

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

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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.

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

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. Sérgio 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.

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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

25
26
27 Compreender os mecanismos e os processos responsáveis pela manutenção da
28 diversidade nos ecossistemas é foco de diversos estudos em biologia da conservação.
29 Relações positivas com a diversidade são propostas a partir de teorias baseadas na
30 diferenciação de nichos ecológicos (Leibold 1995, Tschardt et al. 2012), com a
31 predição de que ambientes mais heterogêneos sejam mais diversos, devido ao aumento
32 das possibilidades de exploração dos recursos, e dos locais para nitificação. Neste caso,
33 é assumido que a heterogeneidade ambiental é responsável pela coexistência de espécies
34 que estruturam a comunidade (Tews et al. 2004, Stein 2014).

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

41 Nas florestas tropicais, a comunidade de plantas é responsável pelas
42 características fisiológicas do sistema, e, possui forte influência sobre as interações
43 tróficas existentes. A produção primária (Novotny et al. 2003) é concentrada no
44 conjunto das copas das árvores que formam o dossel das florestas, sendo este, o
45 principal local de assimilação de energia. Este habitat oferece vasta diversidade de
46 recursos, que são fundamentais para a manutenção de diversidade biológica (Stork et al.
47 1997, Basset et al. 2003). Neste cenário, os insetos herbívoros obtêm destaque como os
48 principais consumidores da biomassa vegetal (Basset et al. 2003, Lewinsohn et al.
49 2005). Apesar do interesse crescente científico, somado a formas mais fáceis de acesso
50 nos últimos anos, o dossel ainda é pouco conhecido (Nadkarni et al. 2011).

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

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

69 As florestas tropicais secas são consideradas de extrema diversidade, muitas
70 espécies estão adaptadas às condições climáticas extremas (Hulshof et al. 2014, Pezzini
71 et al. 2014). Durante a estação chuvosa existe abundância de folhas, e na estação seca,
72 de flores e frutos (Pezzini et al. 2014). Do padrão fenológico das plantas emerge
73 processos adaptativos entre organismos e extrema expressão de nichos ecológicos que
74 interagem com a vegetação do bioma de domínio na paisagem (Avila-Cabadilla 2012,

75 Leal et al. 2015). Portanto as florestas secas são um importante componente para a
76 manutenção da diversidade na região.

77 Todavia, o prolongamento do período seco em um cenário de mudanças
78 climáticas globais, somado a substituição destas florestas por centros de agricultura,
79 pecuária entre outras atividades humanas, representam forte impacto na diversidade e
80 funções ecológicas nestas florestas (Espírito-Santo et al. 2014, Hulshof et al. 2014). A
81 vegetação nativa está fragmentada e em diferentes estágios de sucessão ecológica
82 (Quesada 2009, Madeira et al. 2009). Os efeitos dos processos de sucessão ecológica e
83 sazonalidade na diversidade de insetos em florestas tropicais úmidas ou secas, é pouco
84 conhecido (Lewinsohn et al. 2005). Além disso, a maior parte do conhecimento sobre
85 sucessão em ambientes tropicais foi obtido a partir de estudos em florestas úmidas
86 (Guariguata and Ostertag 2001) e não pode ser aplicada em FTS (Vieira and Scariot
87 2006, Quesada et al.2009).

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CAPÍTULO 1

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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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181 Macedo-Reis et al.: Drives for herbivorous in tropical dry forests

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184 Journal of Insect Science

185 Research

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194 **Heterogeneity at local and forest cover on landscape scales are drives for**

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herbivorous insects diversity in tropical dry forests

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210

Abstract

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

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

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Introduction

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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)

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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).

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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

258 by their home ranges and dispersal abilities. To illustrate this, Kremen et al. (2004)
259 showed that for native bees, forest cover correspond bee foraging ranges and were
260 positive at larger scales when measured as function of the plot radius where insects were
261 collected. Thus, for forest-adapted species we might expect a decrease in niche
262 availability with the increase in percentage of non-forest areas at the landscape scale.
263 This information be used to describe correlations between structural vegetation
264 heterogeneity and insect species diversity in degraded areas within and near preserved
265 forests fragments, and may also be relevant for riparian forest (evergreen) near
266 deciduous forest (Avila-Cabadilla et al. 2012).

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

277 These view is supported by observation of high species β -diversity, among dry
278 forest fragments that contain geologically old, monophyletic clades of endemic plant
279 species, possibly indicating dispersal limitations (Neves et al. 2015). Physiological
280 tolerances of abiotic conditions are also important for explaining the β -diversity patterns
281 among dry forest environments where climate can be most unpredictable (Wardhaugh
282 2014).

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

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297 **Materials and methods**

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299 *Study area and sampling sites*

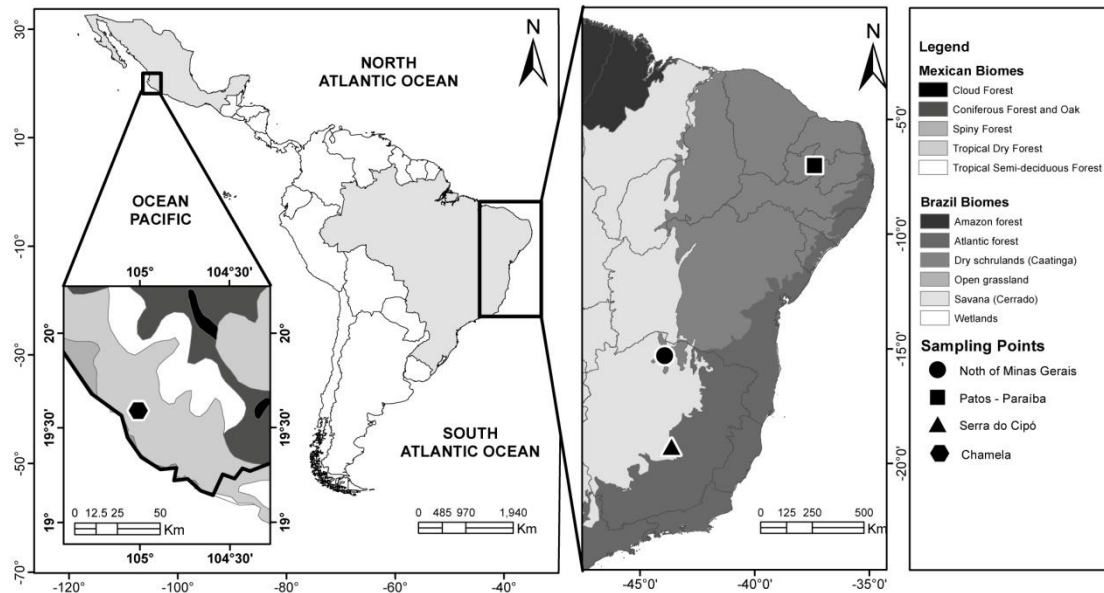
300 The study was carried out in four regions ranging from latitudes 19° south to 19°
301 north: 1) The first region is located in central Minas Gerais state (MG), surrounding the
302 Morro da Pedreira protection area (hereafter Serra do Cipó) (19°19'44.6" S, 43°36'23"
303 W) (Coelho et al. 2012). 2) The second region lies in the São Francisco River Valley in
304 northern Minas Gerais state (hereafter Northern MG) (14°55'12.0" S, 43°56'27" W), and
305 includes three conservations units (Lagoa do Cajueiro State park, 20,500ha; Serra Azul
306 Biological Reserve, 3,840.94ha; Jaíba Biological Reserve, 6,358ha) created as a
307 compensatory measure of the irrigated area called the "Jaíba Project" (Espírito-Santo et

308 al. 2014). 3) The third region is in northeastern Brazil at the Tamanduá farm, an area of
309 approximately 4,000 ha in Paraíba (PB) (hereafter Patos PB) near the city of Patos
310 (7°0'45.5" S, 37°22'48" W). 4) The fourth region is at the central western coast of
311 Mexico in Jalisco state (hereafter Chamela), in and surrounding the Chamela-Cuixmala
312 Biosphere Reserve (19°30'33.2" N, 105°2'36" W, Fig. 1).

313 These regions are subject to severe seasonal variations, with marked differences in
314 rainfall between seasons. The climate in Serra do Cipó is mesothermal according to the
315 Köppen system, with rainy summers (October-March) and dry winters. The average
316 annual rainfall is 1,500 mm, and the average annual temperature is 19.9 °C (Coelho et
317 al. 2012). In North MG the climate is classified as semi-arid, with an average annual
318 temperature of 24.4 °C and average annual rainfall of 818 mm, with rainfall
319 concentrated between October and March (see Pezzini et al. 2014, Macedo-Reis et al.
320 2016). In Patos PB the climate is classified as semi-arid, with an average annual
321 temperature of 32.8 °C and average annual rainfall of 750 mm. However, rainfall is
322 often variable between months, and deviates over 45% from one year to another (Prado
323 2003). The Chamela region has an average annual temperature of 24.6 °C and average
324 annual precipitation of 731 mm, with rainfall concentrated from June to October (Maass
325 et al. 2005).

326 The Serra do Cipó region includes primarily Cerrado *sensu stricto* and altitudinal
327 rocky field vegetation, and the dry forest grows on limestone outcrops and occurs as
328 fragments with unique floristic composition compared to surrounding forest types
329 (Coelho et al. 2012). The northern MG and Patos PB regions have dry forest that are
330 associated with flat and nutrient-rich soils (Espírito-Santo et al. 2014); North of MG is
331 in a transition zone between Cerrado and Caatinga biomes, and Patos PB is in the
332 Caatinga biome (Fig. 1). Dry forest is the predominant vegetation type in Chamela, and

333 is mostly associated with rolling hills (Maass et al. 2005). In all four regions riparian
 334 forest vegetation occurs along permanent rivers and lakes.



335
 336 Fig. 1. Map showing locations of insect herbivore sampling regions and descriptions of
 337 associated biomes.
 338

339 Mining and tourism are the most important economic activities in Serra do Cipó
 340 (Domingues et al. 2012). Agricultural practices (including cattle raising) dominate the
 341 economic activity of northern MG, Patos PB and Chamela regions (Maass et al. 2005,
 342 Espírito-Santo et al. 2014). These anthropogenic activities have caused landscape
 343 patchiness, with forest fragments of different sizes and successional stages scattered
 344 throughout these regions. We selected sampling sites along a gradient of succession in
 345 each region based on the amount of time elapsed since the last major disturbance. This
 346 information was obtained through interviews with members of local communities, and
 347 employees of protected areas. One third of the total sampling sites in each region
 348 represented dry forest abandoned for five to 10 years; one third was abandoned for 17 to
 349 35 years and, and one third existed at least 50 years without any human activities or
 350 disturbance.

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

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

365

366 *Insect Sampling*

367 We collected insects using combined flight Malaise/window traps (Basset 1988,
368 Novais et al. 2016ab). One trap holding two vial collectors with 70% ethanol was
369 placed in the tree canopy in the center of each site. Traps remained in place for 5 days
370 (120 h) per month at the Serra do Cipó, North MG and Patos sites, and 10 days (240 h)
371 per month at Chamela sites. The sampled insect herbivores were grouped into one of
372 three guilds according to their feeding habits: folivorous, sap-sucking, or xylophagous
373 (Novais et al., 2016a). All insects belonging to families that directly or indirectly
374 depend on plant resources for survival were considered herbivores (Moran and
375 Southwood 1982, Neves et al. 2014a, Novais et al. 2016a). All other insects were

376 identified using taxonomic keys (Rafael et al. 2012) and separated into morphospecies
377 based on external morphological characters. The sampled insects in Serra do Cipó,
378 North MG and Patos were deposited in the entomological collection of the Laboratory
379 of Insect Ecology at the Federal University of Minas Gerais (Universidade Federal de
380 Minas Gerais - UFMG), and insects from the Chamela region were deposited at the
381 Ecosystems Research Center of the National Autonomous University of Mexico
382 (Universidad Nacional Autónoma de México, Morelia - UNAM).

383

384 *Data analysis*

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

400

401 *β diversity measures and statistical analysis*

402

403 We calculated multiplicative β -diversity for each guild per region. The β -diversity
404 represents the diversity of differentiation within a region ($\beta_{\text{among-sites}}$). However, β -
405 diversity is sensitive to sample size, which differed among our study regions. To obtain
406 comparable values of β -diversity, we resampled the data (Baselga 2010). To calculate
407 $\beta_{\text{among-sites}}$ for each region, we randomly sampled nine sites without replacement (minor
408 sample value) of the same region 5,000 times (see Solar et al. 2015). $\beta_{\text{among-sites}}$ was
409 calculated using the following formula: $\beta_{\text{among-sites}} = \gamma_{\text{region}}/\alpha_{\text{site}}$ (Whittaker 1972), where
410 γ_{region} is cumulative herbivore species richness in each region, α_{site} is average species
411 richness at a sampling site within a region. In this method, $\beta_{\text{among-sites}}$ values are
412 mathematically independent of α -diversity (Jost 2007), allowing comparison among
413 regions with different α -diversity values.

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

422 We used GLMs to test whether regional heterogeneity and climate variation
423 determine herbivore guild β -diversity and turnover. These models were run using the
424 β -diversity and the proportional turnover ($\beta_{\text{SIM}}/\beta_{\text{SOR}}$) of insect herbivores guilds as
425 response variables. The indicator of heterogeneity (cumulative plant richness) and the
426 climate variation (precipitation coefficient of variation) per region were used as

427 explanatory variables. We calculated the precipitation coefficient of variation for each
428 region, dividing the standard deviation of average monthly rainfall by the average
429 monthly rainfall. We used weather data from four years before the last sample date for
430 each region (N=48 months). Residual analysis was conducted to test the suitability of
431 the model for error distribution (Crawley 2013).

432

433 *Landscape habitat quantification and statistical analysis*

434

435 Assessment of habitat quantity in each 48 sampling sites was based on the
436 classification of RapidEye cloud free, satellite images of years 2011 and 2012. These
437 dates are intermediate in time along the sampling period. Images are from February and
438 early June, corresponding to the dry season when the highest differentiation between
439 pastures, dry, and riparian forest occur. Images were classified based on the first three
440 bands of the RapidEye sensor with a spatial resolution of 5 m. Images were placed into
441 four land-cover classes: (i) forest (intermediate and old growth forest), (ii) crops (e.g.,
442 mango, papaya, watermelon), (iii) water, and (iv) other (e.g., roads, buildings). Image
443 processing was done using Geographical Information System ArcGis 10.2 (ESRI 2012)
444 at 1:15,000 scale. Habitat quantity was determined within concentric circles of 0.25 km,
445 0.5 km, 1 km, and 1.5 km, and 2.0 km. Radii were determined from the centroid of each
446 sample plot, representing a nested set of landscape sectors at five spatial scales.
447 SDMTools was used to obtain the proportion of each land cover class in the R-CRAN
448 environment (v 3.2.2, R Core Team 2015).

449 For each of the five spatial scales (radii) we tested whether proportional forest
450 cover determines insect herbivore diversity. We build GLMs with the mean insect
451 richness and abundance as the response variable, and the percentage of forest cover at
452 each spatial scale as an explanatory variable. To determine at which spatial scale forest

453 cover has the strongest effect, the explanation (deviance) of each of these models was
454 divided by the deviance of a null model using the following formula: Explained
455 deviance = $1 - (\text{deviance H1}/\text{deviance H0})$, thus if the proportion of deviances between
456 H1 and H0 were higher, the explained deviance is low. We plotted the explained
457 deviance for each of the five scales with the $n = 48$ landscapes to illustrate scale-
458 dependence of forest cover on herbivorous insect richness and abundance at these five
459 analyzed spatial scales. All analyses were carried out in R (R Development Core Team,
460 2015).

461

462

Results

463

464 We collected 2,893 herbivorous insects from 438 morphospecies across the four
465 dry forest regions. There were 113 folivorous morphospecies, 225 sap-sucking, and 100
466 xylophagous. Two hundred specimens were folivorous insects, 1,893 specimens were
467 sap-sucking, and 800 specimens were xylophagous. Among the folivorous insects, the
468 families with greatest richness and abundance were Chrysomelidae and Curculionidae;
469 the Cicadellidae and Achilidae families had the highest richness and abundance among
470 the sap-sucking insects. The Cerambycidae family and subfamily Scolytinae had the
471 highest species richness and abundance among the xylophagous insects (Table 1).
472 Cicadellidae and Scolytinae had the highest overall abundance in the study (57% and
473 22% respectively).

474 North MG plots had the highest numbers of morphospecies (160) and individuals
475 (1,578) among the regions, and Patos PB plots had the lowest (with 45 morphospecies
476 and 121 individuals). The Serra do Cipó and the Chamela sites were similar in richness
477 and abundance, with 118 morphospecies and 420 individuals in Serra do Cipó plots, and
478 115 morphospecies and 774 individuals in Chamela plots (Table 1; Fig. 2).

479 Most specimens were considered rare, with only one individual found for 272
480 (62%) of the 438 morphospecies sampled. Nevertheless, the curves approached the
481 Jackknife estimate in 60% for Serra do Cipó species, 67% for North of MG, 62%
482 species for Patos PB, and in 65% for the Chamela region, suggesting that the majority
483 of local species were represented in the analysis (Fig. 2).

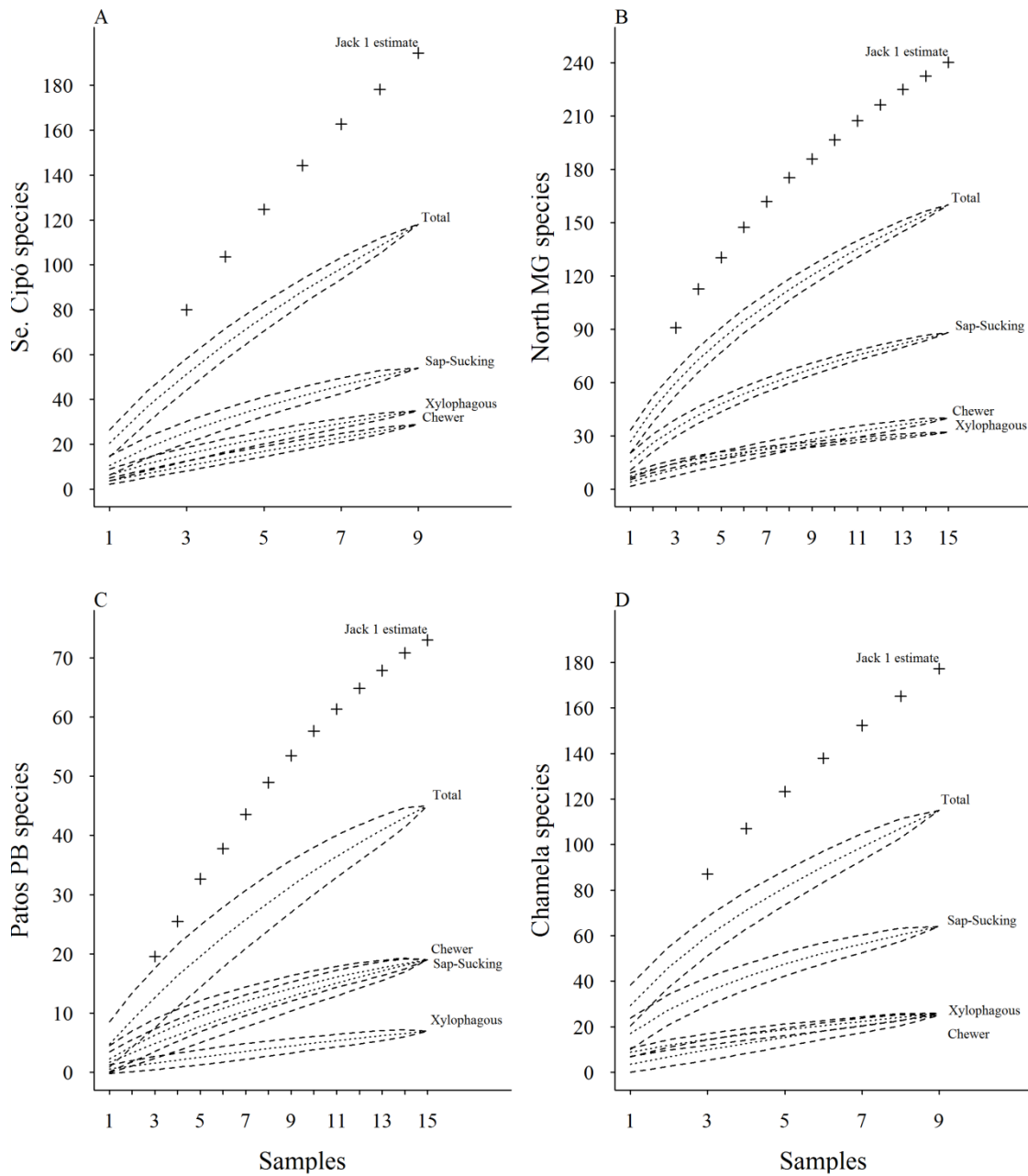
484 Patos PB had lower plant richness (mean±S.D. = 9 ± 1.05 species) than did sites at
485 Serra do Cipó (18.44 ± 3.80 species), Northern MG (24.20 ± 2.10 species) and Chamela
486 (24.44 ± 3.06 species); these three did not differ in mean plant richness (Negative
487 binomial: $_{[3,44]} = 47.05$, $p < 0.001$) (Table 2). The mean temperature was high (above 20
488 °C) for all regions, but rainfall were consistently lower in Patos PB (mean±S.D) than in
489 others regions (mean±S.D) (Table 2).

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

498

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.

Taxon/Guild	Se. Cipó		North MG		Patos PB		Chamela		Total	
	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
Eumastacidae	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



500
 501 Fig. 2. Species accumulation curves and an estimate of the total species richness at Serra
 502 do Cipó (A), North of MG (B), Patos PB (C) and Chamela regions (D) for the complete
 503 data set and for folivorous, sap-sucking and xylophagous species separately. The dotted
 504 lines represent the analytically derived species accumulation curve, and dashed lines
 505 represent the 95% confidence interval. The '+' symbol represents first order jackknife,
 506 using the 'poolaccum' procedure (vegan package) in R.
 507

508

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 (°C)	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

509

510

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

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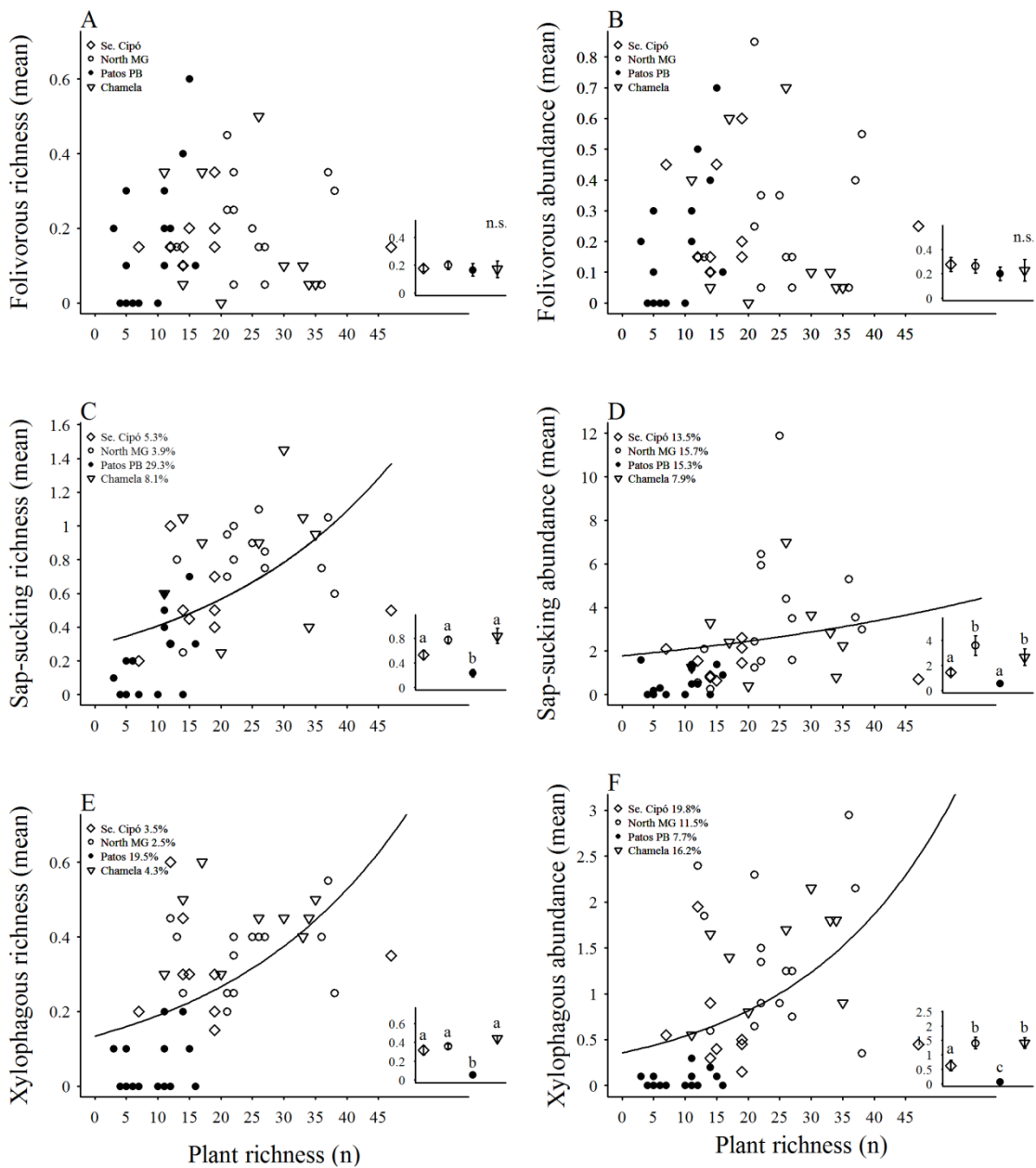
513 *β-diversity among regions*

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

524

525 *Decomposition of β -Diversity*

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



531
 532 Fig. 3. Mean daily species richness and abundance of folivorous (A and B), sap-sucking
 533 (C and D), and xylophagous (E and F) insect herbivores along the sites plant richness
 534 gradient. Parameter estimates used for curve-fitting were obtained from the generalized
 535 linear model (GLM) and adjusted for exponential functions. Mean values from the four
 536 dry forest regions are represented in each subplot, and the different letters above the
 537 symbols represent statistically different means ($P < 0.05$; Table 3). The numbers in the
 538 legend are the calculation of importance variables for regressions, made by scaling the
 539 absolute value of the t-statistic for each model parameter. This was done using the
 540 'varImp' procedure in the 'caret' package in R.
 541

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-Sucking	5.116	95.3
	Xylophagous	5.526	95.1
North MG	Folivorous	6.978	96.5
	Sap-Sucking	4.370	94.8
	Xylophagous	3.527	93.3
Patos PB	Folivorous	7.742	94.5
	Sap-Sucking	6.157	85.8
	Xylophagous	8.409	95.2
Chamela	Folivorous	7.258	92.8
	Sap-Sucking	3.815	88.8
	Xylophagous	2.962	86.5

542
543
544

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

545
546

547 *Landscape effects*

548

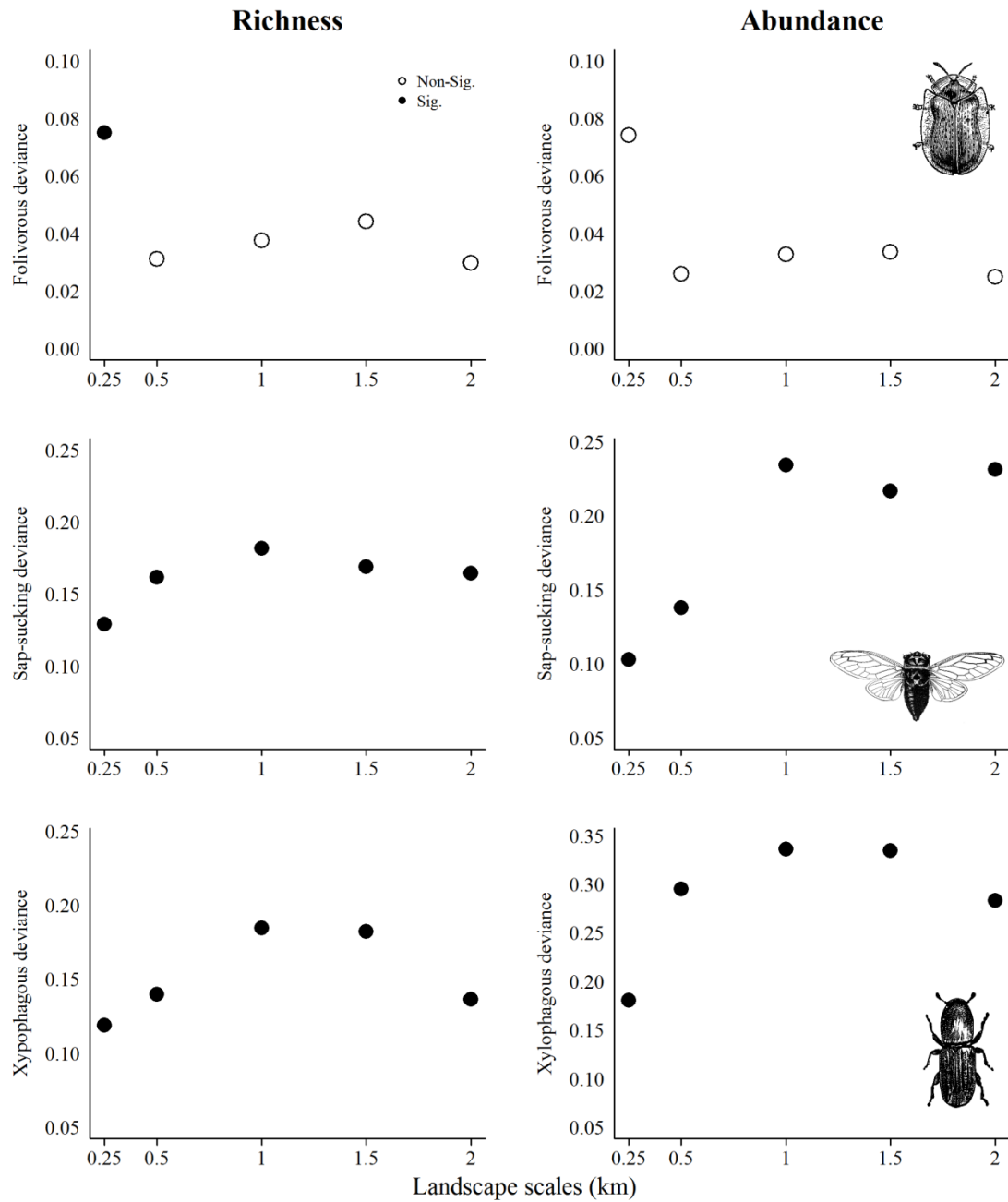
549 The predictive power of forest cover for folivorous, sap-sucking and xylophagous
550 guild diversity differed by spatial scale (0.25 km, 0.5 km, 1km, 1.5 km, 2 km). Although
551 all regressions models showed a positive inclination coefficient, forest cover explained
552 sap-sucking and xylophagous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

557 The proportion of explained variation in folivorous guild richness and abundance
558 decreased from the 0.25 km to 0.5km radii scales, and a similar proportion of variation
559 was explained in the 1 to 2 km scales. In contrast, the proportion of explained variation
560 in sap-sucking richness and abundance increases from 0.25 km to 1 km scale, and
561 remains similar until the 2 km radii scale. The increasing proportion of explained
562 variation was also observed for the xylophage richness and abundance from the 0.25 to
563 0.5 km scales, but the proportion of explained variation was higher at 1 and 1.5 km
564 scales than at the 2 km radius scale.

565

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



566

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

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573

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Discussion

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576

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

584 Folivorous insects were not affected by the differences in plant richness among
585 sites or regions, while the sap-sucking and xylophagous insect richness and abundance
586 were lower in regions with lower plant richness (Patos PB), and higher in regions with
587 higher plant richness. Most sap-sucking and xylophagous insects spend the majority of
588 their cycle on the same host tree, while folivorous insects seek highly nutritious leaf
589 tissue on several hosts (Calderon-Cortez et al 2011, Forister et al. 2015, Neves et al.
590 2014ab). Plant diversity is thus a direct driver of richness and abundance in specialist
591 species, but not as much for generalist species, due to their close association of plants
592 threats (i.g. tolerance to plant defenses) (Price 2002). Folivorous insect diversity is
593 strongly associated with availability of new leaves, niche space, and opportunities for
594 host range expansion, which is a likely explanation for the high folivorous diversity in
595 tropical areas (Novotny et al. 2006, Neves et al. 2014ab).

596 Herbivore β -diversity and the turnover component were not influenced by the
597 cumulative plant richness among regions, showing that effects of habitat heterogeneity
598 depend on the scale at which environmental variables are measured (Stein et al. 2014,
599 Solar et al. 2015). Variation in precipitation (rain CV) among regions did not affect
600 guild β -diversity or the turnover component. In general, β -diversity was higher at the

601 most xeric site (Patos PB region). Many herbivorous insects, especially sap-suckers, are
602 negatively affected by plant water stress, which decrease access to plant nutrients
603 (Huberty and Denno 2004). The high degree of spatial heterogeneity in Patos PB
604 communities may be due to local extinction filters, even with low diversity (Tschardtke
605 et al. 2012, Solar et al. 2015). Further, the Patos PB region has a history of highly
606 unpredictable weather (Prado 2003), with has been reported to negatively affect insect
607 diversity through causing shifts in resource availability, especially in drier forest
608 environments where desiccation is an ever-present threat (Wardhaugh et al. 2014).
609 Nevertheless, we found that turnover is the primary driver of β -diversity in these insect
610 groups. These results were consistent with findings from another study of ambrosia and
611 bark beetle communities in dry forest environment (Macedo-Reis et al. 2016),
612 suggesting a stronger influence of local (site) factors (i.g., temporal shifts in resources)
613 in determining the local species pool (Wardhaugh et al. 2014).

614 These results may be informative for habitat management at the landscape level,
615 particularly in fragmented areas (Avila-Cabadilla et al. 2012, Tschardtke et al. 2012).
616 Differences in landscape forest cover affected the herbivore insect guilds in different
617 ways. This supports the view that species perceive landscape structure at different
618 spatial scales depending on their dispersal abilities or foraging ranges (Weibull et al.
619 2000, Steffan-Dewenter et al. 2002). The distribution of folivorous guild species was
620 only explained by the percentage of forest cover at the smallest spatial scale (0.25 km
621 radius). Similar results were found for Chrysomelidae species (Jonsen et al. 2001, Piper
622 and Compton 2010). Piper and Compton (2010) reported that beetles use host-plants as
623 'stepping stone' to move through its habitat and populations are effectively isolated by
624 relatively small areas of open ground. Therefore, disconnect among forest patches at
625 larger spatial scales might limit the dispersal of the folivorous insects, rendering them

626 more dependent on small-scale processes (Ricketts 2001). Moreover, the degree of
627 available shelter may explain the ability to detect species diversity patterns at smaller
628 spatial scales, since shelter is known to be important for folivorous species, especially to
629 issues related with mortality rates (Weibull et al. 2000, Price 2002, Cornelissen et al.
630 2016)

631 Sap-sucking and xylophagous guilds responded to landscape forest cover at all
632 spatial scales, and landscape factors were more strongly correlated with sap-sucking and
633 xylophagous insect richness and abundance at larger spatial scales (from 1 to 1.5 km).
634 This finding is consistent with the dispersal ability described for sap-sucking and
635 xylophagous species (Turchin and Thoeny 1993, Blackmer et al. 2004). Blackmer et al.
636 (2004) found that the majority (95%) of sap-sucking Cicadellidae were recaptured far
637 from the release site, and another study showed that one half of the released
638 xylophagous bark beetles dispersed more than 0.69 km (Turchin and Thoeny 1993).
639 Therefore, the percentage of forest cover at larger spatial scales should increase
640 colonization potential in these species groups due to strong dispersal capability. Leal et
641 al. (2015) also suggested that riparian forest may be a relevant landscape component for
642 the large-scale heterogeneity effects observed here, since most riparian forests trees
643 maintain leaves year round, and these areas were near our sample sites.

644 The composition of insect herbivore families on the sampled dry forest regions
645 was consistent with findings of earlier studies. The folivorous Chrysomelidae and
646 Curculionidae, the sap-sucking Cicadellidae and Psyllidae, and the xylophagous
647 Scolytinae and Cerambycidae are usually reported as important components of forest
648 insect communities (Basset 2001, Neves et al. 2014a, Leal et al. 2015, Novais et al.
649 2016a). The majority of our morphospecies and individuals were sap-suckers, followed
650 by folivorous and xylophages, respectively. Most of the sampled species were

651 associated with a single plant taxon (i.e., Cicadellidae, Psyllidae), and this is consistent
652 with described patterns of the insect distribution in a rain forest region that used the
653 same sampling methods (Novais et al. 2016a). The distributions generally show higher
654 frequency of more specialized insects, and fewer more generalized species (Forister et
655 al, 2014). The general dominance of monophagy over polyphagy in tropical forests may
656 influence associations between vegetation heterogeneity and local herbivore species
657 diversity.

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

663 **Conclusions**

664 Our results demonstrated that species turnover is important factor for maintaining
665 high diversity in the regions sampled, and reflects the sensitivity of herbivores to plant
666 richness and habitat modification; these effects differed by spatial scale and herbivore
667 feeding guilds (Neves et al. 2014ab, Silva et al. 2016, Macedo-Reis et al. 2016). We
668 suggest prioritizing conservation of areas with higher plant richness, as these areas may
669 be particularly important for maintenance of insect herbivore diversity. The overall
670 landscape patterns indicate that the maintenance of forest cover is increasingly
671 important at larger spatial scales. Strong correlations between forest cover and herbivore
672 abundance and richness at the landscape scale may indicate strong biologically
673 relevance of studies at larger spatial scales. We highlight key structures of the
674 vegetation (i.e., evergreen plants) (Tews et al. 2004, Silva and Neves 2014) as a focus
675

676 for future investigations of insect herbivore foraging requirements and use of regional
677 resources.

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679

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CAPÍTULO 2

880

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

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885 Macedo-Reis et al.: Distribution of dry forest beetles fauna
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887 Journal of Insect Science
888 Research

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897 **Spatio-Temporal Distribution of Bark and Ambrosia Beetles in a Brazilian**
898 **Tropical Dry Forest**
899

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916

Abstract

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918
919 Bark and the ambrosia beetles dig into host plants and live most of their lives in
920 concealed tunnels. We assessed beetle community dynamics in tropical dry forest sites
921 in early, intermediate, and late successional stages, evaluating the influence of resource
922 availability and seasonal variations in guild structure. We collected a total of 763 beetles
923 from 23 species, including 14 bark beetle species, and 9 ambrosia beetle species. Local
924 richness of bark and ambrosia beetles was estimated at 31 species. Bark and ambrosia
925 composition was similar over the successional stages gradient, and beta diversity among
926 sites was primarily determined by species turnover, mainly in the bark beetle
927 community. Bark beetle richness and abundance were higher at intermediate stages;
928 availability of wood was the main spatial mechanism. Climate factors were effectively
929 non-seasonal. Ambrosia beetles were not influenced by successional stages, however
930 the increase in wood resulted in increased abundance. We found higher richness at the
931 end of the dry and wet seasons, and abundance increased with air moisture and
932 decreased with higher temperatures and greater rainfall. In summary, bark beetle species
933 accumulation was higher at sites with better wood production, while the needs of fungi
934 (host and air moisture), resulted in a favorable conditions for species accumulation of
935 ambrosia. The overall biological pattern among guilds differed from tropical rain
936 forests, showing patterns similar to dry forest areas.

937

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

939

Introduction

940

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

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

965 (Baselga 2010). Breaking down β -diversity into these two components may improve our
966 descriptions of bark and ambrosia beetle spatial distribution over structural habitat
967 changes such as historical human land use (Marques and Schoereder 2014, Araujo et al.
968 2015).

969 Plant diversity has been suggested as the primary mechanism preserving the
970 remarkable diversity of tropical herbivore species (Novotny et al. 2010, Neves et al.
971 2014). However, plant diversity does not seem to shape bark and ambrosia beetle
972 diversity. These beetles are likely closely associated with the range of suitable wood
973 availability (Grove 2002, Hulcr et al. 2008b), and wood diameter and moisture content
974 seem better predictors of diversity. Hence, an increase in wood and plant species
975 abundance along a gradient of ecological secondary succession should increase resource
976 availability for them (Guariguata and Ostertag 2001, Kalacska et al. 2004, Madeira et al.
977 2009).

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

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

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

998 **Materials and methods**

999 *Study area*

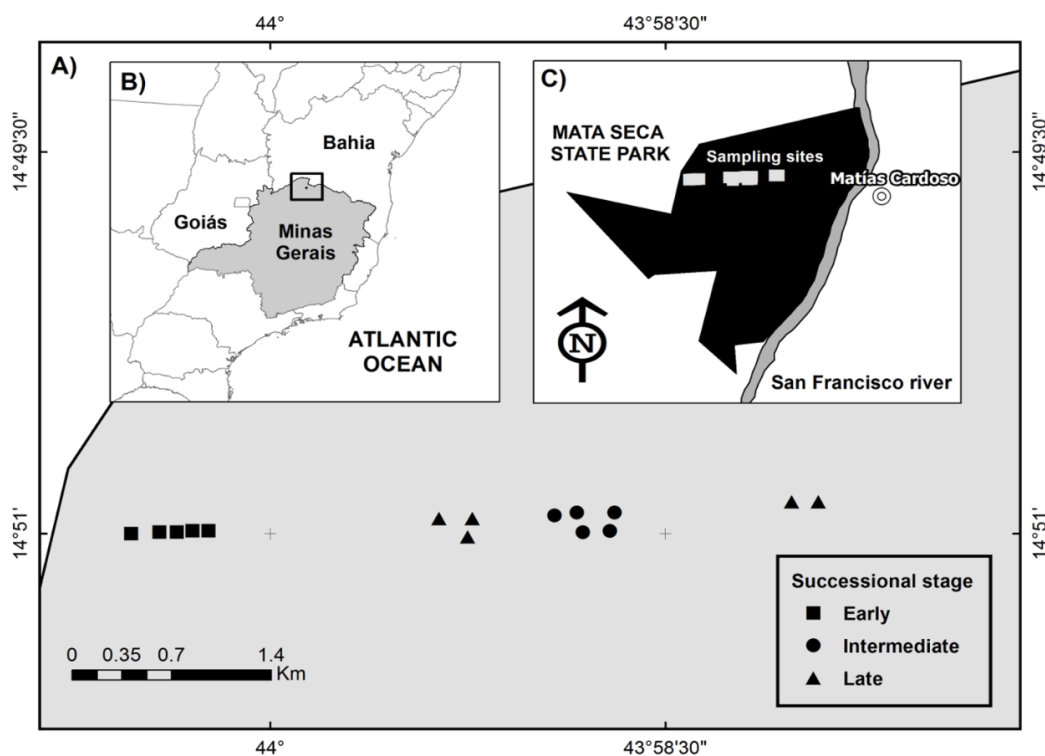
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1001 The study was carried out in the Mata Seca State Park, located in the São
1002 Francisco River Valley in Manga, northern Minas Gerais state, southeastern Brazil
1003 (14°48'36" - 14°56'59" S, 43°55'12" - 44°04'12" W). The park has an area of 15,466
1004 ha, with predominance of seasonal deciduous forest (Madeira et al. 2009). The climate
1005 of the region is classified as semi-arid by the Köppen system, with an average
1006 temperature of 24.4 °C and average annual rainfall of 818 \pm 242 mm (Pezzini et al.
1007 2014). Approximately 1,525 ha consist of abandoned pastures in different stages of
1008 succession (Madeira et al. 2009).

1009 We categorized sampling sites according to number of years in secondary
1010 succession after disturbance, as follows: early = 10 years; intermediate = between 17
1011 and 25 years; and late = over 50 years. The early successional stage was dominated by
1012 herbaceous and shrubby plants, with a discontinuous canopy approximately 4 m in
1013 height. The intermediate stage was composed of trees reaching 10 to 12 m in height

1014 with some emergent trees reaching up to 15 m, with dense understory and with many
 1015 lianas. The late stage was composed of trees forming a closed canopy 18 to 20 m in
 1016 height, with sparse understory with little light penetration and low density of lianas
 1017 (Madeira et al. 2009).

1018 We selected fifteen 20 x 10 m plots, five in each successional stage. Plots were
 1019 established along a 7 km transect. Distance between plots within each stage varied from
 1020 0.2 to 0.8 km, and the distance between plots of different successional stages varied
 1021 from 0.8 to 6 km (Fig. 1). We sampled the plots ten times from 2009 to 2011, during
 1022 rainy and dry seasons (Fig. 2). Sampling was carried out in December 2009, February,
 1023 April, September, and October 2010, and January, April, June, September, and
 1024 December 2011. The dry season occurs from May to October, at which time
 1025 approximately 90-95% of the tree species shed their leaves (Pezzini et al. 2014).

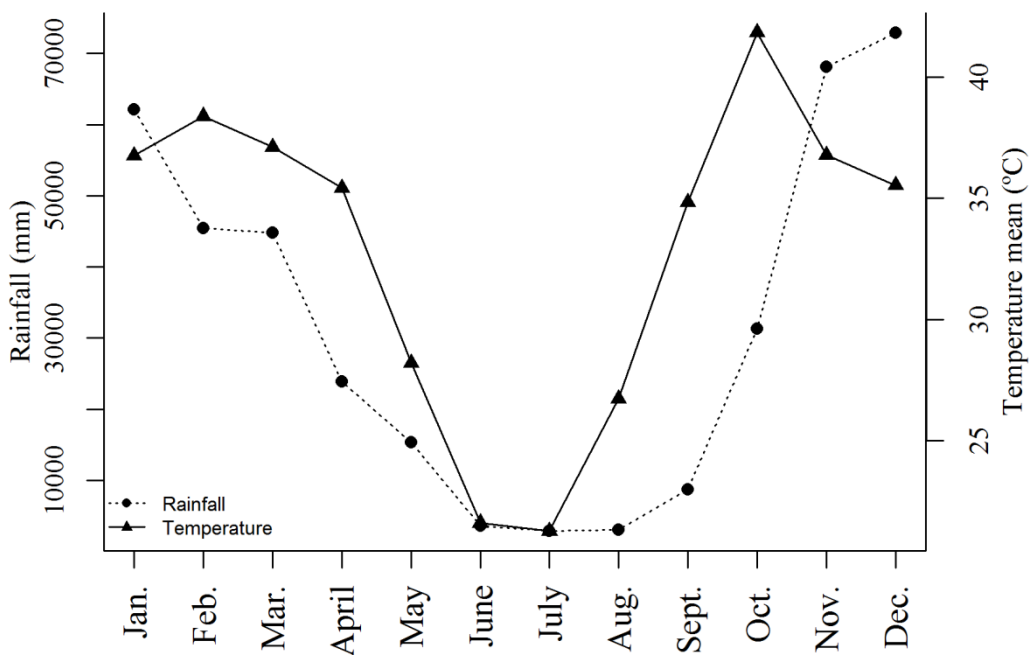


1026

1027 **Fig. 1.** Sampling sites at Mata Seca State Park in southeastern Brazil. Sampling design
 1028 'A' represent the distribution of successional stages, 'B' indicates the location in Brazil
 1029 and 'C' represents the shape of park

1030 In each site, we measured tree circumference at breast height (CBH), wood-area-
 1031 index (WAI) and tree abundance (CBH \geq 15 cm). We measured the WAI using canopy
 1032 photos taken in the dry season (October 2010). We used one photo per site taken with a
 1033 digital camera using an 8 mm fisheye lens (Nassar et al. 2008). The photos represented
 1034 the relative contribution of trunks and branches to canopy structure, and were analyzed
 1035 using Gap Light Analyzer software (Frazer et al. 1999).

1036 We measured cumulative rainfall, average temperature, and air moisture for each
 1037 of the five days required for each sampling period. We used a wireless net station
 1038 located in the study area, which measured temperature and moisture every 30 minutes.



1039
 1040 **Fig. 2.** Total historical average precipitation (filled circle), and monthly average
 1041 temperature (filled triangle) from 1976–2011. Data from Mocambinho Meteorological
 1042 Station located 15 km from Mata Seca State Park.

1043
 1044

1045 *Insect sampling*

1046 We collected beetles using combined flight Malaise/window traps (Basset 1988,
1047 Novais et al. 2016). One trap per site (15 total) holding two vial collectors with 70%
1048 ethanol were exposed for five days (120 h) per month in the tree canopy in the center of
1049 each site. Bark and ambrosia beetles are attracted to ethanol released by dead and dying
1050 trees. Some species tend to be more attracted than others, thus the trapping technique
1051 may be biased towards certain taxonomic group (Hulcr et al., 2008). Specimens were
1052 determined based on Wood (2007), and divided into two feeding habitat guilds: bark
1053 and ambrosia beetles. We calculated the number of species and specimens for each
1054 sampling session. Voucher specimens were deposited in the Museum of Entomology at
1055 FEIS/UNESP (MEFEIS, Ilha Solteira, São Paulo state, Brazil).

1056 *Data analysis*

1057 We used permutational multivariate analysis of variance (PERMANOVA,
1058 Anderson 2001) to evaluate the influence of secondary succession on bark and ambrosia
1059 beetle community composition between early, intermediate, and late stages using
1060 Jaccard dissimilarity measure with 999 permutations. PERMANOVA is a permutational
1061 ANOVA that can test the simultaneous response of one or more variables to one or
1062 more factors in the analyses of variance. We performed the analysis using the "adonis"
1063 procedure in the vegan package in R version 3.2.1.

1064 We tested whether nestedness was the main driver of diversity by decomposing β -
1065 diversity ($\beta_{\text{between sites}}$) using the Sørensen (β_{SOR}) and the Simpson (β_{SIM}) indices (Baselga
1066 2010). β_{SOR} represents the total β -diversity and includes both turnover and nestedness.
1067 β_{SIM} does not consider differences in species richness, and therefore only represents
1068 spatial species replacement, or turnover. Hence, the total species loss due to nestedness
1069 (β_{NES}) is given by the difference between those indices ($\beta_{\text{NES}} = \beta_{\text{SOR}} - \beta_{\text{SIM}}$).

1070 *Beetle diversity along a gradient of resource availability*

1071

1072 The effects of a resource availability gradient on beetle diversity were determined
1073 using generalized linear models (GLMs). In these models, the richness and abundance
1074 of beetles (bark and ambrosia) were pooled by site from 2009 to 2011, whereas
1075 successional stage (early, intermediate and late) and indicators of resource availability
1076 (CBH, WAI, and tree abundance) were used as explanatory variables. The minimal
1077 models were constructed by removing non-significant explanatory variables ($P > 0.05$)
1078 from the full models in the analysis. The models were submitted to residual analysis to
1079 identify the most suitable error distribution, we used the "rldiagnostic" procedure in the
1080 RT4Bio package in R (Crawley 2013).

1081 *Temporal variation*

1082

1083 To test how climate conditions influenced temporal variation in beetle richness
1084 and abundance we used a Generalized Linear Mixed Models analysis (GLMMs, lme4
1085 package), assuming temporal pseudoreplication. The explanatory variables. Collection
1086 month, accumulated rainfall, average moisture (%), and average temperature (°C) were
1087 nested within the random effects of the sites sampled during the study (Bates et al.
1088 2012). All analyses were carried out in the software R (R Development Core Team,
1089 2015).

1090

Results

1091 We collected 763 Scolytinae beetles from 23 species across the successional
1092 gradient, including 14 bark beetle species and nine ambrosia beetle species. Fifty-eight
1093 specimens were bark beetles and 705 specimens were ambrosia beetles. The collected
1094 bark beetles included the Cryphalini, Micracini, Phloeosinini and Scolytini tribes, and
1095 the *Araptus* and *Cryptocarenum* genera. The ambrosia beetles collected included all

1096 Xyleborini species, along with *Euplatypus parallelus*, *Corthylus* sp.1, and *Tricolus*
 1097 *affinis* (Table 1). The tribe Cryphalini had the highest species richness and abundance
 1098 among the bark beetle guild, and the tribe Xyleborini had the highest species richness
 1099 and abundance among the ambrosia beetle guild. *Euplatypus parallelus* was the only
 1100 species of the subfamily Platypodinae, with 12 specimens. *Xyleborus affinis* was the
 1101 only species sampled in all sites and sampling periods, representing 87% of the total
 1102 beetle abundance. In general, most species were considered rare; 15 species had fewer
 1103 than three individuals among sites and sampling periods, and only one individual was
 1104 found for eight species (four species per guild) (Table 1). The species accumulation
 1105 curve did not approach an asymptote for the complete data set or for guilds, indicating
 1106 the need for further sampling to arrive at a reliable estimate of α diversity. However, the
 1107 curve was approaching the Jackknife estimate of 31 species (Fig. 3), suggesting that a
 1108 majority of local species were represented in the analysis.

1109 The sites in early successional stage had lower CBH (Poisson: Deviance [2.12] =
 1110 32.42, $P < 0.001$) and WAI (Quasi-Poisson: Deviance [2.12] = 0.21, $P = 0.007$) than did
 1111 sites at intermediate and late successional stages. Tree abundance was similar between
 1112 successional stages (Negative binomial: Deviance [2.12] = 2.84, $P = 0.24$) (Table 2).

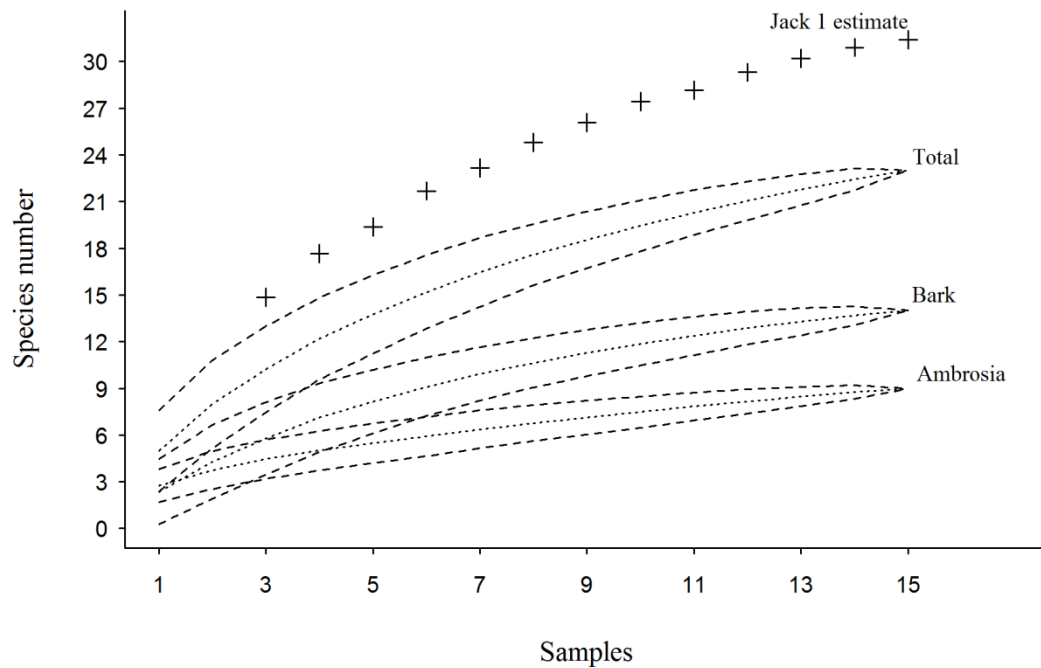
Table 1. List of beetles collected in the Mata Seca State Park in southeastern Brazil. Frequency per sample period (FP, n=10), and abundance per successional stage are reported for each species.

TAXA	GENUS/SPECIES	FP	Early	Inter.	Late	Total
SCOLYTINAE						
Corthylini	<i>Araptus</i> sp.1	1	0	1	0	1
	<i>Corthylus</i> sp.1	1	1	0	0	1
	<i>Cryptocarenum diadematum</i> Eggers	1	0	1	1	2
	<i>Cryptocarenum heveae</i> (Hagedorn)	2	0	1	1	2
	<i>Tricolus affinis</i> Eggers	4	0	2	2	4
Cryphalini	<i>Hypothenemus areolatus</i>	1	0	0	1	1

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

Table 2. Mean values (mean \pm 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 \pm 2.80a	0.246 \pm 0.04a	20.4 \pm 5.58a
Intermediate	40.6 \pm 4.09b	0.348 \pm 0.02b	16.0 \pm 1.05a
Late	47.3 \pm 1.69b	0.412 \pm 0.02b	23.2 \pm 1.77a



1114

1115 **Fig. 3.** Species accumulation and an estimate of total species richness at Mata Seca
 1116 State Park for the complete data set, and for bark and ambrosia beetle species
 1117 separately. The dotted lines represents the analytically derived species accumulation
 1118 curve, and dashed lines represent the 95% confidence interval. The symbol "+"
 1119 represents first order jackknife in abundance-based estimates using the 'poolaccum'
 1120 procedure in the vegan package in R.
 1121

1122

1123 *Beetle composition over the course of ecological secondary succession*

1124 Similarity analysis of bark beetle composition within three categories could not be
 1125 assessed due to absence of species at three of the five early stage sites. However, bark
 1126 beetle composition was similar between the intermediate and the late stages
 1127 (PERMANOVA $r^2= 0.11$, $P = 0.35$). No species were present in all three stages. The
 1128 intermediate and early stages shared two species, and intermediate and late stages
 1129 shared six species. There were no species found in both early and late stages. Two

1130 species were exclusive to the late stage and four to the intermediate stage, with no bark
 1131 beetle found exclusively in the early stage. Ambrosia beetle composition was similar
 1132 among successional stages (PERMANOVA $r^2 = 0.11$, $P = 0.64$). Three ambrosia species
 1133 were common to all stages: *X. affinis*, *X. retusus* and, *E. parallelus*. The intermediate
 1134 stage had two species in common with the late stage and none in common with the early
 1135 stage, despite having three species that were common in all stages. Finally, two species
 1136 were exclusive to early stages and another two exclusive to late stages, with no species
 1137 exclusive to intermediate stages (Table 1).

1138 *Decomposition of β -diversity*

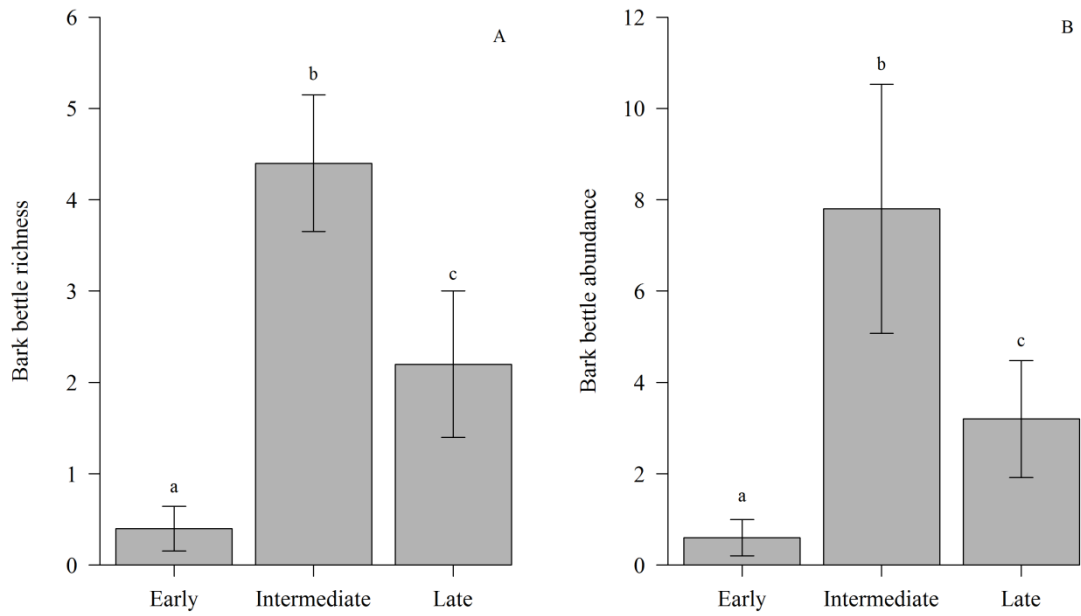
1139 Decomposition of β -diversity revealed species turnover between sites as the main
 1140 driver of the β_{SOR} diversity for both bark ($\beta_{SIM} = 0.77$; $\beta_{SOR} = 0.90$), and ambrosia ($\beta_{SIM} =$
 1141 0.57 , $\beta_{SOR} = 0.76$) beetles, representing 85.6% of the bark beetle β diversity and 74.4%
 1142 of the ambrosia beetle β diversity.

1143 *Beetle diversity along a gradient of resource availability*

1144 We found higher bark beetle richness and abundance at intermediate successional
 1145 stages, followed by the late and the early stages, respectively (Fig. 4). We also detected
 1146 a positive relationship between bark beetle richness and abundance and tree CBH (Table
 1147 3; Figs. 5 A and B). Ambrosia beetles increased in abundance (but not richness) with
 1148 increased tree CBH (Table 3; Fig 5C).

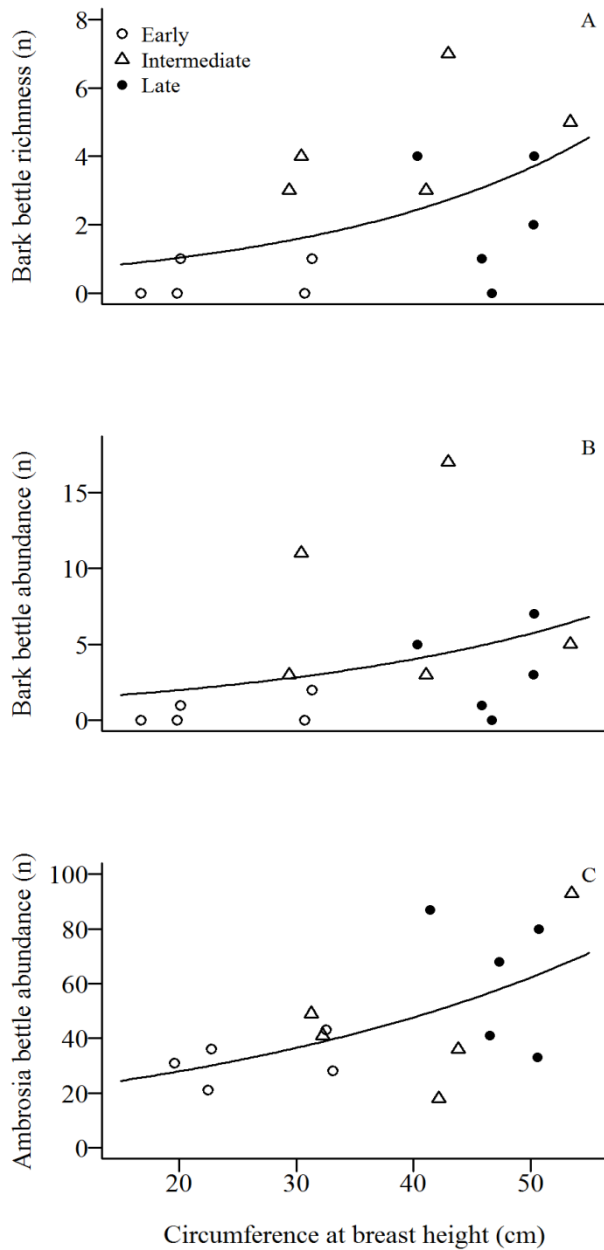
Table 3. Analysis of deviance of the minimal adequate models showing the effects of successional stage and resource CBH on beetle richness and abundance in a Brazilian tropical dry forest.

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



1150

1151 **Fig. 4.** Bark beetle (Curculionidae) richness (A) and abundance (B) (mean \pm SE) in sites
1152 at different successional stages in the Mata Seca State Park in southeastern Brazil.
1153 Different letters above the columns represent statistically different means ($P < 0.05$).
1154



1155

1156 **Fig. 5.** Effect of tree CBH on bark beetle richness (A), bark beetle abundance (B) and
 1157 ambrosia beetle abundance (C) in the Mata Seca State Park in southeastern Brazil.

1158

1159 *Temporal variation*

1160 Bark beetle richness showed no variation among months, and bark beetle
 1161 abundance was higher only in April 2010 (Fig. 6). Climate measures did not affect bark
 1162 beetle richness and abundance (Table 4). Although moisture almost reached statistical
 1163 significance, on explaining the bark beetles abundance increase (Table 4). Ambrosia

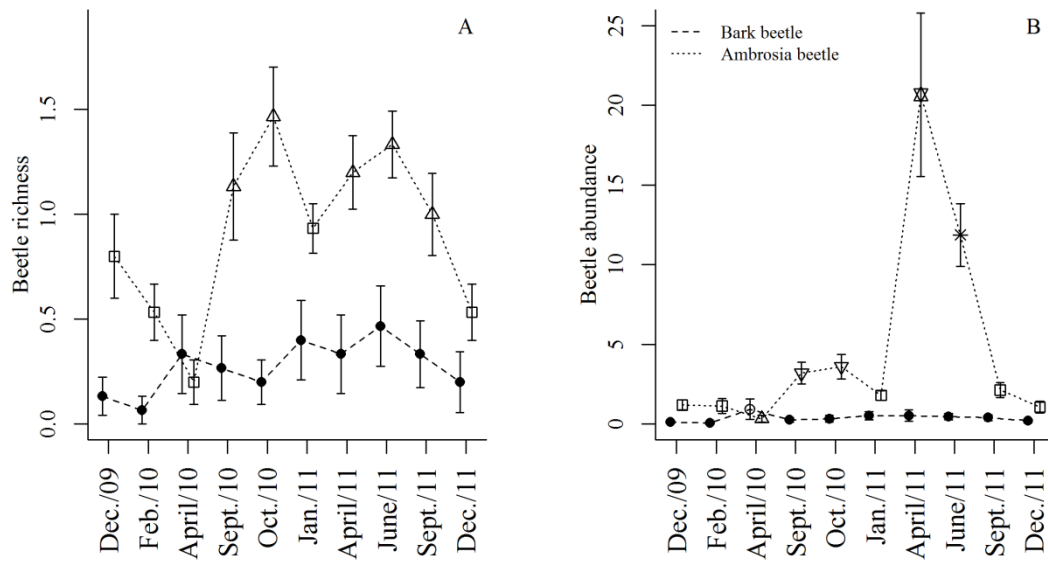
1164 beetle richness was higher in September and October of 2010, and in April, June and
 1165 September of 2011, compared to samples from December, February and April of 2010,
 1166 and January and December of 2011 (Fig. 6A). Overall the driest months were richer
 1167 than the rainy months, and no relationships were found between climate measures and
 1168 ambrosia beetle richness (Table 4). Ambrosia beetle abundance was higher in September
 1169 and October of 2010, with peaks in activity in April and June 2011; these sample
 1170 periods together yielded 69% of the total abundance (Fig. 6B). We found negative
 1171 relationships between monthly variation in ambrosia beetle abundance and increased
 1172 rainfall and temperature, and a positive relationship between variation in abundance and
 1173 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)	<i>P</i>
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

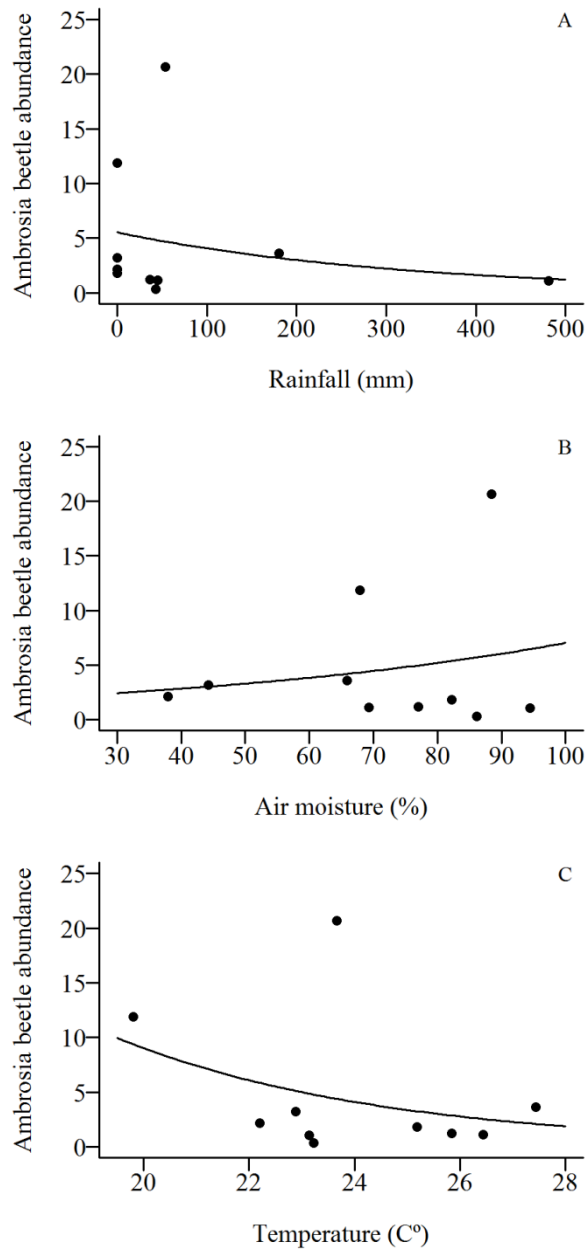
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1177 **Fig. 6.** Bark and ambrosia beetle (Curculionidae) richness (A) and abundance (B) (mean \pm
 1178 SE) during two years of sampling in the Mata Seca State Park in southeastern Brazil.
 1179 Different symbols represent statistically different means ($P < 0.05$).



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1181 **Fig. 7.** Effect of rainfall (A), air moisture (B), and temperature (C) on ambrosia beetle
 1182 abundance in the Mata Seca State Park in southeastern Brazil.

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Discussion

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Studies of variation in composition, richness and abundance of beetles in

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relation to spatial factors and climatic conditions are unprecedented in Brazilian dry

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forests. The current study revealed a total species richness lower than has been found in

1189 to other dry forests in Mexico (Atickson and Equihua 1986), and equal to some other
1190 Brazilian forest biomes (Amazon and Atlantic forest) (Abreu et al. 2012, Muller and
1191 Andreiv 2004). Bark beetle richness (14 species) was greater than ambrosia beetle
1192 richness (9 species); this result may have been affected by the low release of ethanol
1193 during sampling because ethanol tends to attract a greater number of bark beetles (Hulcr
1194 et al. 2008b). However, the dominance of phloeophagous species is a pattern more
1195 common in Mexican dry forest than in Brazilian rainforests (Atickson and Equihua
1196 1986, Abreu et al. 2012, Muller and Andreiv 2004). Phloeophagy as a dominant feeding
1197 habit also occurs in temperate areas, while tropical rainy areas show the opposite trend,
1198 with a greater proportion of ambrosia species typically found (Beaver 1979, Hulcr 2007,
1199 Abreu et al. 2012). Atckson and Equihua (1986) reported that the relative low
1200 importance of ambrosia beetles in dry forests may be associated with the long dry
1201 season, which may limit growth of fungi on wood; this suggestion is supported in the
1202 current study. Although other factors like species interactions are surely involved
1203 (Beaver 1979).

1204 We found similar species compositions with the advancement of secondary
1205 succession, confirming the independence of bark and ambrosia beetles with respect to
1206 local tree community composition (Beaver 1979, Hulcr et al. 2007). However, we found
1207 that turnover is the primary driver of beta diversity for both guilds, and turnover was
1208 higher in bark beetle communities. These results suggest that despite low host-
1209 specificity, site factors may determine the local species pool (mainly in the bark beetle
1210 community).

1211 Bark beetle richness and abundance was higher in intermediate stage sites,
1212 followed by late and early stages, respectively. We found no between-stage differences
1213 in ambrosia beetle richness or abundance, likely due to the different strategies of

1214 obtaining and using food resources among feeding guilds (Hulcr et al. 2007). Overall,
1215 the degree of host specificity is higher in bark beetle species, which favor monophagy
1216 (i.e., restricted to one plant genus) rather than ambrosia species, which tend to favor
1217 polyphagy (i.e., several host families) (Atickson and Equihua 1986). Our results are
1218 analogous to the pattern observed among free-living herbivorous guilds, where the
1219 guilds more closely associated with their host plant traits (e.g., as in sap-sucking
1220 insects) were sensitive to successional stage while the more generalist (chewer) insects
1221 were not (Neves et al. 2014).

1222 Among the structural differences between stages, an increase in tree CBH was
1223 the main mechanism leading to higher diversity, richness and abundance of bark beetles,
1224 and increased abundance of ambrosia beetles. These results suggest that size of wood
1225 affects mainly the bark beetle guild. Large diameter is an important factor for wood
1226 inhabitants due to increased probability of finding resource in a suitable state for
1227 colonization along temporal shifts in spatial parameters (Grove 2002). Wood
1228 availability is thus important for rare bark beetle species, and it is not surprising that
1229 ambrosia species do not follow these patterns because their foraging strategy is closer to
1230 detritivory than to herbivory (Hulcr et al. 2007). For ambrosia beetles, Grove's (2002)
1231 statement with respect to saproxylic beetles that "all wood is good, but bigger is better"
1232 seems to fit our results.

1233 *Xyleborus affinis* was the dominant species in the study area, a consistent pattern
1234 among ambrosia beetles in other studies (Flechtmann et al. 1995, Abreu 2012). This
1235 species has circumtropical distribution, and has been reported to feed on more than 300
1236 plant species. It is considered of high importance among the ambrosia species due to
1237 attacks on Eucalyptus and Pine stands in Brazil and other tropical regions (Flechtmann
1238 1995, Beaver 1988). We demonstrated in the current study that *X. affinis* also has a

1239 strong preference for the Mata Seca State Park, a result in concordance with its high
1240 tolerance for dry and disturbed areas (Hulcr et al 2008b).

1241 Temporal factors did not affect bark beetles richness, and abundance was only
1242 higher in April 2010. Climate factors did not affect guild richness and abundance. Most
1243 of the bark beetle species were trapped in very low numbers, and even the groups of
1244 species reported to occupy dry material such as *Hypothenemus* (Hulcr et al. 2008b) were
1245 found in low abundance. This could be a sampling artifact due to trap bias, however
1246 occurrence was unaffected by seasonality in other studies as well (Hulcr et al 2008b,
1247 Abreu et al. 2012). Our results suggest that the effect of climate seasonality on bark
1248 beetle communities is lower than that of spatial differences between sites.

1249 In contrast, the ambrosia guild showed higher richness in the drier month (June)
1250 and at the end of the dry and wet seasons, and no relationships between community
1251 traits and climate factors. The periods of higher flight activity reflect the emergence of
1252 adults to colonize new, suitable hosts (Wood 1982). According to Wood (1982), these
1253 hosts usually bear senescent leaves that produce attractive substances. The months with
1254 increased percentage of senescent leaves in the study area are the same months with
1255 higher richness of ambrosia beetles (Pezzini et al. 2014). Thus it is likely that host
1256 attractiveness determines ambrosia richness fluctuations. Further studies are necessary
1257 to verify the consistency of the described pattern.

1258 The relatively constant environmental conditions of tropical rainforests allow
1259 year-round beetle activity, and thus there is no clear dispersal pattern for these species
1260 (Hulcr et al. 2008a, Abreu et al. 2012). In tropical dry forests, the abrupt changes among
1261 seasons may lead ambrosia beetles to higher colonization success due to better
1262 conditions for fungal growth.

1289 beetles. Species accumulation was higher in bark beetle species over time, while factors
1290 favorable for fungal growth, such as host and air moisture. Resulted in a broad spatial
1291 distribution of ambrosia species and a greater degree of species redundancy over time.
1292 Detecting spatial and temporal patterns in beetles and insects is not an easy task, and we
1293 highlight interspecific interactions of these beetles as a focus for further investigations.
1294 The overall biological pattern among guilds differed from that of tropical rainforests,
1295 showing patterns similar to other dry forest areas.

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Acknowledgments

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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

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1440 Em nossos resultados, a disponibilidade espacial e temporal de recursos da
1441 vegetação, determinam a distribuição da diversidade de acordo com a estratégia
1442 alimentar e a capacidade de dispersão dos insetos herbívoros. Neste contexto, as
1443 características florestais na escala local e da paisagem estão duplamente envolvidas.
1444 Sugerimos que o uso destes critérios na paisagem florestal, deve ser tão relevante
1445 quanto a definição de áreas fechadas de conservação para a manutenção da diversidade
1446 de insetos herbívoros nas florestas secas.

1447 A sucessão secundária é um indicador de diferenças estruturais da vegetação que
1448 por si, é incapaz de descrever o nível de isolamento do local na paisagem. Todavia a
1449 composição e densidade de plantas foram os mecanismos locais mais importantes para
1450 explicar as diferenças em diversidade no gradiente de sucessão secundária. Em adição a
1451 isso, o aumento da porcentagem de florestas que circundam as áreas amostrais,
1452 determinou o aumento da diversidade dos insetos. Isso demonstra que as possibilidades
1453 de explorar os recursos na matriz são atributos importantes, principalmente para a
1454 manutenção das metacomunidades dos insetos com menor capacidade de dispersão e
1455 mais dependentes dos sistemas florestais.

1456 As florestas secas são ecossistemas cercados por sistemas agrícolas e, os padrões
1457 ecológicos apresentados, podem contribuir para o avanço das estratégias de manejo
1458 atuais, que ainda estão embasadas por poucos critérios relativos principalmente ao
1459 processo de regeneração natural. Nossos resultados demonstram que a complexidade
1460 vegetal deve ser um componente regulador dos insetos herbívoros, diminuindo os riscos
1461 de surtos locais de pragas nos sistemas agrícolas que circundam estas florestas. Todavia
1462 ainda estamos na primeira etapa, definindo os limites e as escalas de análise para
1463 mensurar os serviços ecossistêmicos prestados pelas florestas secas.