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Arthropod facilitation mediated by abandoned dead domatia

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Citation: Novais, S., E. J. Cristóbal-Perez, A. Aguirre-Jaimes, and M. Quesada. 2021. Arthropod facilitation mediated by abandoned dead domatia. Ecosphere 12(1):e03323. 10.1002/ecs2.3323

Abstract. In ant–plant mutualistic interactions, plants provide shelter (domatia) and/or food to ants and in exchange, and ants provide protection against herbivores. After plant tissue senescence, ants are expected to abandon dead domatia, leaving these empty spaces available for other arthropods. In this study, we tested for the role of the mutualistic interaction between *Cordia alliodora* and *Azteca pittieri* in promoting new habitats for arthropods through abandoned dead domatia. We predicted that species richness, abundance, and colonization frequency of secondary arthropods would be greater in dead branch domatia (dead domatia) compared with live branch domatia (live domatia). During March 2019, we selected 38 *C. alliodora* trees in a Mexican tropical dry forest. For each tree, we collected five live and five dead domatia, for 380 domatia in total. We found six morphospecies of secondary arthropods colonizing live domatia, while 42 were present in dead domatia. Ants were the most species-rich group (10 species) in abandoned dead domatia and utilized them as nesting sites (25 nests). Secondary arthropod species richness, abundance, and colonization frequency were greater in dead domatia compared with live domatia. We concluded that the *Azteca–Cordia* mutualistic interaction is an important habitat facilitator by promoting new habitats for arthropods through abandoned dead domatia.

Key words: Arthropod diversity; *Azteca pittieri*; *Cordia alliodora*; Ecosystem engineering; microhabitat.

Received 14 July 2020; accepted 22 July 2020. Corresponding Editor: Debra P. C. Peters.

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Introduction

Several insects modify plant structures to complete their life cycle, such as leafroller caterpillars, gall-inducing insects, bark, and wood-boring beetles. These new habitats might persist on plants and can be later used as shelter by other arthropods in a facilitative interaction process (Vieira and Romero 2013, Cornelissen et al. 2016, Zuo et al. 2016, Novais et al. 2018). Particularly, ants can take advantage of the abandoned shelters made by other insects for nesting, such as wood-boring beetle abandoned cavities (Tschinkel 2002, Satoh et al. 2016, Novais et al. 2017), senescent galls (Fernandes et al. 1988, Mehltreter et al. 2003, Almeida et al. 2014, Santos

et al. 2017, 2019), and empty cocoons (Raath et al. 2017).

In symbiotic ant–plant mutualisms, myrmecophytic plants already possess specialized structures for housing ants, known as domatia. These structures are present in different plant parts, such as in hollow stems (e.g., *Cecropia*, *Cordia*, *Leonardoxa*, *Macaranga*), thorns (*Acacia*), petioles (*Piper*), or leaf pouches (e.g., *Hirtella*, *Maieta*, *Scaphopetalum*, *Tococa*; Heil and Mckey 2003). In addition to nesting spaces, some myrmecophytic plants feed ants directly by producing extrafloral nectar (*Leonardoxa*, African *Acacia* species), cellular food bodies (*Cecropia*, *Macaranga*, *Piper*), or both (Central American *Acacia* species), or indirectly via hemipteran trophobionts tended by resident ants (Heil and Mckey 2003). In exchange for the nesting spaces and food resources, ants protect their myrmecophyte hosts against a broad range of herbivores, as already demonstrated by many experimental studies with different myrmecophytic plant species (Fonseca 1994, Gaume et al. 1997, Vasconcelos and Casimiro 1997, Letourneau 1998, Heil et al. 2001, Alvarez et al. 2001).

In specialized ant–plant mutualistic interactions, senescence of plant tissues is expected to cause the abandonment of dead domatia by ants because of the loss of food resources provided by the plants (e.g., extrafloral nectar, cellular food bodies, hemipteran trophobionts). Under such a scenario, abandoned dead domatia become empty spaces and may facilitate potential refuges for other arthropod species. To understand this new type of ecological facilitation, we test for the role of the well-studied mutualistic interaction between *Cordia alliodora* (Ruiz and Pavón) Oken (Boraginaceae) and *Azteca pittieri* Forel (Dolichoderinae; Pringle et al. 2011) in promoting new habitats for other arthropods through abandoned dead domatia.

Cordia alliodora is a Neotropical myrmecophitic tree with domatia at stem nodes. In the Mexican tropical dry forest, *C. alliodora* is mostly inhabited by the specialized ant species *Azteca pittieri*, although tree domatia may also be inhabited in very lower frequency by generalized stem-nesting species from other genera such as *Crematogaster* (Pringle et al. 2011). To access the domatia, founding ant queens gnaw entrance holes into unoccupied domatia starting egg posture, and as the colony grows, worker ants gnaw openings in other domatia throughout the tree and occupy them (Pringle et al. 2011). *C. alliodora* offers no direct food rewards for ants, and *Azteca* ants host hemipteran insects of the superfamily Coccoidea, known as coccoids, inside the domatia and eat their honeydew (Tillberg 2004, Pringle et al. 2011). Although coccoids compete with their host plant for resources by removing sap, Pringle et al. (2011) demonstrated that *C. alliodora* trees benefit from ant defense against other herbivores.

When a *C. alliodora* branch dies, it usually remains attached to the plant or fall and remains suspended on vegetation under *C. alliodora* canopies (S. Novais, *personal observation*). We observed that *Azteca* ants leave domatia in dead branches, and we asked whether these abandoned structures could be colonized by other arthropods. We hypothesized that ants in specialized ant–plant mutualistic interactions will abandon dead domatia after plant tissue senescence, allowing the colonization of these structures by other arthropods, and consequently, enhancing arthropod diversity. We predicted that species richness, abundance, and colonization frequency of secondary arthropods (non-*Azteca*-coccoids arthropods) would be greater in dead branch domatia compared with live branch domatia. We also investigated the density of *C. alliodora* trees and estimated the amount of live domatia per hectare in order to indirectly demonstrate the importance of the interaction between *A. pittieri* and *C. alliodora* trees in promoting new habitats for arthropod communities through abandoned dead domatia.

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 tropical dry forests (TDFs) with a mean annual rainfall of 748 mm, and a dry season that extends from November to June (García-Oliva et al. 2002).

During March 2019, we selected 38 *C. alliodora* trees at least 20 m apart from each other. For each *C. alliodora* tree, we collected five live

domatia and another five dead domatia, for 380 domatia in total. Dead domatia were localized on dry branches still attached on live *C. alliodora* trees or in felled branches that remain suspended on vegetation under *C. alliodora* tree canopy. Each domatium was placed in an individual fine-mesh bag and transported to the laboratory. These domatia had an average diameter of 1.47 cm (SD ± 0.4 cm). Domatia were frozen to incapacitate any inhabitants, and then carefully opened. Arthropods were transferred to vials with 70% ethanol for further morphotyping to the level of order (García-Aldrete and Ayala 2004). All mites were classified as morphospecies of Acari. Particularly, ant species were identified at genus or species level (see *Acknowledgments*). Species richness (number of morphospecies), abundance (number of individuals), and colonization frequency (percentage of colonized *C. alliodora* trees) of secondary colonizing arthropods (non-*Azteca*-coccoids arthropods) per *C. alliodora* tree were determined. 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.

Density of C. alliodora *trees and live domatia*

In order to estimate the density of *C. alliodora* trees/ha, we utilized data on the abundance of woody tree species sampled in nine 3 × 50 m plots established at the study site (see Lopezaraiza-Mikel et al. 2013). The density of *C. alliodora* live domatia/ha was estimated through the allometric regression model between the number of domatia and *C. alliodora* tree diameter found by Pringle et al. (2012) in a study conducted in the same tropical dry forest.

Statistical analysis

Generalized linear mixed models were used to test whether species richness, abundance, and colonization frequency of secondary arthropods (response variables) are higher in abandoned dead domatia than live domatia of *C. alliodora* trees. Domatium condition (dead and live) was used a fixed explanatory variable, and the 38 individuals of *C. alliodora* as a random effect. Ant individuals were not considered for abundance analysis due to the social character 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. All analyses were performed using R software (R Core Team 2020).

Results

For the total of 190 live domatia collected, ants inhabited 170 (89%), of which 165 (97%) were occupied by *A. pittieri* (13,728 individuals in total), three by *Pseudomyrmex cubaensis* (85), and two by *Crematogaster crinosa* (177). Regarding the occupation of these domatia by coccoids, 153 (81%) contained at least one individual (mean 9.95 ± SD 13.78 coccoids per domatium). None of the 190 dead domatia were occupied by *A. pittieri* or coccoids. We found six morphospecies of non-*Azteca*–coccoids arthropods colonizing live domatia, while 42 morphospecies were present in dead domatia (Table 1; Fig. 1). Ants were the most species-rich group (10 species) in the abandoned dead domatia and utilized them as nesting sites, totaling 863 individuals in 25 nests collected (Table 2; Fig. 2). Among the 425 nonsocial arthropods sampled in dead domatia, mites were the most abundant, followed by psocids, thrips, and beetles (Table 1). The most frequent groups in dead domatia were mites followed by thrips and ants (Table 1). Secondary arthropod species richness, abundance, and colonization frequency were greater in dead domatia compared with live domatia (Appendix S1: Table S1; Fig. 3).

We estimated that the density of *C. alliodora* trees was ~20 individuals/ha at the study site. Of a total of 144 plant species sampled in the nine 3 × 50 plots, *C. alliodora* was the sixteenth woody tree species with the highest density. The average diameter of all *C. alliodora* trees registered was 9.97 cm (SD ± 5.1 cm); a *C. alliodora* tree with this diameter is expected to have ~ 132 live domatia. Therefore, since the density of *C. alliodora* trees was ~ 20 individuals/ha, we estimated the presence of ~2640 live domatia/ha.

Discussion

Our results demonstrated for the first time the role of ant–plant mutualistic interactions in promoting new habitats for arthropods through

Table 1. Variation in secondary arthropod species richness (Rich.), abundance (Abund.), and colonization frequency at tree level (Freq.) in live and dead domatia of *Cordia alliodora* in a tropical dry forest, in Jalisco, Mexico.

		Dead			Live			Total	
Class	Subclass or order	Rich.	Abund.	Freq.	Rich.	Abund.	Freq.	Rich.	Abund.
Arachnida	Acari	8	218	37 (97%)	2	59	16 (42%)	8	277
	Araneae	4	4	4 (11%)				4	4
	Pseudoscorpiones	1	9	9 (23%)				1	9
Chilopoda	Geophilomorpha	3	7	7 (18%)				3	7
Entognatha	Collembola	3	15	7 (18%)				3	15
Insecta	Coleoptera	5	24	13 (34%)				5	24
	Hemiptera (Heteroptera)	1	7	3 (8%)	1	1	1 (3%)	1	8
	Hymenoptera (Formicidae)	10	863	20 (53%)				10	863
	Hymenoptera (Other)	4	14	4 (11%)				4	14
	Psocoptera	1	87	7 (18%)				1	87
	Thysanoptera	3	36	21 (55%)	3	3	3 (8%)	3	39
Malacostraca	Isopoda	1	4	4 (11%)				1	4
Total		42	1288	38 (100%)	6	63	17 (45%)	42	1351

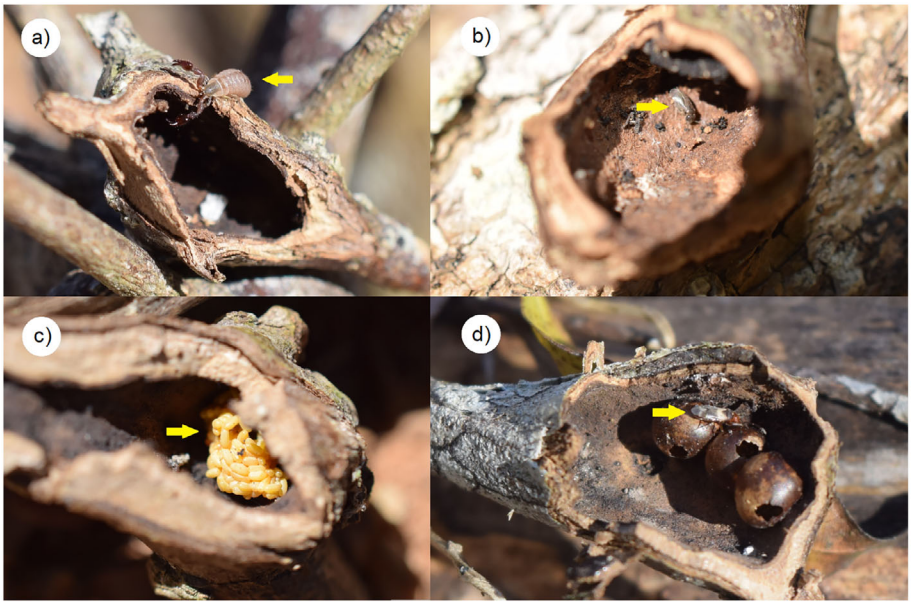


Fig. 1. Arthropods colonizing dead domatia of *Cordia alliodora* in a tropical dry forest, in Jalisco, Mexico. Pseudoscorpion (a), Psocoptera (b), unidentified eggs (c), and Hemiptera (d). Photos by A. Aguirre-Jaimes.

abandoned dead domatia. All living branches of *C. alliodora* had at least one domatium with the presence *A. pittieri* individuals, confirming that this species has a specialized association with the host plant *C. alliodora*. This result also suggests that the few unoccupied domatia in live branches, which had no entrance holes, would probably be occupied as the *Azteca* colonies expanded. In contrast, only three percent of live domatia were colonized by *Pseudomyrmex cubaensis* and *Crematogaster crinosa*, suggesting that these species opportunistically occupy empty domatia in this system. After *C. alliodora* branches with domatia senesce and dried out,

Table 2. Abundance of ant species nesting in dead domatia of *Cordia alliodora* in a tropical dry forest, in Jalisco, Mexico.

Taxon	Abundance	
	Worker	Immature
Camponotus linnaei Forel, 1886	8	0
Camponotus linnaei Forel, 1886	7	15
Camponotus linnaei Forel, 1886	43	6
Camponotus linnaei Forel, 1886	3	0
Camponotus linnaei Forel, 1886	32	12
Camponotus linnaei Forel, 1886	4	0
Camponotus sp1	10	0
Camponotus sp2†	6	23
Cephalotes toltecus	19	25
Crematogaster curvispinosa Mayr, 1862	69	70
Crematogaster curvispinosa Mayr, 1862†	56	35
Crematogaster curvispinosa Mayr, 1862	134	0
Crematogaster curvispinosa Mayr, 1862	77	6
Crematogaster curvispinosa Mayr, 1862	3	11
Crematogaster crinosa Mayr, 1862	12	12
Forelius mccooki McCook, 1879	80	0
Forelius mccooki McCook, 1879	17	0
Forelius mccooki McCook, 1879	204	0
Nesomyrmex wilda Smith, M.R., 1943	5	0
Nesomyrmex wilda Smith, M.R., 1943†	6	6
Pseudomyrmex cubaensis Forel, 1901	9	47
Pseudomyrmex cubaensis Forel, 1901	23	100
Pseudomyrmex cubaensis Forel, 1901	25	151
Pseudomyrmex sp1	8	46
Pseudomyrmex sp1	3	32
Total	863	597

† Represents nests with a queen ant.

Azteca ants leave these dead tissues probably because they no longer serve as a food source for the hemipteran coccoids that, in turn, are not able to provide food resources for ants. In fact, no dead domatium was found occupied by *A. pittieri* or coccoids, but these structures are reused in great majority by a different arthropod community that is not present in live domatia. The abandoned dead domatia, therefore, represent a safe and durable refugia in which many species of secondary arthropods can use as breeding sites, shelter, or nesting sites (Figs. 1, 2).

A recent study conducted in the same tropical dry forest demonstrated the role of wood-boring beetles as important habitat facilitators for arthropods, which utilize the abandoned cavities made by beetle larvae during their development in the wood (Novais et al. 2018). Comparing the arthropod community that reused both abandoned cavities (branches *vs* domatia), Novais et al. (2018) found that spiders (115 individuals), centipedes (37), and crickets (30) were the most abundant nonsocial arthropods in a set of 240 *Spondias purpurea* L. (Anacardiaceae) branch samples. In the present study, we found only four spiders, seven centipedes, and no crickets within a total of 380 domatia samples. These differences are probably related to the variation of entrance hole sizes between both sorts abandoned cavities. *S. purpurea* branches are primary colonized by more than twenty species of wood-boring beetles of various sizes (1.59–21.97 mm; Calderón-Cortes et al. 2011), which leave cavities with a great variety of entrance sizes (0.49–6.25 mm; Novais et al. 2017), allowing the colonization by different-sized arthropod species (S. Novais, personal observation). However, the entrance holes made by *Azteca* ants in domatia are little and homogeneous (≈2 mm; see Fig. 2), allowing only small arthropods to have access.

Ants were an important group colonizing the abandoned dead domatia as nesting sites, as briefly described by Longino (1996) for dead domatia of *C. alliodora* trees in Costa Rica. This author reported that ant species that are generalist inhabitants of dead wood (i.e., stems, branches, and twigs) can take advantage of the abandoned dead domatia as nesting sites. Since most twig-dwelling ants, except for carpenter ants in the genus *Camponotus*, cannot excavate sound wood to build their nests (King et al. 2018), they depend on other organisms to create new cavities for them, nesting almost exclusively in abandoned tunnels of wood-boring beetles (Tschinkel 2002, Powell et al. 2011, Novais et al. 2017). Similarly here, our results suggest that the entrance holes made by ants (e.g., *Azteca*) able to excavate live tissues in domatia of myrmecophytic plants facilitate the access of twig-dwelling ants into dead domatia after their abandonment.

The availability of nesting sites represents a limiting resource for arboreal ants (Philpott and Foster 2005, Mottl et al. 2019, Novais et al. 2020). Previous studies have demonstrated an increase in arboreal ant abundance and distribution when the availability and diversity of nesting sites is increased (Sagata et al. 2010, Powell et al. 2011, Jiménez-Soto and Philpott 2015). In a recent study, Novais et al. (2020) showed that dry fallen

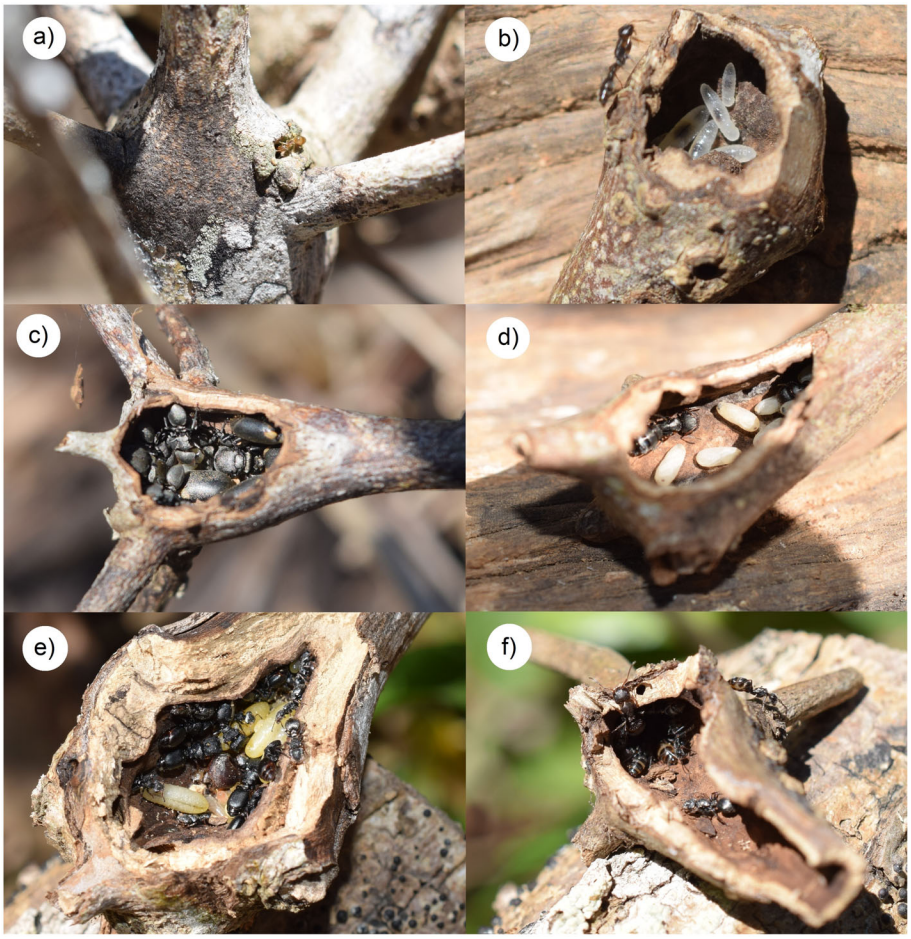


Fig. 2. Ants nesting in dead domatia of *Cordia alliodora* in a tropical dry forest, in Jalisco, Mexico. *Nesomyrmex wilda* (a), *Pseudomyrmex* sp. (b), *Cephalotes* sp. (c, e), and *Camponotus linnaei* (d, f). Photos by A. Aguirre-Jaimes.

petioles of *Cecropia* trees represent an important nesting resource for arboreal twig-nesting ants, and therefore, they suggested that *Cecropia* trees are key components of tropical forests that maintain arboreal ant diversity by promoting a substantial increase in the availability of nesting sites for arboreal twig-nesting ants through dry fallen petioles. In the present study, we suggest that dead domatia of *C. alliodora* trees also represent an important nesting resource for arboreal twig-nesting ants. Compared with *Cecropia* trees that shed a few leaves each day and hundreds of leaves can accumulate on the vegetation below their canopy over time (see Novais et al. 2020), domatia of *C. alliodora* trees do not seem to dry out as often. However, contrary to *Cecropia* petioles which their pith is the most voluminous portion and consists of soft, spongy parenchyma, *C. alliodora* stems consist of sound wood (Devall et al. 1988, Wightman et al. 2001), and therefore, the abandoned dry domatia are likely to remain available for colonization by twig-nesting ants for a much longer period of time until their degradation compared with *Cecropia* petioles.

We found that almost 88% of dead domatia that were occupied by ants did not contain an ant queen. Similar results have also been reported by other abandoned structures made by insects, such senescent galls and wood-boring beetle abandoned cavities, which are mainly colonized by ant species that develop polydomic colonies (Almeida et al. 2014, Santos et al. 2017, Novais et al. 2017). The construction of polydomic nests is a strategy to increase the

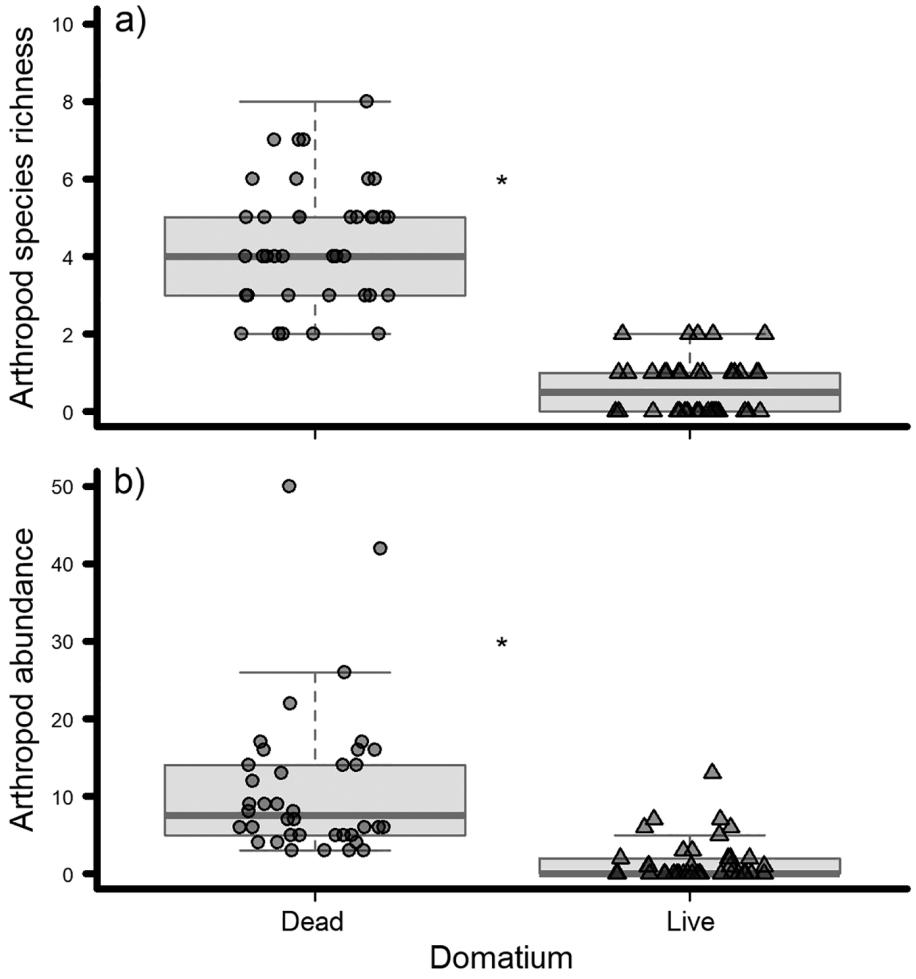


Fig. 3. Boxplots of species richness (a) and abundance (b) of secondary arthropods per tree colonizing live and dead domatia of *Cordia alliodora* in a tropical dry forest, in Jalisco, Mexico. The horizontal thick gray band represents the median value, and the boxplot margins indicate first and third quartiles, the whiskers represent the maximum/minimum value within one and a half times the interquartile range, and each dot represents the arthropod species richness and abundance per tree ($N = 38$). Single asterisk represents significant differences ($P < 0.05$).

distribution of the colony in order to avoid predation and reduce local intraspecific competition for the same resources by bringing workers closer to new food sources (Debout et al. 2007, Lanan et al. 2011, Robinson 2014). In an experimental study to investigate whether colonies of *Crematogaster torosa* form new polydomous nests to better exploit temporally stable food resources, Lanan et al. (2011) found that when food was present, most colonies formed polydomous nests nearby.

Conclusions

We conclude that the *Azteca–Cordia* mutualistic interaction is an important habitat facilitator by promoting new habitats for arthropods through abandoned dead domatia. After senescence of plant tissues, the abandoned dead domatia are occupied by a diverse arthropod community that is not present in live domatia colonized *Azteca* ants, increasing species richness and abundance of arthropods locally. Ants were the most

species-rich group in the abandoned dead domatia, which take advantage of these structures left by *Azteca* ants to expand their polydomic colonies. At large scales, dead wood in the form of dying and dead trees, standing or fallen branches at different stages of decay are important resources (e.g., food, shelter, and breeding sites) for the conservation of a large number of species, such as saproxylic insects, lichens, bryophytes, birds, and mammals; Radu 2006). At a fine scale, we highlight the importance of dead plant tissues in the form dead branches attached on living trees and fallen branches hanged on vegetation as potential refugia that maintain arthropod diversity, which can be mediated by insects such as wood-boring beetles (Novais et al. 2018) or through abandoned dead domatia as demonstrated in the present study.

Acknowledgments

We are grateful to Dora Luz Martinez Tlapa (INECOL) for the identification of ant species. We are grateful to Gumersindo Sánchez-Montoya for field help. We are grateful to anonymous reviewers for their comments on an earlier version of the manuscript. This study was supported by grants from Universidad Nacional Autónoma de México (PAPIIT # IN212714-3, IV200418), SAGARPA-CONACYT 291333, CONACYT-UNAM-UAGro to LANASE (2015-LN250996, 2016-LN271449, 2017-LN280505, 2018-LN293701, and 2019-299033 and Programa Iberoamericana de Ciencia y Tecnología para el Desarrollo RED CYTED SEPODI (417RT0527). Finally, we thank the Chamela-Cuixmala Biosphere Reserve for all the physical structure and logistical support.

Literature Cited

Almeida, M. F. B. D., L. R. D. Santos, and M. A. A. Carneiro. 2014. Senescent stem-galls in trees of *Eremanthus erythropappus* as a resource for arboreal ants. Revista Brasileira De Entomologia 58:265–272.

Alvarez, G., I. Armbrecht, E. Jiménez, H. Armbrecht, and P. Ulloa-Chacón. 2001. Ant-plant association in two *Tococa* species from a primary rain forest of Colombian Choco (Hymenoptera: Formicidae). Sociobiology 38:585–602.

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

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

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

Devall, M. S., B. R. Parresol, and S. J. Wright. 1988. Dendroecological Analysis of *Cordia alliodora*, *Pseudobombax septenatum* and *Annona spraguei* in Central Panama. IAWA Journal 16:411–424.

Fernandes, G. W., W. J. Boecklen, R. P. Martins, and A. G. Castro. 1988. Ants associated with a coleopterous leaf-bud gall on *Xylopia aromatica* (Annonaceae). Proceedings of the Entomological Society of Washington 91:81–87.

Fonseca, C. R. 1994. Herbivory and the long-lived leaves of an Amazonian ant-tree. Journal of Ecology 82:833–842.

García-Aldrete, N. A., and R. Ayala. 2004. Artrópodos de Chamela. Instituto de Biología, Universidad Nacional Autónoma de México, México.

García-Oliva, F., A. Camou, and J. M. Maass. 2002. El clima de la región central de la costa Del Pacífico mexicano. Pages 3–10 *in* A. N. Noguera-Alderte, J. H. Vega-Rivera, A. N. Garcia-Aldrete, and M. Quesada, editors. Historia natural de Chamela. Instituto de Biología, Universidad Nacional Autónoma de México, México.

Gaume, L., D. McKey, and M. C. Anstett. 1997. Benefits conferred by 'timid' ants: active anti-herbivore protection of the rainforest tree *Leonardoxa africana* by the minute ant *Petalomyrmex phylax*. Oecologia 112:209–216.

Heil, M., B. Fiala, U. Maschwitz, and K. E. Linsenmair. 2001. On benefits of indirect defense: short- and long-term studies in antiherbivore protection via mutualistic ants. Oecologia 126:395–403.

Heil, M., and D. McKey. 2003. Protective ant-plant interactions as model systems in ecological and evolutionary research. Annual Review of Ecology, Evolution, and Systematics 34:425–553.

Jiménez-Soto, E., and S. M. Philpott. 2015. Size matters: nest colonization patterns for twig-nesting ants. Ecology and Evolution 5:3288–3298.

King, J. R., R. J. Warren, D. S. Maynard, and M. A. Bradford. 2018. Ants: ecology and impacts in dead wood. Pages 237–262 *in* M. D. Ulyshen, editor. Saproxylic insects - diversity. Ecology and Conservation. Springer, Berlin, Germany.

Lanan, M. C., A. Dornhaus, and J. L. Bronstein. 2011. The function of polydomy: The ant *Crematogaster torosa* preferentially forms new nests near food sources and fortifies outstations. Behavioral Ecology and Sociobiology 65:959–968.

Letourneau, D. K., and L. A. Dyer. 1998. Density patterns of *Piper* ant-plants and associated arthropods: top-predator trophic cascades in a terrestrial system. Biotropica 30:162–169.

Longino, J. T. 1996. Taxonomic characterization of some live-stem inhabiting *Azteca* (Hymenoptera: Formicidae) in Costa Rica, with special reference to the ants of *Cordia* (Boraginaceae) and *Triplaris* (Polygonaceae). Journal Hymenoptera Research 5:131–156.

Lopezaraiza-Mikel, M. et al. 2013. Phenological patterns of tropical dry forests along latitudinal and successional gradients in the neotropics. Pages 101–128 *in* A. Sanchez-Azofeifa, J. S. Powers, G. W. Fernandes and M. Quesada, editors. Tropical Dry Forests in the Americas: Ecology, Conservation, and Management. CRC Press, Boca Raton.

Mehltreter, K., P. Rojas, and M. Palacios-Rios. 2003. Moth larvae-damaged giant leather-fern *Acrostichum danaeifolium* as host for secondary colonization by ants. American Fern Journal 93:49–56.

Mottl, O., J. Yombai, T. M. Fayle, V. Novotný, and P. Klimeš. 2019. Experiments with artificial nests provide evidence for ant community stratification and nest site limitation in a tropical forest. Biotropica 52:277–287.

Novais, S., N. Calderón-Cortés, G. Sánchez-Montoya, and M. Quesada. 2018. Arthropod facilitation by wood-boring beetles: spatio-temporal distribution mediated by a twig-girdler ecosystem engineer. Journal of Insect Science 18:1–7.

Novais, S., W. D. DaRocha, N. Calderón-Cortés, and M. Quesada. 2017. Wood-boring beetles promote ant nest cavities: extended effects of a twig-girdler ecosystem engineer. Basic and Applied Ecology 24:53–59.

Novais, S., V. Hernández-Ortiz, K. Rodríguez-Hernández, M. Quesada, J. Valenzuela, G. W. Fernandes, and A. Aguirre-Jaimes. 2020. Ants nesting in dry fallen petioles of *Cecropia obtusifolia* Bertol. (Urticaceae): vertical stratification and nest site limitation. Insectes Sociaux 67:273–279.

Philpott, S. M., and P. F. Foster. 2005. Nest-site limitation in coffee agroecosystems: Artificial nests maintain diversity of arboreal ants. Ecological Applications 15:1478–1485.

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

Pringle, E. G., R. Dirzo, and D. M. Gordon. 2011. Indirect benefits of symbiotic coccoids for an ant-defended myrmecophytic tree. Ecology 92:37–46.

Pringle E. G., R. Dirzo, and D. M. Gordon. 2012. Plant defense, herbivory, and the growth of Cordia alliodora trees and their symbiotic Azteca ant colonies. Oecologia 170:677–685.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Radu, S. 2006. The ecological role of deadwood in natural forests. Pages 137–141 *in* D. Gafta and J. Akeroyd, editors. Nature Conservation. Springer, Heidelberg, Germany.

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

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

Santos, L. R. D., R. D. S. M. Feitosa, and M. A. A. Carneiro. 2017. The role of senescent stem-galls over arboreal ant communities structure in *Eremanthus erythropappus* (DC.) MacLeish (Asteraceae) trees. Sociobiology 64:7–13.

Santos, M. G., G. F. Porto, I. R. Lancellotti, and R. M. Feitosa. 2019. Ant fauna associated with *Microgramma squamulosa* (Kaulf) de la Sota (Polypodiaceae) fern galls. Revista Brasileira de Entomologia. Revista Brasileira De Entomologia 63:101–103.

Satoh, T., T. Yoshida, S. Koyama, A. Yamagami, M. Takata, H. Doi, T. Kurachi, S. Hayashi, T. Hirobe, and Y. Hata. 2016. Resource partitioning based on body size contributes to the species diversity of wood-boring beetles and arboreal nesting ants. Insect Conservation and Diversity 9:4–12.

Tillberg, C. V. 2004. Friend or foe? A behavioral and stable isotopic investigation of an ant-plant symbiosis. Oecologia 140:506–515.

Tschinkel, W. R. 2002. The natural history of the arboreal ant, *Crematogaster ashmeadi*. Journal of Insect Science 2:1–15.

Vasconcelos, H. L., and A. B. Casimiro. 1997. Influence of *Azteca alfari* ants on the exploitation of Cecropia trees by a leaf-cutting ant. Biotropica 29:84–92.

Vieira, C., and G. Q. Romero. 2013. Ecosystem engineers on plants: indirect facilitation of arthropod

communities by leaf-rollers at different scales. Ecology 94:1510–1518.
Wightman, K. E., T. Shear, B. Goldfarb, and J. Haggar. 2001. Nursery and field establishment techniques to improve seedling growth of three Costa Rican hardwoods. New Forests 22:75–96.
Zuo, J., J. H. Cornelissen, M. M. Hefting, U. Sass-Klaassen, R. S. van Logtestijn, J. van Hal, L. Goudzwaard, J. C. Liu, and M. P. Berg. 2016. The (w) hole story: Facilitation of dead wood fauna by bark beetles? Soil Biology and Biochemistry 95:70–77.

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