

Arthropod Facilitation by Wood-Boring Beetles: Spatio-temporal Distribution Mediated by a Twig-girdler Ecosystem Engineer

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Abstract

The twig-girdler beetle *Oncideres albomarginata chamela* (Cerambycidae: Lamiinae) detaches branches of *Spondias purpurea* L. (Sapindales: 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 by arthropods, we placed 60 branches on the forest floor (ground stratum) and 60 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 8,008 arthropods, which included 7,753 ants (14 species) and 255 nonsocial arthropods (80 species) from 13 different orders. We observed a greater arthropod abundance in the branches in the vegetation stratum in the dry season compared with the rainy season, whereas the richness and abundance of arthropods in the ground stratum were greater in the rainy season compared with 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.

Key words: vertical stratification, seasonality, dead wood, microhabitat, ecosystem engineering

Recent studies have demonstrated the role of caterpillars, gall-inducing insects, and 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, Wetzal 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 1 yr until these branches degrade (S. Novais, personal observation).

The structure of the Mexican TDF where the present study was carried out is characterized by a low canopy ranging from 5- to 10-m 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 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), whereas during the rainy season, there is an increase in abundance and diversity of arboreal arthropods associated with the new foliage growth (Vasconcellos et 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 with the abandoned branches of the tree *S. purpurea* that were previously engineered by *O. albomarginata chamela* in a TDF in Jalisco, Mexico. Based on the evidence

from the literature, we predict that 1) richness, abundance, and colonization frequency of arthropods in the detached branches in the vegetation stratum are greater in the rainy season compared with the dry season and 2) richness, abundance, and colonization frequency of arthropods in the detached branches in the ground stratum are greater in the dry season compared with the rainy season.

Material and Methods

Study Area and Sampling Design

This study was carried out in the Chamela-Cuixmala Biosphere Reserve (19°30' N, 105°03' W) in Jalisco, Mexico. The vegetation within the 13,142 ha of the reserve 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).

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 a greenhouse maintaining 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. We then selected 240 subsamples from this set of fragmented branches (hereinafter referred to as 'branches'); 120 branches were used from February to April (dry season) and 120 branches from August to October 2016 (rainy season). These branches had an average length of 42 cm (SD ± 16 cm) and at least one entrance per emergence cavity made by a beetle. In each season, we placed 60 branches on the forest floor (ground stratum) and hung another 60 branches in trees (vegetation stratum; Fig. 1). Branches were located under the canopy of 15 trees of *S. purpurea* that were at least 30 m apart from each other; 4 branches

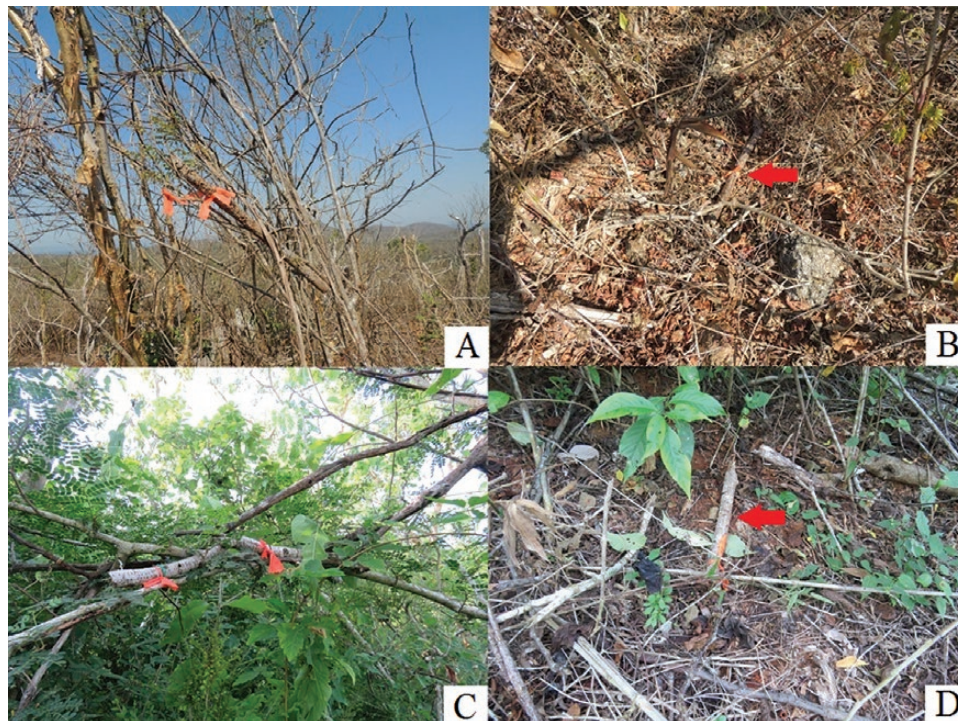


Fig. 1. Examples of *S. purpurea* branch samples that were previously engineering by *O. albomarginata chamela* and placed in two vertical strata and in different seasons in a TDF, in Jalisco, Mexico. Vegetation stratum in dry season (A), ground stratum in dry season (B), vegetation stratum in rainy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

Table 1. Spatio-temporal variation in arthropod richness (Rich.), abundance (Abund.), and colonization frequency (Freq.) in the abandoned cavities left by wood-boring beetles in *S. purpurea* branches that were previously engineered by *O. albomarginata chamela* in a TDF, in Jalisco, Mexico

Taxon	Dry						Rainy						Total	
	Vegetation			Ground			Vegetation			Ground			Rich.	Abund.
	Rich.	Abund.	Freq.	Rich.	Abund.	Freq.	Rich.	Abund.	Freq.	Rich.	Abund.	Freq.		
Arachnida	19	33	25 (42%)	3	7	3 (5%)	15	25	17 (28%)	12	50	25 (42%)	41	115
Opiliones ^a														
Pseudoscorpiones ^a	3	6	6 (10%)	1	1	1 (2%)	2	6	4 (7%)	1	1	1 (2%)	1	1
Scorpiones ^a	1	1	1 (2%)				1	5	4 (7%)				1	6
Solifugae ^a	1	1	1 (2%)											1
Chilopoda	4	32	19 (32%)				3	3	3 (5%)	2	2	2 (3%)	6	37
Diplopoda	2	7	7 (12%)				1	2	2 (3%)	1	2	2 (3%)	2	4
Insecta														
Blattodea	1	9	2 (3%)				1	5	4 (7%)				3	12
Coleoptera							1	2	2 (3%)				2	14
Anthicidae ^a							1	1	1 (2%)				1	2
Carabidae ^a							1	1	1 (2%)				1	1
Cantharidae ^a														1
Cryptophagidae	1	1	1 (2%)										1	1
Laemophloeidae ^a	1	1	1 (2%)										1	1
Scarabaeidae	1	1	1 (2%)										1	1
Silvanidae							1	1	1 (2%)				1	1
Staphylinidae ^a	1	1	1 (2%)										1	1
Coreidae														1
Hemiptera										1	1	1 (2%)	1	1
Pentatomidae										1	1	1 (2%)	1	1
Hymenoptera	10	4315	20 (33%)				11	3438	25 (42%)				14	7753
Formicidae							1	2	1 (2%)				3	4
Other	4	23	15 (25%)				3	7	5 (8%)				6	30
Orthoptera	1	7	6 (10%)										1	7
Gryllidae														
Malacostraca	50	4438	52 (87%)	4	8	3 (5%)	42	3502	46 (77%)	21	60	28 (52%)	94	8008
Isopoda														
Total														

^aTaxa considered as nonsocial predatory arthropods.

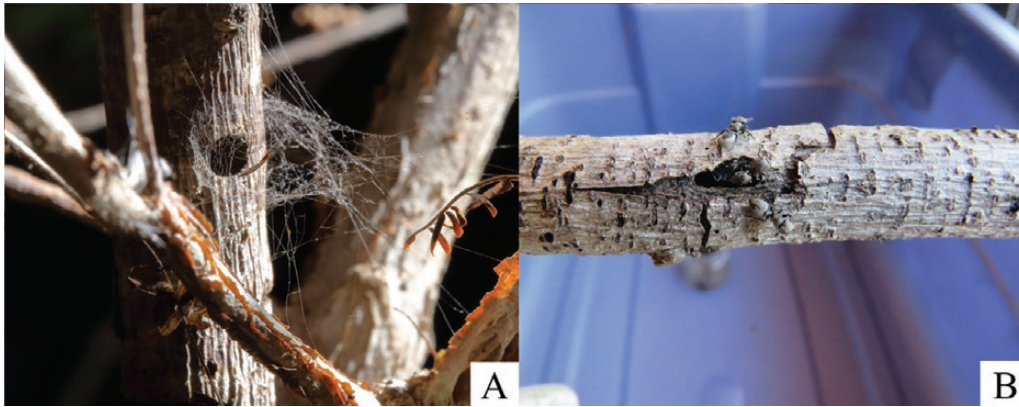


Fig. 2. Spider (A) and ants (B) colonizing cavities abandoned by wood-boring beetles in *S. purpurea* branches were previously engineered by *Oncideres albomarginata chamela* in a TDF, in Jalisco, Mexico. Photos by J. C. Mata and S. Novais, respectively.

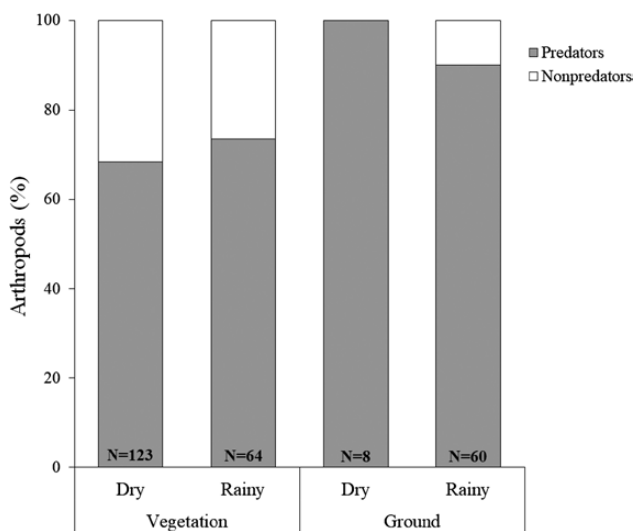


Fig. 3. Percentage of nonsocial predatory arthropods in the abandoned cavities left by wood-boring beetles in *S. purpurea* branches that were previously engineered by *O. albomarginata chamela* sampled in two vertical strata and in different seasons in a TDF, in Jalisco, Mexico.

on the ground stratum and 4 branches on the vegetation stratum. Branches were at least 2 m apart from each other and hung branches in the vegetation stratum were located approximately 1.5 m from the ground. Branches remained in the field for 2 mo to allow colonization and establishment of arthropod communities (Zuo et al. 2016). We then collected each branch in individual fine-mesh bags and transported them to the laboratory.

All collected branches from the field were carefully opened in a large tray, tall enough to prevent arthropods from escaping. The collections were limited to arthropods that could be seen and captured by hand, not considering organisms with a body size of <2 mm, such as Acari and Collembola. Arthropods were transferred to vials with 70% ethanol for further morphotyping at order level and classification into predators or nonpredators (García-Aldrete and Ayala 2004). Individuals belonging to the orders Coleoptera and Hemiptera were identified at family level and considered predators or not depending on the prevailing habit of their respective family (Arnett et al. 2001, 2002; Novais et al. 2016, 2017a). Termites colonizing the branches as food resources were not considered, because they were not using the abandoned wood-boring beetle cavities. Richness (number of morphospecies) and abundance (number of individuals) per branch were determined. We also estimated the

colonization frequency (% of colonized branches) of branches by registering the presence/absence of the arthropod morphospecies on each branch. The sampled arthropods were deposited in the entomological collection of the Laboratory of Evolutionary Ecology and Conservation of Tropical Forests of the National Autonomous University of Mexico.

Statistical Analysis

Generalized Linear Mixed Models 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, seasons (dry and rainy) and vertical strata (vegetation and ground) were used as fixed explanatory variables, and the 15 points (individuals of *S. purpurea*) per year as random effects. 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. The package 'lsmmeans' was used for *a posteriori* comparisons (Lenth et al. 2017). All analyses were performed using R software (R Core Team 2017).

Results

In total, 8,008 adult arthropods from 94 morphospecies were sampled in the 240 *S. purpurea* branches (Table 1). Spiders were the most species-rich group (41 species) followed by ants (14; Table 1; Fig. 2). Ants utilized the abandoned wood-boring beetle cavities as nesting sites, totaling 7,753 individuals in 49 nests, which were found exclusively in the vegetation stratum (Table 1; see Novais et al. 2017b). Among the 255 nonsocial arthropods sampled, most individuals for all strata and seasons were generalist predators, which include mainly spiders, followed by centipedes, beetles, pseudoscorpiones, scorpions, and solifuges (68%–100%; Fig. 3; Table 1).

Arthropod richness, abundance, and colonization frequency in the abandoned branches cavities varied significantly between strata in time (Table 2). Arthropod richness in the vegetation stratum did not differ significantly between seasons, whereas abundance was greater in the dry season compared with the rainy season (Fig. 4). For the ground stratum, arthropod richness and abundance were greater in the rainy season (Fig. 4). Frequency of branch colonization did not differ significantly in the vegetation stratum between seasons (87% in the dry and 77% in the rainy season), whereas for the ground stratum was greater in the rainy (52%) compared with the dry season (5%; Fig. 5).

Table 2. 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 *S. purpurea* branches that were previously engineered by *O. albomarginata chamela* in a TDF, in Jalisco, Mexico

Response variable	Explanatory variable	Error distribution	AIC (H1)	AIC (H0)	P
Arthropod richness	Season*Strata	Negative	566.11	602.00	<0.0001
	Season	Binomial	675.42	673.44	0.88
	Strata		600.43	673.44	<0.0001
Arthropod abundance	Season*Strata	Negative	630.69	664.63	<0.0001
	Season	Binomial	687.38	685.45	0.79
	Strata		663.78	685.45	<0.0001
Colonization frequency	Season*Strata	Binomial	229.05	250.48	<0.0001
	Season		423.37	424.17	0.09
	Strata		389.61	424.17	<0.0001

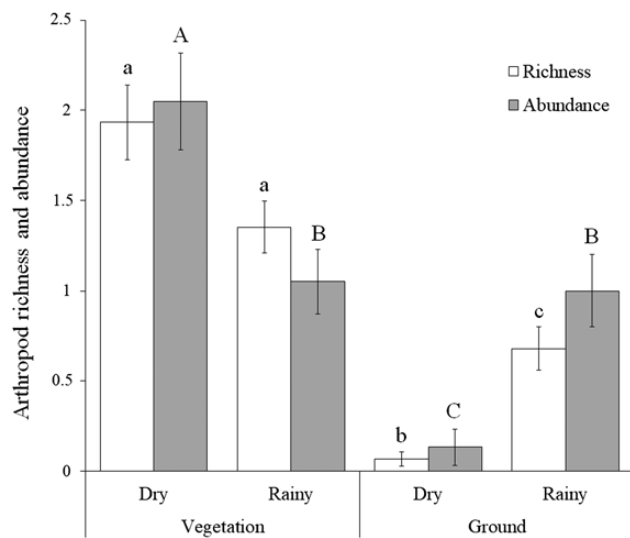


Fig. 4. Spatio-temporal variation in arthropod richness and abundance (mean \pm SE) in abandoned cavities left by wood-boring beetles in *S. purpurea* branches that were previously engineered by *O. albomarginata chamela* in a TDF, in Jalisco, Mexico. Ants were included in the analysis of richness but not in the analysis of abundance. Different letters represent significant differences among groups ($P < 0.05$).

Discussion

A previous study demonstrated that 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 depend on 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 communities, in which wood-boring beetles are important habitat facilitators for arthropods. We found that arthropod richness, abundance, and colonization frequency in the abandoned branch cavities were similar between dry and rainy seasons. However, contrary to expected, arthropod abundance in the vegetation stratum was greater in the dry season compared with rainy season, whereas for the ground stratum, arthropod richness, abundance, and colonization frequency were greater in the rainy season compared with the dry season.

Previous studies showed that arthropod richness and abundance are positively affected by increasing habitat structure (Langellotto and Denno 2004, Tews et al. 2004, Leal et al. 2016). However, we observed that arthropod abundance in the abandoned branch cavities was greater in the seasons when both vegetation and ground

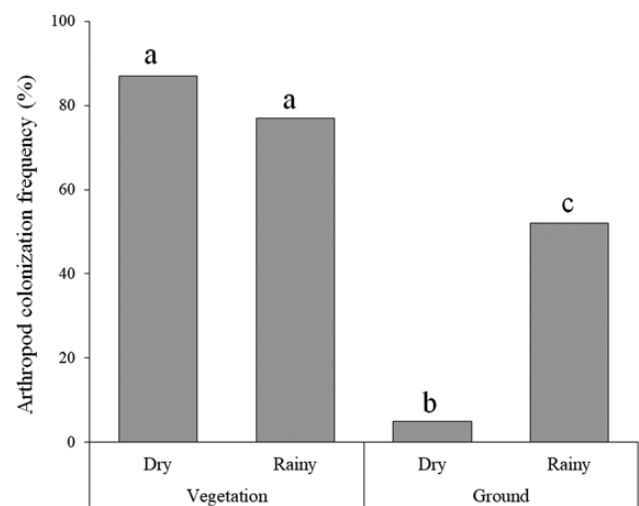


Fig. 5. Arthropod colonization frequency in abandoned cavities left by wood-boring beetles in *S. purpurea* branches that were previously engineered by *O. albomarginata chamela* in a TDF, in Jalisco, Mexico. Different letters represent significant differences among groups ($P < 0.05$).

strata were structurally simpler (i.e., less available microhabitats). During dry season in the TDF studied, 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 quick decomposition of the litterfall in this season leads to a decrease of microhabitats in the ground stratum (Anaya et al. 2012).

Similar 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-Cortés 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-Cortés et al. 2011, Sanders et al. 2014, Wetzel et al. 2016). In our study, although the proportion of predatory arthropods in the branches was probably overestimated by a limitation in our method for collecting potential prey species (e.g., springtails and mites), predatory arthropods were very abundant in all strata and seasons, suggesting that the habitat facilitation by wood-boring beetles also enhance further trophic interactions. We also highlight that most individuals of generalist predators were found in the branches in the vegetation stratum, as well as all sampled ants. Although often overlooked, dead wood that remain hanged on the live vegetation represent a significant phytomass component in the upper forest strata (Maass 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 nonsocial 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. 2017b).

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 enhances 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 nonsocial predatory arthropods and ants.

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