UNIVERSIDADE FEDERAL DE MINAS GERAIS INSTITUTO DE CIÊNCIAS
BIOLÓGICAS PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA,
CONSERVAÇÃO E MANEJO DA VIDA SILVESTRE

LUIZ EDUARDO MACEDO REIS

PADRÕES DE DISTRIBUIÇÃO ESPAÇO-TEMPORAL DE INSETOS HERBÍVOROS EM FLORESTAS TROPICAIS SECAS

Belo Horizonte / 2016

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Tese apresentada ao Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial para obtenção do título de Doutor em Ecologia, Conservação e Manejo da Vida Silvestre.

Orientador: Professor Dr. Frederico de Siqueira Neves (UFMG)

Co-orientador: Professor Dr. Maurício Lopes de Faria (Unimontes)

Belo Horizonte/2016

Agradecimentos

À Universidade Federal de Minas Gerais, particularmente ao Departamento de Ciências Biológicas e ao Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, que me auxiliou através de pessoas competentes durante o tempo do doutorado. Aos professores e demais funcionários, meus sinceros agradecimentos.

À fundação CAPES pela concessão da bolsa de Doutorado. Ao Instituto Estadual de Florestas (IEF) e ICMBIO pelo suporte logístico. Ao suporte financeiro concedido pelo Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), a Fundação de Amparo à Pesquisa de Minas Gerais (FAPEMIG) e a Inter-American Institute for Global Change Research. E também, a todos as pessoas envolvidas na identificação das espécies de vegetais.

Agradeço ao meu orientador Frederico de Siqueira Neves, pela amizade e, por ensinar a ser pesquisador fora da "zona de conforto" através de oportunidades de aprendizado que rei levar para resto da vida, muito obrigado professor.

Ao meu co-orientador Maurício Lopes de Faria pela amizade, incentivos e ensinamentos, ao longo da minha vida acadêmica, e como ele sempre diz: "a Ecologia está em tudo que se vê". Agradeço ao professor Maurício Quesada que muito bem me recebeu no México, sempre disposto a ajudar, serei sempre grato pelo apoio.

Aos membros da banca Dra. Tatiana Cornelissen, Dr. Sérvio P. Ribeiro, Dr. Ricardo Campos e Dr. Wesley Dáttilo por terem aceitado o convite e pela disposição, para contribuir neste trabalho, sinceramente obrigado.

A todos os colegas e amigos do Laboratório de Ecologia de Insetos (LEI) e também a todos colegas da estimada Vila Parentoni, pelos momentos ótimos vividos que certamente deixarão saudades.

Agradeço especialmente aos amigos que me acompanharam durante as amostragens de campo e na triagem dos insetos, Samuel Novais, Graziela Monteiro, Rayanna Melo, Lucas Perillo, Viviane Nolasco, Frederico Macedo, Alex Silva, Cleandson Santos, João Souza, Jacob Edson, Olivério Delgado, Karman Farriol. E também meus agradecimentos aos amigos que ajudaram ao longo deste doutorado: Fernanda Costa, Laura Gagliardi, Marina Beirão, Flavio Siqueira, Reuber Antoniazzi, Affonso de Souza, Ivan Monteiro, Arleu Viana, Leonardo Dias, Alice Leite, Wesley DaRocha, Tadeu Guerra, Newton Barbosa, Marcel Coelho e Thaise Bahia. Muito obrigado a todos, tudo seria mais difícil sem vocês.

À minha família, em especial à Marina Drumond pela paciência, a meus pais Luiz Otoni Reis e Aparecida Macedo, à minha irmã Viviane Macedo Reis e ao meu sogro Marcio Drumond e sogra Tania Oliveira. O apoio e carinho de vocês foi fundamental ao longo destes anos.

Sumário

Apresentação

O presente trabalho fez parte das atividades da rede colaborativa de pesquisas TROPI-DRY, e da rede “Biodiversidade e regeneração natural em florestas tropicais secas brasileiras (SISBIOTA)”, ambos contendo o estudo da sucessão ecológica no contexto dos serviços do ecossistema prestados a sociedade humana.

Entretanto o uso dos serviços ecossistêmicos prestados por florestas secas, está ameaçado em uma paisagem agrícola localizada em áreas culturalmente ricas mas economicamente pobres. Esperamos que os nossos resultados sejam inseridos ao acompanhamento do processo de regeneração natural, consolidando os padrões, e propiciando um levantamento mais robusto da biodiversidade de insetos nas FTS brasileiras.

A tese está dividida em dois capítulos, no primeiro descrevemos os padrões espaciais de insetos herbívoros no contexto da heterogeneidade local e da paisagem em quatro áreas de florestas tropicais secas (3 brasileiras e 1 mexicana), e no segundo descrevemos a distribuição espaço-temporal de besouros (de casa e da ambrosia) em três estágios de sucessão ao longo de dois anos no Parque Estadual da Mata Seca. Toda a tese está nas normas da revista 'Journal of Insect Science' onde o segundo capítulo foi publicado. As legendas e tabelas estão inseridas no decorrer do texto dos manuscritos para facilitar a leitura e as referências estão inseridas ao final de cada capítulo e seção.

Boa leitura.

Introdução Geral

Compreender os mecanismos e os processos responsáveis pela manutenção da diversidade nos ecossistemas é foco de diversos estudos em biologia da conservação. Relações positivas com a diversidade são propostas a partir de teorias baseadas na diferenciação de nichos ecológicos (Leibold 1995, Tscharntke et al. 2012), com a predição de que ambientes mais heterogêneos sejam mais diversos, devido ao aumento das possibilidades de exploração dos recursos, e dos locais para nitificação. Neste caso, é assumido que a heterogeneidade ambiental é responsável pela coexistência de espécies que estruturam a comunidade (Tews et al. 2004, Stein 2014).

Todavia, grupos taxonômicos diferentes percebem o ambiente em diferentes escalas de tempo e espaço (Tews et al. 2004, Tscharntke et al. 2012). De maneira geral, os atributos estruturais que constituem heterogeneidade para um grupo de espécies, podem representar fragmentação ou exclusão de hábitat para outro. Isto significa que as respostas são específicas para cada nível e grupo taxonômico, variando de acordo com a escala usada.

Nas florestas tropicais, a comunidade de plantas é responsável pelas características fisiológicas do sistema, e, possui forte influência sobre as interações tróficas existentes. A produção primária (Novotny et al. 2003) é concentrada no conjunto das copas das árvores que formam o dossel das florestas, sendo este, o principal local de assimilação de energia. Este habitat oferece vasta diversidade de recursos, que são fundamentais para a manutenção de diversidade biológica (Stork et al. 1997, Basset et al. 2003). Neste cenário, os insetos herbívoros obtêm destaque como os principais consumidores da biomassa vegetal (Basset et al. 2003, Lewinsohn et al. 2005). Apesar do interesse crescente científico, somado a formas mais fáceis de acesso nos últimos anos, o dossel ainda é pouco conhecido (Nadkarni et al. 2011).

A ação dos herbívoros, é capaz de reduzir a habilidade competitiva das plantas, que por sua vez, respondem através de estratégias baseadas na presença de compostos químicos, barreiras mecânicas e associações biológicas com predadores, no controle do dano causado (Finke and Denno 2006, Sanders et al. 2008). De maneira geral, a pressão seletiva, e mútua na interação herbívoro-planta é apontada como principal explicação para a diversidade de formas e tipos de interações existentes (Price 2002, Ricklefs and Marquis 2012). Neste sentido, a resposta da diversidade de insetos herbívoros ao longo de gradientes de heterogeneidade ambiental, pode ser uma estratégia vantajosa para o desenvolvimento de programas de conservação e monitoramento de ambientes (Kremen et al.1993).

Nas florestas tropicais secas (FTS) as árvores estão condicionadas a um clima de estações bem definidas (seca e chuvosa), e exibem respostas fisiológicas à escassez de água, com elevado grau de espécies caducifólias (Pezzini et al. 2014). As florestas secas podem ter ocupado extensas áreas no passado recente (entre 18.000 e 12.000 anos), mas, com o aumento da temperatura e umidade na ultima glaciação, estas florestas teriam retraído. Atualmente ocorrem em uma configuração descontínua e em fragmentos de diferentes tamanhos em toda América Latina (Pennington et al. 2000, Neves et al. 2015).

As florestas tropicais secas são consideradas de extrema diversidade, muitas espécies estão adaptadas às condições climáticas extremas (Hulshof et al. 2014, Pezzini et al. 2014). Durante a estação chuvosa existe abundância de folhas, e na estação seca, de flores e frutos (Pezzini et al. 2014). Do padrão fenológico das plantas emerge processos adaptativos entre organismos e extrema expressão de nichos ecológicos que interagem com a vegetação do bioma de domínio na paisagem (Avila-Cabadilla 2012, Leal et al. 2015). Portanto as florestas secas são um importante componente para a manutenção da diversidade na região.

Todavia, o prolongamento do período seco em um cenário de mudanças climáticas globais, somado a substituição destas florestas por centros de agricultura, pecuária entre outras atividades humanas, representam forte impacto na diversidade e funções ecológicas nestas florestas (Espírito-Santo et al. 2014, Hulshof et al. 2014). A vegetação nativa está fragmentada e em diferentes estágios de sucessão ecológica (Quesada 2009, Madeira et al. 2009). Os efeitos dos processos de sucessão ecológica e sazonalidade na diversidade de insetos em florestas tropicais úmidas ou secas, é pouco conhecido (Lewinsohn et al. 2005). Além disso, a maior parte do conhecimento sobre sucessão em ambientes tropicais foi obtido a partir de estudos em florestas úmidas (Guariguata and Ostertag 2001) e não pode ser aplicada em FTS (Vieira and Scariot 2006, Quesada et al.2009).

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CAPÍTULO 1

HETEROGENEITY AT LOCAL AND FOREST COVER ON LANDSCAPE SCALES ARE DRIVES FOR HERBIVOROUS INSECTS DIVERSITY IN TROPICAL DRY FORESTS

Journal of Insect Science
Research

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Heterogeneity at local and forest cover on landscape scales are drives for herbivorous insects diversity in tropical dry forests

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Abstract

Abstract: Insect herbivores are an important component of biodiversity with a narrow relation with plants species and plant parts. We assessed herbivore communities at 48 sites from four disturbed dry forest regions, evaluating the influences of landscape habitat availability at five focal scales in guild structure. We collected 2,893 insects representing 438 morphospecies, including 113 folivorous, 225 sap-sucking and 100 xylophagous insects. We found marked differences in guild richness and abundance responses, and similar patterns of beta diversity. Folivores were only associated with increase in habitat availability at the minor landscape scale, while sap-sucking and xylophagous insects were sensitive to landscape habitat availability, with diversity increasing to a greater extent at larger scales (i.e., 1 to 1.5 km radii). Beta diversity was higher in the region with the most unpredictable weather, and turnover is an important component to preserve high diversity at sampled sites. We demonstrate that the spatial context experienced by insects guilds depends on feeding habits and dispersal abilities. Increased habitat complexity positively affects insect diversity from local to landscape scales. We suggest focusing on key habitat elements for evaluation of herbivore responses to factors in anthropogenic landscapes.

Key words: Dispersal abilities, land use, scales, guild structure, heterogeneity.

Introduction

Most insects are herbivorous, and as a group insect herbivores are an important component of biodiversity due to their ecological and evolutionary radiation with plants (Price 2002). They participate in ecosystem energy flow through their role as primary consumers and as prey for antagonist groups (e.g., insectivorous bats) (Freeman 1979, Basset et al. 2004, Lewinsohn et al. 2005). Investigations of insect herbivore spatial dynamics may prove useful for interpretation of patterns of species diversity in a world increasingly dominated by human modified landscapes (Quesada et al. 2009, Dirzo et al. 2014)

Plant species richness is a good predictor of resource heterogeneity (Stein et al. 2014), and determines insect herbivore diversity at coarse (temperate or tropical biomes) (Basset et al. 2012) or fine (within forest fragments) spatial scales (Neves et al. 2014ab). In general, plant species heterogeneity is positively associated with insect herbivore diversity (Tews et al. 2004), however this pattern can vary by feeding guild (i.e., folivorous, sap-sucking and xylophagous) (Novais et al. 2016a, Macedo-Reis et al. 2016), or spatial scale at which variable are measured (Tews et al. 2004, Stein et al. 2014). Plant density, architecture, and height have been found to impact insect herbivore diversity and metacommunity organization (Ribeiro and Basset 2007, Neves et al. 2014a), as these traits can be associated with resource availability (e.g., plant density) or dispersal ability due to habitat physical characteristics (e.g., wind speed, canopy openness, vertical strata) (Neves et al. 2014a, Basset et al. 2015, Ribeiro and Basset 2016).

Neves et al. (2014a) demonstrated differential responses with respect to heterogeneity of herbivore guilds between fine and local scales. Tews et al. (2004) assert that this scale-dependence is caused by the species operational scales as defined by their home ranges and dispersal abilities. To illustrate this, Kremen et al. (2004) showed that for native bees, forest cover correspond bee foraging ranges and were positive at larger scales when measured as function of the plot radius where insects were collected. Thus, for forest-adapted species we might expect a decrease in niche availability with the increase in percentage of non-forest areas at the landscape scale. This information be used to describe correlations between structural vegetation heterogeneity and insect species diversity in degraded areas within and near preserved forests fragments, and may also be relevant for riparian forest (evergreen) near deciduous forest (Avila-Cabadilla et al. 2012).

Tropical dry forest is the most threatened tropical ecosystem, currently exposed to multiple threats resulting from human activity (Quesada et al. 2009). These areas are subject to severe phenological seasonal variation, with loss of plant leaves during the prolonged dry season (Pezzini et al. 2014). This ecosystem occurs as natural fragments varying in size and disconnectedly distributed across different ecoregions throughout Latin America (Pennington et al. 2009, Neves et al. 2015). In South America, the Pleistocene Arc Hypothesis (Prado and Gibbs 1993, Pennington et al. 2009) postulated that dry forests had a more widespread and contiguous distribution during Pleistocene glaciation phases, and the end of the cool and dry period is thought to have provoked the disrupted distribution in dry forests.

These view is supported by observation of high species β−diversity, among dry forest fragments that contain geologically old, monophyletic clades of endemic plant species, possibly indicating dispersal limitations (Neves et al. 2015). Physiological tolerances of abiotic conditions are also important for explaining the β-diversity patterns among dry forest environments where climate can be most unpredictable (Wardhaugh 2014).

Here we investigated the spatial dynamics of insect herbivore guilds (folivorous, sap-sucking and xylophagous) in insect communities residing in four dry forest fragments. The main goal was to describe herbivore communities by measuring spatial variation in vegetation heterogeneity at the local scale, and variation in forest cover at the landscape scale. We expected herbivore guild diversity to increase with environmental heterogeneity at local and with the increase in forest cover at landscape scales, and for the predictive power of forest cover percentage (with respect to herbivore diversity) to differ between scales. We also evaluated herbivore richness and abundance among dry forests regions and described mechanisms that determine β−diversity, addressing two specific questions: 1) does heterogeneity (plant richness) and weather pattern differences among regions determines β−diversity and species turnover? And 2) Is species turnover among sites more important than species nestedness in communities within a region?

Materials and methods

Study area and sampling sites

The study was carried out in four regions ranging from latitudes 19° south to 19° north: 1) The first region is located in central Minas Gerais state (MG), surrounding the Morro da Pedreira protection area (hereafter Serra do Cipó) (19°19'44.6" S, 43°36'23" W) (Coelho et al. 2012). 2) The second region lies in the São Francisco River Valley in northern Minas Gerais state (hereafter Northern MG) (14°55'12.0" S, 43°56'27" W), and includes three conservations units (Lagoa do Cajueiro State park, 20,500ha; Serra Azul Biological Reserve, 3,840.94ha; Jaíba Biological Reserve, 6,358ha) created as a compensatory measure of the irrigated area called the "Jaíba Project" (Espírito-Santo et al. 2014). 3) The third region is in northeastern Brazil at the Tamanduá farm, an area of approximately 4,000 ha in Paraíba (PB) (hereafter Patos PB) near the city of Patos (7°0'45.5" S, 37°22'48" W). 4) The fourth region is at the central western coast of Mexico in Jalisco state (hereafter Chamela), in and surrounding the Chamela-Cuixmala Biosphere Reserve (19°30'33.2" N, 105°2'36" W, Fig. 1).

These regions are subject to severe seasonal variations, with marked differences in rainfall between seasons. The climate in Serra do Cipó is mesothermal according to the Köppen system, with rainy summers (October-March) and dry winters. The average annual rainfall is 1,500 mm, and the average annual temperature is 19.9 °C (Coelho et al. 2012). In North MG the climate is classified as semi-arid, with an average annual temperature of 24.4 ºC and average annual rainfall of 818 mm, with rainfall concentrated between October and March (see Pezzini et al. 2014, Macedo-Reis et al. 2016). In Patos PB the climate is classified as semi-arid, with an average annual temperature of 32.8 ºC and average annual rainfall of 750 mm. However, rainfall is often variable between months, and deviates over 45% from one year to another (Prado 2003). The Chamela region has an average annual temperature of 24.6 ºC and average annual precipitation of 731 mm, with rainfall concentrated from June to October (Maass et al. 2005).

The Serra do Cipó region includes primarily Cerrado *sensu stricto* and altitudinal rocky field vegetation, and the dry forest grows on limestone outcrops and occurs as fragments with unique floristic composition compared to surrounding forest types (Coelho et al. 2012). The northern MG and Patos PB regions have dry forest that are associated with flat and nutrient-rich soils (Espírito-Santo et al. 2014); North of MG is in a transition zone between Cerrado and Caatinga biomes, and Patos PB is in the Caatinga biome (Fig. 1). Dry forest is the predominant vegetation type in Chamela, and is mostly associated with rolling hills (Maass et al. 2005). In all four regions riparian forest vegetation occurs along permanent rivers and lakes.

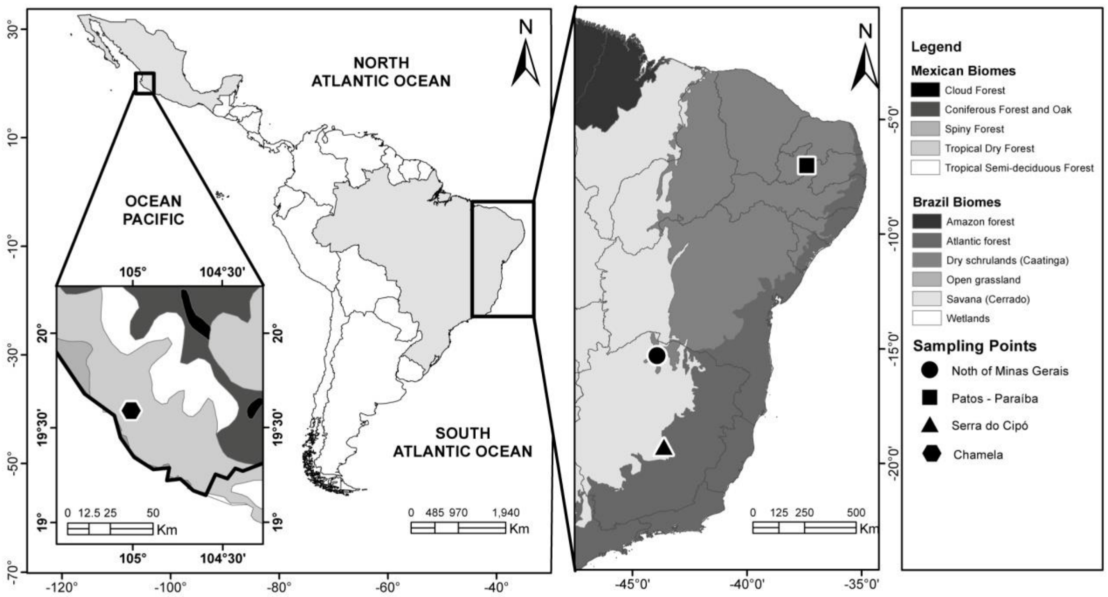

Fig. 1. Map showing locations of insect herbivore sampling regions and descriptions of associated biomes.

Mining and tourism are the most important economic activities in Serra do Cipó (Domingues et al. 2012). Agricultural practices (including cattle raising) dominate the economic activity of northern MG, Patos PB and Chamela regions (Maass et al. 2005, Espírito-Santo et al. 2014). These anthropogenic activities have caused landscape patchiness, with forest fragments of different sizes and successional stages scattered throughout these regions. We selected sampling sites along a gradient of succession in each region based on the amount of time elapsed since the last major disturbance. This information was obtained through interviews with members of local communities, and employees of protected areas. One third of the total sampling sites in each region represented dry forest abandoned for five to 10 years; one third was abandoned for 17 to 35 years and, and one third existed at least 50 years without any human activities or disturbance.

We selected forty-eight 20 x 50 m plots in total. Nine plots were selected in Serra do Cipó and Chamela each and 15 in northern MG and Patos PB region. Sampling sites within regions were at a minimum distance of 100 m. Plots were sampled in rainy and dry seasons, and were sampled four times each in Serra do Cipó and North MG, and two times each in Patos PB and in Chamela. Sampling was carried out in January and August 2012 and 2013 in Serra do Cipó, in March and August 2012 and April and September 2013 in North MG, in May and October 2012 in Patos PB, and in February and August 2015 in Chamela.

In each site, we measured plan richness using the circumference at breast height (CBH) bigger than 15cm as an exclusion criterion. And in each region we measured monthly average rainfall and temperature from the four years before each sampling period. We used the source: INMET - BDMEP (http://www.inmet.gov.br) for the Serra do Cipó, North of MG and Patos PB regions, and the Meteorological Station located in Chamela-Cuixmala Biosphere Reserve for the Chamela region.

Insect Sampling

We collected insects using combined flight Malaise/window traps (Basset 1988, Novais et al. 2016ab). One trap holding two vial collectors with 70% ethanol was placed in the tree canopy in the center of each site. Traps remained in place for 5 days (120 h) per month at the Serra do Cipó, North MG and Patos sites, and 10 days (240 h) per month at Chamela sites. The sampled insect herbivores were grouped into one of three guilds according to their feeding habits: folivorous, sap-sucking, or xylophagous (Novais et al., 2016a). All insects belonging to families that directly or indirectly depend on plant resources for survival were considered herbivores (Moran and Southwood 1982, Neves et al. 2014a, Novais et al. 2016a). All other insects were identified using taxonomic keys (Rafael et al. 2012) and separated into morphospecies based on external morphological characters. The sampled insects in Serra do Cipó, North MG and Patos were deposited in the entomological collection of the Laboratory of Insect Ecology at the Federal University of Minas Gerais (Universidade Federal de Minas Gerais - UFMG), and insects from the Chamela region were deposited at the Ecosystems Research Center of the National Autonomous University of Mexico (Universidad Nacional Autónoma de México, Morelia - UNAM).

Data analysis

Effects of habitat heterogeneity gradient on herbivore guild diversity were determined using generalized linear models (GLMs). In these models, the richness (number of morphospecies) and abundance (number of individuals) of herbivore guilds (folivorous, sap-sucking and xylophagous) were pooled by site per sampling period. Because traps in Patos PB were exposed for 10 days total while traps in other regions were exposed for 20 days total, we divided insect richness and abundance by the number of days that traps were exposed in each region. We then used insect richness and abundance per trap day as the response variable, and region (Serra do Cipó, North MG, Patos PB, and Chamela), habitat heterogeneity (i.e., plant richness) and interactions as explanatory variables. The minimal models were constructed by removing non-significant explanatory variables ($p > 0.05$) from the full model in the analysis. When significant differences were observed between regions, the data were submitted to contrast analysis by aggregating levels, and if the level of aggregation was not significant and did not alter the deviance explained by the null model, the levels were pooled together (Crawley 2013).

β diversity measures and statistical analysis

We calculated multiplicative β-diversity for each guild per region. The β-diversity represents the diversity of differentiation within a region ($\beta_{\text{among-sites}}$). However, β-diversity is sensitive to sample size, which differed among our study regions. To obtain comparable values of β-diversity, we resampled the data (Baselga 2010). To calculate $\beta_{\text{among-sites}}$ for each region, we randomly sampled nine sites without replacement (minor sample value) of the same region 5,000 times (see Solar et al. 2015). $\beta_{\text{among-sites}}$ was calculated using the following formula: $\beta_{\text{among-sites}} = \gamma_{\text{region}}/\alpha_{\text{site}}$ (Whittaker 1972), where γ_{region} is cumulative herbivore species richness in each region, α_{site} is average species richness at a sampling site within a region. In this method, $\beta_{\text{among-sites}}$ values are mathematically independent of α-diversity (Jost 2007), allowing comparison among regions with different α-diversity values.

We decomposed β-diversity ($\beta_{\text{among-sites}}$) using Sørensen ($\beta_{\text{SOR}}$) and Simpson ($\beta_{\text{SIM}}$) indices (Baselga 2010). β_{SOR} represents the total β-diversity and includes both turnover and nestedness. β_{SIM} does not consider differences in species richness, and therefore only represents spatial species turnover. Hence the total species loss due to nestedness (β_{NES}) is given by difference between the Sørenson and Simpson indices ($\beta_{\text{NES}}= \beta_{\text{SOR}} - \beta_{\text{SIM}}$). This approach is also sensitive to sample size, thus we calculated β-values using a resampling procedure. We took 5,000 random samples from the total number of sites within each region, to have a comparable measure of β_{SOR} and β_{SIM} diversities.

We used GLMs to test whether regional heterogeneity and climate variation determine herbivore guild β−diversity and turnover. These models were run using the β−diversity and the proportional turnover ($\beta_{\text{SIM}}/\beta_{\text{SOR}}$) of insect herbivores guilds as response variables. The indicator of heterogeneity (cumulative plant richness) and the climate variation (precipitation coefficient of variation) per region were used as explanatory variables. We calculated the precipitation coefficient of variation for each region, dividing the standard deviation of average monthly rainfall by the average monthly rainfall. We used weather data from four years before the last sample date for each region (N=48 months). Residual analysis was conducted to test the suitability of the model for error distribution (Crawley 2013).

Landscape habitat quantification and statistical analysis

Assessment of habitat quantity in each 48 sampling sites was based on the classification of RapidEye cloud free, satellite images of years 2011 and 2012. These dates are intermediate in time along the sampling period. Images are from February and early June, corresponding to the dry season when the highest differentiation between pastures, dry, and riparian forest occur. Images were classified based on the first three bands of the RapidEye sensor with a spatial resolution of 5 m. Images were placed into four land-cover classes: (i) forest (intermediate and old growth forest), (ii) crops (e.g., mango, papaya, watermelon), (iii) water, and (iv) other (e.g., roads, buildings). Image processing was done using Geographical Information System ArcGis 10.2 (ESRI 2012) at 1:15,000 scale. Habitat quantity was determined within concentric circles of 0.25 km, 0.5 km,1 km, and 1.5 km, and 2.0 km. Radii were determined from the centroid of each sample plot, representing a nested set of landscape sectors at five spatial scales. SDMTools was used to obtain the proportion of each land cover class in the R-CRAN environment (v 3.2.2, R Core Team 2015).

For each of the five spatial scales (radii) we tested whether proportional forest cover determines insect herbivore diversity. We build GLMs with the mean insect richness and abundance as the response variable, and the percentage of forest cover at each spatial scale as an explanatory variable. To determine at which spatial scale forest cover has the strongest effect, the explanation (deviance) of each of these models was divided by the deviance of a null model using the following formula: Explained deviance = 1 - (deviance H1/deviance H0), thus if the proportion of deviances between H1 and H0 were higher, the explained deviance is low. We plotted the explained deviance for each of the five scales with the n = 48 landscapes to illustrate scale-dependence of forest cover on herbivorous insect richness and abundance at these five analyzed spatial scales. All analyses were carried out in R (R Development Core Team, 2015).

Results

We collected 2,893 herbivorous insects from 438 morphospecies across the four dry forest regions. There were 113 folivorous morphospecies, 225 sap-sucking, and 100 xylophagous. Two hundred specimens were folivorous insects, 1,893 specimens were sap-sucking, and 800 specimens were xylophagous. Among the folivorous insects, the families with greatest richness and abundance were Chrysomelidae and Curculionidae; the Cicadellidae and Achilidae families had the highest richness and abundance among the sap-sucking insects. The Cerambycidae family and subfamily Scolytinae had the highest species richness and abundance among the xylophagous insects (Table 1). Cicadellidae and Scolytinae had the highest overall abundance in the study (57% and 22% respectively).

North MG plots had the highest numbers of morphospecies (160) and individuals (1,578) among the regions, and Patos PB plots had the lowest (with 45 morphospecies and 121 individuals). The Serra do Cipó and the Chamela sites were similar in richness and abundance, with 118 morphospecies and 420 individuals in Serra do Cipó plots, and 115 morphospecies and 774 individuals in Chamela plots (Table 1; Fig. 2).

Most specimens were considered rare, with only one individual found for 272 (62%) of the 438 morphospecies sampled. Nevertheless, the curves approached the Jackknife estimate in 60% for Serra do Cipó species, 67% for North of MG, 62% species for Patos PB, and in 65% for the Chamela region, suggesting that the majority of local species were represented in the analysis (Fig. 2).

Patos PB had lower plant richness (mean±S.D. = 9±1.05 species) than did sites at Serra do Cipó (18.44±3.80 species), Northern MG (24.20±2.10 species) and Chamela (24.44±3.06 species); these three did not differ in mean plant richness (Negative binomial: $_{[3,44]}$ = 47.05, $p < 0.001$) (Table 2). The mean temperature was high (above 20 ºC) for all regions, but rainfall were consistently lower in Patos PB (mean±S.D) than in others regions (mean±S.D) (Table 2).

Plant richness had no effect on folivorous guild richness and abundance, and effectively explained the increase in sap-sucking and the xylophagous guild species richness and abundance in the four dry forest regions (Table 3; Fig. 3). Patos PB sites contributed most to plant richness explanation among regions for the sap-sucking (29%) and xylophagous (19%) guilds richness (Fig. 3). Folivorous guild richness and abundance were similar among regions, and the sap-sucking and xylophagous species richness and abundance was higher in the Northern MG and the Chamela sites (Table 3; Fig.3).

Table 1. Morphospecies richness (Rich) and abundance (Ab) of herbivorous insects sampled in four tropical dry forests. The predominant feeding guild (folivorous, sap-sucking and xylophagous) is presented for each taxa.

	Se. Cipó		North MG		Patos PB		Chamela		Total	
Taxon/Guild	Rich	Ab	Rich	Ab	Rich	Ab	Rich	Ab	Rich	Ab
Coleoptera/Folivorous										
Chrysomelidae	17	31	10	15	6	10	14	17	47	73
Curculionidae	10	16	13	34	7	9	6	8	36	67
Elateridae	1	2	2	2	0	0	1	1	4	5
Megalopodidae	0	0	0	0	0	0	3	12	3	12
Orthoptera/Folivorous										
Acrididae	0	0	0	0	1	1	0	0	1	1
Eumastacidade	0	0	1	2	0	0	0	0	1	2
Gryllidae	1	1	5	14	2	2	1	3	9	20
Proscopiidae	0	0	1	1	1	5	0	0	2	6
Tettigoniidae	0	0	8	11	2	3	0	0	10	14
Hemiptera/Sap-sucking										
Achilidae	1	1	9	62	1	1	4	6	15	70
Aetalionidae	0	0	1	1	0	0	0	0	1	1
Aphididae	1	1	0	0	0	0	0	0	1	1
Aphrophoridae	1	1	0	0	0	0	0	0	1	1
Ceratocombidae	0	0	0	0	0	0	1	5	1	5
Cicadellidae	37	174	63	982	16	78	43	428	159	1662
Cicadidae	0	0	0	0	0	0	1	1	1	1
Coreidae	1	1	1	1	0	0	1	1	3	3
Dictyopharidae	1	1	1	1	0	0	0	0	2	2
Flatidae	0	0	0	0	1	2	1	1	2	3
Hebridae	0	0	1	2	0	0	0	0	1	2
Issidae	1	1	0	0	0	0	0	0	1	1
Lygaeidae	1	3	0	0	0	0	2	2	3	5
Membracidae	2	2	2	2	0	0	1	1	5	5
Miridae	2	16	6	8	0	0	5	9	13	33
Nogodinidae	0	0	1	1	1	1	0	0	2	2
Psyllidae	2	50	2	12	0	0	4	23	8	85
Rhopalidae	3	5	0	0	0	0	0	0	3	5
Tingidae	0	0	1	4	0	0	1	1	2	5
Triozidae	1	1	0	0	0	0	0	0	1	1
Coleoptera/Xylophagous										
Anobiidae	2	6	3	4	0	0	3	5	8	15
Anthribidae	1	1	1	1	1	1	0	0	3	3
Bostrichidae	2	2	4	25	3	5	2	21	11	53
Cerambycidae	9	13	12	51	2	2	5	5	28	71
Platypodinae	3	4	2	20	1	1	1	1	7	26
Scolytinae	18	87	10	322	0	0	15	223	43	632

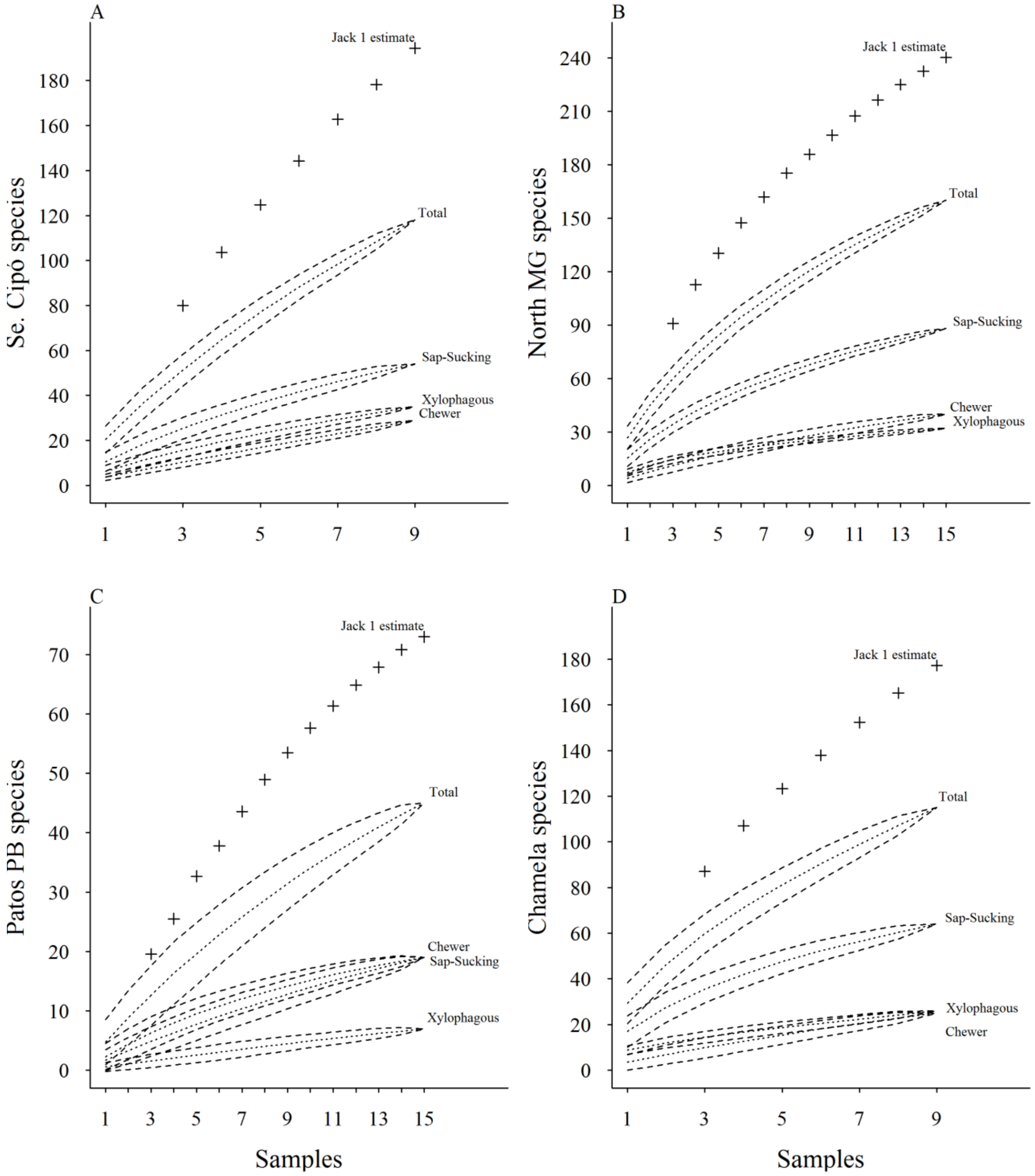

Fig. 2. Species accumulation curves and an estimate of the total species richness at Serra do Cipó (A), North of MG (B), Patos PB (C) and Chamela regions (D) for the complete data set and for folivorous, sap-sucking and xylophagous species separately. The dotted lines represent the analytically derived species accumulation curve, and dashed lines represent the 95% confidence interval. The '+' symbol represents first order jackknife, using the 'poolaccum' procedure (vegan package) in R.

Table 2. Mean values (mean±SE) of plant richness, monthly average temperature, and monthly average precipitation over four years in four dry forest regions. GLMs were used to test for differences among regions. Different letters represent statistically different means (P<0.05) by aggregating levels in contrast analysis.

Region	Plant richness	Temperature (ºC)	Precipitation (mm)
Se. Cipó	18.44±3.80a	22.10±0.68	129.25±22.40
North MG	24.20±2.10a	25.21±0.44	76.66±18.91
Patos PB	9.00±1.10b	27.88±0.18	47.50±11.66
Chamela	24.44±3.06a	26.55±0.50	98.95±17.50

Table 3. Analysis of deviance showing the effects of plant richness, region, and interaction on insects herbivore richness and abundance in tropical dry forests.

Response Variable	Explanatory variable	GL	Deviance	p
Folivore richness	Plant richness	1	0.0395	0.557
	Region	3	0.0263	0.972
	Plant richness:Region	3	0.8552	0.070
Folivore abundance	Plant richness	1	0.0937	0.490
	Region	3	0.1206	0.890
	Plant richness:Region	3	1.3499	0.089
Sap-sucker richness	Plant richness	1	3.5286	**<0.001**
	Region	3	2.6395	**0.001**
	Plant richness:Region	3	0.8457	0.097
Sap-sucker abundance	Plant richness	1	21.1263	**<0.001**
	Region	3	21.5707	**0.005**
	Plant richness:Region	3	2.7030	0.601
Xylophage richness	Plant richness	1	1.8248	**<0.001**
	Region	3	3.3464	**<0.001**
	Plant richness:Region	3	0.1059	0.610
Xylophage abundance	Plant richness	1	8.5963	**<0.001**
	Region	3	18.3684	**<0.001**
	Plant richness:Region	3	0.7102	0.507

β-diversity among regions

β-diversity was greater for the sap-sucking and the xylophage guilds in Patos PB, and for the folivore guild in Serra do Cipó (Table 4). However, heterogeneity (accumulated plant richness) and precipitation coefficient of variation did not affect β-diversity or turnover (among sites) for each guild, although sap-sucking β-diversity showed a toward significance (Table 5). Accumulated plant richness was higher in the Chamela and Serra do Cipó sites with 111 and 100 plant species respectively, followed by North MG sites with 84 species, and Patos PB with 22 plant species. Precipitation coefficient of variation was roughly equal in Serra do Cipo, North MG and Chamela regions (1.20, 1.28, and 1.21, rain CV respectively), and higher in Patos PB (1.45 rain CV).

Decomposition of β-Diversity

Decomposition of β-diversity revealed species turnover among sites as the main driver of the β_{SOR} for the three guilds in all four dry forests regions (Table 4). Turnover explained more than 90% of the total diversity for all groups except the sap-sucking guild in Patos PB and Chamela regions, and the xylophage guild in the Chamela region (Table 4).

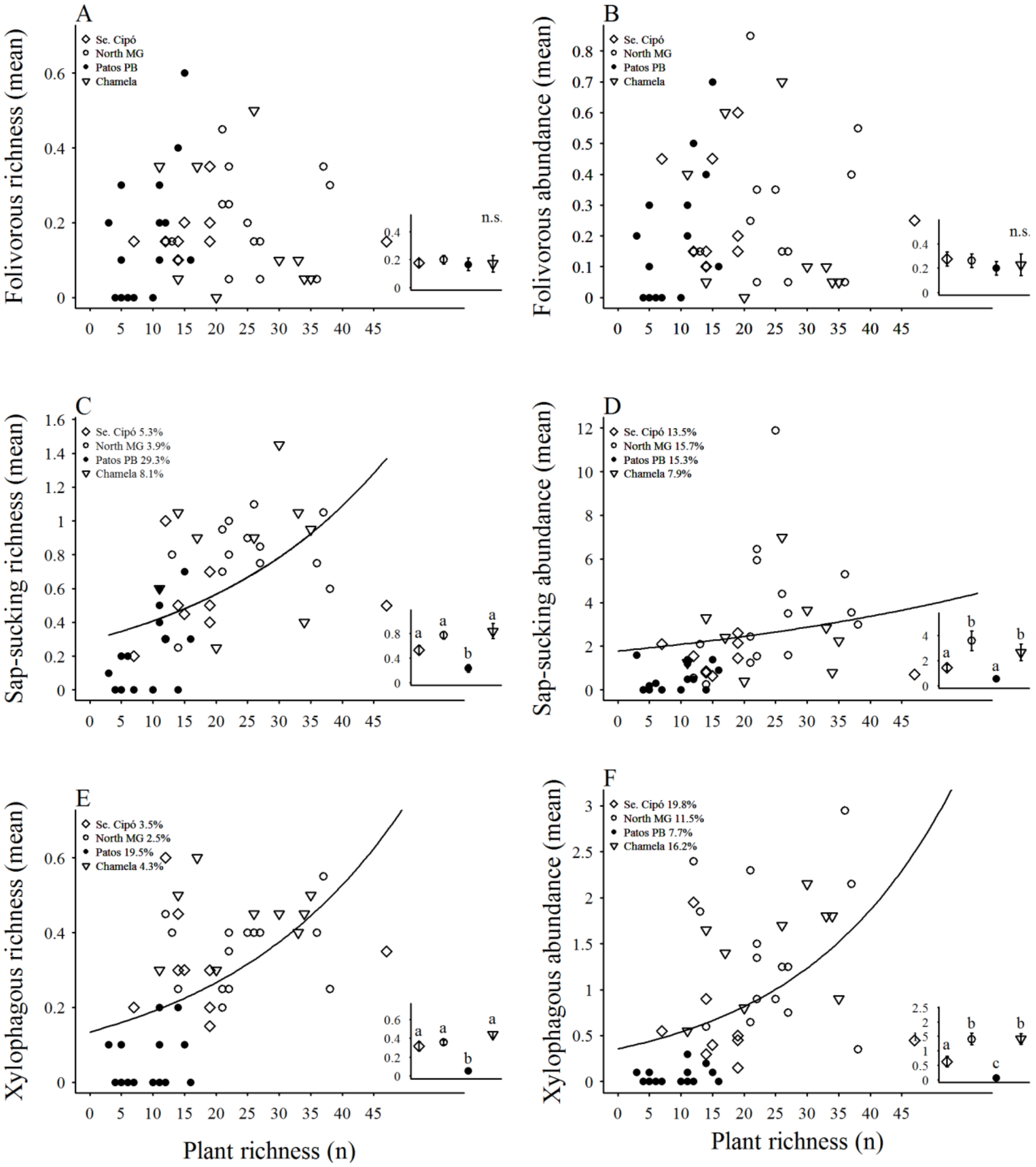

Fig. 3. Mean daily species richness and abundance of folivorous (A and B), sap-sucking (C and D), and xylophagous (E and F) insect herbivores along the sites plant richness gradient. Parameter estimates used for curve-fitting were obtained from the generalized linear model (GLM) and adjusted for exponential functions. Mean values from the four dry forest regions are represented in each subplot, and the different letters above the symbols represent statistically different means ($P < 0.05$; Table 3). The numbers in the legend are the calculation of importance variables for regressions, made by scaling the absolute value of the t-statistic for each model parameter. This was done using the 'varImp' procedure in the ‘caret’ package in R.

Table 4. Diversity measure ($\beta_{\text{among-sites}}$) for herbivorous insects collected in four tropical dry forests regions. The importance (%) of turnover ($\beta_{\text{SIM}}/\beta_{\text{SOR}}$) is reported for each guild in each region.

Region	Guild	β-Diversity	Turnover
Se. Cipó	Folivorous	8.156	99.4
	Sap-Suking	5.116	95.3
	Xylophaous	5.526	95.1
North MG	Folivorous	6.978	96.5
	Sap-Suking	4.370	94.8
	Xylophaous	3.527	93.3
Patos PB	Folivorous	7.742	94.5
	Sap-Suking	6.157	85.8
	Xylophaous	8.409	95.2
Chamela	Folivorous	7.258	92.8
	Sap-Suking	3.815	88.8
	Xylophaous	2.962	86.5

Table 5. Analysis of deviance showing the effects of the precipitation coefficient of variation (CV) and cumulative plant richness on insect herbivore guild diversity ($\beta_{\text{among-sites}}$) and turnover ($\beta_{\text{SIM}}/\beta_{\text{SOR}}$) in four tropical dry forests regions.

Response variable	Explanatory variable	GL	Deviance	p
Folivore β-diversity	Rain CV	2	0.0001	0.970
	Plant richness	1	0.0857	0.299
Sap-sucker β-diversity	Rain CV	2	0.3649	0.051
	Plant richness	1	0.2589	0.061
Xylophage β-diversity	Rain CV	2	2.0668	0.123
	Plant richness	1	1.2820	0.155
Folivore β-turnover	Rain CV	2	0.0024	0.617
	Plant richness	1	0.0004	0.307
Sap-sucker β-turnover	Rain CV	2	0.0038	0.484
	Plant richness	1	0.0029	0.683
Xylophage β-turnover	Rain CV	2	0.0012	0.458
	Plant richness	1	0.0033	0.311

Landscape effects

The predictive power of forest cover for folivorous, sap-sucking and xylophagous guild diversity differed by spatial scale (0.25 km, 0.5 km, 1km, 1.5 km, 2 km). Although all regressions models showed a positive inclination coefficient, forest cover explained sap-sucking and xylophagous insect diversity better than folivorous. Folivorous guild morphospecies richness (but not abundance) increased with forest cover only at the 0.25 km radii scale (Table 6; Fig. 4). Percentage of forest cover sufficiently explained sap-sucking and xylophagous species richness and abundance at all spatial scales (Table 6; Fig 4).

The proportion of explained variation in folivorous guild richness and abundance decreased from the 0.25 km to 0.5km radii scales, and a similar proportion of variation was explained in the 1 to 2 km scales. In contrast, the proportion of explained variation in sap-sucking richness and abundance increases from 0.25 km to 1 km scale, and remains similar until the 2 km radii scale. The increasing proportion of explained variation was also observed for the xylophage richness and abundance from the 0.25 to 0.5 km scales, but the proportion of explained variation was higher at 1 and 1.5 km scales than at the 2 km radius scale.

Table 6. Dependence of insect herbivore guilds on the percentage of forest cover (i.e., landscape complexity) in 48 dry forest landscapes at five spatial scales. P-values are from Generalized Linear Models (GLM) with quasipoisson error distribution for guild richness and abundance. The correlation coefficient (Deviance %) was calculated using the formula: "1-(deviance H1/deviance H0)", and values from 0 to 1 represent the total model contribution, each with N = 48 landscape sectors.

Factor	Deviance (%)	P	Regression model
Folivore richness			
Scale: 0.25 km	0.075	**0.048**	Y= e-2.53+0.99*x
Scale: 0.5 km	0.031	0.212	Y= e-2.19+0.64*x
Scale: 1 km	0.037	0.171	Y= e-2.22+0.73*x
Scale: 1.5 km	0.044	0.137	Y= e-2.25+0.76*x
Scale: 2 km	0.030	0.222	Y= e-2.21+0.71*x
Folivore abundance			
Scale: 0.25 km	0.074	0.055	Y= e-2.34+1.10*x
Scale: 0.5 km	0.026	0.265	Y= e-1.91+0.64*x
Scale: 1 km	0.033	0.210	Y= e-1.96+0.76*x
Scale: 1.5 km	0.033	0.204	Y= e-1.95+0.74*x
Scale: 2 km	0.025	0.275	Y= e-1.93+0.72*x
Sap-sucker richness			
Scale: 0.25 km	0.129	**0.007**	Y= e-1.49+1.12*x
Scale: 0.5 km	0.162	**0.002**	Y= e-1.55+1.29*x
Scale: 1 km	0.182	**0.001**	Y= e-1.54+1.37*x
Scale: 1.5 km	0.169	**0.002**	Y= e-1.48+1.28*x
Scale: 2 km	0.164	**0.002**	Y= e-1.58+1.42*x
Sap-sucker abundance			
Scale: 0.25 km	0.103	**0.039**	Y= e-0.52+1.45*x
Scale: 0.5 km	0.138	**0.019**	Y= e-0.65+1.75*x
Scale: 1 km	0.234	**0.002**	Y= e-0.93+2.25*x
Scale: 1.5 km	0.217	**0.003**	Y= e-0.83+2.11*x
Scale: 2 km	0.231	**0.002**	Y= e-1.07+2.43*x
Xylophage richness			
Scale: 0.25 km	0.119	**0.007**	Y= e-2.32+1.22*x
Scale: 0.5 km	0.140	**0.003**	Y= e-2.35+1.35*x
Scale: 1 km	0.185	**0.001**	Y= e-2.42+1.55*x
Scale: 1.5 km	0.182	**0.001**	Y= e-2.39+1.41*x
Scale: 2 km	0.136	**0.004**	Y= e-2.35+1.45*x
Xylophage abundance			
Scale: 0.25 km	0.180	**0.002**	Y= e-1.94+2.09*x
Scale: 0.5 km	0.295	**0.001**	Y= e-2.34+2.72*x
Scale: 1 km	0.336	**0.001**	Y= e-2.18+2.70*x
Scale: 1.5 km	0.335	**0.001**	Y= e-2.16+2.65*x
Scale: 2 km	0.283	**0.001**	Y= e-2.17+2.69*x

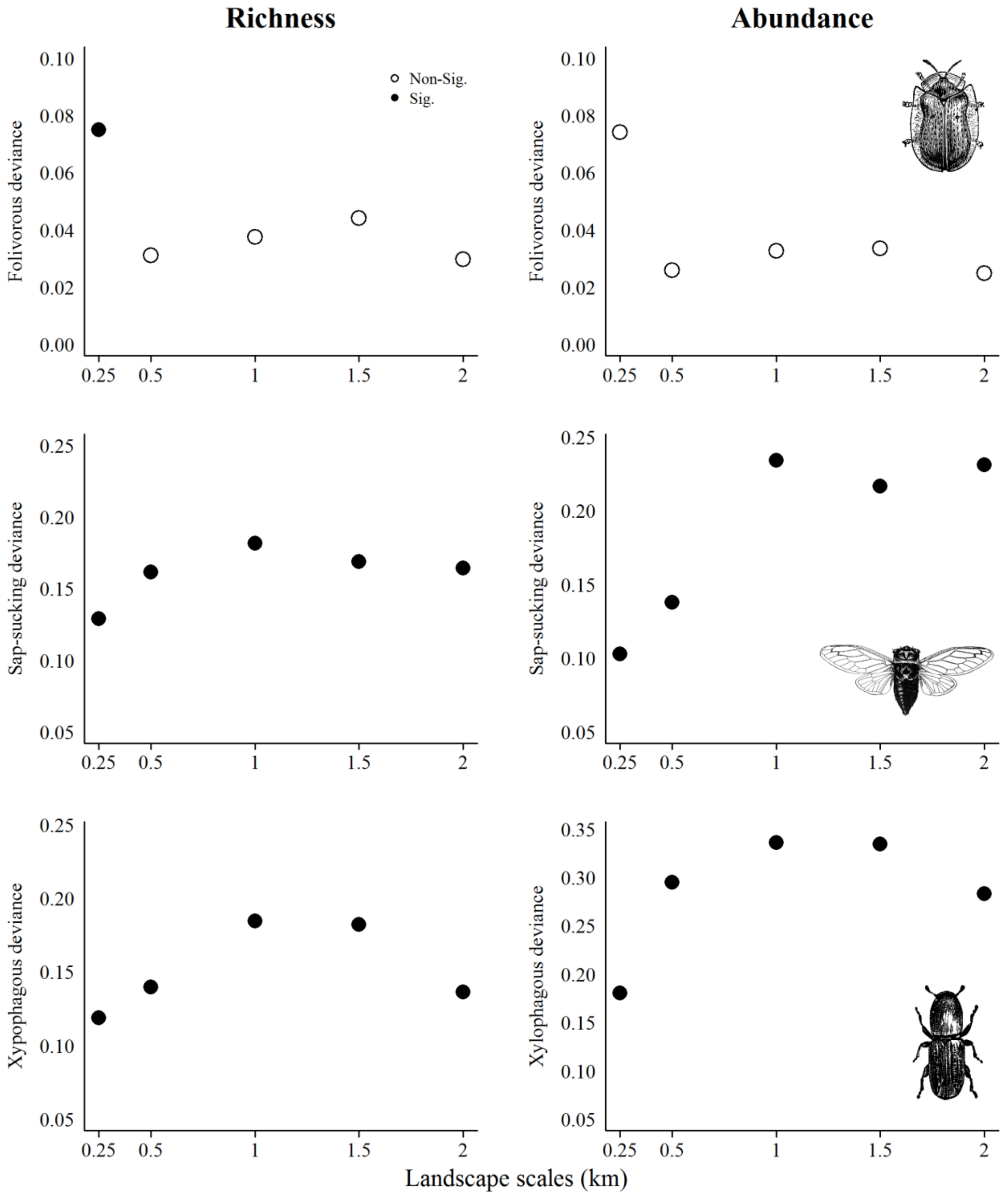

Fig. 4. Explained deviance of the richness and abundance (columns) of folivorous, sap-sucking and xylophagous insects (lines) versus the percentage of forest cover (i.e., landscape complexity) at five spatial scales. Significant regressions ($p<0.05$) are indicated by filled symbols, for explanation of statistics see Table 6. Font: http://etc.usf.edu/clipart/, for the insects' images.

Discussion

Our results indicate that higher herbivore diversity is sometimes associated with local heterogeneity and structural complexity of the landscape, as well as high percentage of forest cover and relatively little land conversion for other activities. Species turnover is the primary driver of β-diversity for the three insect herbivore guilds in all of our dry forests regions. These results generally agree with the common expectation that loss of forest cover and habitat homogenization negatively affect insect diversity (Thies et al. 2003, Wilby et al. 2006, Stein et al. 2014, Novais et al. 2016a).

Folivorous insects were not affected by the differences in plant richness among sites or regions, while the sap-sucking and xylophagous insect richness and abundance were lower in regions with lower plant richness (Patos PB), and higher in regions with higher plant richness. Most sap-sucking and xylophagous insects spend the majority of their cycle on the same host tree, while folivorous insects seek highly nutritious leaf tissue on several hosts (Calderon-Cortez et al 2011, Forister et al. 2015, Neves et al. 2014ab). Plant diversity is thus a direct driver of richness and abundance in specialist species, but not as much for generalist species, due to their close association of plants threats (i.g. tolerance to plant defenses) (Price 2002). Folivorous insect diversity is strongly associated with availability of new leaves, niche space, and opportunities for host range expansion, which is a likely explanation for the high folivorous diversity in tropical areas (Novotny et al. 2006, Neves et al. 2014ab).

Herbivore β-diversity and the turnover component were not influenced by the cumulative plant richness among regions, showing that effects of habitat heterogeneity depend on the scale at which environmental variables are measured (Stein et al. 2014, Solar et al. 2015). Variation in precipitation (rain CV) among regions did not affect guild β-diversity or the turnover component. In general, β-diversity was higher at the most xeric site (Patos PB region). Many herbivorous insects, especially sap-suckers, are negatively affected by plant water stress, which decrease access to plant nutrients (Huberty and Denno 2004). The high degree of spatial heterogeneity in Patos PB communities may be due to local extinction filters, even with low diversity (Tscharntke et al. 2012, Solar et al. 2015). Further, the Patos PB region has a history of highly unpredictable weather (Prado 2003), with has been reported to negatively affect insect diversity through causing shifts in resource availability, especially in drier forest environments where desiccation is an ever-present threat (Wardhaugh et al. 2014). Nevertheless, we found that turnover is the primary driver of β-diversity in these insect groups. These results were consistent with findings from another study of ambrosia and bark beetle communities in dry forest environment (Macedo-Reis et al. 2016), suggesting a stronger influence of local (site) factors (i.g., temporal shifts in resources) in determining the local species pool (Wardhaugh et al. 2014).

These results may be informative for habitat management at the landscape level, particularly in fragmented areas (Avila-Cabadilla et al. 2012, Tscharntke et al. 2012). Differences in landscape forest cover affected the herbivore insect guilds in different ways. This supports the view that species perceive landscape structure at different spatial scales depending on their dispersal abilities or foraging ranges (Weibull et al. 2000, Steffan-Dewenter et al. 2002). The distribution of folivorous guild species was only explained by the percentage of forest cover at the smallest spatial scale (0.25 km radius). Similar results were found for Chrysomelidae species (Jonsen et al. 2001, Piper and Compton 2010). Piper and Compton (2010) reported that beetles use host-plants as 'stepping stone' to move through its habitat and populations are effectively isolated by relatively small areas of open ground. Therefore, disconnect among forest patches at larger spatial scales might limit the dispersal of the folivorous insects, rendering them more dependent on small-scale processes (Ricketts 2001). Moreover, the degree of available shelter may explain the ability to detect species diversity patterns at smaller spatial scales, since shelter is known to be important for folivorous species, especially to issues related with mortality rates (Weibull et al. 2000, Price 2002, Cornelissen et al. 2016)

Sap-sucking and xylophagous guilds responded to landscape forest cover at all spatial scales, and landscape factors were more strongly correlated with sap-sucking and xylophagous insect richness and abundance at larger spatial scales (from 1 to 1.5 km). This finding is consistent with the dispersal ability described for sap-sucking and xylophagous species (Turchin and Thoeny 1993, Blackmer et al. 2004). Blackmer et al. (2004) found that the majority (95%) of sap-sucking Cicadellidae were recaptured far from the release site, and another study showed that one half of the released xylophagous bark beetles dispersed more than 0.69 km (Turchin and Thoeny 1993). Therefore, the percentage of forest cover at larger spatial scales should increase colonization potential in these species groups due to strong dispersal capability. Leal et al. (2015) also suggested that riparian forest may be a relevant landscape component for the large-scale heterogeneity effects observed here, since most riparian forests trees maintain leaves year round, and these areas were near our sample sites.

The composition of insect herbivore families on the sampled dry forest regions was consistent with findings of earlier studies. The folivorous Chrysomelidae and Curculionidae, the sap-sucking Cicadelidae and Psyllidae, and the xylophagous Scolytinae and Cerambycidae are usually reported as important components of forest insect communities (Basset 2001, Neves et al. 2014a, Leal et al. 2015, Novais et al. 2016a). The majority of our morphospecies and individuals were sap-suckers, followed by folivorous and xylophages, respectively. Most of the sampled species were associated with a single plant taxon (i.e., Cicadellidae, Psyllidae), and this is consistent with described patterns of the insect distribution in a rain forest region that used the same sampling methods (Novais et al. 2016a). The distributions generally show higher frequency of more specialized insects, and fewer more generalized species (Forister et al, 2014). The general dominance of monophagy over polyphagy in tropical forests may influence associations between vegetation heterogeneity and local herbivore species diversity.

Three of the four sampled dry forest regions are surrounded by extensive agricultural crop areas (North MG, Patos PB and Chamela). Further, these forests surely provide ecosystem services (i.e., pollination and pest control) that should be quantified in future studies (Thies and Tscharntke 1999, Maass et al. 2005, Boerema et al. 2016, Novais et al. 2016b).

Conclusions

Our results demonstrated that species turnover is important factor for maintaining high diversity in the regions sampled, and reflects the sensitivity of herbivores to plant richness and habitat modification; these effects differed by spatial scale and herbivore feeding guilds (Neves et al. 2014ab, Silva et al. 2016, Macedo-Reis et al. 2016). We suggest prioritizing conservation of areas with higher plant richness, as these areas may be particularly important for maintenance of insect herbivore diversity. The overall landscape patterns indicate that the maintenance of forest cover is increasingly important at larger spatial scales. Strong correlations between forest cover and herbivore abundance and richness at the landscape scale may indicate strong biologically relevance of studies at larger spatial scales. We highlight key structures of the vegetation (i.e., evergreen plants) (Tews et al. 2004, Silva and Neves 2014) as a focus for future investigations of insect herbivore foraging requirements and use of regional resources.

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CAPÍTULO 2

SPATIO-TEMPORAL DISTRIBUTION OF BARK AND AMBROSIA BEETLES IN A BRAZILIAN TROPICAL DRY FOREST

Journal of Insect Science
Research

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Spatio-Temporal Distribution of Bark and Ambrosia Beetles in a Brazilian Tropical Dry Forest

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Abstract

Bark and the ambrosia beetles dig into host plants and live most of their lives in concealed tunnels. We assessed beetle community dynamics in tropical dry forest sites in early, intermediate, and late successional stages, evaluating the influence of resource availability and seasonal variations in guild structure. We collected a total of 763 beetles from 23 species, including 14 bark beetle species, and 9 ambrosia beetle species. Local richness of bark and ambrosia beetles was estimated at 31 species. Bark and ambrosia composition was similar over the successional stages gradient, and beta diversity among sites was primarily determined by species turnover, mainly in the bark beetle community. Bark beetle richness and abundance were higher at intermediate stages; availability of wood was the main spatial mechanism. Climate factors were effectively non-seasonal. Ambrosia beetles were not influenced by successional stages, however the increase in wood resulted in increased abundance. We found higher richness at the end of the dry and wet seasons, and abundance increased with air moisture and decreased with higher temperatures and greater rainfall. In summary, bark beetle species accumulation was higher at sites with better wood production, while the needs of fungi (host and air moisture), resulted in a favorable conditions for species accumulation of ambrosia. The overall biological pattern among guilds differed from tropical rain forests, showing patterns similar to dry forest areas.

Key words: moisture, Platypodinae, Scolytinae, succession, seasonality

Introduction

The Scolytinae and Platypodinae (Coleoptera, Curculionidae) are insects with two different main feeding strategies, commonly referred to as bark and ambrosia beetles. Bark beetles feed mostly on phloem tissue (i.e., phoeophagy), while ambrosia beetles feed on fungi growing on tree trunks and branches (i.e., myelophagy), or on portions of xylem and fungal tissue (i.e., xylomycetophagy) (Atkinson and Equihua, 1986). The term 'bark beetle' is used here strictly for phloeophagous species, while the term 'ambrosia beetle' applies to both xylomycetophagy and myelophagy (Hulcr et al. 2007). With both strategies, larvae and adults create a system of cavities that protect them from external risks until they bore a new gallery, typically in another host tree. The cavity system resulting from the colonization process can be secondarily occupied by other beetle species such as inquilines and predators (Feller and Mathis 1997, Calderón-Cortés et al. 2011). Hence, the beetle community influences cascade effects in natural ecosystems, and investigations of bark and ambrosia beetle spatio-temporal dynamics may prove useful for future research targeting wood-associated fauna in tropical ecosystems (Wardhaugh 2014, Seibold et al. 2015).

Hulcr and collaborators (2008a) found low ambrosia beetle beta diversity (β) at a scale of 1,000 km in Papua New Guinea rainforests, where most species were evenly distributed over large areas in an idiosyncratic pattern. Low host specificity likely explained this broad distribution and low β-diversity (Hulcr et al. 2008b). The same pattern occurs in other generalist herbivorous insect guilds (Novotny et al. 2007). β-diversity can be decomposed into two components: (1) species turnover, which consists of replacement of species at a given site with different species from another site, and (2) nestedness, which describes the loss (or gain) of species such that a site with lower species richness harbors a subset of species found in a site with higher species richness

(Baselga 2010). Breaking down β-diversity into these two components may improve our descriptions of bark and ambrosia beetle spatial distribution over structural habitat changes such as historical human land use (Marques and Schoereder 2014, Araujo et al. 2015).

Plant diversity has been suggested as the primary mechanism preserving the remarkable diversity of tropical herbivore species (Novotny et al. 2010, Neves et al. 2014). However, plant diversity does not seem to shape bark and ambrosia beetle diversity. These beetles are likely closely associated with the range of suitable wood availability (Grove 2002, Hulcr et al. 2008b), and wood diameter and moisture content seem better predictors of diversity. Hence, an increase in wood and plant species abundance along a gradient of ecological secondary succession should increase resource availability for them (Guariguata and Ostertag 2001, Kalacska et al. 2004, Madeira et al. 2009).

There are few studies reporting an influence of season on ambrosia beetle abundance in Brazil. Furthermore, season is rarely clearly defined, and catches among seasons not statistically compared; when these variables are controlled for some patterns emerge. While the majority of species are active throughout the year, most species are more abundant in the rainy/warm season, and a smaller number are either more active in the dry/cold season, or show no significant differences in activity between seasons (Dall’Oglio and Peres-Filho 1997, Flechtmann et al. 2001).

In contrast with tropical rainforests, leaf primary production in tropical dry forests is concentrated in the rainy season (Pezzini et al. 2014). There is a demonstrated increase in herbivorous insect activity in this season (Neves et al. 2014), especially for Scarabaeinae beetles (Neves et al. 2010) and butterflies (Neves et al. 2013).

We investigated spatio-temporal dynamics of beetles (Curculionidae: Platypodinae and Scolytinae) in tropical dry forests. The main goal of this study was to describe the bark and ambrosia beetle community by measuring temporal climate factors and variation in resource availability over a gradient of ecological secondary succession. We then described mechanisms that determine beetle β-diversity, addressing two questions: 1) Is nestedness more important than species turnover in this group? and 2) does species composition differ between successional stages? We expected beetle richness and abundance to increase over the course of secondary succession, and to find temporal variation in beetle richness and abundance.

Materials and methods

Study area

The study was carried out in the Mata Seca State Park, located in the São Francisco River Valley in Manga, northern Minas Gerais state, southeastern Brazil (14º48’36” - 14º56’59” S, 43º55’12”- 44º04’12” W). The park has an area of 15,466 ha, with predominance of seasonal deciduous forest (Madeira et al. 2009). The climate of the region is classified as semi-arid by the Köppen system, with an average temperature of 24.4 ºC and average annual rainfall of 818 ± 242 mm (Pezzini et al. 2014). Approximately 1,525 ha consist of abandoned pastures in different stages of succession (Madeira et al. 2009).

We categorized sampling sites according to number of years in secondary succession after disturbance, as follows: early = 10 years; intermediate = between 17 and 25 years; and late = over 50 years. The early successional stage was dominated by herbaceous and shrubby plants, with a discontinuous canopy approximately 4 m in height. The intermediate stage was composed of trees reaching 10 to 12 m in height with some emergent trees reaching up to 15 m, with dense understory and with many lianas. The late stage was composed of trees forming a closed canopy 18 to 20 m in height, with sparse understory with little light penetration and low density of lianas (Madeira et al. 2009).

We selected fifteen 20 x 10 m plots, five in each successional stage. Plots were established along a 7 km transect. Distance between plots within each stage varied from 0.2 to 0.8 km, and the distance between plots of different successional stages varied from 0.8 to 6 km (Fig. 1). We sampled the plots ten times from 2009 to 2011, during rainy and dry seasons (Fig. 2). Sampling was carried out in December 2009, February, April, September, and October 2010, and January, April, June, September, and December 2011. The dry season occurs from May to October, at which time approximately 90-95% of the tree species shed their leaves (Pezzini et al. 2014).

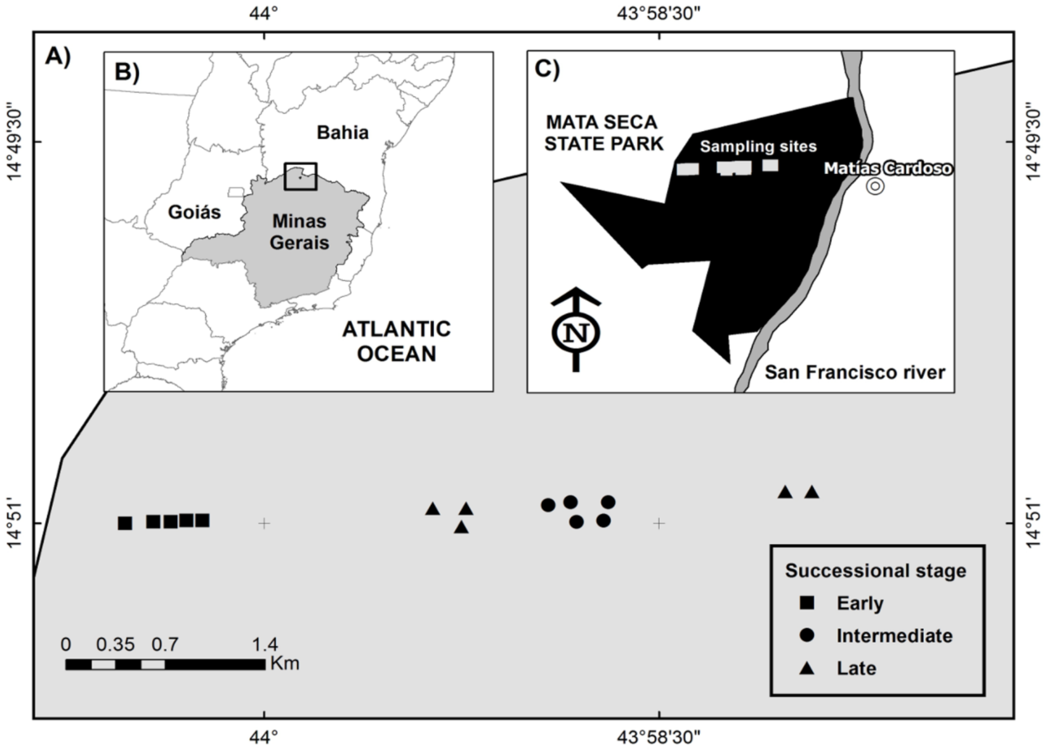

Fig. 1. Sampling sites at Mata Seca State Park in southeastern Brazil. Sampling design 'A' represent the distribution of successional stages, 'B' indicates the location in Brazil and 'C' represents the shape of park

In each site, we measured tree circumference at breast height (CBH), wood-area-index (WAI) and tree abundance (CBH ≥ 15 cm). We measured the WAI using canopy photos taken in the dry season (October 2010). We used one photo per site taken with a digital camera using an 8 mm fisheye lens (Nassar et al. 2008). The photos represented the relative contribution of trunks and branches to canopy structure, and were analyzed using Gap Light Analyzer software (Frazer et al. 1999).

We measured cumulative rainfall, average temperature, and air moisture for each of the five days required for each sampling period. We used a wireless net station located in the study area, which measured temperature and moisture every 30 minutes.

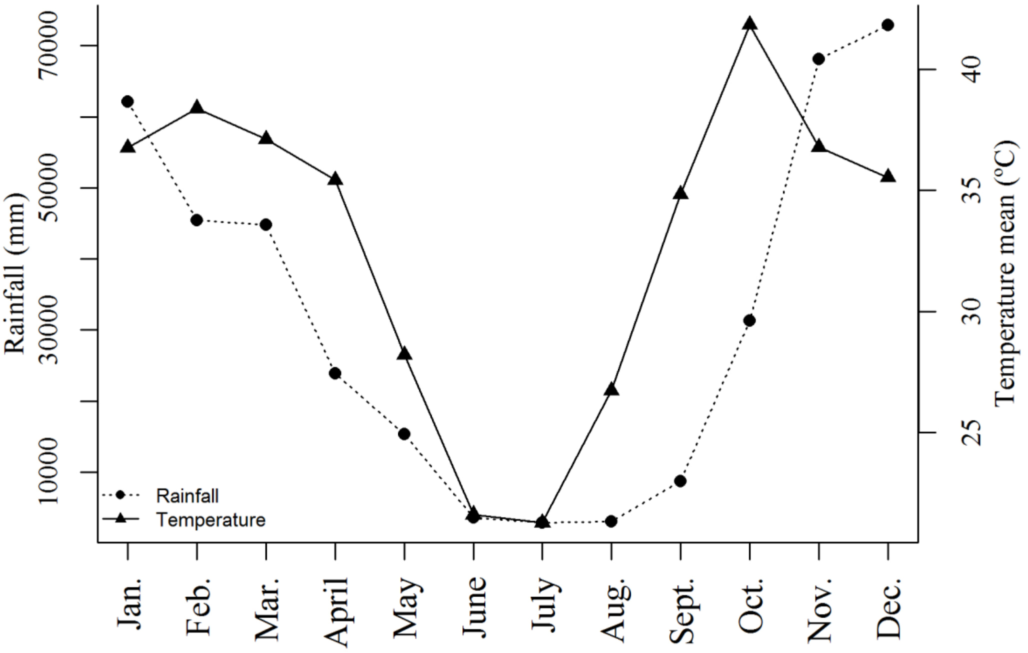

Fig. 2. Total historical average precipitation (filled circle), and monthly average temperature (filled triangle) from 1976–2011. Data from Mocambinho Meteorological Station located 15 km from Mata Seca State Park.

Insect sampling

We collected beetles using combined flight Malaise/window traps (Basset 1988, Novais et al. 2016). One trap per site (15 total) holding two vial collectors with 70% ethanol were exposed for five days (120 h) per month in the tree canopy in the center of each site. Bark and ambrosia beetles are attracted to ethanol released by dead and dying trees. Some species tend to be more attracted than others, thus the trapping technique may be biased towards certain taxonomic group (Hulcr et al., 2008). Specimens were determined based on Wood (2007), and divided into two feeding habitat guilds: bark and ambrosia beetles. We calculated the number of species and specimens for each sampling session. Voucher specimens were deposited in the Museum of Entomology at FEIS/UNESP (MEFEIS, Ilha Solteira, São Paulo state, Brazil).

Data analysis

We used permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) to evaluate the influence of secondary succession on bark and ambrosia beetle community composition between early, intermediate, and late stages using Jaccard dissimilarity measure with 999 permutations. PERMANOVA is a permutational ANOVA that can test the simultaneous response of one or more variables to one or more factors in the analyses of variance. We perfomed the analysis using the "adonis" procedure in the vegan package in R version 3.2.1.

We tested whether nestedness was the main driver of diversity by decomposing β-diversity ($\beta_{\text{between sites}}$) using the Sørensen ($\beta_{SOR}$) and the Simpson ($\beta_{SIM}$) indices (Baselga 2010). β_{SOR} represents the total β-diversity and includes both turnover and nestedness. β_{SIM} does not consider differences in species richness, and therefore only represents spatial species replacement, or turnover. Hence, the total species loss due to nestedness (β_{NES}) is given by the difference between those indices ($\beta_{NES} = \beta_{SOR} - \beta_{SIM}$).

Beetle diversity along a gradient of resource availability

The effects of a resource availability gradient on beetle diversity were determined using generalized linear models (GLMs). In these models, the richness and abundance of beetles (bark and ambrosia) were pooled by site from 2009 to 2011, whereas successional stage (early, intermediate ad late) and indicators of resource availability (CBH, WAI, and tree abundance) were used as explanatory variables. The minimal models were constructed by removing non-significant explanatory variables ($P > 0.05$) from the full models in the analysis. The models were submitted to residual analysis to identify the most suitable error distribution, we used the "rdiagnostic" procedure in the RT4Bio package in R (Crawley 2013).

Temporal variation

To test how climate conditions influenced temporal variation in beetle richness and abundance we used a Generalized Linear Mixed Models analysis (GLMMs, lme4 package), assuming temporal pseudoreplication. The explanatory variables. Collection month, accumulated rainfall, average moisture (%), and average temperature (ºC) were nested within the random effects of the sites sampled during the study (Bates et al. 2012). All analyses were carried out in the software R (R Development Core Team, 2015).

Results

We collected 763 Scolytinae beetles from 23 species across the successional gradient, including 14 bark beetle species and nine ambrosia beetle species. Fifty-eight specimens were bark beetles and 705 specimens were ambrosia beetles. The collected bark beetles included the Cryphalini, Micracini, Phloeosinini and Scolytini tribes, and the *Araptus* and *Cryptocarenus* genera. The ambrosia beetles collected included all

Xyleborini species, along with *Euplatypus parallelus*, *Corthylus* sp.1, and *Tricolus affinis* (Table 1). The tribe Cryphalini had the highest species richness and abundance among the bark beetle guild, and the tribe Xyleborini had the highest species richness and abundance among the ambrosia beetle guild. *Euplatypus parallelus* was the only species of the subfamily Platypodinae, with 12 specimens. *Xyleborus affinis* was the only species sampled in all sites and sampling periods, representing 87% of the total beetle abundance. In general, most species were considered rare; 15 species had fewer than three individuals among sites and sampling periods, and only one individual was found for eight species (four species per guild) (Table 1). The species accumulation curve did not approach an asymptote for the complete data set or for guilds, indicating the need for further sampling to arrive at a reliable estimate of α diversity. However, the curve was approaching the Jackknife estimate of 31 species (Fig. 3), suggesting that a majority of local species were represented in the analysis.

The sites in early successional stage had lower CBH (Poisson: Deviance $_{[2.12]}$ = 32.42, P < 0.001) and WAI (Quasi-Poisson: Deviance $_{[2.12]}$ = 0.21, P = 0.007) than did sites at intermediate and late successional stages. Tree abundance was similar between successional stages (Negative binomial: Deviance $_{[2.12]}$ =2.84, P = 0.24) (Table 2).

Table 1. List of beetles collected in the Mata Seca State Park in southeastern Brazil. Frequency per sample period (FP, n=10), and abundance per successional stage are reported for each species.

TAXA	GENUS/SPECIES	FP	Early	Inter.	Late	Total
SCOLYTINAE						
Corthylini	*Araptus* sp.1	1	0	1	0	1
	Corthylus sp.1	1	1	0	0	1
	*Cryptocarenus diadematu*Eggers	1	0	1	1	2
	Cryptocarenus heveae (Hagedorn)	2	0	1	1	2
	Tricolus affinis Eggers	4	0	2	2	4
Cryphalini	*Hypothenemus areccae*	1	0	0	1	1

	Weswood					
	Hypothenemus eruditus Weswood	2	0	2	0	2
	Hypothenemus plumeriae (Nordlinger)	3	2	3	0	5
	Hypothenemus sp.1	2	0	2	0	2
	Pityophthorus sp.1	6	0	3	3	6
	Pityophthorus sp.2	6	0	16	3	19
	Pityophthorus sp.3	3	0	1	2	3
	Pityophthorus sp.4	1	0	0	1	1
Micracini	*Hylocurus* sp.1	3	0	2	4	6
Phloeosinini	*Pseudochramesus acuteclavatus* (Hagedorn)	1	0	1	0	1
Scolytini	*Scolytopsis* sp.1	4	1	6	0	7
Xyleborini	*Cnestus retusus* (Eichhoff)	6	3	7	10	20
	Dryocoetoides sp.1	1	0	0	1	1
	Xyleborus affinis Eichhoff	10	152	223	288	663
	Xyleborus ferrugineus (Fabricius)	1	0	0	1	1
	Xyleborus spinulosus Blandford	1	1	0	0	1
	Xylosandrus curtulus (Eichhoff)	1	0	1	1	2
PLATYPODINAE						
Platypodini	*Euplatypus parallelus* (Fabricius)	5	2	4	6	12

Table 2. Mean values (mean ± S.E.) of the resource CBH (circumference at breast height), WAI (wood-area-index) and tree abundance, in 20 X 10 m plots in three successional stages in a Brazilian tropical dry forest. Generalized linear models were used, and the different letters represent statistically different means ($P < 0.05$).by aggregating levels in a contrast analysis.

Successional stage	CBH	WAI	Tree abundance
Early	20.1±2.80a	0.246±0.04a	20.4±5.58a
Intermediate	40.6±4.09b	0.348±0.02b	16.0±1.05a
Late	47.3±1.69b	0.412±0.02b	23.2±1.77a

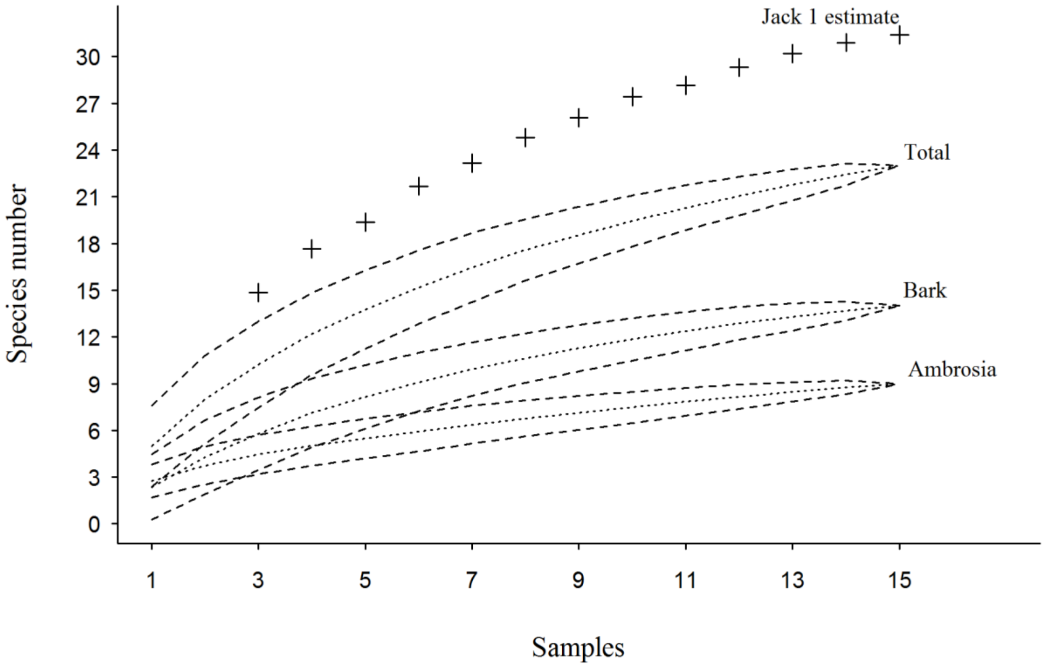

Fig. 3. Species accumulation and an estimate of total species richness at Mata Seca State Park for the complete data set, and for bark and ambrosia beetle species separately. The dotted lines represents the analytically derived species accumulation curve, and dashed lines represent the 95% confidence interval. The symbol " +" represents first order jackknife in abundance-based estimates using the 'poolaccum' procedure in the vegan package in R.

Beetle composition over the course of ecological secondary succession

Similarity analysis of bark beetle composition within three categories could not be assessed due to absence of species at three of the five early stage sites. However, bark beetle composition was similar between the intermediate and the late stages (PERMANOVA r^2= 0.11, P = 0.35). No species were present in all three stages. The intermediate and early stages shared two species, and intermediate and late stages shared six species. There were no species found in both early and late stages. Two species were exclusive to the late stage and four to the intermediate stage, with no bark beetle found exclusively in the early stage. Ambrosia beetle composition was similar among successional stages (PERMANOVA r^2= 0.11, P = 0.64). Three ambrosia species were common to all stages: *X. affinis*, *X. retusus* and, *E. parallelus*. The intermediate stage had two species in common with the late stage and none in common with the early stage, despite having three species that were common in all stages. Finally, two species were exclusive to early stages and another two exclusive to late stages, with no species exclusive to intermediate stages (Table 1).

Decomposition of β-diversity

Decomposition of β-diversity revealed species turnover between sites as the main driver of the β_{SOR} diversity for both bark (β_{SIM} = 0.77; $\beta_{SOR\,=}$ 0.90), and ambrosia (β_{SIM} = 0.57, $\beta_{SOR;=}$ 0.76) beetles, representing 85.6% of the bark beetle β diversity and 74.4% of the ambrosia beetle β diversity.

Beetle diversity along a gradient of resource availability

We found higher bark beetle richness and abundance at intermediate successional stages, followed by the late and the early stages, respectively (Fig. 4). We also detected a positive relationship between bark beetle richness and abundance and tree CBH (Table 3; Figs. 5 A and B). Ambrosia beetles increased in abundance (but not richness) with increased tree CBH (Table 3; Fig 5C).

Table 3. Analysis of deviance of the minimal adequate models showing the effects of successional stage and resource CBH on beetle richness and abundance in a Brazilian tropical dry forest.

Response variable	Explanatory variable	df	Deviance	*P*
Bark beetle richness	CBH	1	25.99	0.007
	Successional stage	2	13.16	0.001
Bark beetle abundance	CBH	1	28.64	0.036
	Successional stage	2	16.13	0.001
Ambrosia beetle abundance	CBH	1	15.12	0.005

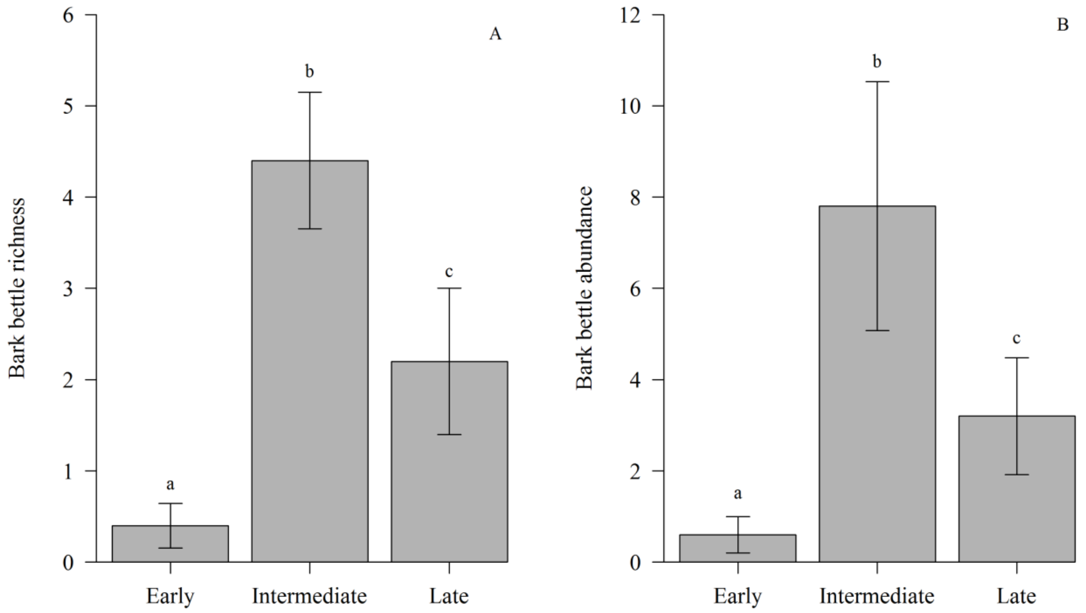

Fig. 4. Bark beetle (Curculionidae) richness (A) and abundance (B) (mean ± SE) in sites at different successional stages in the Mata Seca State Park in southeastern Brazil. Different letters above the columns represent statistically different means ($P < 0.05$).

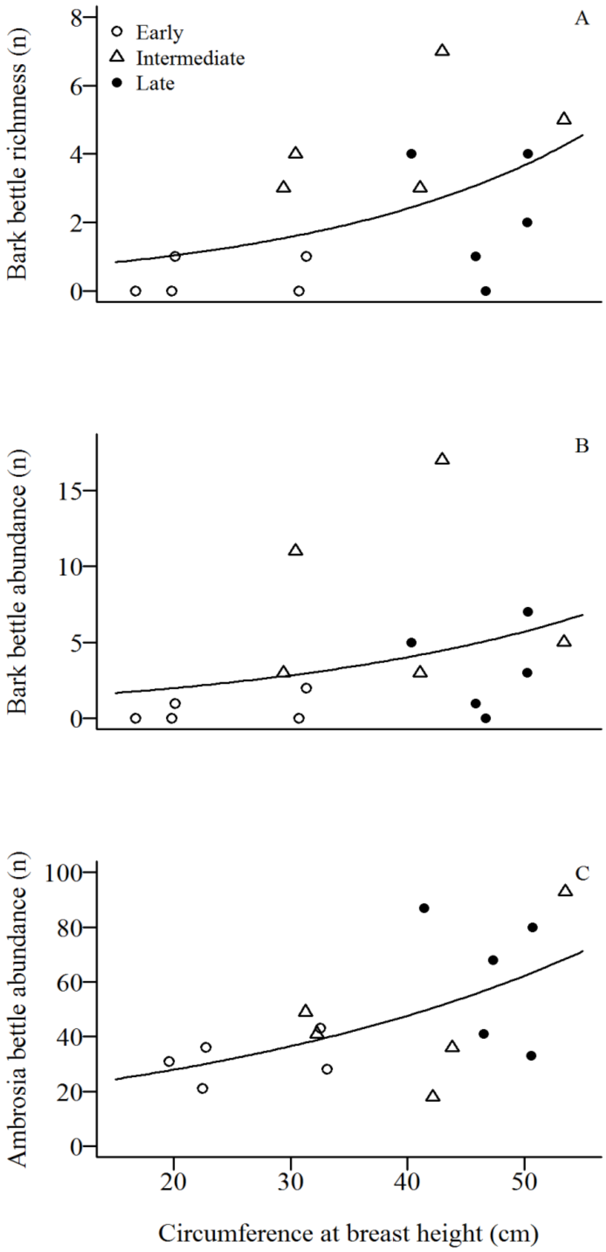

Fig. 5. Effect of tree CBH on bark beetle richness (A), bark beetle abundance (B) and ambrosia beetle abundance (C) in the Mata Seca State Park in southeastern Brazil.

Temporal variation

Bark beetle richness showed no variation among months, and bark beetle abundance was higher only in April 2010 (Fig. 6). Climate measures did not affect bark beetle richness and abundance (Table 4). Although moisture almost reached statistical significance, on explaining the bark beetles abundance increase (Table 4). Ambrosia beetle richness was higher in September and October of 2010, and in April, June and September of 2011, compared to samples from December, February and April of 2010, and January and December of 2011 (Fig. 6A). Overall the driest months were richer than the rainy months, and no relationships were found between climate measures and ambrosia beetle richness (Table 4). Ambrosia beetle abundance was higher in September and October of 2010, with peaks in activity in April and June 2011; these sample periods together yielded 69% of the total abundance (Fig. 6B). We found negative relationships between monthly variation in ambrosia beetle abundance and increased rainfall and temperature, and a positive relationship between variation in abundance and increased air moisture (Table 4; Fig. 7).

Table 4. Results of linear mixed effects model (LME), showing the temporal variation and effects of the rainfall, moisture, and temperature on bark and ambrosia beetle richness and abundance. Significance was estimated by ANOVA comparing complete (H1) and null models (H0). The Akaike's information criterion (AIC) represents the uncertainty of the model whereby lower AIC values represent the more parsimonious models.

Response variable	Explanatory variable	d.f.	AIC (H1)	AIC (H0)	*P*
Bark beetle richness	Month	9	205.76	196.14	0.497
	Rainfall	1	198.58	197.87	0.254
	Moisture	1	200.73	198.58	1.000
	Temperature	1	199.41	200.73	0.068
Bark beetle abundance	Month	9	252.93	256.75	0.009
	Rainfall	1	256.88	256.75	0.172
	Moisture	1	255.12	256.88	0.052
	Temperature	1	253.92	255.12	0.073
Ambrosia beetle richness	Month	9	343.11	352.07	0.001
	Rainfall	1	352.82	352.07	0.264
	Moisture	1	352.14	352.82	0.101
	Temperature	1	354.13	352.14	0.931
Ambrosia beetle abundance	Month	9	778.19	1668.59	<0.001
	Rainfall	1	746.58	750.41	0.015
	Moisture	1	746.58	754.54	0.001
	Temperature	1	746.58	752.97	0.003

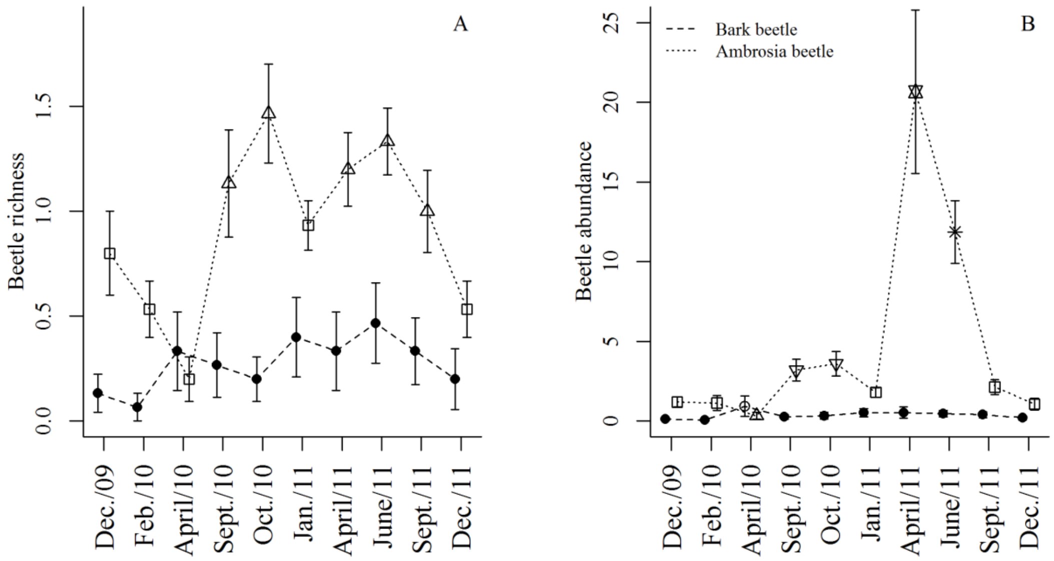

Fig. 6. Bark and ambrosia beetle (Curculionidae) richness (A) and abundance (B) (mean ± SE) during two years of sampling in the Mata Seca State Park in southeastern Brazil. Different symbols represent statistically different means ($P < 0.05$).

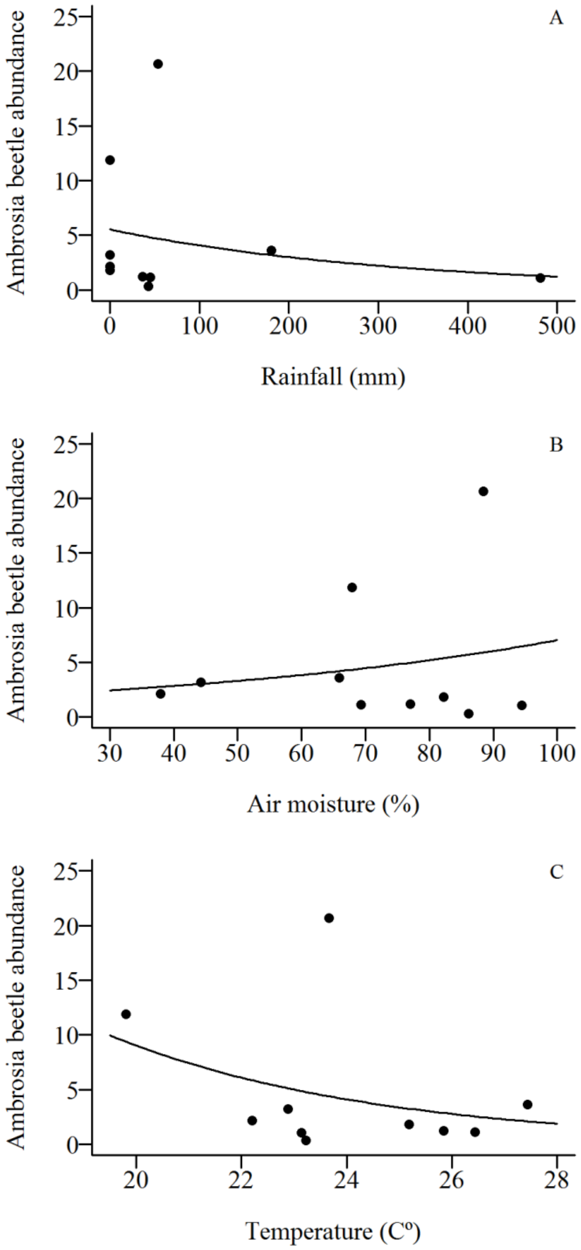

Fig. 7. Effect of rainfall (A), air moisture (B), and temperature (C) on ambrosia beetle abundance in the Mata Seca State Park in southeastern Brazil.

Discussion

Studies of variation in composition, richness and abundance of beetles in relation to spatial factors and climatic conditions are unprecedented in Brazilian dry forests. The current study revealed a total species richness lower than has been found in to other dry forests in Mexico (Atickson and Equihua 1986), and equal to some other Brazilian forest biomes (Amazon and Atlantic forest) (Abreu et al. 2012, Muller and Andreiv 2004). Bark beetle richness (14 species) was greater than ambrosia beetle richness (9 species); this result may have been affected by the low release of ethanol during sampling because ethanol tends to attract a greater number of bark beetles (Hulcr et al. 2008b). However, the dominance of phloeophagous species is a pattern more common in Mexican dry forest than in Brazilian rainforests (Atickson and Equihua 1986, Abreu et al. 2012, Muller and Andreiv 2004). Phloeophagy as a dominant feeding habit also occurs in temperate areas, while tropical rainy areas show the opposite trend, with a greater proportion of ambrosia species typically found (Beaver 1979, Hulcr 2007, Abreu et al. 2012). Atckson and Equihua (1986) reported that the relative low importance of ambrosia beetles in dry forests may be associated with the long dry season, which may limit growth of fungi on wood; this suggestion is supported in the current study. Although other factors like species interactions are surely involved (Beaver 1979).

We found similar species compositions with the advancement of secondary succession, confirming the independence of bark and ambrosia beetles with respect to local tree community composition (Beaver 1979, Hulcr et al. 2007). However, we found that turnover is the primary driver of beta diversity for both guilds, and turnover was higher in bark beetle communities. These results suggest that despite low host-specificity, site factors may determine the local species pool (mainly in the bark beetle community).

Bark beetle richness and abundance was higher in intermediate stage sites, followed by late and early stages, respectively. We found no between-stage differences in ambrosia beetle richness or abundance, likely due to the different strategies of obtaining and using food resources among feeding guilds (Hulcr et al. 2007). Overall, the degree of host specificity is higher in bark beetle species, which favor monophagy (i.e., restricted to one plant genus) rather than ambrosia species, which tend to favor polyphagy (i.e., several host families) (Atickson and Equihua 1986). Our results are analogous to the pattern observed among free-living herbivorous guilds, where the guilds more closely associated with their host plant traits (e.g., as in sap-sucking insects) were sensitive to successional stage while the more generalist (chewer) insects were not (Neves et al. 2014).

Among the structural differences between stages, an increase in tree CBH was the main mechanism leading to higher diversity, richness and abundance of bark beetles, and increased abundance of ambrosia beetles. These results suggest that size of wood affects mainly the bark beetle guild. Large diameter is an important factor for wood inhabitants due to increased probability of finding resource in a suitable state for colonization along temporal shifts in spatial parameters (Grove 2002). Wood availability is thus important for rare bark beetle species, and it is not surprising that ambrosia species do not follow these patterns because their foraging strategy is closer to detritivory than to herbivory (Hulcr et al. 2007). For ambrosia beetles, Grove’s (2002) statement with respect to saproxylic beetles that "all wood is good, but bigger is better" seems to fit our results.

Xyleborus affinis was the dominant species in the study area, a consistent pattern among ambrosia beetles in other studies (Flechtmann et al. 1995, Abreu 2012). This species has circumtropical distribution, and has been reported to feed on more than 300 plant species. It is considered of high importance among the ambrosia species due to attacks on Eucalyptus and Pine stands in Brazil and other tropical regions (Flechtmann 1995, Beaver 1988). We demonstrated in the current study that *X. affinis* also has a strong preference for the Mata Seca State Park, a result in concordance with its high tolerance for dry and disturbed areas (Hulcr et al 2008b).

Temporal factors did not affect bark beetles richness, and abundance was only higher in April 2010. Climate factors did not affect guild richness and abundance. Most of the bark beetle species were trapped in very low numbers, and even the groups of species reported to occupy dry material such as *Hypothenemus* (Hulcr et al. 2008b) were found in low abundance. This could be a sampling artifact due to trap bias, however occurrence was unaffected by seasonality in other studies as well (Hulcr et al 2008b, Abreu et al. 2012). Our results suggest that the effect of climate seasonality on bark beetle communities is lower than that of spatial differences between sites.

In contrast, the ambrosia guild showed higher richness in the drier month (June) and at the end of the dry and wet seasons, and no relationships between community traits and climate factors. The periods of higher flight activity reflect the emergence of adults to colonize new, suitable hosts (Wood 1982). According to Wood (1982), these hosts usually bear senescent leaves that produce attractive substances. The months with increased percentage of senescent leaves in the study area are the same months with higher richness of ambrosia beetles (Pezzini et al. 2014). Thus it is likely that host attractiveness determines ambrosia richness fluctuations. Further studies are necessary to verify the consistency of the described pattern.

The relatively constant environmental conditions of tropical rainforests allow year-round beetle activity, and thus there is no clear dispersal pattern for these species (Hulcr et al. 2008a, Abreu et al. 2012). In tropical dry forests, the abrupt changes among seasons may lead ambrosia beetles to higher colonization success due to better conditions for fungal growth.

The fluctuations in species abundance decrease with higher rainfall and in warmer months, and increase with higher air moisture. Dispersal from the parental gallery to a new host plant/gallery imposes high energy costs for ambrosia beetles, as the cultivation of symbiotic fungi frequently fails (Biedermann et al. 2011). Our results show that peaks in abundance are closely followed by an additional peak, as in April and June 2011. This pattern of emergence has been observed in *X. affinis* (Biedermann et al. 2011, Iidzuka et al. 2014), the most abundant species in the present study. Those peaks in dispersal occurred on days with lower rainfall and higher air moisture, with temperature varying from 20 to 23 ºC. Other studies showed that the flight activity of Scolytinae beetles is stimulated by light and high temperature, varying from 20 to 40 ºC (Wood 1982), and that a temperature around 30 ºC seems to be optimal for ontogenetic stages of development (Walgama and Zalucki 2007). Rainfall usually negatively affects Scolytinae flight (McMullen and Atkins 1962, Moser and Dell 1979), whereas the decreased rain in the end of the dry season sufficiently maintains air moisture to avoid heat exposure and desiccation (Wardhaugh 2014). Hence, the sampling periods characterized by hot days, but high enough humidity to avoid desiccation represent favorable abiotic conditions for beetle flight and selection of new hosts.

Conclusions

The data presented above describe a diverse array of spatio-temporal distributions among bark and ambrosia beetle guilds. The spatial and the temporal factors have mixed contributions to shaping the observed patterns, and the main differences among guilds reflect their use of resources. In summary, bark beetles are more sensitive to wood content along the secondary succession than are ambrosia beetles, and they have higher density at sites with greater availability of wood. Further, climate factors were effectively non-seasonal for bark beetles and seasonal for ambrosia beetles. Species accumulation was higher in bark beetle species over time, while factors favorable for fungal growth, such as host and air moisture. Resulted in a broad spatial distribution of ambrosia species and a greater degree of species redundancy over time. Detecting spatial and temporal patterns in beetles and insects is not an easy task, and we highlight interspecific interactions of these beetles as a focus for further investigations. The overall biological pattern among guilds differed from that of tropical rainforests, showing patterns similar to other dry forest areas.

Acknowledgments

We are grateful to the staff of the Instituto Estadual de Florestas (IEF - MG) and ICMBIO for allowing us to work at the Mata Seca State Park (MSSP), and for logistical support. This work was funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), the Fundação de Amparo à Pesquisa de Minas Gerais (FAPEMIG), and the Inter-American Institute for Global Change Research (IAI-CRN II-021). This study was in partial fulfillment of requirements for the PhD degree at Universidade Federal de Minas Gerais.

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Conclusão geral

Em nossos resultados, a disponibilidade espacial e temporal de recursos da vegetação, determinam a distribuição da diversidade de acordo com a estratégia alimentar e a capacidade de dispersão dos insetos herbívoros. Neste contexto, as características florestais na escala local e da paisagem estão duplamente envolvidas. Sugerimos que o uso destes critérios na paisagem florestal, deve ser tão relevante quanto a definição de áreas fechadas de conservação para a manutenção da diversidade de insetos herbívoros nas florestas secas.

A sucessão secundária é um indicador de diferenças estruturais da vegetação que por si, é incapaz de descrever o nível de isolamento do local na paisagem. Todavia a composição e densidade de plantas foram os mecanismos locais mais importantes para explicar as diferenças em diversidade no gradiente de sucessão secundária. Em adição a isso, o aumento da porcentagem de florestas que circundam as áreas amostrais, determinou o aumento da diversidade dos insetos. Isso demonstra que as possibilidades de explorar os recursos na matriz são atributos importantes, principalmente para a manutenção das metacomunidades dos insetos com menor capacidade de dispersão e mais dependentes dos sistemas florestais.

As florestas secas são ecossistemas cercados por sistemas agrícolas e, os padrões ecológicos apresentados, podem contribuir para o avanço das estratégias de manejo atuais, que ainda estão embasadas por poucos critérios relativos principalmente ao processo de regeneração natural. Nossos resultados demonstram que a complexidade vegetal deve ser um componente regulador dos insetos herbívoros, diminuindo os riscos de surtos locais de pragas nos sistemas agrícolas que circundam estas florestas. Todavia ainda estamos na primeira etapa, definindo os limites e as escalas de análise para mensurar os serviços ecossistêmicos prestados pelas florestas secas.