7.63
			Lepidoptera		
	1	Pest	Acrolophidae	-22.46	6.48
	1	Pest	Crambidae	-26.66	3.88
	1			-26.43	0.43
	3			-16.81	12.22
	2			-29.13	10.55
	1	Forest Pest	Geometridae	-31.89	7.71
	4	Pest	Noctuidae	-12.50	2.07
	4			-13.90	2.13
	3			-16.76	12.57
	2			-16.55	11.09

Appendix D – Continued. Isotopic values of carbon and nitrogen (‰) of insects of the University of São Paulo, Piracicaba, represented by taxon (order and family), site of sampling, cluster group (1-5) and economic relevance.

Local	Cluster Group	Importance	Ordem	^{13}C	^{15}N
Pasture	3	Pest	Noctuidae	-15.80	5.58
			Diptera		
	3	-	No family defined	-18.94	10.83
	4			-11.13	0.05
	1	Predator	Tachinidae	-24.14	4.33
	1	Pest	Tephritidae	-26.33	7.58
			Hemiptera (Heteroptera)	-29.35	6.07
	1	-	Rhopalidae		
			Hymenoptera		
	3	-	Apidae	-15.29	8.43
	3	Predator	Ichneumonidae	-19.56	8.09
			Lepidoptera		
	2	Pest	Crambidae	-29.17	10.49
	1	Pest	Gelechiidae	-27.42	7.57
	1	Pest	Geometridae	-27.37	2.90
	2			-30.88	13.24
	1			-29.68	7.91
Silviculture	2			-27.34	9.48
	1	Pest	Noctuidae	-31.46	5.85
	3			-15.35	8.46
	3			-18.39	11.18
	2			-27.29	10.66
	3			-21.68	12.05
	2	Pest	Pyralidae	-27.46	14.53
	2			-27.28	9.07
	1			-27.18	4.85
	2			-29.67	9.84
	3			-13.86	7.82
	2			-27.35	9.17
	1			-25.76	6.84
	2			-24.85	14.05
	3			-13.51	8.08
	5	Pest	Tortricidae	-34.48	-2.63

Appendix D – Conclusion. Isotopic values of carbon and nitrogen (‰) of insects of the University of São Paulo, Piracicaba, represented by taxon (order and family), site of sampling, cluster group (1-5) and economic relevance.

Local	Cluster Group	Importance	Order	^{13}C	^{15}N
			Neuroptera		
Silviculture	1	Predator	Chrysopidae	-24.42	2.62
			Odonata		
	3	Predator	Libellulidae	-21.96	8.73

Appendix E - Stable isotope mixing model (*MixSIAR*) results with predicted diet proportions (2.5th to 97.5th percentile) of each group source item compared to $\delta^{13}C$ and $\delta^{15}N$ mixture values for bat species. Median isotope values are in parentheses. Values in bold are the highest prey item contribution to each bat category.

Consumers	Source 1	Source 2	Source 3	Source 4	Source 5	Source 6
Frugivore	0.005 - 0.274 (0.064)	0.052 - 0.389 (0.178)	0.039 - 0.415 (0.173)	0.022 - 0.264 (0.098)	0.019 - 0.283 (0.098)	**0.082 - 0.588 (0.315)**
Insectivore	0.004 - 0.314 (0.071)	0.069 - 0.467 (0.231)	0.065 - 0.433 (0.203)	**0.082 - 0.446 (0.226)**	0.005 - 0.15 (0.046)	0.021 - 0.356 (0.151)
Nectarivore	0.003 - 0.387 (0.072)	0.023 - 0.504 (0.182)	0.051 - 0.554 (0.221)	0.011 - 0.359 (0.108)	0.004 - 0.278 (0.061)	**0.029 - 0.583 (0.222)**
A. lituratus	0.003 - 0.213 (0.065)	0.019 - 0.213 (0.1)	0.041 - 0.306 (0.168)	0.024 - 0.169 (0.101)	0.048 - 0.335 (0.203)	**0.117 - 0.594 (0.348)**
A. planirostris	0.002 - 0.288 (0.043)	**0.043 - 0.75 (0.475)**	0.014 - 0.472 (0.137)	0.007 - 0.373 (0.081)	0.005 - 0.155 (0.047)	0.018 - 0.316 (0.128)
C. planirostris	0.002 - 0.444 (0.061)	**0.028 - 0.64 (0.256)**	0.025 - 0.46 (0.186)	0.03 - 0.453 (0.25)	0.002 - 0.159 (0.036)	0.009 - 0.342 (0.113)
G. soricina	0.002 - 0.416 (0.066)	0.013 - 0.358 (0.183)	0.063 - 0.512 (0.279)	0.006 - 0.203 (0.077)	0.003 - 0.217 (0.053)	**0.021 - 0.507 (0.28)**
H. velatus	0.002 - 0.473 (0.072)	0.026 - 0.475 (0.198)	**0.032 - 0.454 (0.217)**	0.043 - 0.354 (0.205)	0.002 - 0.2 (0.047)	0.01 - 0.407 (0.18)
M. molossus	0.002 - 0.205 (0.051)	0.052 - 0.414 (0.267)	0.072 - 0.363 (0.201)	**0.262 - 0.504 (0.366)**	0.002 - 0.077 (0.023)	0.008 - 0.164 (0.067)
M. nigricans	0.003 - 0.58 (0.073)	0.023 - 0.447 (0.162)	0.021 - 0.449 (0.158)	0.03 - 0.334 (0.174)	0.002 - 0.282 (0.058)	**0.012 - 0.553 (0.237)**
M. rufus	0.002 - 0.263 (0.049)	0.039 - 0.652 (0.327)	0.026 - 0.403 (0.188)	**0.07 - 0.491 (0.295)**	0.002 - 0.106 (0.025)	0.007 - 0.212 (0.074)
P. lineatus	0.002 - 0.308 (0.048)	0.016 - 0.211 (0.092)	0.013 - 0.403 (0.133)	0.008 - 0.132 (0.053)	0.006 - 0.352 (0.097)	**0.062 - 0.768 (0.53)**
S. lillium	0.002 - 0.391 (0.052)	0.015 - 0.251 (0.102)	0.012 - 0.39 (0.125)	0.008 - 0.155 (0.057)	0.006 - 0.365 (0.102)	**0.055 - 0.766 (0.493)**

ANNEX

Annex A – Carbon and nitrogen isotopic values (‰) of discrimination factors in different tissues of bat species obtained from specific literature.

Species	Tissue	$\delta^{13}C$	$\delta^{15}N$	References
Glossophaga soricina	blood	2	4.4	(MIRÓN et al., 2006)
Glossophaga soricina	blood	0.1	3.3	(MIRÓN et al., 2006)
Glossophaga soricina	blood	-	3.2	(VOIGT; MATT, 2004)
Glossophaga soricina	wing	-	4	(VOIGT; MATT, 2004)
Glossophaga soricina	hair/wing/blood	2.6	-	(VOIGT et al., 2003)
Leptonycteris curasoae	hair/wing/blood	2.8	-	(VOIGT et al., 2003)
Leptonycteris curasoae	Blood	-	3	(VOIGT; MATT, 2004)
Leptonycteris curasoae	Wing	-	4.7	(VOIGT; MATT, 2004)
Myotis myotis	Hair	3.6	2.6	(SIEMERS et al., 2011)
Myotis nattereri	Hair	3.2	3.2	(SIEMERS et al., 2011)
Nyctalus noctula	Wing	4	3.7	(ROSWAG;BECKER; ENCARNAÇÃO, 2015)
Nyctalus noctula	Hair	5.9	3.4	(ROSWAG;BECKER; ENCARNAÇÃO, 2015)