



Universidade Federal de Goiás

Instituto de Ciências Biológicas

Programa de Pós-Graduação em Ecologia e Evolução



**IMPORTÂNCIA DE PROCESSOS DETERMINÍSTICOS E ESTOCÁSTICOS SOBRE PADRÕES DE
DIVERSIDADE TAXONÔMICA, FUNCIONAL E FILOGENÉTICA DE MARIPOSAS ARCTIINAE**

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Orientadora: Viviane Gianluppi Ferro

Goiânia - GO

Março de 2017

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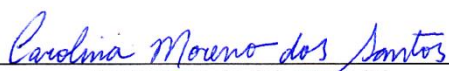
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Tese apresentada à Universidade Federal de Goiás, como parte das exigências do Programa de Pós-Graduação em Ecologia e Evolução para obtenção do título de Doutora em Ecologia e Evolução.

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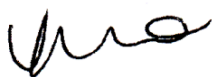


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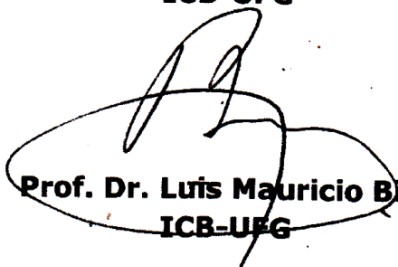
ATA DA SESSÃO PÚBLICA DE DEFESA DE TESE DE Nº 52

Aos vinte e sete dias do mês de março de 2017 (27/03/2017), às quatorze horas (14h), no Auditório do ICB I, UFG, reuniram-se os componentes da banca examinadora: **Profa. Dra. Viviane Gianluppi Ferro, ICB-UFG; Prof. Dr. Luis Mauricio Bini, ICB-UFG; Prof. Dr. Mário Almeida Neto, ICB-UFG; Profa. Dra. Sarah Siqueira de Oliveira, ICB-UFG; Profa. Dra. Livia Rodrigues Pinheiro, Museu de Zoologia da Universidade de São Paulo** para, em sessão pública presidida pelo (a) primeiro(a) examinador(a) citado(a), procederem à avaliação da defesa de tese intitulada: **"Importância de processos determinísticos e estocásticos sobre padrões de diversidade taxonômica, funcional e filogenética de mariposas Arctiinae"**, em nível de doutorado, área de concentração em Ecologia e Evolução, de autoria de **Carolina Moreno dos Santos**, discente do Programa de Pós-Graduação Ecologia e Evolução da Universidade Federal de Goiás. A sessão foi aberta pelo(a) presidente(a), que fez a apresentação formal dos membros da banca. A palavra, a seguir, foi concedida a(o) autor(a) da tese que, em cerca de 40 minutos, procedeu à apresentação de seu trabalho. Terminada a apresentação, cada membro da banca arguiu a(o) examinada(o), tendo-se adotado o sistema de diálogo sequencial. Terminada a fase de arguição, procedeu-se à avaliação da tese. Tendo-se em vista o que consta na Resolução nº 1127 de dezembro de 2012 do Conselho de Ensino, Pesquisa, Extensão e Cultura (CEPEC), que regulamenta o Programa de Pós-Graduação em Ecologia e Evolução, a tese foi aprovada, considerando-se integralmente cumprido este requisito para fins de obtenção do título de Doutor(a) em Ecologia e Evolução pela Universidade Federal de Goiás. A conclusão do curso dar-se-á quando da entrega da versão definitiva da tese na secretaria do programa, com as devidas

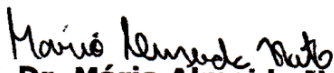
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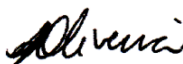
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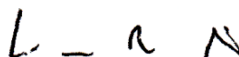
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“Ciência é conhecimento organizado. Sabedoria é vida organizada.”

Immanuel Kant

Aos meus pais, pelo incentivo constante.

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RESUMO

Arctiinae, uma das subfamílias mais diversas e cosmopolitas de Lepidoptera, é dividida em quatro tribos: Lithosiini, Amerilini, Syntomini e Arctiini. Somente Arctiini e Lithosiini ocorrem nos Neotrópicos. Apesar de serem da mesma subfamília, mariposas destas duas tribos Neotropicais se diferenciam muito em tamanho, padrões de coloração, dieta, tipo de substância secundária que sequestram e uso de habitat. Todas as diferenças morfológicas, fisiológicas e comportamentais destas mariposas influenciam muito em suas distribuições ao longo de gradientes ambientais. A distribuição das espécies também pode ser fortemente influenciada por processos determinísticos (baseados em modelos de nicho, como por exemplo, interações ecológicas e filtragem ambiental) e por processos estocásticos (exemplos: deriva ecológica, limitação na dispersão, especiação e extinção aleatórias). Para responder quais processos melhor determinam a distribuição de mariposas Arctiinae, esta Tese foi composta por três capítulos. No primeiro capítulo testei qual modelo de metacomunidades (relacionados com variáveis ambientais e espaciais), melhor determinam a distribuição de espécies comuns, raras, especialistas de habitat, generalistas de habitat e de espécies pertencentes às tribos Arctiini e Lithosiini. No segundo capítulo testei se a estrutura funcional de Arctiini e de Lithosiini e se a estrutura filogenética de Arctiini são influenciadas da mesma forma por processos estocásticos e determinísticos. Mariposas Arctiinae foram influenciadas tanto por variáveis ambientais (relacionadas a processos determinísticos) quanto por espaciais (relacionadas a processos estocásticos), mas o ambiente foi mais importante tanto para a maioria dos grupos da diversidade taxonômica (capítulo 1) quanto para as diversidades funcional e filogenética (capítulo 2). Como os processos determinísticos são muito importantes em determinar a distribuição de Arctiinae ao longo das comunidades, no terceiro capítulo testei qual destes processos determinísticos (especificamente se interações antagônicas ou se filtragem ambiental) é mais importante em determinar a estrutura funcional de mariposas Arctiinae ao longo de diferentes fitofisionomias e de diferentes estações climáticas, marcantes da área de estudo. Os resultados mostraram que mariposas Arctiinae são fortemente influenciadas por filtros ambientais, e que interações antagônicas (ex.: exclusão competitiva) não são tão importantes em determinar a estrutura funcional de mariposas Arctiinae nas comunidades.

Palavras-chave: Atributos funcionais, Lepidoptera, relações filogenéticas

ABSTRACT

Arctiinae is one of the most diverse and cosmopolitan subfamilies of Lepidoptera, and is composed of four tribes: Lithosiini, Amerilini, Syntomini and Arctiini. In the Neotropics occur Arctiini and Lithosiini only. Moths of these two tribes are very different in body size, coloration patterns, diet, in the type of secondary compounds they sequester, and in habitat use. The morphological, physiological, and behavioral characteristics of these moths are very important in influencing their distribution in the environment. The distribution of species can also be highly influenced by deterministics (based in the niche models, like as ecological interactions and environmental filtering) and stochastic processes (i.e.: ecological drift, dispersion limitations, random speciation and extinction). To answer which processes best determine the distribution of Arctiinae moths, this Thesis was composed by three chapters. In the first chapter I tested which model of metacommunity (related to environmental and spatial variables) best determine the distribution of groups of species: common, rare, habitat specialist, habitat generalist and species belonging to tribes Arctiini and Lithosiini. In the second chapter, I tested if the functional structure of Arctiini and of Lithosiini and if the phylogenetic structure of Arctiini are influenced in the same way by stochastic and deterministic processes. Arctiinae moths (both tribes) were influenced by environmental (also related to deterministic processes) and spatial (also related to stochastic processes) variables, but the environment was more important to the majority of the groups of taxonomic diversity (chapter 1) and to the functional and phylogenetic diversities (chapter 2). As the deterministic processes are very important to determine the distribution of Arctiinae on communities, in the third chapter I tested which deterministic process (specifically, antagonistic interactions or environmental filtering) is more important in determine the functional structure of these moths along different physiognomies and in two marked weather seasons, characteristics of the study area. The results showed that Arctiinae moths are strongly influenced by environmental filters, and that antagonistic interactions (i.e. competition) are not so important in determine the functional structure of Arctiinae moths on communities.

Key-words: Functional traits, Lepidoptera, phylogenetic relationships

INTRODUÇÃO GERAL

Arctiinae é uma das subfamílias mais ricas de Lepidoptera (Heppner, 1991; Weller *et al.*, 2009), sendo composta por uma grande radiação de mariposas crípticas, aposemáticas e miméticas (Simmons, 2009; Zahiri *et al.*, 2012; Zaspel *et al.*, 2014). Aproximadamente 11000 espécies foram descritas em todo mundo (Watson & Goodger, 1986; Weller *et al.*, 2009), sendo que o pico de diversidade ocorre na região Neotropical, com aproximadamente 6000 espécies (Brehm, 2009; Weller *et al.*, 2009). No Brasil já foram estimadas cerca de 1400 espécies (Ferro & Diniz, 2010).

Pertencente a família Erebidae (Zahiri *et al.*, 2011; 2012), Arctiinae é dividida em quatro tribos: Lithosiini, Amerilini, Syntomini e Arctiini (Zaspel *et al.*, 2014; Zenker *et al.*, 2016). Na região Neotropical ocorrem as tribos Arctiini e Lithosiini (Heppner, 1991). Membros da tribo Lithosiini compartilham uma característica que é a presença de uma mandíbula molar alargada, importante para macerar líquens, briófitas e algas, suas fontes alimentares na fase larval (Singer & Bernays, 2009; Wagner, 2009; Weller *et al.*, 2009; Scott *et al.*, 2014). Lithosiini é o único grupo conhecido que possui a capacidade de sequestrar polifenóis de líquens, que são substâncias tóxicas importantes para conferir proteção contra inimigos naturais (Scott *et al.*, 2014). Apesar da maioria das espécies que sequestram substâncias tóxicas apresentar coloração de advertência (Simmons, 2009), Lithosiini é em sua maioria críptica na fase larval e algumas espécies continuam crípticas na fase adulta (Simmons, 2009; Wagner, 2009). Porém, grande parte dos adultos de Lithosiini, assim como de Arctiini, apresenta sinal visual com coloração de advertência (coloração aposemática) (Simmons, 2009; Scott *et al.*, 2014). As espécies que são aposemáticas variam muito nos padrões de coloração, combinando cores fortes e brilhantes, como laranjas, vermelhos, rosas, amarelos, azuis iridescentes, pretos e até a cor branca se torna aposemática em voos noturnos. Estas cores são combinadas de diversas maneiras (Simmons, 2009; Figura 1). Adultos de

Lithosiini se diferenciam morfologicamente de Arctiini por possuírem envergadura de tamanho pequeno a médio, com corpo pequeno e delgado e a grande maioria possui asas estreitas (Weller *et al.*, 2009; Bayarsaikhan *et al.*, 2016).

A tribo Arctiini é composta por mariposas altamente diversas, de tamanho pequeno, médio e grande (Weller *et al.*, 2009). Na fase larval, se alimentam de uma grande variedade de plantas, incluindo gramíneas, herbáceas, arbustos e árvores (Singer & Bernays, 2009; Weller *et al.*, 2009). Por serem polípagas, elas podem ocorrer em diferentes formações vegetais (Kitching *et al.*, 2000; Hilt & Fiedler, 2006; Brehm, 2009; Singer & Bernays, 2009). Contudo, apesar de seu alto grau de polifagia (Weller *et al.*, 1999; Kitching *et al.*, 2000; Hilt & Fiedler, 2006; Singer & Bernays, 2009; Weller *et al.*, 2009), Arctiini se especializou em plantas hospedeiras que possuem metabólitos secundários tóxicos, sendo então chamadas de “generalistas especializadas” por Singer & Bernays (2009). Tais substâncias tóxicas são importantes para protegê-las contra predação e parasitismo (Bezzerides *et al.*, 2004; Bowers, 2009; Hartmann, 2009). Estes aleloquímicos são alcaloides pirrolizidínicos, glicosídeos cardíacos e glicosídeos de iridoide (Weller *et al.*, 1999; Bowers, 2009; Zaspel *et al.*, 2014). Muitas espécies conseguem transferir estas substâncias da fase larval para a fase adulta (Hartmann, 2009), outras espécies só as adquirem na fase adulta através de farmacofagia (Boppré, 1981; Zaspel *et al.*, 2014).

Tanto Arctiini quanto Lithosiini apresentam várias estratégias de defesa para alertar seus inimigos naturais de sua impalatabilidade (Weller *et al.*, 1999; Conner *et al.*, 2009; Dowdy & Conner, 2016). Dentre elas, a coloração aposemática (sinal visual) e o aposematismo acústico (ultrassom produzido pelos órgãos timpânicos, ou sons de baixa frequência produzidos pelas cerdas de lagartas), podem ocorrer nas fases larval e adulta (Weller *et al.*, 1999; Conner & Wilson, 2009; Conner *et al.*, 2009). Os sinais visual e o acústico são principalmente expressados por espécies que adquirem substâncias tóxicas

(Conner *et al.*, 2009; Simmons, 2009), mas mimetismo Batesiano (espécies palatáveis mimetizando espécies tóxicas) e Mülleriano (espécies impalatáveis se assemelhando umas as outras) são muito comuns entre mariposas Arctiinae (Conner *et al.*, 2009; Simmons, 2009).

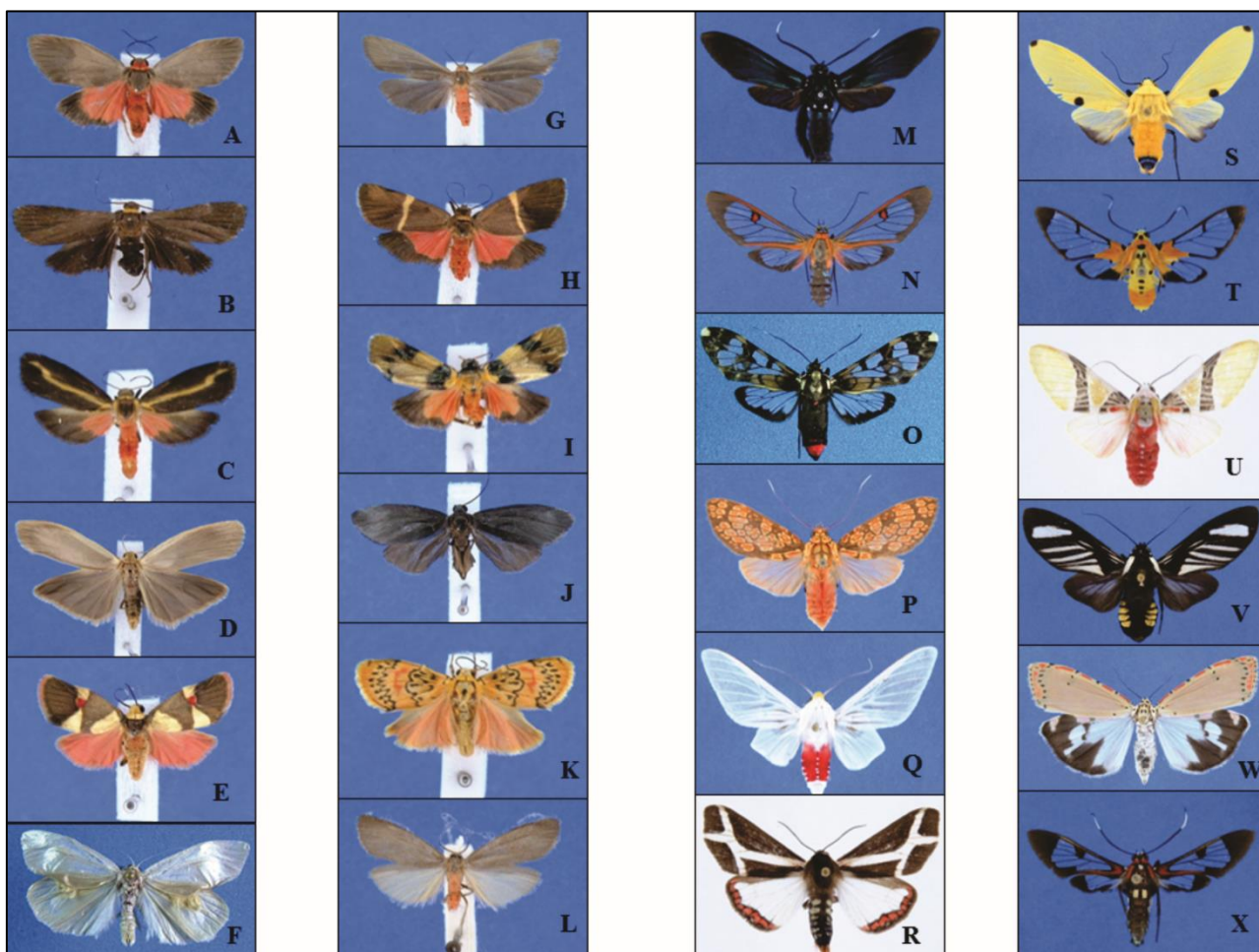


Figura 1. Exemplos de mariposas Arctiinae, mostrando a diversidade dos padrões de coloração das asas. A tribo Lithosiini é representada pelas letras A a L. (A) *Cisthene subruba*, (B) *Cisthene ruficollis*, (C) *Metalobosia diaxantha*, (D) *Parablavia sadima*, (E) *Nodozana jucunda*, (F) *Aglylla argentea*, (G) *Odozana domina*, (H) *Zonoda dives*, (I) *Cisthene croesus*, (J) *Odozana obscura*, (K) *Barsinella mirabilis*, e (L) *Talara grisea*. A tribo Arctiini é representada pelas letras M a X. (M) *Macrocneme aurifera*, (N) *Lepidoneiva erubescens*, (O) *Pseudohyalocerea vulnerata*, (P) *Cresera optima*, (Q) *Eupseudosoma grandis*, (R) *Dysschema sacrificata*, (S) *Viviennea salma*, (T) *Hyda basilutea*, (U) *Idalus carinosa*, (V) *Ripha strigosa*, (W) *Utetheisa ornatrix*, (X) *Pheia seraphina*.

Todas as diferenças nas características morfológicas (por exemplo, diferentes tamanhos de corpo, de coloração e padrões de mimetismo), fisiológicas (por exemplo, busca e sequestro de substâncias tóxicas e transferência destas substâncias em diferentes fases de

desenvolvimento) e comportamentais (por exemplo, emissão de ultrassom na presença de predadores, Conner *et al.*, 2009) são importantes para determinar a distribuição de mariposas Arctiinae ao longo de diferentes gradientes ambientais (Hilt & Fiedler, 2006; Brehm, 2009; Simmons, 2009). Por exemplo, as mariposas Arctiinae são muito sensíveis à mudança ambiental que ocorre no bioma Cerrado (Moreno *et al.*, 2014). As fitofisionomias do Cerrado abrangem desde áreas abertas, sem nenhum extrato arbóreo-arbustivo (formações campestres), até áreas com grande densidade de árvores altas (formações florestais) (Oliveira-Filho & Ratter, 2002). As formações vegetais pertencentes ao cerrado *sensu lato* (formações campestres e savânicas) representam um gradiente de vegetação que aumenta em densidade de arbóreas e diminui em densidade de herbáceas e subarbustos (Oliveira-Filho & Ratter, 2002). No bioma Cerrado também ocorrem formações florestais que não são consideradas pertencentes ao cerrado *sensu lato*, como por exemplo, as matas estacionais decíduas e semidecíduas, as matas sempre verdes, as matas de vale e as matas de galeria (Oliveira-Filho & Ratter, 2002). Desta forma, o bioma Cerrado pode ser dividido em formações florestais, savânicas e campestres (Oliveira-Filho & Ratter, 2002; Ribeiro & Walter 2008, Figura 2). Nós amostramos as mariposas Arctiinae em duas formações campestres (campo sujo e campo cerrado), uma formação savânica (cerrado *sensu stricto*) e uma formação florestal (mata estacional semidecídua) para representarmos bem a fauna de mariposas que ocorrem em diferentes formações vegetais.

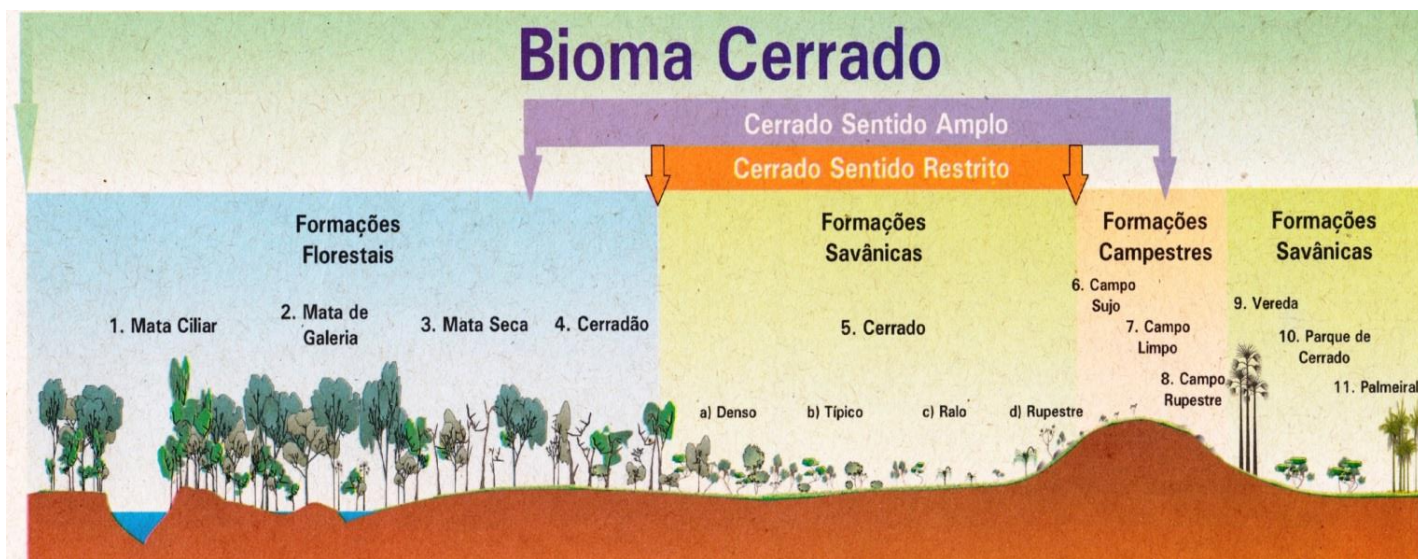


Figura 2. Fitofisionomias que ocorrem no bioma Cerrado. Fonte: Ribeiro & Walter (2008).

A distribuição das espécies ao longo de comunidades também pode ser fortemente influenciada por processos determinísticos e estocásticos (Kraft *et al.*, 2008; Chase, 2010; Pavoine & Bonsall, 2011). Processos determinísticos são os baseados em modelos de nicho, como por exemplo, interações ecológicas e filtragem ambiental (Chase, 2010; Pavoine & Bonsall, 2011). Já os processos estocásticos incluem deriva ecológica, limitação na dispersão, especiação e extinção aleatórias e neutralidade no fitness das espécies (Kraft *et al.*, 2008; Chase, 2010; Pavoine & Bonsall, 2011). Os processos estocásticos e determinísticos estão interligados entre si, e podem agir simultaneamente (Ellwood *et al.*, 2009). Para conjuntos de comunidades ligadas pela dispersão dos indivíduos (conceito de metacomunidade, Wilson, 1992; Leibold *et al.*, 2004; Presley *et al.*, 2010), foram propostos quatro modelos que explicam como processos estocásticos e determinísticos podem atuar na distribuição de espécies (Leibold *et al.*, 2004). O primeiro, *patch dynamics*, prediz que todos os fragmentos possuem características ambientais idênticas e que a riqueza de espécies nos fragmentos é limitada pela dispersão dos indivíduos. O segundo, *mass effect*, assume variação ambiental nos fragmentos e frisa no forte impacto que a migração dos indivíduos tem sobre as dinâmicas de colonização de novos fragmentos a partir de populações fontes (Leibold *et al.*, 2004;

Winegardner *et al.*, 2012). O terceiro, *neutral model*, assume que todas as espécies são ecologicamente equivalentes em suas interações e capacidades de dispersão e habilidades competitivas (Hubbell, 2001). O quarto, *species sorting*, assume que a heterogeneidade ambiental e as interações ecológicas têm uma influencia mais forte na composição das espécies nas comunidades do que a dispersão dos indivíduos (Leibold *et al.*, 2004; Winegardner *et al.*, 2012). Os três primeiros modelos estão mais relacionados com processos espaciais (variáveis espaciais), enquanto que *species sorting* é mais relacionado com processos de nicho (por exemplo, com variáveis ambientais) (Leibold *et al.*, 2004; Pandit *et al.*, 2009).

Para responder quais processos melhor determinam a distribuição das espécies de Arctiinae, propuz três capítulos. O primeiro teve como objetivo geral testar se grupos de espécies de mariposas Arctiinae respondem diferentemente a variáveis ambientais e espaciais, e qual modelo (*patch dynamics*, *mass effect*, *neutral model* ou *species sorting*) melhor explica a distribuição das espécies ao longo da metacomunidade. Para isso, as espécies de mariposas Arctiinae foram divididas em generalistas e especialistas de hábitat, comuns e raras, e em tribos Arctiini e Lithosiini. Especificamente testei três hipóteses:

(1) espécies generalistas de habitat (espécies que ocorrem em todas ou na maioria das comunidades) são mais influenciadas por mecanismos relacionados à dispersão das espécies (relacionadas a variáveis espaciais) do que por variáveis ambientais. Estas espécies ocorrem em praticamente todos os tipos de vegetação e podem ocupar distintos microhábitats, com diferentes recursos disponíveis, então as variáveis ambientais não seriam um fator limitante, mas o que poderia limitar a ocorrência destas espécies seria a capacidade delas se dispersarem para comunidades distantes. Ao contrário, espécies especialistas de habitat (aquelas que ocorrem em poucas comunidades, em tipos específicos de habitat) seriam mais influenciadas

por variáveis ambientais, já que elas requerem condições ambientais específicas para persistirem (Pandit *et al.*, 2009).

(2) espécies raras (que são as que têm poucos indivíduos nas comunidades) são mais influenciadas por processos espaciais (como por exemplo, deriva ecológica) porque sua ausência em ambientes adequáveis (em que elas poderiam ocorrer com maior abundância) pode resultar em uma estruturação espacial muito forte (Hubbell, 2001). Seguindo essa lógica, as espécies comuns (aquelas que ocorrem em alta abundância) seriam mais influenciadas por variáveis ambientais. Por serem abundantes, estas espécies podem ser competitivamente dominantes em uma comunidade (Abugov, 1982), e um fator que limitaria a abundância destas espécies seria algum tipo de variação ambiental, como por exemplo, deficiência de recursos no habitat (Siqueira *et al.*, 2012)

(3) espécies que pertencem à tribo Lithosiini são mais influenciadas por variáveis ambientais, já que elas são especialistas de dieta (se alimentam de líquens, briófitas e algas; Singer & Bernays, 2009; Wagner, 2009; Weller *et al.*, 2009) e, por isso, devem ser restritas a ambientes que fornecem esses recursos. Ao contrário, espécies que pertencem à tribo Arctiini são mais influenciadas por variáveis espaciais, já que a maioria destas espécies é generalista de dieta (se alimentam de uma variedade de plantas, incluindo herbáceas, arbustos e árvores; Kitching *et al.*, 2000; Hilt & Fiedler, 2006; Singer & Bernays, 2009; Weller *et al.*, 2009). Em geral mariposas Arctiini podem ocupar uma ampla variedade de tipos de vegetação (Hilt & Fiedler, 2006; Moreno *et al.*, 2014). Logo, acredito que elas seriam mais limitadas por suas capacidades de dispersão.

No segundo capítulo mantive a ideia de que variáveis espaciais (relacionadas a processos estocásticos) são mais importantes em determinar comunidades de mariposas Arctiini e que variáveis ambientais (relacionadas a processos determinísticos) são mais importantes em determinar comunidades de mariposas Lithosiini. Contudo, neste capítulo

incorporei informações de atributos funcionais (para as tribos Arctiini e Lithosiini) e de relações filogenéticas (para a tribo Arctiini) das mariposas. Duas filogenias de mariposas Arctiinae, construídas com dados moleculares, foram publicadas recentemente (Zaspel *et al.*, 2014; Zenker *et al.*, 2016). Ambas apresentam uma grande quantidade de exemplares de Arctiinae, especialmente a de Zenker *et al.* (2016) que incorporaram muitas espécies da região Neotropical. As duas filogenias são importantes em demonstrar a diversidade de linhagens, as relações de parentesco entre as tribos e subtribos, e a história evolutiva destas mariposas (Zaspel *et al.*, 2014; Zenker *et al.*, 2016). Eu construí uma árvore filogenética menor, com algumas das espécies que amostréi em meu sistema de estudo, para poder incorporar mais um componente da biodiversidade (diversidade filogenética) e responder como processos estocásticos e determinísticos influenciam a distribuição destas espécies nas comunidades.

As tribos Arctiini e Lithosiini pertencem a um clado altamente diverso (Weller *et al.*, 2009; Zaspel *et al.*, 2014) e apresentam muitas diferenças morfológicas, como por exemplo, tamanho do corpo, e padrões de coloração (Simmons, 2009; Weller *et al.*, 2009). Além disso, possuem dietas distintas (Singer & Bernays, 2009; Weller *et al.*, 2009) e buscam por diferentes substâncias tóxicas (Zaspel *et al.*, 2014; Scott *et al.*, 2014). Suas diferenças morfológicas e de dieta influenciam muito em suas distribuições ao longo de diferentes habitats (Hilt & Fiedler, 2006; Brehm, 2009; Simmons, 2009), e suas relações funcionais e filogenéticas podem fornecer informações que o simples nome das espécies (taxonomia) não pode (McGill *et al.*, 2006; Gavilanez & Stevens, 2013), tais como, as similaridades ecológicas e as relações de parentesco entre as espécies (Pavoine & Bonsall, 2011; Siefert *et al.*, 2013). Portanto, as diversidades funcionais e filogenéticas podem revelar respostas aos processos estocásticos e determinísticos que não são revelados somente pela diversidade taxonômica (McGill *et al.*, 2006; Pavoine & Bonsall, 2011; Gavilanez & Stevens, 2013).

Como as espécies de Lepidoptera são fortemente influenciadas por processos exclusivamente determinísticos (Gonçalves-Sousa *et al.*, 2014; Moreno *et al.*, 2016), no terceiro capítulo testei quais processos determinísticos (especificamente se filtragem ambiental ou se exclusão competitiva) são mais importantes em determinar a distribuição de Arctiinae nas comunidades. Estudos discutem que a competição pode não ser frequente entre insetos herbívoros porque eles são raramente limitados pela grande quantidade de recursos no ambiente (revisões de Lawton & Strong Jr., 1981; e de Denno *et al.*, 1995; Nishida *et al.*, 2015). Porém, evidências de que a competição interespecífica em insetos herbívoros é comum no ambiente foi comprovada em vários sistemas (revisado por Denno *et al.*, 1995; Kursar *et al.*, 2006). A escassez de alimento pode ser um fator limitante, aumentando a força da competição em herbívoros, principalmente entre indivíduos de espécies mais relacionadas, mas a competição é menos comum em espécies de mandibulados de vida livre (Lawton & Strong Jr., 1981; Denno *et al.*, 1995; Kursar *et al.*, 2006). A competição entre herbívoros também pode ocorrer por processos indiretos, como a competição por espaço livre de inimigos naturais (competição aparente, Jeffries & Lawton, 1984; Denno *et al.*, 1995; Ramirez & Eubanks, 2016). Além disso, a competição entre polinizadores (adultos de Arctiinae, por exemplo) por recursos florais é comum na natureza (Kevan & Baker, 1983; de Camargo *et al.*, 2016). A competição por recursos semelhantes pode levar a uma maior dissimilaridade de atributos funcionais do que o esperado ao acaso na comunidade (Webb *et al.*, 2002). Em contrapartida, um padrão de maior similaridade de atributos funcionais do que o esperado ao acaso pode ser em resposta a filtragem ambiental, que selecionam espécies com características similares, capazes de coexistir em condições ambientais particulares (Webb *et al.*, 2002).

Diante disso, fiz as seguintes predições: (1) em ambientes simples, que fornecem menor quantidade de recursos e de abrigos (Bazzaz, 1975; Tews *et al.*, 2004) e em condições

climáticas xéricas, que apresenta déficit hídrico, maior variação na temperatura e qualidade de recursos reduzida (Morais *et al.*, 1999; Pinheiro *et al.*, 2002), as espécies tendem a apresentar uma maior similaridade de atributos funcionais do que o esperado ao acaso (agrupamento funcional, Webb *et al.*, 2002), pois filtros ambientais tendem a selecionar espécies com características similares, capazes de sobreviver em condições ambientais desfavoráveis (Webb *et al.*, 2002).

(2) em contrapartida, espécies que ocorrem em habitats estruturalmente complexos (com maior disponibilidade de recursos e abrigos) e em condições climáticas mais amenas (estação chuvosa, com melhor qualidade nutricional dos recursos), apresentam uma maior dissimilaridade de seus atributos funcionais em resposta a interações antagônicas entre as espécies (Webb *et al.*, 2002). Habitats estruturalmente complexos fornecem diferentes nichos (Bazzaz, 1975; Tews *et al.*, 2004), e portanto as espécies podem apresentar maior dissimilaridade funcional em resposta a partição de nichos, e não devido a força das interações competitivas (Webb *et al.*, 2002). Por isso, também testei a relação entre a riqueza e a diversidade funcional das espécies. Caso a relação seja positiva (quanto maior a riqueza, maior a diversidade funcional em habitats estruturalmente complexos), então provavelmente o padrão de maior dissimilaridade de atributos é devido à partição de nichos e não às interações antagônicas entre as espécies (Webb *et al.*, 2002; Carvalho & Tejerina-Garro, 2015). Entretanto, caso a relação seja negativa (quanto maior a riqueza de espécies, menor a diversidade funcional), então a filtragem ambiental é um processo forte em determinar a distribuição das espécies nas comunidades, mesmo em ambientes estruturalmente complexos, com maior quantidade de nichos (Webb *et al.*, 2002).

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CAPÍTULO 1

Plant species richness as the main driver of moth metacommunities¹

¹Moreno, C., Landeiro, V.L., & Ferro, V.G. (2016) Plant species richness as the main driver of moth metacommunities. *Ecological Entomology*, 41: 704-715. doi: 10.1111/een.12348

Plant species richness as the main driver of moth metacommunities

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Abstract

Ecologists have recognized several factors that may explain the distribution of species in a metacommunity. These factors may be related to the dispersal of individuals among the patches and to environmental conditions. Here, we attempted to determine which of the four different metacommunity frameworks (patch dynamics, mass effect, neutral processes, and species sorting) explain the distribution of Arctiinae moths in Brazilian savanna areas with different tree species richness. We categorized the Arctiinae moths as habitat specialists or generalists, common or rare, and belonging to the tribes Arctiini and Lithosiini. We hypothesized that environmental variables best explain the abundance and occurrence of habitat specialist species, common species, and members of Lithosiini; while spatial processes are more closely related to habitat generalists, rare species, and members of Arctiini. Contrary to our expectations, we found that the species sorting (mainly dictated by the species richness of trees) best explained the variation in abundance and occurrence of the majority of species groups. Spatial processes (more related to patch dynamics, mass effect and neutral), although they were significantly related to some species groups, were not strong enough to explain the distribution of these species in our study area. The plant species richness was the most important environmental condition, related to moth species niches, therefore, species sorting best explained the distribution of the species of Arctiinae in the Brazilian savanna.

Keywords: Arctiinae, Cerrado biome, light traps, species sorting, tiger moths, variation partitioning

Introduction

The mechanisms underlying the occurrence and abundance of species are related to the dispersal of individuals among sets of local communities (metacommunity concept, Leibold *et al.*, 2004; Presley *et al.*, 2010) (Wilson, 1992; Winegardner *et al.*, 2012). There are four models (proposed by Leibold *et al.*, 2004) that explain the mechanisms dictating species distributions within a metacommunity: (1) The patch dynamics considers that all patches in the metacommunity are environmentally identical and that species diversity is limited by dispersal, in which spatial dynamics are guided by local extinction and colonization (Leibold *et al.*, 2004). (2) The mass effect focuses on the important role of migration in the source-sink dynamic of local populations. This aspect highlights the importance of spatial dynamics (i.e. species dispersal) in affecting the density of local populations and the rescue effect of source populations (Leibold *et al.*, 2004; Winegardner *et al.*, 2012). (3) In the neutral model, all species are assumed to be ecologically equivalent in terms of their dispersal capacity and competitive ability (Hubbell, 2001). The interactions between species are random and can modify their frequencies in the environment. In the neutral model, the difference in species richness among fragments is due to probabilities of extinction, speciation, emigration and immigration (Leibold *et al.*, 2004). (4) In the species-sorting model, the quality of the patches (for example, habitat heterogeneity and plant species richness) has a strong influence on the composition of local communities. Dispersal is still important (to allow changes in species composition), but it has a weak signal in the community structure. In this case, environmental gradients are more important than dispersal (Leibold *et al.*, 2004; Winegardner *et al.*, 2012). The first three models are more related to spatial processes, while species sorting is more related to niche processes (Leibold *et al.*, 2004; Pandit *et al.*, 2009).

The environmental complexity (is related to niche processes) is in its majority dictated by the plant community (Tews *et al.*, 2004; Stein *et al.*, 2014). Thus, the plant species richness, density and composition can exert a strong influence on the animal species distribution in metacommunities, mainly on herbivores and pollinators, such as butterflies and moths (Gonçalves-Sousa *et al.*, 2014). The very diverse moth subfamily Arctiinae comprises approximately 11,000 species worldwide (Heppner, 1991), with 1,400 in Brazil (Ferro & Diniz, 2010). These moths respond quickly to environmental changes, especially in vegetation cover and climate (Brown Jr., 1997), making them an appropriate group to understand the different models of metacommunities. The Arctiinae moths vary widely in body size (Weller *et al.*, 2009), coloration patterns (Simmons, 2009), diet (Wagner, 2009) and habitat use (Hilt & Fiedler, 2006). All these differences allow the moths of this subfamily to diverge in several aspects of their ecological niches. Therefore, different species groups may respond differently to the same environmental gradients.

The metacommunity models can act in different ways for different species groups (Pandit *et al.*, 2009; Siqueira *et al.*, 2012), since the species are not equivalent in their responses to environmental gradients (Lomolino, 2000). Thus, we evaluated three hypotheses to explain Arctiinae distributions. First, as proposed by Pandit *et al.* (2009) for marine invertebrates, habitat generalists and habitat specialists species possess different levels of environmental tolerances, as the habitat generalist can occur in different microhabitats and the habitat specialists cannot. We tested if this hypothesis applies to a terrestrial animal group. We postulated that the habitat generalist species (those species that occur in all or almost all communities, Figure 1) are more influenced by mechanisms related to species dispersal (spatial variables as proxies), because they usually occur in a wide variety of vegetation types and can occupy distinct microhabitats with different available resources, so the environmental variables are not the main factor limiting their occurrence. On the other hand, habitat

specialist species (those species that occur in a few communities, in specific habitat types, Figure 1) are more influenced by environmental variables, as they require specific environmental conditions to persist (Pandit *et al.*, 2009).

Second, we postulated that rare species (those species that do not have many individuals in communities, Figure 1) are more affected by spatial processes (as ecological drift, for example) because their absence from suitable environments (in habitats that they could have more individual abundance) may result in strong spatial structuring (Hubbel, 2001). Following this logic, the common species (those species that occur in higher abundance, Figure 1) should be more influenced by environmental variables; and since these species are abundant, they can be the competitive dominant species in a community (habitat) (Abugov, 1982) and one of the possible causes that can limit their abundance in a specific habitat would be the variations (resource shortcomings, for example) of the environmental conditions in that habitat (Siqueira *et al.*, 2012).

Third, species belonging to the tribe Lithosiini should be more influenced by environmental variables because they feed on bryophytes, lichens and algae (Weller *et al.*, 2009), so that they are restricted to vegetation types that provide these resources. On the other hand, members of the tribe Arctiini should be more influenced by spatial variables, in accordance with mass effects (Leibold *et al.*, 2004), since most of these moths are “specialized generalists” (Singer & Bernays, 2009). Many Arctiini species are polyphagous, with some exceptions in the subtribes Phaegopterina, Euchromiina, and Ctenuchina (Weller *et al.*, 1999; Kitching *et al.*, 2000; Hilt & Fiedler, 2006; Rab Green *et al.*, 2011). They feed on a wide variety of plants, including grasses, herbs, shrubs and trees (Weller *et al.*, 1999; Kitching *et al.*, 2000; Hilt & Fiedler, 2006; Singer & Bernays, 2009; Weller *et al.*, 2009), and the majority (mainly the subtribes Phaegopterina, Euchromiina and Ctenuchina, Zaspel *et al.*, 2014) of them include in their diet, plants that possess secondary compounds (mainly

pyrrolizidine alkaloids, PAs) (Hartmann, 2009; Zaspel *et al.*, 2014) that make them unpalatable to some natural enemies (Bowers, 2009). In general, Arctiini species can occupy a wide variety of vegetation types (Hilt & Fiedler, 2006; Moreno *et al.*, 2014). Thus, we believe that they could be mainly limited by their dispersal capabilities.

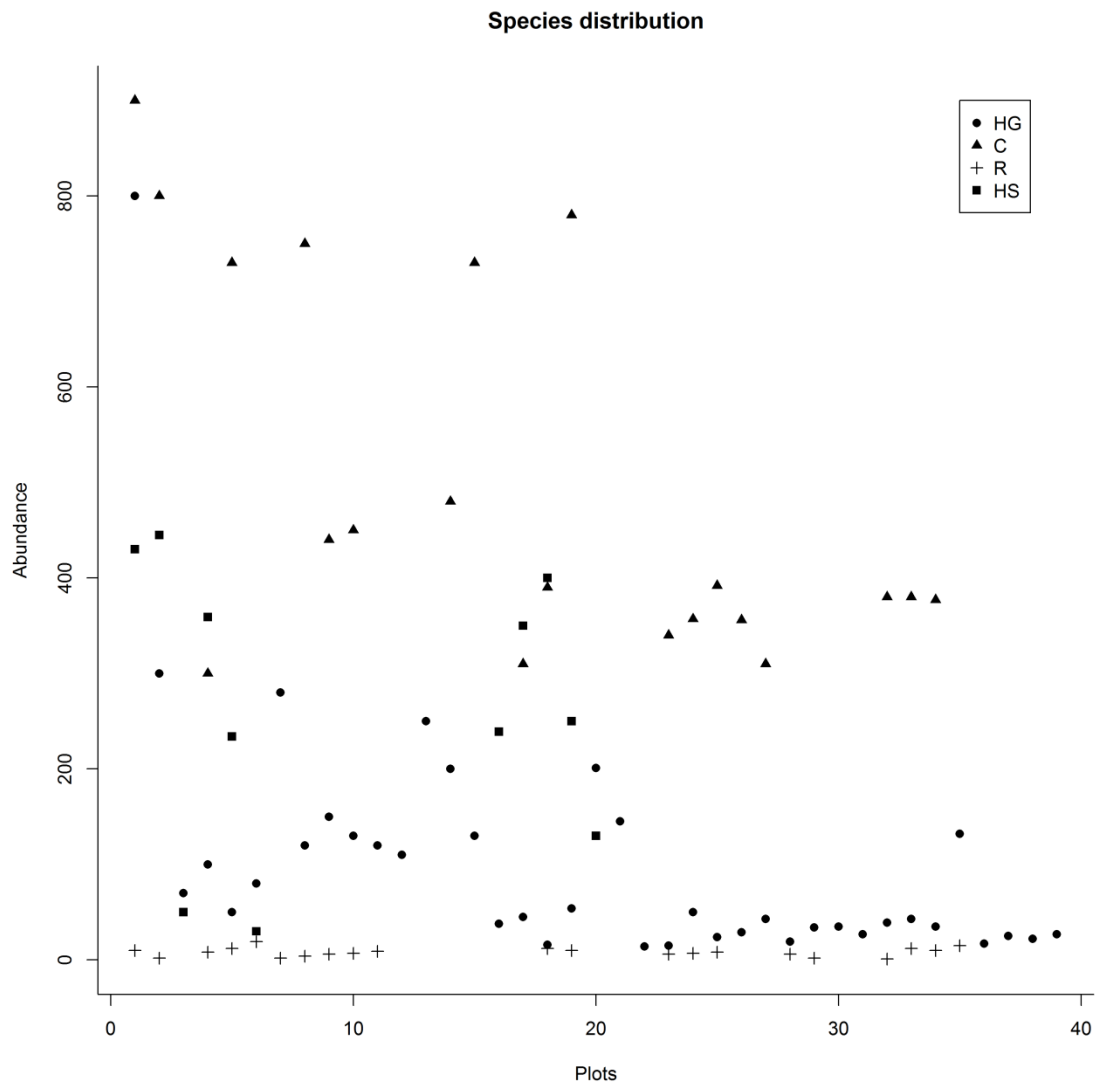


Figure 1. Hypothetical distribution of the species groups. The x axis represent the 39 plots of our metacommunity and the y axis, the individual abundance of the species (representative numbers). Habitat generalist species (HG) are those that occur in all or almost all plots (with high or low abundance). Habitat specialists species (HS) are those that occur in a few plots (they can have a high or a low abundance). Common species (C) are those with the highest

abundance (no matter if they occur in a few or in many plots) and rare species (R) are those that have few individuals.

Methods

We collected the data in the Emas National Park (ENP), central Brazil (17°49' - 18°28'S and 052°39' - 53°10'W). ENP is located in the Cerrado biome, one of the 25 world biodiversity hotspots (Myers *et al.*, 2000). The climate of this region is the Köppen Aw type, with a total annual rainfall varying from 1200 to 2000 mm and a mean annual temperature of around 25°C (Ramos-Neto & Pivello, 2000).

The Cerrado biome is characterized by very distinct vegetation types. The vegetation types included in the cerrado *sensu lato* range from grasslands, which are composed of grasses and herbs (called *campo limpo*), to savanna formations, which are composed of sparser grasses and herbs with trees growing in low to higher densities, in some locations forming a nearly closed canopy (called *cerradão*) (Oliveira-Filho & Ratter, 2002). To a lower extent, but still very representative of the Cerrado biome, are forest formations that occur in moister and richer soils (Oliveira-Filho & Ratter, 2002). We sampled the Arctiinae moths in 39 plots of 10 x 10 m distributed in three vegetation types of the cerrado *sensu lato* (*campo sujo*, *campo cerrado* and *cerrado sensu stricto*, N = 29 plots), and one forest formation (semideciduous forest, N = 10 plots). These vegetation types represent a gradient where the density and height of trees increases from *campo sujo* to semideciduous forest, while the density of herbaceous cover decreases (Oliveira-Filho & Ratter, 2002). In each plot, we use a Luiz de Queiroz light trap, equipped with a 15W black (UV) lamp (Silveira-Neto & Silveira, 1969). To avoid attracting individuals from other plots, we established our plots at least 100 m and at most 30 km apart (A minimum distance of 50 m between plots was used to test metcommunity theory for Lepidoptera species by Gonçalves-Souza *et al.*, 2014). The distance

of 100 m corresponds to the maximum attraction radius of a 125W black lamp (Muirhead-Thompson, 1991), which is more powerful than the lamp that we used in our study. We sampled the moths in three consecutive years, during the dry (June 2010, July 2011 and July 2012) and rainy seasons (December 2010 through January 2011, November 2011 and December 2012). In each plot, we sampled the moths in two non-consecutive nights, totaling 12 nights of sampling in each plot (six in the dry and six in the rainy seasons). We identified the specimens to the lowest possible taxonomic level, using the appropriate literature (Hampson, 1898, 1900, 1901, 1914; Watson & Goodger, 1986; Piñas-Rubio *et al.*, 2000; Piñas-Rubio & Manzano, 2003), and comparing our material with specimens in the Becker Collection (Camacan, Brazil). The Becker Collection is the best collection of tiger moths of the Cerrado, and most of its specimens were identified by comparison with types found in European and American museums. Individuals were deposited in the Zoological Collection of the Federal University of Goiás (Goiânia, Brazil).

Definition of the species groups

Habitat specialists and habitat generalists

We separated the species into habitat generalists and habitat specialists, based on presence and absence data, using the species specialization index (SSI; Julliard *et al.*, 2006). This index is calculated from the number of habitat classes (h) occupied by a species within all the habitat classes (H) that exist in the study area: $SSI = ((H/h)-1)^{1/2}$ (Julliard *et al.*, 2006). We defined each plot is a habitat class, making a total of 39 habitat classes. Prior to the analyses, we excluded all species (= 60) that occurred only once or twice in the study area, to remove the possible bias of classifying these species as habitat specialists (Pandit *et al.*, 2009), when they are merely more difficult to detect (MacKenzie *et al.*, 2002).

We also separated the groups of habitat generalists and specialists with the coefficient of variation (CV) of the individual densities among the plots (Julliard *et al.*, 2006). In this method, a species can be considered a habitat generalist if it occupies all the classes (in our case, all the plots) in relatively equal abundance in each class. However, if a species occupies all the classes, but in some of them is highly abundant compared with other classes, it can be considered a habitat specialist (Devictor *et al.*, 2008). A species may also be considered a habitat specialist if it does not occupy all classes and has low abundance (Julliard *et al.*, 2006). To better separate the habitat generalists from habitat specialists, we selected the 30 species with the lowest CV values as generalists, and the 30 species with the highest CV values as specialists. The 27 species with intermediate coefficients of variation were excluded from the analysis.

We performed the analyses using these two methods separately. Later, we verified whether the results remained consistent regardless of the method used.

Common and rare

To distinguish between common and rare species, we used the inflection point of the species abundance curve (Siqueira *et al.*, 2012), using the whole database of the metacommunity. The inflection point is the region of the curve in which the curvature changes (Figure 2). We defined the species on the left side of the inflection point as common, and those on the right side as rare. The first eight most abundant species listed in Supplementary material Appendix 1 were selected as being the most common by the inflection-point method.

We also classified these groups of species by labelling the 25% most abundant as common, and the remaining 75% as rare (Siqueira *et al.*, 2012). With this method, 36 species were selected as common (Supplementary material Appendix 1) and 111 as rare species.

We performed the analyses separately for these two kinds of datasets. Later, we verified whether the results remained consistent regardless of the method used.

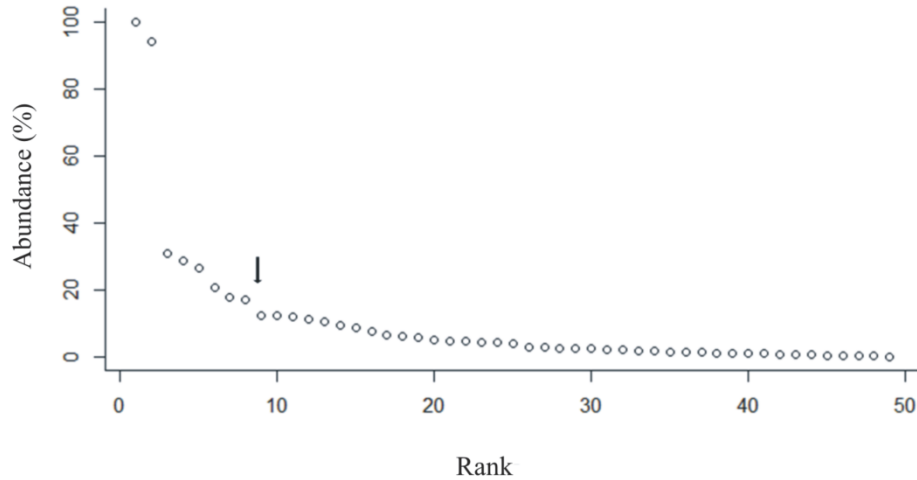


Figure 2. Rank-abundance curve (made with the relative species abundance) and the percentage of the total abundance of Arctiinae in the metacommunity. The arrow indicates the inflection point of the curve. Species on the left side of the arrow are common, and those on the right side are rare.

Separation by tribes

We also performed the analyses separately for each tribe of the subfamily Arctiinae. The tribe Arctiini is more diverse and abundant (Weller *et al.*, 2009), and our database contained 117 species of this group. The tribe Lithosiini totaled 30 species in our database.

Spatial variables

We first calculated an Euclidean distance matrix between all sampling sites. Then, we generated the spatial variables using the Moran's Eigenvector Maps through the PCNM

technique (Principal Coordinates of Neighbor Matrices, Borcard & Legendre, 2002). Each spatial variable generated represents a different spatial pattern that might fit or not the variance in our response data (see Dray *et al.*, 2006, for further details of spatial variables generated through this technique). We used all the MEM axes (eigenvectors) with positive eigenvalues as spatial predictors in the Redundancy analyses (see below; Dray *et al.*, 2006). All MEM axes are orthogonal, and those with high eigenvalues associated are said to represent broad-scale patterns, while the MEM with lower eigenvalues associated represent finer scales (Griffith & Peres-Neto, 2006). For example, if our response data is related to MEM 1 (higher eigenvalue) we can assume that our response data have a spatial pattern in broad scale (e.g. increase in community differentiation through distance). On the other hand, a MEM with low associated eigenvalue related to the response matrix indicates a spatial pattern at a finer scale (e.g. some habitat differences between closer sites that might not exist between distant sites).

Environmental variables

We measured ten environmental variables related to the vegetation present within each plot. Only one was related to the herbaceous layer (herbaceous cover); the others were related to woody plants. In each plot, all woody plants with a stem circumference greater than 10 cm at soil level were sampled. The richness, density, height, petiole, perimeter, leaf length, leaf toughness, leaf mass, and specific leaf area of the woody plant species were measured (see Zava & Cianciaruso, 2014, for more details). As there was more than one individual of the same plant species in each plot, we calculated the coefficient of variation of the above variables measured for each individual.

We measured the herbaceous cover on each plot with a 1-m² quadrat subdivided into 100 cells of 10 x 10 cm. We placed this quadrat on the soil level and counted the number of

cells that contained herbaceous vegetation. We made two measurements per plot, and then calculated the mean number of cells filled with herbaceous vegetation. We measured the herbaceous cover on two occasions, once in the dry season and once in the wet season, to neutralize the effect of a possible influence of seasonality on the vegetation. We used the mean of these two measurements in the analyses.

Collinearity among the environmental variables

We explored the multicollinearity of the variables with a variance inflation factor (VIF, Satoh, 2001). We removed the density of woody plants from the analyses because it had the highest VIF value (more than five, Simões *et al.*, 2013).

Statistical analysis

We used Redundancy Analysis (RDA) to evaluate which factors best explain moth species composition. RDA is a multivariate analysis quite similar to multiple regression in which the variance in a response variable is related to multiple predictor variables. In the RDA analysis the community data matrix (Sites in rows and species abundance in columns) is related to one matrix of predictor variables (i.e. the variance in species data is related to the set of environmental predictors). To understand the factors that best explained the distribution of each group of Arctiinae moths, we first performed two Redundancy Analysis (RDA), one with all the spatial variables as predictors of moth species composition (moth species data with sites in rows and species in columns) and another with all the environmental variables as predictors. In case of significant global RDA models, we were able to use Blanchet *et al.* (2008) recommendations to select the most important variables through forward selection. We used the adjusted R^2 of the global model and the p values (≤ 0.05) of each variable as selection criteria (i.e. the reduced model could not have a higher adjusted R^2 than global model). Then,

we used the environmental and spatial variables selected by the forward selection procedure in a partial RDA (i.e. two sets of predictors, the environmental and the spatial one) followed by variation partitioning (Borcard *et al.*, 1992; Peres-Neto *et al.*, 2006) for each group of species. The variation partitioning show how much variation is explained by the environmental variables, how much by the spatial variables and how much variance are explained by both, spatial and environmental.

Through the variation partitioning, it is possible to evaluate the contribution of spatial and environmental variables to the composition of the species groups. The components of the explanation given by variation partitioning are: the total variance explained (in the composition of each group of species) $[a+b+c]$; the variance explained by the environmental variables $[a+b]$; the variance explained by the spatial variables $[b+c]$; the variance explained exclusively by the environmental variables $[a]$, the variance explained exclusively by the spatial variables $[c]$; the variance shared by the environment and space $[b]$ and the unexplained variance $[d]$ (Peres-Neto *et al.*, 2006).

The response matrices (sampling sites in rows and species in columns) were composed of: (i) habitat generalists, (ii) habitat specialists, (iii) common species, (iv) rare species, and tribes (v) Arctiini and (vi) Lithosiini.

All matrices were transformed with the Hellinger method to reduce the effect of many zeros on lower-abundance matrices (Legendre & Gallagher, 2001). We performed the analyses in the R program (R Core Team 2014).

Results

In our 39 plots, we sampled 5632 Arctiinae moths belonging to 147 species (Supplementary material Appendix 2). The matrix with all arctiine species (tribes Arctiini and Lithosiini together) was influenced by the environment (Table 1, Figure 3), with the richness

of woody plants and the herbaceous cover as the main environmental variables selected for the RDA models.

Habitat generalists versus habitat specialists

The habitat-specialist species (those species that just occur in some communities) were influenced by both the spatial and the environmental variables, regardless of the selection method of the species (SSI or Coefficient of Variation) (Table 1, Figure 3). Despite the low value of the adjusted R^2 (Table 1), both the spatial and the environmental variables helped to explain the variation of the data matrix including only habitat-specialist species (Table 1, Figure 3). The spatial and environmental variables also explained part of the variation in habitat-generalist species (those species that occur in all or almost all communities of the metacommunity); however, they were more influenced by the environment (Table 1, Figure 3), regardless of the separation method (SSI or coefficient of variation) of these species. The habitat-generalist species showed a higher percentage of explanation than the habitat-specialist species (Table 1, Figure 3).

Rare versus common species

The rare species (the 75% least abundant species, and the inflection point method) were influenced by the spatial and the environmental variables, but the common species (those species with higher individual abundance) (selected by both methods) were influenced only by environmental factors. The matrix including only common species showed a higher percentage of explained variation than the matrix of rare species (Table 1, Figure 3). As we sampled moths for three years (and thus some species could be rare in one year, but abundant in subsequent years), we performed the analysis for each year separately and found that the percentage of explanation of both space and environment tend to be lower in the dataset of

each year than in a combined three-year dataset, but the overall interpretation of the results are the same.

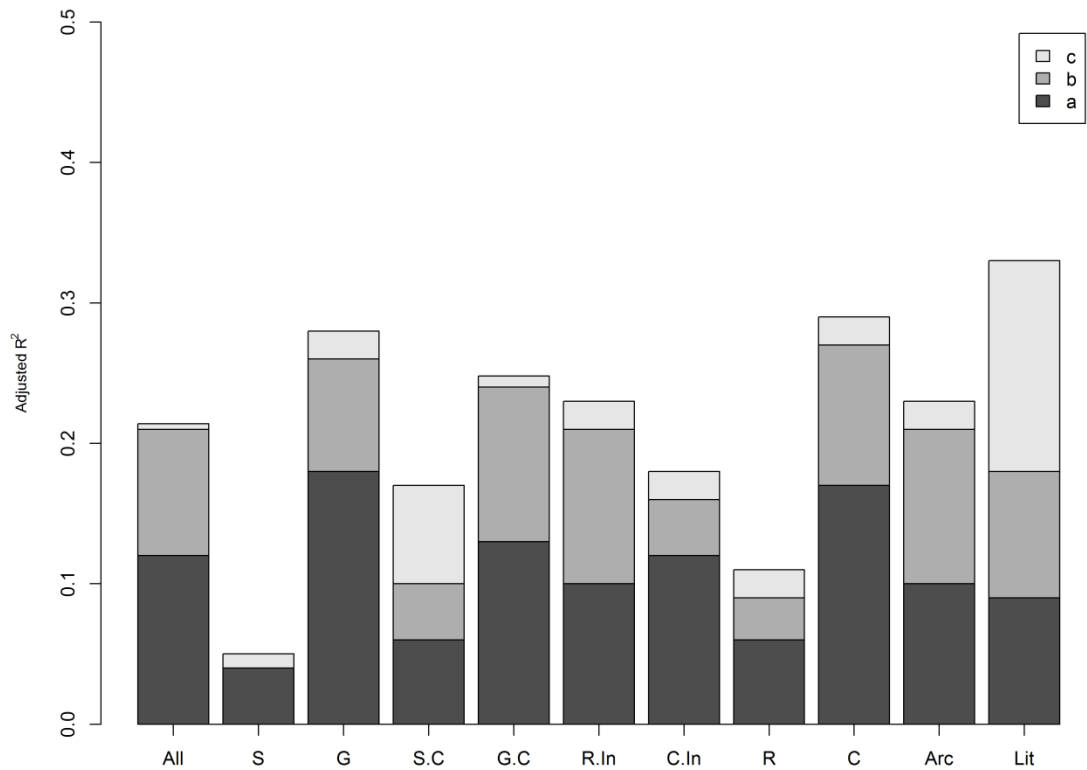


Figure 3. Percentage of explained variation (variation partitioning calculated from pRDA) of the composition of the species groups. "All" means the total dataset of the arctiine moths. S and G mean habitat specialists and generalists (respectively) by the SSI method. S.Co and G.Co mean habitat specialists and generalists (respectively) by the coefficient of variation. R.In and C.In mean rare and common (respectively) by the inflection point method. R.75 means the rare species by the 75% least abundant, and C.25 means the common species by the 25% most abundant. Arc means the tribe Arctiini and Lit means the tribe Lithosiini. The components are represented by letters: environment [a], shared [b] and spatial [c].

Table 1. Results from Partial Redundancy Analysis showing the environmental and spatial variables selected by the forward selection, the percentage of explanation of each component, and the p-value of the environment and space. SSI: species specialization index; CV: coefficient of variation of individual densities (Julliard *et al.*, 2006). Inflection point, 75% and 25% quartiles are the methods of separation of the rare and common species (respectively), in agreement with Siqueira *et al.*, (2012). Env. Sel. and Spa. Sel. are the environmental and spatial variables selected (respectively) for each group in the forward selection.

Group	Method	Env. Sel.	Spa. Sel.	adjusted R ²					
				[a]	[b]	[c]	[d]	P[a]	P[c]
All		Herb.,Riq.	2,4,7	0.12	0.09	0.004	0.78	0.00	0.59
Specialists	SSI	Herb.,LT	3	0.04	0.00	0.01	0.94	0.00	0.01
Specialists	CV	Herb.,Riq.	3,4,10,12,14	0.06	0.04	0.07	0.81	0.00	0.00
Generalists	SSI	Herb.,Riq.	1,2,4	0.18	0.08	0.02	0.70	0.00	0.03
Generalists	CV	Herb.,Riq.	2,4,7	0.13	0.11	0.008	0.73	0.00	0.27
Rare	Inflection	Herb.,Riq.,Per.,LL	1,2,3,4,6,7,24	0.10	0.11	0.02	0.75	0.00	0.03
Rare	75%	Herb.,Riq.	3,4,7	0.03	0.01	0.01	0.94	0.00	0.14
Common	Inflection	Riq.,Herb.	1,2,4,	0.12	0.04	0.02	0.80	0.00	0.19
Common	25%	Riq.,Herb.	1,2,4,7	0.17	0.10	0.02	0.69	0.00	0.09
Arctiini	-----	Herb.,Riq.	2,3,4,7	0.10	0.11	0.02	0.75	0.00	0.06
Lithosiini	-----	Herb.,Riq.	1,3,4,6,7,12,14, 22,24,25	0.09	0.09	0.15	0.64	0.00	0.00

Herb. means herbaceous cover; Riq., the richness of woody plants; coefficient of variation of: leaf toughness (LT), of the perimeter (Per.) and of the leaf length (LL) of woody plants. The letters a, b, c and d mean the adjusted R² values to the environment, shared (between environment and spatial), spatial and error components (respectively). The p (a) and p (c) mean the significance of the environmental and spatial components.

Tribe Arctiini versus tribe Lithosiini

The composition of Arctiini and Lithosiini species were influenced by the environment (herbaceous cover and the richness of woody plants; Table 1, Figure 3). However, Lithosiini species were mainly affected by spatial factors (Table 1, Figure 3).

In general, when comparing pure fractions of the variation partitioning ([a] = environmental and [c] = space), the environmental fraction was more important for most of the species groups (habitat generalists, common, and tribe Arctiini), regardless of the classification method (Table 1). However, the tribe Lithosiini was more influenced by the space. The rare and habitat-specialist species did not show any difference between the spatial and environmental components (Table 1).

The richness of woody plants and the herbaceous cover were the main environmental variables retained for major RDA models (Table 1). The spatial variables selected represent both large-scale and small-scale patterns, since the first, intermediate and last MEMs were retained by the forward selection procedure to the variation partitioning (Table 1).

Discussion

We found that environmental variables affected most of the species groups of arctiine moths, regardless of the separation method. So, the species sorting was the metacommunity model that best explained the distributions of the majority of tiger moth groups in Brazilian savanna areas. These results suggest that the plots with similar environmental conditions have a similar composition of arctiine moth species, independently of the distance between the plots. Other researchers have also found that the environmental variables (e.g. environmental heterogeneity) were more important to explain the composition of different species groups (Cottenie, 2005; Siqueira *et al.*, 2012; Algarte *et al.*, 2014; Padial *et al.*, 2014). Although the herbivorous insects show a smaller proportion of species sorting than other trophic groups

(Soininen, 2014), our results indicated the importance of species sorting in controlling the species distribution (Cottenie, 2005; Van der Gucht *et al.*, 2007) of these moths.

The relative importance of species sorting may differ among different animal taxa, trophic positions and ecosystems (Soininen, 2014), while the importance of spatial structures result from extrinsic factors such study extend and ecosystem type and intrinsic factors such as biological, ecological, and physiological aspects of species (Soininen, 2015). In any case, according to the species sorting, a predominance of ecological interactions among the species and their requirements for resources and environmental conditions dictate the structure of communities (Leibold *et al.*, 2004). The spatial variables may not have been as influential for our species groups because all the individuals can fly during the adult stage. As demonstrated by De Bie *et al.* (2012), flying animals, including insects, have a very weak signal for dispersal limitations. Furthermore, our study was done in a small spatial scale (the longest distance between the plots is 30 km), and according to Soininen (2014) species sorting tends to be more important than dispersal processes at small spatial scales because the species can disperse throughout the area.

Our prediction that the tribe Lithosiini would be more influenced by environmental variables was not supported. We postulated that environmental variables would be more influential for this species group because they feed on a limited set of plants (lichens, bryophytes and algae, Weller *et al.*, 2009) and may occupy habitats that provide these resources. However, our results showed that the tribe Lithosiini is more influenced by the space than by the environment. This result may be due to the small size of most of these moths, as small organisms can be more stochastically distributed, because of their rapid population dynamics (Soininen *et al.*, 2013). Still, although small organisms, like bacteria, can also be strongly driven by local environment, because their dispersal rates are high (Van der Gucht *et al.*, 2007), we agree that the smaller-sized and the fragility of Lithosiini moths

(Hilt & Fiedler, 2006; Weller *et al.*, 2009) suggest that they have limited dispersal capabilities (Hilt & Fiedler, 2006) and the spatial variables can exert a strong influence in them. Most arctiine moths feed on a wide variety of plants, including herbs, shrubs and trees (Weller *et al.*, 2009). Because they are polyphagous, they can occur in different vegetation types (Singer & Bernays, 2009), and therefore their occurrence in the environment would be more limited by parasitoids or pathogens (Ricklefs, 2015). However, the distribution of the members of this tribe was not related to spatial variables. On the contrary, the Arctiini species responded significantly to environmental variables, showing the potential influence of species sorting in structuring its moth assemblage.

Most species groups were related to the spatial variables, although with very low adjusted R^2 values (habitat-specialist, habitat-generalists, rare species and tribe Lithosiini). In agreement with Winegardner *et al.* (2012), the mass effect and the patch models are special cases of species sorting. These models, mainly the mass effect, interact with the species sorting in the way that they affect species distribution (as found by others, e.g. Cottenie, 2005; Pandit *et al.*, 2009; Padial *et al.*, 2014), also observed here. One explanation for the low adjusted R^2 values for the spatial variables is that the dispersal mechanisms may act over a larger spatial extent (e.g. De Bie *et al.*, 2012; Soininen, 2015) than we sampled. Larger spatial scales would allow the detectability of spatial patterns caused by limited dispersal of the individuals, mainly for those species with low flight capacity.

The low percentage of explanation is common in metacommunity studies (Pandit *et al.*, 2009; De Bie *et al.*, 2012; Siqueira *et al.*, 2012) and may result from the very high variation or noise commonly present in abundance data (Cottenie, 2005). In addition, sampling errors (spatial and temporal differences) and stochastic factors (De Bie *et al.*, 2012) might increase the model residuals. Recently, Ricklefs (2015) commented on the importance of community ecologists to include specialized pathogens or other antagonists in the models,

and the lack of these information might be the cause for the low explanation of most modeling approaches.

Groups of habitat-specialist species and rare species had the lowest percentages of explanation, probably because of the difficulty of modeling the distributions of rare species that are present in low abundance (Siqueira *et al.*, 2012). Heino & Soininen (2010) found that common and rare species of aquatic metacommunities are influenced by both, the environment and the space. Despite our different results, we agree with Heino & Soininen (2010) that we can use only the common species (or the most abundant species) to describe the relationships between space and environment structuring metacommunities. Yet, the low values of the coefficients of determination observed in our models may be due to the lack of environmental variables that moth species composition actually responds to. These variables are difficult to measure in the field, such as ecological interactions (e.g. competition and predation; Chase *et al.*, 2002), as well as the pathogen effects discussed by Ricklefs (2015).

The main environmental variables retained by the forward selection procedure were the richness of woody plants, and the herbaceous cover. As demonstrated by other authors, the plant species richness (sometimes indicated as the environmental heterogeneity, Stein *et al.*, 2014), is the main driver of animal species richness and composition among communities (Moreno *et al.*, 2014; Stein *et al.*, 2014). The richness of woody plants and the herbaceous cover are important in structuring the vegetation gradient that occurs in the Cerrado biome (Brazilian savanna) (Oliveira-Filho & Ratter, 2002). For some species groups, these variables had a higher percentage of explanation (common, Arctiini and habitat generalists), indicating that these moths are influenced by the vegetation characteristics, since both larval (leaves) and adults (i.e. feeding on plants to obtain secondary compounds through pharmacophagy, Zaspel *et al.*, 2014) depend on a great variety of woody and herbaceous plants. There are few studies addressing variation partitioning in terrestrial arthropods (see reviews by Soininen, 2014;

Soininen, 2015), and the majority of them showed a lower percentage of explanation of the pure environmental component structuring terrestrial arthropods (Sattler *et al.*, 2010; Baldissera *et al.*, 2012). Sattler *et al.*, (2010) found that the environment did not show any explanation on bee variation in urban metacommunities, and this result might have been caused because they did not measure plants variables. Then, we showed that the richness of woody plants and the herbaceous cover can shape the richness, abundance and distribution of the Arctiinae metacommunity. In addition, in accordance with our results, other studies also found that the vegetation richness was the most important in determining the species composition of Lepidoptera (Panzer & Schwartz, 1998; Usher & Keiller, 1998; Beck *et al.*, 2002) and other herbivorous insects (Panzer & Schwartz, 1998; Lewinsohn & Roslin, 2008; Schuldt *et al.*, 2010).

The environmental (related to deterministic processes) and the spatial variables (related to some stochastic processes and endogenous processes) are important in structuring species assemblages, in this and in other metacommunities (Pandit *et al.*, 2009; Siqueira *et al.*, 2012; Padial *et al.*, 2014) and may be occurring simultaneously (Cottenie, 2005; Chase & Myers, 2011). It must be recognized that other factors not analyzed in this study are important in structuring species in the environment, and may affect the relative importance of the spatial and environmental variables, such as the species interactions (Siqueira *et al.*, 2012; Mehrparvar *et al.*, 2014), the spatial scale analyzed, seasonality of the moths, body size, type and the dispersal capacity of the individual (Cottenie, 2005; De Bie *et al.*, 2012). These are some of the variables that can be addressed in future studies and may improve our knowledge of the moth metacommunity dynamics. Despite the low values of the R^2 of the environmental and spatial components (as in the majority of metacommunity studies, e.g. Pandit *et al.*, 2009; Siqueira *et al.*, 2012; Padial *et al.*, 2014), we showed that the plant species richness and the herbaceous cover dictate the metacommunity of arctiine moths in the Brazilian savanna.

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Contribution of authors

CM and VGF conducted fieldwork, conceived and designed the text/analysis. CM analyzed the data and wrote the manuscript, as this is part of her Thesis. VLL and VGF helped in writing, preparation and provided editorial advice to this manuscript.

Disclosure

We declare that we do not have any conflict of interest.

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CAPÍTULO 2

Deterministic and stochastic processes determine the functional and phylogenetic structure of moth communities

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Abstract

Deterministic and stochastic processes are of great importance in influencing the structure of communities. Deterministic processes are the niche-based models, for example environmental filtering, and fitness-dependent interactions between species. While stochastic processes are mainly related to neutral community models, like as ecological drift, dispersal limitations, random speciation and extinction, and fitness equivalence of species interactions. Here we tested if deterministic and stochastic processes have the same force of influence on functional and phylogenetic structure of moth communities. Specifically, we hypothesized that Arctiini functional and phylogenetic structure would be more influenced by stochastic processes because this tribe of moths belongs to a high diverse clade and present a high dissimilarity of their morphological traits. They are mainly diet generalists, and can occupy a wide range of vegetation habitats. Thus spatial variables, like dispersal limitations would be a greater limitation for them to migrate to distant communities. On the other hand, we hypothesized that Lithosiini functional structure would be more influenced by deterministic processes, because moths within this tribe are mainly diet specialists and occur with more abundance in specific vegetation types. Thus, their functional traits might respond to environmental filtering, in vegetation types that provide the narrow range of resources this group of species explore. Contrary to our expectations, both, deterministic and stochastic processes are important to determine the functional and phylogenetic structure of Arctiini and Lithosiini

moths. However, the percentage of explanation of environmental and spatial variables is contrasting, depending on the functional and phylogenetic relationships among species.

Key-words: Arctiini; environment; Lithosiini; phylogeny; space; traits; variation partitioning

Introduction

The distribution of species in communities can be influenced by deterministic or stochastic processes, or both (Leibold *et al.*, 2004; Winegardner *et al.*, 2012; Arnan *et al.*, 2015; Moreno *et al.*, 2016). Deterministic processes are mainly related to environmental filtering, and to species interactions and their relationships to abiotic and biotic factors, corresponding to the niche-based models (Kraft *et al.*, 2008; Pavoine & Bonsall 2011). While stochastic processes are mainly related to ecological drift, dispersal limitations, random speciation and extinction, and fitness equivalence of all individuals (Leibold *et al.*, 2004; Hubbell, 2001; Pavoine & Bonsall, 2011).

Recent studies have shed new light on how spatial and environmental processes may shape species diversity at the community scale (Carvalho & Tejerina-Garro, 2014; Arnan *et al.*, 2015). Both, space (related to stochastic forces) and environment (related to deterministic forces) show different results of influence on distinct groups of species, like as habitat generalists and specialists, species that occur in rarity or are common, and groups of species based on their body size and dispersal ability (Padial *et al.*, 2009; De Bie *et al.*, 2012; Siqueira *et al.*, 2012; Gonçalves-Souza *et al.*, 2014; Moreno *et al.*, 2016). Thus, the structure of communities can be influenced by species' functional traits (Webb *et al.*, 2002; Siefert *et al.*, 2013; Carvalho & Tejerina-Garro, 2014; Arnan *et al.*, 2015), which are, in large part, dictated by their phylogenetic history (Webb *et al.*, 2002; Gavilanez & Stevens, 2013; Arnan *et al.*, 2015).

Characteristics that affect the growth, reproduction, and survival of the individual can be considered as a functional trait (Violle *et al.*, 2007), revealing the ecological similarities on communities (Cianciaruso *et al.*, 2009; Pavoine & Bonsall, 2011). However, the choice of a group of traits might not show the general answer to the influence of stochastic or deterministic processes on communities (Pavoine & Bonsall, 2011). Phylogenetic data can add much more information about species relationships and shared ancestry (Webb *et al.*, 2002; Pavoine & Bonsall, 2011). Thus, using the functional traits and phylogenetic information of the species, instead of just their taxonomy, can help us to better understand the mechanisms of species distributions within communities (McGill *et al.*, 2006). Phylogenetic and functional structure can provide critical information that cannot be extracted from scientific nomenclature (McGill *et al.*, 2006; Gavilanez & Stevens, 2013), primarily because taxonomic identities alone, offer little insight into the ecological similarities of species (Pavoine & Bonsall, 2011; Siefert *et al.*, 2013), and might not reveal the correctly influence of stochastic and deterministic processes on communities (Pavoine & Bonsall, 2011).

There is a lack of information about the influence of stochastic and deterministic processes on terrestrial arthropods (reviews by Soininen, 2014; 2016), and the few studies addressing this variation partitioning showed a lower percentage of explanation of the pure deterministic factors (i.e. Sattler *et al.*, 2010; Baldissera *et al.*, 2012, but see Gonçalves-Souza *et al.*, 2014; Moreno *et al.*, 2016). However, terrestrial arthropods, like as Lepidoptera species are highly influenced by the environmental conditions of their habitats (Panzer & Schwartz, 1998; Usher & Keiller, 1998; Beck *et al.*, 2002; Gonçalves-Souza *et al.*, 2014; Moreno *et al.*, 2014; Moreno *et al.*, 2016), as they are often closely associated with plant species, in both the larval (i.e., as herbivores) and adult stages (i.e., as pollinators). Here we analyzed one of the richest groups of Lepidoptera, the Arctiinae subfamily (Brehm, 2007; Weller *et al.*, 2009). About 11,000 species of Arctiinae have been described worldwide (Zahiri *et al.*, 2012), with

roughly 6,000 occurring in the Neotropics (Watson & Goodger, 1986; Weller *et al.*, 2009). Arctiinae moths belong to the Erebidae family (Zahiri *et al.*, 2012), and are composed of tribes Lithosiini, Amerilini, Syntomini and Arctiini (Zaspel *et al.*, 2014). Species within tribes Arctiini and Lithosiini have different morphological characteristics and highly divergent feeding habits (Hilt & Fiedler, 2006; Singer & Bernays, 2009; Wagner, 2009). The vast majority of Lithosiini tribe is represented by relatively small moths (Weller *et al.*, 2009), that are mainly lichen feeders (diet specialists, Singer & Bernays, 2009; Weller *et al.*, 2009; Wagner, 2009). Arctiini are the most diverse tribe, including species variable in their morphology and life histories. They are small to medium-size moths that feed on a variety of plants as larvae, including grasses, herbs, shrubs and trees (most of them are diet generalists, Singer & Bernays, 2009; Weller *et al.*, 2009). Some Arctiini and Lithosiini species sequester noxious substances from their hosts (mainly pyrrolizidine alkaloids, and lichen polyphenolics, respectively), that provide to them protection against natural enemies (Hartmann, 2009; Scott *et al.*, 2014; Zaspel *et al.*, 2014). Many species warn their natural enemies about their unpalatability with bright coloration and mimicry of unpalatable insects like other Arctiinae moths, wasps, beetles and butterflies (Bowers, 2009; Zaspel *et al.*, 2014).

The differences in morphology, like as body size, and coloration of Arctiini and Lithosiini moths can be the main response for them to occupy different habitat types (Hilt & Fiedler, 2006). Also, the body size can influence the population growth, the distribution of the species in the environment (De Bie *et al.*, 2012; Vogt *et al.*, 2013), and can affect the main ecosystem process realized by moths in the adult phase (pollination, as described for Sphingidae moths, Agosta & Janzen, 2005). Besides, some traits, mainly the colors of wings, can affect the regulation of the community structure, realized on moths, like predation and parasitism, as most Arctiinae moths signal its unpalatability through warning coloration (Simmons, 2009).

As showed, Arctiini and Lithosiini diverge in several aspects of their ecological niches and their functional structure might respond differently to stochastic and to deterministic processes. Thus, we predicted that Arctiini functional and phylogenetic structure would be more influenced by space (related to stochastic processes) because they are diet generalists, feed on a wide variety of plants (Wagner, 2009; Weller *et al.*, 2009), their traits allow them to explore a wide variety of vegetation types (Hilt & Fiedler, 2006), and probably could be mainly limited by their dispersal capabilities. On the other hand, we postulate that Lithosiini functional structure should be more influenced by environmental variables (related to deterministic processes) because they present a restrict diet, feeding mainly on lichens (Wagner, 2009; Weller *et al.*, 2009), so their ecological niche might be conserved (Futuyma & Moreno, 1988), and their functional traits might respond to environmental filtering on the types of vegetation that provide these resources (Hilt & Fiedler, 2006).

Methods

Study site

We collected the Arctiinae moths in the Emas National Park (ENP), located in the Cerrado biome, an area of Brazilian savanna (17°49'–18°28'S, 52°39'–53°10'W), which is one of the 25 documented biodiversity hotspots in the world (Myers *et al.*, 2000). The climate of this tropical region is humid, with three dry months in the winter. The annual rainfall varies from 1200 to 2000 mm and the average annual temperature is around 25°C (Ramos-Neto & Pivello, 2000). This Brazilian savanna encompasses distinct physiognomies that varies from areas without shrubs or trees, composed by 100% of grasses and herbs (called *campo limpo*) to areas with a very complex structure, with a lot of taller trees and fewer grasses and herbs (forest formations) (Oliveira-Filho & Ratter, 2002).

Community data

We sampled Arctiinae moths in 39 plots of 10 x 10 m using *Luiz de Queiroz* light traps, with a 15W black lamp (Silveira-Neto & Silveira, 1969). The plots had a minimum distance of 100m from each other to avoid attracting individuals from other plots (Muirhead-Thompson, 1991). We sampled moths over a three-year period during the dry (June of 2010, July of 2011 and July of 2012) and rainy seasons (December of 2010, November of 2011 and December of 2012). Specimens were identified to the lowest possible taxonomic level (Hampson, 1898; 1900; 1901; 1914; Watson & Goodger, 1986; Piñas-Rubio *et al.*, 2000; Piñas-Rubio & Manzano, 2003). We also compared our specimens with digital images and the reference collection of Becker (Camacan, Bahia, Brazil). Specimens that were identified to species level were used in the final dataset. All voucher specimens were deposited in the Coleção Zoológica da Universidade Federal de Goiás (Goiânia, Brasil).

Functional trait data

We measured the following four functional traits for each species included in our dataset: wingspan, body length, thorax width, and fore wing colors. We used three male individuals of each species to measure the wingspan, body length, and the thorax width; then we calculated the mean of each variable to each species and used these values in the subsequent analyses.

We performed a Pearson's correlation between the three traits that reflect the body size (wingspan, body length and chest width). As these three traits were highly correlated with each other (> 82%), we performed a Principal Component Analysis (PCA) and used the first axis of the PCA as the body size variable in the subsequent analysis.

DNA extraction, PCR and Sequencing

We extracted the DNA of two legs of each specimen using a DNeasy Extraction kit (Qiagen, Valencia, CA). For specimens in which little DNA was recovered (25 samples), we performed whole genome amplification (WGA) using a REPLI-g kit (Qiagen, Valencia, CA). Samples for which ample quantities of DNA could be recovered were used in downstream polymerase chain reaction (PCR) assays following the methods of Zaspel *et al.* (2014). We amplified six target regions for each sample: (1) the barcode region of the COI gene (COI), (2) the D2 region of the 28S ribosomal subunit sequence (28S), (3) wingless (WGS), (4) elongation factor 1- α protein (EF1- α), (5) ribosomal protein subunit S5 (RpS5) and (6) glyceraldehydes-3-phosphate dehydrogenase (GAPDH).

Purified PCR products were sent to the Genomic Core Facility at Purdue University, USA, for Illumina library preparation and sequencing and bioinformatics pipeline were developed at Purdue University, called "WideSeq". WideSeq involves Nextera transposon tagging/fragmentation ("tagmentation") of template DNAs, multiple loci PCR product pools, followed by dual index/flowcell oligo-complementary adapter extension. A standard alignment program, (i.e., Bowtie2), was then used to map resulting reads to known reference sequences from Zaspel *et al.* (2014).

Alignment and phylogenetic analysis

We performed alignments using ClustalW implemented in Geneious v.10.0.3 (Kearse *et al.*, 2012) and also using MAFFT v. 7 online (Katoh & Standley, 2013; <http://mafft.cbrc.jp/alignment/server/>). To determine the best partitioning scheme for codon positions and the best evolutionary models for the dataset, we used Partition Finder v. 1.1.1 (Lanfear *et al.*, 2012). We performed a maximum likelihood (ML) using RAxML (Stamatakis *et al.*, 2008) along with 1,000 bootstrap replicates on the CIPRES Web Portal (Miller *et al.*,

2010). The phylogenetic tree was visualized using the statistical software package R (R Core Team 2016).

Environmental variables (one of the features of deterministic factors)

In all plots that we sampled Arctiinae moths, ten environmental variables related to the vegetation were obtained. Nine of these variables were related to the woody plants (richness, density, and coefficient of variation of height, petiole, perimeter, leaf length, leaf toughness, leaf mass and specific leaf area) (see Zava & Cianciaruso, 2014; for more details). The tenth variable was herbaceous cover, measured by the filling of 100 little squares (of 10x10cm) in a square of 1m² (mean of two measures in each plot).

We tested for correlations between the environmental variables using the VIF (Variance Inflation Factors, Satoh, 2001) method. The density of woody plants was highly correlated with the richness of woody plants ($r = 0.86$), thus we removed the variable density of woody plants in the analyses, due to its higher VIF value.

Spatial variables (related to stochastic factors)

We generated the spatial variables using the PCNM technique (Principal Coordinates of Neighbour Matrices, Borcard & Legendre, 2002), from the Euclidean distance matrix of the geographical coordinates of each sampled plot. We used all the axes (eigenvectors) with positive eigenvalues resulting from PCNM as the spatial descriptors in the Redundancy analyses (Dray *et al.*, 2006).

Statistical analysis

Functional and phylogenetic structure

We calculated the net relatedness index (NRI) and the nearest taxon index (NTI) for the functional and phylogenetic data for each community (each plot). The NRI quantifies overall clustering of taxa on a functional or phylogenetic tree. The NTI quantifies the extent of terminal clustering on a functional or phylogenetic tree (Webb *et al.*, 2002). Both metrics are very dependent on the species pool of each community and their values increase when the species of a community are more related (functional or phylogenetic grouping) to each other and become negative when the species are not so related to each other (functional or phylogenetic overdispersion) (Webb *et al.*, 2002).

The traits variables consisted of quantitative and categorical variables. Thus, we calculated the distances matrices with the Gower's distance (Podani & Schmera, 2006) and the NRI as -1 X ses.mpd and NTI as -1 X ses.mntd using the package Picante (Kembel *et al.*, 2010) in the statistical software R (R Core Team 2016).

Forward selection and variation partitioning

We performed global multiple regressions for functional and phylogenetic structure (NRI and NTI) with all the spatial and environmental variables. Then we selected the most important spatial and environmental variables with forward selection, where the adjusted R^2 of the global model and the p values (≤ 0.05) of each variable are used as selection criteria (Blanchet *et al.*, 2008). We used the environmental and spatial variables selected in the partial multiple regressions, followed by variation partitioning (Borcard *et al.*, 1992; Peres-Neto *et al.*, 2006) for each dataset separately (functional and phylogenetic structure of tribe Arctiini, and functional structure of tribe Lithosiini).

Through variation partitioning, we know the total explained variance (environment, space, shared by environment and space; and residuals); the variance explained exclusively by the environmental variables, the variance explained exclusively by the spatial variables; the variance shared by the environment and space and the unexplained variance (Peres-Neto *et al.*, 2006). All the analyses were performed in the statistical software package R (R Core Team 2016).

Results

The dataset with the functional traits has 107 species of Arctiinae, in which 91 species belong to tribe Arctiini and 16 to tribe Lithosiini (Supplementary material Appendix 3). In total, the phylogenetic tree is composed by 25 species (Figure 1), in which 18 of them are our species that the WideSeq sequencing worked well, four of them are from Zaspel *et al.* (*in preparation*) (*Carales arizonensis* (Rothschild, 1909), *Hyda basilutea* (Walker, 1854), *Nyridela acroxantha* (Perty, 1833), and *Pheia albisigna* (Walker, 1854)) and three of them are outgroups related to the Arctiinae subfamily (*Arctornis* sp. Germar, 1810, Lymantriinae; *Calyptra thalictri* (Roach, 2008), Calpinae; *Orgyia antiqua* (Linnaeus, 1758), Lymantriinae). The three subtribes represented in our phylogenetic tree are recognized to be derived clades within tribe Arctiini (Zaspel *et al.*, 2014): Phaegopterina (N = 11), Euchromiina (N = 8) and Ctenuchina (N = 3). Species belonging to the same genus were placed together (Figure 1). The outgroups species (N = 3) did not enter in the statistical analyses because they are not part of the Arctiini communities.

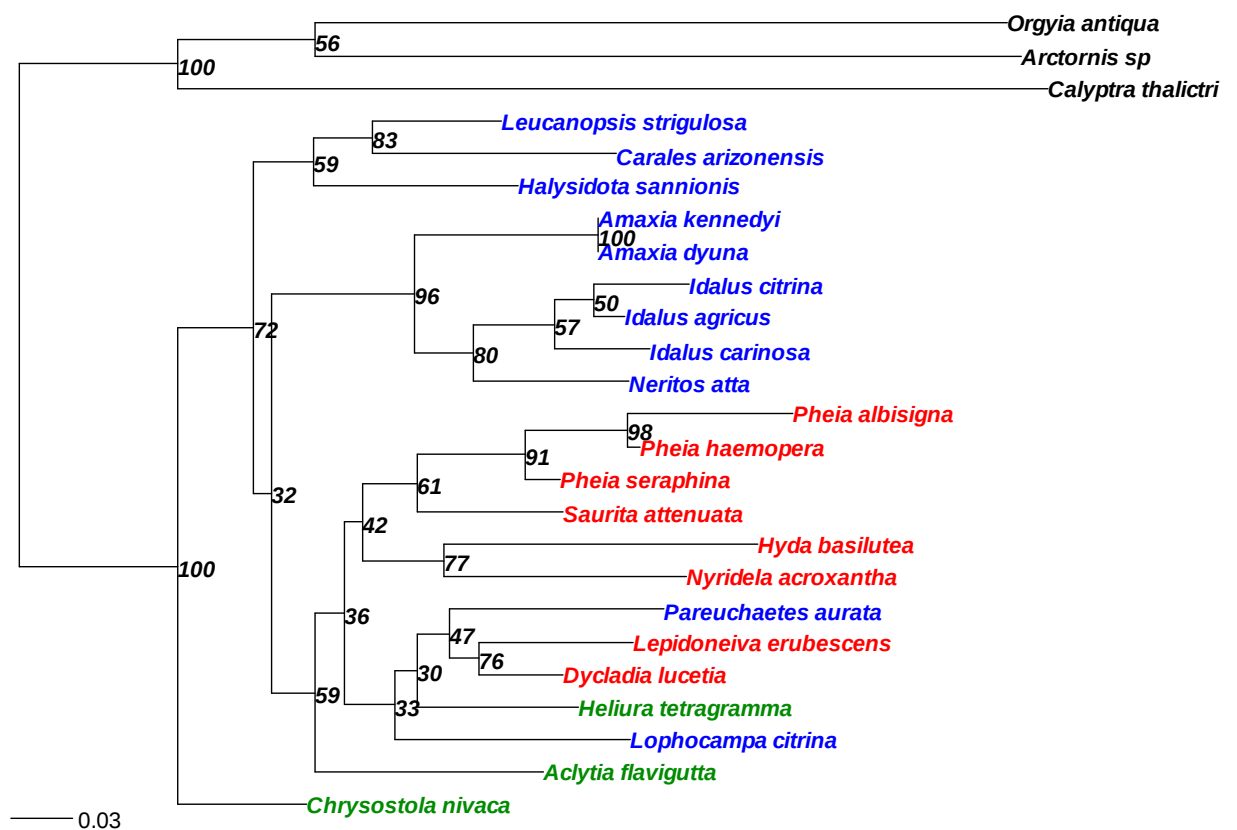


Figure 1. Phylogenetic hypothesis of the 22 species of tribe Arctiini based on molecular data, showing the species relationships across the tribe. The subtribes Phaegopterina, Euchromiina and Ctenuchina are separated by the colors blue, red and green, respectively. The bootstrap values are given on branches.

The environmental variables selected for the multiple regressions models were the richness of woody plants, the herbaceous cover, and the coefficient of variation of the leaf mass, leaf toughness, and perimeter of woody plants (Table 1). The spatial variables selected represent large, intermediate and small-scale patterns, since the first, intermediate and last MEMs were retained for the multiple regressions models (Table 1).

The functional traits of the entirely dataset of Arctiinae were more influenced by space than by the environment (Table 1), even though they were significantly influenced by both (Table 1).

The functional and the phylogenetic structure of the tribe Arctiini were influenced by both, the space and the environment (Table 1). However, the environment was more important to the net relatedness index (NRI, which quantifies the average functional and phylogenetic similarity of all species in a community, Webb *et al.*, 2000; Vogt *et al.*, 2013) and the space was more important to the nearest taxon index (NTI, which quantifies the mean of the distance between species that share the most similarities in their traits and in their phylogenetic history for each community, Webb *et al.*, 2000; Vogt *et al.* 2013) (Table 1).

Just the environment explained the variance of the nearest taxon index (NTI) and the space was slightly more important than the environment in explaining the net relatedness index (NRI) of the tribe Lithosiini (Table 1).

Table 1. Results from Partial Multiple Regressions showing the environmental and spatial variables selected by the forward selection, the percentage of explanation of each component, and the p-value of the environment and space. Env. Sel. and Spa. Sel. are the environmental and spatial variables selected (respectively) for each diversity information in the forward selection.

Group	Information	Env. Sel.	Spa. Sel.	adjusted R ²					
				[a]	[b]	[c]	[d]	P[a]	P[c]
Arctiinae	Funct. (NTI)	H.,R.,LM.	3.8.9.12.18.19	0.19	0.12	0.32	0.35	0.00	0.00
Arctiinae	Funct. (NRI)	LM.	2.8.11.12.18.20	0.12	0.00	0.48	0.38	0.00	0.00
Arctiini	Funct. (NTI)	H.R.P.	3.8.9.12.18.19	0.15	0.13	0.29	0.40	0.00	0.00
Arctiini	Funct. (NRI)	LM.	2.3.7.18.22	0.24	0.00	0.16	0.58	0.00	0.04
Arctiini	Phylo. (NTI)	H.,LT	4.11.21.23	0.04	0.18	0.21	0.55	0.10	0.01
Arctiini	Phylo. (NRI)	H.,R.	2.8	0.16	0.07	0.08	0.67	0.00	0.054
Lithosiini	Funct. (NTI)	P.	2.3.7.8.9	0.15	0.07	0.03	0.72	0.01	0.27
Lithosiini	Funct. (NRI)	P.	2.4.7.15.25	0.17	0.10	0.21	0.50	0.01	0.01

H. means herbaceous cover; R., the richness of woody plants; coefficient of variation of: leaf mass (LM), leaf toughness (LT) and of the perimeter (P.) of woody plants. The letters a, b, c and d mean the adjusted R^2 values to the environment, shared (between environment and spatial), spatial and error components (respectively). The p (a) and p (c) mean the significance of the environmental and spatial components.

Discussion

The functional and phylogenetic structures of communities were influenced by both, the environment and space. Although the space and the environment are important in dictating the communities of Arctiinae species, the relative importance of the environment and space was different for each different index of functional and phylogenetic structure (NRI and NTI). The environment was more important to the total range of traits and overall phylogenetic clustering (NRI) among communities of the tribe Arctiini. Environmental variables are related to deterministic processes, like facilitation, competition and environment filtering, which comprehend the niche-based models (Leibold *et al.*, 2004; Pavoine & Bonsall, 2011), thus species interactions and environmental filters influences the distribution of species taking into account the functional and phylogenetic relationships among all species on communities, as already found to the Arctiini taxonomic diversity (Moreno *et al.*, 2016). The net relatedness index (NRI) measures the functional or phylogenetic distances among the overall species analysed in the trees, thus if the environment was more important than space to the overall functional and phylogenetic structures, we argue that deterministic processes dictate the high dissimilarity of Arctiini species composition along the different types of vegetation that occur in the study area (Moreno *et al.*, 2014).

The environment was also more important to the functionally closer species of Lithosiini (measured by the nearest taxon index, NTI). Lithosiini species do not show many differences in their food resources and occupy similar vegetation types (Hilt & Fiedler, 2006; Wagner, 2009; Weller *et al.*, 2009), thus this result suggests that the environment might be

functioning as a filter to functionally closer species that habit in similar environmental conditions (Keddy, 1992; Weiher *et al.*, 1998). This result was just found to the functional structure and not to the taxonomic diversity (Moreno *et al.*, 2016), showing that just the names of species do not show all the ecological patterns along communities. Moreno *et al.* (2016) showed that Lithosiini species are mainly influenced by space and argued that as they have small size they might be more stochastically structured due mainly to their limited dispersal capabilities (Soininen *et al.*, 2013; Hilt & Fiedler, 2006; Moreno *et al.*, 2016). However, we showed here that Lithosiini can be environmentally structured if we consider their functional traits.

Neutral processes (Hubbel, 2001), related to spatially structured factors, were important to the nearest phylogenetic and functional neighbours of Arctiini, indicating that the distribution of more related species on communities can be dictated by stochastic factors, like random speciation, extinction, and ecological drift (Pavoine & Bonsall, 2011). Purely stochastic processes can indicate that these species (mainly tribe Arctiini) do not present a consistent pattern of evolutionary and ecological similarities (Swenson *et al.*, 2012). Despite the close evolutionary relationship between species belonging to Phaegopterina, Euchromiina and Ctenuchina, this clade is the most rich in species of the entirely Arctiinae subfamily (Zaspel *et al.*, 2014), and the few species represented in our tree might not responding to the environment as it could with addition of more related species belonging to these subtribes. Also, stochastic processes can point to intrinsic factors, like biological, ecological and physiological aspects of species that might be more important in response to the functional and phylogenetic structures on communities than the environmental variables analysed here (Soininen, 2016). But, this result can also be due to some spatially structured environmental variables more important to species traits and to phylogenetic structure that we did not measure in the field. If this is the case, the functional and phylogenetic structures could reveal

answers to deterministic processes that are not showed by species diversity alone (Swenson *et al.*, 2011).

The main environmental variables selected to the variation partitioning analyses were the richness of woody plants and the herbaceous cover, as already shown by Moreno *et al.* (2016). These two are the main variables that structure the gradient of vegetation that occur in Cerrado biome (Oliveira-Filho & Ratter, 2002) and they are very important in dictating the richness and composition of animal species (Rodrigues *et al.*, 2002; Ribas *et al.*, 2003; Almeida & Louzada, 2009; Moreno *et al.*, 2014). These variables were selected to the functional and phylogenetic structure of the tribe Arctiini, but not to functional structure of Lithosiini. Three different variables were also selected to the functional and phylogenetic structure: the coefficients of variation of leaf mass, of leaf toughness and of perimeter of woody plants. Leaf mass and leaf toughness are related to food resource, but also might be related to the concentration of pyrrolizidine alkaloids (PAs) in the plant (Hartmann, 1999). PAs are the most studied secondary compounds sequestered by moths of the tribe Arctiini (Zaspel *et al.*, 2014), and are involved in protect them against predation and parasitism (Bezzares *et al.*, 2004; Bowers, 2009; Singer & Bernays, 2009). Lithosiini do not sequester PAs (Weller *et al.*, 1999). The main secondary compounds sequestered by Lithosiini are lichen polyphenolics (Scott *et al.*, 2014). The presence of lichens in the plant might be related to the perimeter (diameter) of trees (which was the only variable related to the functional structure of Lithosiini), as larger-diameter trees present more richness of lichens (Hofmeister *et al.*, 2016).

Our results showed that we can achieve different results and amplify our understanding of community ecology if we consider more components of diversity (functional and phylogenetic), as already suggested by other authors (i.e. Pavoine & Bonsall, 2011; Swenson *et al.*, 2011). Although the functional and phylogenetic structure of Arctiini showed

similar responses to environmental and spatial variables, it is important to analyse these two facets of diversity separately, as phylogeny might not be a good proxy for functional diversity, even if there are strong phylogenetic signals in the functional traits (Arnan *et al.*, 2015). In addition, the two metrics (NRI and NTI) of the functional diversity of Arctiini were significantly related to environmental variables and just the NRI of phylogenetic diversity was related to the environment. This result indicates that functional diversity might be a better indicator of community assembly processes than phylogenetic diversity (Arnan *et al.*, 2015), as functional traits give a direct response of the species characteristics and to how species interact to each other and to environmental gradients at local scales (Cianciaruso *et al.*, 2009; Pavoine & Bonsall, 2011; Vogt *et al.*, 2013; Carlucci *et al.*, 2015). Although it is still necessary to analyze both, functional and phylogenetic structures of communities because phylogenetic details add more information on diversity (Pavoine & Bonsall, 2011) and as the traits can be conserved or convergent along the evolution (Webb *et al.*, 2002), the responses to stochastic or deterministic factors might be distinct between these two diversity metrics.

Deterministic and stochastic processes can affect in a distinct way different groups of species, for example: common, rare, habitat specialists, habitat generalists species (Pandit *et al.*, 2009; Siqueira *et al.*, 2012; Moreno *et al.*, 2016), and related clades, like tribes Arctiini and Lithosiini (Moreno *et al.*, 2016). Both processes determine the functional and phylogenetic structures of Arctiinae moth. The functional structure showed significant relationships to the environment and to space. The phylogenetic structure was influenced either by space or by environment, depending on the index of measure of the phylogenetic relationships among species. The environment was more important to the higher phylogenetic diversity measured to all species in the tree (NRI) and the space was more important to the closer phylogenetically species (NTI). Thus, stochastic and deterministic processes are important but they also respond differently to the community structure, depending on the

functional and phylogenetic relationships among species (Arnan *et al.*, 2015; Carvalho & Tejerina-Garro, 2015), as showed by our results.

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CAPÍTULO 3

Environmental filtering is stronger than competitive exclusion in dictating moth functional structure

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Abstract

Environmental filtering and competitive exclusion are two strong forces that influence the species community structure. If the community is composed by species more related to each other than expected by chance (functional attraction), they share more ecological similarities and the coexistence of those species is mainly governed by environmental filters. In contrary, if the community is composed by species less functionally related than expected by chance (functional repulsion), thus some previous antagonistic interactions, like as competition, excluded highly similar species from coexisting at the same space and time. Here we hypothesized that communities of Arctiinae moths present a clustered pattern (more related than expected by chance) in simple habitats (with low quantity of food resources and shelters) and in xeric weather conditions (with water deficit, higher range of temperature, and reduced food quality), as these habitats might select traits of species that can survive on unfavorable conditions. In contrary, we hypothesized that structurally complex habitats and better weather conditions present more richness and abundance, highlighting the prevalence of competition for resources, and thus showing an overdispersed pattern in their communities. Opposed to our expectations, most communities presented a significant functionally clustered pattern, and just two communities showed a significant overdispersed pattern. Even in physiognomies higher in species richness, the communities showed a tendency to cluster, thus the species present a narrowed range of important functional traits analyzed in this study. In addition,

environmental variables were strongly related to the functional structure on most communities. Thus, environmental variables are acting as filters, selecting species with similar traits able to coexist at the same time and space. We argue that environmental filtering is a strong force influencing the occurrence of species on communities of moths and that competition is a weak force to this group of insects.

Key-words: Cerrado biome; clustering; dry season; overdispersion; physiognomies; rainy season

Introduction

Environmental filtering and competitive exclusion are two strong forces that influence the community structure (Webb *et al.*, 2002; Lebrija-Trejos *et al.*, 2010; Vogt *et al.*, 2013; Carvalho & Tejerina-Garro, 2015; Nunes *et al.*, 2016). If a community is composed by species with more similar traits than expected by chance, which might share common ecological niche, thus this community is mainly governed by some kind of environmental filtering that selected species to survive in particular environmental conditions (Webb *et al.*, 2002; Lebrija-Trejos *et al.*, 2010; Vogt *et al.*, 2013; Nunes *et al.*, 2016). In contrary, if a community is composed by species with traits that are less similar than expected by chance, thus phenotypically similar species were excluded from the community by competition (Webb *et al.*, 2002; Lebrija-Trejos *et al.*, 2010; Vogt *et al.*, 2013).

In recent years, many studies used phylogenies as proxy for functional patterns to respond about ecological relationships between species in community scale (Webb *et al.*, 2002; Kembel, 2009; Cianciaruso, 2011). Although, the use of functional traits to respond if environmental filtering or competitive exclusion is stronger in dictating communities has been recognized to be better than the use of phylogenetic relationships between species

(Cianciaruso *et al.*, 2009; Carlucci *et al.*, 2015). The functional traits give a direct response of the species characteristics; they provide a direct quantification of how species interact to each other, and how they respond to environmental gradients (Cianciaruso *et al.*, 2009; Vogt *et al.*, 2013; Carlucci *et al.*, 2015).

Here, we tested if environmental filtering or competition is more important in dictating the Actiinae moth species occurrence in communities, based on some of their functional similarities. Arctiinae is a rich subfamily of Lepidoptera, composed by species with a high range of morphological and ecological variation. For example, they vary widely in body and wingspan sizes, in patterns of body and wings coloration, in food resources and in the type of secondary compounds they sequester (Simmons, 2009; Weller *et al.*, 2009; Scott *et al.*, 2014). The majority of species of tribe Arctiini is diet generalist, feeding on a wide range of plants and is specialized (“specialized generalists”, Singer & Bernays, 2009) in searching for noxious substances, like as pyrrolizidine alkaloids, cardiac glycosides and iridoid glycosides from their hosts plants (Bowers, 2009; Zaspel *et al.*, 2014). In contrary, Lithosiini are smaller moths, mainly lichen-feeders, and many species sequester lichen polyphenolics from their hosts (Bowers, 2009; Weller *et al.*, 2009; Scott *et al.*, 2014). All these morphological and ecological variation within the subfamily influence the species distribution on the environment (Hilt & Fiedler, 2006), and thus the species richness and composition are highly dissimilar along different vegetation types (Hilt & Fiedler, 2006; Brehm & Axmacher, 2006; Hawes *et al.*, 2009; Moreno *et al.*, 2014).

Arctiinae richness and composition are strongly correlated to the vegetation characteristics that occur in Cerrado biome (Ferro & Diniz, 2007; Moreno *et al.*, 2014; 2015; 2016). This biome presents a continuum gradient of vegetation ranging from simple to structurally complex habitats and presents a highly seasonal weather, with marked dry and wet seasons (Morais *et al.*, 1999; Oliveira-Filho & Ratter, 2002). Simple habitats (with less

quantity of resources and shelters against natural enemies, for example) and xeric weather conditions (with low precipitation, reduced food quality, and higher range of temperature) might select species (through environmental filtering) more functionally similar, presenting characteristics that make them able to survive in unfavorable environments. Following this logic, we hypothesize that (1) species occurring in simple habitats (*campo sujo* and *campo cerrado* physiognomies) and (2) species occurring in xeric weather conditions (dry season) will show more functionally cluster communities than expected by chance. In contrary, we hypothesize that (1) species occurring in structurally complex habitats (*cerrado sensu stricto* and semideciduous forest physiognomies) and (2) species occurring in mesic weather conditions (rainy season) will show more functionally overdispersed communities than expected by chance, as a result of the higher species richness and abundance (Moreno *et al.*, 2014), and consequently more prevalence of antagonistic interactions (Webb *et al.*, 2002).

However, the overdispersion pattern would be response to the occupation of different niches in structurally complex habitats, and not to antagonistic interactions between species (Webb *et al.*, 2002). Thus, we tested if in structurally complex habitats and in the rainy season the moth species richness show a negative relationship with the functional structure (the indexes used to calculate the functional structure become negative in functional dissimilarity - overdispersion) (Webb *et al.*, 2002). In this case, the negative relationship means that habitats with higher species richness offer more quantity of niches (Bazzaz, 1975; Webb *et al.*, 2002; Tews *et al.*, 2004), diminishing the competition for resources (Webb *et al.*, 2002). In contrary, a positive relationship means that even communities with high species richness tend to present a higher degree of functional similarity (clustering), as a reflex of a strong process of environmental filtering (Webb *et al.*, 2002).

Methods

Study site

We collected the Arctiinae moths in the Emas National Park (ENP), located in Cerrado biome, which is one of the 25 biodiversity hotspots of the world (Myers *et al.*, 2000). ENP presents a humid tropical climate, with three dry months in winter (June, July and August). The annual rainfall varies from 1200 to 2000 mm and the average annual temperature is around 25°C (Ramos-Neto & Pivello, 2000). The climate of Cerrado biome is highly seasonal. The dry season is from May to September, when the average rainfall is 23.9 mm (with relative humidity of 58.2%), the average minimum temperature is 12°C and the maximum temperature is 25°C. The wet season occur in the rest of the seven months of the year. The average rainfall is 184.7 mm (with relative humidity of 75.7%), the average minimum temperature is 17°C and the average maximum temperature is 26°C (Pinheiro *et al.*, 2002).

The Cerrado biome, also called Brazilian savanna, encompasses distinct physiognomies that varies from open areas, composed by 100% of grasses and herbs (called *campo limpo*) to areas with a high complex structure, with a lot of taller trees and fewer grasses and herbs (forest formations) (Oliveira-Filho & Ratter, 2002).

Community data

To test if simple habitats present species that are more functionally related (clustered) and if structurally complex habitats present species that are less functionally related (overdispersed) (see hypotheses), we sampled Arctiinae moths in four different physiognomies of the Cerrado biome: *campo sujo*, *campo cerrado*, *cerrado sensu stricto* and semideciduous forest. These physiognomies represent a crescent gradient of shrubs and trees

and a decrescent gradient of herbs, from simple habitats (*campo sujo*) to structurally complex habitats (semideciduous forest) (Oliveira-Filho & Ratter, 2002).

To test if the species occurring in the dry season represent functionally cluster communities and if the moth communities are functionally overdispersed in the rainy season (see hypotheses), we sampled the Arctiinae moths in ten sampling occasions, five during the dry season (June of 2010, July of 2011, July of 2012, August of 2013 and August of 2014) and five during the rainy season (December of 2010, November of 2011, December of 2012, January of 2014 and January of 2015).

We sampled the moths in 40 plots of 10 x 10 m using a *Luiz de Queiroz* light trap (Silveira-Neto & Silveira, 1969), with a 15W black lamp. The plots have a minimum distance of 100m from each other to avoid attracting individuals from other plots (Muirhead-Thompson, 1991). We identified the specimens until the lowest possible taxonomic level through literature (Hampson, 1898; 1900; 1901; 1914; Watson & Goodger, 1986; Piñas-Rubio *et al.*, 2000; Piñas-Rubio & Manzano, 2003), comparing digital images and with the specimens of the Becker Collection. The data used in this paper was composed just by the specimens that we sorted to the species level and by the specimens that we measured the functional traits (N = 107 species). All sampled individuals were deposited in the *Coleção Zoológica da Universidade Federal de Goiás* (Goiânia, Brasil).

Functional trait data

We measured three morphometric functional traits of each species: wingspan, body length, thorax width (in centimeters). We took three individuals of each species to measure the wingspan, body length and the thorax width; then we calculated the mean of each variable to each species and used these values in the subsequent analyses. We also measured one trait

related to the adaptive coloration of the species. For this, we noted all the colors occurring on the fore wings (Supplementary material Appendix 3).

We chose these morphological traits to better separate the Arctiinae moths. The differences in morphology, body size, and coloration of Arctiinae moths can influence their distributions on different environments (Hilt & Fiedler, 2006). The body size can influence the population growth (De Bie *et al.*, 2012; Vogt *et al.*, 2013), and can affect the main ecosystem process realized by moths in the adult phase (pollination, as described for Sphingidae moths, Agosta & Janzen, 2005). Also, these traits, mainly the colors of the wings, can affect the regulation of the moth community structure, like predation and parasitism (Fujiwara & Nishikawa, 2016), as most Arctiinae moths signal its unpalatability through warning coloration (Simmons, 2009).

We performed a Pearson's correlation between the quantitative variables. As the three traits that reflect body size (wingspan, body length and chest width) were much correlated with each other, we performed a Principal Component Analysis (PCA) and used the first axis of the PCA as the body size variable in the subsequent analyses.

Statistical analyses

Functional structure

We calculated the functional structure for each community (each of the 40 plots) as the nearest taxon index (NTI). This metric is mostly used for phylogenetic structure, but it can also be used to calculate the functional structure in communities (Pavoine & Bonsall, 2011). For this, we substituted the phylogenetic distance matrix by a functional distance matrix. We converted the traits matrix to distances matrices with the Gower's distance (Pavoine *et al.*, 2009), because we have quantitative and qualitative traits. Later, we created a functional dendrogram, with the Unweighted Pair Group Method using Arithmetic averages (UPGMA)

as the clustering method. We used this distance to calculate the NTI for each community. As the functions of NTI (`ses.mntd`) (of package `picante`) calculate the $-NTI$, we multiplied the results of the standard effect size by (-1) (Webb *et al.*, 2002). The NTI quantifies the extent of terminal clustering on a functional tree (Webb *et al.*, 2002). This metric is very dependent on the species pool. Thus, we calculated the null models using the “sample.pool” method (with 999 runs), in which randomize the “community data matrix by drawing species from pool of species occurring in at least one community (sample pool) with equal probability”. The values of NTI increase when the species of a community are more functionally related (clustered) than expected by chance ($p < 0.05$) and become negative when the species within a community are less functionally related (overdispersed) than expected by chance ($p > 0.95$) (Webb *et al.*, 2002; Kembel & Hubbell, 2006).

We tested the presence of environmental filtering by the influence of environmental variables on the functional structure of communities (Pavoine & Bonsall, 2011). We performed a multiple linear regression between environmental variables and the metric of functional structure (NTI), using a forward stepwise selection to reduce the collinearity between variables. As we performed the analyzes for each type of physiognomy, we did not have many degrees of freedom, thus we analyzed four environmental variables previously selected for the entire dataset: richness of trees (1), coefficient of variation of perimeter (2), coefficient of variation of leaf mass (3) and herbaceous cover (4) (see Moreno *et al.*, 2016 for details). All analyses were performed in the statistical software R (R Core Team 2016).

Results

The majority of the communities had positive values of functional structure (NTI), both, in the dry and rainy seasons (Table 1), showing a tendency of moth assemblages to clustering. The nearest taxon index (NTI) showed significant positive values in 47.5% (19) of

the communities in the dry season and 37.5% (15) of the communities in the rainy season (Table 1). Of the 40 plots sampled, 10 were clustered only in the dry, 6 only in rainy and 9 in both seasons (Table 1).

In relation to the complexity of habitat, the NTI showed that in the dry season, the plots of *campo sujo*, which is the simplest habitat type, showed only one (16.6%) clustered community (Table 1). *Campo cerrado* (that is simpler than *cerrado sensu stricto* and semideciduous forest) had 8 (57.14%) clustered communities (Table 1). The *cerrado sensu stricto* plots had 7 (70%) functionally clustered communities, and semideciduous forest had 3 (30%) clustered communities (Table 1). In the rainy season, the NTI showed that the proportion of the clustered communities was 0% in *campo sujo*, 57.14% in the *campo cerrado*, 50% in the *cerrado sensu stricto* and 20% in the semideciduous forest (Table 1). If we categorize the physiognomies of *campo sujo* and *campo cerrado* as simple habitats and *cerrado sensu stricto* and semideciduous forest as complex habitats, the NTI showed that 40% (8) of simple habitat plots and 35% (7) of the complex habitat plots were clustered in the rainy season. In the dry season these values were 45 (9) and 50% (10), respectively (Table 1).

Table 1. Results of the nearest taxon index (NTI) with a null model approach for moths communities sampled in Emas National Park (ENP) in different physiognomies and in the dry and rainy seasons. Bold values correspond to significant NTI values (at 0.05 level: $P < 0.05$ correspond to a cluster pattern and $P > 0.95$ to an overdispersed pattern) under the null expectation. SF means semideciduous forest, CSS *cerrado sensu stricto*, CC *campo cerrado* and CS *campo sujo*.

Plot Code	Dry season			Rainy season		
	NTI	p(NTI)	Structure	NTI	p(NTI)	Structure
1 SF	-0.79626411	0.769	Random	-0.01146066	0.516	Random
2 SF	2.40015498	0.006	Clustered	0.08270662	0.482	Random

3 SF	-0.03061531	0.519	Random	1.41375407	0.079	Random
4 SF	1.66269192	0.047	Clustered	1.88230422	0.024	Clustered
5 SF	0.52760408	0.299	Random	0.56388525	0.296	Random
6 SF	1.25941124	0.104	Random	1.04397259	0.152	Random
7 SF	0.55725463	0.291	Random	1.55705659	0.059	Random
8 SF	1.84078397	0.031	Clustered	1.66090637	0.035	Clustered
9 SF	1.41677084	0.085	Random	1.01444658	0.168	Random
10 SF	1.50986602	0.065	Random	1.12445972	0.139	Random
1 CSS	2.74366173	0.001	Clustered	2.83882225	0.001	Clustered
2 CSS	2.04143317	0.018	Clustered	0.74009672	0.229	Random
3 CSS	1.9787803	0.023	Clustered	0.98648451	0.163	Random
4 CSS	-1.08316781	0.867	Random	0.07526199	0.464	Random
5 CSS	1.24227247	0.11	Random	-0.32922307	0.625	Random
6 CSS	-0.05575988	0.521	Random	2.02015443	0.02	Clustered
7 CSS	1.9299062	0.031	Clustered	1.94820667	0.026	Clustered
8 CSS	2.14908353	0.02	Clustered	2.45011155	0.008	Clustered
9 CSS	2.36570802	0.008	Clustered	1.6655144	0.045	Clustered
10 CSS	1.81157976	0.035	Clustered	0.88748446	0.178	Random
9 CC	0.01551999	0.509	Random	2.55981545	0.005	Clustered
10 CC	2.07642584	0.016	Clustered	0.60080542	0.276	Random
11 CC	1.84302483	0.028	Clustered	1.08850538	0.135	Random
12 CC	1.86245042	0.03	Clustered	2.18598722	0.015	Clustered
13 CC	1.23971601	0.111	Random	1.63990901	0.049	Clustered
14 CC	2.50816539	0.007	Clustered	-0.37758322	0.654	Random
18 CC	3.25323813	0.001	Clustered	4.11858291	0.001	Clustered
19 CC	1.22396461	0.115	Random	3.25562164	0.001	Clustered
27 CC	1.7866842	0.034	Clustered	1.07863934	0.153	Random
28 CC	2.65691778	0.004	Clustered	2.02063603	0.021	Clustered
29 CC	2.55995055	0.006	Clustered	1.11824924	0.126	Random
32 CC	-0.51622875	0.679	Random	2.18541141	0.015	Clustered
33 CC	1.29926856	0.101	Random	0.67899702	0.258	Random
37 CC	1.20643158	0.108	Random	1.96359231	0.03	Clustered
16 CS	1.85257755	0.03	Clustered	0.63363618	0.27	Random
17 CS	0.39058457	0.352	Random	1.11492759	0.138	Random
30 CS	1.00219375	0.178	Random	0.16901139	0.431	Random
31 CS	-0.31417847	0.632	Random	0.55279594	0.286	Random
38 CS	0.7029638	0.255	Random	0.71515743	0.244	Random
39 CS	1.42796056	0.058	Random	0.02656079	0.481	Random

Campo sujo was the only physiognomy that didn't show any association between the functional structure and the environmental variables (Table 2). Environmental variables explained 83% of the total variation in *campo cerrado* in NTI values (NTI: adjusted $R^2 = 0.83$, $p = 0.001$, Table 2). *Cerrado sensu stricto* showed a significant relationship with environmental variables in NTI values (adjusted $R^2 = 0.65$, $p = 0.02$, Table 2). Semideciduous forest had a significant relationship with environmental variables NTI values (NTI: adjusted $R^2 = 0.49$, $p = 0.04$, Table 2). Only leaf mass and perimeter of trees influenced significantly the functional structure of Arctiinae moths along the physiognomies (Table 2).

Table 2. Results of the multiple linear regression between the functional structure index (NTI) and environmental variables (selected by the forward selection) in different physiognomies. SF means semideciduous forest, CSS *cerrado sensu stricto*, CC *campo cerrado* and CS *campo sujo*.

Physiognomy	NTI		
	Variables	R^2	P - value
SF	Richness (-)	0.49	0.13
	Leaf Mass (+)		0.67
	Perimeter (-)		0.04*
	Herbaceous (+)		0.87
CSS	Richness (+)	0.65	0.19
	Leaf Mass (+)		0.07
	Perimeter (+)		0.02*
	Herbaceous (+)		0.94
CC	Richness (-)	0.83	0.21
	Leaf Mass (+)		0.001*
	Perimeter (-)		0.39
	Herbaceous (-)		0.03*
CS	Richness (-)	-0.03	0.55
	Herbaceous (-)		0.59

The sign means a positive (+) or negative (-) effect of the variable on the functional structure indexes.

Discussion

The majority of the Arctiinae moth communities showed positive values of the functional structure index (NTI), showing a tendency of functionally clustered assemblages, as a response to environmental filtering in dictating the distributions of these insects in the study area. We hypothesised that moths occurring in simple habitats, composed by less density and richness of shrubs and trees (*campo cerrado* and *campo sujo*, Oliveira-Filho & Ratter, 2002) and in xeric weather conditions (dry season), marked by low temperatures, water stress and less nutritional quality of food resources (Morais *et al.*, 1999; Pinheiro *et al.*, 2002) would show clustered patterns of functional structure, because the environment would filter and select species more functionally similar (than expected by chance) that are adapted to survive on those conditions (Webb *et al.*, 2002; Pavoine & Bonsall, 2011). Part of these hypotheses was corroborated, as a high percentage of communities showed functional grouping in simpler habitats and in xeric weather conditions. However, a high percentage of communities more functionally clustered than expected by chance were also found on structurally complex habitats (higher richness and density of shrubs and trees, *cerrado sensu stricto* and semideciduous forest, Oliveira-Filho & Ratter, 2002) and on mesic weather conditions (rainy season). These physiognomies are richer in Arctiinae moth species (Moreno *et al.*, 2014), proving that a few functional groups dominated a large number of species. Thus, we argue that environmental filtering is a strong ecological process in influencing the Arctiinae traits distributions and this effect is constant along the gradient of vegetation and the two marked weather seasons of the study area. Also, environmental filtering was confirmed by the significant relationship between the functional traits index and the environmental variables. Thus, environmental variables are important and act as filters to the distribution of the functional groups that occur in different types of vegetation, as already shown to the

richness and composition of these moths in the study area (Moreno *et al.*, 2014; Moreno *et al.*, 2016).

Our hypotheses that the rainy season and the structurally complex habitats would have a high percentage of overdispersed communities were not corroborated, since any community showed a significant overdispersed pattern. Thus, antagonistic interactions, like competition are not so strong in dictating the Arctiinae moth functional structure. Many studies pointed out that the interspecific competition for resources in herbivorous insects (larval phase in Lepidoptera) is not frequent (reviewed by Lawton & Strong Jr., 1981; Nishida *et al.*, 2015), but other studies showed that scarcity of food can be a limiting factor, raising the force of competition on herbivores, mainly on those closely related, but less common in free-living, mandibulate insects, like as Lepidoptera (Denno *et al.*, 1995; Kursar *et al.*, 2006). However, competition between pollinators (adult phase in Lepidoptera) for floral resources is common in nature (Kevan & Baker, 1983; de Camargo *et al.*, 2016). In addition, competition in insects can occur via an indirect process, as apparent competition (Ramirez & Eubanks, 2016). The competition in herbivores might be higher among individuals of the same species (intraspecific competition, Lawton & Strong Jr., 1981) and this is an issue that could be tested in a wide scale, for example, in different types of vegetation and in different weather seasons, as we performed here, to disentangle the effects of environment and climate on competition among herbivores insects.

Most of the Arctiinae moth communities showed a tendency to cluster, independently of the physiognomy and weather season. Two environmental variables accounted for these patterns of functional grouping and might be functioning as environmental filters on communities. The coefficients of variation of leaf mass and of perimeter of trees were the only variables that presented a significant relationship with the functional structure on communities. Leaf mass is related to food resource and to the concentration of noxious

substances, important to the unpalatability of Arctiini moths, like pyrrolizidine alkaloids (Hartmann, 1999; Zaspel *et al.*, 2014). The perimeter of trees can be related to the occurrence of lichens, which possess polyphenolics (Hofmeister *et al.*, 2016), the main food resource and secondary compounds that also confer protection to Lithosiini moths (Scott *et al.*, 2014). Arctiinae moths use their bright aposematic coloration to warn natural enemies about their unpalatability (Simmons, 2009). The colour of the first pair of wings was one of the variables that we used to separate the functional groups of Arctiinae moths. Despite we have sampled the adults and took traits of the adult specimens, they search for good conditions for mating and oviposition, thus their offspring will be able to feed and sequester the secondary compounds that they might need on larval and adult phases (Hartmann, 2009).

The differences in the body size and in the colors of the wings of Arctiinae moths might reduce the overlap on the use of resources. The body size might influence the distribution of species along the habitats (De Bie *et al.*, 2012; Vogt *et al.*, 2013) and the colors of the wings may protect Arctiinae moths from predation and parasitism through warning advertence (Simmons, 2009; Fujiwara & Nishikawa, 2016). Besides Arctiinae moths present a higher dissimilarity of these traits (Simmons, 2009; Weller *et al.*, 2009), their community composition present similar traits occurring at the same space and at the same time and the coexistence of those ecological similarities are influenced by the environment. Thus, environmental filtering is more important than antagonistic interactions in determining the functional structure of Arctiinae moths in the study area.

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CONCLUSÕES GERAIS

- A composição de espécies de mariposas Arctiinae foi influenciada tanto pelo ambiente quanto pelo espaço. Contudo, o ambiente foi mais importante do que espaço para praticamente todos os grupos de espécies: especialistas de habitat, generalistas de habitat, espécies comuns, raras e tribo Arctiini. Desta forma, o modelo de *species sorting*, que está principalmente relacionado a filtros ambientais e as interações entre espécies, explica melhor o padrão de distribuição de espécies ao longo da metacomunidade.
- Entretanto, a composição de espécies de mariposas da tribo Lithosiini foi mais influenciada por variáveis espaciais do que pelo ambiente. Este resultado pode ser devido ao pequeno tamanho corporal destas mariposas, que podem ser estocasticamente distribuídas devido à rápida dinâmica de suas populações e também pode ser devido a sua fragilidade e maior limitação para dispersão, e então variáveis espaciais podem exercer uma força maior sobre elas.
- De todas as variáveis ambientais testadas (riqueza de arbóreas, cobertura de herbáceas, coeficientes de variação do perímetro, do comprimento foliar, e da dureza das folhas de arbóreas), riqueza de arbóreas foi selecionada para todos os grupos de espécies, evidenciando a importância desta variável na composição de espécies de mariposas Arctiinae ao longo de toda metacomunidade.
- A estrutura funcional e a estrutura filogenética de mariposas Arctiinae também são influenciadas por processos estocásticos (relacionados a variáveis espaciais) e determinísticos (também relacionados a variáveis ambientais). Contudo, o poder de explicação de variáveis ambientais e espaciais na estrutura funcional e filogenética dependeu da forma como as relações funcionais e filogenéticas das espécies foram mensuradas. O ambiente foi mais relacionado com o índice de parentesco líquido

(NRI, do inglês net relatedness index, que quantifica a média da similaridade entre todas as espécies na árvore) de mariposas da tribo Arctiini. O ambiente foi mais relacionado ao índice do táxon mais próximo (NTI, nearest taxon index, que quantifica a média da distância entre espécies que compartilham maiores similaridades) de mariposas da tribo Lithosiini.

- Ao contrário, as espécies mais semelhantes na estrutura funcional e filogenética (NTI) de Arctiini e a média da distância funcional entre todas as espécies (NRI) de Lithosiini foram mais influenciadas por variáveis espaciais.
- A estrutura funcional de Lithosiini mostrou relações significativas com o ambiente, o que não havia sido mostrado para a riqueza taxonômica. Este resultado corrobora o fato de que a simples informação taxonômica não mostra os reais padrões de similaridades ecológicas entre as espécies nas comunidades.
- As variáveis ambientais selecionadas para as análises de partição de variância nos dados de estrutura funcional e filogenética foram: cobertura de herbáceas, riqueza de arbóreas, coeficientes de variação da massa foliar, da dureza foliar e do perímetro de arbóreas. Todas estas variáveis, principalmente a riqueza de arbóreas e a densidade de herbáceas são importantes no gradiente de vegetação que ocorre na área de estudo e influenciam muito a riqueza e composição de espécies animais. O coeficiente de variação no perímetro de arbóreas foi a única variável que influenciou a estrutura funcional de mariposas Lithosiini. O perímetro de arbóreas pode estar relacionado à quantidade de líquens na planta, que é o principal recurso alimentar destas mariposas. As informações de seus atributos mostraram claramente a relação entre esta variável e suas estruturas funcionais nas comunidades.
- Dentre os processos determinísticos, os filtros ambientais são mais importantes do que interações antagônicas em influenciar a estrutura funcional de mariposas Arctiinae.

- A maioria das comunidades apresentou um padrão aglomerado de estrutura funcional, mostrando que as espécies que coexistem apresentam maior similaridade de atributos ecológicos. Até comunidades mais ricas apresentaram espécies mais similares entre si do que o esperado ao acaso.
- Em geral, os padrões de maior similaridade funcional não foram diferentes nas distintas fitofisionomias (*habitats simples versus habitats complexos*) e nem nas distintas estações marcantes (*seca versus chuva*) do bioma Cerrado.
- A maioria das comunidades tendeu a ter espécies mais funcionalmente similares do que o esperado ao acaso. As variáveis ambientais foram significativamente correlacionadas com estes padrões de similaridade na maioria das fitofisionomias. Estes resultados confirmam que a filtragem ambiental é um importante processo sobre a distribuição de traços funcionais de mariposas Arctiinae na área de estudo.
- Somente duas comunidades apresentaram espécies com maior dissimilaridade funcional do que o esperado ao acaso. Este resultado pode ser em resposta a interações antagônicas entre as espécies, como exclusão competitiva ou competição aparente.

Supplementary material Appendix 1. Most abundant species selected by the methods of the first quartile (25% most abundant) and by the inflection point (the first eight most abundant).

Species	Abundance
<i>Lithosiini</i> sp. 14	1038
<i>Lepidoneiva erubescens</i> (Butler, 1876)	962
<i>Leucanopsis strigulosa</i> (Walker, 1855)	320
<i>Lophocampa citrina</i> (Sepp, [1852])	297
<i>Parablavia sadima</i> (Schaus, 1896)	274
<i>Idalus carinosa</i> (Schaus, 1905)	217
<i>Pheia seraphina</i> (Herrich-Schäffer, 1854)	182
<i>Pseudalus limona</i> Schaus, 1896	173
<i>Halysidota sannionis</i> (Rothschild, 1909)	130
<i>Dycladia lucetius</i> (Stoll, 1781)	128
<i>Cisthene subruba</i> (Schaus, 1905)	126
<i>Phoenicoprocta baeri</i> Rothschild, 1911	113
<i>Leucanopsis squalida</i> (Herrich-Schäffer, [1855])	96
<i>Pseudosphex nivaca</i> (Jones, 1914)	93
<i>Cisthene</i> sp. 1	87
<i>Aclytia heber</i> (Cramer, 1780)	78
<i>Amaxia dyuna</i> Schaus, 1896	66
<i>Cisthene triplaga</i> (Hampson, 1905)	66
<i>Odozana obscura</i> (Schaus, 1896)	64
<i>Idalus citrina</i> Druce, 1890	62
<i>Utetheisa ornatix</i> (Linnaeus, 1758)	56
<i>Hyperthaema</i> sp. 1	51
<i>Nodozana jucunda</i> Jones, 1914	51
<i>Elysia joiceyi</i> Talbot, 1928	48
<i>Pheia haemopera</i> Schaus, 1898	47
<i>Heliura tetragramma</i> (Walker, 1854)	44
<i>Pheia albisigna</i> (Walker, 1854)	44
<i>Pareuchaetes aurata</i> (Butler, 1875)	43
<i>Barsinella mirabilis</i> Butler, 1878	31
<i>Macrocneme aurifera</i> Hampson, 1914	28
<i>Aclytia flavigutta</i> (Walker, 1854)	27
<i>Saurita attenuata</i> Hampson, 1905	26
<i>Pheia haematosticta</i> Jones, 1908	24
<i>Paracles</i> sp. 1	21
<i>Rhipha pulcherrima</i> (Rothschild, 1935)	19
<i>Arctiini</i> sp. 1	17

Supplementary material Appendix 2. List of the tiger moth species and their abundances in four vegetation types in an area of Cerrado. The codes indicate grassland (G), savanna (S), woodland savanna (WS) and semideciduous forest (SF).

Species	Vegetation types				Total
	G	S	WS	SF	
Arctiinae					
Arctiini					
Arctiini sp. 1		8	8	1	17
Arctiini sp. 2			1		1
Arctiini sp. 3			2	11	13
Arctiini sp. 4		1			1
Ctenuchiina sp. 1	1	1			2
Arctiina					
<i>Hypercompe mus</i> (Oberthür, 1881)			1		1
<i>Paracles phaeocera</i> (Hampson, 1905)		2	2		4
<i>Paracles</i> sp. 1	4	14	2	1	21
<i>Paracles</i> sp. 2			1		1
<i>Pseudalus limona</i> Schaus, 1896	43	104	20	6	173
Callimorphina					
<i>Utetheisa ornatix</i> (Linnaeus, 1758)	10	33	10	3	56
Ctenuchina					
<i>Aclytia flavigutta</i> (Walker, 1854)	7	8	9	3	27
<i>Aclytia heber</i> (Cramer, 1780)	5	12	35	26	78
<i>Aclytia</i> sp. 1		7	4	2	13
<i>Argyrodes braco</i> (Herrich-Schäffer, [1855])				1	1
<i>Cercopimorpha postflavia</i> Rothschild, 1912				2	2
<i>Correbidia calopteridia</i> (Butler, 1878)				4	4
<i>Correbidia</i> sp. 1				1	1
<i>Delphyre discalis</i> (Druce, 1905)	1	4	3	6	14
<i>Delphyre dizona</i> (Druce, 1898)		1	2	2	5
<i>Episcepsis klagesi</i> Rothschild, 1911			1		1
<i>Episcepsis lenaeus</i> (Cramer, 1780)			1		1
<i>Episcepsis thetis</i> (Linnaeus, 1771)			2	1	3
<i>Eucereon albidia</i> Rothschild, 1912			1	1	2
<i>Eucereon arenosun</i> Butler, 1877	1				1
<i>Eucereon dorsipuncta</i> Hampson, 1905			1	3	4
<i>Eucereon pseudarchias</i> Hampson, 1898				10	10
<i>Eucereon setosum</i> (Sepp, [1830])		1	1	10	12
<i>Eucereon</i> sp. 1		1	1	1	3
<i>Heliura rhodophila</i> (Walker, 1856)			1		1
<i>Heliura tetragramma</i> (Walker, 1854)	1	13	19	11	44
<i>Napata leucotela</i> Butler, 1876	1				1
<i>Philoros rubriceps</i> (Walker, 1854)	2	10	3		15
<i>Pseudohyaleucerea vulnerata</i> (Butler, 1875)			1	1	2
<i>Pseudosphex discoplaga</i> (Schaus, 1905)			1		1

<i>Pseudosphex fulvisphex</i> (Druce, 1898)		1	1	1	3
<i>Pseudosphex nivaca</i> (Jones, 1914)	10	68	13	2	93
Euchromiina					
<i>Autochloris enagrus</i> (Cramer, 1780)		3	1		4
<i>Cosmosoma achemon</i> (Fabricius, 1781)	1	2	1	2	6
<i>Cosmosoma auge</i> (Linnaeus, 1767)		1		1	2
<i>Cosmosoma nigriscens</i> Rothschild, 1911		1			1
<i>Cosmosoma rasera</i> Jones, 1914		1	1	3	5
<i>Cosmosoma theuthras restrictum</i> Butler, 1876	1	2	3	8	14
<i>Cosmosoma</i> sp. 1		1	1	2	4
<i>Cosmosoma</i> sp. 2	1				1
<i>Cosmosoma</i> sp. 3	2		1	1	4
<i>Dycladia lucetius</i> (Stoll, 1781)	13	61	52	2	128
<i>Erruca hanga</i> (Herrich-Schäffer, [1854])	1				1
<i>Eurota histrio</i> (Guérin, 1843)			1		1
<i>Hyda basilutea</i> (Walker, 1854)		3	4		7
<i>Lepidoneiva erubescens</i> (Butler, 1876)	41	817	53	51	962
<i>Macrocneme aurifera</i> Hampson, 1914	5	14	6	3	28
<i>Nyridela acroxantha</i> (Perty, 1833)		1		1	2
<i>Nyridela chalciope</i> (Hübner, [1827])			1		1
<i>Pheia albisigna</i> (Walker, 1854)	1	20	17	6	44
<i>Pheia gaudens</i> (Walker, 1856)		1			1
<i>Pheia haematosticta</i> Jones, 1908	3	5	13	3	24
<i>Pheia haemopera</i> Schaus, 1898	5	32	7	3	47
<i>Pheia seraphina</i> (Herrich-Schäffer, 1854)	14	129	25	14	182
<i>Pheia</i> sp. 1	4		1		5
<i>Phoenicoprocta baeri</i> Rothschild, 1911	8	67	30	8	113
<i>Phoenicoprocta</i> sp. 1		8	1	2	11
<i>Poliopastea plumbea</i> Hampson, 1898		1	1		2
<i>Poliopastea</i> sp. 1				1	1
<i>Saurita attenuata</i> Hampson, 1905		2		24	26
<i>Sphecosoma aenetus</i> (Schaus, 1896)			1		1
Pericopina					
<i>Dysschema boisduvalli</i> (van der Hoeven & de Vriese, 1840)	1				1
<i>Dysschema sacrifica</i> (Hübner, [1831])		1	3	1	5
<i>Hyalurga fenestra</i> (Linnaeus, 1758)			1		1
<i>Hyalurga partita</i> (Walker, 1854)				1	1
Phaegopterina					
<i>Agaraea semivitrea</i> Rothschild, 1909				1	1
<i>Amaxia dyuna</i> Schaus, 1896	1	1	12	52	66
<i>Amaxia kennedyi</i> (Rothschild, 1909)				2	2
<i>Biturix diversipes</i> (Walker, [1855])		3			3
<i>Carales astur</i> (Cramer, 1777)				1	1
<i>Cresera affinis</i> (Rothschild, 1909)				1	1
<i>Cresera ilioides</i> (Schaus, 1905)		1			1
<i>Cresera optima</i> (Butler, 1877)				3	3
<i>Echeta junio</i> (Schaus, 1892)				10	10
<i>Elysium hermia</i> (Cramer, 1777)			1		1

<i>Elysium joiceyi</i> Talbot, 1928	5	32	11		48
<i>Eupseudosoma grandis</i> Rothschild, 1909		2	1	1	4
<i>Eupseudosoma involuta</i> (Sepp, [1855])			3	1	4
<i>Halysidota sannionis</i> (Rothschild, 1909)		3	9	118	130
<i>Hyperandra appendiculata</i> (Herrich-Schäffer, [1856])				5	5
<i>Hyperthaema</i> sp. 1		5	10	36	51
<i>Hyperthaema</i> sp. 2		2	9		11
<i>Hyponerita lavinia</i> (Druce, 1890)	1				1
<i>Idalus agricus</i> Dyar, 1910		2	5	2	9
<i>Idalus carinosa</i> (Schaus, 1905)	3	97	112	5	217
<i>Idalus citrina</i> Druce, 1890	3	29	28	2	62
<i>Idalus dares</i> Druce, 1894		1			1
<i>Idalus lineosus</i> Walker, 1869		3	9		12
<i>Lepidokirbyia vittipes</i> (Walker, 1855)	1	1	7	6	15
<i>Leucanopsis rosetta</i> (Schaus, 1896)	2	5	2	1	10
<i>Leucanopsis squalida</i> (Herrich-Schäffer, [1855])	3	33	56	4	96
<i>Leucanopsis strigulosa</i> (Walker, 1855)	36	109	141	34	320
<i>Lophocampa annulosa</i> (Walker, 1855)			1		1
<i>Lophocampa atrimaculata</i> (Hampson, 1901)				1	1
<i>Lophocampa citrina</i> (Sepp, [1852])		158	122	17	297
<i>Mazaeras francki</i> Schaus, 1896		1			1
<i>Melese incertus</i> (Walker, 1855)		1	4		5
<i>Melese paranensis</i> Dognin, 1911				4	4
<i>Neritos atta</i> Schaus, 1920		4	2	1	7
<i>Neritos flavimargo</i> Joicey & Talbot, 1916		1	1		2
<i>Neritos hampsoni</i> Rothschild, 1909			4	6	10
<i>Neritos sanguipuncta</i> Schaus, 1901				1	1
<i>Pareuchaetes aurata</i> (Butler, 1875)	3	14	16	10	43
<i>Pelochyta arontes</i> (Stoll, 1782)				6	6
<i>Psychophasma erosa</i> (Herrich-Schäffer, [1858])		2		1	3
<i>Rhipha pulcherrima</i> (Rothschild, 1935)	4	7	1	7	19
<i>Rhipha strigosa</i> (Walker, 1854)			2		2
<i>Robinsonia dewitzi</i> Gundlach, 1881		1			1
<i>Scaptius submarginalis</i> (Rothschild, 1909)				1	1
<i>Viviennea salma</i> (Druce, 1896)		3	4		7
Lithosiini					
Lithosiinii sp. 1			3	3	6
Lithosiinii sp. 2		2	2	2	6
Lithosiinii sp. 3		1	1	1	3
Lithosiinii sp. 4	9	1			10
Lithosiinii sp. 5			3		3
Lithosiinii sp. 6				8	8
Lithosiinii sp. 7				1	1
Lithosiinii sp. 8		2	9	2	13
Lithosiinii sp. 9				4	4
Lithosiinii sp. 12			3		3
Lithosiinii sp. 14	113	442	459	24	1038
Cisthenina					

<i>Barsinella mirabilis</i> Butler, 1878			3	28	31
<i>Cisthene dives</i> (Schaus, 1896)		1	1	1	3
<i>Cisthene ruficollis</i> (Schaus, 1896)	1	4			5
<i>Cisthene subruba</i> (Schaus, 1905)	3	4	106	13	126
<i>Cisthene triplaga</i> (Hampson, 1905)	2	5	57	2	66
<i>Cisthene</i> sp. 1		1	22	64	87
<i>Cisthene</i> sp. 2		1	2	1	4
<i>Cisthene</i> sp. 3			2	1	3
<i>Illice croesus</i> Hampson, 1914		1			1
<i>Illice griseola</i> (Rothschild, 1913)				4	4
<i>Odozana domina</i> (Schaus, 1896)		4	2	6	12
<i>Odozana obscura</i> (Schaus, 1896)	2	14	2	46	64
<i>Talara grisea</i> Schaus, 1896		12	2	1	15
Eudesmiina					
<i>Antona fallax</i> (Butler, 1877)			1		1
Lithosina					
<i>Agylla argentea</i> (Walker, 1863)	2	7	3	2	14
<i>Agylla marcata</i> (Schaus, 1894)	3	2			5
<i>Agylla</i> sp. 1	2	2	3	2	9
<i>Apistosis judas</i> Hübner, [1819]				1	1
<i>Metalobosia diaxantha</i> Hampson, 1914				2	2
<i>Nodozana jucunda</i> Jones, 1914	1	11	29	10	51
<i>Parablavia sadima</i> (Schaus, 1896)	12	70	191	1	274

Supplementary material Appendix 3. List of Arctiinae species (tribes Arctiini and Lithosiini) and their functional traits values. Mean values of wingspan, body length and thorax width (measured in centimeters).

Species	Wingspan	Body_length	Body_width	Fore wing_colors
Arctiini				
<i>Aclytia flavigutta</i> (Walker, 1854)	2.8	1.1	0.3	black_yellow
<i>Aclytia heber</i> (Cramer, 1780)	3	1.2	0.3	black_yellow
<i>Agaraea semivitre</i> a Rothschild, 1909	3.2	1.2	0.4	white_gray
<i>Amasia dyuna</i> Schaus, 1896	3.1	1.3	0.3	yellow_brown_red
<i>Amasia kennedyi</i> (Rothschild, 1909)	3	1.2	0.3	yellow_brown_red
<i>Argyrodes braco</i> (Herrich-Schäffer, [1855])	2.2	1.3	0.3	transparent_black
<i>Autochlois enagrus</i> (Cramer, 1780)	3	1.1	0.25	transparent_black
<i>Carales astur</i> (Cramer, 1777)	4.5	2	0.6	gray_brown
<i>Cercopimorpha postflavia</i> Rothschild, 1912	2.8	1.25	0.3	black
<i>Correbidia calopteridia</i> (Butler, 1878)	2.7	1.1	0.3	black_brown
<i>Cosmosoma achemon</i> (Fabricius, 1781)	2.4	0.9	0.3	transparent_black_red
<i>Cosmosoma auge</i> (Linnaeus, 1767)	3.7	1.5	0.4	transparent_black
<i>Cosmosoma nigriscens</i> Rothschild, 1911	4.1	1.6	0.4	transparent_black_red
<i>Cosmosoma raser</i> a Jones, 1914	2.3	0.9	0.3	transparent_black
<i>Cosmosoma theuthras restrictum</i> Butler, 1876	3.9	1.4	0.4	transparent_black_red
<i>Cresera ilioides</i> (Schaus, 1905)	3.6	1.6	0.5	orange_brown
<i>Cresera optima</i> (Butler, 1877)	2.9	1.2	0.3	brown_orange
<i>Delphyre discalis</i> (Druce, 1905)	3.1	1.2	0.3	black_grey
<i>Delphyre dizona</i> (Druce, 1898)	2.9	1.2	0.3	black_grey
<i>Dycladia lucetius</i> (Stoll, 1781)	2.3	0.9	0.3	black_orange_transparent
<i>Dysschema boisduvalli</i> (van der Hoeven & de Vriese, 1840)	5	2	0.7	white_red_black
<i>Dysschema sacrific</i> a (Hübner, [1831])	4.4	1.8	0.6	black_white
<i>Echeta jun</i> o (Schaus, 1892)	3.5	1.5	0.4	brown_yellow_red
<i>Elysium cingulata</i> (Walker, 1856)	6	2.7	0.8	brown_yellow_red
<i>Elysium hermia</i> (Cramer, 1777)	5.6	2.1	0.8	orange_yellow
<i>Elysium joiceyi</i> Talbot, 1928	6.3	2.5	0.8	brown_yellow
<i>Episcepsis klagesi</i> Rothschild, 1911	2.8	1.1	0.3	black_white
<i>Episcepsis lenaeus</i> (Cramer, 1780)	3.1	1.5	0.4	black_white
<i>Episcepsis thetis</i> (Linnaeus, 1771)	3	1.5	0.3	black_white
<i>Erruca hanga</i> (Herrich-Schäffer, [1854])	3.5	1.6	0.4	transparent_black_orange
<i>Eucereon albidia</i> Rothschild, 1912	3	1	0.3	gray_brown
<i>Eucereon arenosun</i> Butler, 1877	3.4	1.4	0.3	polka_dot_brown
<i>Eucereon dorsipuncta</i> Hampson, 1905	2.8	1.2	0.3	polka_dot_brown
<i>Eucereon pseudarchias</i> Hampson, 1898	3.7	1.6	0.5	brown_black
<i>Eucereon setosum</i> (Sepp, [1830])	3.9	1.6	0.4	polka_dot_brown
<i>Eupseudosoma grandis</i> Rothschild, 1909	3.5	1.5	0.5	white
<i>Eupseudosoma involuta</i> (Sepp, [1855])	3.1	1.5	0.5	white
<i>Eurota histrio</i> (Guérin, 1843)	2.7	1.25	0.35	transparent_black
<i>Halysidota sannionis</i> (Rothschild, 1909)	2.5	1.1	0.3	brown_yellow_red

<i>Heliura rhodophila</i> (Walker, 1856)	2.8	0.9	0.2	polka_dot_brown
<i>Heliura tetragramma</i> (Walker, 1854)	2.7	0.9	0.2	polka_dot_brown_transparent
<i>Hyalurga fenestra</i> (Linnaeus, 1758)	6	2.5	0.4	transparent_yellow_black
<i>Hyalurga partita</i> (Walker, 1854)	2.9	1.1	0.3	transparent_yellow_black
<i>Hyda basilutea</i> (Walker, 1854)	2.2	1.1	0.3	transparent_black_orange
<i>Hyperandra appendiculata</i> (Herrich-Schäffer, [1856])	2.8	1	0.3	brown_yellow
<i>Hypercompe mus</i> (Oberthür, 1881)	5.1	1.85	0.65	transparent_gray_black
<i>Hyperthaema granifera</i> Rawlins	2.9	1.4	0.4	red_white_brown
<i>Idalus agricus</i> Dyar, 1910	3	1.35	0.45	yellow_gray_red
<i>Idalus carinosa</i> (Schaus, 1905)	3.4	2	0.5	yellow_gray_red
<i>Idalus citrina</i> Druce, 1890	3.3	1.1	0.3	yellow_gray_red
<i>Idalus dares</i> Druce, 1894	3	1.35	0.4	white_brown_black
<i>Idalus lineosus</i> Walker, 1869	3.6	1.4	0.5	yellow_gray_black
<i>Lepidokirbyia vittipes</i> (Walker, 1855)	3.2	1.3	0.3	orange_brown_black
<i>Lepidoneiva erubescens</i> (Butler, 1876)	3.4	1.3	0.3	transparent_black_red
<i>Leucanopsis rosetta</i> (Schaus, 1896)	3.4	1.7	0.5	yellow_brown
<i>Leucanopsis strigulosa</i> (Walker, 1855)	3.4	1.6	0.6	yellow_brown
<i>Lophocampa atrimaculata</i> (Hampson, 1901)	4.5	1.7	0.5	yellow_brown
<i>Lophocampa citrina</i> (Sepp, [1852])	3.2	1.2	0.3	yellow_brown
<i>Macrocneme aurifera</i> Hampson, 1914	4	1.7	0.4	metallic_dark_green
<i>Melese dorothea</i> (Stoll, 1782)	3.5	1.5	0.5	brown_orange
<i>Melese incertus</i> (Walker, 1855)	2.7	1.1	0.4	brown
<i>Napata leucotela</i> Butler, 1876	2.3	0.9	0.3	black_transparent
<i>Neritos atta</i> Schaus, 1920	2.1	0.9	0.2	red_yellow
<i>Neritos flavimargo</i> Joicey & Talbot, 1916	2.1	1	0.3	red_yellow
<i>Neritos hampsoni</i> Rothschild, 1909	2.5	1.1	0.3	yellow_brown_white
<i>Nyridela acroxantha</i> (Perty, 1833)	4.1	1.8	0.5	transparent_black
<i>Paracles phaeocera</i> (Hampson, 1905)	5	1.9	0.9	brown
<i>Pareuchaetes aurata</i> (Butler, 1875)	3.5	1.1	0.3	yellow
<i>Pelochyta arontes</i> (Stoll, 1782)	3.8	1.5	0.4	brown
<i>Pheia albisigna</i> (Walker, 1854)	2.6	1.1	0.3	transparent_black_red
<i>Pheia gaudens</i> (Walker, 1856)	2.3	1.1	0.3	black_transparent_yellow
<i>Pheia haematosticta</i> Jones, 1908	2.7	1.1	0.3	transparent_black_red
<i>Pheia haemopera</i> Schaus, 1898	2.5	1.1	0.2	transparent_black_red
<i>Pheia seraphina</i> (Herrich-Schäffer, 1854)	2.7	1.1	0.2	transparent_black_red
<i>Philoros rubriceps</i> (Walker, 1854)	2.6	1	0.3	black
<i>Phoenicoprocta baeri</i> Rothschild, 1911	2.5	1.2	0.2	black
<i>Poliopastea plumbea</i> Hampson, 1898	2.7	1	0.3	black
<i>Pseudalus limona</i> Schaus, 1896	3.1	1.7	0.4	yellow
<i>Pseudohyaleucerea vulnerata</i> (Butler, 1875)	3.7	1.6	0.5	transparent_black_brown
<i>Pseudosphex discoplaga</i> (Schaus, 1905)	2.1	0.95	0.3	transparent_black
<i>Pseudosphex fulvisphex</i> (Druce, 1898)	2.4	1.3	0.3	transparent_black_orange
<i>Pseudosphex nivaca</i> (Jones, 1914)	2.2	1	0.3	transparent_black_yellow
<i>Psychophasma erosa</i> (Herrich-Schäffer, [1858])	4.5	1.7	0.5	transparent_gray_brown_black
<i>Rhipha pulcherrima</i> (Rothschild, 1935)	4.5	2.3	0.6	white_red_black
<i>Rhipha strigosa</i> (Walker, 1854)	3.5	1.6	0.6	black_white
<i>Robinsonia dewitzi</i> Gundlach, 1881	4.4	1.9	0.5	white_brown

<i>Saurita attenuata</i> Hampson, 1905	2.5	0.8	0.2	black_transparent
<i>Scaptius submarginalis</i> (Rothschild, 1909)	2.6	1.2	0.3	yellow_gray_red
<i>Sphecosoma aenetus</i> (Schaus, 1896)	2.9	1.25	0.35	black
<i>Utetheisa ornatrix</i> (Linnaeus, 1758)	3.7	1.9	0.3	white_red_black
<i>Viviennea salma</i> (Druce, 1896)	3.4	1.5	0.5	yellow_black
Lithosiini				
<i>Agylla argentea</i> (Walker, 1863)	3.4	1.2	0.2	white
<i>Antona fallax</i> (Butler, 1877)	3.1	1	0.3	black_yellow
<i>Apistosis judas</i> Hübner, [1819]	5	1.6	0.4	metallic_dark_green
<i>Barsinella mirabilis</i> Butler, 1878	1.3	0.6	0.2	yellow_black_orange
<i>Cisthene dives</i> (Schaus, 1896)	1.6	0.6	0.2	black_yellow
<i>Cisthene ruficollis</i> (Schaus, 1896)	1.6	0.6	0.2	black
<i>Cisthene subruba</i> (Schaus, 1905)	1.2	0.6	0.1	gray
<i>Cisthene triplaga</i> (Hampson, 1905)	1.5	0.7	0.2	gray_yellow
<i>Illice croesus</i> Hampson, 1914	1.5	0.6	0.2	brown_black
<i>Illice griseola</i> (Rothschild, 1913)	1.6	0.6	0.2	gray
<i>Metalobosia diaxantha</i> Hampson, 1914	1.4	0.5	0.2	black_yellow
<i>Nodozana jucunda</i> Jones, 1914	1.4	0.5	0.2	black_yellow_pink
<i>Odozana domina</i> (Schaus, 1896)	1.7	0.5	0.2	gray
<i>Odozana obscura</i> (Schaus, 1896)	1.6	0.7	0.2	black
<i>Parablavia sadima</i> (Schaus, 1896)	2	0.6	0.2	gray
<i>Talara grisea</i> Schaus, 1896	1.5	0.5	0.2	gray