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

TESE DE DOUTORADO

INFLUÊNCIA DE FATORES ESPACIAIS E TEMPORAIS SOBRE AS COMUNIDADES DE ARTRÓPODES ASSOCIADOS A UMA ENGENHARIA ECOSSISTÊMICA

SAMUEL MATOS ANTUNES DE NOVAIS

Belo Horizonte– 2018

SAMUEL MATOS ANTUNES DE NOVAIS

INFLUÊNCIA DE FATORES ESPACIAIS E TEMPORAIS SOBRE AS COMUNIDADES DE ARTRÓPODES ASSOCIADOS A UMA ENGENHARIA ECOSSISTÊMICA

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. Mauricio Quesada (UFMG/UNAM-México)

Co-orientadora: Professora Dra. Nancy Calderón Cortez (UNAM-México)

Belo Horizonte– 2018

DEDICATÓRIA

À minha mãe Celma Maria Antunes Novais (*in memorium*),
e aos meus três filhos (*in futurium*)
dedico.

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. Meus mais sinceros agradecimentos ao então coordenador do PPG-ECMVS, Frederico Neves, e ao secretário Frederico Teixeira, por toda ajuda nos trâmites associados ao doutorado Brasil-México.

À CAPES pela concessão das bolsas de Doutorado (Demanda Social e Sanduíche).

Agradeço ao meu orientador Mauricio Quesada pela confiança, ensinamentos e excelente orientação. Serei sempre grato por todo apoio.

À minha co-orientadora Nancy Calderón Cortés por aceitar colaborar nesse projeto, por toda ajuda em campo, identificação dos insetos e sugestões de escrita.

Aos co-autores, Dudu, Jacob, Milan, Gume, Paul, Spixo e Fred pelas contribuições ao trabalho.

A todos os colegas e amigos do Laboratorio de Ecología Evolutiva y Conservación de Bosque Tropicales e Laboratorio Nacional de Análisis y Síntesis Ecológica pelos momentos vividos que certamente deixarão saudades.

Agradeço especialmente aos amigos que me acompanharam durante as amostragens de campo e na triagem dos insetos: Dudu, Pelé Jacob, Olegario (no tan) Delgado, Erika, Thaise, Marichui, HombreCarro, Benji, Rodrigo, Ivette, Alejandro, Vitor, Fortino e Tomás.

À Alessandra Braga, esposa, amiga, companheira dentro e fora de campo. Obrigado por viver essa aventura ao meu lado, você foi fundamental em todas as etapas desse trabalho. Te amo.

SUMÁRIO

Introdução geral

O estudo dos fatores que causam variações espaciais e temporais na distribuição e abundância das espécies é o principal objetivo de investigação da ecologia de comunidades (Begon et al., 2006). Em ecossistemas terrestres, as comunidades de artrópodes são fortemente influenciadas pela estrutura da vegetação, pois essa afeta a disponibilidade de recursos, heterogeneidade ambiental e condições microclimáticas (Lawton et al., 1983; McCoy & Bell 1991). Estudos prévios têm demonstrado que a riqueza e abundância de artrópodes respondem positivamente ao aumento da complexidade estrutural do habitat (Halaj et al., 2000; Tews et al., 2004; Langellotto & Denno 2004; Neves et al., 2014).

Além das variações estruturais da vegetação dentro de um mesmo habitat (por exemplo, entre os estratos verticais de uma floresta), as mudanças ambientais causadas pelo ser humano constituem importantes fatores que alteram a estrutura das comunidades vegetais (Vellend et al., 2007; Arroyo-Rodriguez et al., 2013;Newbold et al., 2015). Os distúrbios antropogênicos frequentemente causam uma simplificação dos habitats naturais, resultando em uma redução geral da diversidade de artrópodes e alterações na abundância das espécies persistentes (Lawton et al., 1998; Gardner et al., 2009; Solar et al., 2015). Apesar do crescente número de estudos avaliando as respostas de diferentes artrópodes às alterações antropogênicas em florestas tropicais, os efeitos desses distúrbios sobre alguns grupos, como os insetos saproxílicos, ainda permanecem pouco estudados (Seibold et al., 2015). Os insetos saproxílicos são aqueles que dependem, direta ou indiretamente, de madeira morta durante parte do seu ciclo de vida, e incluem, principalmente, besouros e seus parasitóides (Speight 1989).

As mudanças sazonais das condições e recursos também constituem importantes fatores que podem determinar a composição e estrutura das comunidades de artrópodes, principalmente em ambientes extremamente sazonais como as florestas tropicais secas (FTS; Kishimoto-Yamada & Itioka 2015). As FTS são caracterizadas principalmente por possuírem duas estações bem definidas (seca e chuvosa), onde a maioria das árvores perde suas folhas durante a estação seca como uma resposta fisiológica à escassez de água (Lopezaraiza-Mikel et al., 2013; Pezzini et al., 2014). Apesar das condições altamente sazonais determinarem os padrões temporais das comunidades de artrópodes em FTS (Janzen 1973; Duarte-Junior & Schlindwein 2005; Neves et al., 2010; Vasconcellos et al., 2010; Liberal et al., 2011; Nobre et al., 2012; Kishimoto-Yamada & Itioka 2015), fatores denso-independentes como os distúrbios naturais podem mudar abruptamente a disponibilidade de recursos e condições ambientais, afetando as populações de artrópodes (Schowalter et al., 2012).

Embora existam diversos estudos que avaliam a influência de fatores espaciais e temporais sobre as comunidades de artrópodes, estudos que avaliam a influência desses fatores sobre as comunidades de artrópodes associados a uma engenharia ecossistêmica são extremamente raros (ver Vieira & Romero 2013). Os engenheiros ecossistêmicos são organismos que, direta ou indiretamente, causam mudanças físicas no ambiente, controlando a disponibilidade de recursos para outras espécies (Jones et al., 1994). Diversos autores têm demonstrado o papel de artrópodes, principalmente insetos, atuando como engenheiros ecossistêmicos para outros artrópodes (Martinsen et al., 2000; Lill & Marquis 2003; Kagata et al., 2004; Jouquet et al., 2006; Calderón-Cortés et al., 2011; Vieira & Romero 2013; Cornelissen et al., 2016; Harvey et al., 2016; Satoh et al., 2016; Sydenham et al., 2016; Wetzel et al., 2016; Zuo et al., 2016; Raath et al., 2017).

O principal objetivo dessa tese foi determinar os efeitos de fatores espaciais e temporais sobre as comunidades de artrópodes associados diretamente e indiretamente com a engenharia ecossistêmica realizada pelo besouro *Oncideres albomarginata chamela* (Cerambycidae: Lamiinae). As fêmeas de *O. albomarginata chamela* cortam ramos de 2-3 cm de diâmetro da árvore *Spondias purpurea* (Anacardiaceae). Os ramos de *S. purpúrea* podem cair sobre o solo ou ficar suspendidos sobre a vegetação, e em seguida, as fêmeas fazem incisões ao longo da casca onde colocam ovos (Uribe-Mú &Quesada 2006). Posteriormente, esses ramos são colonizados por outras espécies de artrópodes, principalmente besouros saproxílicos (Calderón-Cortés et al., 2011). Depois que os besouros emergem como adultos dos ramos de *S. purpurea*, as cavidades onde suas larvas se desenvolveram permanecem disponíveis para outros artrópodes como sítios de nidificação e abrigo.

A tese está dividia em quatro capítulos: O **capítulo 1** teve como objetivo determinar como as comunidades de insetos saproxílicos associados com a engenharia ecossistêmica de *O. albomarginata chamela* respondem a modificações do habitat causadas pelo homem, e como essas comunidades variam ao longo do tempo após um distúrbio natural (Furacão Patricia).

O **capítulo 2** teve como objetivo determinar como as variações na estrutura do habitat em diferentes estratos verticais (solo e vegetação) entre estações (seca e chuvosa) afetam a riqueza, abundância e frequência de colonização de artrópodes que se beneficiam indiretamente da engenharia ecossistêmica de *O. albomarginata chamela*.

O**capítulo 3**, já publicado na revista *Basic and Applied Ecology* (Anexo I), teve como objetivo avaliar a importância das cavidades abandonadas pelos besouros na organização das comunidades de formigas arborícolas.

O **capítulo 4**, particularmente, não se refere às comunidades de insetos associados à engenharia ecossistêmica de *O. albomarginata chamela*. Este capítulo teve como objetivo determinar os efeitos do Furacão Patricia sobre três guildas de insetos herbívoros (sugadores, folívoros e xilófagos) e besouros predadores associados ao dossel de uma floresta tropical seca. Nesse capítulo também avaliamos a dinâmica temporal dessas guildas por três anos, um ano antes e dois anos depois do furacão.

Referências

Arroyo-Rodriguez, V., Roes, M., Escobar, F., Melo, F.P.L., Santos, B.A., Tabarelli, M. et al. (2013). Plant beta-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. Journal of Ecology, 101: 1449-1458.

Begon, M., Townsend, C. R., Harper, J. L. (2006). Ecology: from individuals to ecosystems. 4th ed. Oxford: Blackwell Publishing. 746 pp.

Calderón-Cortes, N., Quesada, M., Escalera-Vazquez, L.H. (2011). Insects as stem engineers: Interactions mediated by the twig-girdler *Oncideres albomarginata chamela* enhance arthropod diversity. PLoS One, 6: e19083.

Cornelissen, T., Cintra, F., Santos, J.C. (2016) Shelter-building insects and their role as ecosystem engineers. Neotropical Entomology, 45: 1–12.

Duarte-Junior, J. A., Schlindwein, C. (2005). The highly seasonal hawkmoth fauna (Lepidoptera Sphingidae:) of the caatinga of northeast Brazil: a case study in the state of Rio Grande do Norte. The Lepidopterists' Society, 59,212.

Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A., Sodhi, N.S. (2009). Prospects for tropical forest biodiversity in a human-modified world. Ecology Letters, 12(6): 561-582.

Halaj, J., Ross, D.W., Moldenke, A.R. (2000). Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos, 90(1): 139-152.

Harvey, J.A., Ode, P.J., Malcicka, M., Gols, R. (2016). Short-term seasonal habitat facilitation mediated by an insect herbivore. Basic and Applied Ecology, 17(5): 447-454

Janzen, D.H. (1973). Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology, 54: 687-708.

Jones, C.G., Lawton, J.H., Shachak, M. (1994). Organisms asecosystem engineers. Oikos, 69: 373-386.

Jouquet, P., Dauber, J., Lagerlof, J., Lavelle, P., Lepage, M. (2006). Soil invertebrates asecosystem engineers: intended and accidental effects on soil and feedback loops. Apllied Soil Ecology, 32:153-164.

Kagata, H., Ohgushi, T. (2004). Leaf miner as a physical ecosystem engineer: secondaryuse of vacant leaf-mines by other arthropods. Annals of the EntomologicalSociety of America, 97: 923-927.

Kishimoto-Yamada, K. Itioka, T. (2015). How much have we learned about seasonality in tropical insect abundance since Wolda (1988)? Entomological Science, 18: 407-419.

Lawton, J. (1983). Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology, 28(1): 23-39.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M. et al. (1998). Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature, 391(6662): 72.

Liberal, C.N., Farias, A.M.I., Meiado, M.V., Filgueiras, B.K., Iannuzzi, L. (2011). How habitat change and rainfall affect dung beetle diversity in Caatinga, a Brazilian semi-arid ecosystem. Journal of Insect Science, 11: 1–11.

Lill, J.T., Marquis, R.J. (2003). Ecosystem engineering by caterpillars increases insectherbivore diversity on white oak. Journal of the Lepidopterists` Society, 84: 682-690.

Lopezaraiza-Mikel, M., Quesada, M., Álvarez-Añorve, M., Ávila-Cabadilla, L., Martén-Rodríguez, S., Calvo-Alvarado, J.et al. (2013). Phenological Patterns of Tropical Dry Forests along Latitudinal and Successional Gradients in the Neotropics. In: Sanchez-Azofeifa, A., Powers, J.S., Fernandes, G.W., Quesada, M. (eds.) Tropical Dry Forests in the Americas: Ecology, Conservation, and Management. CRC Press, 2013.101-128pp.

Langellotto, G.A., Denno, R.F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia, 139: 1-10

McCoy, E.D., Bell, S.S. (1991). Habitat structure: the evolution and diversification of a complex topic. In: Bell, S.S., McCoy, E.D, Mushinsky, H.R. (eds). Habitat structure – The Physical Arrangement of Objects in Space. Chapman & Hall, London. pp. 169-196.

Martinsen, G.D., Floate, K.D., Waltz, A.M., Wimp, G.M., Whitham, T.G. (2000). Positiveinteractions between leafrollers and other arthropods enhance biodiversity on hybrid cottonwoods. Oecologia, 123:82-89.

McCoy, E.D., Bell, S.S. (1991). Habitat structure: the evolution and diversifications of acomplex topic. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (eds.) Habitat Structure:The Physical Arrangement of Objects in Space. Chapman & Hall. pp. 3-27.

Neves, F.S., Oliveira, V.H.F., Espírito-Santo, M.M., Vaz-de-Mello, F.Z., Louzada, J., Sanchez-Azofeifa, A., Fernandes, G.W. (2010). Successional and seasonal changes in a community of dung beetles (Coleoptera: Scarabaeinae) in a tropical dry forest. Natureza e Conservação, 8: 160-164.

Neves, F.S., Silva, J.O., Espírito-Santo, M.M., Fernandes, G.W. (2014). Insect herbivores and leaf damage along successional and vertical gradients in a tropical dry forest. Biotropica, 46:14-24.

Newbold, T., Hudson, L. N., Hill, S. L., Contu, S., Lysenko, I., Senior, R. A. et al. (2015). Global effects of land use on local terrestrial biodiversity. Nature, 520(7545), 45.

Nobre, C.E.B., Iannuzzi, L. Schlindwein, C. (2012). Seasonality of fruit-feeding butterflies (Lepidoptera, Nymphalidae) in a Brazilian semiarid area. ISRN Zoology, 268159.

Pezzini, F.F., Ranieri, B.D., Brandão, D.O., Fernandes, G.W., Quesada, M., Espírito-Santo, M.M., Jacobi, C.M. (2014). Changes in tree phenology along natural regeneration in a seasonally dry tropical forest. Plant Biosystems, 148:965-974.

Raath, M.J., le Roux, P.C., Veldtman, R., Campbell, H., Buyens, I.P.R., Greve, M. (2017). Empty *Gonometa postica* cocoons function as nest sites and shelters for arboreal ants. Journal of Arid Environments, 144: 42-47.

Satoh, T., Yoshida, T., Koyama, S., Yamagami, A., Takata, M., Kurachi, T. et al.(2016). Resource partitioning based on body size contributes to the species diversity of wood-boring beetles and arboreal nesting ants. Insect Conservation and Diversity, 9(1): 4-12

Schowalter, T.D. (2012). Insect responses to major landscape-level disturbance. Annual Review of Entomology, 57: 1-20.

Solar, R.C., Barlow, J., Ferreira, J., Berenguer, E., Lees, A. C., Thomson, J. R., Chaul, J. (2015). How pervasive is biotic homogenization in human-modified tropical forest landscapes? Ecology Letters, 18(10): 1108-1118.

Speight, M.C.D. (1989). Saproxylic Invertebratesand their Conservation. Strasbourg. Council Europe, 79 pp.

Sydenham, M.A., Häusler, L.D., Moe, S.R., Eldegard, K. (2016). Inter-assemblage facilitation: the functional diversity of cavity-producing beetles drives the size diversity of cavity-nesting bees. Ecology and Evolution, 6(2): 412-425

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography, 31(1): 79-92.

Uribe-Mú, C. A., Quesada, M. (2006). Preferences, patternsand consequences of branch removal on the dioecious tropical tree *Spondias purpurea* (Anacardiaceae) by the insect borer *Oncideres albomarginata chamela* (Cerambycidae). Oikos, 112: 691-697.

Vasconcellos, A., Andreazze, R., Almeida, A.M., Araujo, H.F., Oliveira, E.S., Oliveira, U. (2010). Seasonality of insects in the semi-arid Caatinga of northeastern Brazil. Revista Brasileira de Entomologia, 54: 471-476.

Vellend, M., Verheyen, K., Flinn, K.M., Jacquemyn, H., Kolb, A., Van Calster, H. et al. (2007). Homogenization of forest plant communitiesand weakening of species-environment relationships via agriculturalland use. Journal of Ecology, 95: 565–573.

Vieira, C., Romero, G.Q. (2013). Ecosystem engineers on plants: indirect facilitation of arthropod communities by leaf-rollers at different scales. Ecology, 94(7): 1510-1518

Wetzel, W.C., Screen, R.M., Li, I., McKenzie, J., Phillips, K.A., Cruz, M.et al.(2016). Ecosystem engineering by a gall-forming wasp indirectly suppresses diversity and density of herbivores on oak trees. Ecology, 97(2): 427-438.

Zuo, J., Cornelissen, J.H., Hefting, M.M., Sass-Klaassen, U., van Logtestijn, R.S., van Hal, J.et al.(2016). The (w) hole story: Facilitation of dead wood fauna by bark beetles? Soil Biology and Biochemistry,95: 70-77.

CAPÍTULO 1

EFFECTS OF ANTHROPOGENIC AND NATURAL DISTURBANCES ON SAPROXYLIC INSECT COMUNITIES ASSOCIATED WITH AN ECOSYSTEM ENGINEERING

Effects of anthropogenic and natural disturbances on saproxylic insect communities associated with an ecosystem engineering

Samuel Novais[a,b,c], Paul Hanson[d] and Mauricio Quesada[a,b,c*]

[a] Laboratório de Ecologia de Insetos, Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, 31270-901, Brazil

[b] Laboratorio Nacional de Análisis y Síntesis Ecológica, Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, 58190, México

[c] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, 58190, México

[d] Escuela de Biología, Universidad de Costa Rica, San Pedro, Costa Rica

* Laboratorio Nacional de Análisis y Síntesis Ecológica, Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, 58190, México.

E-mail address: mquesada@cieco.unam.mx (M. Quesada) Tel: +52 4436893517.

Abstract: Females of *Oncideres albomarginata chamela* (Cerambycidae) girdler branches of *Spondias purpurea* (Anacardiaceae) for oviposition. Later many saproxylic insects (those that depend on dead wood during part of their life cycle) colonize the same branches. The objective of our study was to evaluate the effects of anthropogenic and natural disturbances on saproxylic insect communities associated with the ecosystem engineering carried out by *O. albomarginata chamela*. After the large-scale windthrow caused by Hurricane Patricia (category 5) in October 2015 in a tropical dry forest of Jalisco, Mexico, we started an experimental two-year study (January 2016 and 2017) comparing the richness and abundance of saproxylic beetles and parasitoids that emerged from *S. purpurea* branches between two treatments: continuous forest and disturbed forest fragments. Early-decay beetles with short developmental time (Scolytinae and Bostrichidae) and their associated parasitoids were more abundant in the sampling soon after the hurricane, probably as an immediate response to the increased amount of dead wood after the hurricane (bottom-up effects). In the second sampling year, top-down effects (predation and parasitism), bottom-up effects (decrease of freshly dead wood), and competition by beetles species with longer developmental time could be factors regulating early-decay beetle populations. Although the differences in abiotic conditions and forest structure between continuous forest and disturbed forest fragments were probably reduced after the hurricane, continuous forests presented a greater number of exclusive species and frequency of rare species of both beetles and parasitoids in 2016. In addition, continuous forest presented greater beetle richness in 2017, as well as a greater abundance of Scolytinae and Cerambycidae beetles in both sampling years. We conclude that anthropogenic and natural disturbances are important factors that affect saproxylic insect communities associated with the ecosystem engineering carried out by *O. albormaginata chamela.*

Keywords: Saproxylic beetles, saproxylic parasitoids, predatory beetles, trophic interactions, dead wood, tropical dry forest

Introduction

In terrestrial ecosystems, dead wood represents an important resource of which many species depend upon, directly or indirectly, during part of their life cycle (saproxylic species; Speight 1989). In temperate and boreal forests, where most studies on saproxylic fauna have been conducted (Seibold et al. 2015a), there has been a growing interest in investigating the effects of increasing habitat management practices on saproxylic beetles and their associated parasitoids (Grove 2002; Hilszczanski et al. 2005; Johansson et al. 2007; Gibb et al. 2008; Stenbacka et al. 2010; Seibold et al. 2015b). Saproxylic beetles and parasitoids are positively dependent on dead wood amount and diversity (e.g. tree species, diameters and decay stages), which tend to be reduced in managed compared to primary forests (Grove 2002; Hilszczajski et al. 2005; Jonsell et al. 2007; Johansson et al. 2007; Hjaltén et al. 2007; Gibb et al. 2008; Ulyshen and Hanula 2009; Brin et al. 2011). In addition, differences in abiotic conditions among original and managed habitats could also affect the distribution of these insects (Ranius and Jansson 2000; Sverdrup-Thygeson and Ims 2002; Lindhe et al. 2005; Hjaltén et al. 2007; Gibb et al. 2008; Stenbacka et al. 2010; Ulysen et al. 2011; Seibold et al. 2016). In general, managed forests present lower species richness and abundance of saproxylic species, and different assemblages compared to primary forests (Grove 2002; Simila et al. 2003).

In contrast to the negative effects of changes in biotic and abiotic conditions caused by anthropogenic disturbances on saproxylic insect communities, density-independent factors such as natural disturbance events can abruptly increase dead wood availability and favorable habitat conditions for these insects (Bouget and Duelli 2004; Schowalter 2012). For example, strong winds associated with hurricanes cause several damages on forest structure, which include large-scale tree mortality, increased standing dying trees and live trees with broken parts, as well as the fall of wood debris of different tree species (Lugo 2008; Kimberlain et al. 2016). It is expected that an increase in the amount and diversity of dead wood following windthrow events may lead to a rapid increase in abundance of saproxylic insect populations (Bouget and Duelli 2004; Wermelinger et al. 2017). As the high-quality dead wood resources decline over time (e.g. newly fallen and stressed trees), saproxylic beetles and their natural enemies tend to decrease in abundance (Wermelinger et al. 2013).

The ecosystem engineering carried out by the twig-girdler beetle *Oncideres albomarginata chamela* (Cerambycidae: Lamiinae) is a keystone process that structure an arthropod community composed mainly by saproxylic beetles (Calderón-Cortés et al. 2011). Adult females of *O. albomarginata chamela* detach branches of the tree *Spondias purpurea* (Anacardiaceae) and make incisions along them for oviposition (Uribe-Mú and Quesada 2006). Consequently, they provide a suitable habitat for secondary colonization, mainly by beetles that oviposit in the same branches (Calderón-Cortés et al. 2011). Later, natural enemies (e.g. predatory beetles and parasitoids) also take advantage of the cut branches by attacking beetle larvae (Calderón-Cortés et al. 2011).

The objective of our study was to evaluate the effects of anthropogenic and natural disturbances on saproxylic insect communities associated with the ecosystem engineering carried out by *O. albomarginata chamela*. In October 2015, Hurricane Patricia, the strongest tropical hurricane (category 5) that has been reported in the Western Hemisphere so far, struck directly the Chamela-Cuixmala Biosphere Reserve and the surrounding forest fragments in the state of Jalisco, Mexico. Nearly all trees were defoliated, stripped off their branches, snapped, or uprooted by the strong winds (Kimberlain et al. 2016). Immediately after the Hurricane Patricia, we started an experimental two-year study comparing the richness and abundance of saproxylic beetles and parasitoids that emerged from *S. purpurea* branches in continuous forest disturbed by Hurricane Patricia and forest fragments already disturbed by anthropic activities also affected by Hurricane Patricia. We also analyzed the mechanisms determining the β-diversity between these treatments, which can be partitioned into turnover (species replacement between sites) and nestedness (species loss or gain between sites) components (Baselga 2010). We tested the following predictions: I) the richness and abundance of saproxylic species are greater in the first sampling after Hurricane Patricia than in the followed year; II) the richness and abundance of saproxylic species are greater in continuous forest than in disturbed forest fragments; and III) the β-diversity of saproxylic species between continuous forest and disturbed forest fragments is mainly shaped by species turnover.

Material and methods

Study site

This study was conducted in the Chamela-Cuixmala Biosphere Reserve (CCBR, 19º30’N, 105º03’W) and three surrounding forest fragments, located on the Pacific coast of Jalisco, Mexico (Fig. 1). The vegetation of the region consists primarily of TDF with a mean annual rainfall of 748 mm, and a dry season that extends from November to June (García-Oliva et al. 2002). Land use around the CCBR has been transformed by human activity, mainly related to agriculture and livestock production. In addition, the remaining forest fragments have been under continuous pressures such as selective logging and as additional cattle grazing areas (Quesada et al. 2009).

Our samplings were carried out during two consecutive years, from January to December 2016 and 2017. At 23 of October 2015 Hurricane Patricia, estimated as a category 5 on the Saffir-Simpson Hurricane Wind Scale, reached the southwestern coast of Mexico in the state of Jalisco, heavily affecting the Chamela-Cuixmala Biosphere Reserve region (Fig. 1). Hurricane Patricia is considered as the strongest hurricane that made landfall in the Western Hemisphere which has been reported so far (Kimberlain et al. 2016).

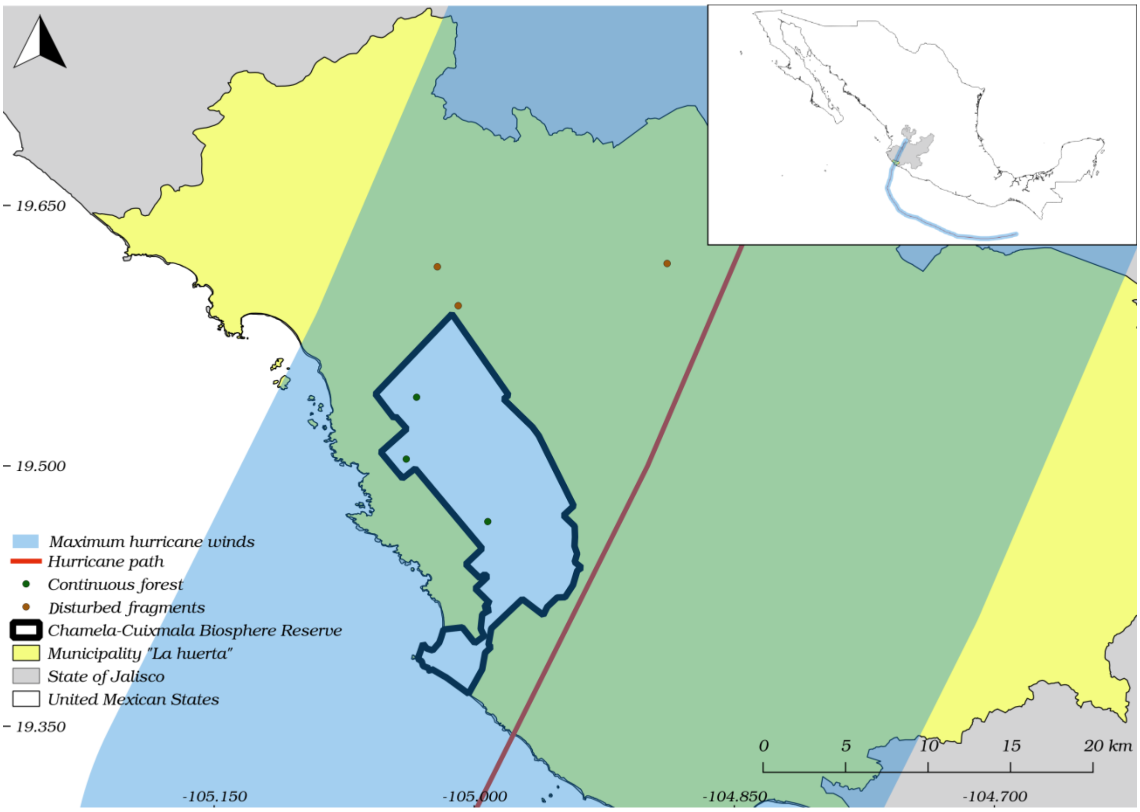


Figure 1. Map of municipality of La Huerta, Jalisco, showing the location of the Chamela-Cuixmala Biosphere Reserve and the six study sites. The red line and the blue boundaries represent respectively the path of Hurricane Patricia and their maximum winds obtained from historical hurricane tracks of the National Oceanic and Atmospheric Administration (https://coast.noaa.gov/hurricanes/).

Experimental design

In order to assess the saproxylic insect communities associated with the ecosystem engineering by *O. albomarginata chamela* we conducted a field experiment utilizing artificially simulated engineered branches. Branches exhibiting similar characteristics (reproductive branches from ≈2–3 cm in diameter) to those detached and colonized by *O. albomarginata chamela* were artificially cut off from *S. purpurea* trees.

We artificially simulated the structural modification of branches made by adult females of *O. albomarginata chamela* by making numerous incisions with scissors (every 5 mm) on the bark of the branches (see Calderón-Cortés et al. 2011). Experimentally, working with artificially cut branches has the advantage of standardizing the exact cut date. Because the natural cut by *O. albomarginata chamela* goes from November to February it is not possible to determine the exact cut date of these branches when encountering them in the field. The composition, richness and abundance of beetles that emerge from artificially-engineered branches are similar to those that emerge from branches of *S. purpurea* naturally detached and colonized by *O. albomarginata chamela* (Calderón-Cortés et al. 2011).

The effects of anthropogenic disturbances on saproxylic species were assessed comparing the emerging insect communities from the artificially-engineered branches in two treatments: continuous forest disturbed by Hurricane Patricia (hereinafter referred to as “continuous forest”) and forest fragments already disturbed by anthropic activities also affected by Hurricane Patricia (hereinafter referred to as “disturbed forest fragments”). Three transects located at least 3 km apart were selected within the CCBR, and other three transects were established in distinct forest fragments. All selected fragments were characterized by forest remnants surrounded by a pasture matrix and also used as additional cattle grazing areas. In each transect, we select five individuals of *S. purpurea* (points) distant from each other by at least 50 meters. Next, we attached up to three artificially-engineered branches in distinct trees under the canopy of the *S. purpurea* trees (N=12 branches/transect), for 72 branch samples in total (N=36 branches/treatment). All branches were marked, and remained in field for 45 days (January to February 2016) to allow the colonization of the saproxylic beetles and parasitoids (Fig. S1). After 45 days, we collected the branches that were enclosed in mesh bags (0.5 mm mesh size) and additionally placed inside emergence traps made of black cloth to prevent further colonization and escape of the established fauna. The emergence traps were placed in an open room at the study site, and maintained at local environmental conditions (Fig. S2). Emerging arthropods from each branch were recorded monthly from March to December 2016. The same experiment was repeated with another set of artificially-engineered branches, from January to December 2017, in the same transects and points. We used respectively 37 and 39 branches in continuous forest and disturbed forest fragments in 2017, for 148 branch samples in total during the two-year sampling period. Taxonomic identification of the beetles to family level was carried out using available taxonomic literature (Arnett 2000), while parasitoids were identified by the second author.

Statistical analysis

In order to visualize the general differences of the saproxylic species among continuous forest and disturbed forest fragments in the two sampling years, we built distribution networks using the Cytoscape software (Kohl et al. 2011). The networks were constructed based on species abundance data.

We used Generalized Mixed Linear Models (GLMERs; lme4 package in R) to test whether the richness and abundance of saproxylic beetles and parasitoids were affected by treatments and sampling years. Models were also performed separately for the abundance of the most abundant families/subfamilies of beetles: Bostrichidae, Cerambycidae, Histeridae, Lyctinae (Bostrichidae), Scolytinae (Curculionidae) and Tenebrionidae. Particularly, Bostrichidae family showed two general traits in size and developmental time: a) species with small body size and short developmental time (hereinafter referred to as “Bostrichidae I”) and b) species with large body size and longer developmental time (hereinafter referred to as "Bostrichidae II"), which were analyzed in different models (see Calderón-Cortéz et al. 2011). These models used: (i) the number of species and adult individuals that emerged from the branches as the response variable, (ii) treatment, year and their interaction as fixed explanatory variables, and (iii) the transect points (individuals of *S. purpurea*) per year as random effects. We applied a "*Poisson"* distribution of errors to the models, and eventual data overdispersion were adjusted with a "*Negative Binomial"* distribution of errors. Significance was estimated with an ANOVA between the complete (H1) and the null model (H0). The Akaike Information Criterion (AIC) was used to rank the models, since it represents the uncertainty of the model a lower value of the AIC represents the more parsimonious model. The package "*lsmeans*" was used for *a posteriori* comparisons (Lenth et al. 2017). All analyses were performed using R software (R Core Team 2016).

We decomposed β-diversity to determine the primary mechanisms shaping the community composition of saproxylic beetles and parasitoids between treatments. The decomposition of β-diversity was performed using the Sørensen ($\beta_{SØR}$) and Simpson (β_{SIM}) dissimilarity indices (Baselga 2010). $\beta_{SØR}$ represents the total β-diversity and incorporates both species turnover and the nestedness. β_{SIM} shows only species replacement, or turnover, and does not consider variation in species richness. The difference between these indices indicates the total loss of species due to nestedness (β_{NES}), such that ($\beta_{NES}=\beta_{SØR} - \beta_{SIM}$). We also performed an analysis in order to evaluate the effects of the treatments and years on the frequency of colonization of the *S. purpurea* branches by rare species of beetles and parasitoids. We consider rare species those that presented less than three individuals or were sampled in less than three of the 148 branches during the two-year sampling period. Treatment, year and their interaction were also included as fixed variables, and the transect points per year as random effects. We used the GLMERs in R software with a "*Binomial*" distribution of errors. The AIC was used to rank the models, and the package "*lsmeans*" was used for *a posteriori* comparisons (Lenth et al. 2017).

Results

A total of 30,427 saproxylic beetles emerged from the 148 artificially-engineered branches of *S. purpurea* in the two consecutive studied years. These included 114 species from at least 28 families,of which Bostrichidae was the most abundant, comprising 53% of all individuals, followed by Scolytinae (Curculionidae; 27%) and Histeridae (18%),totaling together more than 98% of the sampled beetles (Table S1). Scolytinae was the richest group (16 spp.), followed by Bostrichidae (12) and Cerambycidae (11; Table S1). For parasitoids, 4,152 individuals were collected from 52 species (Table S2).

A total of 137 species of saproxylic insects were collected in 2016 (94 beetles and 43 parasitoids) compared to 81 species in 2017 (52 beetles and 29 parasitoids). In 2016, 60 species were exclusively found in continuous forest areas, 22 in the disturbed fragments and 55 were shared between treatments (Fig. 2). In 2017, 24 species were exclusively found in continuous forest areas, 17 in the disturbed fragments and 40 were shared between treatments (Fig. 2). The most abundant species changed between years; in 2016 was the xylophagous beetle *Prostephanus truncates* (Bostrichidae I), while in 2017 was the predatory beetle *Teretriosoma nigrescens* (Histeridae; Fig. 2).

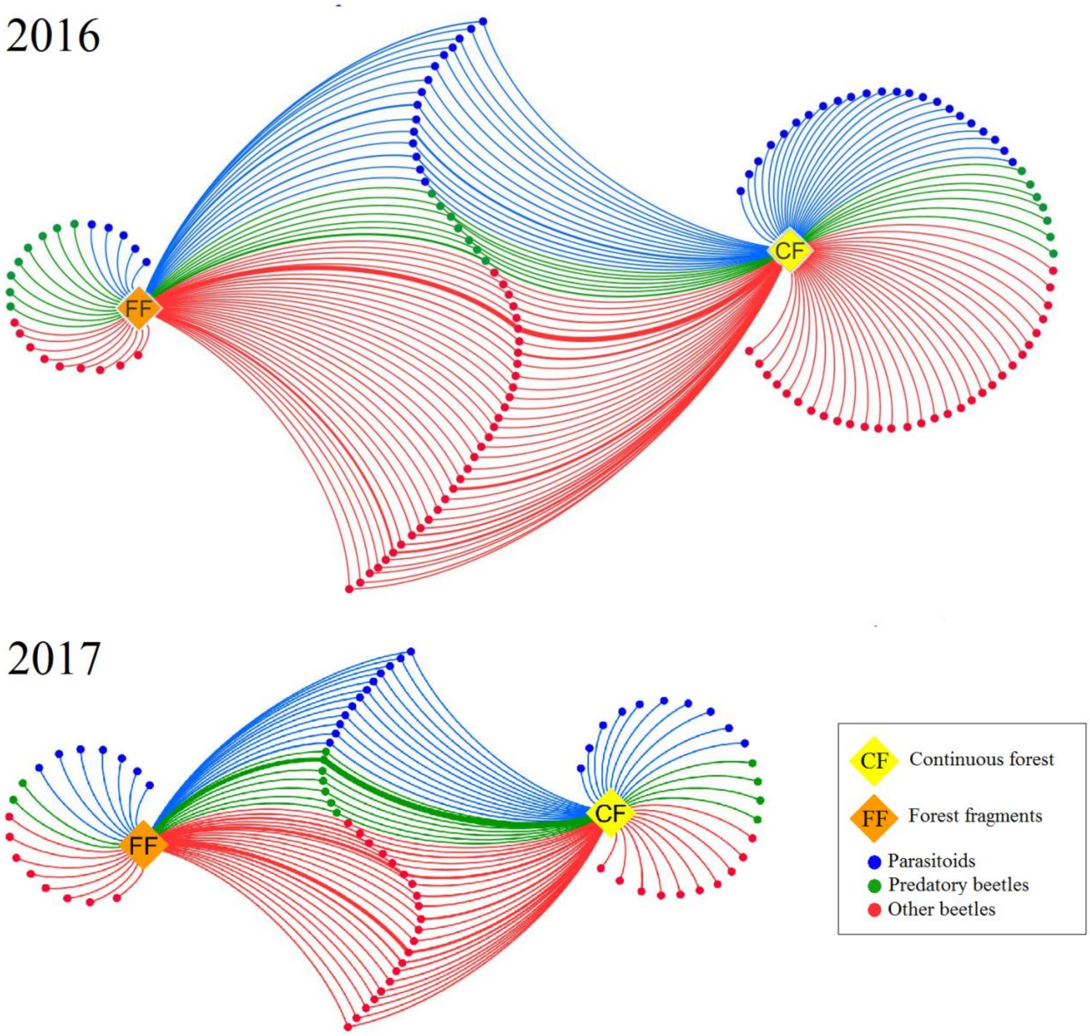


Figure 2. Distribution networks of saproxylic insect species between continuous forest (CF) and disturbed forest fragments (FF) in 2016 and 2017. Each circle represents different species of parasitoids (blue), predatory beetles (green) or other beetles (red). The width of the lines indicates the relative abundance of each species. Saproxylic beetle species belonging to families with prevailing predatory habits were considered predators (Table S1). The insects emerged from *Spondias purpurea* branches in a tropical dry forest, in Jalisco, Mexico.

There was a significant effect of treatment, and the interaction between treatment and year on the richness of saproxylic beetles, while parasitoid richness was affected by treatment and year (Table 1). Beetle richness was greater in continuous forests only in 2017, while parasitoid richness in continuous forests and in 2016 (Table 1; Fig. 3). Beetle and parasitoid abundance did not differ between treatments and was greater in 2016 compared to 2017, but we found contrasting results between beetle families/subfamilies. Cerambycidae, Scolytinae and Tenebrionidae were more abundant in continuous forests, while Lyctinae was more abundant in disturbed forest fragments. The abundance of Bostrichidae I, Bostrichidae II and Histeridae did not differ between treatments. Bostrichidae I and Scolytinae were more abundant in 2016, while Bostrichidae II, Histeridae, Lyctinae and Tenebrionidae in 2017. Cerambycidae did not differ in abundance between years. A significant effect of interaction between treatment and year was found for Scolytinae and Histeridae (Table 1; Fig 4).

Table 1. Results of Generalized Mixed Linear Models showing the effects of treatment (continuous forest and disturbed forest fragments), year and their interaction on the richness and abundance of saproxylic beetles and parasitoids. Models for beetle abundance were also performed separately per family/subfamily. Bostrichidae I refers to species with small body size and short developmental time, while Bostrichidae II refers to species with large body size and longer developmental time. The insects emerged from *Spondias purpurea* branches in a tropical dry forest, in Jalisco, Mexico. * p < 0.05.

Taxa	Explanatory Variable	AIC (H0)	AIC (H1)	p-value	Comparisons
Beetle richness	Treatment	774.83	762.58	0.0001*	Forest>Fragment
	Year	774.83	776.8	0.89	
	Treatment*Year	764.08	761.57	0.03*	
Parasitoid richness	Treatment	605.8	602.5	0.02*	Forest>Fragment
	Year	605.8	584.4	<0.0001*	2016>2017
	Treatment*Year	578.9	580.49	0.51	
Beetle abundance	Treatment	1860.3	1860.7	0.19	
	Year	1849.2	1842.1	0.003*	2016>2017
	Treatment*Year	1838.1	1840.1	0.97	
Bostrichidae I abundance	Treatment	1489.5	1491	0.47	
	Year	1489.5	1479.5	<0.0001*	2016>2017
	Treatment*Year	1487.2	1490.8	0.25	
Bostrichidae II abundance	Treatment	561.33	563.33	0.98	
	Year	561.33	537.5	<0.0001*	2017>2016
	Treatment*Year	539.45	540.97	0.49	
Cerambycidae abundance	Treatment	264.59	238.48	<0.0001*	Forest>Fragment
	Year	264.59	263.36	0.07	
	Treatment*Year	237.15	238.21	0.33	
Histeridae abundance	Treatment	1336.7	1338.7	0.96	
	Year	1336.7	1325.7	0.0003*	2017>2016
	Treatment*Year	1327.5	1321	0.004*	
Lyctinae abundance	Treatment	944.58	934.78	0.0005*	Fragment>Forest
	Year	944.58	905.88	<0.0001*	2017>2016
	Treatment*Year	894.69	895.38	0.25	
Scolytinae	Treatment	1391.4	1345.4	<0.0001*	Forest>Fragment

abundance	Year	1391.4	1379.3	0.0002*	2016>2017
	Treatment*Year	1323.7	1307.4	<0.0001*	
Tenebrionidae	Treatment	284.75	288.62	0.004*	Forest>Fragment
abundance	Year	284.75	276.85	0.002*	2017>2016
	Treatment*Year	272.6	273.35	0.26	
Parasitoid	Treatment	1158	1158.7	0.24	
abundance	Year	1158	1118.7	<0.0001*	2016>2017
	Treatment*Year	1116.7	1118.7	0.927	

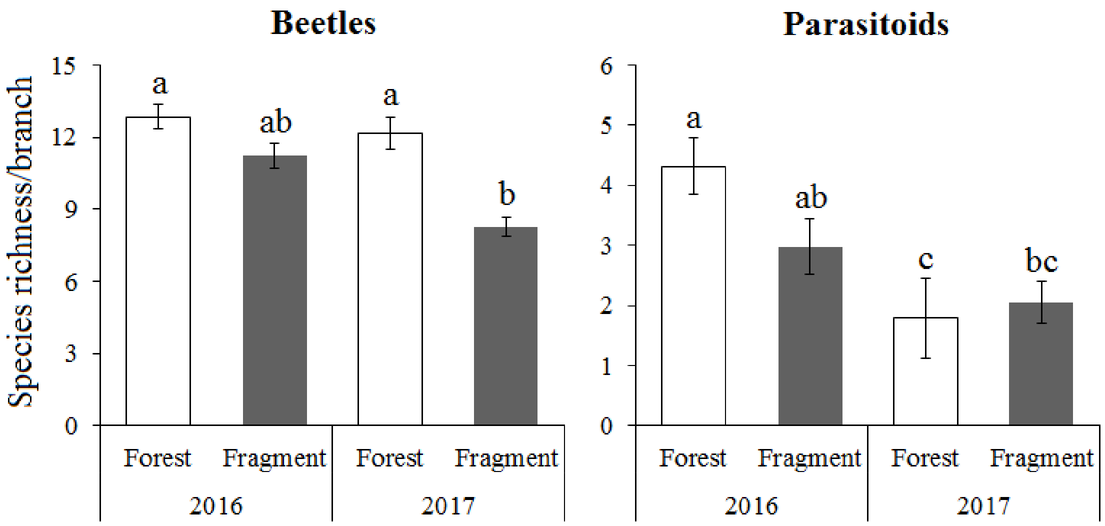


Figure 3. Mean richness (±SE) of saproxylic beetles and parasitoids between continuous forests and disturbed forest fragments in 2016 and 2017. Insects emerged from *Spondias purpurea* branches in a tropical dry forest, in Jalisco, Mexico. Different letters represent significant differences among groups ($p < 0.05$).

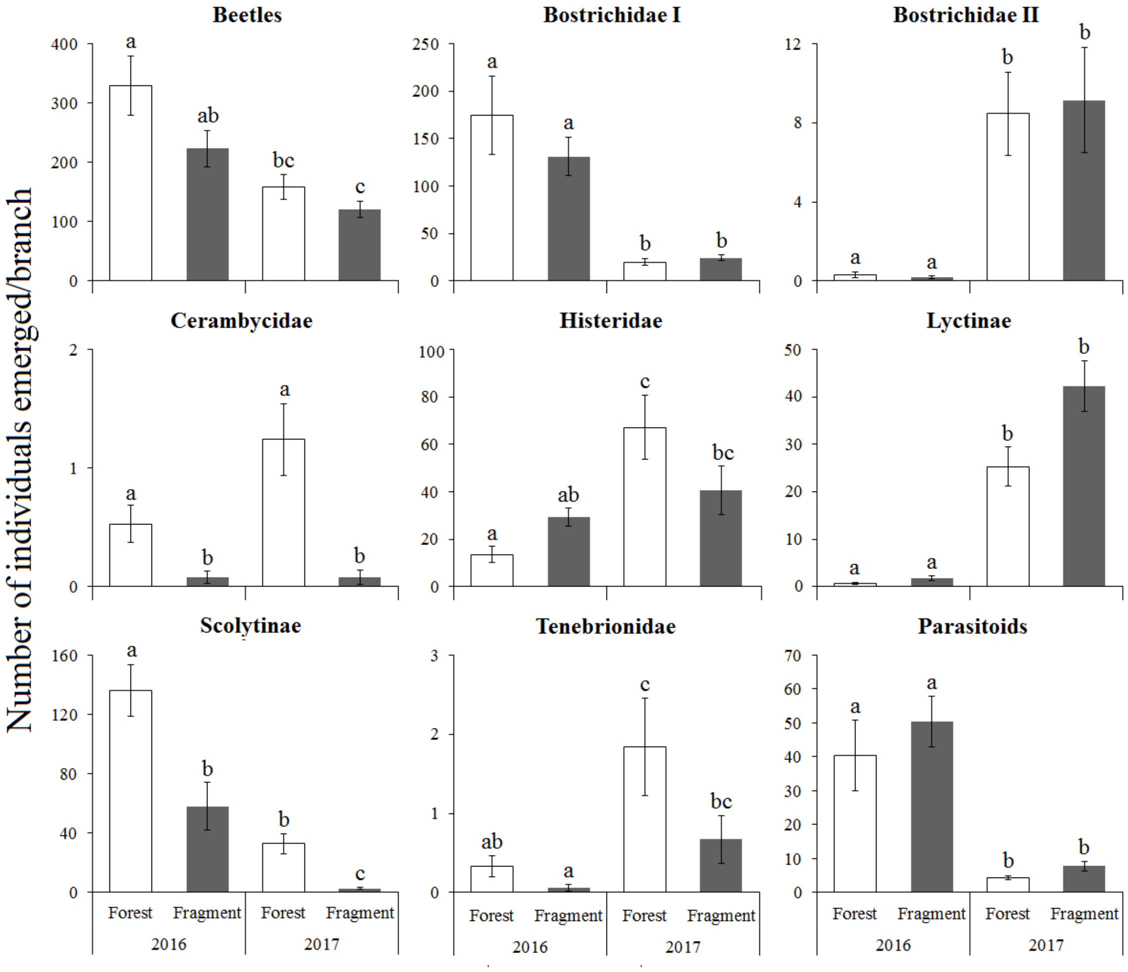


Figure 4. Mean abundance (±SE) of saproxylic beetles (total and per family/subfamily) and parasitoids between continuous forests and disturbed forest fragments in 2016 and 2017. The insects emerged from *Spondias purpurea* branches in a tropical dry forest, in Jalisco, Mexico. Bostrichidae I refers to species with small body size and short developmental time, while Bostrichidae II refers to species with large body size and longer developmental time. Different letters represent significant differences among groups ($p < 0.05$).

Partitioning of β-diversity revealed species turnover (β_{SIM}) between continuous forests and disturbed forest fragments as the main driver of the β_{SOR} diversity for saproxylic beetles and parasitoids in both sampled years (Table 2). The importance of β_{SIM} between treatments increased for both groups from 2016 to 2017 (Table 2). There was a significant effect of treatment, year and the interaction between treatment and year on the colonization frequency of rare species of beetles and parasitoids (Table 3). The rare species of beetles and parasitoids were more frequent in the continuous forest in 2016 (Fig. 5).

Table 2.Results from partitioning of β-diversity for saproxylic beetles and parasitoids are reported between treatments (continuous forests and disturbed forest fragments) for 2016 and 2017. The insects emerged from *Spondias purpurea* branches in a tropical dry forest, in Jalisco, Mexico.

Period	**Group**	β_{SIM}	β_{NES}	β_{SOR}
2016	Beetles	0.298 (73.9%)	0.105 (26.1%)	0.403
	Parasitoids	0.250 (51.8%)	0.233 (48.2%)	0.483
2017	Beetles	0.263 (88.0%)	0.036 (12.0%)	0.299
	Parasitoids	0.368 (88.9%)	0.046 (11.1%)	0.414

Table 3. Results of Generalized Mixed Linear Models showing the effects of treatment (continuous forest and disturbed forest fragments), year and their interaction on the colonization frequency of rare species of saproxylic beetles and parasitoids. The insects emerged from *Spondias purpurea* branches in a tropical dry forest, in Jalisco, Mexico. * p < 0.05.

Taxa	Explanatory Variable	AIC (H0)	AIC (H1)	p-value	Comparisons
Rare beetles	Treatment	774.83	762.58	0.03*	Forest>Fragment
	Year	181.53	174.98	0.003*	2016>2017
	Treatment*Year	170.83	167.42	0.02*	
Rare parasitoids	Treatment	135.12	131.86	0.045*	Forest>Fragment
	Year	135.12	133.12	0.02*	2016>2017
	Treatment*Year	129.09	125.91	0.02*	

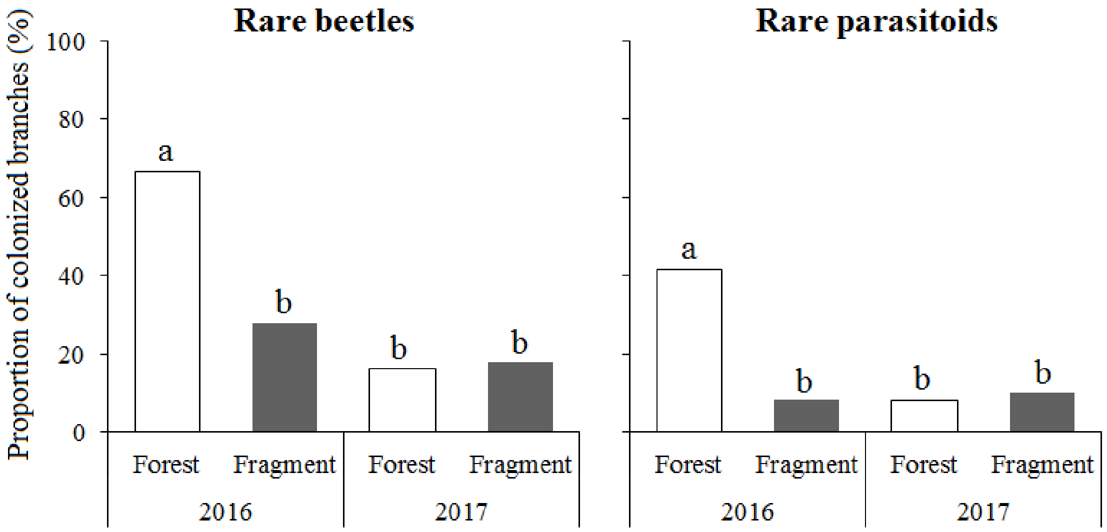


Figure 5. Branch colonization frequency by rare species of beetles and parasitoids between continuous forests and disturbed forest fragments in 2016 and 2017. The insects emerged from *Spondias purpurea* branches in a tropical dry forest, in Jalisco, Mexico. Different letters represent significant differences among groups ($p < 0.05$).

Discussion

Our results showed significant variations in the structure of the saproxylic insect community associated with the ecosystem engineering of *O. albomarginata chamela* between the sampled years, suggesting that hurricane disturbances are important density-independent factors that affect these organisms in TDFs. The richness and abundance of beetles and parasitoids were greater in the sampling soon after the passage of the Hurricane Patricia compared to the next year. However, this was not a pattern shared by all beetle families/subfamilies, with some of them showing a greater abundance in the second sampling year. Although the differences in abiotic conditions and forest structure between continuous forest and disturbed forest fragments were probably reduced by the landfall of the Hurricane Patricia, our results demonstrated that anthropogenic disturbances had important negative effects on the saproxylic insect communities associated with the ecosystem engineering of *O. albomarginata chamela*.

The general pattern for beetle abundance was mainly determined by individuals of Scolytinae and Bostrichidae I, which represented almost 70% of the all beetles sampled. Both taxa were more abundant in the first sampling year, when the artificially-engineered *S. purpurea* branches were exposed to colonization only three months after the landfall of the Hurricane Patricia. Species from Scolytinae and Bostrichidae I had a small body size with a short developmental time, and are considered early-decay species, breeding mainly in the phloem or xylem of freshly dead wood (Wood 1982). These characteristics probably allowed them to rapidly increase in abundance in the months following the hurricane (see Cap. 4), and greatly colonize the *S. purpurea* branches. On the other hand, the time between the landfall of the hurricane and our first sampling was probably not enough for species with large body size (e.g. Bostrichidae II) and/or longer developmental time (e.g. Lyctinae, Tenebrionidae) to increase their population sizes, being able to greatly colonize the *S. purpurea* branches in the second sampling year.

Parasitoid abundance presented a similar pattern between years to that found for Scolytinae and Bostrichidae I, which suggests these taxa as their main hosts. A previous study conducted in subalpine spruce forests in the Swiss Prealps after Hurricane Vivian (1990) demonstrated that the populations of bark beetles (Scolytinae) and their associated parasitoids increased and declined rather synchronously after the disturbance (Wermelinger et al. 2013). They documented that these beetles took advantage of the increased amount of freshly dead wood and produced many offspring, which immediately served as hosts for the parasitoids, while the subsequent decline was mainly determined by a reduction in dead wood quality. In our system, several factors could be acting together leading to a decrease in the abundance of early-decay species and their associated parasitoids in the second sampling year: (1) Top-down effects, predatory beetles and parasitoids are important outbreak regulators of saproxylic after windthrow disturbances (Bouget and Duelli 2004; Wermelinger et al. 2013). In our study, predatory beetles from Histeridae family were the third most abundant taxon, with a significant greater number of individuals collected in the second year; (2) Bottom-up effects, a lower availability of freshly dead wood compared to the months after the hurricane; (3) Competition by other beetles, individuals from Bostrichidae II and Lyctinae were greatly more abundant in the second year, which could be competing with the early-decay species and maintaining their populations at lower levels.

Our results also suggest that the landfall of the Hurricane Patricia had important effects on the patterns found for the saproxylic insect communities between continuous forest and disturbed forest fragments. Probably the large-scale windthrow caused by the hurricane increases dead wood amount in both treatments, resulting in the general no-significant pattern in abundance of both saproxylic beetles and parasitoids. However, continuous forests presented a greater number of exclusive species and frequency of rare species of beetles and parasitoids in the first sampling year. Since density-independent factors affect any and all populations regardless of their densities, this result suggests that continuous forests have a greater species pool of saproxylic insects compared to human-disturbed forest fragments, which were able to increase their abundance and distributions soon after the landfall of the Hurricane Patricia. In addition, differences in saproxylic insect communities between treatments would be expected to increase over time as the forest structure and associated environmental conditions more closely resembled the pre-disturbance state. This hypothesis was supported by ours results, in which the importance of species turnover for the β-diversity between treatments increased from the first to the second sampling for both saproxylic beetles and parasitoids. In addition, while a no-significant difference in beetle richness was found between treatments in the first sampling, the continuous forest presented a greater richness in the second year.

Conclusions

We concluded that hurricane disturbances are important density-independent factors that affect the saproxylic insect communities associated with the ecosystem engineering carried out by the twig-girdler beetle *O. albomarginata chamela.* The overall richness and abundance of both saproxylic beetles and parasitoids were greater in the sampling soon after the Hurricane Patricia compared to the sampling in the next year. However, the response time of the saproxylic beetles to post-hurricane conditions varied between beetle families and species traits (e.g. size and developmental time), which affected the species richness, abundance and interactions (predation, parasitism and competition) in the *S. purpurea* branches between the sampling years. Although the differences in abiotic conditions and forest structure between treatments were probably reduced by the landfall of the Hurricane Patricia, our results demonstrated that anthropogenic disturbances have negative effects on the saproxylic insect communities associated with the ecosystem engineering carried out by *O. albormaginata chamela*.

Acknowledgments

We are grateful to A. Costa, N. Calderón-Cortés, O. Carrillo, B. Bravo, R. Garcia and E. Cristobal-Pérez for field help. We thank L. Villanueva-Espino for help with map construction. We thank M. Santiago-Hernández for help with the network figure. S. Novais thank CAPES (PDSE- Sandwich Doctoral Programme Abroad) for research grants awarded during the development of this study. This study was supported by grant from Universidad Nacional Autónoma de México (PAPIIT # IN212714-3, IV200418), CONACyT (# 2009-131008 and # 155016) SAGARPA-CONACYT 291333 and CONACYT-UNAM-UAGro to LANASE (2015-LN250996, 2016-LN271449, 2017-LN280505, 2018-LN293701). Finally, we thank the Chamela-Cuixmala Biosphere Reserve for all the physical structure, logistical support and for providing rainfall data. This study was performed in partial fulfillment of the requirements of the Ph.D. degree of S. Novais in Ecology, Conservation and WildLife Management, Federal University of Minas Gerais, Brazil.

References

Arnett RHJr (2000) American Insects, a Handbook of Insects of America North of Mexico. USA, FL-Boca Raton: CRC Press. pp. 1-1024.

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography, 19, 134–143.

Bouget C, Duelli P (2004) The effects of windthrow on forest insect communities: a literature review. Biological Conservation, 118(3), 281-299.

Brin A, Bouget C, Brustel H, Jactel H (2011) Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. Journal of insect conservation, 15(5), 653-669.

Calderón-Cortes N, Quesada M, Escalera-Vazquez LH (2011) Insects as stem engineers: Interactions mediated by the twig-girdler *Oncideres albomarginata chamela* enhance arthropod diversity. PLoS One, 6, e19083.

García Oliva F, Camou A, Maass JM (2002) El clima de la region central de la costa del pacific mexicano. In: Noguera-Alderte AN, Vega-Rivera JH, Garcia-Aldrete AN, Quesada M, editors. Historia natural de Chamela: Instituto de Biología, UNAM. pp. 3–10.

Gibb H, Hilszczański J, Hjältén J, Danell K, Ball JP, Pettersson RB, Alinvi O (2008) Responses of parasitoids to saproxylic hosts and habitat: a multi-scale study using experimental logs. Oecologia, 155(1), 63-74.

Grove SJ (2002) Saproxylic insect ecology and the sustainable management of forests. Annual review of ecology and systematics, 33(1), 1-23.

Hilszczański J, Gibb H, Hjältén J, Atlegrim O, Johansson T, Pettersson RB et al (2005) Parasitoids (Hymenoptera, Ichneumonoidea) of saproxylic beetles are affected by forest successional stage and dead wood characteristics in boreal spruce forest. Biological Conservation, 126(4), 456-464.

Hjältén J, Johansson T, Alinvi O, Danell K, Ball JP, Pettersson R, et al (2007) The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. Basic and Applied Ecology, 8(4), 364-376.

Johansson T, Gibb H, Hjältén J, Pettersson RB, Hilszczański J, Alinvi O, et al (2007) The effects of substrate manipulations and forest management on predators of saproxylic beetles. Forest Ecology and Management, 242(2-3), 518-529.

Jonsell M, Hansson J, Wedmo L (2007) Diversity of saproxylic beetle species in logging residues in Sweden–comparisons between tree species and diameters. Biological conservation, 138(1-2), 89-99

Kimberlain TB, Blake ES, Cangialosi JP (2016) Hurricane Patricia (EP202015). National Hurricane Center Tropical Cyclone Report, NOAA, Miami, Florida.

Kohl M, Wiese S, Warscheid B (2011) Cytoscape: software for visualization and analysis of biological networks. In Data Mining in Proteomics, Humana Press. pp. 291-303.

Lenth RV (2017) Using lsmeans. https://cran.r-project.org/web/packages/lsmeans/vignettes/using-lsmeans.pdf

Lindhe A, Lindelöw Å, Åsenblad N (2005) Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. Biodiversity & Conservation, 14(12), 3033-3053.

Lugo AE (2008) Visible and invisible effects of hurricanes on forest ecosystems: an international review. Austral Ecology, 33(4), 368-398.

Quesada M, Sanchez-Azofeifa GA, Alvarez-Anorve M, Stoner KE, Avila-Cabadilla L, Calvo-Alvarado J, et al (2009) Succession and management of tropical dry forests in the Americas: Review and new perspectives. Forest Ecology and Management, 258(6), 1014-1024.

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Ranius T, Jansson N (2000) The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biological Conservation, 95(1), 85-94.

Schowalter TD (2012) Insect responses to major landscape-level disturbance. Annual Review of Entomology, 57, 1-20.

Seibold S, Bässler C, Brandl R, Büche B, Szallies A, Thorn S, et al (2016). Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. Journal of Applied Ecology, 53(3), 934-943.

Seibold S, Bässler C, Brandl R, Gossner MM, Thorn S, Ulyshen MD, Müller J (2015a) Experimental studies of dead-wood biodiversity—a review identifying global gaps in knowledge. Biological Conservation, 191, 139-149.

Speight MCD (1989) Saproxylic invertebrates and their conservation. Council of Europe. 79 pp.

Stenbacka F, Hjältén J, Hilszczański J, Ball JP, Gibb H, Johansson T, et al (2010) Saproxylic parasitoid (Hymenoptera, Ichneumonoidea) communities in managed boreal forest landscapes. Insect Conservation and Diversity, 3(2), 114-123.

Sverdrup-Thygeson A, Ims RA (2002) The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. Biological Conservation, 106(3), 347-357.

Ulyshen MD, Hanula JL (2009) Habitat associations of saproxylic beetles in the southeastern United States: a comparison of forest types, tree species and wood postures. Forest Ecology and Management, 257(2), 653-664.

Ulyshen MD, Pucci TM, Hanula JL (2011) The importance of forest type, tree species and wood posture to saproxylic wasp (Hymenoptera) communities in the southeastern United States. Journal of Insect Conservation, 15(4), 539-546.

Uribe-Mú CA, Quesada M (2006) Preferences, patterns and consequences of branch removal on the dioecious tropical tree Spondias purpurea (Anacardiaceae) by the insect borer *Oncideres albomarginata chamela* (Cerambycidae). Oikos, 112, 691–

697.

Wermelinger B, Obrist MK, Baur H, Jakoby O, Duelli P (2013). Synchronous rise and fall of bark beetle and parasitoid populations in windthrow areas. Agricultural and forest entomology, 15(3), 301-309.

Wood SL (1982) The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Brigham Young University. 1365 pp.

Supporting Information

Figure S1. Example of an artificially-engineered *Spondias purpurea* branch exposed to colonization by saproxylic insects in the understory of a disturbed fragment in a tropical dry forest, in Jalisco, Mexico.

Figure S2. Emergence traps for the collection of the saproxylic insects from artificially-engineered *Spondias purpurea* branches that were previously exposed in a tropical dry forest, in Jalisco, Mexico.

Table S1. Morphospecies richness (Rich.) and abundance (Abun.) of saproxylic beetles sampled in continuous forest and disturbed forest fragments in 2016 and 2017. Bostrichidae (I) refers to species with small body size and short developmental time, while Bostrichidae (II) refers to species with large body size and longer developmental time. The beetles emerged from *Spondias purpurea* branches in a tropical dry forest, in Jalisco, Mexico.

Family/Subfamily	2016				2017				Total	
	Forest		Fragment		Forest		Fragment			
	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.
Anobiidae	2	2							2	2
Anthicidae [a]			1	1					1	1
Anthribidae	8	13	2	6	1	3	1	1	6	23
Bostrichidae (I)	5	6280	5	4723	5	735	6	955	7	12693
Bostrichidae (II)	3	11	2	7	4	313	3	356	5	687
Brentidae	2	2			1	1	1	1	4	4
Bruchidae	1	1	1	1					2	2
Bubrestidae	1	2	2	11					2	13
Cantharidae [a]	2	2			1	2			2	4
Carabidae [a]					1	1			1	1
Cerambycidae	8	19	2	3	4	46	2	3	11	71
Cleridae [a]	2	3	3	5	2	3	3	6	5	17
Corylophidae	1	6	1	4					1	10
Curculionidae	3	13	2	2					4	15
Curculionidae/Scolytinae	13	4894	11	2089	8	1220	9	109	16	8312
Dermestidae	2	3							2	3
Histeridae [a]	2	486	2	1056	2	2483	2	1583	2	5608
Laemophloeidae [a]	3	7	1	1	1	6	1	1	3	15
Latridiidae			1	1					1	1
Lyctidae	2	25	2	67	2	936	2	1646	2	2674
Monotomidae [a]	1	12	1	1					1	13
Mordelidae	1	1							1	1
Mycetophagidae			1	1					1	1
Nitidulidae	1	1							1	1
Passandridae [a]			2	3	2	20	2	4	2	27
Scarabaeidae	1	2	1	1					2	3
Silvanidae	3	32	4	27	2	2	2	2	7	63
Staphylinidae [a]	5	8	4	6					6	14
Tenebrionidae	2	12	2	2	4	68	3	26	6	108
Trogossitidae [a]			1	2	2	15	1	5	2	22
Not identified	6	16	2	2					6	18
Total	80	11853	56	8022	42	5854	38	4698	114	30427

[a] Families of beetles considered predatory.

Tabla S2. Number of individuals of saproxylic parasitoid morphospecies sampled in continuous forest and disturbed forest fragments in 2016 and 2017. The parasitoids emerged from *Spondias purpurea* branches in a tropical dry forest, in Jalisco, Mexico.

Species	2016		2017		Total
	Forest	Fragment	Forest	Fragment	
Sp.1	10	318	72	204	604
Sp.2	235	879	33	60	1207
Sp.3	370	380			750
Sp.4	6	5	1		12
Sp.5	48	15	4		67
Sp.6	1016	4	1		1021
Sp.7		1			1
Sp.8	17	7	1		25
Sp.9		2	1	2	5
Sp.10	93	5	1	4	103
Sp.11	10	20	7	3	40
Sp.12	75	1	1		77
Sp.13		3	8	2	13
Sp.14	1	13	11	2	27
Sp.15	9	1			10
Sp.16	4				4
Sp.17	35	1	1		37
Sp.18	24			1	25
Sp.19	1	3			4
Sp.20	1				1
Sp.21	2	1			3
Sp.22	3		1		4
Sp.23	1				1
Sp.24	1				1
Sp.25	2		3		5
Sp.26	1				1
Sp.27	1				1
Sp.28	1			1	2
Sp.29	10				10
Sp.30	7				7
Sp.31	1				1
Sp.32	1				1
Sp.33	5				5
Sp.34	3				3
Sp.35	1				1
Sp.36	16				16
Sp.37	6				6
Sp.38	2				2
Sp.39	2		1	1	4
Sp.40	7				7
Sp.41		2			2

Sp.42		1		1	2
Sp.43	1		2		3
Sp.44				2	2
Sp.45			1	2	3
Sp.46			2	2	4
Sp.47			1	10	11
Sp.48			1	1	2
Sp.49				1	1
Sp.50				1	1
Sp.51				2	2
Sp.52			5		5
Total	2029	1662	159	302	4152

CAPÍTULO 2

ARTHROPOD FACILITATION BY WOOD-BORING BEETLES: SPATIO-TEMPORAL DISTRIBUTION MEDIATED BY A TWIG-GIRDLER ECOSYSTEM ENGINEER

Arthropod facilitation by wood-boring beetles: spatio-temporal distribution mediated by a twig-girdler ecosystem engineer

Samuel M. A. Novais[1,2], Nancy Calderón-Cortés[3], Gumersindo Sánchez-Montoya[2]& Mauricio Quesada[2,3]

[1] Laboratório de Ecologia de Insetos, Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil

[2] Laboratorio Nacional de Análisis y Síntesis Ecológica and Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, México

[3] Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, 58190, México

*Corresponding author: Mauricio Quesada, mquesada@cieco.unam.mx, Tel: +5214436893517.

Running title: Arthropod facilitation by wood-boring beetles

**O capítulo está formatado conforme as instruções de submissão da revista *Arthropod-Plant Interactions*. As figuras e tabelas estão inseridas no corpo do manuscrito para facilitar a leitura.

Abstract The twig-girdler beetle *Oncideres albomarginata chamela* (Cerambycidae: Lamiinae) detaches branches of *Spondias purpurea* (Anacardiaceae) that fall on the forest floor or remain suspended on vegetation. Many wood-boring beetles also oviposit in these branches and larval development creates cavities that are abandoned when the adults emerge. The objective of this study was to evaluate the role of wood-boring beetles as facilitators by creating new habitats for arthropods, and test for vertical stratification and temporal variation of arthropods associated with *S. purpurea* branches that were previously engineered by *O. albomarginata chamela* in a tropical dry forest (TDF) in Jalisco, Mexico. In order to determine the effects of vertical strata and seasons on branch colonization, we placed sixty branches on the forest floor (ground stratum) and sixty were placed in trees (vegetation stratum) from February to April (dry season), and from August to October 2016 (rainy season), for 240 branch samples in total. We collected 8,007 arthropods, which included 7,753 ants and other 254 arthropods from 13 different orders. We observed a greater arthropod abundance in the branches in the vegetation stratum in the dry season compared to the rainy season, while the richness and abundance of arthropods in the ground stratum were greater in the rainy season compared to the dry season. We concluded that wood-boring beetles are important habitat facilitators for arthropods, and that the vertical position of branches and the seasonal variations in TDFs differently affect the colonization of the abandoned cavities by arthropods.

Keywords. Vertical stratification, seasonality, dead wood, microhabitats, ecosystem engineering

Introduction

Recent studies have demonstrated the role of caterpillars, gall-inducing insects, bark and wood-boring beetles as facilitators for arthropods (Vieira and Romero 2013; Cornelissen et al. 2016; Harvey et al. 2016; Satoh et al. 2016; Sydenham et al. 2016; Wetzel et al. 2016; Zuo et al. 2016; Raath et al. 2017). Particularly, when adult wood-boring beetles emerge from tree hosts, they leave behind cavities where their larvae develop, thus promoting new habitats for other species to occupy (Buse et al. 2008; Zuo et al. 2016). Some groups of insects like ants and bees can take advantage of the abandoned beetle cavities in the wood for nesting (Satoh et al. 2016; Sydenham et al. 2016). However, little is known about the role of wood-boring beetles promoting new habitats for arthropod communities (but see Zuo et al. 2016).

In this work, we utilized dead wood resources provided by the twig-girdler beetle *Oncideres albomarginata chamela* (Cerambycidae: Lamiinae) in a tropical dry forest (TDF) to test for the role of wood-boring beetles as facilitators for arthropods. *O. albomarginata chamela* beetles girdle and detach branches 2–3 cm in diameter from the tree *Spondias purpurea* L.(Anacardiaceae) that fall on the forest floor or remain suspended on vegetation, and oviposit in them (Uribe-Mú and Quesada 2006). Consequently, they provide a suitable environment for secondary colonization, mainly wood-boring beetles that opportunistically oviposit in the same girdle branches (Calderón-Cortés et al. 2011). After wood-boring beetles emerge as adults, the abandoned cavities remain available for the colonization of other arthropods for at least one year until these branches degrade (S. Novais, personal observation).

The structure of the Mexican tropical dry forest where the present study was carried out is characterized by a low canopy ranging from five to ten meters high, and a dense understory due to the high abundance of shrubs and vines that together represent

39% of the flora species (Durán et al. 2002). These characteristics allow a large amount of dead wood to remain suspended in the vegetation without directly reaching the ground; broken branches of 2–20 cm in circumference that remain hanged on the live vegetation represent 29% of the dead aboveground phytomass in this ecosystem (Maass et al. 2002). Wood-boring beetle communities are significantly affected by the vertical distribution of resources from the canopy to the forest floor, changing in species composition, richness and abundance according to the position of dead wood (Ulyshen and Hanula 2009; Vodka et al. 2009; Bouget et al. 2011). However, little attention has been given to the distribution patterns of the arthropods that can be utilizing wood-boring beetle abandoned cavities (Ulyshen et al. 2011).

Seasonal variations in TDFs along the year change the availability of resources and microhabitats between forest strata. Most trees shed their leaves at the beginning of the dry season, and a rapid budding of new leaves occur after the first rains at the beginning of the wet season (Lopezaraiza-Mikel et al. 2013; Pezzini et al. 2014). During dry season, there is an increase in ground arthropods due to the greater amount of litterfall (Palacios-Vargas et al. 2007), while during the rainy season, there is an increase in abundance and diversity of arboreal arthropods associated to the new foliage growth (Vasconcelloset al. 2010; Kishimoto-Yamada and Itioka 2015). Therefore, these seasonal changes may differentially affect arthropod colonization of the abandoned branch cavities left by the wood-boring beetles along the vertical strata of the forest.

The objective of this study was to evaluate the role of wood-boring beetles as facilitators by creating new habitats for arthropods. We tested for temporal variation and vertical stratification of the arthropod community associated to the abandoned branches of the tree *S. purpurea* that were previously engineered by *O. albomarginata chamela* in a TDF in Jalisco, Mexico. We tested the following predictions: i. richness, abundance and colonization frequency of arthropods in the detached branches in the dry season are greater in the ground stratum, whereas for the rainy season are greater in the vegetation stratum; ii. richness, abundance and colonization frequency of arthropods in the detached branches in the vegetation stratum are greater in the rainy season, whereas for the ground stratum are greater in the dry season.

Material and methods

Study area and sampling design

This study was carried in the Chamela-Cuixmala Biosphere Reserve (CCBR, 19º30’N, 105º03’W), in Jalisco, Mexico. The vegetation within the 13,142 ha of the reserve consists primarily of tropical dry forest with a mean annual rainfall of 748 mm, and a dry season that extends from November to June (García-Oliva et al. 2002).

During February and March 2015, we collected 80 branches that were detached and colonized by *O. albomarginata chamela*, and also colonized by other secondary wood-boring beetles. All branches were marked and enclosed in mesh bags (<0.5 mm mesh size), placed in an open room at the study site, and maintained at local environmental conditions until January 2016 for the emergence of all associated arthropods (see Calderón-Cortés et al. 2011). Larval development of the beetles led to a partial fragmentation of the branches. In February (dry season) and August (rainy season) 2016, we selected 120 sub-samples of branch parts, 240 sub-samples of the original detached branches (hereinafter referred to as "branches"). These branches contained at least one entrance/emergence cavity made by a beetle. To experimentally test the colonization of empty detached branches by the arthropod community, we placed four branches on the forest floor (ground stratum) at least 5 meters apart from each other, and hanged another four branches in trees (vegetation stratum) under the canopy of 15 individuals of *S. purpurea* at least 30 meters apart from each other. Each of the four hanged branches was located in four trees, without canopy connection, at a height ranging from 1.5 to 2.0 m. A total of 60 branch samples per stratum (vegetation and ground), and 120 branches per season were used (dry and rainy; Fig 1). The branches remained in the field for two months, to allow colonization and the establishment of the arthropod community (Zuo et al. 2016). In April and October 2016, we collected the exposed branches and immediately placed them in individual fine mesh bags and transported them to the laboratory.

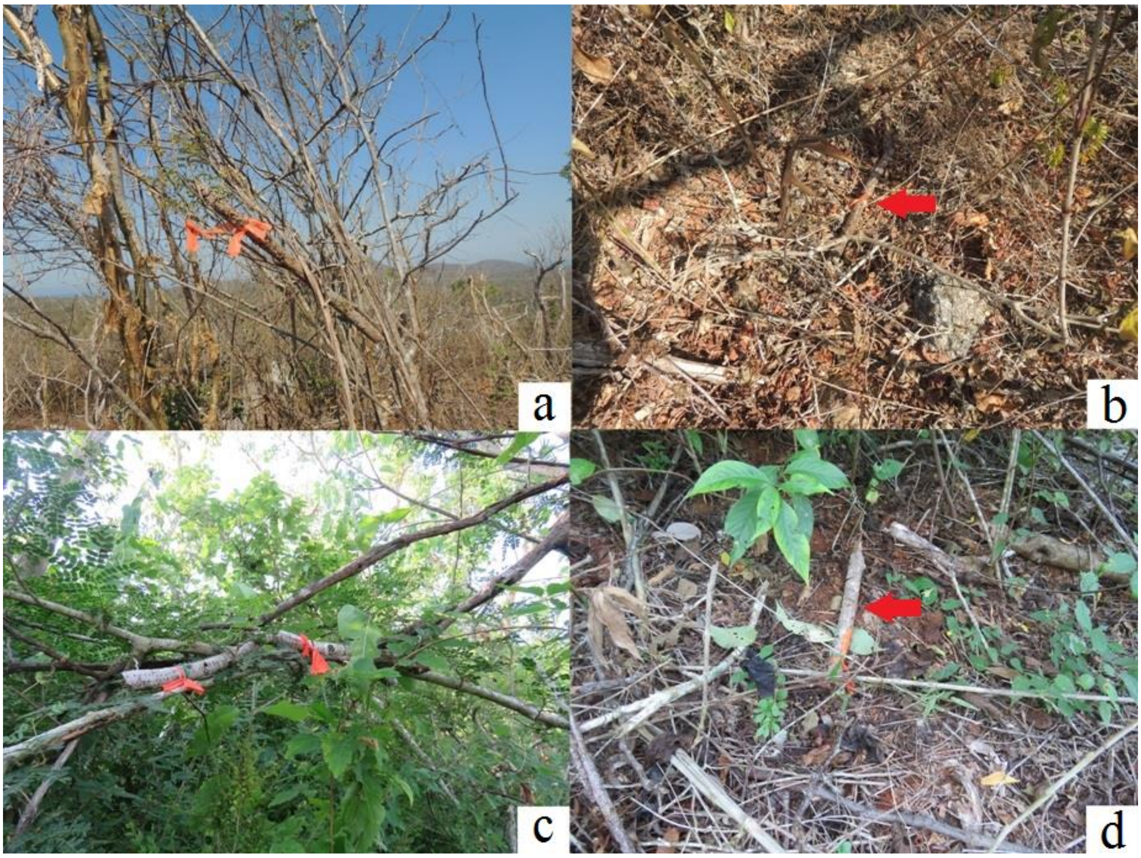


Fig. 1. Examples of *Spondias purpurea* branch samples that were previously engineering by *Oncideres albomarginata chamela* and placed in two vertical strata and in different seasons in a tropical dry forest, in Jalisco, Mexico. Vegetation stratum in dry season (A), ground stratum in dry season (B), vegetation stratum in rainy season (C) and ground stratum in rainy season (D).

All collected branches from the field were carefully opened in a large tray, tall enough to prevent arthropods from escaping. Arthropods were transferred to vials with 70% ethanol for further taxonomic identification at order or family level (García-Aldrete and Ayala 2004). Mesofauna such as springtails and mites was not considered in this study. Termites colonizing the branches as food resources were also not considered because they were not using the abandoned wood-boring beetle cavities. Richness, abundance and colonization frequency of arthropods per branch were determined.

Statistical analysis

Generalized Linear Mixed Models (GLMMs) were used to determine the occurrence of temporal variation and vertical stratification on arthropod community. Richness, abundance and colonization frequency of arthropods were used as response variables, whereas seasons (dry and rainy) and vertical strata (vegetation and ground) were used as explanatory variables. Ant individuals were not considered for abundance analysis due to the social characteristic of the group. The Akaike Information Criterion (AIC) was used to rank the models, since it represents the uncertainty of the model, a lower value of the AIC represents the more parsimonious model. When significant differences were observed between sample periods and strata, the data were submitted to contrast analysis by aggregating levels (Crawley, 2013). The package "*lsmeans*" was used for *a posteriori* comparisons (Lenth et al. 2017). All analyses were performed using R software (R Core Team 2016).

Results

A total of 8,007 adult arthropods from 93 morphospecies were sampled in the 240 *S. purpurea* branches (S1 Appendix). Spiders were the most diverse group (41 species) followed by ants (14; Fig. 2). Ants were the most abundant group, totaling 7,753 individuals. Among the 254 non-social arthropods sampled, most individuals for all strata and seasons were generalist predators, which include mainly spiders, followed by centipedes, pseudoscorpiones and scorpions (59-100%; Fig. 3; S1 Appendix).

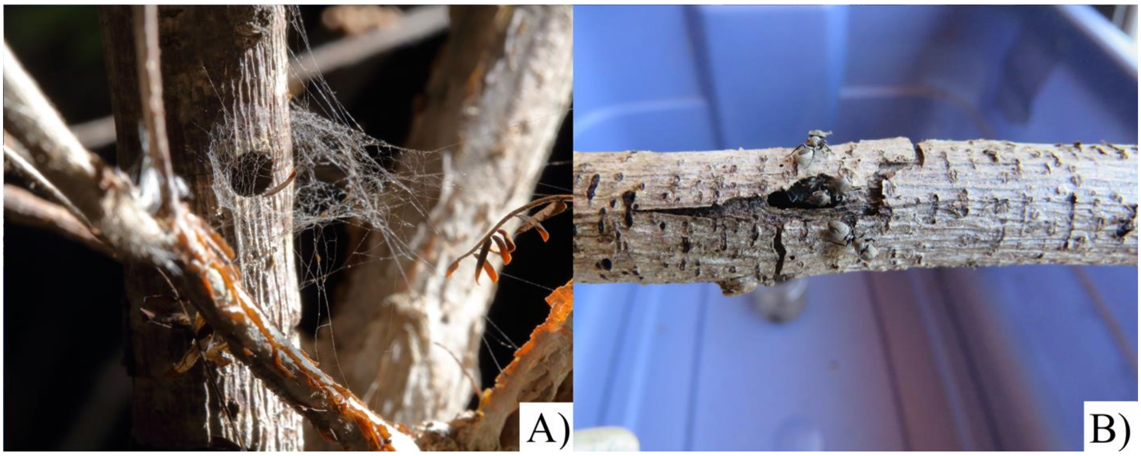


Fig. 2. Spider (A) and ants (B) colonizing cavities abandoned by wood-boring beetles in *Spondias purpurea* branches that were previously engineered by *Oncideres albomarginata chamela* in a tropical dry forest, in Jalisco, Mexico. Photos by J. C. Mata and S. Novais, respectively.

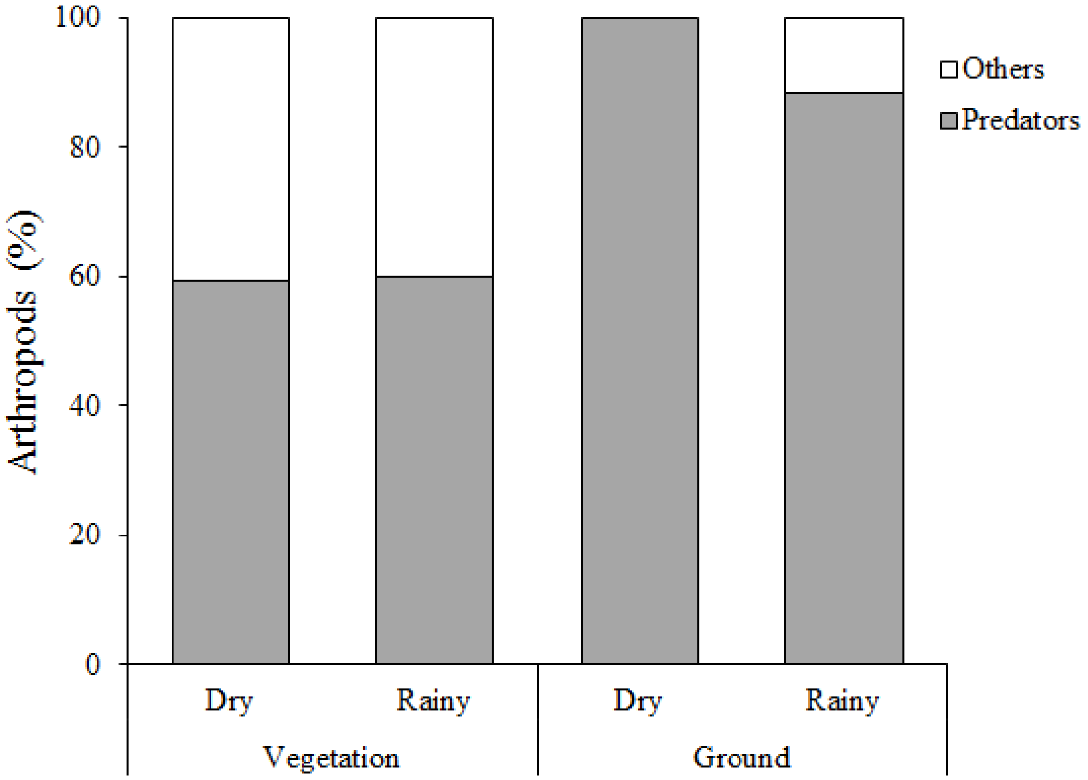


Fig. 3. Percentage of predatory arthropods in the abandoned cavities left by wood-boring beetles in *Spondias purpurea* branches that were previously engineered by *Oncideres albomarginata chamela* sampled in two vertical strata and in different seasons in a tropical dry forest, in Jalisco, Mexico.

Arthropod richness, abundance and colonization frequency in the abandoned branches cavities varied significantly between strata in time (Table 1). For the dry season, we observed a greater arthropod richness and abundance in the branches in the vegetation stratum compared to the ground stratum. For the rainy season, arthropod richness was greater in the vegetation stratum, whereas abundance was similar between strata (Fig. 4). Branch colonization was greater in the vegetation stratum compared to ground stratum in both seasons: 87%*versus* 5% in dry season and 77% *versus* 52% in the rainy season.

Arthropod richness in the vegetation stratum did not differ significantly between seasons, while abundance was greater in the dry season compared to the rainy season. For the ground stratum, arthropod richness and abundance were greater in the rainy season (Fig. 4). Branch colonization did not differ significantly in the vegetation stratum between seasons (87% in the dry and 77% in the rainy season), while for the ground stratum was greater in the rainy (52%) compared to the dry season (5%).

Table 1. Results of Generalized Linear Mixed Models showing spatio-temporal variation in richness, abundance and colonization frequency of arthropods in the abandoned cavities left by wood-boring beetles in *Spondias purpurea* branches that were previously engineered by *Oncideres albomarginata chamela* in a tropical dry forest, in Jalisco, Mexico.

Response variable	Explanatory variable	Error distribution	AIC (H1)	AIC (H0)	P
Arthropod richness	Season*Strata	Negative Binomial	564.26	600.7	<0.0001
	Season		673.87	671.9	0.92
	Strata		599.02	671.9	<0.0001
Arthropod abundance	Season*Strata	Negative Binomial	629.33	663.8	<0.0001
	Season		686.17	684.3	0.76
	Strata		662.81	684.3	<0.0001
Colonization frequency	Season*Strata	Binomial	229.05	250.5	<0.0001
	Season		423.37	424.2	0.09
	Strata		389.61	424.2	<0.0001

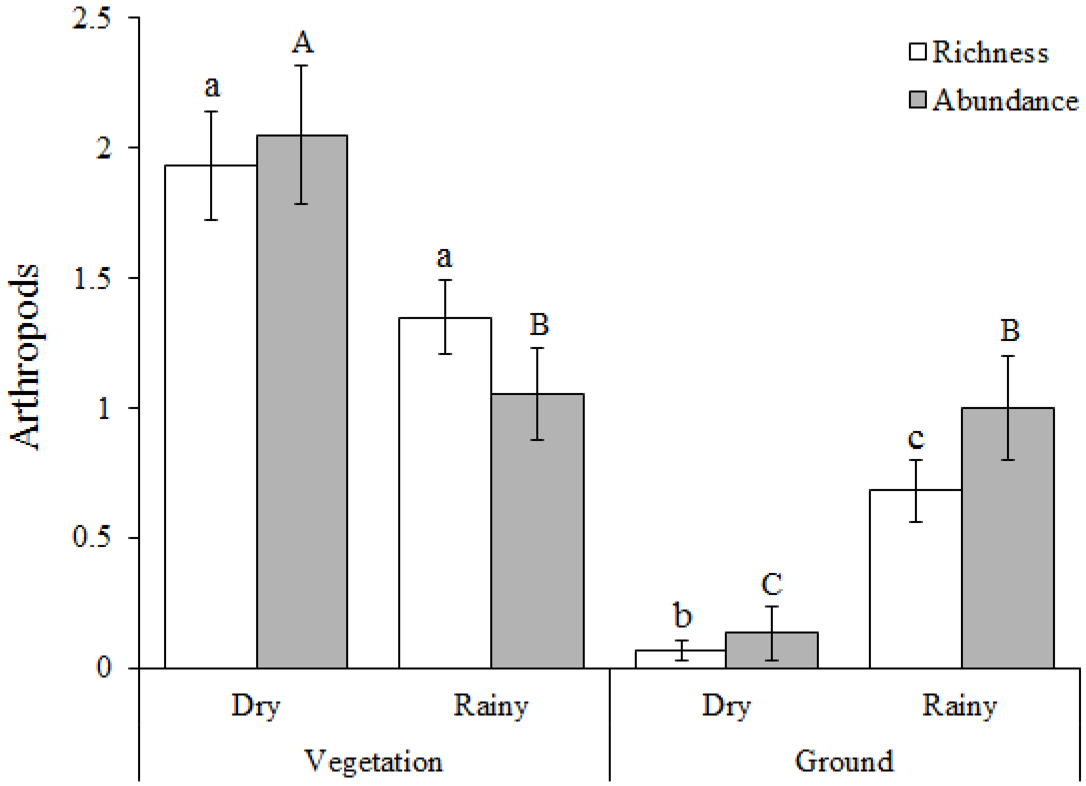


Fig. 4. Spatio-temporal variation in arthropod richness and abundance (mean ± SE)in the abandoned cavities left by wood-boring beetles in *Spondias purpurea* branches that were previously engineered by *Oncideres albomarginata chamela* in a tropical dry forest, in Jalisco, Mexico. Different letters represent significant differences among

groups ($p < 0.05$).

Discussion

The twig-girdler beetle *O. albomarginata chamela* is an important ecosystem engineer that detaches *S. purpurea* branches and provides a suitable environment for secondary colonization, mainly for other wood-boring beetle species, which depends of the detached branches to develop its offspring (Calderón-Cortés et al. 2011). Our results showed that this ecosystem engineering had extended indirect effects on the arthropod community, in which wood-boring beetles are important habitat facilitators for arthropods. However, contrary to expected, in the dry season a greater richness, abundance and colonization frequency of arthropods were found in the branches in the vegetation compared to ground stratum. Moreover, also contrary to expected, arthropod abundance in the vegetation stratum was greater in the dry season compared to rainy season, whereas for the ground stratum an opposite pattern was found for richness and abundance.

Previous studies showed that arthropod richness and abundance are positively affected by increasing habitat structure (Tews et al. 2004; Langellotto and Denno 2004; Leal et al. 2016). However, we observed that arthropod abundance in the abandoned branch cavities was greater when the habitats were structurally simpler, for both vegetation and ground strata. During dry season in the studied TDF, most trees shed their leaves, and consequently, the forest floor accumulates a large amount of litterfall (Lopezaraiza-Mikel et al. 2013). Therefore, it is possible that the increase of available microhabitats (i.e., refuges or nesting sites) for the ground arthropod community negatively affects the colonization of *S. purpurea* branches in this season. For the vegetation stratum, an opposite mechanism must be acting in the dry season; where a reduction of available microhabitats for arthropods caused by leaf fall may have contributed to a greater colonization rate of the branches in this stratum. During the rainy season, when tree species recovered their leaves, the amount of available microhabitats changes between vegetation and ground strata, since a complex architecture of tree foliage increases the availability of potential microhabitats in the vegetation stratum; meanwhile the quickly decomposition of the litterfall in this season leads to a decrease of microhabitats in the ground stratum (Anaya et al. 2012).

Similarly to our results for the vegetation stratum, Vieira and Romero (2013) analyzing the role of leaf-rolling caterpillars as facilitators for arboreal arthropod communities, found that the magnitude of the engineering effect on arthropod abundance was greater in the dry season than in the rainy season. These authors proposed that leaf shelters could function as favorable refuges against drought, attracting more arthropods during periods of low rainfall. This mechanism may also contribute to the greater abundance of arthropods in the abandoned cavities of *S. purpurea* branches in the vegetation stratum during the dry season.

Most studies that evaluate the effects of ecosystem engineering by insects on the structure of arthropod communities have focused on species that directly benefit from the habitat modifications (Cornelissen et al. 2016, Harvey et al. 2016; Satoh et al. 2016; Sydenham et al. 2016; Zuo et al. 2016). However, ecosystem engineering could initiate cascades of interactions affecting indirectly the abundance and diversity of communities that do not directly interact with the habitat modifications (Sanders et al. 2014; Wetzel et al. 2016). For example, *Trogon citreolus* is a species of bird present in our study area that builds its nests in abandoned arboreal termitaria. After *T. citreolus* leave their nests, the cavities are reused by other organisms, such as mammals and arthropods. This implies that *T. citreolus* provides a critical role in creating necessary cavities for many organisms in a space that was initially modified by termites (Valdivia-Hoeflich et al. 2005). In our study, we also demonstrated a “facilitation in cascade”, in which the twig-girdler beetle ecosystem engineer *O. albomarginata chamela* acts as facilitator for wood-boring beetles (Calderón-Cortes et al. 2011) that provide cavities that are reused by a different arthropod community that do not directly interact with the initial habitat modifications.

In addition to positively affecting the structure of arthropod communities, insect ecosystem engineers can positively affect the abundance of species of higher trophic levels, and consequently, enhance trophic interactions (Calderón-Corteset al. 2011; Sanders et al. 2014; Wetzel et al.2016). In our study, for all strata and seasons, most non-social arthropods utilizing the abandoned branch cavities were generalist predators, mainly spiders, suggesting that this habitat facilitation by wood-boring beetles also enhance further trophic interactions. We also highlight that most individuals of generalist predators was found in the branches in the vegetation stratum, as well as all sampled ants (S1 Appendix). Although often overlooked, dead woodthat remain hanged on the live vegetation represent a significant phytomass component in the upper forest strata (Mass et al. 2002; Nordén et al. 2004), and are an important resource for wood-boring beetle communities (Bouget et al. 2011). Our results demonstrated that these resources are also important for the arboreal arthropod community that utilizes the cavities left by wood-boring beetles, mainly predatory arthropods and ants. The importance of habitat facilitation by wood-boring beetles for arboreal ant communities was discussed in another manuscript (Novais et al. 2017).

We conclude that the ecosystem engineering carried out by the twig-girdler *O. albomarginata chamela* besides having positive direct effects on the diversity of wood-boring beetles in *S. purpurea* branches (Calderón-Cortés et al. 2011), had extended indirect effects on the arthropod community. Our study showed a case of “facilitation in cascade”, in which the wood-boring beetles that colonized the branches detached by the twig-girdler *O. albomarginata chamela* act as habitat facilitators for a different arthropod community that do not directly interact with the initial habitat modifications. Seasonal variations are important factors that affected arthropod colonization in the abandoned branch cavities between vertical strata in the TDF studied. Generalist predators, mainly spiders, widely used the abandoned cavities as refuges and nesting sites, which imply that habitat facilitation by wood-boring beetles also enhance trophic interactions. Finally, we highlight the importance of dead wood hanged on the live vegetation as important habitats for arboreal arthropod communities that utilize the abandoned cavities left by wood-boring beetles, mainly predatory arthropods and ants.

Acknowledgments

We are grateful to A. Costa, L. Macedo-Reis and E. Cristobal-Perez for field help. S. Novais thank the CAPES (PDSE- Sandwich Doctoral Programme Abroad) for research grants awarded during the development of this study. This study was supported by grant from Universidad Nacional Autónoma de México (Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (PAPIIT) # IN212714-3 to MQ, and IA202514 to NCC), Consejo Nacional de Ciencia y Tecnologia (CONACYT # 2009-131008 and # 155016 to MQ, and CB-2015-253420 to NCC) and CONACYT-UNAM-UAGro to LANASE (2015-LN250996, 2016-LN271449and 2017-LN280505). Finally, we thank the Chamela-Cuixmala Biosphere Reserve for all the physical structure and logistical support. This study was performed in partial fulfillment of the requirements of the Ph.D. degree of SMAN in Ecology, Conservation and Wild Life Management, Federal University of Minas Gerais, Brazil.

References

Anaya CA, Jaramillo VJ, Martínez-Yrízar A, García-Oliva F (2012) Large rainfall pulses control litter decomposition in a tropical dry forest: evidence from an 8-year study. Ecosystems 15(4): 652-663

Bouget C, Brin A, Brustel H (2011) Exploring the “last biotic frontier”: Are temperate forest canopies special for saproxylic beetles? For Ecol Manage 261: 211–220

Buse J, Ranius T, Assmann T (2008) An Endangered Longhorn Beetle Associated with Old Oaks and Its Possible Role as an Ecosystem Engineer. Conserv Biol 22(2): 329–337

Calderón-Cortes N, Quesada M, Escalera-Vazquez LH (2011) Insects as Stem Engineers: Interactions Mediated by the Twig-Girdler *Oncideres albomarginata chamela* Enhance Arthropod Diversity. PloS ONE 6:e19083

Cornelissen T, Cintra F, Santos JC (2016) Shelter-building insects and their role as ecosystem engineers. Neotrop Entomol 45: 1–12

Crawley MJ (2013) The R Book. Willey, New York

Durán E, Balvanera P, Lott E, Segura G, Pérez-Jiménez A, Islas A, Franco M (2002) Estructura, composición y dinámica de la vegetación. In: Noguera-Alderte AN, Vega-Rivera JH, Garcia-Aldrete AN, Quesada M (ed)Historia natural de Chamela. Instituto de Biología, UNAM, México,pp 443-472

García-Aldrete NA, Ayala R (2004) Artrópodos de Chamela. Instituto de Biología, UNAM, México

García-Oliva F, Camou A, Maass JM (2002) El clima de la región central de la costa Del Pacífico mexicano. In: Noguera-Alderte AN, Vega-Rivera JH, Garcia-Aldrete AN, Quesada M (ed) Historia natural de Chamela. Instituto de Biología, UNAM, México, pp 3–10

Harvey JA, Ode PJ, Malcicka M, Gols R (2016) Short-term seasonal habitat facilitation mediated by an insect herbivore. Basic Appl Ecol17(5): 447-454

Kishimoto-Yamada K, Itioka T (2015)How much have we learned about seasonality in tropical insect abundance since Wolda (1988)? Entomol Sci 18: 407-419.

Langellotto GA, Denno RF (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia 139: 1-10

Leal CRO, Silva JO, Sousa-Souto L, Neves FS (2016) Vegetation structure determines insect herbivore diversity in seasonally dry tropical forests. J Insect Conserv 20(6): 979-988

Lenth RV(2017) Using lsmeans. https://cran.r-project.org/web/packages/lsmeans/vignettes/using-lsmeans.pdf

Lopezaraiza-Mikel M, Álvarez-Añorve M, Ávila-Cabadilla L, Martén-Rodríguez S, Calvo-Alvarado J, Espírito-Santo MMet al (2013) Phenological Patterns of Tropical Dry Forests along Latitudinal and Successional Gradients in the Neotropics. In: Sanchez-Azofeifa A, Powers JS, Fernandes GW, Quesada M (ed)Tropical Dry Forests in the Americas: Ecology, Conservation, and Management. CRC Press, pp101-128

Palacios-Vargas JG, Castaño-Meneses G, Gómez-Anaya JA, Martínez-Yrizar A, Mejía-Recamier BE, Martínez-Sánchez J (2007) Litter and soil arthropods diversity and density in a tropical dry forest ecosystem in Western Mexico. Biodivers Conserv 16(13): 3703-3717.

Maass MJ, Martinez-Irizar A, Patino C, Sarukhan J (2002) Distribution and annual net accumulation of above-ground dead phytomass and its influence on throughfall quality in a Mexican tropical deciduous forest ecosystem. J Trop Ecol 18: 821–834

Nordén B, Götmark F, Tönnberg M, Ryberg M (2004) Dead wood in seminatural temperate broadleaved woodland: contribution of coarse and fine dead wood, attached dead wood and stumps. For EcolManage 194: 235–248

Pezzini FF, Ranieri BDI, Brandão DO, Fernandes GW, Quesada M, Espírito-Santo MM, Jacobi CM (2014) Changes in tree phenology along natural regeneration in a seasonally dry tropical forest. Plant Biosyst 148(5): 1-10

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Raath MJ, le Roux PC, Veldtman R, Campbell H, Buyens IPR, Greve M (2017) Empty Gonometa postica cocoons function as nest sites and shelters for arboreal ants. J Arid Environ 144: 42–47

Sanders D, Jones CG, Thébault E, Bouma TJ, van der Heide T, van Belzen J, Barot S (2014) Integrating ecosystem engineering and food webs. Oikos 123(5): 513-524

Satoh T, Yoshida T, Koyama S, Yamagami A, Takata M, Kurachi T et al (2016) Resource partitioning based on body size contributes to the species diversity of wood-boring beetles and arboreal nesting ants. Insect Conserv Divers 9(1): 4-12

Sydenham MA, Häusler LD, Moe SR, Eldegard K (2016) Inter-assemblage facilitation: the functional diversity of cavity-producing beetles drives the size diversity of cavity-nesting bees. Ecol Evol 6(2): 412-425

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31(1): 79-92.

Vasconcellos A, Andreazze R, Almeida AM, Araujo HFP, Oliveira ES, Oliveira U (2010)Seasonality of insects in the semi-arid Caatinga of northeastern Brazil. Rev Bras Entomol 54: 471-476.

Valdivia-Hoeflich T, Vega Rivera JH, Stoner KE (2005) The Citreoline Trogon as an Ecosystem Engineer. Biotropica37(3): 465-467

Vieira C, Romero GQ (2013) Ecosystem engineers on plants: indirect facilitation of arthropod communities by leaf-rollers at different scales. Ecology 94(7): 1510-1518

Vodka S, Konvicka M, Cizek L (2009) Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. J Insect Conserv 13: 553–562

Ulyshen MD (2011) Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. For EcolManage 261(9): 1479-1489

Ulyshen MD, Hanula JL (2009) Habitat associations of saproxylic beetles in the southeastern United States: A comparison of forest types, tree species and wood postures. For EcolManage 257: 653–664

Uribe-Mú CA, Quesada, M. (2006) Preferences, patterns and consequences of branch removal on the dioecious tropical tree *Spondias purpurea* (Anacardiaceae) by the insect borer *Oncideres albomarginata chamela* (Cerambycidae). Oikos 112: 691-697

Wetzel WC, Screen RM, Li I, McKenzie J, Phillips KA, Cruz Met al (2016) Ecosystem engineering by a gall-forming wasp indirectly suppresses diversity and density of herbivores on oak trees. Ecology 97(2): 427-438

Zuo J, Cornelissen JH, Hefting MM, Sass-Klaassen U, van Logtestijn RS, van Hal J et al(2016) The (w) hole story: Facilitation of dead wood fauna by bark beetles? Soil Biol Biochem 95: 70-77

Supporting Information

S1 APPENDIX. Spatio-temporal variation in arthropod richness (Rich.), abundance (Abund.) and colonization frequency (Freq.) in the abandoned cavities left by wood-boring beetles in *Spondias purpurea* branches that were previously engineered by *Oncideres albomarginata chamela* in a tropical dry forest, in Jalisco, Mexico.

S1 Appendix.Spatio-temporal variation in arthropod richness (Rich.), abundance (Abund.) and colonization frequency (Freq.) in the abandoned cavities left by wood-boring beetles in *Spondias purpurea* branches that were previously engineered by *Oncideres albomarginata chamela* in a tropical dry forest, in Jalisco, Mexico.

Taxon	Vegetation						Ground						Total	
	Dry			Rainy			Dry			Rainy				
(Class/Order/Family)	Rich.	Abund.	Freq.	Rich.	Abund.	Freq.	Rich.	Abund.	Freq.	Rich.	Abund.	Freq.	Rich.	Abund.
Arachnida/Araneae[a]	19	33	25 (42%)	15	25	17(28%)	3	7	3 (5%)	12	50	25(42%)	41	115
Insecta/Blattodea	2	7	7 (12%)	1	5	4 (7%)							3	12
Insecta/Coleoptera	5	13	6 (10%)	3	8	7 (12%)							8	21
Chilopoda/Geophilomorpha[a]	4	32	19 (32%)	3	3	3 (5%)				2	2	2 (3%)	6	37
Arachnida/Scorpiones[a]	1	1	1 (2%)	1	5	4 (7%)							1	6
Insecta/Orthoptera/Gryllidae	4	23	15 (25%)	3	7	5 (8%)							6	30
Arachnida/Pseudoscorpiones[a]	3	6	6 (10%)	2	6	4 (7%)	1	1	1 (2%)	1	1	1 (2%)	4	14
Arachnida/Solifugae[a]	1	1	1 (2%)										1	1
Malacostraca/Isopoda	1	7	6 (10%)										1	7
Insecta/Hymenoptera/Formicidae	10	4315[b]	20 (33%)	11	3438[b]	25 (42%)							14	7753[b]
Insecta/Hymenoptera/Other				1	2	1 (2%)				2	2	2 (3%)	3	4
Diplopoda				1	2	2 (3%)				1	2	2 (3%)	2	4
Insecta/Heteroptera										2	2	2 (3%)	2	2
Arachnida/Opiliones										1	1	1 (2%)	1	1
Total	50	4438	52 (87%)	39	3501	46 (77%)	3	8	3 (5%)	21	60	28 (52%)	93	8007

[a] Taxa considered as generalist predatory arthropods

[b] Ants were not considered for abundance analysis.

CAPÍTULO 3

WOOD-BORING BEETLES PROMOTE ANT NEST CAVITIES: EXTENDED EFFECTS OF A TWIG-GIRDLER ECOSYSTEM ENGINEER

Wood-boring beetles promote ant nest cavities: extended effects of a twig-girdler ecosystem engineer

Samuel M. A. Novais[a,b,c], Wesley D. DaRocha[d,e], Nancy Calderón-Cortés[f] and Mauricio Quesada[a,b,c,f *]

[a]Laboratório de Ecologia de Insetos, Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, 31270-901, Brazil

[b] Laboratorio Nacional de Análisis y Síntesis Ecológica (LANASE), Universidad Nacional Autónoma de México ,Morelia, Michoacán, 58190, México

[c] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, 58190, México

[d]Departamento de Ciências Agrárias e Ambientais – DCAA/PRODEMA, Universidade Estadual de Santa Cruz – UESC, Ilhéus, Bahia, 45662-900, Brazil

[e] Laboratório de Mirmecologia, Centro de Pesquisa do Cacau, Itabuna, Bahia, 45600-900, Brazil

[f] Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, 58190, México

*Corresponding author. Tel.: +52 4436893517.
E-mail address: mquesada@cieco.unam.mx.

**O capítulo está formatado conforme as instruções de submissão da revista *Basic and Applied Ecology*. As figuras e tabelas estão inseridas no corpo do manuscrito para facilitar a leitura.

Abstract

Oncideres albomarginata chamela (Cerambycidae: Lamiinae) is a stem-boring beetle that girdles branches of *Spondias purpurea* (Anacardiaceae) for oviposition. Many beetles opportunistically oviposit in these branches and larvae create cavities that are abandoned when the adults emerge. Our objective was to evaluate the role of wood-boring beetles in promoting ant nest cavities mediated by a twig-girdler engineer. We collected 120 abandoned branches that had been detached by *O. albomarginata chamela*, in a tropical dry forest, in Jalisco, Mexico. Sixty abandoned branches were placed in trees from February to April, and another sixty from August to October 2016. In order to test the effects of nest characteristics on ant species, we measured the diameter of each branch and the diameter of the ant nest entrance as explanatory variables, whereas the size of ant species was used as response variable. We found 49 nests of arboreal ants from 14 species. The body size of the ants nesting in the abandoned branches was positively correlated with the diameter of the nest entrance. Ants used abandoned branches mainly as polydomic nests. Our result confirms that ants partitioning resources according to the size of entrance holes made by wood-boring beetles in dead wood. Polydomic nests have been reported as a strategy to promote the colonization of new nesting sites and the reduction of intraspecific competition. We conclude that the ecosystem engineering carried out by the twig-girdler *O. albomarginata chamela* had extended effects on the arboreal ant community, that takes advantage of the cavities abandoned by wood-boring beetles for nesting, especially for polydomic nests.

Keywords: Cerambycidae;dead wood; ecosystem engineering; resource availability; species coexistence; twig-dwelling ants

Introduction

Recent studies have demonstrated that non-trophic interactions mediated by ecosystem engineering are relevant ecological drivers of diversity (Jones et al. 2010; Romero, Gonçalves-Souza, Vieira, & Koricheva 2014; Sanders et al. 2014). Ecosystem engineers directly or indirectly modify habitats and increase resource availability for other organisms (Jones, Lawton, & Shachak 1994). In terrestrial ecosystems many species of herbivorous insects such as leaf rollers, gall-makers, leaf miners and stem-borers act as ecosystem engineers, increasing the diversity of arthropod communities and enhancing trophic interactions (Marquis & Lill 2007; Calderón-Cortes, Quesada, & Escalera-Vazquez 2011; Cornelissen, Cintra, & Santos 2016; Sanders et al. 2014).

The stem-boring beetle *Oncideres albomarginata chamela* (Cerambycidae: Lamiinae) is an ecosystem engineer that girdles branches 2-3 cm in diameter of the tree *Spondias purpurea* (Anacardiaceae) for the development of its own progeny (Uribe-Mú & Quesada 2006). These branches usually fall and remain suspended on vegetation under the canopy of *S. purpurea* trees, due to the dense understory of the Mexican tropical dry forest where the present study was carried out (Quesada et al. 2014). Later other wood-boring beetles, mainly Bostrichidae and Cerambycidae species, oviposit in the same girdled branches (Calderón-Cortes et al. 2011). The beetle larvae develop inside detached branches and during this process they feed on wood creating galleries and tunnels that are abandoned, thereby creating new habitats for other species to occupy (Calderón-Corteset al. 2011). Twig-dwelling ants are a potential group that colonizes abandoned cavities made by wood-boring beetles (Powell, Costa, Lopes, & Vasconcelos 2011; Satoh et al. 2016). Although some ants are able to excavate nests themselves, mainly in fallen twigs (Byrne 1994; Carvalho & Vasconcelos 2002; Silva, Fernandes, Silva, Souza-Campana, & Morini 2016) they usually take advantage of and build them in plant cavities (DaRocha, Neves, Dáttilo, & Delabie 2016; Cereto, Schmidt, Martins, Castellani, & Lopes 2011) or in cavities made by other insects (Almeida, Santos, & Carneiro 2014; Raath et al. 2017).

Nest sites are a limiting resource for twig-nesting ants, which have their distribution influenced by nest availability and characteristics (Tschinkel 2002; Armbrecht, Perfecto, & Vandermeer 2004; Philpott & Foster 2005; Armbrecht, Perfecto, & Silverman 2006; Sagata, Mack, Wright, & Lester 2010; Powell et al. 2011; Jimenez-Soto & Philpott 2015). Previous studies have demonstrated that richness and abundance of colonies of twig-nesting ants are positively correlated with twig density, and are also greater in a set of twigs belonging to many tree species compared to twigs belonging to a single species (Armbrecht et al. 2004; Sagata et al. 2010). In addition, the diversity of nest entrance sizes is a critical mechanism structuring ant communities (Powell et al. 2011; Jimenez-Soto & Philpott 2015). Previous studies utilizing artificial nests demonstrated that some ant species were more frequently found in nests with certain entrance sizes; this result implies in niche differentiation in cavity use based on ant body size, which leads to the maintenance of species coexistence and diversity in arboreal ant communities (Powell et al. 2011; Jimenez-Soto & Philpott 2015). However, few studies have analyzed the possible role of other organisms, such as wood-boring beetles, promoting wood cavitiesfor ant communities. Satoh and colleagues (2016), for example, conducted an experimental study where tree branches of different sizes were artificially removed. They documented that wood-boring beetles colonized those branches according to their size and generated galleries and tunnels of different sizes, which were subsequently colonized by different-sized ant species. For our study system, Calderón-Cortes and colleagues (2011) found that more than twenty species of wood-boring beetles of various sizes (1.59 - 21.97 mm) colonize the branches detached by the twig-girdler beetle *O. albormaginata chamela*, and leave cavities of various sizes after emerging.

Nesting space is a limiting resource for ants (Hölldobler & Wilson 1990; Blüthgen & Feldhaar 2010) at several organizational levels (Fonseca 1999). Nesting ecology is fundamental to understand the organization of ant communities, and at the colony level, colony size is expected to grow to a greater size, which is determined by nest space limitations (Fonseca 1993). The twigs resulting from the breakdown of tree branches represent an important resource for many arboreal and litter ants (Carvalho & Vasconcelos 2002; Armbrecht et al. 2004; Silva et al. 2016). Twig-dwelling ants can utilize twigs as the main nest, when a queen ant colonizes the twig and starts a new colony; or as a satellite nest, when polydomic nests (i.e. nests without queens) are created because the main nest is not large enough to shelter the entire colony (Debout, Schatz, Elias, & Mckey 2007; Robinson 2014). Therefore, small cavities are an important resource to polydomous ant species, which take advantage of these spaces to increase their colony size and foraging areas (Debout et al. 2007; Tanaka, Yamane, & Itioka 2010).

The main objective of this study was to evaluate the role of wood-boring beetles promoting ant nest cavities mediated by the twig-girdler engineer *O. albomarginata chamela*. This study asked the following questions: (1) Do ants colonize the abandoned branches previously engineered by *O. albomarginata chamela* after the wood-boring beetles have emerged as adults? (2) Does branch diameter and nest entrance size (diameter) made by wood-boring beetles directly determine the size of the ant species colonizing these cavities? (3) Do twig-dwelling ants use the abandoned branches mainly as polydomic nests?

Materials and methods

Study area and sampling design

This study was carried out in the Chamela-Cuixmala Biosphere Reserve (CCBR, 19º30’N, 105º03’W) located on the Pacific coast of Jalisco, Mexico. The vegetation is tropical dry forest with a mean annual rainfall of 748 mm and a dry season that extends from November to June (García-Oliva et al. 2002).

During February and March 2015, we collected 80 branches that had been detached and inhabited by *O. albomarginata chamela*, and also colonized by secondary wood-boring beetles. All branches were marked and collected in mesh bags (<0.5 mm mesh size), placed in an open room at the study site, and maintained at local environmental conditions until January 2016 for the emergence of all associated arthropods (see Calderón-Corteset al. 2011). The larval development of the beetles led to a partial fragmentation of the branches (Fig. 1A). In February and August 2016, we selected 60 sub-samples of branches of different sizes, for 120 sub-samples (hereinafter referred to as "branches") in total, which were originally used by *O. albomarginata chamela* or other secondary colonizers (Fig. 1B). These branches contained at least one entrance/emergence hole made by a beetle. From each branch we measured the diameter and length, which ranged from 5-33 mm and 11-77 cm, respectively. To experimentally test the colonization of empty detached branches by the ant community, we utilized flagging tapes to attach four branches of different diameters in trees under the canopy of 15 individuals of *S. purpurea* distant from each other by at least 30 meters. Each of the four branches was located in four trees, without canopy connection, at a height ranging from 1.5 to 2.0 m for two months, sufficient time for invertebrate community colonization (Zuo et al. 2016). In April and October 2016, we collected all branches, immediately placed them in individual bags of fine mesh, and transported them to the laboratory.

All branches collected from the field were carefully opened to collect ants and, in the cases where ants were found, we measured the size of the ant nest entrance with a digital caliper (Stainless Hardened 150 mm; Fig. 1C). Each branch was placed in a large tray, big enough to prevent ants from escaping. Ants were transferred to vials with 70% ethanol for further taxonomic identification, counting and measurements. We calculated the number of individuals per branch and measured the length of the body of ten workers to estimate the average size of ant species. The length of the ants was measured by the software ZEN Lite 2011 from pictures taken with a digital camera (Axio Cam ICc5, Zeiss) attached to a microscope (Stemi 2000-C, Zeiss). Taxonomic identification of species was carried out by W. D. DaRocha using taxonomic keys (Andrade & Baroni-Urbani 1999; Longino 2003).

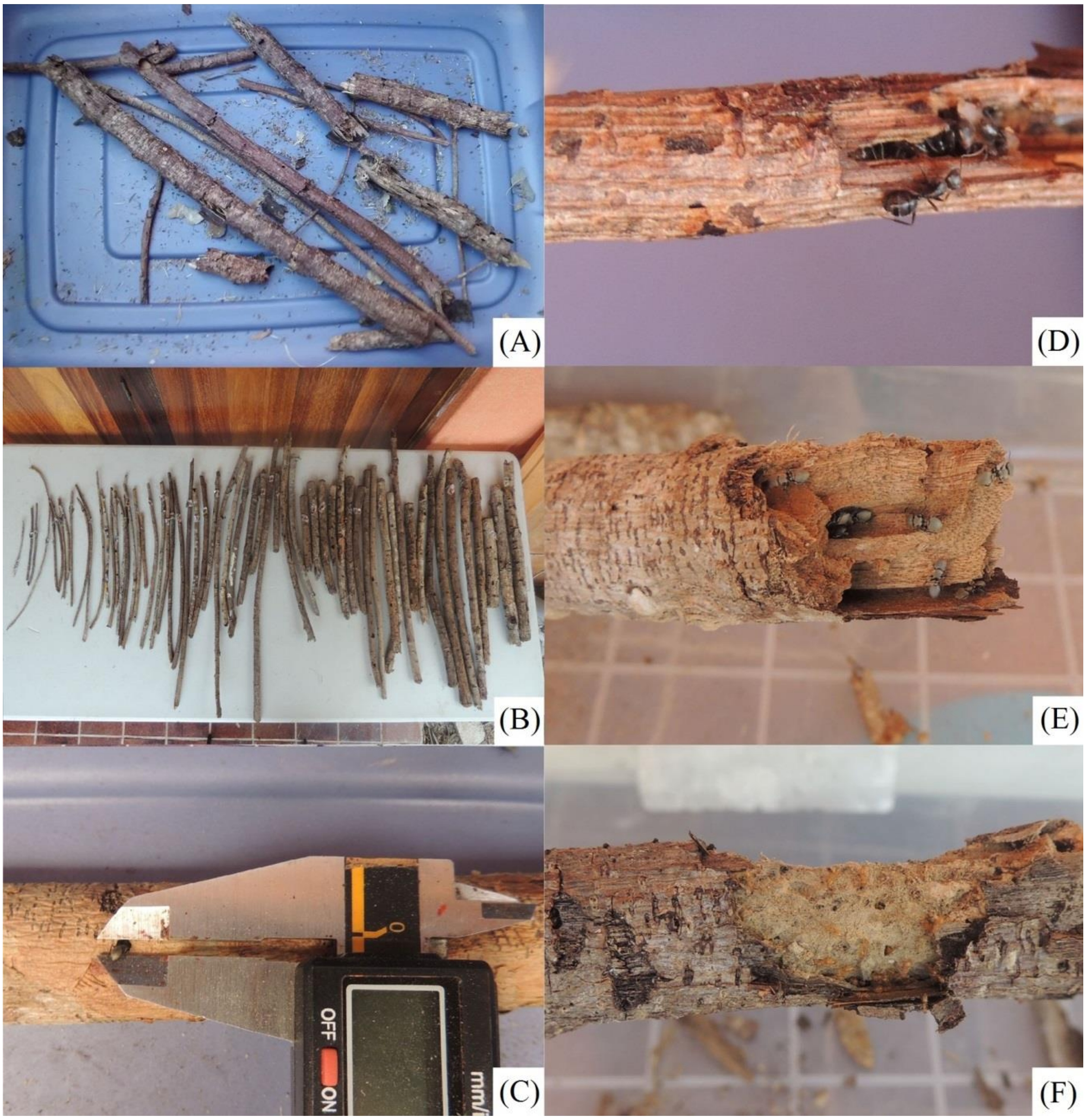


Fig. 1. Degradation state of *Spondias purpurea* branches one year after engineering by *O. albomarginata chamela* (A); 60 abandoned branches samples (B); measuring a nest entrance cavity with a caliper (C); ants nesting in the abandoned branches samples (D, E and F).

Statistical analysis

A Linear Mixed Model (LMER; lme4 package in R) was used to determine the effects of nest characteristics on ant species colonizing the abandoned branches, assuming spatial pseudoreplication. For this model, ant body size was used as response variable, whereas branch diameter and nest entrance diameter were used as explanatory variables. The explanatory variables were nested within the random effects of the fifteen points (individuals of *S. purpurea*) sampled during the study (Bates, Maechler, Bolker, & Walker 2015). Significance was estimated with an ANOVA between the complete (H1) and the null model (H0). The Akaike Information Criterion (AIC) was used to rank the models, since it represents the uncertainty of the model, a lower value of the AIC represents the more parsimonious model. The model was adjusted with Gaussian error distribution. The package “MuMIn” was used with the function “r.squaredGLMM” to obtain the value of R^2 (Bartoń 2016).Abandoned branches with a queen ant present but without workers were counted as nests, but were not included in the regression analysis. All analyses were performed using R software (R Core Team 2016).

Results

We observed 49 nests of arboreal ants in the 120 abandoned branches sampled (see Appendix A; Fig. 1D, E and F). Forty-one branches contained one colony and four branches contained two colonies of different species. We sampled 7753 adult and 3325 immature ants from 14 species. Sixteen queens were sampled in the 49 nests; nine branches only contained workers, while 24 contained both adults and immature stages without a queen ant (see Appendix A).

The body size of the ants nesting in the abandoned branches was not affected by branch diameter ($p=0.40$; Table 1), but was positively correlated with the diameter of nest entrance cavity ($p<0.0001$; $n=45$; $R^2= 0.58$; Table 1; Fig. 2).

Table 1. Linear Mixed Models to test the effects of branch diameter and diameter of nest entrance on ant body size. Ant nests were sampled in association with cavities made by wood-boring beetles in *S. purpurea* branches previously engineered by *O. albomarginata chamela* in a tropical dry forest, in Jalisco, Mexico.

Response variable	Explanatory variable	AIC (H1)	AIC (H0)	P
Ant body size	Branch diameter	142.7	141.4	0.40
Ant body size	Nest entrance size	141.4	173.5	<0.0001

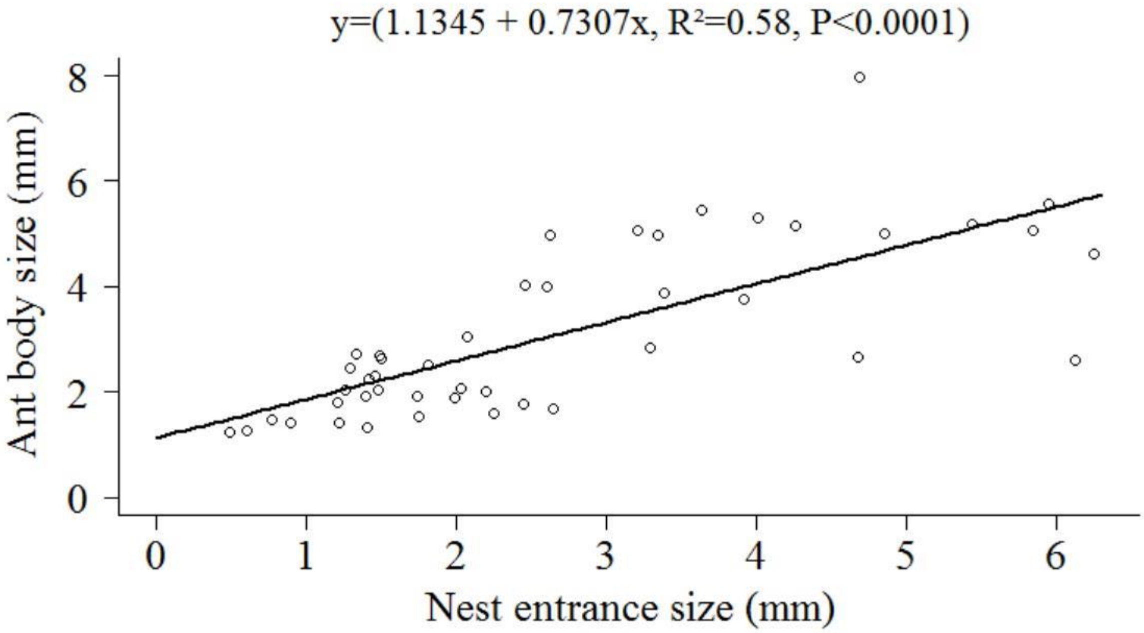


Fig. 2. Relationship between diameter of the nest entrance holes made by wood-boring beetles and ant body size sampled from *S. purprea* abandoned branches previously engineered by *O. albomarginata chamela* in a tropical dry forest, in Jalisco, Mexico.

Discussion

The availability of nest sites is a major mechanism structuring ant communities (Blüthgen & Feldhaar 2010). Our results demonstrated for the first time the role of a twig-girdler beetle in promoting nest space for twig-dwelling ants. After the wood-boring beetles have emerged from the branches detached by the twig-girdler ecosystem engineer *O. albomarginata chamela*, the abandoned cavities become important nest sites for twig-dwelling ants. This study was also pioneer in determining the role of the size of natural entrance holes made by wood-boring beetles for arboreal twig-dwelling ants. Finally, our results demonstrated that arboreal ants use the abandoned cavities in the branches mainly as polydomic nests.

Previous studies have demonstrated that foraging areas of arboreal ant species are limited by their nesting sites (Tanaka et al. 2010; Klimes, Fibich, Idigel, & Rimandai 2015). Therefore, organisms that are able to create cavities, which are colonized by ants for nesting, play an important role in ant community organization (Tschinkel 2002; Satoh et al. 2016). For example, *Crematogaster ashmeadi* Emery is the most dominant arboreal ant in the pine forests of northern Florida, United States; and because their newly mated queens are not able to excavate nest sites, they found colonies in abandoned wood-boring beetle cavities in the first dead branches that form on pine saplings (Tschinkel 2002). We found 14 ant species nesting in the abandoned cavities of wood-boring beetles in the detached branches, which implies that the ecosystem engineering carried out by twig-girdler beetle *O. albomarginata chamela* had extended indirect effects on arboreal ant community organization by increasing the availability of nest sites.

In another similar experimental study, Satoh and colleges (2016) artificially removed branches of ubame oak (*Quercus phillyraeoides* A. Grey) trees and found a positive relationship between wood diameter and ant body size. These authors first demonstrated a positive relationship between wood-boring beetle body size and wood diameter, and suggested that larger ants colonize larger branches mediated by the larger cavities left by the beetles, whereas smaller ants colonize branches with smaller cavity diameters. Our result contrasts with this study because we did not find a relationship between branch diameter and ant body size. In our system, after the ecosystem engineer *O. albomarginata chamela* detached branches of *S. pupurea,* it makes incisions along the branch bark, thus providing oviposition niches for both large and small beetle species (Calderón-Cortes et al. 2011). The small entrance/emergence holes left by small wood-boring beetles in larger branches allow colonization by smaller ant species (Fig. 1F).

We found a positive correlation between the size of the entrance hole made by wood-boring beetles and ant body size. This result confirms the indirect evidence suggested by Satoh and colleges (2016) of a resource partitioning by the ants according to the sizes of nest entrance holes in dead wood. Previous studies utilizing artificial bamboo twigs, with distinct entrance sizes, have already demonstrated how the diversity of nesting sites influences the colonization process of arboreal twig-dwelling ants (Powell et al. 2011; Jimenez-Soto & Philpott 2015). A wider diversity of nest entrance sizes allows for greater niche differentiation in cavity use by ants, increasing the overall richness of the ant community (Blüthgen & Feldhaar 2010; Jimenez-Soto & Philpott 2015).

We found that almost 70% of the occupied branches were utilized as polydomic nests by ants. In addition, of the 14 ant species found in our study, 12 had at least one polydomic nest sampled, which suggests that some nests with queens could be founding nests of a potential polydomic colony or the main nest of a polydomic colony. These results imply that the abandoned cavities left by wood-boring beetles in the branches normally represent a limited space resource for the development and shelter of entire arboreal ant colonies. However, polydomic nests, where a queen ant is capable of founding several different nests without occupying them, have been related as a strategy to promote the colonization of new nesting sites and the reduction of intraspecific competition for the same resources by crowding in a unique place, thereby increasing foraging capacity in places with other food supplies (Debout et al. 2007; Robinson 2014). Therefore, the ecosystem engineering carried out by *O. albomarginata chamela* may have a more pronounced effect on ant species that develop polydomic colonies, which take advantage of the cavities left by the wood-boring beetles to increase their nest distribution, and consequently, their foraging areas.

Acknowledgments

We are grateful to A. Costa, L. Macedo-Reis, E. Cristobal-Perez and G. Sánchez-Montoya for field help. We are also immensely grateful to L. Macedo-Reis and three anonymous reviewers for their comments on an earlier version of the manuscript. S. Novais thank the CAPES (PDSE- Sandwich Doctoral Programme Abroad) for research grants awarded during the development of this study. This study was supported by grant from Universidad Nacional Autónoma de México (PAPIIT # IN212714-3), CONACyT (# 2009-131008 and # 155016) and CONACYT-UNAM-UAGro to LANASE (2015-LN250996, 2016-LN271449 and 2017-LN280505). Finally, we thank the Chamela-Cuixmala Biosphere Reserve for all the physical structure and logistical support. This study was performed in partial fulfillment of the requirements of the Ph.D. degree of SMAN in Ecology, Conservation and WildLife Management, Federal University of Minas Gerais, Brazil.

References

Almeida, M. F. B. D., Santos, L. R. D., & Carneiro, M. A. A. (2014). Senescent stem-galls in trees of *Eremanthus erythropappus* as a resource for arboreal ants. *Revista Brasileira de Entomologia*, *58*(3), 265-272.

Andrade, M. L., & Baroni-Urbani, C. (1999). Diversity and adaptation in the ant genus *Cephalotes,* past and present (Hymenoptera, Formicidae). Stuttgart: Stuttgarter Beiträge zur Naturkunde. Serie B (Geologie und Paläontologie), pp. 889.

Armbrecht, I., Perfecto, I., & Vandermeer, J. (2004). Enigmatic biodiversity correlations: ant diversity responds to diverse resources. *Science*, *304*(5668), 284-286.

Armbrecht, I., Perfecto, I., & Silverman, E. (2006). Limitation of nesting resources for ants in Colombian forests and coffee plantations. *Ecological Entomology*, *31*, 403-410.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Bartoń K. (2016). MuMIn: Community Ecology Package. In: R package version 1.15.6. Available: https://cran.r-project.org/web/packages/MuMIn/index.html

Blüthgen, N., & Feldhaar, H. (2010). Food and shelter: how resources influence ant ecology. In L. Lach, C. L. Parr, & K. L. Abbott (Eds.), *Ant ecology* (pp. 115-136). New York: Oxford University Press.

Byrne, M. M. (1994). Ecology of twig-dwelling ants in a wet lowland tropical forest. *Biotropica*, *26*, 61-72.

Calderón-Cortes, N., Quesada, M., & Escalera-Vazquez, L.H. (2011). Insects as stem engineers: interactions mediated by the twig-girdler *Oncideres albomarginata chamela* enhance arthropod diversity. *PLOS ONE*, *6*, e19083.

Carvalho, K. S., & Vasconcelos, H. L. (2002). Comunidade de formigas que nidificam em pequenos galhos da serrapilheira em floresta da Amazônia Central, Brasil. *Revista Brasileira de Entomologia*, *46*(2), 115-121.

Cereto, C. E., Schmidt, G. O., Martins, A. G., Castellani, T. T., & Lopes, B. C. (2011). Nesting of ants (Hymenoptera, Formicidae) in dead post-reproductive plants of Actinocephalus polyanthus (Eriocaulaceae), a herb of coastal dunes in southern Brazil. *Insectes sociaux*, *58*(4), 469-471.

Cornelissen, T., Cintra, F., & Santos, J. C. (2016). Shelter-building insects and their role as ecosystem engineers. *Neotropical Entomology*, *45*, 1–12.

DaRocha, W. D., Neves, F. S., Dáttilo, W., & Delabie, J. H. (2016). Epiphytic bromeliads as key components for maintenance of ant diversity and ant–bromeliad interactions in agroforestry system canopies. *Forest Ecology and Management*, *372*, 128-136.

Debout, G., Schatz, B., Elias, M., & Mckey, D. (2007). Polydomy in ants: what we know, what we think we know, and what remains to be done. *Biological Journal of the Linnean Society*, *90*(2), 319-348.

Fonseca, C. R. (1993). Nesting space limits colony size of the plant-ant *Pseudomyrmex concolor*. *Oikos*, *67*(3), 473-482.

Fonseca, C. R. (1999). Amazonian ant–plant interactions and the nesting space limitation hypothesis. *Journalof Tropical Ecology*, *15*(6), 807-825.

García-Oliva, F., Camou, A., & Maass, J. M. (2002). El clima de la región central de la costa Del Pacífico mexicano. In A. N. Noguera-Alderte, J. H. Vega-Rivera, A. N. Garcia-Aldrete, & M. Quesada (Eds.). *Historia natural de Chamela*. (pp. 3–10). UNAM: Instituto de Biología.

Hölldobler, B., & Wilson, E.O. (1990). *The ants*. Cambridge: Harvard University Press. pp. 732.

Jones, C. G., Lawton, J. H., & Shachak. M. (1994). Organisms as ecosystem engineers. *Oikos*, *69*, 373-386.

Jones, C.G., Gutiérrez, J.L., Byers, J.E., Crooks, J.A., Lambrinos, J.G., & Talley, T.S. (2010). A framework for understanding physical ecosystem engineering by organisms. *Oikos*, *119*, 1862-1869.

Jiménez-Soto, E., & Philpott, S. M. (2015). Size matters: nest colonization patterns for twig-nesting ants. *Ecology and evolution*, *5*(16), 3288-3298.

Klimes, P., Fibich, P., Idigel, C., & Rimandai, M. (2015). Disentangling the diversity of arboreal ant communities in tropical forest trees. *PLOS ONE*, *10*(2), e0117853.

Longino, J. T. (2003). The *Crematogaster* (Hymenoptera, Formicidae, Myrmicinae) of Costa Rica. *Zootaxa*, *151*, 1-150.

Marquis, R.J., & Lill, J.T. (2007). Effects of arthropods as physical ecosystem engineers on plant-based trophic interaction webs. In T. Ohgushi, T. P. Craig, & P. W. Price (Eds.), *Ecological communities: plant mediation in indirect interactions webs* (pp. 246–274). New York: Cambridge University Press.

Quesada, M., Álvarez-Añorve, M., Ávila-Cabdilla, L., Castillo, A., Lopezaraiza-Mikel, M., Martén-Rodríguez, S., et al. (2014). Tropical dry forest ecological succession in Mexico: synthesis of a long-term study. In:A. Sánchez-Azofeifa, J.S. Powers, G.W. Fernandes, &M. Quesada (Eds.), *Tropical dry forests in the Americas*(pp.17–33). Boca Raton: CRC Press.

Philpott, S. M., & Foster, P. F. (2005). Nest-site limitation in coffee agroecosystems: Artificial nests maintain diversity of arboreal ants. *Ecological applications*, *15*(4), 1478-1485.

Powell, S., Costa, A. N., Lopes, C. T., & Vasconcelos, H. L. (2011). Canopy connectivity and the availability of diverse nesting resources affect species coexistence in arboreal ants. *Journal of Animal Ecology*, *80*, 352–360.

R Core Team. (2016). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. (http://www.R-project.org/).

Raath, M. J., le Roux, P. C., Veldtman, R., Campbell, H., Buyens, I. P. R., & Greve, M. (2017). Empty *Gonometa postica* cocoons function as nest sites and shelters for arboreal ants. *Journal of Arid Environments*, *144*, 42-47.

Robinson, E. J. (2014). Polydomy: the organisation and adaptive function of complex nest systems in ants. *Current Opinion in Insect Science*, *5*, 37-43.

Romero, G. Q., Gonçalves-Souza, T., Vieira, C., & Koricheva, J. (2014). Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biological Reviews*, *90*, 877-890.

Sagata, K., Mack, A. L., Wright, D. D., & Lester, P. J. (2010). The influence of nest availability on the abundance and diversity of twig-dwelling ants in a Papua New Guinea forest. *Insectes Sociaux*, *57*(3), 333-341.

Sanders, D., Jones, C. G., Thébault, E., Bouma, T. J., Heide, T. V. D., Belzen, J. V., & Barot, S. (2014). Integrating ecosystem engineering and food webs. *Oikos*, *123*, 513-524.

Satoh, T., Yoshida, T., Koyama, S., Yamagami, A., Takata, M., Kurachi, T., et al. (2016). Resource partitioning based on body size contributes to the species diversity of wood-boring beetles and arboreal nesting ants. *Insect Conservation and Diversity*, *9*(1), 4-12.

Silva, O. G. M., Fernandes, T. T., da Silva, R. R., de Souza-Campana, D. R., & de Castro Morini, M. S. (2016). Twigs of *Albizia niopoides* (Spruce ex Benth.) Burkart as a nesting resource for ants (Hymenoptera: Formicidae). *Revista Brasileira de Entomologia*, *60*(2), 182–185.

Tanaka, H. O., Yamane, S., & Itioka, T. (2010). Within-tree distribution of nest sites and foraging areas of ants on canopy trees in a tropical rainforest in Borneo. *Population Ecology*, *52*(1), 147.

Tschinkel, W. R. (2002). The natural history of the arboreal ant, *Crematogaster ashmeadi*. *Journal of Insect Science*, *2*(12), 1-15.

Uribe-Mú, C. A., & Quesada, M. (2006). Preferences, patterns and consequences of branch removal on the dioecious tropical tree *Spondias purpurea* (Anacardiaceae) by the insect borer *Oncideres albomarginata chamela* (Cerambycidae). Oikos, *112*, 691-697.

Zuo, J., Cornelissen, J. H., Hefting, M. M., Sass-Klaassen, U., van Logtestijn, R. S., van Hal, J., et al. (2016). The (w) hole story: Facilitation of dead wood fauna by bark beetles? *Soil Biology and Biochemistry*, *95*, 70–77.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at

Appendix A

Table 1.Abundance and size of ant species nesting in cavities abandoned by wood-boring beetles in *Spondias purpurea* branches previously engineered by *O. albomarginata chamela* in a tropical dry forest, in Jalisco, Mexico. *Represents nests with a queen ant.

Taxon	Abundance		Worker body	Nest entrance
	Worker	Immature	size (mm)	size (mm)
Azteca sp1	223	353	3.04	2.07
Brachymyrmex sp1	125	114	2.04	1.48
Brachymyrmex sp1*	1376	362	2.05	1.26
Camponotus novogranadensis Mayr, 1870	32	12	3.75	3.91
Camponotus novogranadensis Mayr, 1870	38	11	3.87	3.38
Camponotus novogranadensis Mayr, 1870	19	9	3.99	2.6
Camponotus novogranadensis Mayr, 1870	78	10	4.03	2.45
Camponotus rectangularis Emery, 1890	37	10	4.61	6.25
Camponotus rectangularis Emery, 1890	27	0	4.99	3.34
Camponotus rectangularis Emery, 1890	119	314	5	4.85
Camponotus rectangularis Emery, 1890	34	0	5.14	4.26
Camponotus rectangularis Emery, 1890	26	3	5.31	4.01
Camponotus rectangularis Emery, 1890	13	10	5.58	5.95
Cephalotes multispinosus Norton, 1868	250	211	5.07	5.84
Cephalotes multispinosus Norton, 1868	158	66	5.18	5.43
Cephalotes multispinosus Norton, 1868	173	84	5.46	3.63
Cephalotes multispinosus Norton, 1868*	578	556	4.99	2.62
Cephalotes multispinosus Norton, 1868*	0	0	-	4.8
Cephalotes multispinosus Norton, 1868*	0	0	-	3.64
Cephalotes multispinosus Norton, 1868*	0	7	-	4.89
Cephalotes multispinosus Norton, 1868*	0	9	-	5.43
Crematogaster curvispinosa Mayr, 1862	63	0	2.31	1.45
Crematogaster erecta Mayr, 1866	18	0	2.45	1.29
Crematogaster erecta Mayr, 1866	172	0	2.61	6.12
Crematogaster erecta Mayr, 1866	8	0	2.63	1.5
Crematogaster erecta Mayr, 1866	69	0	2.66	4.67
Crematogaster erecta Mayr, 1866	28	0	2.74	1.33
Crematogaster erecta Mayr, 1866	24	0	2.86	3.29
Crematogaster erecta Mayr, 1866*	8	0	1.78	2.44
Crematogaster erecta Mayr, 1866*	4	13	1.79	1.2

Crematogaster erecta Mayr, 1866*	12	3	2.02	2.19
Crematogaster sp1	415	102	2.5	1.81
Crematogaster sp1*	142	42	2.24	1.41
Crematogaster sp1*	210	94	2.68	1.49
Pseudomyrmex ferrugineus (Smith, F., 1877)	5	3	7.98	4.68
Pseudomyrmex gracilis (Fabricius, 1804)	29	36	5.06	3.21
Solenopsis sp1*	253	72	1.55	1.75
Solenopsis sp1*	46	14	1.6	2.25
Solenopsis sp2	15	9	1.23	0.49
Solenopsis sp2	8	13	1.33	1.4
Solenopsis sp2	9	13	1.42	1.21
Solenopsis sp2	12	7	1.42	0.89
Solenopsis sp2	45	108	1.48	0.77
Solenopsis sp2*	2	0	1.26	0.6
Tapinoma sp1*	823	77	1.89	1.99
Tapinoma sp1*	455	309	1.92	1.39
Tapinoma sp2	316	7	1.69	2.64
Tapinoma sp2	944	133	1.91	1.74
Tapinoma sp2	312	129	2.06	2.03
Total	7753	3325		

CAPÍTULO 4

POSITIVE EFFECTS OF THE CATASTROPHIC HURRICANE PATRICIA ON INSECTS COMMUNITIES

Positive effects of the catastrophic Hurricane Patricia on insect communities

Samuel Novais[1,2,3], Luiz Eduardo Macedo-Reis[1,2], Edson Cristobal-Peréz[2,3], Gumersindo Sánchez-Montoya[2,3], Milan Janda[3], Frederico Neves[1] & Mauricio Quesada[1,2,3*]

[1] Laboratório de Ecologia de Insetos, Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, 31270-901, Brazil

[2] Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, México

[3] Laboratorio Nacional de Análisis y Síntesis Ecológica, Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, México

*Email: mquesada@cieco.unam.mx

**O capítulo está formatado conforme as instruções de submissão da revista *Scientific Reports*. As figuras e tabelas estão inseridas no corpo do manuscrito para facilitar a leitura.

Abstract: Highly seasonal conditions of tropical dry forests (TDFs) determine the temporal patterns of insect abundance. However, density-independent factors such as natural disturbances can abruptly change environmental conditions, affecting insect populations. We address the effects of the Hurricane Patricia (category 5) on the richness and abundance of three feeding guilds of herbivorous insects and predatory beetles associated to the canopy of a TDF. This is the strongest tropical hurricane ever reported in the Western Hemisphere. We also analyzed the seasonal dynamics of these insect guilds during three consecutive years, one year before and two years after the hurricane. The richness and abundance of all insect guilds presented small variations between seasons in the first sampling year, probably due to the heavy rains that occur during the dry season. Most insect guilds increased in richness and abundance in the following months after the hurricane, compared to samples before it. Despite this increase, the insect communities oscillated seasonally through the two years that followed the hurricane. We demonstrated that catastrophic hurricane disturbances may be important events that positively affect insect communities in TDFs, which tend to oscillate over time due to the strong seasonality of the environmental conditions in this ecosystem.

Introduction

Insect communities vary seasonally due to changes in climatic conditions and the availability of food resources (1, 2). Seasonal patterns become more evident when insect abundance and diversity are compared between the dry and wet seasons of highly seasonal environments, such as tropical dry forests (TDFs; 2, 3, 4, 5, 6 , 7, 8, 9). In these ecosystems, water stress is a major factor that determines the timing and duration of leafing phenological events regulating plant-insect interactions (3, 10, 11). During the dry season, most trees shed their leaves as a drought-resistant mechanism, and then the first rains determine synchronous leaf flushing of most plant species (12, 13). In the case of free-feeding herbivorous insects (e.g. folivorous and sap-suckers), there is a general reduction in abundance and diversity in the dry season (3, 6, 14). However, this pattern can vary among insect guilds; for example, xylophagous beetles show increased activity at the transitions between wet and dry seasons due to favorable abiotic conditions for flight and selection of new hosts (15). The temporal patterns for some other insect guilds, such as predatory insects, are often unknown in TDFs.

In addition to variations in abiotic conditions among seasons (e.g., dry and wet season) and years (e.g., a drier year compared to a wetter year) in TDFs, density-independent factors such as natural disturbance events can abruptly change resource availability and habitat conditions (16). Post-disturbance conditions can facilitate the colonization of less competitive species that increase their abundance and expand their distribution (17, 18). Among natural disturbance events, hurricanes play an important role affecting the structure and dynamics of forests around the world (19, 20, 21, 22, 23, 24, 25, 26). Death or architecture simplification of many tree species following hurricanes change abiotic (light, temperature and moisture) and biotic (increase of organic matter in soil, decreased species density) conditions, allowing the growth of weed gap species (21, 25). Consequently, structural and compositional changes in plant communities, coupled with an increase in availability of resources (wood debris and foliage regrowth) following hurricanes can have direct and indirect effects on insect communities (27, 28, 29). For example, positive or negative effects on primary consumers can propagate throughout the food chain, causing changes at other trophic levels (30, 31).

Given the difficulty to anticipate the occurrence of such natural disturbances, most studies have attempted to estimate hurricane effects on insect populations comparing abundances among different post-hurricane plots, or after a long period of time have passed between the sampling period before and after hurricane disturbance occurred (28, 32, 33, 34). Other studies have attempted to simulate the effect of hurricanes experimentally by trimming tree crowns and comparing arboreal insect abundances before and after manipulations (35, 36). However, these experimental studies did not simulate the effects of a hurricane over larger spatial scales, underestimating their effects on insect communities. Plots with experimental tree defoliations are influenced more rapidly by the colonization of insects from nearby intact forests than plots affected by a hurricane (37). Understanding the effects of hurricane disturbances on forest ecosystem dynamics is of critical importance because the frequency of intense hurricanes (category 4 and 5) is expected to increase in many regions as a consequence of global climate change (38, 39, 40). Therefore, studies that analyze the structure of insect communities before and immediately after hurricanes are needed (but see 41).

In 2015 we started a study with the objective of evaluate temporal variations in the abundance and richness of three feeding guilds of herbivorous insects (xylophagous, sap-sucking, and folivorous) and predatory beetles in a TDF canopy. At the end of the rainy season on October 2015 Hurricane Patricia (category 5), the strongest tropical hurricane that has been reported in the Western Hemisphere so far, struck directly on our study sites in Chamela, Jalisco, on the central Pacific coast of México (Fig. 1). Nearly all trees were defoliated, stripped off their branches, snapped, or uprooted by the strong winds, and then the heavy rains associated with the hurricane caused a new vegetative growth (26, 42). The main objective of this study was to evaluate the effects of the catastrophic Hurricane Patricia on different insect guilds in a TDF canopy, by comparing samples taken before and in the following months after the hurricane. We addressed the following prediction: (I) there is an increase in abundance and richness of herbivores following Hurricane Patricia due to foliage regrowth right after the hurricane (sap-sucking and folivorous) and an increase in the availability of dead wood resources (xylophagous). There is also an increase in abundance and richness of predatory beetles following Hurricane Patricia due to an increase in the availability of prey. We also evaluated temporal variations in insect communities across different seasons (rainy season, transition and dry season) for three consecutive years, one year before and two years after Hurricane Patricia. Despite the effects of the hurricane, we expected that the strong seasonality of environmental conditions in the TDF affects the temporal patterns of the insect communities. We addressed the following prediction: (II) there is an increase in abundance and richness of free-feeding herbivorous insects (sap-sucking and folivorous beetles) and predatory beetles during the rainy season, and an increase in abundance and richness of xylophagous beetles in the transition between rainy and dry seasons.

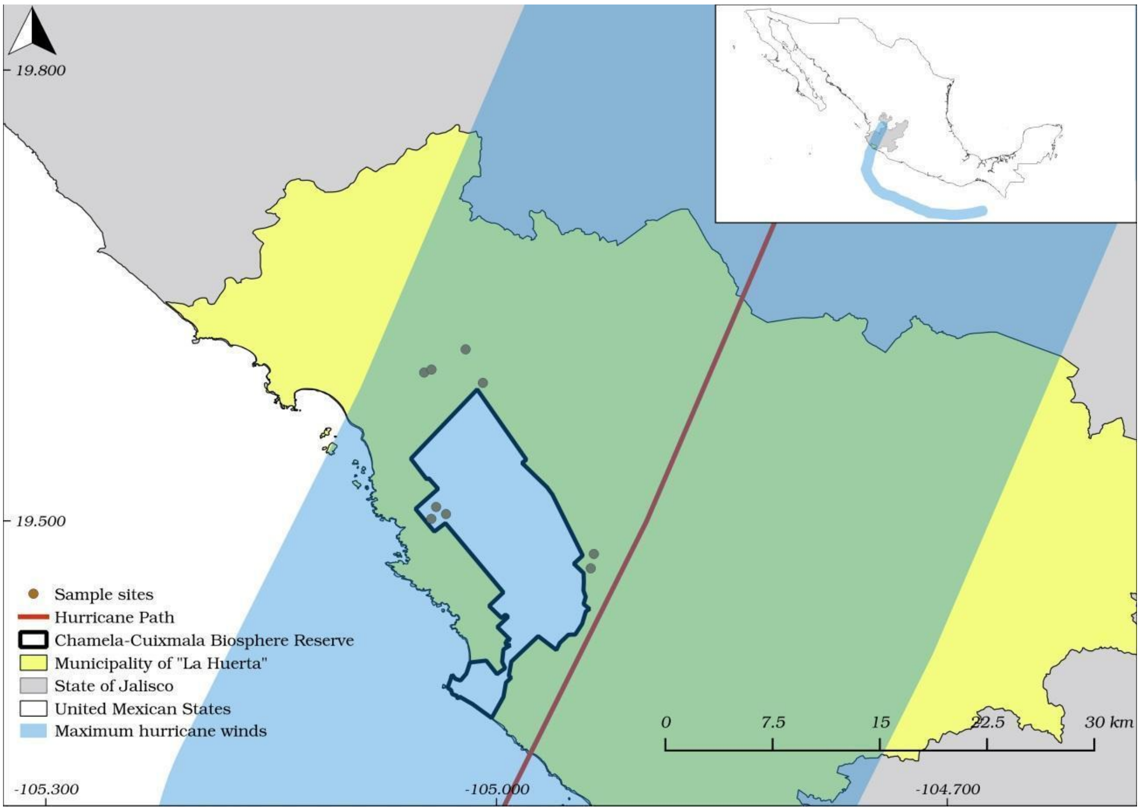


Figure 1.

Results

A total of 5,103 insect herbivores was sampled, 2,284 (44.7%) sap-sucking, 116 (2.3%) folivorous beetles and 2,703 (53%) xylophagous. Herbivores were divided among 275 morphospecies, including 151 sap-sucking, 53 folivorous and 71 xylophagous. For predatory beetles, a total of 1,890 individuals were sampled, divided in 104 morphospecies (Supplementary Table S1). In terms of number of individuals and morphospecies, Cicadellidae and Scolytinae were the most representative subfamilies/families for sap-sucking and xylophagous guilds, respectively. For folivorous, Chrysomelidae and Curculionidae presented the highest number of individuals, and for predatory beetles Carabidae and Staphylinidae (Supplementary Table S1).

Richness and abundance of all insect guilds varied significantly between sampling periods (Table 1, Fig. 2). However, the seasonal responses varied within guilds and between the years, mainly from the first sampling year (2015) to the following (2016 and 2017; Fig. 2). The 2015 dry season was abnormal in terms of the rainfall, with a precipitation 1000% higher than expected for this season. Sap-sucking herbivores were more abundant in the abnormal dry season compared to the rainy season in 2015. This guild increased respectively 4 and 3 fold in abundance and richness after Hurricane Patricia (October 2015) compared to the samples in the previous rainy season (August 2015). In 2016 and 2017, sap-sucking herbivores were more rich and abundant in the rainy seasons compared to the dry seasons (Fig. 2A and B). The richness and abundance of the folivorous beetles was similar between the abnormal dry and the rainy season in 2015. In the following months after Hurricane Patricia their richness and abundance remained similar to previous samples. In 2016, folivorous beetles were more rich and abundant in the rainy season compared to the dry season, whereas for 2017 were similar between seasons (Fig. 2C and D). The xylophagous guild was less rich and abundant in the rainy season of 2015. This guild increased approximately 3 fold in abundance three months after Hurricane Patricia compared to the samples in 2015, and their richness also increased compared to the samples before the hurricane. In 2016, the richness and abundance of xylophagous were similar along the sampling periods, but in 2017 were greater in the transition between seasons (Fig. 2E and F). Predatory beetles were more abundant in the rainy season compared to the abnormal dry season in 2015. This guild increased respectively 8 and 3 fold in abundance and richness two months after Hurricane Patricia compared to the samples before it. In 2016 and 2017, predatory beetles were more rich and abundant in the rainy seasons compared to the dry seasons (Fig. 2G and H).

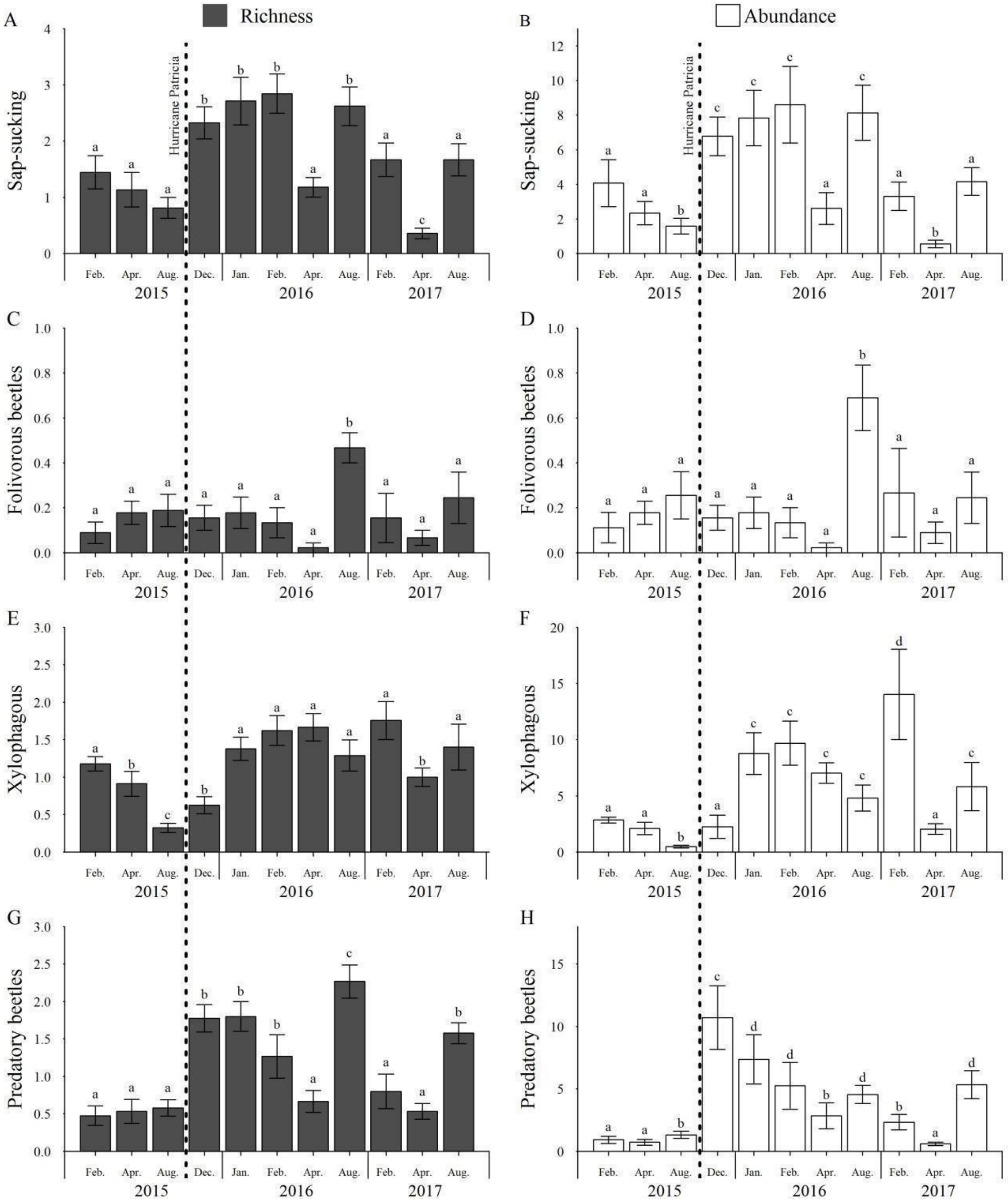

Richness
Abundance
A
B
C
D
E
F
G
H
Hurricane Patricia
Sap-sucking
Folivorous beetles
Xylophagous
Predatory beetles
Feb.
Apr.
Aug.
Dec.
Jan.
Feb.
Apr.
Aug.
Feb.
Apr.
Aug.
2015
2016
2017
0
1
2
3
4
0
2
4
6
8
10
12
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
5
10
15
20
a a a b b b a b a c a
a a b c c c a c a b a
a a a a a a a b a a a
a a a a a a a b a a a
a b c b a a a a a b a
a a b a c c c c d a c
a a a b b b a c a a b
a a b c d d b d b a d

Figure 2.

Discussion

Our results showed that catastrophic hurricane disturbances are important density-independent factors that positively affect insect communities in TDFs. The abrupt changes in forest structure and plant phenology caused by the Hurricane Patricia at the end of the rainy season of 2015 lead to an increase in the richness and abundance of most studied insect guilds in the following months compared to the samples before the hurricane. Despite this increase, the insect communities oscillated seasonally (i.e. in the following wet and dry seasons) through two years after the hurricane. The arrival of the regular dry season of 2016, for example, caused a reduction in the community structure of most insect guilds. Overall, for 2016 and 2017, the abundance and richness of free-feeding herbivores (sap-sucking and folivorous beetles) and predatory beetles were greater in the rainy seasons, while for xylophagous beetles were greater in the transitions between wet and dry seasons.

Sap-sucking herbivores were more rich and abundant in the months following Hurricane Patricia, compared to the samples before it. Previous studies carried out in a tropical rainforest in Puerto Rico after Hurricane Hugo (1989) reported a greater abundance of sap-sucking herbivores in post-hurricane gaps compared to closed canopy forests (29, 32, 33). The main mechanism attributed to this pattern was related to an increase in the availability of new shoots and leaf meristems due to natural coppicing by the hurricane (43). Sap-sucking herbivores prefer feeding on these structures because they have increased translocation of nutrients via phloem and xylem vessels (44, 45). In our study, the heavy rains associated with Hurricane Patricia also caused an immediate new vegetative growth of most deciduous plant species, explaining this increase of sap-sucking herbivores. However, the arrival of the regular dry season in 2016 lead to a reduction in the richness and abundance of this guild, which increased again in the next rain season of 2016. This seasonal pattern was also consistent between seasons in 2017. These results corroborated previous studies conducted in TDFs which found that sap-sucking populations were severely reduced by stressful conditions in the dry seasons and due to fluctuations in the abundance of new leaves, which are mostly available for them in the rainy seasons (3, 6, 46).

The richness and abundance of folivorous beetles did not differ between the samples before and in the following months after Hurricane Patricia. Despite the fact that an increase in the availability of young leaves should lead to an increase in folivorous beetle populations, other changes in abiotic and biotic conditions following Hurricane Patricia may have prevented this from happening. Loss of canopy cover after hurricanes immediately results in increase of temperature and reduction of moisture (47), the conditions that limit the development, survivorship and fecundity of folivorous beetles (48, 49). For example, Novais and colleagues (50) demonstrated that folivorous beetles were very sensitive to habitat simplification, and that only a few species were able to remain in habitats with low canopy cover. The quality of regrowth foliage could be another factor negatively affecting folivorous beetle populations; for example, Hunter and Forkner (51) demonstrated that regrowth foliage following Hurricane Opal in United States had higher condensed tannin concentrations, an anti-herbivore defense. Furthermore, the life cycle of folivorous beetles is longer, compared to sap-sucking herbivores, and because most larvae feed and develop on leaves they could be more susceptible to attack from natural enemies that tend to increase their populations following hurricanes (43, 52), as also observed by our study. For example, Torres (53) showed an outbreak of 15 species of Lepidoptera caterpillars probably due to a flush of new foliage that occurred after Hurricane Hugo in Puerto Rico, but this outbreak was subsequently controlled by Dipteran and Hymenopteran parasitoids. Similar to sap-sucking herbivores, folivorous beetles also presented a tendency of decrease in richness and abundance with the arrival of the dry season of 2016, and later increase in the rainy season. A tendency to this seasonal pattern was also found in 2017. These results corroborate studies in TDFs for other folivorous insects, such as Lepidoptera caterpillars, which demonstrated that their abundance and species richness through the year is seasonal and correlated with rainfall (4, 8, 54).

Xylophagous beetles took longer to demonstrate a positive response to post-hurricane conditions compared to sap-sucking and predatory beetles. This delay may be associated with the heavy rains that accompanied the hurricane, disfavoring the colonization of new hosts due to an increase in the moisture content of the available deadwood resources (55). Later, at the end of the rains was accompanied by an increase in the richness and abundance of xylophagous beetles. Strong winds associated with hurricanes cause an increase in the amount and diversity of susceptible deadwood resources, such as tree falls, stem breakage, as well as the fall of coarse and fine wood debris of different tree species, which lead to an increase in xylophagous beetle populations (27, 28). In addition, standing dying trees, live trees with broken parts or partially uprooted also constitute an important resource for this guild, explaining together their high population levels throughout 2016. During 2017, the xylophagous guild presented clear seasonal variations, with a high abundance in the transition between the previous wet (2016) and the dry season of 2017. These results are in agreement with a previous study conducted in a Brazilian tropical dry forest, which found a greater abundance of Scolytinae beetles at the beginning of a dry season (15). In our study, a large portion of the xylophagous guild (90% of the individuals, 50% of species) belongs to the Scolytinae subfamily. These beetles spend most of their life cycle protected within the host plant, where the microclimatic conditions are stable and adults only emerge from their brood tree to mate and colonize a new host (54). During the selection of new hosts the scolytids are attracted to volatile substances emitted by the plants, usually from recently injured, stressed, dying or dead trees (56,57,58), and the new entrance hole is usually located at a leaf scar, axil, crevice, or other irregularity in the host bark (55). The flight activity of scolytid adults is usually short, and they seems to avoid very dry and rainy periods to search for a new host, due to the desiccation and the increased moisture content of available deadwood resources, respectively (15, 55). A previous study has shown that the transition between wet and dry seasons may be a more favorable period for beetle flight because air moisture still remains high (15). In addition, during this period in TDFs most plants begin to lose their leaves due to water limitation, increasing the availability of susceptible stressed hosts and nest entrance sites, such as leaf scars (12).

Richness and abundance of predatory beetles also increased during post-hurricane period. This positive response of predatory beetles may be result of the greater availability of prey after hurricanes, as observed for sap-sucking and xylophagous guilds in our study, and for other groups of invertebrates such as detritivores (29, 33) and dipteran species (41). However, predatory beetles also decrease in richness and abundance with the arrival of the dry season of 2016, presenting clear seasonal variations with a high species richness and abundance in the rainy seasons compared to the dry seasons of 2016 and 2017. In addition to disfavoring abiotic conditions during dry seasons, a decrease in the availability of prey (other arthropods) may be an important factor regulating predatory beetle populations in TDFs (2, 3, 4, 5, 6, 8). In our study, the richness and abundance of predatory beetles was similar to the pattern presented by sap-sucking and folivorous beetles but differ from that observed for xylophagous guild. Similarly, a previous study conducted in an Australian rainforest also showed that the seasonality of predatory beetles is more similar to that of folivorous, fungivorous and saprophagous beetles than to xylophagous (59).

We observed that the richness and abundance of most insect guilds presented small variations between seasons in 2015. The El Niño–Southern Oscillation caused changes in the rainfall pattern in the region of our study during 2015, with a 1,000% above normal precipitation in the dry season (60). Different from expected for the temporal fluctuations in insect communities between seasons in TDFs, 2015 presented small differences, no differences or even a greater richness and abundance of insect guilds during the abnormal dry season. An experimental irrigation study conducted in the same TDF of the present study revealed that at least 200 mm of rainfall during a dry season are needed to cause a full canopy of newly emerged leaves (61). The heavy rains that occur during the dry season of 2015 exceed this value, allowing all deciduous trees to recover their canopy, which probably lead to an increase in insect populations.

Our results demonstrated that catastrophic hurricane disturbances may be important events that increase the richness and abundance of insects in TDFs. Particularly, the positive effects of the Hurricane Patricia on the studied insect communities were probably associated to the increase in the availability of resources to herbivores (new vegetative growth and wood debris) and prey to predatory beetles. We also demonstrated that despite these positive effects, the insect communities oscillated through the years that followed the hurricane due to the strong seasonality of the environmental conditions in the TDF. In fact, a seasonal pattern congruent to all insect guilds was a lower species richness and abundance in the dry seasons, confirming the role of this season in TDFs as an ecological filter that lead to a reduction in insect populations (62).

Materials and Methods

Study area

This study was conducted in the Chamela-Cuixmala Biosphere Reserve (CCBR, 19º30’N, 105º03’W) and its surroundings, in Jalisco, Mexico (Fig. 1). The vegetation of the region consists primarily of tropical dry forests with a mean annual rainfall of 748 mm, and a dry season that normally extends from November to May (Fig. 3A, 63).

The year 2015 was abnormal in terms of the rainfall by influence of the El Niño–Southern Oscillation (60). February and March, usually dry months with low rainfall (<10 mm), presented a total rainfall of 116 mm and 282 mm respectively (Fig. 3B). In addition, at 23 of October 2015 Hurricane Patricia, estimated as a category 5 on the Saffir-Simpson Hurricane Wind Scale, reached the southwestern coast of Mexico in the state of Jalisco, near Playa Cuixmala, heavily impacting the Chamela-Cuixmala Biosphere Reserve region (Fig. 1). Heavy rains were associated with the hurricane, for a total of 350 mm in October, extending the rainy season until December (Fig. 3B). Hurricane Patricia is considered as the strongest hurricane that made landfall in the Western Hemisphere which has been reported so far (26). The village of Chamela was one of the most affected, in which the strong winds tore roofs off of homes and businesses, uprooted, snapped and defoliated nearly all trees (Fig. 4A, 26). On the other hand, the years 2016 and 2017 were normal in relation to rainfall, with well-defined dry and rainy seasons (Fig. 3C and D).

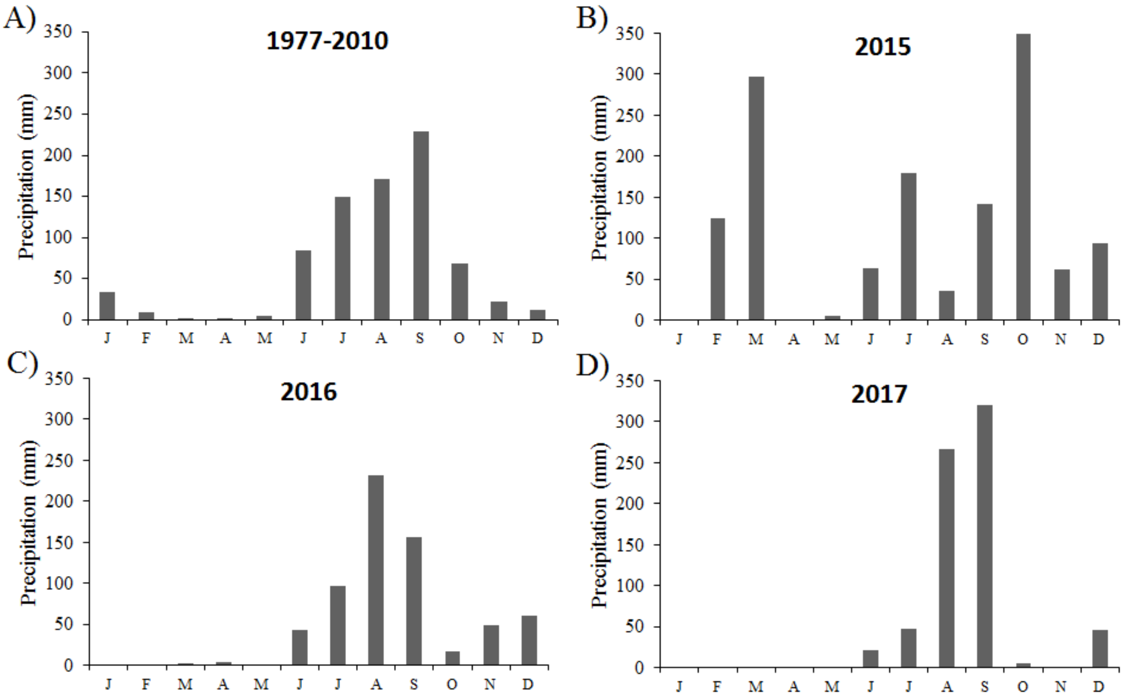


Figure 3.

Figure 4.

Sampling design

In 2015, nine 20 m x 50 m plots were selected in CCBR region at a minimum distance of 200 m (Fig. 1), in which the community of insects was sampled in the following periods: transition between wet and dry seasons (February), dry season (April) and rainy season (August) for three consecutive years (2015-2017). Insect communities were also sampled in two months after Hurricane Patricia struck directly our study sites (December 2015 and January 2016), for eleven sampling periods in total.

Sampling of insects

We collected the insects using combined flight Malaise/window traps (Fig. 3B; 50, 64). With an exception, one trap per plot (9 total) holding two vial collectors with 70% ethanol were exposed for five days (120 h) in the canopy of the same tree during all sampling periods, at a height ranging from 4 to 7 m in the center of each plot. If any of these trees broke after the hurricane, the traps were placed in the canopy of the nearest neighboring tree. August/2015 traps were exposed for 10 days (240 h).

All of the insects belonging to families with prevailing herbivorous habits were considered herbivores (64, 65). The sampled herbivorous insects were grouped into three guilds according to their feeding habit – sap-sucking, folivorous and xylophagous (see 64). Insects belonging to the suborders Auchenorrhyncha and Sternorrhyncha were considered sap-sucking herbivores, while insects belonging to the suborder Heteroptera were considered herbivores or not depending on the prevailing habit of their respective family. Chrysomelidae, Curculionidae and Megalopodidae were considered folivorous. Butterflies and moths were excluded from the sampled. The subfamilies Platypodinae and Scolytinae (Curculionidae) and families Anobiidae and Cerambycidae were included in the guild of xylophagous herbivorous insects, which are groups that preferentially feed on wood parts or build galleries to cultivate fungi for feeding, depending directly or indirectly from the wood resource for survival. Beetles belonging to families with predominantly predatory habits were grouped into the guild of predatory beetles (50). All insects were identified to family level and morphotyped based on external morphological characters (66).

Statistical analysis

We used Linear Mixed Models (LMER; lme4 package in R) to test whether the abundance and richness of herbivorous insects and predatory beetles were affected by sample period. To have comparable values among sampling periods we divided insect abundance and richness per guild (sap-sucking, folivorous, xylophagous and predatory beetles) by the number of days that the traps were exposed in each sampling period. We then used the insect abundance and richness per day trap, as response variables. Collection month was nested within the random effects of the sites sampled during the study (67). Significance was estimated with an ANOVA between the complete (H1) and the null model (H0). The Akaike Information Criterion (AIC) was used to rank the models, since it represents the uncertainty of the model a lower value of the AIC represents the more parsimonious model. When significant differences were observed between sample periods, contrast analysis was conducted using aggregating levels (68). If the level of aggregation was not significant and did not alter the deviance explained by the null model, the levels were pooled together (contrast analyses). All analyses were performed using R software version 3.4.1 (69).

Data availability

The datasets generated and analysed during the current study are available from the corresponding author upon reasonable request.

References

1. Wolda, H. Insect seasonality: why? *Annu. Rev. Ecol. Syst.***19**, 1-18(1988).

2. Kishimoto-Yamada, K. & Itioka, T. How much have we learned about seasonality in tropical insect abundance since Wolda (1988)? *Entomol. Sci*. **18**, 407-419 (2015).

3. Janzen, D. H. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* **54**, 687–708 (1973).

4. Duarte-Junior, J. A. & Schlindwein, C. The highly seasonal hawkmoth fauna (Lepidoptera Sphingidae:) of the caatinga of northeast Brazil: a case study in the state of Rio Grande do Norte. *J. Lepid. Soc*. **59**, 212 (2005).

5. Neves, F. S. *et al.* Successional and seasonal changes in a community of dung beetles (Coleoptera: Scarabaeinae) in a tropical dry forest. *Nat. Conserv.* **8,** 160–164 (2010).

6. Vasconcellos, A. *et al.* Seasonality of insects in the semi-arid Caatinga of northeastern Brazil. *Rev. Bras. Entomol*. **54**, 471-476 (2010).

7. Liberal, C. N., Farias, A.M.I., Meiado, M. V., Filgueiras, B. K. & Iannuzzi, L. How habitat change and rainfall affect dung beetle diversity in Caatinga, a Brazilian semi-arid ecosystem. *J. Insect. Sci.* **11**, 1–11 (2011).

8. Nobre, C. E. B., Iannuzzi, L.& Schlindwein, C. Seasonality of fruit-feeding butterflies (Lepidoptera, Nymphalidae) in a Brazilian semiarid area. *ISRN Zoology* 268159; 10.5402/2012/268159 (2012).

9. Beirão, M. V., Neves, F. S., Penz, C. M., DeVries, P. J. & Fernandes, G. W. High butterfly beta diversity between Brazilian cerrado and cerrado–caatinga transition zones. *J. Insect Conserv*. **21**, 849-860 (2017).

10. van Schaik, C. P., Terborgh, J. W. & Wright, S. J. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst*. **24**, 353-377 (1993).

11. Borchert, R. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* **75**, 1437-1449 (1994).

12. Lopezaraiza-Mikel, M. *et al.* Phenological Patterns of Tropical Dry Forests along Latitudinal and Successional Gradients in the Neotropics in *Tropical Dry Forests in the Americas: Ecology, Conservation, and Management* (eds Sanchez-Azofeifa, A., Powers, J. S., Fernandes, G. W. & Quesada, M.), 101-128 (CRC Press, 2013).

13. Pezzini, F. F. *et al.* Changes in tree phenology along natural regeneration in a seasonally dry tropical forest. *Plant Biosyst.* **148**, 965-974 (2014).

14. Creão-Duarte, A., Hernández, M., Rothéa, R.& Santos, W. Temporal variation of Membracidae (Hemiptera: Auchenorrhyncha) composition in areas of caatinga with different vegetation structures. *Sociobiology* **63**, 826-830 (2016).

15. Macedo-Reis, L. E.*et al*. Spatio-Temporal Distribution of Bark and Ambrosia Beetles in a Brazilian Tropical Dry Forest. *J. Insect Sci.* **16,** 48 (2016).

16. Schowalter, T. D. Insect responses to major landscape-level disturbance. *Annu. Rev. Entomol* .**57**, 1-20(2012).

17. Levin, S. A. & Paine, R. T. Disturbance, patch formation, and community structure. *P. Natl. Acad. Sci.* **71**, 2744-2747 (1974).

18. Connell, J. H. Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302-1310 (1978).

19. Brokaw, N. V. L. & Grear, J. S. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. *Biotropica* **2**, 386–392 (1991).

20. Scatena, F. N., Moya, S., Estrada, C. & Chinea, J. D. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo

in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica* **28,** 424–440 (1996).

21. Vandermeer, J., Boucher, D., Perfecto, I. & Cerda, I. G. A theory of disturbance and species diversity: evidence from Nicaragua after Hurricane Joan. *Biotropica* **28**,600-613 (1996).
22. Lomascolo, T. & Aide, T. M. Seed and seedling bank dynamics in secondary forests following Hurricane Georges in Puerto Rico. *Caribb. J. Sci.* **37**, 259-270 (2001).
23. Gouvenain, R. C. & Silander, J. A. Do tropical storm regimes influence the structure of tropical lowland rain forests? *Biotropica* **35,** 166–180 (2003).
24. Beard, K. H. *et al*. Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. *Ecol. Monogr.* **75(3),** 345-361 (2005).
25. Lugo, A. E. Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecol.* **33(4),** 368-398 (2008).
26. Kimberlain, T.B., Blake, E.S. & Cangialosi, J.P. Hurricane Patricia (EP202015). National Hurricane Center Tropical Cyclone Report (NOAA, Miami, Florida, 2016).
27. Bouget, C. & Duelli, P. The effects of windthrow on forest insect communities: a literature review. *Biol. Conserv.* **118**,281-299 (2004).
28. Grimbacher, P. S. & Stork, N. E. How do beetle assemblages respond to cyclonic disturbance of a fragmented tropical rainforest landscape? *Oecologia***161**, 591-599 (2009).
29. Schowalter, T. D., Willig, M. R. & Presley, S. J. Post-hurricane successional dynamics in abundance and diversity of canopy arthropods in a tropical rainforest. *Environ. Entomol.* **46**, 11-20 (2017).
30. Price, P. W. *et al.* Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Ann. Rev. Ecol. Syst.* **11,** 41-65 (1980).
31. Polis, G. A. & Strong, D. R. Food web complexity and community dynamics. *Am. Nat.* **147**, 813-846 (1996).
32. Schowalter, T. D. & Ganio, L. M. Invertebrate communities in a tropical rain forest canopy in Puerto Rico following Hurricane Hugo. *Ecol. Entomol.* **24**, 191-201 (1999).
33. Schowalter, T. D. & Ganio, L. M. Diel, seasonal and disturbance induced variation in invertebrate assemblages in *Arthropods of Tropical Forests (*eds Basset, Y., Navotny, V., Miller, S. & Kitching, R.) 315–328 (Cambridge University Press, Cambridge, United Kingdom, 2003).
34. Hirao, T., Murakami, M., Iwamoto, J., Takafumi, H. & Oguma, H. Scale-dependent effects of windthrow disturbance on forest arthropod communities. *Ecol. Res.* **23**, 189-196 (2008).
35. Schowalter, T. D., Willig, M. R. & Presley, S. J. Canopy arthropod responses to experimental canopy opening and debris deposition in a tropical rainforest subject to hurricanes. *Forest Ecol. Manag.* **332,** 93-102 (2014).
36. Shiels, A. B., González, G. & Willig, M. R. Responses to canopy loss and debris deposition in a tropical forest ecosystem: Synthesis from an experimental

manipulation simulating effects of hurricane disturbance. *Forest Ecol. Manag.* **332**, 124-133 (2014).

37. Willig, M. R. *et al.* Cross-scale responses of biodiversity to hurricane and anthropogenic disturbance in a tropical forest. *Ecosystems* **10,** 824–838 (2007).

38. Knutson, T. R. *et al*. Global projections of intense tropical cyclone activity for the late twenty-first century from dynamical downscaling of CMIP5/RCP4.5 scenarios. *J. Climate*. **28**,7203-7224 (2015).

39. Sugi, M., Murakami, H. & Yoshida, K. Projection of future changes in the frequency of intense tropical cyclones. *Clim. Dynam.* **49**,1-14 (2016).

40. Sobel, A. H. *et al*.Human influence on tropical cyclone intensity. *Science* **353**, 242-246 (2016).

41. Barberena-Arias, M. F. & Aide, T. M. Variation in Species and Trophic Composition of Insect Communities in Puerto Rico. *Biotropica* **34**, 357-367 (2002).

42. Parker, G., Martínez-Yrízar, A., Álvarez-Yépiz, J. C., Maass, M. & Araiza, S. Effects of hurricane disturbance on a tropical dry forest canopy in western Mexico. *Forest Ecol. Manag.*10.1016/j.foreco.2017.11.037 (2017).

43. Angulo-Sandoval, P., Fernandez-Marin, H., Zimmerman, J. K. & Aide, T. M. Changes in patterns of understory leaf phenology and herbivory following hurricane damage. *Biotropica* **36**, 60-67 (2004).

44. Raven, J. A. Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. *Adv. Ecol. Res.***13**, 135-234 (1983).

45. Douglas, A. E. The nutritional quality of phloem sap utilized by natural aphid populations. *Ecol. Entomol.***18**, 31-38 (1993).

46. Wolda, H. Seasonal fluctuations in rainfall, food and abundance of tropical insects. *J. Anim. Ecol.* **47**, 369-381(1978).

47. Turton, S. M. & Siegenthaler, D. T. Immediate impacts of a severe tropical cyclone on the microclimate of a tropical rainforest canopy in northeast Australia. *J. Trop. Ecol.* **20**, 583–586 (2004).

48. Zhou, Z. S., Guo, J. Y., Chen, H. S. & Wan, F. H. Effect of humidity on the development and fecundity of *Ophraella communa* (Coleoptera: Chrysomelidae). *Bio. Control*. **55**, 313-319 (2010).

49. Hou, Y. & Weng, Z. Temperature-dependent development and life table parameters of *Octodontanipae* (Coleoptera: Chrysomelidae). *Environ. Entomol*. **39**, 1676-1684 (2010).

50. Novais, S. M., Macedo-Reis, L. E. & Neves, F. S. Predatory beetles in cacao agroforestry systems in Brazilian Atlantic forest: a test of the natural enemy hypothesis. *Agroforest. Syst.* **91**, 201-209 (2017).

51. Hunter, M. D. & Forkner, R. E. Hurricane damage influences foliar polyphenolics and subsequent herbivory on surviving trees. *Ecology*, **80(8)** 2676-2682 (1999).

52. Godfray, H. C. J. & Hassell, M. P. Natural enemies may be a cause of discrete generations in tropical insects. *Nature* **327**, 144-147(1987).

53. Torres, J. A. Lepidoptera outbreaks in response to successional changes after the passage of Hurricane Hugo in Puerto Rico. *J. Trop. Ecol.* **8**, 285-298 (1992).

54. Janzen, D. H. Ecological characterization of a Costa Rican dry forest caterpillar fauna. *Biotropica* **20**,120-135(1988).

55. Wood, S. L. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph (ed. Wood, S. L), 1365pp.(Brigham Young University, 1982).

56. Schroeder, L. M. & A. Lindelow. Attraction of scolytids and associated beetles by different absolute amounts and proportions of α-pinene and ethanol. *J. Chem. Ecol.* **15**, 807-817(1989).

57. Hulcr, J., Beaver, R. A., Puranasakul, W., Dole, S. A. & Sonthichai, S. A comparison of bark and ambrosia beetle communities in two forest types in Northern Thailand (Coleoptera: Curculionidae: Scolytinae and Platypodinae). *Environ. Entomol*. **37**, 1461-1470 (2008).

58. Ranger, C. M., Reding, M. E., Persad, A. B. & Herms, D. A. Ability of stress-related volatiles to attract and induce attacks by *Xylosandrus germanus* and other ambrosia beetles. *Agric Forest Entomol*. **12**, 177-185 (2010).

59. Grimbacher, P. S. & Stork, N. E. Seasonality of a diverse beetle assemblage inhabiting lowland tropical rain forest in Australia. *Biotropica* **41**, 328-337 (2009).

60. Onogi K., Goto, A. & Mochizuki, Y. TCC News. Tokyo Climate Center, Japan Meteorological Agency. **43**, 1-11 (2016).

61. Hayden, B., Greene, D. F.& Quesada, M. A field experiment to determine the effect of dry-season precipitation on annual ring formation and leaf phenology in a seasonally dry tropical forest. *J. Trop. Ecol.* **26**, 237-242 (2010).

62. Young, A. M. Effects of Seasonality on Insect Populations in the Tropics in *Population biology of tropical insects* (ed Young, A. M), 273-333 (Springer Science & Business Media, 2012).

63. García-Oliva, F., Camou, A. & Maass, J. M. El clima de la region central de la costa del pacific mexicano in *Historia Natural de Chamela (*eds Noguera-Alderte, A. N., Vega-Rivera, J. H., Garcia-Aldrete, A. N. & Quesada, M) 3–10 (Instituto de Biología, UNAM, 2002)

64. Novais, S. M., Macedo-Reis, L. E., DaRocha, W. D. & Neves, F. S. Effects of habitat management on different feeding guilds of herbivorous insects in cacao agroforestry systems. *Rev. Biol. Trop*. **64**, 763-777 (2016).

65. Neves, F. S., Silva, J. O., Espirito-Santo, M. M. & Fernandes, G. W. Insect herbivores and leaf damage along successional and vertical gradients in a tropical dry forest. *Biotropica*. **46,** 14-24 (2014).

66. Arnett, R. H. Jr. American Insects, a Handbook of Insects of America North of Mexico (ed Arnett, R. H. Jr.) 1024pp. (USA, FL-Boca Raton: CRC Press, 2000).

67. Bates D., Maechler, M. Bolker, B. & Walker S. Fitting linear mixed effects models using lme4. *J. Stat. Softw*. **67**, 1–48 (2015).

68. Crawley, M. J. The R Book (ed. Crawley, M. J.), 1051pp.(John Wiley & Sons, Chichester,2013).

69. R Development Core Team. R: A language and environment for statistical computing. https://cran.r-project.org/ (2018).

Acknowledgments

We are grateful to A. Costa, O. Carrillo, M. Aguilar-Aguilar, B. Bravo, R. Garcia, K. Sanchez-Gomez, E. Perez, A. Rivera, T. Bahia, S. Lopez, N. Valdespino and R. Duran for field help. We thank L. Villanueva-Espino for help with map construction. S. Novais and L.E. Macedo-Reis thank CAPES (PDSE- Sandwich Doctoral Programme Abroad) for research grants awarded during the development of this study. This study was supported by grant from Universidad Nacional Autónoma de México (PAPIIT # IN212714-3, IV200418), CONACyT (# 2009-131008 and # 155016) SAGARPA-CONACYT 291333 and CONACYT-UNAM-UAGro to LANASE (2015-LN250996, 2016-LN271449, 2017-LN280505, 2018-LN293701). Finally, we thank the Chamela-Cuixmala Biosphere Reserve for all the physical structure, logistical support and for providing rainfall data. This study was performed in partial fulfillment of the requirements of the Ph.D. degree of S. Novais in Ecology, Conservation and WildLife Management, Federal University of Minas Gerais, Brazil.

Author Contributions

S.N., L.E.M.R., F.N. and M.Q designed the study. S.N., L.E.M.R., E.C.P and G.S.M. collected the insects. S.N. and L.E.M.R. identified the insects and performed analyzes. S.N. drafted the manuscript. S.N., L.E.M.R., E.C.P., M.J., F.N. and M.Q. completed and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Figure Legends

Figure 1. Map of municipality of La Huerta, Jalisco, showing the location of the Chamela-Cuixmala Biosphere Reserve and the nine study sites. The red line and the blue boundaries represent respectively the path of Hurricane Patricia and their maximum winds obtained from historical hurricane tracks of the National Oceanic and Atmospheric Administration (https://coast.noaa.gov/hurricanes/).

Figure 2. Mean (±SE) richness and abundance of sap-sucking (**A, B**), folivorous beetles (**C, D**), xylophagous (**E, F**) and predatory beetles (**G, H**) sampled in eleven periods in the canopy of a tropical dry forest, Jalisco, Mexico. Samples were carried out in the transition wet/dry, dry and rainy season (February, April and August, respectively) from 2015-2017. Two samples were also conducted in December 2015 and January 2016 after the passage of the Hurricane Patricia (October 2015). Different letters represent significant differences among groups ($p < 0.05$).

Figure 3. Long-term mean monthly precipitation for the period 1977–2010 (**A**) and total monthly precipitation from January 2015 to December 2017 (**B-D**) at Chamela-Cuixmala Biosphere Reserve, in Jalisco, Mexico.

Figure 4. Tropical dry forest with fallen and denuded trees one week after Hurricane Patricia (October 2015) struck the Chamela region, in Jalisco, México (**A**). Malaise/window trap exposed in the canopy of a tree in January 2016, three months after Hurricane Patricia (**B**). Photos by E. Cristobal-Pérez and S. Novais, respectively.

Tables

Table 1. Results of Linear Mixed Models showing temporal variation in richness and abundance of herbivorous insects (sap-sucking, folivorous and xylophagous) and predatory beetles sampled in eleven periods in the canopy of a tropical dry forest, Jalisco, Mexico. Samples were carried out in the transition wet/dry, dry and rainy season (February, April and August, respectively) from 2015-2017. Two samples were also conducted in December 2015 and January 2016 after the passage of the Hurricane Patricia (October 2015).

Response variable	Explanatory variable	AIC (H1)	AIC (H0)	P
Sap-sucking richness	Month	264.58	309.18	<0.0001
Sap-sucking abundance		543.14	572.08	<0.0001
Folivorous beetles richness		-15.43	-6.41	<0.0001
Folivorous beetles abundance		53.56	64.4	<0.0001
Xylophagous richness		171.38	205.56	<0.0001
Xylophagous abundance		612.08	642.31	<0.0001
Predatory beetles richness		168.73	239.97	<0.0001
Predatory beetles abundance		532.23	577.55	<0.0001

Electronic supplementary material

Positive effects of the catastrophic Hurricane Patricia on insect communities

Samuel Novais, Luiz Eduardo Macedo-Reis, Edson Cristobal-Peréz, Gumersindo Sánchez-Montoya, Milan Janda, Frederico Neves& Mauricio Quesada

TABLE S1. Morphospecies richness (Rich.) and abundance (Abun.) of herbivorous insects (xylophagous, sap-sucking and folivorous) and predatory beetles sampled in eleven periods in the canopy of a tropical dry forest, Jalisco, Mexico. Samples were carried out in the transition wet/dry, dry and rainy season (February, April and August, respectively) from 2015-2017. Two samples were also conducted in December 2015 and January 2016 after the passage of the Hurricane Patricia (October 2015).

Guild/Taxon	Feb-15		Apr-15		Aug-15		Dec-15		Jan-16		Feb-16		Apr-16		Aug-16		Feb-17		Apr-17		Aug-17		Total	
	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.	Rich.	Abun.
Sap-sucking/Hemiptera																								
Auchenorrhyncha																								
Achilidae					4	5	2	4	3	3					3	4					4	6	11	22
Cicadellidae	24	166	24	57	34	122	30	226	39	288	40	322	23	110	37	346	33	143	9	22	25	165	84	1967
Cicadidae					1	1																	1	1
Cixiidae															1	1	1	1			1	2	2	4
Flatidae					1	2									1	1							1	3
Membracidae	1	1							2	2	1	1			1	2					3	3	4	9
Sternorrhyncha																								
Psyllidae	3	7	3	25	3	8	4	6	11	12	7	14	4	5	2	3	1	1			3	3	25	84
Heteroptera																								
Alydidade															1	1							1	1
Coreidae			1	1																			1	1
Cydnidae			2	2			1	2	1	1	1	1	1	1	1	1			1	1	3	3	2	12
Enicocephalidae					1	3	1	1			1	1											1	5
Largidae					1	1	1	4	1	2					3	3					1	1	5	11
Lygaeidae	1	1					2	2			1	1					2	2			1	1	5	7
Miridae	3	7	3	20			3	25	3	44	3	45	1	1	1	3	1	2	1	2	1	1	3	150

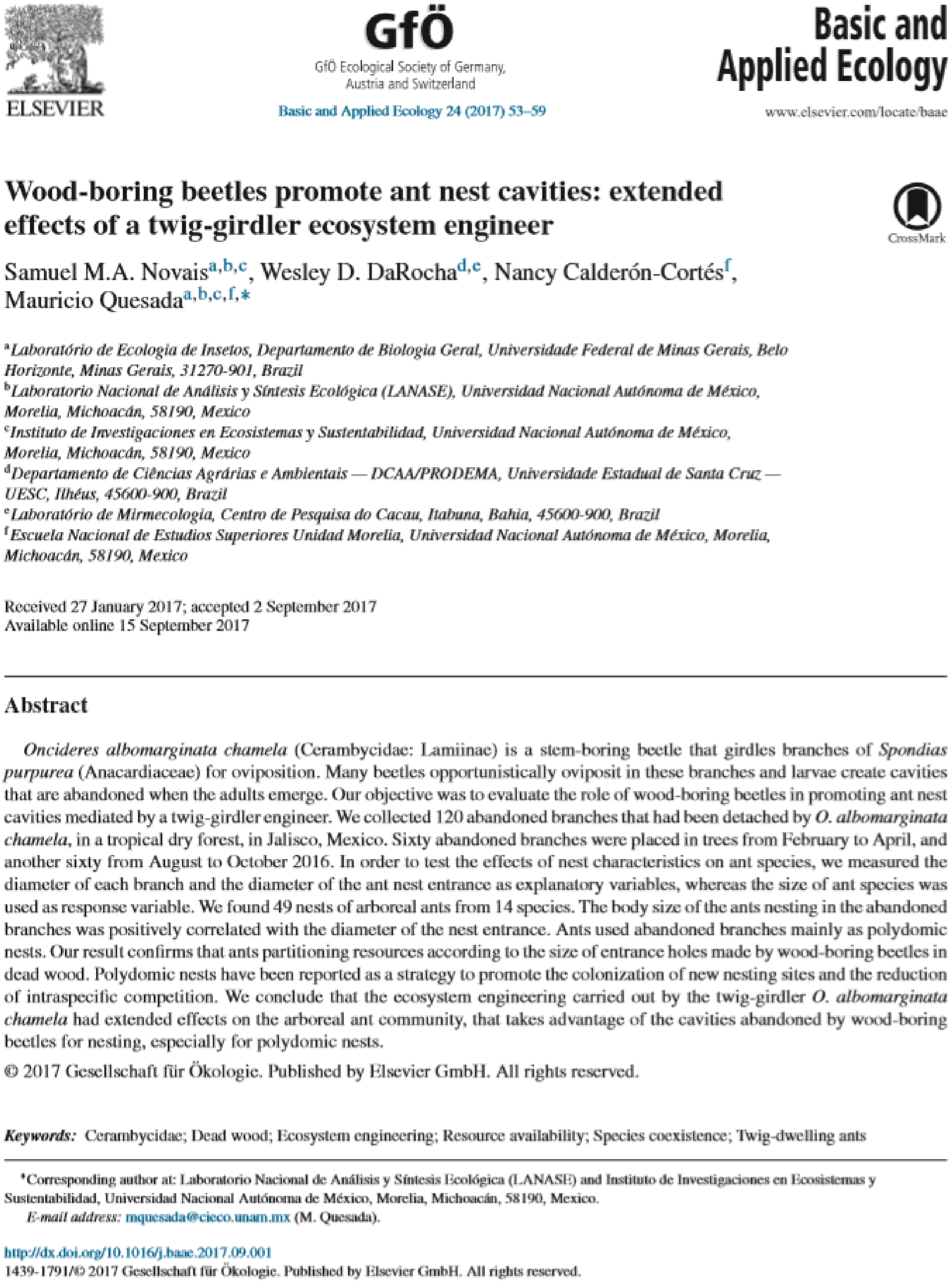
Rhopalidae											1	1											1	1
Tingidae	1	1																			1	1	2	2
Not Identified							1	1			1	1			1	1					1	1	2	4
Folivorous/Coleoptera																								
Curculionidae	1	1	1	1	4	6	5	6	4	4	1	1	1	1	8	13	6	12	2	3	3	3	24	51
Chrysomelidae	3	4	6	7	9	10	1	1	3	3	5	5			8	17					8	9	26	56
Megalopodidae					1	7			1	1					1	1							3	9
Predators/Coleoptera																								
Anthicidae					1	1	2	3	3	3	1	3			8	23	1	1	1	1	4	7	10	42
Carabidae	2	17	5	10	3	9	5	249	4	180	3	97	2	36	5	15	2	3	3	4	1	1	9	617
Cleridae			1	1	5	5					1	2			2	5					7	8	11	25
Coccinelidae	2	3	3	4	3	9	4	6	4	18	2	5	2	2	6	26	2	2			3	3	13	78
Histeridae					6	64	1	1			1	1			6	51	1	3	3	3	7	188	11	311
Laemopholeidae									3	6	2	2	1	1	3	3	2	3	1	1	2	3	7	19
Lamparidae					1	7																	1	7
Monotomidae	1	1			1	1	1	2	2	7	2	10	2	20	1	6	2	41	3	8			6	96
Passandridae																	1	1					1	1
Staphylinidae	4	16	6	18	9	23	19	167	17	118	10	224	6	69	18	76	9	51	6	10	14	30	35	694
Xylophagous/Coleoptera																								
Anobiidae			3	6	2	3	1	1	2	3	4	4	3	6	3	9	1	2	2	2	7	36	12	72
Bostrichidae	2	13	2	8	2	2	1	1	1	51	3	39	3	18			4	13	3	3	2	4	5	152
Cerambycidae	1	1			4	4	1	1							3	3	1	1	2	2	9	12	16	25
Curculionidae (Platipodinae)	1	1							2	3	1	2	3	6	2	17	2	2					3	31
Curculionidae (Scolytinae)	10	113	9	80	10	35	8	87	9	337	16	391	15	286	16	187	20	613	15	84	14	210	35	2423
TOTAL	60	353	69	240	106	328	94	796	115	1086	108	1173	67	562	142	818	92	897	52	146	125	701	379	6993

Conclusão Geral

Nos dois primeiros capítulos da tese avaliamos a importância de diferentes fatores espaciais e temporais sobre as comunidades de artrópodes associados diretamente e indiretamente com a engenharia ecossistêmica realizada pelo besouro *Oncideres albormaginata chamela*. No Capítulo 1, demonstramos que distúrbios antropogênicos e naturais são importantes fatores que causam variação espacial e temporal nas comunidades de insetos saproxílicos associados diretamente com a engenharia ecossistêmica de *O. albormaginata chamela.* No Capítulo 2, demonstramos que a estratificação vertical e a sazonalidade são importantes fatores que causam variação espacial e temporal nas comunidades de artrópodes associados indiretamente com a engenharia ecossistêmica de *O. albormaginata chamela*. No Capítulo 3, utilizando ramos de *Spondias purpurea* previamente cortados por *O. albormaginata chamela*, demonstramos que os besouros brocadores são importantes facilitadores para formigas arborícolas, afetando a estrutura e organização de suas comunidades. As espécies de formigas utilizam as cavidades abandonadas como sítios de nidificação e particionam o uso dessas cavidades de acordo com o tamanho dos seus corpos. No Capítulo 4, demonstramos que a sazonalidade e o distúrbio ambiental causado por um furacão são importantes fatores que causam variação temporal nas comunidades de insetos associados ao dossel de uma floresta tropical seca.

Anexo I

Capa: Novais et al. 2017. Wood-boring beetles promote ant nest cavities: extended effects of a twig-girdler ecosystem engineer



ELSEVIER

GfÖ
GfÖ Ecological Society of Germany,
Austria and Switzerland

Basic and Applied Ecology 24 (2017) 53–59

Basic and
Applied Ecology

www.elsevier.com/locate/baae

Wood-boring beetles promote ant nest cavities: extended effects of a twig-girdler ecosystem engineer

Samuel M.A. Novais[a,b,c], Wesley D. DaRocha[d,e], Nancy Calderón-Cortés[f],
Mauricio Quesada[a,b,c,f,*]

[a] *Laboratório de Ecologia de Insetos, Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, 31270-901, Brazil*
[b] *Laboratorio Nacional de Análisis y Síntesis Ecológica (LANASE), Universidad Nacional Autónoma de México, Morelia, Michoacán, 58190, Mexico*
[c] *Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, 58190, Mexico*
[d] *Departamento de Ciências Agrárias e Ambientais — DCAA/PRODEMA, Universidade Estadual de Santa Cruz — UESC, Ilhéus, 45600-900, Brazil*
[e] *Laboratório de Mirmecologia, Centro de Pesquisa do Cacau, Itabuna, Bahia, 45600-900, Brazil*
[f] *Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, 58190, Mexico*

Received 27 January 2017; accepted 2 September 2017
Available online 15 September 2017

Abstract

Oncideres albomarginata chamela (Cerambycidae: Lamiinae) is a stem-boring beetle that girdles branches of *Spondias purpurea* (Anacardiaceae) for oviposition. Many beetles opportunistically oviposit in these branches and larvae create cavities that are abandoned when the adults emerge. Our objective was to evaluate the role of wood-boring beetles in promoting ant nest cavities mediated by a twig-girdler engineer. We collected 120 abandoned branches that had been detached by *O. albomarginata chamela*, in a tropical dry forest, in Jalisco, Mexico. Sixty abandoned branches were placed in trees from February to April, and another sixty from August to October 2016. In order to test the effects of nest characteristics on ant species, we measured the diameter of each branch and the diameter of the ant nest entrance as explanatory variables, whereas the size of ant species was used as response variable. We found 49 nests of arboreal ants from 14 species. The body size of the ants nesting in the abandoned branches was positively correlated with the diameter of the nest entrance. Ants used abandoned branches mainly as polydomic nests. Our result confirms that ants partitioning resources according to the size of entrance holes made by wood-boring beetles in dead wood. Polydomic nests have been reported as a strategy to promote the colonization of new nesting sites and the reduction of intraspecific competition. We conclude that the ecosystem engineering carried out by the twig-girdler *O. albomarginata chamela* had extended effects on the arboreal ant community, that takes advantage of the cavities abandoned by wood-boring beetles for nesting, especially for polydomic nests.

Keywords: Cerambycidae; Dead wood; Ecosystem engineering; Resource availability; Species coexistence; Twig-dwelling ants

---

[*] Corresponding author at: Laboratorio Nacional de Análisis y Síntesis Ecológica (LANASE) and Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, 58190, Mexico.
E-mail address: mquesada@cieco.unam.mx (M. Quesada).

http://dx.doi.org/10.1016/j.baae.2017.09.001
1439-1791/© 2017 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.