

UNIVERSIDADE ESTADUAL DE CAMPINAS INSTITUTO DE BIOLOGIA

GISELLE MARTINS LOURENÇO

SPATIO-TEMPORAL PATTERNS OF FRUIT-FEEDING BUTTERFLY DISTRIBUTION AND DIVERSITY IN TRANSITIONAL HABITATS

PADRÕES ESPAÇO-TEMPORAIS DE DISTRIBUIÇÃO E DIVERSIDADE DE BORBOLETAS FRUGÍVORAS EM HABITATS TRANSICIONAIS

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RESUMO

Em florestas tropicais, a distribuição dos insetos no espaço e no tempo é determinada por fatores que variam ao longo das dimensões horizontal (habitats), vertical (estratos) e temporal (tempo), sendo influenciada pela fragmentação dessas florestas. A expansão de interfaces entre florestas fragmentadas e habitats não-florestais (plantações, pastagens, estradas e áreas urbanas) cria transições antrópicas (bordas) que diferem drasticamente da cobertura original da floresta e em condições microclimáticas, podendo comprometer a sincronia conhecida entre a emergência de insetos e as condições favoráveis para sua emergência. Por outro lado, as transições naturais (ecótonos) são distintas das bordas antrópicas. Enquanto as bordas antrópicas usualmente têm um contorno bem definido associado a perturbações, com mudanças abruptas nas condições microclimáticas, os ecótonos naturais mesmo quando abruptos são compostos por uma fisionomia vegetal complexa, onde as árvores crescem inclinadas para o habitat aberto, tornando o habitat mais sombreado e úmido. Assim, a tese integra as ideias expostas acima em três capítulos: 1) o primeiro capítulo investiga se as assembleias de borboletas frugívoras em ecótonos naturais se assemelham mais ao interior da floresta do que às bordas antrópicas, demonstrando as diferenças e similaridades na abundância, riqueza, diversidade e composição de borboletas frugívoras observadas entre os habitats e estratos; 2) o segundo capítulo investiga a distribuição temporal de borboletas frugívoras entre os meses durante um ano, verificando como as diferenças e similaridades observadas em cada habitat no capítulo 1 variam ao longo dos meses; e 3) o terceiro capítulo descreve a movimentação e algumas características populacionais de seis espécies de borboletas frugívoras que apresentaram mais de 3% sucesso de recaptura. Amostramos as borboletas mensalmente durante um ano no Parque Estadual do Rio Doce, Sudeste do Brasil, seguindo um desenho padronizado utilizando armadilhas atrativas, instaladas no sub-bosque e dossel de três habitats distintos (interior da floresta, ecótono e borda). Capturamos 11.594 indivíduos de 98 espécies de borboletas frugívoras, sendo 411 indivíduos (3,5%) recapturados ao menos uma vez. Os resultados mostram que a riqueza e diversidade de espécies de borboletas foram maiores nas áreas de transição. Porém, o ecótono reúne uma combinação de borboletas do interior da floresta e da borda antrópica, ainda que no ecótono, a composição e dominância de espécies sejam similares ao observado no interior da floresta nos dois estratos. Desse modo, os resultados demonstram que o ecótono apresenta condições únicas e distintas de bordas antrópicas. Ao analisarmos as variações mensais das comunidades de borboletas frugívoras notamos uma distribuição não uniforme em todos os habitats estudados com maior abundância, riqueza e beta diversidade na estação quente. A

abundância de borboletas frugívoras aumenta com elevação da temperatura em todos os habitats. Para riqueza de borboletas, no entanto, esse efeito da temperatura só pode ser observado no interior da floresta. Embora a beta diversidade de borboletas frugívoras varie ao longo do ano, sobrepondo-se com as mudanças sazonais em todos os habitats, em geral as transições (ecótono e borda) foram mais ricas e abundantes do que o interior da floresta durante todo o ano. Entretanto, os resultados mostram que as transições são mais variáveis do que o interior da floresta ao longo do ano. Logo, a manutenção das populações nos habitats de transição tende a ser mais difícil. Portanto, conhecer como as taxas de turnover variam ao longo do tempo em diferentes habitats pode nos ajudar a entender a sensibilidade dos sistemas ecológicos as mudanças ambientais. Ao analisar os dados de recaptura encontramos razão sexual desviada para machos em todos os meses e estrutura etária com sutil aumento no recrutamento no final da estação seca. Durante a estação chuvosa notamos o gradual envelhecimento das populações, porém a estrutura etária foi relativamente constante durante todo o ano. A movimentação das espécies na paisagem mostra que poucos indivíduos percorreram longas distâncias, a maioria foi recapturado no mesmo local ou a poucos metros de onde foi capturado pela primeira vez. As recapturas foram mais frequentes no ecótono, o que demonstra que possivelmente as condições ecofisiológicas do ecótono favorecem a permanência dos indivíduos. Todos os resultados obtidos nos três capítulos demonstram que os ecótonos são habitats únicos capazes de acomodar espécies adaptadas a condições ecológicas distintas, apresentando características ecofisiológicas que o fazem um habitat chave em termos de diversidade e estrutura da comunidade.

ABSTRACT

In tropical forests, insect distribution in space and time are determined by factors that vary along the horizontal (habitats), vertical (strata) and temporal (time) dimensions, being influenced by the fragmentation of those forests. The expansion of interfaces between fragmented forests and non-forest habitats (e.g., croplands, pasture, roads and urban areas) creates human-made edges that are dramatically different from the original forest cover and microclimatic conditions, which may jeopardize the known synchrony between insect emergence and favorable conditions for their development. In the other hand, natural transition habitats (ecotones) are distinct from human-made forest edges, while the human made are usually sharp associated with disturbances, with abrupt changes in microclimatic conditions, the ecotones, even when abrupt, are composed of a complex vegetation physiognomy, where the trees grow leaning toward the open habitat, creating the habitat more shaded and humid. Thus, the thesis integrates the ideas presented above into three chapters: 1) the first chapter investigates whether the fruitfeeding butterfly assemblages are more similar between ecotone and forest interior than to anthropic edges, showing the differences and similarities in abundance, species richness, diversity and composition of fruit-feeding butterflies observed among habitats; 2) the second chapter investigates the fruit-feeding butterfly distribution among months during a year in each habitat, verifying how the differences and similarities observed in chapter 1 vary over the months; and 3) the third chapter describes the movement and some population characteristics of six fruit-feeding butterfly species that presented more than 3% recapture success. We sampled butterflies monthly over one year in the Rio Doce State Park, Southeastern Brazil, following a standardized design using bait traps, settled up in the canopy and understory of three distinct habitats (forest interior, ecotone and edge). We captured 11,594 individuals from 98 fruit-feeding butterfly species, 411 individuals (3.5%) of which recaptured at least once. The results showed that the butterfly richness and species diversity were higher in transition areas. However, the ecotone showed a combination of butterflies from the forest interior and from anthropic edges, although in the ecotone, species composition and dominance were similar to the forest interior in both vertical strata. Therefore, the results demonstrate that the ecotone presents unique and distinct conditions of anthropic edges. When analyzing the monthly variations of the fruit-feeding butterfly communities we noticed a nonuniform distribution in all studied habitats, with greater abundance, richness and beta diversity in the wet season. Butterfly abundance increased with high temperatures in all habitats. For species richness, however, this effect was only detected in the forest interior. Although the beta diversity varies through the year, overlapping in all habitats with the seasonal changes, the transition habitats (ecotone and edge) were generally richer and with a greater abundance compared with the forest interior all year round. However, the results also show that the transition habitats were more variable than the forest interior throughout the year. Hence, maintaining populations in transitional habitats tends to be more difficult. Therefore, knowing how rates of species turnover vary over time in different habitats can help in understanding the sensitivity of ecological systems to environmental changes. When analyzing the recapture data, we found the sex ratio male biased in all months and the age structure with subtle increase in recruitment at the end of the dry season. During the wet season we noticed the gradual aging of the population, but the age structure was relatively constant during the year. The species movement in the landscape shows that few individuals travel long distances, most were recaptured in the same site or a few meters away from where it was first captured. Recaptures were more frequent in the ecotone, possibly the eco-physiological conditions favor the individual permanence. All the results obtained in the three chapters demonstrate that ecotones are unique habitats capable of accommodating species adapted to distinct ecological conditions, presenting eco-physiological characteristics that make it a key habitat in terms of diversity and community structure.

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Introdução Geral

Entender os mecanismos determinantes de padrões de distribuição dos organismos é uma questão fundamental na ecologia. Em florestas tropicais, a distribuição dos insetos é determinada por fatores que variam ao longo das dimensões horizontal (habitats), vertical (estratos) e temporal (tempo) (Basset et al., 2015). Horizontalmente, as distribuições das populações de insetos tropicais variam devido a fatores como a presença e qualidade nutricional de plantas hospedeiras ou outros recursos alimentares, distancia da borda florestal, capacidade de dispersão, interações entre organismos, entre outros (Basset et al., 2012, 2015; Didham et al., 1996; Novotny et al., 2007). Por outro lado, a estratificação vertical da ocorrência de organismos e recursos é um dos fatores responsáveis pela elevada diversidade em florestas tropicais (Basset et al., 2003). A dimensão vertical da floresta determina a distribuição dos insetos tropicais ao longo do gradiente de características abióticas e bióticas que variam do chão da floresta ao topo das árvores (ou seja, microclimas que respondem ao conjunto das copas de todas as árvores na floresta, incluindo folhas, galhos, ramos e epífitas; Basset et al., 2003; Nadkarni, 1995; Parker e Brown, 2000). Já a variação temporal, apesar de não ser tão marcante como em ecossistemas temperados onde os picos de atividade são restritos aos períodos quentes, também contribui para a variação das populações de insetos tropicais ao longo do ano (Kishimoto-Yamada e Itioka, 2015; Wolda, 1988). De modo geral, os picos de atividade e populacionais de insetos tropicais coincidem com os períodos que concentram condições favoráveis para o desenvolvimento, tais como disponibilidade de recursos e aumento da temperatura, pluviosidade e umidade (Kishimoto-Yamada e Itioka, 2015; Wolda, 1988).

Em florestas tropicais, a heterogeneidade ambiental ao longo da dimensão horizontal resulta em diferentes disponibilidades de recursos e condições microclimáticas entre os tipos de habitat (Didham et al., 1996). Assim, o conjunto de características do habitat pode determinar a permanência das espécies, limitando ou favorecendo a diversidade local e regional (Beirão et al., 2017; Ribeiro et al., 2008; Saunders et al., 1991; Uehara-Prado et al., 2007). Todos estes fatores, somados à fragmentação das florestas, são determinantes da distribuição dos insetos tropicais. A expansão de interfaces entre florestas fragmentadas e habitats não-florestais (plantações, pastagens, estradas e áreas urbanas) cria transições antrópicas (bordas) que diferem drasticamente da cobertura original da floresta, não somente em cobertura vegetal, mas também em condições microclimáticas (temperatura, umidade, velocidade do vento e quantidade de radiação solar que penetra no habitat) (Murcia, 1995; Steffen et al., 2015). A fragmentação da floresta causa mudanças na estrutura das comunidades levando a mudanças não só na

abundância e diversidade de muitos grupos de insetos, como também modifica as interações ecológicas entre esses e outros organismos (Didham et al., 1996). Estudos sobre transições florestais estão cada vez mais presentes na literatura da ecologia florestal (Melo et al., 2013; Steffen et al., 2015; Solar et al., 2015). Porém, sabemos pouco sobre as transições naturais entre florestas e habitats não florestais, como quando ocorre súbita interrupção da ocorrência de árvores em transições para formações abertas, os chamados ecótonos, os quais devem ter aspectos ecológicos-funcionais e processos evolutivos completamente distintos daqueles observados em bordas oriundas de distúrbios (Fonseca-Silva et al., 2015).

Transições naturais entre florestas e habitats não florestais

Existem vários tipos de ecótonos, tais como as interfaces com lagoas, rios, matas ciliares, dunas, savanas e campos. Segundo Holland (1988), ecótonos são definidos como "zonas de transição entre sistemas ecológicos adjacentes, com um conjunto de características únicas definido pelas escalas de espaço e tempo e pela força das interações entre os sistemas ecológicos adjacentes". Por serem transições naturais, os ecótonos diferem das bordas antrópicas (Fig. 1). As bordas antrópicas usualmente têm um contorno bem definido associado a perturbações, com mudanças abruptas na temperatura, umidade, luminosidade e incidência de vento para o interior da floresta. Por outro lado, os ecótonos naturais mesmo quando abruptos são compostos por uma fisionomia vegetal complexa, com estruturas de copa aproximando do solo e uma composição de espécies herbáceas e arbóreas bem adaptadas a esta faixa de transição. As árvores nos ecótonos crescem inclinadas para o habitat aberto, podendo chegar perto do nível do solo, tornando o habitat mais sombreado e úmido, oferecendo condições mais amenas quando comparadas as condições das bordas antrópicas.

Além disso, no dossel dos ecótonos a folhagem permanece próxima ao solo e ainda apresenta várias características similares ao dossel superior da floresta (Barbosa, 2014). Por exemplo, as folhas do dossel apresentam alta esclerofilia e os atributos morfológicos típicos de folhas sob elevada insolação (Sanches et al., 2010; Ribeiro e Basset, 2007, 2016). Adicionalmente, as taxas de respiração foliar são similares às de árvores emergentes (Sanches et al., 2010) e a arquitetura da copa é típica de dossel superior (isto é, relação entre biomassa de tronco e folhas, dados qualitativos das características das folhas e ramificações de tronco (Barbosa, 2014). Assim, semelhanças ecofisiológicas já foram identificadas entre o dossel superior e o dossel inclinado do ecótono.



Fig. 1 Habitats estudados (interior da floresta, ecótono, borda antrópica) no Parque Estadual do Rio Doce, Minas Gerais, Brasil. Vista externa (imagens superiores), Vista interna (imagens inferiores).

Borboletas (Ordem Lepidoptera)

No Brasil são registradas mais de 3.250 espécies de borboletas (Freitas e Marini-Filho, 2011), que de um modo geral, podem ser divididas em duas guildas conforme o hábito alimentar dos adultos: nectarívoras, borboletas que se alimentam principalmente do néctar das flores; e as frugívoras, borboletas que se alimentam de frutas fermentadas, seiva fermentada, fezes e matéria orgânica em decomposição (DeVries, 1987). No Brasil, as borboletas frugívoras pertencem à família Nymphalidae, sendo representadas pelas subfamílias: Biblidinae, Charaxinae, Nymphalinae (tribo Coeini) e Satyrinae (tribos Brassolini, Haeterini, Morphini e Satyrini) (Freitas e Brown Jr., 2004; Freitas et al., 2014; Wahlberg et al., 2009).

Em florestas tropicais, as borboletas frugívoras são consideradas um excelente modelo para estudos de estrutura da comunidade e variação temporal da diversidade, pois são ecologicamente diversas, sensíveis às variações do clima, possuem taxonomia relativamente bem resolvida e podem ser amostradas de forma simultânea e padronizada em várias áreas utilizando armadilhas de fruta (Fig. 2; DeVries et al., 2016; Freitas et al., 2014; Grøtan et al., 2012, 2014; Molleman et al., 2006). Além disso, o papel das borboletas frugívoras como indicadoras biológicas é reforçado pois elas respondem tanto à estratificação vertical da floresta como a vários tipos de perturbação, sendo sensíveis à fragmentação e mudanças na cobertura florestal (Barlow et al., 2007; DeVries et al., 1997; Fermon et al., 2003, 2005; Filgueiras et al., 2016; Ribeiro et al., 2012; Ribeiro e Freitas, 2012; Sant'Anna et al., 2014; Shahabuddin e Terborgh, 1999; Thomas, 2016; Uehara-Prado et al., 2007).



Fig. 2 Amostragem de borboletas frugívoras com armadilhas portáteis (Van Someren-Rydon) instaladas em cada habitat nos estratos (dossel, sub-bosque), utilizando como isca atrativa uma mistura de banana e garapa fermentada por 48 horas, Parque Estadual do Rio Doce, Minas Gerais, Brasil.

Borboletas frugívoras apresentam um padrão consistente de estratificação vertical da composição das espécies em florestas tropicais (Molleman et al., 2006; Fordyce e DeVries, 2016). Diferenças na abundância, riqueza, diversidade e composição de espécies de borboletas frugívoras entre os estratos foram verificadas em muitos estudos (DeVries, 1987; Fermon et al., 2003, 2005; Hill et al., 2001; Molleman et al., 2006; Ribeiro e Freitas, 2012; Santos et al., 2017; Spitzer et al., 1993). Entretanto, estes padrões de distribuição das espécies observados no interior da floresta são alterados em áreas de transição. A radiação solar que alcança o subbosque de bordas florestais é maior, logo outros parâmetros microclimáticos também são alterados, as temperaturas diárias são mais altas e variáveis, e há redução de umidade (Murcia, 1995). Essas mudanças no sub-bosque podem se estender até 40 m para dentro da floresta, podendo se estender mais quando os fragmentos são pequenos (Murcia, 1995).

Estrutura da tese

Esta tese integra as ideias expostas acima em três capítulos:

1) Equal but different: natural ecotones are dissimilar to anthropic edges. O primeiro capítulo investiga se as assembleias de borboletas frugívoras em ecótonos naturais se assemelham mais ao interior da floresta do que às bordas antrópicas, demonstrando as diferenças e similaridades na abundância, riqueza, diversidade e composição de borboletas frugívoras observadas entre os habitats. Especificadamente, testamos as seguintes hipóteses: i) as assembleias de borboletas frugívoras são mais similares entre o ecótono e o interior da floresta do que entre ecótono e borda antrópica para os dois estratos estudados, com predição de que o dossel inclinado do ecótono resulta em um sub-bosque mais sombreado similar ao subbosque do interior da floresta, e ao mesmo tempo o dossel inclinado mantem as características ecofisiológicas observadas no dossel superior do interior da floresta; e ii) a estratificação vertical da composição de espécies de borboletas frugívoras é diferente entre os três habitats, com predição de que no ecótono a proximidade física entre o dossel inclinado e o sub-bosque pode aumentar as chances das espécies se moverem entre os estratos verticais, diferindo da estratificação observada no interior da floresta onde a diferença de altura e condições microclimáticas entre os estratos são empecilhos para a movimentação de muitas espécies. Por outro lado, a estratificação em bordas impactadas diferirá dos habitats naturais (interior da floresta e ecótono da floresta) em ambos os estratos, devido às diferenças na cobertura vegetal e às distintas condições microclimáticas que estão submetidas.

2) Temporal variation of fruit-feeding butterfly in natural and anthropic forest transitions. O segundo capítulo investiga a distribuição temporal de borboletas frugívoras entre os meses durante um ano em cada habitat, verificando como as diferenças e similaridades observadas em cada habitat no capítulo 1 variam ao longo dos meses. Especificadamente, testamos as seguintes hipóteses: i) a distribuição das borboletas frugívoras é concentrada em determinados períodos do ano nos três habitats estudados, com predição de que os picos de atividade de insetos tropicais coincidem com os períodos de maior disponibilidade de recursos e aumento da temperatura, pluviosidade e umidade; ii) a variação da diversidade beta entre os meses é similar entre os habitats naturais (interior da floresta e ecótono), com predição de que os habitats naturais apresentam condições favoráveis para o desenvolvimento de diferentes espécies, mantendo uma heterogeneidade em termos de espécies ao longo do ano; e iii) o aumento da temperatura e umidade afetam positivamente a abundância e riqueza de borboletas frugívoras nos três habitats estudados, com predição temporal das condições de temperatura e umidade regulam os padrões de atividade de borboletas frugívoras.

3) Movement patterns and biological traits related to the sex of fruit-feeding butterflies: using mark-recapture data. O terceiro capítulo descreve a movimentação de seis espécies de borboletas frugívoras que apresentaram mais de 3% de recaptura em todo estudo realizado no Parque Estadual do Rio Doce. Analisamos para cada espécie foco a razão sexual e a estrutura etária ao longo dos meses, bem como a permanência máxima de cada espécie. Descrevemos os movimentos realizados por cada espécie e sexo entre armadilhas, estratos e habitats, calculando as distâncias máxima e média.

Capítulo 1

Equal but different: natural ecotones are dissimilar to anthropic edges

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Abstract

Increasing deforestation worldwide has expanded the interfaces between fragmented forests and nonforest habitats. Human-made edges are very different from the original forest cover, with different microclimatic conditions. Conversely, the natural transitions (i.e., ecotones) are distinct from humanmade forest edges. The human-made forest edges are usually sharp associated with disturbances, with abrupt changes in temperature, humidity, luminosity and wind incidence towards the forest interior. However, the natural forest-lake ecotones, even when abrupt, are composed of a complex vegetal physiognomy, with canopy structures close to the ground level and a composition of herbaceous and arboreal species well adapted to this transition range. In the present study, fruit-feeding butterflies were used as models to investigate whether faunal assemblages in natural ecotones are more similar to the forest interior than to the anthropic edges. Butterflies were sampled monthly over one year in the Rio Doce State Park, Southeastern Brazil, following a standardized design using a total of 90 bait traps, in three different forest habitats (forest interior, forest ecotone and anthropic edges), in both canopy and understory. A total of 11,594 individuals from 98 butterfly species were collected (3,151 individuals from 79 species in the forest interior, 4,321 individuals from 87 species in the ecotone and 4,122 individuals from 83 species in the edge). The results indicated that the butterfly richness and diversity were higher in transition areas (ecotones and edges). The ecotone included a combination of butterfly species from the forest interior and from anthropic edges. However, species composition and dominance in the ecotone were similar to the forest interior in both vertical strata. These results suggest that human made forest edges are quite distinct from ecotones. Moreover, ecotones represent unique habitats accommodating species adapted to distinct ecological conditions, while anthropic edges accommodate only opportunistic species from open areas or upper canopies.

Keywords Atlantic forest, canopy, fruit-feeding butterflies, Nymphalidae, tropical rainforest, vertical stratification

Introduction

Increasing deforestation worldwide has expanded the interfaces between fragmented forests and non-forest habitats (e.g., croplands, pasture, roads and urban areas), and studies of these interfaces dominates the forest ecology literature (Melo et al., 2013; Steffen et al., 2015). Human-made edges are very different from the original forest cover, with different microclimatic conditions, including temperature, humidity, wind speed and the amount of solar radiation that penetrates the habitat (Murcia, 1995). These changes in the microclimate can extend into the forest understory and may extend further when the fragments are small (Murcia, 1995). All these edge effects cause changes in the natural community structure, not only in terms of abundance and diversity, but also in the ecological interactions between organisms (Didham et al., 1996).

As well as human-made edges, there are many kinds of natural transitions between forests and non-forest habitats, such as interfaces with lakes, rivers, riparian forests, dunes, savannas and grasslands, all falling into the category of "ecotones". Following Holland (1988), ecotones are defined as a "zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems". As natural transition habitats, forest ecotones are distinct from human-made forest edges. The human-made forest edges are usually sharp and associated with disturbances, with abrupt changes in temperature, humidity, luminosity and wind incidence from the forest interior towards the edge (Murcia, 1995). In contrast to human edges, natural forest-lake ecotones, for example, even when abrupt are composed of a complex vegetation physiognomy, with trees growing leaning toward to the open habitat and canopy structures close to the ground level (hereafter "brought low canopy") (Barbosa, 2014). Additionally, the forest-lake ecotone has a composition of herbaceous and arboreal species well adapted to this transition range (Barbosa, 2014). In these particular ecotones between forest and lakes, the foliage remains close to the ground and yet presents several characteristics similar to the typical forest upper canopy (Barbosa, 2014). For example, canopy leaves present a high degree of sclerophylly and typical morphological attributes resulting from high insolation (Sanches et al., 2010; Ribeiro and Basset, 2007, 2016). In

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addition, rates of leaf respiration are similar to those of emergent trees (Sanches et al., 2010) and the crown architecture is typical of a canopy tree (i.e., trunk-leaf biomass ratio, qualitative data on leaf characteristics and trunk ramifications) (Barbosa, 2014). Hence, there are eco-physiological similarities already identified between the upper canopy and the brought low canopy.

The difference in height between the ecotone canopy and the canopy of the forest interior or anthropic edges is remarkable. Knowing that the vertical stratification of organisms and resources is maintained mainly by the height differentiation between strata, as well as the amount of light that arrives in each forest stratum (DeVries, 1988), it is expected that this stratification will be lost in the ecotone. However, other studies have shown that, even at a lower height, the forest-lake ecotone presents vast territories of dominant ants such as those in the genus *Azteca*, which is a typical ant distribution pattern of the upper canopies (Campos et al., 2006; Ribeiro et al., 2013). Also, a high number of galls are found in the ecotones, and in wet forests, those are typical of the upper canopy as well (Ribeiro and Basset, 2007; Ribeiro, 2003). On the other hand, investigating organisms that present a consistent vertical stratification distribution, such as butterflies, is an opportunity to understand how the characteristics of each habitat type (e.g., natural or human-made transitions), may influence species distribution in the landscape and ultimately the whole community.

In tropical forests, fruit-feeding butterflies (i.e., those whose adults primarily obtain nutrients by feeding on rotten fruits or fermenting sap; DeVries, 1987) are considered an excellent model for studies of community structure and temporal variation in diversity. Mainly because fruit-feeding butterflies are ecologically diverse, sensitive to seasons and to habitat quality, have a taxonomy relatively well resolved and are sampled with traps baited with rotting fruits, allowing for simultaneous and standardized sampling in several areas (revised by Freitas et al., 2014). In addition, fruit-feeding butterflies respond to the vertical structure of forest and several types of disturbance, which reinforces their role as biological indicators (DeVries et al., 1997; Ribeiro et al., 2012; Shahabuddin and Terborgh, 1999; Thomas, 2016; Uehara-Prado et al., 2007). Previous studies have shown that butterflies are highly sensitive to fragmentation and to changes in forest cover (Barlow et al., 2007; Fermon et al., 2003, 2005; Filgueiras et al., 2016; Ribeiro and Freitas, 2012; Sant'Anna et al., 2014; Uehara-Prado et al., 2007), responding to variation in the immediate surrounding vegetation and to different intensities of disturbance (Ribeiro et al., 2012). Less intense land use tends to increase the abundance and richness species, while the more intensive land use tends to decrease (Ribeiro et al., 2012). Intense land

use causes, for example, a decline in butterfly populations and changes in butterfly community, mainly due to loss and/or reduction of breeding areas, as well as in the number of host plants for larval feeding (Casagrande et al., 1998; Basset et al., 2015; Thomas, 2016).

In this study, fruit-feeding butterfly assemblages were sampled in three different forest habitats (forest interior, forest ecotone and anthropic edges), in both canopy and understory. Specifically, the following hypotheses were tested: i) fruit-feeding butterfly assemblages are more similar between ecotone and forest interior than to anthropic edges. It follows that the "brought low canopy" in the ecotone causes a shaded understory similar to the understory within the forest, at the same time, it has the eco-physiological characteristics typically found in the upper canopy of the forest interior (Barbosa, 2014); ii) the stratification of the butterfly species composition varies differently between the three habitats. It follows that ecotone and forest interior should be more similar among them than to anthropic edges, which differs from a natural habitat (forest interior and forest ecotone) in both strata, due to type of vegetation and microclimatic conditions. The anthropic edge may vary severely in type of vegetation and microclimatic condition, and despite similarities between ecotone and interior forest, the physical proximity between strata in the ecotone may allow some species, coming from the understory, moving in and out the canopy.

Material and methods

Study site

The study was carried out in the Rio Doce State Park (PERD in the Portuguese abbreviation) (19°48'-19°29'S and 42°38'-42°28'W), in the municipalities of Marliéria, Timóteo and Dionísio, state of Minas Gerais, southeastern Brazil (Fig. 1). The PERD covers an area of approximately 36,000 ha of Atlantic rainforest varying from 200 and 500 m above sea level, where the forest surrounds a complex system of about 42 lakes. These lakes were formed by the closure of the secondary valleys of the Doce river, after tectonic movements during the middle Holocene (Fonseca-Silva et al., 2015), around 10-8 thousand years ago. The surrounding rainforest, on the other hand, arose more recently (about 4,500 years old), substituting a more xeric ecosystem (Fonseca-Silva et al., 2015). The present climate in the region is tropical seasonal (Aw, based on the Köppen classification), with a rainy season between October-April and a dry season between May-September. The average annual

temperature is 21.9°C and the average annual precipitation is 1,480 mm (Alvares et al., 2014; CBH-Doce, 2009).



Fig. 1 Rio Doce State Park, approximately 36,000 ha of Atlantic rainforest, in the municipalities of Marliéria, Timóteo and Dionísio, Minas Gerais State, Brazil.

Sampling methods

Sampling of fruit-feeding butterflies occurred in three different habitats within the PERD: i) interior of the forest (hereafter called "forest interior"), at least 50 m distant from any border, with a canopy height similar to the anthropic edges (10-25 m high); ii) natural forest-lake or flooded grassland (hereafter "ecotone"), with high sun light availability resulting in the formation of a "brought low canopy" (5-15 m high) with main branches bent towards the lakes at 1 - 3 meters above the ground and with similar characteristics of forest canopy (Barbosa, 2014); iii) anthropic edges (hereafter "edge"), a result of planned cut within the park, as in borders of dirt roads and facilities, with a canopy higher than the ecotone (between 10-30 m) but dominated by saplings and young trees close to the ground, right on the edge.

The sample design follows DeVries (1999), modified after Ribeiro and Freitas (2012). Three transects of approximately 250 m in length were selected per habitat. Each habitat transect was separated by at least 1 km in distinct locations, constituting random and truly independent samples. Only two ecotone and forest interior transects were somehow in the same region, but even those were more than 300 meters apart (Fig. 2). Thus, a total of nine independent transects were set: three in forest interiors, three in ecotones (from three distinct lakes) and three in edges. Each transect contained a sampling unit of 10 portable traps (Van Someren-Rydon – VSR, Fig. 2) containing attractive bait (a mix of banana and sugar cane juice at a ratio 3:1, fermented for 48 hours), totaling 90 bait traps. The traps were installed 25 m apart

from each other, alternating between canopy and understory, so that the canopy traps were suspended right in the upper canopy, to a distance of only 1-3 m below the canopy surface (i.e. interface between the uppermost layer of leaves and the atmosphere; Basset et al., 2003): 6.2-21.9 m, average of 11.14 m in the forest interior; 3.5-11.7 m, average of 7.25 m in the ecotone; 6.8-24.1 m, average of 11.44 m in the edge. The understory traps were suspended 1-1.5 m above the ground. Butterflies were sampled monthly from August 2015 to July 2016 (n=12 months), with the traps remaining open for four consecutive days with revisions at 48 h intervals. Therefore, the total effort was 4,320 trap-days (90 traps x 4 sampling days x 12 months), a sampling effort higher than recommended by Ribeiro et al. (2016). During each revision, baits were replaced and all butterfly individuals captured were recorded and marked with a sequential number on the right posterior wing to avoid to overestimate butterfly abundance, thus those eventually recaptured were not counted as new individuals. Those individuals not identified in the field or that died in the traps (n = 5,958; 51.4%) were taken to the lab for later identification. At least three individuals of each butterfly species (except those with less than three individuals recorded throughout the study) were pinned and deposited at the Museu de Zoologia of the Universidade Estadual de Campinas, São Paulo, Brazil (ZUEC), as well as in the Laboratório de Ecologia Evolutiva de Insetos de Dossel e Sucessão Natural, of the Universidade Federal de Ouro Preto, Minas Gerais, Brazil. Permits for the field studies were issued by the state authority Instituto Estadual de Florestas (IEF) and the national authority Sistema de Autorização e Informação em Biodiversidade/ Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO/ ICMBio).

42°37'30''W 42°27'0''W Brazil South 19°39'0''S Atlantic Ocean Legend Rio Doce State Park area 4 ⊐Km Intermunicipal boundaries Sampling habitats Vegetation Lakes Forest Interior Sampling habitats 19°49'30"S Forest Interior Ecotone Edge 35cm Transects Ecotone Canopy Lake Bait trap 100cm Understory 0m 25m 50m Edge 44cm Dirt Road 5cm 44cm

Fig. 2 Location of the study area, Rio Doce State Park, Minas Gerais State, Brazil. Layout of the sampling design with 10 traps in each habitat (forest interior, ecotone, edge) alternating the strata (canopy, understory), in Rio Doce State Park, Brazil.

Data analysis

To estimate the expected richness of fruit-feeding butterflies in the habitats (i.e., forest interior, ecotone, edge) and strata (i.e., canopy, understory) and to evaluate the representation of each sample according to the total community, the Chao 1 estimator was used. The Chao 1 estimator uses only the singletons, doubletons and the observed richness to obtain the lower bound for the expected richness (Gotelli and Chao, 2013). Rarefaction curves were built integrating the interpolation and extrapolation (prediction) of species diversity, based on individuals, to compare species diversity among habitats and strata, using Hill numbers (q = 0, q = 1, q = 2). This unified standardization method allows the quantification and comparison of species diversity across multiple assemblages (Hsieh et al., 2016), even if they have unequal

abundances (Gotelli and Graves, 1996). Hill numbers are parameterized by a diversity order q, which determines the measures' sensitivity to species relative abundances (Hsieh et al., 2016). In diversity of order q = 0 all the abundances are raised to 0, in this way rare species have the same weight as abundant, so q = 0 represents species richness. In diversity of order q = 1 all the abundances are raised to 1, that is, diversity in effective species number calculated by Shannon Diversity. In diversity of order q = 2 all the abundances are raised to 2, that is, diversity in effective species number calculated by Simpson Diversity, which increases the weight of the dominant species. The package "iNEXT" in the R software was used to construct these integrated curves and the curve size was extrapolated to three times the size of the lowest observed richness to compare different samples until an estimated asymptote (Hsieh et al., 2016).

To examine factors affecting the distribution of fruit-feeding butterflies, Generalized Linear Models (GLMs) were used, where the abundance, species richness and subfamily-tribe abundances were used as response variables, and study habitats (forest interior, ecotone, edge), strata (canopy, understory) and the interaction between these two factors were used as explanatory variables. For this, the Poisson distribution of errors corrected for Negative Binominal distribution were used when overdispersion was verified. In addition, non-significant variables were removed until reaching the reduced model, with application of a posthoc test to examine the difference among levels. For comparing proportion of individuals from each species between strata were used G-tests, and values were corrected using the sequential Bonferroni method (Rice, 1989).

In order to test what scale most contributes to the gamma diversity (γ), an analysis of additive partitioning of diversity was done using the "*vegan*" and "*betapart*" packages in R. The scales analyzed were the diversity within transects (set of five traps for each stratum) (α), the diversity distributed among transects of the same stratum and habitat (β 1), between strata of the same habitat (β 2) and among habitats (β 3), and the total diversity of the Park (γ). Beta diversity (β 1, β 2 and β 3) is composed of two components: turnover (i.e. replacement of some species by others) and nestedness (i.e. species found on one site represent a subset of another site), and the Jaccard index was used to separate the contribution of each process. Expected values were generated by a series of null models (with 999 simulations) and the comparisons between the observed and expected diversity were considered different when p < 0.05.

Species composition was described comparing canopy and understory in the three different habitats, using Non-Metric Multidimensional Scaling (NMDS) with Bray-Curtis similarity measure. A Permutational Multivariate Analysis of Variance (PERMANOVA) was performed to test the significance of the groupings formed by habitats and strata. The Bray-Curtis index was used to compare the similarity among and within habitats, and the coefficient of variation in the species composition within each habitat was used as a measure of biotic homogeneity. All of the statistical analyses were performed using the software R 3.4.0 (R Core Team, 2017).

For comparative purposes with previous studies, in all analyses the Nymphalidae taxonomy followed Freitas and Brown Jr. (2004) modified after Wahlberg et al. (2009) (subfamilies Biblidinae, Charaxinae, Satyrinae and Nymphalinae). The subfamily Satyrinae was subdivided into three tribes (Satyrini, Morphini and Brassolini) since they are distinct in several morphological, ecological and behavioral traits (see Freitas et al., 2014). Only a single individual of tribe Haeterini (Satyrinae) has been captured, therefore, it was excluded from the analyzes.

Results

In total, 11,594 individuals from 98 fruit-feeding butterfly species were captured in all habitats and strata during 12 months, with Biblidinae subfamily being the most abundant (5,339 individuals, 46.05%), followed by Satyrinae (3,650 individuals, 31.48%), Charaxinae (2,495 individuals, 21.52%) and Nymphalinae (110 individuals, 0.95%). Richness estimators showed that 91.9% of the total richness was sampled, which can be considered a good representation of the local assemblage (Tab. 1). The forest interior registered 3,151 individuals from 79 species (four exclusive species), with nine species predominantly captured in the understory, nine predominantly captured in the canopy and 48 shared between strata (Appendix 1). The ecotone registered 4,321 individuals from 87 species (six exclusive species), with 15 species predominantly captured in the understory, only three predominantly captured in the canopy and 59 shared between strata (Appendix 1). The edge registered 4,122 individuals from 83 species (six exclusive species), with 16 species predominantly captured in the understory, nine predominantly captured in the canopy and 57 shared between strata (Appendix 1). The three habitats shared 70 out of the 98 recorded species (Appendix 8 – Tab. 3).

		Diversity			Richness estimators		
Habitats	Abundance	q0	q1	q2	Chao 1	SD	Coverage %
Forest							
Interior							
Canopy	1408	60	19.03	12.40	70.9	7.6	84.63
Understory	1743	67	18.20	10.27	77.9	7.6	86.01
Total	3151	79	21.15	12.44	100.3	14.5	78.76
Ecotone							
Canopy	1587	73	24.06	14.33	85.5	8.5	85.38
Understory	2734	73	24.32	13.51	89.9	12.7	81.20
Total	4321	87	26.52	14.60	96.4	6.8	90.25
Edge							
Canopy	1901	71	26.99	19.07	94.1	14.8	75.45
Understory	2221	69	32.01	20.78	72.1	3.1	95.70
Total	4122	83	35.26	23.58	98.1	12.5	84.61
Total	11594	98	31.59	19.26	106.6	6.8	91.93

Table 1. Abundance, richness and diversity of the fruit-feeding butterflies in different habitats

 and strata in Rio Doce State Park, MG, Brazil.

SD, standard deviation.

The studied habitats did not differ in fruit-feeding butterfly abundance ($\chi^2 = 18.21 \text{ p} = 0.093$) and there was no interaction among habitats and strata ($\chi^2 = 18.19 \text{ p} = 0.320$). On the other hand, understory had more individuals than canopy (mean ± SD: 744.2 ± 222.3 and 544 ± 174.7 respectively; $\chi^2 = 22.95 \text{ p} = 0.009$). The tribes Morphini and Brassolini and Satyrini were more abundant in the understory (Morphini and Brassolini $\chi^2 = 24.49 \text{ p} < 0.001$; Satyrini $\chi^2 = 30.12 \text{ p} < 0.001$) and varied among the habitats (Morphini and Brassolini $\chi^2 = 17.59 \text{ p} = 0.032$; Satyrini $\chi^2 = 18.98 \text{ p} = 0.004$; Tab. 2). Morphini and Brassolini abundances were greater in the ecotone (n = 228 individuals) than in the forest interior and in the edge (n = 163 and 190, respectively). Satyrini abundance observed in the ecotone and in the edge (n = 1,250 and 1,069, respectively) were greater than in the forest interior (n = 750). Interaction between habitats and strata was significant only for Nymphalinae ($\chi^2 = 22.02 \text{ p} = 0.021$), indicating greater abundance in the canopy in the forest interior and edge, but in the ecotone this subfamily was most abundant in the understory. Biblidinae and Charaxinae abundances did not vary among habitats and strata.

		Habitats	Strata		
Subfamilies/Tribe	Forest Interior Ecotone		Edge	Canopy	Understory
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Biblidinae	229.5 ± 138.8	321.5 ± 229.6	338.8 ± 38.1	285.4 ± 143.3	307.8 ± 174.0
Charaxinae	138.8 ± 73.4	146.3 ± 36.8	130.7 ± 50.9	158.4 ± 45.3	118.8 ± 54.6
Morphini and Brassolini	27.17 ± 25.1 ^b	38.0 ± 33.5 ^a	31.7 ± 27.1 ^b	7.3 ± 4.0 ^a	57.2 ± 13.4 ^b
Nymphalinae	4.7 ± 2.3	6.0 ± 3.4	7.7 ± 3.6	5.9 ± 4.1	6.3 ± 2.2
Satyrini	125.0 ± 79.0 ^b	208.3 ± 110.5 ^a	178.2 ± 112.2 ª	86.9 ± 36.3 ^a	254.1 ± 70.9 ^b

Table 2. Mean abundance for subfamilies and tribes fruit-feeding butterfly species by habitats and strata, Rio Doce State Park, Brazil.

SD, standard deviation. Different letters in front of mean indicate significant differences based on Tukey tests.

The species rank abundance showed a similar distribution among strata and habitats, with a predominance of rare species (Fig. 3). In the canopy, 54.5% of the species (n = 48), and in the understory, 42.5% (n = 37) were represented by 10 or fewer individuals. The contributions of singletons and doubletons (species represented by one and two individuals, respectively) were 20.4% in the canopy and 21.8% in the understory (n = 18 and 19 species, respectively). In the forest interior, the most abundant species in the canopy was *Hamadryas amphinome* (n = 224 individuals; 15.9%) and in the understory, *Taygetis rufomarginata* (n = 395 individuals; 22.7%). In the ecotone, *T. rufomarginata* was the most abundant species in both strata, with 218 individuals in the canopy (15.5%) and 543 in the understory (19.7%). In the edge, the most abundant species in the canopy was *H. amphinome* (219 individuals; 11.5%) and in the understory, *H. epinome* (262 individuals; 11.8%). Among the five most common butterfly species, some were recorded in more than one stratum and habitat, such as *T. rufomarginata*, *H. amphinome*, *Fountainea ryphea*, *H. epinome* and *H. laodamia*. From these more common species, only *H. amphinome* occurred in all strata and habitats.



Fig. 3 Rank-abundance distribution of fruit-feeding butterflies by habitats and strata (canopy above; understory below) in Rio Doce State Park, Brazil. The symbols represent the habitats: forest interior (circle), ecotone (square) and edge (triangle).

Despite the understory having a greater abundance of fruit-feeding butterflies, there was almost the same number of species in both vertical strata, and the rarefaction and extrapolation curves reveal that the species richness (q = 0) did not vary between strata (Fig. 4). However, mean species richness differed among habitats, being lower in the forest interior, without difference between ecotone and edge (q = 0: χ^2 = 8.57 p = 0.003) (Fig. 5). The same can be observed for species diversity (q = 1) and species dominance (q = 2), no variation between strata (q = 1: F = 23.08 p = 0.601; q = 2: F = 0.29 p = 0.601) and differences among habitats (q = 1: F = 8.53 p < 0.001; q = 2: F = 14.06 p < 0.001) (Fig. 4). The diversity (q1) of fruit-feeding butterflies was also lower in the forest interior, without difference between ecotone and edge. Meanwhile, species dominance (q = 2) was higher in the edge, without difference between ecotone and edge. Meanwhile, species dominance (q = 2) F = 0.64 p = 0.543).



Fig. 4 Interpolation (solid line) and extrapolation (dashed line) curves with species richness (q = 0) of fruit-feeding butterflies in Rio Doce State Park, Brazil. Shaded area represents the standard error – SE; light grey lines represent the canopy and dark grey lines the understory.



Fig. 5 Hill's diversity (q0 diversity – Species richness, q1 diversity – Shannon Diversity, q2 diversity – Simpson Diversity) of mean fruit-feeding butterfly species by habitats (left) and strata (right), Rio Doce State Park, Brazil. The lines represent the first and four quartiles, the box represents the second and first quartiles and the line within the box represents the median. Different letters above boxplot indicate significant differences based on Tukey tests. The points outside of the boxplot represent atypical data.

The partitioning of species diversity analysis indicated that the average diversity among transects (α) was responsible for 50.9% of the total diversity, lower than expected at random (63.2% p = 0.001) (Appendix 6). The diversities among transects in the same stratum and habitat (β 1), between strata of the same habitat (β 2) and among habitats (β 3) were higher than expected at random (β 1 19.3%, expected 15.4%, p = 0.001; β 2 14.4%, expected 8.5%, p = 0.001; β 3 15.3%, expected 12.9%, p = 0.003). Thus, β 1 had the greatest contribution to the β diversity of fruit-feeding butterflies, followed by β 3 and β 2. The decomposition into β 1, β 2 and β 3 allowed us to verify that turnover was the main process responsible for the β diversity compared to transects (80.3%), strata (84.6%) and habitats (76.5%), while the nestedness processes explained only 19.7%, 15.4% and 24.5% respectively.

Species composition was distinct between canopy and understory in all habitats (stress = 0.12; PERMANOVA: F = 7.53, R = 0.28, p = 0.001) and, further, among habitats (PERMANOVA: F = 2.82, R = 0.21, p = 0.001) (Fig. 6). Besides habitats differed among them, the patterns of the species distribution varied differently within each habitat. The variation in species occurrence among transects was greater in the forest interior (19.2%) than ecotone (11.7%) and also greater in the forest interior than in the edge (3.2%), which had quite homogenous samples.



Fig. 6 Non-metric multidimensional scaling ordination based on the composition of fruit-feeding butterfly species within habitats and strata (Bray-Curtis similarity; stress = 0.12;

PERMANOVA: strata F = 7.53, R = 0.28, p = 0.001; habitats F = 2.82, R = 0.21, p = 0.001), Rio Doce State Park, Brazil. The symbols represent the habitats: forest interior (circle), ecotone (square) and edge (triangle); and colour represents the strata: canopy (write) and understory (grey).

Discussion

BUTTERFLY DIVERSITY. The sampled fruit-feeding butterfly species richness (98 species) in the State Park of Rio Doce (PERD) was equivalent to those of other areas in the Atlantic rainforest, where species richness varies from 90 to 120 species (Brown Jr., 2005). However, in the present study, species richness was not different between strata, while in most previous studies the understory was richer than the canopy (DeVries, 1997, 1999; Fermon et al., 2003, 2005; Hill et al., 2001; Molleman et al., 2006). Still, in one study in the Amazonian forest (Ribeiro and Freitas, 2012) and another in the Atlantic Forest (Santos et al., 2017), the opposite was recorded, with greater fruit-feeding butterfly species richness in the canopy than in the understory. Given these idiosyncrasies one must be cautious in trying to identify a mechanism behind patterns that appear from a limited number of studies in the Atlantic Forest.

The present results showed higher abundance in the understory as found in other tropical forests (DeVries et al., 1997, 1999; Fermon et al., 2003, 2005; Molleman et al., 2006; Ribeiro and Freitas, 2012). A distinct pattern was found in a study carried out in an area of montane Atlantic Forest where higher abundances of fruit-feeding butterflies were observed in the canopy (Santos et al., 2017). In that case, the greater abundance in the canopy was explained by the difference in the temperature between strata (due to a combination of altitude and latitude). The canopy of montane forests maintains higher temperatures throughout the year even in the colder months, favoring the butterfly activity in this stratum through the year (Santos et al., 2017). In the PERD, the absence of a cold season provides high temperatures in both strata throughout the year, allowing high butterfly activity in the shaded understory all year round.

EFFECTS OF VERTICAL STRATIFICATION FOR SPECIES DISTRIBUTION. The stratification of abundance varied by taxon. Groups known to be dominant in the canopy, such as Biblidinae and Charaxinae, did not differ between strata. Morphini and Brassolini and Satyrini, which commonly occupy lower strata, were more abundant in the understory, even in

the ecotone where the brought low canopy was observed. Additionally, only Nymphalinae showed an interaction between habitat and strata, being more abundant in the ecotone understory while in the other habitats it appears to be more abundant in the canopy. This indicates that the brought low canopy in the ecotone allows typical canopy species to also occupy the understory.

Considering the vertical dimension among habitats, although the ecotone canopy is lower than the canopy of forest interior and edge, the results with fruit-feeding butterflies indicated that it still presents stratification as in other habitats. The ecotone canopy is a smooth continuation of the upper foliage surface from the interior towards the branches bent towards the lake (Barbosa, 2014). The butterfly species that commonly dominate the canopy of the forest interior are also present in the ecotone canopy. This shows that even though it is lower, the brought low canopy in the ecotone maintains the characteristics of an upper canopy of the forest interior. Other studies in forest-lake ecotones in the PERD with other taxa (Azteca ant genus and galls) have also demonstrated that the ecotone maintains distribution patterns typical of upper canopy (Ribeiro and Basset, 2007; Campos et al., 2006; Ribeiro et al., 2013; Ribeiro, 2003), being a continuation of the upper canopy and differing from the understory from the forest interior. However, the present study showed that fruit-feeding butterflies maintain the vertical stratification even in the ecotone, presenting distinct species composition between strata. On the other hand, the brought low canopy in the ecotone may allow opportunistic exploitation of its resources, as predicted. Some butterfly species such as Taygetis rufomarginata is a good example of this; in the present study, this species dominate the understory of the forest interior but occurred in both strata in the ecotone.

EFFECTS OF HABITAT TYPE FOR SPECIES DISTRIBUTION. It is largely known that transitions (both natural and anthropic) are usually richer and more diverse than adjacent habitats, since they combine characteristics of the two nearby environments (Holland, 1988) (in the present study, a forest and an open habitat). However, there are few studies comparing fruit-feeding butterfly communities between natural and anthropic transitions (Filgueiras et al., 2016; Ribeiro and Freitas, 2012; Ribeiro et al., 2012; Sant'Anna et al., 2014; Uehara-Prado et al., 2007). A meta-analysis using ground beetles (Coleoptera: Carabidae) showed that different edge maintenance processes (natural or anthropic) reflected in the diversity and assemblage composition of inhabitants (Magura et al., 2017). Forest edges maintained by natural processes had higher species richness forest interiors, while edges with continued anthropic influence did

not (Magura et al., 2017). By comparing two distinct forests studied at different times, DeVries et al. (1999) anticipated a pattern, showing that natural transitions presented lower abundance, species richness and diversity of fruit-feeding butterflies than anthropic edges, which is consistent with findings that disturbance has a positive effect on abundance and richness of butterflies (as largely known, see Uehara-Prado et al., 2007, 2009; DeVries et al., 1999). Nevertheless, the present study is the first to investigate with direct comparisons whether the natural transitions (forest ecotones) differ from anthropic transitions (forest edges) within a same landscape mosaic. The present study clearly indicated that both, species richness and species diversity of fruit-feeding butterflies were higher in the transition habitats (ecotone and edge) than in the forest interior, and transitional habitats did not differ markedly from each other, in contrast to the findings of DeVries et al. (1999). However, the results of the present study also showed that species composition and species dominance are distinct between ecotones and edges. Therefore, the disturbance origin directly affects which species will be present, as well as the community dynamics.

When comparing some of the most abundant butterfly species among habitats, several idiosyncratic responses were observed. *Taygetis rufomarginata* (the most abundant in the ecotone and the forest interior) had low abundance in the edge. This result corroborated the pattern described by Uehara-Prado et al. (2007) that showed that large Satyrinae species prefer shaded habitats. Other species commonly recorded in edge, such as *Hamadryas amphinome* and *H. epinome* (Biblidinae), are also among the five most abundant species in both ecotone and forest interior. These two species are described as common in open or disturbed habitats (Uehara-Prado et al., 2007), as well as *H. laodamia* (a species common in the edge understory and the ecotone canopy), indicating that species commonly abundant in the edge may find favorable conditions to establish themselves also in the ecotone.

The partitioning of diversity analysis showed that the β diversity among transects of the same stratum and habitat (β 1) was the one that contributed most to the total fruit-feeding butterfly diversity. This indicates that transects were mainly responsible for adding new butterfly species. Therefore, the mere spatial spreading of the sampling design resulted in an important β diversity driver, even more important than strata and habitats. Hence, the spatial variation of a set of characteristics (e.g., vegetation structure, host plants and microclimatic conditions) alone may regulate the permanence of species (Beirão et al., 2017; Ribeiro et al., 2008; Saunders et al., 1991; Uehara-Prado et al., 2007). The differences in habitat characteristics and resource distribution among areas have already been indicated as a possible
explanation for the high β diversity of fruit-feeding butterflies (Ribeiro et al., 2008). As a consequence, species turnover was the main process responsible for the structuring the butterfly community, with the predominance of replacement some species with others among transects, strata and habitats. Natural habitats provide favorable conditions and resources for the maintenance of butterfly populations, while anthropic edges change or eliminate breeding areas and areas essential for larval feeding, drives to changes in butterfly assemblages (Thomas, 2016; Casagrande et al., 1998; Basset et al., 2015).

Despite the similarities observed between ecotone and edge, due to the characteristics of transitional habitats (the highest species richness and diversity of fruit-feeding butterflies), these two types of habitats were quite distinct in species composition, with the edges showing the most homogeneous assemblages. The edge is very homogeneous compared to the natural habitats (ecotone or forest interior), so losing an edge is different from losing an ecotone. The high unpredictability caused by ongoing succession and different microclimatic conditions in the edges may favor the high dominance of a few generalist species, leading to taxonomic and functional simplification. On the other hand, the large number of lakes (42, summed up an area of 11% of the 36,000 ha of the Park) results in natural ecotones with a forest that are a habitat of great relevance at a landscape scale and also highly constant and predictable, favoring so different butterfly species. In special, this constancy in ecological conditions allowed a brought low canopy that grows occupying all possible light gaps, thus, resulting in an upper canopy-type of habitat closer to the ground. A quite unique and different situation compared to the edges.

The growing importance of human-made edges and fragmented forests to conservation resulted in natural ecotones to be neglected by ecological literature. Here, the NMDS (Fig. 6) was one of the analyses that indicated that ecotones were a key habitat in terms of diversity, with a unique species composition and heterogeneous assemblages. The lower height facilitates the occupation of different butterfly species as well as the eco-physiological conditions, since many species are not able to live in the extreme temperature, wind and humidity of a typical canopy. The unique brought low canopy is capable of accommodating species adapted to distinct ecological conditions, being a repository for several populations. It is also possible to extrapolate that forest-lake ecotone is a key habitat for diversity conservation because its unique species composition and dynamics spread along a very extensive area, i.e., the huge linear extension of water-forest contacts, separated in various lakes with distinct shapes and size. This study is the first to investigate and report differences between natural and anthropic transitions in fruit-feeding assemblages in Atlantic Forest. The main findings showed that the fruit-feeding assemblages living in the ecotones show similarities with the forest interior as well as particularities that make ecotones unique and distinct of anthropic borders. Particular characteristics attributed to ecotones favor the maintenance of butterfly populations from different habitats, consolidating their importance for the biodiversity conservation in the region. More studies are needed to better define how different ecotones are from the ecosystems stablished in human generated borders and how essential they are for biodiversity conservation in each scenario.

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Capítulo 2

Temporal variation of fruit-feeding butterfly in natural and anthropic forest transitions Giselle M. Lourenço¹, Pedro Luna², Roger Guevara³, Wesley Dáttilo², André V. L. Freitas¹, Sérvio P. Ribeiro^{1,4}

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Abstract

Butterfly species often synchronize their life cycles to seasonal fluctuations of weather. Increasing temperature and humidity act as clues of resource availability, triggering a response to favorable time for flight, foraging, courting and oviposition. Nevertheless, human-made forest edges drive major changes in the microclimatic conditions that may jeopardized the synchrony between insect emergence and favorable conditions. Here, the distribution of fruitfeeding butterflies was studied over one year in three different habitats (forest interior, forest ecotone, forest edge) to verify: i) if species density varies seasonally; ii) if species composition varies among habitats over the year; and iii) if temperature and humidity affect the abundance and temporal distribution of butterflies. The present study was carried out in the Rio Doce State Park, where forest surrounds the largest natural lake system of the Atlantic Forest. A total of 11,594 individuals representing 98 butterfly species were collected. The butterflies presented a nonuniform distribution in all studied habitats, with greater abundance, richness and species diversity during the wet season. Butterfly abundance increased with high temperatures in all habitats. For species richness, however, this effect was only detected in the forest interior. Although butterfly diversity varied through the year, transition habitats were generally richer and with a greater abundance of butterflies compared with the forest interior all year round. The contributions of turnover and nestedness processes change over the months, overlap the seasonal changes in all the habitats. Understanding how rates of species turnover vary over time in different habitats can help in understanding the sensitivity of species to environmental changes, allowing quantification and comparison of community variation over time.

Keywords Beta diversity, ecotone, insect seasonality, Lepidoptera

Introduction

Most tropical insects show seasonality all year long, although not as extreme as in temperate ecosystems where their peaks are restricted to the warmer seasons (Kishimoto-Yamada and Itioka, 2015; Wolda, 1988). In tropical regions, insect populations vary throughout the year often synchronizing their life cycles at or about the beginning of the wet seasons (Wolda, 1989), when conditions for the development of most tropical organisms, such as high temperature and humidity and resource availability, reach their optima (Kishimoto-Yamada and Itioka, 2015). The duration and peaks of organisms' activities vary greatly among groups, with multivoltinism (i.e., several generations in one year; Gullan and Cranston, 2010) probably being the most common among tropical insects (Wolda, 1988). Rainfall is recognized as a predictor of insect activity pulses (Wolda, 1988, 1989). Hence, wet and dry seasons can differently affect both species abundance and species diversity (Grøtan et al., 2012). However, although rainfall might be the cue hatching and breaking diapause of tropical organisms, other factors such as temperature, resource availability and the abundance of enemies may actually drive growth, survival and reproduction (Didham and Springate, 2003).

A temporal increase in temperature, along with constancy in rainfall, apparently act as clues of resource availability, triggering behaviors such as flight/dispersion, foraging and reproduction of tropical insects (Didham and Springate, 2003; Kishimoto-Yamada and Itioka, 2015; Torres-Vila and Rodríguez-Molina, 2002). Even though some resources (e.g. leaves) are available all year round, their quality may vary over time generating some favorable periods throughout (Aeide, 1993; Hunter and Lechowicz, 1992). In general, herbivorous insects prefer young, tender, leaves than mature leaves (Aeide, 1993; Coley, 1983; Ribeiro et al., 1994). Specifically, for butterflies the leaf availability and new plant tissues regulate the optimum period for caterpillar development (Murakami et al., 2008). For adult butterflies, the temporal variation in the availability of resources could regulate the activity pattern in each site as previous data suggest (Hamer et al., 2006; Ribeiro et al., 2010).

However, the synchrony between insect emergence and favorable conditions for their emergence may be jeopardized by the fragmentation of tropical forests (Hamer et al., 2005; Ribeiro and Freitas, 2011). The expansion of the interfaces between fragmented forests and non-forest habitats (e.g., croplands, pasture, roads and urban areas) creates human-made edges that are dramatically different from the original forest cover not only in plant cover, but also in microclimatic conditions (e.g. temperature, humidity, wind speed and the amount of solar radiation that penetrates the habitat) (Murcia, 1995; Steffen et al., 2015). The human-made forest edges present abrupt changes in microclimatic conditions and for butterflies, for example, high temperatures increase their activity, with possible consequences for their life cycles (Ribeiro and Freitas, 2010). In addition, the loss and reduction of breeding areas, as well as the number of larval host plants, mainly due to intense land use exerting pressures, could result in the decline of butterfly populations and changes in butterfly communities (Basset et al., 2015; Casagrande et al., 1998; Thomas, 2016). Consequently, the loss of synchrony with the favorable period for the emergence of butterfly species can affect the temporal dynamics of its demography and diversity through different habitats. Indeed, recent evidence has shown that community composition of fruit-feeding butterflies (i.e., those whose adults primarily obtain resources by feeding on rotten fruits or fermenting sap; DeVries, 1987) was similar between natural transitions (ecotones) and the forest interior, although the ecotones and the forest edges (anthropic transitions) were richer and more diverse than the forest interior (see Chapter 1). The temporal variation in the fruit-feeding butterfly assemblage among habitats therefore offers an opportunity to investigate how the variation in climatic and micro-climatic conditions throughout the year influence butterfly species and ultimately the whole butterfly community.

The Brazilian Atlantic rainforest has experienced a long history of anthropic impacts resulting from the early colonization in Southeastern Brazil becoming one of the most fragmented tropical forest biomes in South America (Ribeiro et al., 2009) with an obvious expansion of forest edges. Fruit-feeding butterflies are considered an excellent model for studies of community structure and temporal variation in diversity, as they are ecologically diverse, sensitive to seasons and to fragmentation, allowing for simultaneous and standardized sampling in several areas (Barlow et al., 2007; Bonebrake et al., 2010; DeVries et al., 2016; Fermon et al., 2003, 2005; Filgueiras et al., 2016; Freitas et al., 2014; Grøtan et al., 2012, 2014; Molleman et al., 2006; Ribeiro and Freitas, 2012; Sant'Anna et al., 2014; Uehara-Prado et al., 2007). In view these, investigating the abundance, richness and diversity of butterfly community over time is relevant to understanding the sensitivity of ecological systems to environmental change. Accordingly, the present study investigates the fruit-feeding butterfly distribution among months during a year in each habitat. Specifically, the following hypotheses were tested: i) the fruit-feeding butterflies is concentrated at certain periods of the year in the three habitats studied, with predictions that the peaks of tropical insect activity synchronize with periods of increase resources availability and increases in temperature, rainfall and humidity; ii) the beta diversity among months is similar among natural habitats (forest interior and ecotone), with predictions that the natural habitats present favorable conditions for different species to develop, maintaining the heterogeneity in terms of species throughout the year; and iii) the increase in temperature and humidity positively affect the abundance and species richness of butterflies in the three habitats studied, with the predictions that the temporal variation of temperature and humidity conditions regulate the activity patterns of fruit-feeding butterflies.

Material and methods

Study site

The study was carried out in the Rio Doce State Park (hereafter PERD, following the Portuguese abbreviation) (19°48'-19° and 42°38'- 42°28'W), in the municipalities of Marliéria, Timóteo and Dionísio, Minas Gerais State, southeastern Brazil. The PERD covers an area of approximately 36,000 ha of Atlantic rainforest with an elevational range from 200 up to 500 m encompassing a complex system of lakes that includes over 40 lakes. These lakes were formed by the closure of the secondary valleys of the Doce river, after tectonic movements during the Holocene (Fonseca-Silva et al., 2015), around 10-8 thousand years ago. The surrounding rainforest, on the other hand, arose more recently (about 4,500 years old), substituting a more xeric ecosystem (Fonseca-Silva et al., 2015). Current prevailing conditions correspond to Aw climate (tropical seasonal) on the Köppen classification, with a wet season between October-April and a dry season between May-September. The average annual temperature and precipitation are 21.9°C and 1,480 mm respectively (Alvares et al., 2014; CBH-Doce, 2009).

Sampling methods

The butterflies were sampled in three different habitats in the PERD (for more details, see Chapter 1): i) interior of the forest (hereafter forest interior), at least 50 m distant from any border, with a canopy up to 10-25 m in height; ii) forest-lake or forest-flooded grassland ecotones (hereafter ecotone), with high light availability resulting in the formation of a brought-low canopy (5 - 15 m high), with main branches at 1 - 3 meters above the ground and with similar characteristics of forest canopy (Barbosa, 2014); and iii) anthropic edges (hereafter edge), a result of planned cut within the Park, as in borders of dirt roads and facilities, with a

canopy higher than the ecotone (between 10 - 30 m) but dominated by saplings and young trees close to the ground, right on the edge.

The sample design follows DeVries (1999), modified after Ribeiro and Freitas (2012). In each habitat, three transects 250 m long placed but with the conditions that the transect were at least 1 km apart (see Chapter 1). The separation among transects within each habitat is enough to consider them as independent samples. At each transect (sampling unit) we placed 10 portable traps (Van Someren-Rydon - VSR) spaced every 25 m and baited with a mix of banana and sugar cane juice at a ratio 3:1, fermented for 48 hours. The traps were placed alternate at 1.5 m above the ground level to sample the understory and 1 - 3 m below the canopy surface (i.e. interface between the uppermost layer of leaves and the atmosphere; Basset et al., 2003) to sample the canopy. Sampling was done monthly from August 2015 to July 2016 (n = 12) months). Every month at each transect traps remaining open for four consecutive days with revisions and bait refreshment every 48 hours totaling 4,320 trap-days (10 traps \times 3 transects \times 3 habitats \times 4 sampling days \times 12 months). All captured butterflies were recorded and marked with a sequential number on the right posterior wing to avoid recaptures overestimating butterfly abundance. Those individuals that died in the trap were taken to the lab, as were individuals not identified in the field (n = 5,958; 51.4%). For every species captured, whenever possible, three individuals were mounted and deposited at the zoology museum of the Universidade Estadual de Campinas, São Paulo, Brazil (ZUEC) and the Laboratório de Ecologia Evolutiva de Insetos de Dossel e Sucessão Natural, of the Universidade Federal de Ouro Preto, Minas Gerais, Brazil. Permits for the field studies were issued by the state authority Instituto Estadual de Florestas (IEF) and the national authority Sistema de Autorização e Informação em Biodiversidade/ Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO/ ICMBio).

Data analyses

For comparative purposes with previous studies, in all analyses the Nymphalidae taxonomy followed Freitas and Brown Jr. (2004) modified after Wahlberg et al. (2009) (subfamilies Biblidinae, Charaxinae, Satyrinae and the Nymphalinae tribe Coeini). The subfamily Satyrinae was subdivided into three tribes (Satyrini, Morphini and Brassolini) since they are distinct in several morphological, ecological and behavioral traits (see Freitas et al.,

2014). Only a single individual of tribe Haeterini (Satyrinae) has been captured, therefore, it was excluded from the analyzes.

To test whether fruit-feeding butterflies were evenly distributed throughout the year a circular statistically approaches was used (Jammalamadaka and SenGupta, 2001). Cyclical changes such as those occurring on daily and yearly basis are cyclical in nature and therefore their description an analysis must follow circular statistical methods that help to address for instance whether species are evenly distributed along the year or whether they are clustered around some specific time periods (Jammalamadaka and SenGupta, 2001). All analyses were done at the taxonomic levels of subfamily or tribe (Biblidinae, Charaxinae, Nymphalinae, Satyrinae: Brassolini, Morphini and Satyrini). Monthly samplings were coded as 30 degrees intervals of circumference and then expressed as radians that when transformed in sine and cosine are truly circular. Every observation is represented as a vector defined by the sine and cosine of the bearings in radians, therefore the bearings of the overall resulting vector represent the mean orientation (μ) and the average length of the resulting vector is used to test whether the orientation, in this case occurrence through the year, is random. The average length of the resulting vector ranges from zero (random orientation) to one (if all records occurred in the same sampling period). Specifically, Rayleigh test of uniformity was used and implemented in the R software 3.4.0 (R Core Team, 2017) in the package "circular" (Agostinelli and Lund, 2017).

Rarefaction curves were used to compare species richness for each month in each habitat. To assess the variation in butterfly species composition through time, the pooled data from all transects were aggregated by habitat and months (12 units per habitat). The scales analyzed were the accumulated diversity among the three transects of each habitat per months (α), and the β 1 represents the differences among months. The additive partitioning of species diversity is an approach that allows to disentangle the temporal variation in the distribution of species, where the components of diversity (turnover and nestedness) can be observed monthly, as well as changing them over time (Baselga et al., 2015). An analysis of additive partition of diversity was performed using the "vegan" and "betapart" packages in R, and were used with the "beta.pair.abund" function that takes into account the species abundance (Baselga et al., 2015). This analysis results in three dissimilarity matrices based on the Bray-Curtis index: the beta.bray.bal expresses the temporal turnover (i.e. replacement of some species by others from time to time), the beta.bray.gra expresses the nestedness (i.e. species found on one site represent a subset of another site from time to time) and the beta.bray expresses the total β . It is important

to stress that temporal changes in species composition can be related to both temporal turnover and nestedness from time to time (Baselga et al., 2015).

To test if the mean temperature can explain the temporal distribution of abundance and richness of butterflies, data were analyzed with regression analysis (ANCOVA), using total sampled assemblage abundance and richness of the transects in each month and the mean temperature for transects in each month (measured in the field during of traps revisions). Temporal autocorrelation (time-lag) was looked to detect if there was independence between the values observed in the sampling months. All the statistical analyses were performed using the software R 3.4.0 (R Core Team, 2017).

Results

In total, 11,594 individuals of 98 fruit-feeding butterfly species were captured during 12 months, with the subfamily Biblidinae being the most abundant (5,339 individuals, 46.05%), followed by Charaxinae (2,495 individuals, 21.52%), Nymphalinae (110 individuals, 0.95%) and Satyrinae (3,650 individuals, 31.48%) (Appendix 9 and 10 – Tab. 1 and 2).

Both, richness and abundance, varied over the months (Fig. 1, Appendix 11 - Tab. 3). Rarefaction analysis revealed that in the all three habitats the wet months (January to March) presented lower species richness than the remaining months (Fig. 2). The month variation in the proportion of subfamilies/tribes was similar in the three habitats, with abundance peaks usually coincident (Fig. 3).



Fig. 1 Richness and abundance of fruit-feeding butterfly species by habitats throughout a year, Rio Doce State Park, Brazil. The symbols represent the habitats: forest interior dark grey circle, ecotone light grey square, edge white triangle; the shaded area represents wet season.



Fig. 2 Rarefaction analyses of fruit-feeding butterfly species for habitat (forest interior, ecotone, edge), Rio Doce State Park, Brazil. Actual monthly species richness plotted against an individual-based accumulation curve for the total assemblage for habitat; Jan = January; Feb = February; Mar = March; Apr = April; Oct = October, Nov = November.



Fig. 3 Proportion of fruit-feeding subfamily abundance by habitats throughout a year, Rio Doce State Park, Brazil.

The circular analysis showed nonuniform distributions of fruit-feeding butterflies throughout the year in all habitats for the total sampled assemblage and for each subfamily/tribe tested (Fig. 4). The mean vector (μ) and the standard deviation of the total sampled assemblage were similar among habitats, with 73.7% of the total abundance in the forest interior concentrated from August to March. On the other hand, the period from September to March concentrated 66.3% and 68.9% of the total abundance in the ecotone and the edge, respectively. Considering the abundance distribution of each subfamily/tribe, Biblidinae presented a concentration in December in the forest interior, while in the ecotone and in the edge, it occurred in January. Charaxinae and Morphini concentrated in November for all habitats. However, the Morphini *Morpho helenor* showed a clearly bimodal distribution, with peaks in November and April. Nymphalinae concentrated in December in the ecotone, while in the forest interior it occurred in February and in the edge in March. The Brassolini concentrated in November in the forest interior and in the ecotone and one month later (December) in the edge. For the Satyrini, concentration occurred in August in the forest interior, in September in the edge and in October in the ecotone.



Fig. 4 Circular histogram of the number of individuals observed for the total sampled assemblage and for subfamily/tribe of fruit-feeding butterflies in each habitat throughout the year, Rio Doce State Park, Brazil. The arrows represent the average vector length (r) and indicate the average dates, the red area represent standard deviation.

Overall, the temporal partition of the β diversity of all months (β 1) was similar across the studied habitats, overlapping with seasonal changes (when there is a fluctuation in resource availability for larval and adults). However, the fluctuation of the β diversity among months was clearer in the forest interior (Fig. 5), indicating that the forest interior is more heterogeneous in terms of species throughout the year. When verifying the components of β diversity, it was observed that the contributions by turnover and nestedness change over the months, coinciding with seasonal changes. For example, at the transition from the wet to the dry season (March to April), the forest interior presented a greater contribution generated by species nestedness, i.e., the species were similar among the months. In this same period, there was a greater contribution by turnover in ecotone and edge, that is, species composition was changing throughout the months. During the following period, the early dry season (April and May), nestedness remained as the main process in the forest interior, that is, the community remains similar to previous months, but not in the edge, where seasonal turnover remains as a main process driving species variation, nor in the ecotone where a growth of nestedness contribution is noted, indicating little temporal variation in the community in the period. On the other hand, in the beginning of the wet season (October and November) the turnover process prevails in all the habitats, suggesting a high faunal replacement following in this period, followed again by changes due to nestedness processes in the following period (November and December).



Fig. 5 Temporal partitioning of species diversity of fruit-feeding butterflies among months (β 1) of a year by habitat, Rio Doce State Park, Brazil. The dark grey color represents Turnover, the light grey color represents Nestedness and the shaded area represents wet season.

Regression analysis showed that fruit-feeding butterfly abundance is positively correlated with mean temperature (F = 21.2, df = 2, P < 0.05), and this pattern was observed for all habitats (Fig. 6). The mean temperature also explained species richness (F = 5.28, df = 2, P < 0.05), but this pattern was only significant in the forest interior (Fig. 6). There was no statistical interaction among mean temperature and habitat (abundance F = 0.10, df = 2, P = 0.902; richness F = 0.21, df = 2, P = 0.808). Rainfall was not related to either, abundance or species richness.



Fig. 6 Fruit-feeding butterfly abundance (above) and richness (below) per habitat corresponding to mean temperature (°C), Rio Doce State Park, Brazil. The symbols represent the habitats: circle forest interior, square ecotone and triangle edge; the solid lines represent the tendency and dashed lines represent the non-significant slopes for each habitat.

Discussion

Although there are very few long term studies that investigated the annual variation of butterfly richness and abundance, the seasonal pattern reported in the present study is similar to that previously reported for Neotropical species, with peaks of abundance and richness during the wet season (Brown Jr., 1992; DeVries et al., 1999; Grøtan et al., 2012, 2014; Ribeiro et al., 2010). Moreover, similar patterns have been reported for other tropical insects, such as beetles, bees and mosquitoes (see Kishimoto-Yamada and Itioka, 2015), supporting the hypothesis that the onset of wet season provides essential information to start the activity of some tropical organisms (Kishimoto-Yamada and Itioka, 2015; Wolda, 1989). The peaks of abundance, richness and diversity observed in the State Park of Rio Doce (PERD) during the wet season, start with the seasonal changes that occur during the transition from dry to rainy season. During these periods there is seasonal variation in the resource availability, where the intense leaf production is decisive for immatures and the greater availability of decaying fruits is essential for adults (Aide, 1993; Morellato et al., 2000). The butterfly life cycle synchronizes with the season with greater resource availability, low herbivory pressure and mating behavior (Brown Jr., 1992; Ribeiro et al., 2010).

Additionally, with the seasonal changes there is variation in temperature that is wellsupported with the main predictor of species richness for taxonomically broad communities, both of plants and animals (Peters et al., 2016; Wolda, 1988). Hence, in the present study, higher temperatures increased the butterfly abundance and richness as reported by other studies with fruit-feeding butterfly (Grøtan et al., 2012; Ribeiro and Freitas, 2010; Ribeiro et al., 2010; Santos et al., 2017). This positive effect of temperature on abundance and species richness was observed in all habitats studied here. For richness, however, this positive effect was only detected in the forest interior. Temperature does not predict the butterfly richness in transitional habitats (natural and anthropic transitions) only increases the population sizes of those species already found in these habitats, demonstrating that in these habitats other factors are more important to predict the species richness. Is possible that in transitional habitats other local factors may be interfering more in the butterfly richness than the summer raise in temperature, as transitional habitats receive more sunshine than the forest interior all year round, even in the colder months. It is known that the vegetation structure, host plants and microclimatic conditions can determine the permanence of species (Beirão et al., 2017; Hamer et al., 2006; Saunders et al., 1991; Shahabuddin and Terborgh, 1999). Therefore, as in transitional habitats the temperature does not vary much over the year, the butterfly richness is possibly responding first to vegetation variation and availability of host plants.

On the other hand, although the fruit-feeding butterfly annual variation was observed in all the habitats studied here, the natural transitions (ecotone) and anthropic transitions (edge) were generally richer and more abundant than the forest interior throughout the year. This was expected because it is largely known that transitions (both natural and anthropic) are usually richer and more diverse than adjacent habitats, since they present characteristics of two environments (Holland, 1988). The subfamily/tribe abundance and its proportions varied similarly among the habitats throughout the year. Seasonal patterns were evident for some subfamilies/tribes that coincide with that described in the literature. For example, *Morpho helenor* (Morphini) showed two peaks, in November and April, a clearly bimodal distribution similar to that reported by Carreira (2015), Freire et al. (2014), Ribeiro et al. (2010) and Santos et al. (2017) that is maintained in all habitats. Also studying areas of Atlantic Forest, Ribeiro et al. (2010) reports *M. helenor* peaking between January and February. These different peak periods between localities may be associated with variation in availability of fleshy fruits and regrowth period in the different sites (Morellato and Leitão-Filho, 1992; Morellato et al., 2000).

In general, the monthly fluctuation of temporal beta diversity was similar among habitats, although the variation was more evident in the forest interior. The beta diversity varies more in the forest interior than in transitional habitats, showing that the forest interior is more heterogeneous in terms of species throughout the year. The contribution of turnover and nestedness process changes over the months, overlapping in all habitats with the season changes, when the fluctuation in resource availability occurs. This variability in the fruitfeeding butterfly community can be related to the presence of a favorable season (hot and wet) with great resource abundance both plant-derived and animal, and other unfavorable (cold and dry) with little available resource (Brown Jr., 1992). The butterfly community fluctuates more clearly in the forest interior, although in the other habitats the pattern was similar. In the transition between dry and wet seasons (September-October-November) the higher temperature and the more constant rain lead to the regrowth of many plants that will provide ample food resources for the Nymphalidae family first generation (Brown Jr., 1992). The next period (November-December) overlaps with the adult emergence peak of the species already present in the population, which explains the greater diversities observed in the three habitats. At the wet season peak, there were changes in community composition with a prevalence of the turnover process in all habitats. These changes decrease significantly at the end of the wet season and at the beginning of the dry season, although in this period the transitional habitats kept changing more than the forest interior. During the dry season there was an increase in diversity and changes in community structure in all habitats, completing the annual cycle. Previous studies that showed low diversity in dry season driven by the dry and intense winter cold (Brown Jr., 1992; Ribeiro et al., 2010). However, different from that observed in previous studies during the dry season in the PERD the second generation of several butterfly species was observed, as well as the common species emergence in this period. It is important to note that the PERD has a comparatively higher mean monthly temperature than other Atlantic Forest areas, which favors the butterfly development and activity since the temperature determines both adult development rates and adult reproductive activity (Ribeiro and Freitas, 2010; Wolda, 1988).

Moreover, the present results help guide the sampling effort in environmental diagnostics. In general, these diagnostics do not include long studies, therefore, knowing the best sampling period of an increasingly used indicator group such as butterflies helps to focus the samplings at the best periods (in this case, dry-wet transition and/or only wet season), combining the period richer and more abundant of the group. Moreover, present results showed that transitional habitats (natural or anthropic transitions) are more variable than the forest interior throughout the year. Thus, in transitional habitats the maintenance of populations is more difficult, begin able to occur in some months local extinction of some species and in other months may occur recolonizations. So, the next step is to investigate if this is repeated in other sites. Determining how rates of species turnover vary over time in different habitats is relevant to understanding the sensitivity of ecological systems to environmental change and quantify these sensitivities to future climatic change.

Capítulo 3

Movement patterns and biological traits related to the sex of fruit-feeding butterflies: using mark-recapture data

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Abstract

The movement patterns are the cumulate product of all the individual decisions and can be shaped by the interaction among morphology, behavior and landscape structure. Butterfly movement patterns are known to depend also on host plant distribution and resource availability for adults. Hence, the ongoing process of habitat fragmentation increases the distance among suitable habitats and changes the habitat in such a way that it generates strong selection pressures favoring movement behavior. In addition, the habitat fragmentation can affect different biological traits of the population. This present study describes the movements of six species of fruit-feeding butterflies between strata (canopy, understory) and among habitats: forest interior, natural transition between forest and lake (ecotone) and anthropic transition (edge), as well as biological traits throughout the year (sex ratio, age structure and individual permanence). Butterflies were sampled monthly over one year in the Rio Doce State Park, Southeastern Brazil, following a standardized design using banana-bait traps, settled up in alternating strata. Six butterfly species were analyzed, totaling 411 individuals recaptured at least once. For all species analyzed, the sex ratio of captured individuals was male biased and the age structure showed an increase in recruitment in the dry season and a noticeable aging of the population in the wet season, although the age structure has been relatively constant throughout the year. Considering all species analyzed and both sexes, few individuals traveled long distances in meters and most individuals were recaptured in the same trap, suggesting that the habitats are providing the necessary conditions for the maintenance of butterfly populations, favoring lower movements and narrow home ranges for both sexes throughout the year. However, the recapture in the ecotone was higher than in the interior and in the edge. Thus, the eco-physiological conditions of the ecotone favor the individual permanence, which reinforces the importance of this habitat for the conservation of butterfly populations of different species.

Keywords Bait trap, canopy, ecotone, Lepidoptera, mark-release-recapture

Introduction

Every butterfly, as well as other organisms, has to make decisions over whether to go elsewhere or to stay where it is, and the movement patterns are the cumulate product of all these individual decisions (Baker, 1984). Although flying organisms display a high potential of vagility (i.e., ability to cross physical barriers) (Ehrlich, 1961), they usually move much less than they could (Baker, 1984; Ehrlich, 1961; Da Silveira et al., 2016; Thomas, 2016). Some butterflies visit areas 2000-3000 km away from their birthplaces, others, on the other hand, continuously choose to stay rather than to move, never going more than a few meters from the place where their mother oviposed them (Baker, 1984). Moreover, vagility is variable and saving some migration events, most individuals in a given population are sedentary and generation after generation individuals are born and stay in the same area of their birthplace respecting barriers intrinsic to dispersal (Baker, 1984; Ehrlich, 1961).

So, what do determine, favoring or limiting, the individual movements among areas? The different movements signatures observed result from the interaction among morphology, behavior and landscape structure and conservation (Da Silveira et al., 2016). Variation in matrix quality, for example, can be differently perceived by different individuals, generating variation in movements related to distinct habitats (i.e., contrasted boundaries, corridors, or barriers) and/or individual phenotypes (i.e., sex, age or sex ratio) (Legrand et al., 2015; Turlure et al., 2011). For instance, butterfly movement patterns are known to depend on host plant distribution and resource availability for adults (Ehrlich, 1984; Baker, 1984; Fermon et al., 2003). Hence, the ongoing process of habitat fragmentation increase the distance among suitable habitats and changes the habitat in such a way that it generates strong selection pressures favoring movement behavior (Baker, 1984; Fermon et al., 2003; Schtickzelle et al., 2007). Fermon et al. (2003) showed that butterfly movement parameters among distinct land use reveals the largest mean movement in the plantation, while in the natural forest the home range tend to be smaller. Therefore, in natural sites the recaptures tend to be higher, since most butterfly individuals remain where the suitable conditions are provided and remain stable over generations (Baker,

1984; Fermon et al., 2003), thus also reflecting on the age structure of populations throughout the year.

The stimulus as well as the ability to movements may differ between sexes (Legrand et al., 2015; Reim et al., 2018; Turlure et al., 2011). For many butterfly species, males are more active than females, due for example to mate location, inspection flights and territorial disputes, which increases the chances of males to be captured (Reim et al., 2018). Butterfly females generally move more than males due to straighter flight trajectories (Reim et al., 2018), either to found host plant and distribute eggs strategically over a wider area (Petr and Novotny, 2015; Hopper, 1999) or to start new populations (Hill et al., 1999; Hanski et al., 2004). In addition, butterfly females need to escape from male harassment (Trochet et al., 2013), which increases the distances they travel. Knowledge on movement patterns is an important step for a better understanding of dispersal and its crucial role in the conservation and evolution of species facing major environmental changes, such as habitat loss and fragmentation, climate change and their interactions (Reim et al., 2018; Stevens et al., 2010). In view of these, the present study describes the movements of six species of fruit-feeding butterflies between strata (canopy, understory) and among habitats: forest interior, natural transition between forest and lake (ecotone) and anthropic transition (edge), as well as biological traits throughout the year (sex ratio, age structure and individual permanence). Specifically, the main objectives are: 1) describe the sex ratio and the age structure throughout the months, as well as the maximum permanence of each species; and 2) describe the movements by each species and sex among traps, strata and habitats.

Material and Methods

Study site

The study was carried out in the Rio Doce State Park (PERD in the Portuguese abbreviation) (19°48'-19° and 42°38'-42°28'W), in the municipalities of Marliéria, Timóteo and Dionísio, state of Minas Gerais, southeastern Brazil. The PERD covers an area of approximately 36,000 ha of Atlantic rainforest varying from 200 and 500 m above sea level, where the forest surrounds a complex system of about 42 lakes. These lakes were formed by the closure of the secondary valleys of the Doce river, after tectonic movements during the middle Holocene (Fonseca-Silva et al., 2015), around 10-8 thousand years ago. The surrounding rainforest, on the other hand,

arose more recently (about 4,500 years old), substituting a more xeric ecosystem (Fonseca-Silva et al., 2015). The present climate in the region is tropical seasonal (Aw, based on the Köppen classification), with a wet season between October-April and a dry season between May-September. The average annual temperature is 21.9°C and the average annual precipitation is 1,480 mm (Alvares et al., 2014; CBH-Doce, 2009).

Sampling methods

Butterflies were captured in three different habitats in the PERD (for more details, see Chapter 1): i) interior of the forest (hereafter forest interior), at least 50 m distant from any border, with a canopy up to 10-25 m in height; ii) forest-lake or forest-flooded grassland ecotones (hereafter ecotone), with high light availability resulting in the formation of a brought-low canopy (5 - 15 m high), with main branches bent towards the lakes at 1 - 3 meters above the ground and with similar characteristics of forest canopy (Barbosa, 2014); and iii) anthropic edges (hereafter edge), a result of planned cut within the park, as in borders of dirt roads and facilities, with a canopy higher than the ecotone (between 10 - 30 m) but dominated by saplings and young trees close to the ground, right on the edge.

Studies of tropical butterfly movements usually are based on active capture using insect nets, have rarely been assessed using bait traps (Fermon et al., 2003) and the benefits and drawbacks of each method have been previously discussed (Daily and Ehrlich, 1995; DeVries et al., 1997; Fermon et al., 2003; Vlasanek et al., 2013). In the present case, besides all advantages related to the method (see Freitas et al., 2014), the use of bait traps allows to verify the species movements between strata (canopy and understory), since the canopy can hardly be accessed otherwise. The sample design follows DeVries (1999), modified after Ribeiro and Freitas (2012). In each habitat, three transects 250 m long were randomly placed but with the conditions that the transect were at least 1 km apart. At each transect (sampling unit) we placed 10 portable traps (Van Someren-Rydon - VSR) spaced every 25 m and baited with a mix of banana and sugar cane juice at a ratio 3:1, fermented for 48 hours. The traps were placed alternate at 1.5 m above the ground level to sample the understory and 1 - 3 m below the canopy surface (i.e. interface between the uppermost layer of leaves and the atmosphere; Basset et al., 2003) to sample the canopy. Sampling was done monthly from August 2015 to July 2016 (n = 12 months). Every month at each transect traps remaining open for four consecutive days with

revisions and bait refreshment every 48 hours totaling 4,320 trap-days (10 traps \times 3 transects \times 3 habitats \times 4 sampling days \times 12 months).

All captured butterflies were marked with a sequential number on the right posterior wing with a permanent marker to avoid recaptures overestimating butterfly abundance and released to monitor the individual movements among strata and habitats (Fig. 1). Individual characteristics of each individual (age, sex, point of capture) were recorded and the butterflies already marked were recorded as recapture. Recapture rates were calculated by removing all individuals that died in the trap and were taken to the lab, as were individuals not identified in the field (n = 5,958; 51.4%). For every species captured, whenever possible, three individuals were pinned and deposited at the zoology museum of the Universidade Estadual de Campinas, São Paulo, Brazil (ZUEC) and the Laboratório de Ecologia Evolutiva de Insetos de Dossel e Sucessão Natural, of the Universidade Federal de Ouro Preto, Minas Gerais, Brazil. Permits for the field studies were issued by the state authority Instituto Estadual de Florestas (IEF) and the national authority Sistema de Autorização e Informação em Biodiversidade/ Instituto Chico Mendes de Conservação da Biodiversidade (SISBIO/ ICMBio).



Fig. 1 Marking butterflies with a sequential number on the right posterior wing with a permanent marker, Rio Doce State Park, Brazil. A – *Hamadryas amphinome*, B – *H. laodamia*, C – *Paulogramma pygas*.

Data analyses

The present study was carried out with the species that showed more than 3% of recapture success. Age structure was based on wing wear, based on three categories (new, intermediate and old; as in Ramos and Freitas, 1999). Individual permanence time (survival) in population (equals maximum permanence, an indirect measure of longevity) was calculated as

days elapsed between marking and last recapture and the mean was calculated to indicate the

species permanence mean (following Brussard et al., 1974). Due to the low number of individuals for age structure and permanence males and females were analyzed together.

Although the captures were carried out in both canopy and understory, the distances traveled in meters (m) were calculated based on the vertical and horizontal vector, considering the distances traveled among traps and including recaptures in the same day. The maximum distance (m) recorded was calculated as maximum distance traveled by each individual and the mean distance was calculated as mean distance traveled by total individuals per species and for each sex. To test if there was difference between the distances traveled (m), by sex in each species, the T-test was used. To analyze the butterfly movments among strata, transects and habitats were considered the multiple recapture of the same individual. To test whether there was a difference in the recapture numbers of fruit-feeding butterflies among habitats the G-test was used.

Results

A total of 11,594 individuals from 98 fruit-feeding butterfly species were captured in the three habitats (forest interior, ecotone and edge), 411 of which were recaptured at least once. Only six species were analyzed, representing those with more than 3% of recapture success (in order of recapture rate, *Hamadryas feronia*, *H. amphinome*, *Paulogramma pygas*, *H. laodamia*, *Fountainea ryphea* and *Taygetis rufomarginata*) totaling 335 individuals (Tab. 1). The sex ratio of captured individuals was male biased for these six species analyzed, with males dominating in all months (Fig. 2, Tab. 1).

Table 1 Fruit-feeding butterfly species (male/female) with more the 3% of recapture, Rio Doce

 State Park, Brazil.

Subfamilies	N° ind (Male/Female)	Total recapture (Male/Female)	% recapture
BIBLIDINAE			
Hamadryas			
amphinome	1125 (767/358)	103 (77/26)	10.7
Hamadryas feronia	679 (427/252)	114 (72/42)	22.6
Hamadryas laodamia	538 (339/199)	29 (18/11)	7.6
Paulogramma pygas	305 (166/139)	20 (10/10)	7.5



Fig. 2 Sex ratio for species over the months, Rio Doce State Park, Brazil. Males (dark grey) and females (light grey).

The age structure of the six species studied showed an increase in recruitment between August-September and a noticeable aging of the population in November-December, followed by a subtle increase in January and a relatively constant age structure in the following months (Fig. 3). The maximum individual permanence (survival) was of 151 days for one *H*. *amphinome* individual (mean \pm SD: 21 \pm 33.1 days, n = 103), followed by 92 days for one *H*.

feronia individual (mean \pm SD: 13.2 \pm 17.3 days, n = 114), 60 days for one *P. pygas* individual (mean \pm SD: 10.3 \pm 19.9 days, n = 20), 57 days for two *H. laodamia* individuals (mean \pm SD: 9.7 \pm 15.9 days, n = 29), 34 days for two *T. rufomarginata* individuals (mean \pm SD: 5.8 \pm 8.9 days, n = 31), and only 3 days for 28 *F. ryphea* individuals (mean \pm SD: 2.7 \pm 0.7 days, n = 38).



Fig. 3 Age structure for species over the months, Rio Doce State Park, Brazil. Categories: new individuals (black), intermediate individuals (dark grey) and old individuals (light grey).

Few individuals traveled long distances and most individuals were recaptured in the same site, often using the same trap or a trap few meters away from where it was first captured (Fig. 4, Appendix 12 Tab. 2). *Hamadryas feronia* was the only species that traveled more than 4 km away (4,678 m for a male and 4,747 m for a female), from an edge to an ecotone site. The maximum distance traveled by *H. amphinome* was 1,253 m for a male and 925 m for a female,

followed by *P. pygas* (200 m for a male and 50 m for three females), *F. ryphea* (157 m for a male and 175 m for a female), *T. rufomarginata* (100 m for two male and a female) and *H. laodamia* (75 m for three male and 50 m for five female) (Appendix 12 Tab. 2). There was no difference between the mean distance traveled by sexes for six species studied. In addition, it is noted that most individuals of all species analyzed were recaptured in the same trap of the first capture (*H. feronia* 50 individuals, 43.9%; *H. amphinome* 50 individuals, 48.5%; *H. laodamia* 15 individuals, 51.7%; *P. pygas* 13 individuals, 61.9%; *F. ryphea* 19 individuals, 50%; *T. rufomarginata* 14 individuals, 45.2%) (Fig. 4, Appendix 13 Tab. 3).



Fig. 4 Distances traveled (m) for species, Rio Doce State Park, Brazil. Total of individuals (black), males (dark grey) and females (white).

Most recaptures were in the same strata for all habitats studied (forest interior = 68 individuals - 80%, ecotone = 143 individuals - 72.6%, edge = 80 individuals - 72.7%; Fig. 5).

The number of individuals recaptured at least once in the ecotone (205 individuals, 9.47% of total) was higher than in the interior (90 individuals, 5.73% of total) and in the edge (116 individuals, 6.3% of total) (G-test = 22.9, p < 00001, df = 2). Movements among habitats were low than movements between strata, considering all species only five individuals captured in the interior changed habitat (three individuals were recaptured in the ecotone and two in the edge), eight in the ecotone (five individuals recaptured in the forest interior and three in the edge) and six in the edge (one individual recaptured in the forest interior and five in the ecotone). Movements among different transects of the same habitat did not occur.



Fig. 5 Total individuals number recaptured per habitat and movement description within each habitat, among habitats and between strata (canopy, understory), Rio Doce State Park, Brazil. Movements between the same strata – SS and movements between the different strata – DS.

Discussion

The permanence time of butterfly individuals can be determined by vegetation structure, host plants, microclimatic conditions and the best season for both high resource availability and low

enemy pressure (Beirão et al., 2017; Ribeiro et al., 2008; Ribeiro and Freitas, 2011; Saunders et al., 1991; Uehara-Prado et al., 2007). All these factors can also determine how much a species will move in the landscape (Baker, 1984; Fermon et al., 2003). In the present study, most individuals of all species analyzed were recaptured in the same trap from where it was first captured or a few meters away, showing that few individuals are moving through long distances (Fig. 4, Appendix 12 Tab. 2). Also, the present study detected no differences between sexes in the average distances traveled, a patter previously detected for many butterfly species both, nectar and fruit feeding (Beirão et al., 2012; Fermon et al., 2003; Legrand et al., 2015; Ramos and Freitas, 2009; Reim et al., 2018; Scott, 1975; Turlure et al., 2011). This suggests that the habitats are providing the necessary conditions for the maintenance of butterfly populations,

favoring lower movements and narrow home ranges for both sexes, and suggests that the same dispersal ability between the sexes. However, the existence of intrinsic barriers within each habitat cannot be discarded, and these could be also involved in the maintenance of the narrow home ranges here reported, besides the high dispersal potential of several species (e.g. *F. ryphea* and *P. pygas*, both strong flyers) (see also Ehrlich, 1961).

Forest fragmentation drives habitat modification, changing resources distribution and availability, thus affecting the behavior in butterflies that will have to move more in search of resources (Baker, 1984; Fermon et al., 2003). The comparison of movement parameters between different management sites reveals larger mean movement within the crops, compared to control forest (Fermon et al., 2003), so increase the recapture chance in natural sites. In the present study, the recaptures were more frequent in the natural ecotone, resulting in small movements of individuals. Consequently, individual permanence may have been favored by the eco-physiological conditions in the ecotone, such as the habitat more shaded and humid than anthropic edge, due a complex vegetation physiognomy, where the trees grow leaning toward the open habitat (see Chapter 1). In addition, the ecotone is warmer than the forest interior throughout the year (see Chapter 2), presenting the optimal conditions for the individual permanence. On the other hand, movements in the same strata and between strata were recorded for all habitats studied. However, movement among habitats was small, most individuals remained where they were, so that those individuals who have made such large movements show that the species is able to disperse, but most individuals choose to stay.

The observed male biased sex ratios, with males dominating in all months, are commonly reported in population studies of nectar feeding butterflies (Gilbert and Singer, 1975; Ehrlich, 1984; Tyler et al., 1994), and this is attributed to the behavioral differences between

sexes (Beirão et al., 2012; Ramos and Freitas, 1999; Reim et al., 2018). Females are generally less recaptured because they need to move more than males to find host plants, spread strategically their eggs, found new populations and may need to escape from male harassment (Hill et al., 1999; Hanski et al., 2004; Reim et al., 2018; Trochet et al., 2013). Curiously, some few studies with fruit feeding butterflies reported non-male biased sex ratios (e.g. Uehara-Prado et al., 2005). The alleged reasons were that by using a food resource attractive to both sexes and a sampling method independent of collector efficiency, this sampling bias could be minimized. Nonetheless, more mark-recapture studies are necessary to a better understanding of this pattern.

The reported increase of recruitment of adults in the end of the dry season (August-September) precedes the peak in the production of fleshy fruits (one of the main resources for the adults; DeVries, 1987) that will increase through the wet season (Morellato et al., 2000). In addition, after September, there was an increase in average temperatures, one of the main predictors of abundance and species richness for taxonomically broad communities, both of plants and animals (Peters et al., 2016; Wolda, 1988). For example, with the same data-set (see Chapter 2), detected a positive effect of temperature on abundance and species richness in all habitats, as pattern previously reported by other studies with fruit-feeding butterflies (Grøtan et al., 2012; Ribeiro and Freitas, 2010; Ribeiro et al., 2010; Santos et al., 2017). High temperatures observed in PERD during practically the whole year can also be associated with the relatively constant age structure during the year. Therefore, despite the gradual aging of the population observed in some months (wet season), the monthly temperature favors the constant birth of individuals throughout the year.

In view of these, the conservation of a set of heterogeneous habitats is even more important for the maintenance of populations, both of those sedentary butterflies and of those that move large distances with potential for colonization new or vacant patches. A better understanding of species ecologies and of the processes that drive population changes is important and makes it possible to restore suitable conditions, since conservation of plant diversity alone is not enough to conserve the butterfly assemblages (Thomas, 2016).

Conclusão Geral

O presente estudo mostrou como as borboletas frugívoras estão distribuídas ao longo do espaço e do tempo em diferentes habitats: interior da floresta, transição natural (ecótono) e transição antrópica (borda). Nossos resultados do Capítulo 1 demonstraram que os ecótonos são distintos das bordas antrópicas. O dossel inclinado dos ecótonos resulta em condições ecofisiológicas distintas do interior da floresta e da borda. Essas condições ecofisiológicas tornam os ecótonos capazes de acomodar espécies adaptadas a distintos habitats, reunindo uma combinação de borboletas frugívoras do interior da floresta, mas também da borda antrópica. Ou seja, o ecótono conserva algumas características comuns com a borda antrópica, apresentando maior riqueza e diversidade de espécies de borboletas frugívoras do que o interior da floresta, como consequência. Ainda assim, a composição e a dominância de borboletas frugívoras observadas no ecótono são similares ao interior da floresta nos dois estratos verticais, reforçando o quanto as transições naturais são únicas e distintas das transições artificiais.

Nossos resultados do Capítulo 2 demonstram como as diferenças e similaridades observadas em cada habitat no Capítulo 1 variam ao longo do ano. Verificamos uma distribuição não uniforme em todos os habitats estudados, com maior abundância, riqueza e beta diversidade no verão, a estação quente e úmida. A abundância de borboletas frugívoras aumenta com elevação da temperatura em todos os habitats. Para riqueza de borboletas, no entanto, esse efeito do aumento da temperatura só pode ser observado no interior da floresta. Embora a beta diversidade de borboletas frugívoras flutue mensalmente de modo similar nos três habitats, em geral as transições (ecótono e borda) foram mais ricas e abundantes do que o interior da floresta durante todo o ano (mantendo o padrão observado no Capítulo 1). As contribuições dos processos de turnover e aninhamento mudam ao longo dos meses, sobrepondo em todos os habitats com as mudanças sazonais. Entretanto, os resultados mostram que as transições são mais variáveis do que o interior da floresta ao longo do ano. Logo, a manutenção das populações nos habitats de transição tende a ser mais difícil, podendo ocorrer extinções em alguns meses e recolonizações em outros. Conhecer como as taxas de turnover variam ao longo do tempo em diferentes habitats pode nos ajudar a entender a sensibilidade dos sistemas ecológicos as mudanças ambientais e climáticas.

No Capítulo 3 analisamos os dados de recaptura de seis espécies (com recaptura acima de 3%), descrevendo a movimentação delas na paisagem assim como suas características biológicas. A razão sexual foi deslocada para machos em todos os meses, o que pode ser

resultado de diferenças comportamentais entre os sexos. O aumento do recrutamento de indivíduos no final da estação seca indica que novos indivíduos nascem para a estação de maior disponibilidade de recursos (estação chuvosa), porém a estrutura etária foi relativamente constante durante todo o ano. A movimentação das espécies na paisagem confirma o padrão encontrado para outras espécies, com poucos indivíduos percorrendo longas distâncias, a maioria foi recapturado no mesmo local ou a poucos metros de onde foi capturado pela primeira vez. As recapturas foram mais frequentes no ecótono, o que demonstra que possivelmente as condições ecofisiológicas do ecótono favorecem a permanência dos indivíduos.

Os resultados obtidos nos três capítulos nos permitem concluir que os ecótonos são habitats únicos capazes de acomodar espécies adaptadas a condições ecológicas distintas. Sendo um habitat que recebe espécies do interior da floresta e da borda, funcionando como uma mescla dos dois habitats ao longo do ano, já que compartilha propriedades de ambos, porém não é igual a nenhum. Desse modo, as características do ecótono o fazem um habitat chave em termos de diversidade e heterogeneidade da comunidade, favorecendo a permanência de diferentes espécies ao longo de todo ano. Ao extrapolamos para toda região, considerando toda a extensão de ocorrência de ecótonos ao longo da Bacia do Rio Doce por exemplo, podemos ter uma noção do quanto temos de região biodiversa. Os ecótonos vem sendo negligenciados em vista da urgência de se estudar as bordas antrópicas. Dessa maneira, a tese ressalta o papel dos ecótonos na conservação da biodiversidade local e regional, e a importância de entendermos como funcionam esses sistemas naturais que representam um oásis para diferentes espécies ao longo do ano.

Os padrões encontrados nos ecótonos com lagos podem ser replicados em outros ecótonos naturais, tais como: transições com rios (matas ciliares), dunas (arbustos xéricos) e pradarias (savanas rochosas), que também podem sustentar espécies únicas e serem um componente importante da heterogeneidade da comunidade. Desse modo, o próximo passo é investigar se os padrões encontrados aqui se repetem em outros ecótonos naturais. Mais estudos são necessários para definir o quão diferente qualquer ecótono pode ser das fronteiras artificiais do ecossistema e como eles são essenciais para a conservação da diversidade em cada cenário.

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Apêndices



Appendix 1 Fig. Exclusive and shared butterfly species between strata per habitats, Rio Doce State Park, Brazil.



Appendix 2 Fig. Abundance of fruit-feeding butterfly species per habitats (above) and strata (below), Rio Doce State Park, Brazil. The lines represent the first and four quartiles, the box represents the second and first quartiles and the line within the box represents the median. Different letters above boxplot indicate significant differences based on Tukey tests. The points outside of the boxplot represent atypical data.



Appendix 3 Fig. Abundance for subfamilies and tribes fruit-feeding butterfly species for habitats (left) and strata (right), Rio Doce State Park, Brazil. The lines represent the first and four quartiles, the box represents the second and first quartiles and the line within the box represents the median. Different letters above boxplot indicate significant differences based on Tukey tests. The points outside of the boxplot represent atypical data.



Appendix 4 Fig. Abundance of Nymphalinae subfamily fruit-feeding butterfly species that presented interaction among habitats and strata, Rio Doce State Park, Brazil. The lines represent the first and four quartiles, the box represents the second and first quartiles and the line within the box represents the median. Different letters above boxplot indicate significant differences based on Tukey tests. The colour represents the strata: light grey canopy and dark grey understory.



Appendix 5 Fig. Hill's diversity (q0 diversity – Species richness, q1 diversity – Shannon Diversity, q2 diversity – Simpson Diversity) of fruit-feeding butterflies associated with the habitats and strata in Rio Doce State Park, Brazil. Bars represent the standard error – SE.



Appendix 6 Fig. Spatial partitioning of fruit-feeding butterfly diversity in Rio Doce State Park, Brazil. Observed and expected diversity across multiple scales: $\alpha 1$ (black) = diversity within transects (set of five traps for each stratum); $\beta 1$ (dark grey) = difference of diversity among transects of the same stratum and habitat; $\beta 2$ (grey) = difference of diversity between strata of the same habitat; and $\beta 3$ (light grey) = difference of diversity among habitats.



Appendix 7 Fig. Cluster analyses of the fruit-feeding butterfly assemblages (Bray-Curtis similarity, Cluster method: average), Rio Doce State Park, Brazil. The numbers above the branch represent the p-values: left number is the approximately unbiased (AU) and right number is bootstrap probability (BP). The numbers below the branch represent the grouping sequence of Cluster analyses.

		For	est Interio	or		F	Ecotone				Edge		
Subfamilies/Tribes	С	U	G-test	p*	С	U	G-test	p*	С	U	G-test	p*	Total
BIBLIDINAE	710	667			797	1132			1062	971			5339
Biblis hyperia	0	0			0	0			1	2			3
Callicore astarte	98	37	28.59	< 0.0001	42	33	1.08	0.2981	132	56	31.62	< 0.0001	398
Callicore sorana	0	0			1	0			7	2			10
Callicore texa	1	0			1	1			2	0			5
Catonephele acontius	4	9	1.97	0.1601	2	7	1.73	0.1879	1	7			30
Catonephele numilia	12	4	4.19	0.0408	19	28			26	8	10.03	0.0015	97
Diaethria clymena	10	1	8.55	0.0035	66	14	36.71	< 0.0001	13	6	2.64	0.1042	110
Ectima thecla	0	0			0	1			0	0			1
<i>Epiphile</i> sp.	0	0			1	0			0	0			1
Eunica eurota	1	0			0	0			0	0			1
Eunica maja	3	14	7.72	0.0055	14	28			4	13	5.02	0.0255	76
Eunica malvina	2	3			9	3			3	0			20
Eunica mygdonia	1	0			2	0			4	1			8
Eunica tatila	1	0			3	0			1	0			5
Haemathera pyrame	0	0			0	0			1	0			1
Hamadryas amphinome	224	182	4.35	0.0370	122	158	4.35	0.0370	219	259	3.35	0.0672	1164
Hamadryas arete	49	19	13.70	0.0002	13	11	13.70	0.0002	42	23	5.64	0.0176	157
Hamadryas chloe	0	1			1	22	23.66	< 0.0001	0	19			43
Hamadryas epinome	110	208	30.70	0.0001	64	225	95.03	< 0.0001	81	262	100.53	< 0.0001	950
Hamadryas februa	0	8			7	29	14.44	0.0001	5	4			53
Hamadryas feronia	29	64	13.50	0.0002	212	271	7.23	0.0072	61	57	0.14	0.7127	694
Hamadryas iphthime	6	1			3	1			1	2			14
Hamadryas laodamia	51	66	1.93	0.1649	94	121	3.40	0.0652	93	114	2.13	0.1441	539
Myscelia orsis	4	26	18.03	< 0.0001	6	101	102.10	< 0.0001	2	49	53.83	< 0.0001	188
Nica flavilla	1	6			8	27	10.89	0.0010	14	40	13.05	0.0003	96
Paulogramma pygas	46	7	32.10	< 0.0001	44	15	14.89	0.0001	178	26	127.15	< 0.0001	316
Pyrrhogyra neaeria	0	0			0	0			2	0			2
Temenis huebneri	30	4	22.50	< 0.0001	37	19	5.89	0.0152	98	8	90.22	< 0.0001	196
Temenis laothoe	27	7	12.56	0.0004	26	17	1.90	0.1683	71	13	44.06	< 0.0001	161

Appendix 8 Table 3. List of the fruit-feeding butterfly species recorded in Rio Doce State Park, state of Minas Gerais, Brazil.

		For	est Interio	or		ŀ	Cotone				Edge		T - 4 - 1
Subfamilies/ 1 ribes	С	U	G-test	p*	С	U	G-test	p *	С	U	G-test	p *	Total
CHARAXINAE	496	337			425	453			505	279			2495
Archaeoprepona amphimachus	2	5			0	5			5	10	1.70	0.1924	27
Archaeoprepona demophon	6	17	5.48	0.0192	15	27	3.48	0.0622	30	47	3.78	0.0517	142
Archaeoprepona demophoon	5	5			7	4	0.83	0.3627	14	6	3.29	0.0696	41
Archaeoprepona meander	0	1			0	1			0	0			2
Fountainea glycerium cratais	1	0			1	0			0	0			2
Fountainea ryphea	202	164	3.95	0.0468	185	187	0.01	0.9174	86	59	5.06	0.0245	883
Hypna clytemnestra	1	11	9.75	0.0018	4	39	33.00	< 0.0001	0	5			60
Memphis acidalia	15	21	1.01	0.3162	37	43	0.45	0.5021	33	43	1.32	0.2507	192
Memphis moruus	63	29	12.87	0.0003	59	64	0.20	0.6521	127	58	26.37	< 0.0001	400
Memphis xenocles	47	6	36.04	< 0.0001	24	7	9.86	0.0017	56	5	49.97	< 0.0001	145
Agrias claudina	4	0			2	0			0	1			7
Prepona dexamenus	1	0			1	0			1	0			3
Prepona eugenes	2	0			1	1			7	0			11
Prepona laertes	4	2			7	7			8	0			28
Prepona pseudomphale	8	2	3.86	0.0496	12	3	5.78	0.0162	6	0			31
Prepona sp.	1	0			0	0			0	0			1
Siderone galanthis	23	1	24.96	< 0.0001	16	1	15.96	< 0.0001	37	4	30.62	< 0.0001	82
Zaretis strigosus	111	73	7.91	0.0049	54	64	0.85	0.3570	95	41	22.04	< 0.0001	438
NYMPHALINAE	14	14			11	25			28	18			110
Colobura dirce	2	9	4.82	0.0282	1	16	15.96	< 0.0001	1	16	15.96	< 0.0001	45
Historis acheronta	5	2			7	2			10	0			26
Historis odius	7	3	1.65	0.1996	3	7	1.65	0.1996	17	2	13.55	0.0002	39
SATYRINAE	188	725			354	1124			306	953			3650
Brassolini	12	65			24	105			21	60			287
Caligo brasiliensis	0	0			0	2			1	6			9
Caligo illioneus	0	5			4	29	21.37	< 0.0001	0	15			53
Catoblepia amphirhoe	0	2			2	2			1	3			10
Catoblepia berecynthia	1	2			0	3			1	9	7.36	0.0067	16
Eryphanis automedon	6	52	41.82	< 0.0001	8	64	49.58	< 0.0001	1	12	10.97	0.0009	143

		For	est Interio	or		J	Ecotone				Edge		
Subfamilies/Tribes	С	U	G-test	p*	С	U	G-test	p*	С	U	G-test	p*	Total
Opoptera aorsa	0	0			0	0			0	1			1
Opsiphanes cassiae	0	0			1	1			0	0			2
Opsiphanes invirae	5	4			7	4	0.83	0.3627	15	13	0.14	0.7053	48
Opsiphanes quiteria	0	0			2	0			2	1			5
Haeterini	0	1			0	0			0	0			1
Pierella lamia	0	1			0	0			0	0			1
Morphini	2	84			6	93			1	108			294
Antirrhea archaea	0	2			0	0			0	0			2
Morpho helenor	2	82	97.55	< 0.0001	6	93	91.97	< 0.0001	1	108	139.73	< 0.0001	292
Satyrini	174	575			324	926			284	785			3068
Archeuptychia cluena	1	16	15.96	< 0.0001	0	3			0	6			26
Caeruleuptychia brixius	5	8	0.70	0.4033	0	0			0	2			15
Caeruleuptychia sp.1	12	1	10.97	0.0009	13	7	1.83	0.1764	1	0			34
Caeruleuptychia sp.3	0	0			0	0			1	0			1
Chloreuptychia arnaca	0	4			0	1			0	19			24
Chloreuptychia herseis	0	3			1	2			0	4			10
Cissia eous	1	0			2	4			3	40	37.85	< 0.0001	50
Cissia myncea	3	1			15	24	2.10	0.1477	101	64	8.37	0.0038	208
Cissia phronius	0	1			0	7			6	39	27.04	< 0.0001	53
Euptychoides castrensis	0	0			1	0			0	1			2
Hermeuptychia sp.	2	0			4	4			6	3			19
Magneuptychia lea	0	0			0	1			0	0			1
Magneuptychia libye	0	0			3	0			0	0			3
Magneuptychia sp.2	0	0			0	1			0	0			1
Pareuptychia ocirrhoe	1	5			9	58	40.01	< 0.0001	11	94	75.12	< 0.0001	178
Pareuptychia summandosa	0	1			10	35	14.71	0.0001	5	70	67.23	< 0.0001	121
Paryphthimoides grimon	0	0			5	1			0	2			8
Paryphthimoides poltys	2	2			5	13	3.68	0.0550	11	20	2.65	0.1035	53
Paryphthimoides sp.2	0	0			0	1			1	0			2
Pharneuptychia sp.1	0	1			1	2			3	5			12
Pseudodebis celia	0	0			1	0			59	112	16.70	< 0.0001	172
Pseudodebis euptychidia	0	16			0	28			7	59	46.85	< 0.0001	110

Subfomilios/Tribos		Fore	est Interio	or		F	Ecotone				Edge		Total
Sublammes/1 fibes	С	U	G-test	p *	С	U	G-test	p *	С	U	G-test	p*	Total
Satyrinae	0	1			4	0			2	2			9
Splendeuptychia doxes	4	3			8	8			3	1			27
Taygetina kerea	0	4			0	1			0	0			5
Taygetis fulginia	0	0			0	0			0	1			1
Taygetis laches	0	9			8	69	55.38	< 0.0001	1	69	86.56	< 0.0001	156
Taygetis leuctra	1	5			1	3			0	0			10
Taygetis mermeria	2	2			3	11	4.86	0.0275	2	14	10.12	0.0015	34
Taygetis rufomarginata	132	395	137.33	< 0.0001	218	543	143.36	< 0.0001	41	76	10.63	0.0011	1405
Taygetis sosis	3	88	99.78	< 0.0001	1	75	94.71	< 0.0001	1	24	26.26	< 0.0001	192
Taygetis virgilia	0	5			0	10			2	34	34.46	< 0.0001	51
Yphthimoides affinis	0	2			2	11	6.86	0.0088	7	22	8.15	0.0043	44
Yphthimoides renata	3	1			5	3			9	2	4.82	0.0282	23
Zischkaia pacarus	0	1			2	0			1	0			4
Zischkaia saundersii	2	0			2	0			0	0			4
Total of individuals	1408	1743			1587	2734			1901	2221			11594

C, samples in canopy; U, samples in understory. Bold numbers represent significant p values (after Bonferroni's correction). * Corrected critical p-value: Forest Interior = 0.002, Ecotone = 0.001, Edge = 0.001.

Appendix 9 Table 1 Fruit-feeding butterflies species recorded in the wet season in each habitat (forest interior, ecotone, edge), Rio Doce State Park, state of Minas Gerais, Brazil. Some species absent in these months (wet season) were maintained here because this continues in the following table.

	0	ctober-	-15	No	vembei	-15	De	cember	-15	Ja	nuary-	-16	Fe	bruary	-16	N	/larch-1	6		April-1	6
Subfamilies/Tribes	F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge												
BIBLIDINAE																					
Biblis hyperia	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Callicore astarte	28	13	53	18	10	36	2	0	2	9	6	16	5	7	7	10	10	12	23	12	24
Callicore sorana	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Callicore texa	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Catonephele acontius	2	3	0	0	2	0	0	0	1	1	0	2	1	0	0	2	0	1	2	0	2
Catonephele numilia	2	8	4	1	9	6	0	2	0	3	1	1	1	1	1	0	4	4	2	1	0
Diaethria clymena	1	7	5	0	1	0	0	0	0	0	0	0	0	2	0	0	2	0	0	6	0
Ectima thecla	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Epiphile</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eunica eurota	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eunica maja	1	1	0	3	2	1	0	0	0	0	2	0	3	15	7	0	4	1	3	1	0
Eunica malvina	1	4	1	1	0	0	2	2	1	0	1	0	0	1	0	0	0	0	0	1	0
Eunica mygdonia	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Eunica tatila	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haemathera pyrame	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hamadryas amphinome	26	19	36	35	17	42	16	5	16	79	43	98	41	40	108	53	58	71	71	61	51
Hamadryas arete	24	2	15	13	2	14	2	0	2	3	6	10	4	3	7	4	2	6	4	1	3
Hamadryas chloe	0	7	2	1	8	2	0	1	3	0	3	2	0	3	2	0	0	3	0	0	0
Hamadryas epinome	51	34	51	65	60	48	67	23	40	47	37	38	24	56	77	11	34	37	27	21	18
Hamadryas februa	1	0	0	1	1	0	1	2	2	0	3	2	2	7	0	1	4	2	2	10	2
Hamadryas feronia	16	43	8	19	56	16	4	21	11	3	48	14	9	78	20	8	71	14	16	70	16
Hamadryas iphthime	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hamadryas laodamia	30	40	17	35	22	41	3	10	3	14	29	34	0	12	29	4	37	26	12	30	16
Myscelia orsis	8	32	5	4	7	3	1	1	1	3	0	0	2	1	0	1	2	7	2	2	2
Nica flavilla	1	5	4	1	1	7	0	0	0	0	1	0	0	1	4	0	3	5	0	0	2
Paulogramma pygas	2	3	8	1	0	2	0	0	1	13	12	33	3	3	35	9	22	50	16	9	49
Pyrrhogyra neaeria	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Temenis huebneri	4	5	15	8	9	14	0	1	2	1	1	9	2	7	13	1	1	6	0	2	11
Temenis laothoe	3	4	10	9	7	13	1	2	4	0	1	6	0	1	16	0	3	5	1	4	7
CHARAXINAE																					
Archaeoprepona amphimachus	0	2	4	2	1	5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0

	0	ctober-	15	No	vember	-15	De	cember	-15	Ja	anuary-	16	Fe	bruary	-16	N	/larch-1	6	1	April-1(6
Subfamilies/Tribes	F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge												
Archaeoprepona demophon	5	7	20	5	6	12	0	0	2	2	0	5	0	0	2	1	1	1	1	11	9
Archaeoprepona demophoon	3	2	4	2	6	6	0	0	0	0	0	0	0	0	2	0	1	0	0	0	1
Archaeoprepona meander	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fountainea glycerium cratais	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Fountainea ryphea	19	30	11	51	48	21	2	10	1	44	39	13	35	42	8	51	68	22	52	39	30
Hypna clytemnestra	2	5	1	0	6	1	3	2	0	0	2	0	1	3	1	2	4	0	1	6	2
Memphis acidalia	8	8	9	12	35	35	0	1	4	1	3	1	1	8	7	2	1	3	3	1	4
Memphis moruus	13	25	19	11	19	28	0	1	2	5	2	4	8	10	40	1	8	9	10	17	18
Memphis xenocles	5	6	6	6	1	0	2	0	0	0	3	3	0	0	0	2	1	4	6	2	11
Prepona claudina	1	0	0	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prepona dexamenus	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prepona eugenes	1	0	3	0	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Prepona laertes	2	3	0	0	7	3	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0
Prepona pseudomphale	1	1	1	5	3	1	1	0	0	1	2	0	0	3	0	1	1	1	1	1	1
Prepona sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Siderone galanthis	6	7	9	6	5	9	2	0	0	1	1	5	1	0	5	0	0	4	1	1	3
Zaretis strigosus	34	25	20	63	56	38	2	3	0	8	1	9	4	3	7	1	0	4	18	8	22
NYMPHALINAE																		-			
Colobura dirce	1	2	0	0	3	3	0	1	0	2	1	0	0	1	2	3	2	3	3	5	2
Historis acheronta	0	0	0	0	3	2	1	1	0	1	0	4	2	1	1	0	0	1	0	1	1
Historis odius	3	3	1	3	0	2	0	1	0	0	1	0	0	0	3	1	2	0	0	1	4
SATYRINAE																					
Brassolini																					
Caligo brasiliensis	0	0	3	0	2	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Caligo illioneus	2	5	6	2	7	1	0	2	0	0	0	0	0	8	5	0	1	0	0	3	1
Catoblepia amphirhoe	0	0	0	0	0	0	0	0	0	0	0	0	2	4	4	0	0	0	0	0	0
Catoblepia berecynthia	1	0	1	0	2	6	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0
Eryphanis automedon	7	10	3	15	21	5	2	4	0	2	1	0	6	5	1	4	5	0	6	8	0
Opoptera aorsa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opsiphanes cassiae	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opsiphanes invirae	1	3	1	1	0	2	0	0	2	1	4	6	1	0	0	0	0	4	4	4	9
Opsiphanes quiteria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	1
Haeterini																					
Pierella lamia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Morphini																					
Antirrhea archaea	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Morpho helenor	9	3	12	48	74	66	3	3	4	0	0	0	2	1	1	3	3	4	14	12	21
Satyrini																					

	0	ctober-	15	No	vember	-15	De	cember	-15	Ja	anuary	-16	Fe	bruary	-16	N	/larch-1	6	1	April-1	6
Subfamilies/Tribes	F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge												
Archeuptychia cluena	3	1	3	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Caeruleuptychia brixius	5	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Caeruleuptychia sp.1	4	6	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caeruleuptychia sp.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chloreuptychia arnaca	4	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	2	0	0	2
Chloreuptychia herseis	1	0	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cissia eous	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	7
Cissia myncea	0	3	27	0	1	3	0	0	0	0	0	2	0	1	10	0	0	0	3	4	9
Cissia phronius	0	1	13	0	0	2	0	0	3	0	1	3	0	0	8	0	1	2	0	0	0
Euptychoides castrensis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hermeuptychia sp.	0	2	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1
Magneuptychia lea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Magneuptychia libye	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Magneuptychia sp.2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pareuptychia ocirrhoe	3	9	8	0	2	4	0	0	1	0	4	5	0	2	4	0	1	3	0	8	6
Pareuptychia summandosa	0	4	10	0	6	5	0	2	0	0	0	1	0	2	4	0	1	3	0	11	5
Parvphthimoides grimon	0	4	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Paryphthimoides poltys	1	1	4	2	0	3	0	0	0	0	1	1	0	1	0	0	1	1	0	2	6
Paryphthimoides sp.2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pharneuptychia sp.1	1	0	1	0	1	2	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0
Pseudodebis celia	0	1	15	0	0	6	0	0	0	0	0	6	0	0	13	0	0	20	0	0	6
Pseudodebis euptychidia	2	5	13	3	9	8	0	1	3	0	1	8	2	5	1	0	1	8	1	0	4
Satvrinae	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Splendeuptychia doxes	3	12	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tavgetina kerea	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Tavgetis fulginia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taygetis laches	0	3	7	0	18	10	0	1	0	0	2	6	0	6	12	0	6	7	3	10	7
Taygetis leuctra	0	1	0	1	2	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0
Tavgetis mermeria	1	3	5	1	6	5	0	2	0	0	1	1	1	0	3	0	0	0	0	0	1
Tavgetis rufomarginata	52	79	32	51	165	7	7	12	0	19	21	2	89	126	29	27	17	0	50	92	5
Tavgetis sosis	8	5	4	9	25	5	2	6	2	1	4	2	20	19	4	7	0	0	15	11	4
Tavgetis virgilia	2	3	4	1	2	1	0	0	1	0	1	1	1	0	8	0	0	5	0	1	
Yphthimoides affinis	0	0	8	0	2	6	0	0	0	0	0	0	0	1	1	0	0	0	1	1	5
Yphthimoides renata	1	4	5	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2
Zischkaia pacarus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Zischkaia saundersii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Total of individuals	417	533	544	528	768	569	127	123	116	266	291	358	278	494	521	211	388	363	379	497	421

Appendix 10 Table 2 Fruit-feeding butterflies species recorded in the dry season in each habitat (forest interior, ecotone, edge), Rio Doce State Park, state of Minas Gerais, Brazil. Note that due to the temporal window of the study the dry season was broken between the end of dry season of 2015 and the early of dry season of 2016. Some species absent in these months (dry season) were maintained here because this is a continuity of previous table.

	А	ugust-1	15	Sep	otember	-15	\\		May-16	ó		June-16	i		July-16	i
Subfamilies/Tribes	F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge		F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge
BIBLIDINAE																
Biblis hyperia	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Callicore astarte	21	8	21	6	4	5		5	4	9	8	1	1	0	0	2
Callicore sorana	0	0	0	0	0	9		0	0	0	0	0	0	0	0	0
Callicore texa	0	0	0	0	0	0		0	1	0	0	1	0	0	0	1
Catonephele acontius	3	2	1	0	2	0		1	0	0	1	0	0	0	0	1
Catonephele numilia	3	8	8	1	3	4		1	4	2	1	1	4	1	5	0
Diaethria clymena	9	40	11	1	8	2		0	1	0	0	5	0	0	8	1
Ectima thecla	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
<i>Epiphile</i> sp.	0	1	0	0	0	0		0	0	0	0	0	0	0	0	0
Eunica eurota	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Eunica maja	0	0	0	0	0	0		1	5	2	0	3	1	6	9	5
Eunica malvina	0	0	1	0	1	0		0	0	0	0	0	0	1	2	0
Eunica mygdonia	0	1	0	0	0	0		0	0	1	0	0	1	0	0	0
Eunica tatila	0	0	0	0	0	0		0	1	1	0	1	0	0	1	0
Haemathera pyrame	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Hamadryas amphinome	18	7	6	8	3	10		23	3	16	7	9	3	29	15	21
Hamadryas arete	7	3	2	2	2	3		3	2	1	0	0	0	2	1	2
Hamadryas chloe	0	1	4	0	0	0		0	0	0	0	0	0	0	0	1
Hamadryas epinome	9	7	5	4	2	11		6	8	10	3	1	2	4	6	6
Hamadryas februa	0	0	0	0	0	0		0	5	0	0	3	1	0	1	0
Hamadryas feronia	7	40	2	4	11	2		3	21	5	0	7	2	4	17	8
Hamadryas iphthime	5	4	3	2	0	0		0	0	0	0	0	0	0	0	0
Hamadryas laodamia	11	19	19	3	2	6		2	5	6	2	3	0	1	6	10
Myscelia orsis	7	39	21	2	12	7		0	3	1	0	0	2	0	8	2
Nica flavilla	2	19	28	1	2	3		1	1	1	0	1	0	1	1	0
Paulogramma pygas	3	2	2	0	0	1		3	5	15	3	2	5	0	1	3
Pyrrhogyra neaeria	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Temenis huebneri	10	13	18	3	1	12		1	5	4	2	5	2	2	6	0
Temenis laothoe	10	9	13	3	2	3		2	2	4	2	2	1	3	6	2

	А	ugust-1	5	Sep	tember	-15	١١	1	May-16			June-16	i		July-16	
Subfamilies/Tribes	F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge		F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge
CHARAXINAE	0		1					1		0				1		0
Archaeoprepona amphimachus	1	0	2	2		4		1	1	0	1	0	1	1		
Archaeoprepona demophon	2	1	<u> </u>	1		o		1	1	9		2	1 2	4	3	/
Archaeoprepona aemophoon			2	1	1			0	0	1	0	0		1		0
Arcnaeoprepona meanaer	0	0	0	0	1	0		0	1	0	0	0	0	0	0	0
Fountainea glycerium cratais	25	40	10	20	15			40	1	5		11	0			0
Foundanea rypnea	35		19	0	15			49	20			11	0	4		0
Mamphia apidalia	1		2	4	כ ד	5		2		2	1	2	0	0		2
Memphis actaatta	1	9	10		11			3		12		2		0		
Memphis moruus	0	10	19	17	11			- 9	0 6	12		0	1	1		S
Prepong alguding	0		19	17	4			0	0	0	0	1	0	1		0
Propona dayamanus	0	0	0	0	0	0		0	0	0	0	0	0	0		0
Propona augonos	0	0	0	0	0	0		0	0	0	0	0	0	1	0	1
Prepona la artes	0	0	1	1	1	1		0	0	0	0	0	0	1 2		1
Prepona laeries	0	0	1	I	າ	1 		0	0	0	0	1	0	2	1	1
Prepona pseudompnate	0	0	0	0		1		0	0	0	0	0	0	0	0	0
Sidarana aglanthia	1	1	1		0			2	0	1	0	0	0	2		0
Suerone galaninis	1	2	0	27	0				5	5		1	0	2		0
	15		0	21					5	5		1	0		+	0
NYMPHALINAE					••••••	••••••			••••••				•••••			
Colobura dirce	1	1	4	0	0	1		1	1	1	0	0	1	0	0	0
Historis acheronta	1	0	0	0	1	0		0	1	0	1	0	0	1	1	1
Historis odius	0	2	2	0	0	3		1	0	3	0	0	0	2	0	1
SATYRINAE						•••••										
Brassolini			-							-		-				-
Caligo brasiliensis	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Caligo illioneus	0	0	0	1	3	1		0	2	1	0	0	0	0	2	0
Catoblepia amphirhoe	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Catoblepia berecynthia	0	0	0	1	0	0		0	0	0	0	1	0	0	0	0
Eryphanis automedon	0	2	0	3	1	1		2	4	0	6	6	2		5	1
Opoptera aorsa	0	0	0	0	0	1		0	0	0	0	0	0	0	0	0
Opsiphanes cassiae	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Opsiphanes invirae	0	0	0	0	0	3		0	0	1	1	0	0	0	0	0
Opsiphanes quiteria	0	0	0	0	0	0		0	0	0	0	0	1	0	0	0
Haeterini						•••••										
Pierella lamia	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Morphini																

	А	ugust-1	15	Sep	tember	·-15	١١		May-16	5		June-16	i		July-16	
Subfamilies/Tribes	F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge		F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge	F. Interior	Ecotone	Edge
Antirrhea archaea	1	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Morpho helenor	2	0	0	0	0	0		2	1	1	1	2	0	0	0	0
Satyrini																
Archeuptychia cluena	4	0	3	6	2	0		2	0	0	0	0	0	0	0	0
Caeruleuptychia brixius	1	0	0	1	0	0		1	0	0	0	0	0	3	0	0
Caeruleuptychia sp.1	3	2	0	4	8	1		0	1	0	0	0	0	0	1	0
Caeruleuptychia sp.3	0	0	0	0	0	0		0	0	1	0	0	0	0	0	0
Chloreuptychia arnaca	0	0	3	0	0	1		0	0	3	0	0	5	0	0	0
Chloreuptychia herseis	0	0	1	2	1	0		0	0	0	0	0	0	0	0	0
Cissia eous	0	2	8	0	0	18		0	1	4	0	1	0	0	1	3
Cissia myncea	0	10	39	1	4	21		0	2	20	0	3	16	0	11	18
Cissia phronius	1	4	9	0	0	2		0	0	0	0	0	1	0	0	2
Euptychoides castrensis	0	0	1	0	0	0		0	0	0	0	0	0	0	0	0
Hermeuptychia sp.	2	0	2	0	1	0		0	0	1	0	1	0	0	3	3
Magneuptychia lea	0	0	0	0	0	0		0	0	0	0	1	0	0	0	0
Magneuptychia libye	0	0	0	0	1	0		0	0	0	0	0	0	0	0	0
Magneuptychia sp.2	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Pareuptychia ocirrhoe	0	4	11	1	11	28		1	8	15	1	12	16	0	6	4
Pareuptychia summandosa	0	1	4	0	0	3		0	5	24	1	8	11	0	5	5
Paryphthimoides grimon	0	0	0	0	0	0		0	0	0	0	0	1	0	1	0
Paryphthimoides poltys	0	0	7	0	4	3		0	3	2	1	1	2	0	4	2
Paryphthimoides sp.2	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Pharneuptychia sp.1	0	0	0	0	0	0		0	0	0	0	1	1	0	0	2
Pseudodebis celia	0	0	8	0	0	58		0	0	25	0	0	10	0	0	4
Pseudodebis euptychidia	1	1	3	6	2	7		0	1	6	0	1	4	1	1	1
Satyrinae	0	0	0	0	1	0		1	0	3	0	0	0	0	0	0
Splendeuptychia doxes	4	2	0	0	2	0		0	0	0	0	0	0	0	0	0
Taygetina kerea	0	0	0	1	0	0		1	0	0	0	0	0	0	0	0
Tavgetis fulginia	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0
Tavgetis laches	0	3	2	2	13	11		2	7	7	2	7	1	0	1	0
Taygetis leuctra	0	0	0	1	1	0		0	0	0	0	0	0	1	0	0
Taygetis mermeria	0	0	0	1	2	0		0	0	0	0	0	0	0	0	1
Tavgetis rufomarginata	24	26	8	74		29		43	36	3	68	88	2	23	16	0
Tavgetis sosis	3	2	0	2	1	1		8	2	0	10	1	2	6	0	1
Tavgetis virgilia	0	0	1	1	2	3		0	1	5	0	0	2	0	0	1
Yphthimoides affinis	1	0	4	0	- 2	2		0	3			1	- 1	0	3	1
Yphthimoides renata	0	 0	2	0	- 0	1		0	0	0		2	0	2	0	1
Zischkaia pacarus	0	0		0	0	0		0	0	0	0	0	0	- 1	0	0
Zischkaia saundersii	2	0	0	0		0		0	0	0	0	0	0	0	0	0
Total of individuals	251	361	364	244	266	370	. \ \	196	209	247	136	209	110	118	182	139

		Forest 1	Interior			Eco	tone			Ed	lge	
Months	Al	oundance	F	Richness	Al	oundance	ŀ	Richness	A	bundance	F	lichness
	Total	Mean ± SD	Total	Mean ± SD	Total	Mean ± SD	Total	Mean ± SD	Total	Mean ± SD	Total	Mean ± SD
January	266	88.7 ± 60.9	26	15.7 ± 2.1	291	97.0 ± 37.0	37	20.7 ± 0.6	358	119.3 ± 39.4	38	25.0 ± 4.0
February	278	92.7 ± 23.7	32	16.3 ± 4.2	494	164.7 ± 69.8	52	24.7 ± 0.6	521	173.7 ± 70.2	48	30.7 ± 5.9
March	211	70.3 ± 5.1	26	15.3 ± 1.5	388	129.3 ± 83.8	39	22.0 ± 3.6	363	121.0 ± 49.0	39	25.7 ± 4.2
April	379	126.3 ± 9.0	37	22.7 ± 5.7	497	165.7 ± 74.0	45	29.0 ± 1.7	421	140.3 ± 24.1	50	33.7 ± 2.5
May	196	65.3 ± 11.9	34	19.3 ± 3.2	209	69.7 ± 19.3	42	23.7 ± 3.2	247	82.3 ± 38.9	43	24.7 ± 7.5
June	136	45.3 ± 21.5	25	13.0 ± 1.7	209	69.7 ± 10.7	40	22.3 ± 4.9	110	36.7 ± 10.4	34	18.0 ± 4.6
July	118	39.3 ± 5.8	30	16.3 ± 2.1	182	60.7 ± 19.7	42	24.0 ± 3.6	139	46.3 ± 13.0	38	20.0 ± 4.4
August	251	83.7 ± 47.6	39	22.7 ± 3.2	361	120.3 ± 36.6	40	26.3 ± 2.5	364	121.3 ± 19.3	48	32.0 ± 5.2
September	244	81.3 ± 17.9	40	21.3 ± 7.6	266	88.7 ± 33.8	47	27.3 ± 5.1	370	123.3 ± 22.7	47	29.3 ± 4.0
October	417	139.0 ± 32.9	53	30.7 ± 2.3	533	177.7 ± 49.1	61	41.0 ± 3.6	544	181.3 ± 66.1	60	42.7 ± 1.5
November	528	176.0 ± 54.1	48	30.3 ± 7.1	768	256.0 ± 62.5	64	36.0 ± 1.7	569	189.7 ± 19.1	55	37.3 ± 7.0
December	127	42.3 ± 24.8	22	12.3 ± 0.6	123	41.0 ± 13.2	28	15.7 ± 1.5	116	38.7 ± 7.6	27	15.0 ± 1.7

Appendix 11 Table 3 Abundance and richness of fruit-feeding butterflies (total and mean) per months in each habitat, Rio Doce State Park, Brazil. SD = standard deviation.

]	Distance Travele	d (m)			
Subfamilies	Max	ximum		Mean ± SD				
	Male	Female	Specie	Male	Female	T-test	df	р
BIBLIDINAE								
Hamadryas amphinome	1,253	925	52.6 ± 153.3	48.5 ± 144 ^a	65.4 ± 181.7 ^a	0.43	35.78	0.67
Hamadryas feronia	4,678	4,747	128.6 ± 633.4	121 ± 576.7 ª	141.6 ± 728.9 ª	0.16	70.63	0.88
Hamadryas laodamia	75	50	25 ± 28.3	25 ± 30.9 ^a	25 ± 25 ª	0	24.72	1
Paulogramma pygas	200	50	22.6 ± 45.3	27.3 ± 59.6 ^a	17.5 ± 23.7 ^a	0.5	13.33	0.62
CHARAXINAE								
Fountainea ryphea	157	175	34.2 ± 48.8	27.1 ± 41.6 ^a	46.4 ± 58.7 ^a	1.08	20.74	0.29
SATYRINAE								
Taygetis rufomarginata	100	100	29.8 ± 33.8	27.1 ± 33.7 ^a	39.3 ± 34.9 ª	0.82	9.52	0.43

Appendix 12 Table 2 Distances traveled by fruit-feeding butterfly species (male/female) with more the 3% of recapture, Rio Doce State Park, Brazil. The letters in front of mean distances traveled indicate there was no difference between sexes based on T-test.

Cubfomiliag	Say Displacements among traps (m)									Total			
Sublamines	Sex	0	25	50	75	100	125	150	175	200	225	>500	Total
BIBLIDINAE													
	М	36	17	14	3	2	3	2	1	0	1	1	80
Hamadryas amphinome	F	14	4	3	0	1	1	2	0	0	0	1	26
	Т	50	21	17	3	3	4	4	1	0	1	2	106
	М	30	17	9	5	6	1	2	1	0	0	2	73
Hamadryas feronia	F	20	8	5	4	3	0	1	0	0	0	1	42
	Т	50	25	14	9	9	1	3	1	0	0	3	115
	М	10	1	4	3	0	0	0	0	0	0	0	18
Hamadryas laodamia	F	5	1	5	0	0	0	0	0	0	0	0	11
	Т	15	2	9	3	0	0	0	0	0	0	0	29
	М	7	2	1	0	0	0	0	0	1	0	0	11
Paulogramma pygas	F	6	1	3	0	0	0	0	0	0	0	0	10
	Т	13	3	4	0	0	0	0	0	1	0	0	21
CHARAXINAE													
	М	13	5	2	2	0	1	1	0	0	0	0	24
Fountainea ryphea	F	6	2	2	1	1	0	1	1	0	0	0	14
	Т	19	7	4	3	1	1	2	1	0	0	0	38
SATYRINAE													
	М	12	4	4	2	2	0	0	0	0	0	0	24
Taygetis rufomarginata	F	2	1	3	0	1	0	0	0	0	0	0	7
	Т	14	5	7	2	3	0	0	0	0	0	0	31

Appendix 13 Table 3 Fruit-feeding butterfly displacements among traps (m) by species with more the 3% of recapture, Rio Doce State Park, Brazil. Male (M), female (F) and total (T).

Anexos

Anexo I. Licenças ambientais – IEF/ IBAMA



GOVERNO DO ESTADO DE MINAS GERAIS SECRETARIA DE ESTADO DE MEIO AMBIENTE E DESENVOLVIMENTO SUSTENTÁVEL INSTITUTO ESTADUAL DE FLORESTAS DIRETORIA DE PESQUISA E PROTEÇÃO À BIODIVERSIDADE GERÊNCIA DE PROJETOS E PESQUISAS

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Sérv	io Pontes Ribeiro		UFOP	665.848.766-9		Orientador	
André	Victor Lucci Freit	as	UNICAMP	253.834.388-74	1	Co-orientador	
Ana	a Beatriz Borges	2	· · · · ·	087.634.696-42	2	Colaborador	
Glór	ria Ramos Soares		UFMG	013.411.106-0	5	Colaborador	
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Ministério do Meio Ambiente - MMA Instituto Chico Mendes de Conservação da Biodiversidade - ICMBio

Sistema de Autorização e Informação em Biodiversidade - SISBIO

Autorização para atividades com finalidade científica

Número: 45788-1	Data da Emissão: 08/10/2014 10:21	Data para Revalidação*: 07/11/2015
* De acordo com o art. 33 da mas deverá ser revalidada a a contar da data do aniversár	a IN 154/2009, esta autorização tem prazo de validade ec nualmente mediante a apresentação do relatório de ativid io de sua emissão.	uivalente ao previsto no cronograma de atividades do projeto, ades a ser enviado por meio do Sisbio no prazo de até 30 dias

Dados do titular

Nome: Giselle Martins Lourenço	CPF: 073.538.876-80
Título do Projeto: Padrões de distribuição de borbol <mark>etas: os</mark> e <mark>feitos de habitat</mark> s f	florestais e ecótones
Nome da Instituição : UNIVER SIDADE ESTADUAL DE CAMPINAS	CN PJ: 46.068.425/0001-33

Cronograma de atividades

#	Descrição da atividade	Início (mês/ano)	Fim (mês/ano)
1	Reconhecimento das areas e seleção dos pontos de amostragem e coleta inicial.	11/2014	12/2014
2	Coletas de espècimes.	01/2015	01/2018

Observações e ressalvas

1	As atividades de campo exercidas por pessoa natural ou jundica estrangeira, em todo o território nacional, que impliquem o deslocamento de recursos humanos e materiais, tendo por objeto coletar dados, materiais, espécimes biológicos e minerais, peças integrantes da cultura nativa e cultura popular, presente e passada, obtilos por meio de recursos e térmisos que se destinema ne studica à difúsión ou à negruisa e estito a subtraca
2	Esta autorização NAO exime o pesquisador titular e os membros de sua equipe da necessidade de obter as anuências previstas em outros instrumentos legais, bem como do consentimento do responsável pela área, pública ou privada, onde será realizada a atividade, inclusive do órgão gestor de terra indígena (FUNAI), da unidade de conservação estadual, distrital ou municipal, ou do proprietário, amendatário, posseiro ou morador de área dentro dos limites de unidade de conservação federal cujo processo de regularização fundiária encontra-se em curso.
3	Este documento somente poderá ser utilizado para os íns previstos na histrução Normativa ICMBio nº 03/2014 ou na histrução Normativa ICMBio nº 10/2010, no que especifica esta Autorização, não podendo ser utilizado para fins comenciais, industriais ou esportivos. O material biológico coletado deverá ser utilizado para atividades derefícas ou didáticas no ámbito do ensino superior.
4	O titular de licença ou autorização e os membros da sua equipe deverão optar por métodos de coleta e instrumentos de captura direcionados, sempre que possivel, ao grupo taxonômico de interesse, evitando a morte ou dano significativo a outros grupos; e empregar esforço de coleta ou captura que não comprometa a viabilidade de populações do grupo taxonômico de interesse em condição in situ.
5	O titular de autoriz ação ou de licença permanente, assim como os membros de sua equipe, quando da vidação da legislação vigente, ou quando da inadequação, omissão ou faisa descrição de informações relevantes que subsidiaram a expedição da or, poderá, mediante decisão motivada, ter a autorização ou licença sustensa ou revocada pelo ICMB oe o material biológico coletado apreendido nos termos da lecislação besteira em vicor.
6	Este documento não dispensa o cumprimento da legisfação que dispõe sobre acesso a componente do patrimônio genético existente no território nacional, na plataforma continental e na zona econômica exclusiva, ou ao conhecimento tradicional associado ao patrimônio genético, para fins de pesquisa científica, bioprospecção e desenvolvimento tecnológico. Veja maiores informações em uww.mna.gov.brAgen.
7	Em caso de pesquisa em UNIDADE DE CONSERVAÇÃO, o pesquisador titular desta autorização deverá contactar a administração da unidade a fim de CONFIRMAR AS DATAS das expedições, as condições para realização das coletas e de uso da infra-estrutura da unidade.

#	Nome	Função	CPF	Doc. Identidade	Nacionalidade
1	Laura Braga de Oliveira	Colaborador	071.272.486-99	MG13146767 SSP-MG	Brasileira
2	André Motor Lucci Freitas	Co-orientador	253.834.388-74	19296024 SSP-SP	Brasileira
3	Sérvio Pontes Ribeiro	Orientador	665.848.766-91	M2288405 SSP-MG	Brasileira
4	Ana Beatriz Borges da Silva	Colaborador	087.634.696-42	MG-14.882.838 SSP-MG	Brasileira
5	Gloria Ramos Scares	Colaborador	013.411.106-05	10904714 SSP-MG	Brasileira

Locais onde as atividades de campo serão executadas

#	Município	UF	Descrição do local	Tipo
1	MARLIERIA	MG	Parque Estadual do Rio Doce	Fora de UC Federal

Material e métodos

Este documento (Autorização para atividades com finalidade científica) foi expedido com base na Instrução Normativa nº154/2007. Através do código de autenticação abaixo, qualquer cidadão poderá verificar a autenticidade ou regularidade deste documento, por meio da página do Sisbio/ICMBio na Internet (www.icmbio.gov.br/sisbio).

Código de autenticação: 74959868



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Anexo II. Declaração Bioética e Segurança



COORDENADORIA DE PÓS-GRADUAÇÃO INSTITUTO DE BIOLOGIA Universidade Estadual de Campinas Caixa Postal 6109. 13083-970, Campinas, SP, Brasil Fone (19) 3521-6378. email: cpgib@unicamp.br

DECLARAÇÃO

Em observância ao §5° do Artigo 1° da Informação CCPG-UNICAMP/001/15, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Tese de Doutorado, intitulada "Spatio-temporal patterns of fruit-feeding butterfly distribution and diversity in transitional habitats (Padrões espaço-temporais de distribuição e diversidade de borboletas frugívoras em habitats transicionais)", desenvolvida no Programa de Pós-Graduação em Ecologia do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

Assinatura: Giselle laitino t aurenco Nome do(a) aluno(a): Giselle Martins Lourenço

Assinatura: _______ Nome do(a) orientador(a): Sérvio Pontes Ribeiro

Data: 30 de novembro de 2018

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Anexo III. Declaração Direitos Autorais

Declaração

As cópias de artigos de minha autoria ou de minha co-autoria, já publicados ou submetidos para publicação em revistas científicas ou anais de congressos sujeitos a arbitragem, que constam da minha Dissertação/Tese de Mestrado/Doutorado, intitulada "Spatio-temporal patterns of fruit-feeding butterfly distribution and diversity in transitional habitats" (Padrões espaço-temporais de distribuição e diversidade de borboletas frugívoras em habitats transicionais), não infringem os dispositivos da Lei n.º 9.610/98, nem o direito autoral de qualquer editora.

Campinas, 30 de novembro de 2018

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