



Revisiting ecological dominance in arboreal ants: how dominant usage of nesting resources shapes community assembly

Flávio Camarota^{1,2,3} · Heraldo L. Vasconcelos² · Robert J. Marquis⁴ · Scott Powell¹

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Abstract

Ecologically dominant species can shape the assembly of ecological communities via altering competitive outcomes. Moreover, these effects may be amplified under limited niche differentiation. Nevertheless, the influences of ecological dominance and niche differentiation on assembly are rarely considered together. Here, we provide a novel examination of dominance in a diverse arboreal ant community, defining dominance by the prevalent usage of nesting resources and addressing how it influences community assembly. We first used a series of quantitative observational and experimental studies to address the natural nesting ecology, colony incidence on surveyed trees, and level of dominance over newly available nesting resources by our focal species, *Cephalotes pusillus*. The experimental studies were then used further to examine whether *C. pusillus* shapes assembly via an influence on cavity usage by co-occurring species. *C. pusillus* was confirmed as a dominant user of cavity nesting resources, with highly generalized nesting ecology, occupying about 50% of the trees within the focal system, and accounting for more than a third of new cavity occupation in experiments. Our experiments showed further that the presence of *C. pusillus* was associated with modest effects on species richness, but significant decreases in cavity-occupation levels and significant shifts in the entrance-size usage by co-occurring species. These results indicate that *C. pusillus*, as a dominant user of nesting resources, shapes assembly at multiple levels. Broadly, our findings highlight that complex interactions between a dominant species and the resource-usage patterns of other species can underlie species assembly in diverse ecological communities.

Keywords Community assembly · Ecological dominance · Interspecific competition · Niche differentiation · Resource specialization

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✉ Flávio Camarota
camarotaflavio@gmail.com

- ¹ Department of Biological Sciences, The George Washington University, Washington, USA
- ² Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, Brazil
- ³ Instituto de Biologia Geral, Universidade Federal de Viçosa, Viçosa, MG, Brazil
- ⁴ Department of Biology and the Whitney R. Harris World Ecology Center, University of Missouri-St. Louis, St. Louis, MO 63121, USA

Introduction

Ecological dominance has long been thought to have important implications for the assembly of biological communities (Connell 1961; MacArthur 1965; Whittaker 1965; McNaughton and Wolf 1970; May 1975; He and Legendre 2002; Hillebrand et al. 2008). Ecologically dominant species have been defined by a number of characteristics, including an unusually high density and biomass within the community (Whittaker 1965; McNaughton 1968; Guo and Rundel 1997), interacting with most other species, and using a substantial proportion of essential or limited resources (McNaughton and Wolf 1970; Price 1971). Moreover, the potential effects of ecological dominance may interact with the degree to which competing species share limited resources (Morse 1974), with the impacts of the dominant species amplified when niche differentiation is limited (McNaughton and Wolf 1970; Price 1971). Despite the

potential interconnection between ecological dominance and niche differentiation, these two influences on community assembly are rarely considered together in highly diverse communities. Experimental tests of the interactions between these processes are rarer still. Whether dominance and niche structure interact in ways that meaningfully shape community assembly, therefore, remains an open question in community ecology, especially in diverse tropical systems.

The presence of dominant species is often considered a remarkable feature of arboreal ant communities (Blüthgen and Stork 2007), and much research attention has been given to assessing the role of dominance in community assembly (e.g., Diaz-Castelazo et al. 2004; Sanders et al. 2007; Dáttilo et al. 2014). This issue is of particular importance, because arboreal ants comprise a significant part of the species diversity and biomass of tropical ecosystems and they have a wide-reaching footprint on the food web (Majer 1990; Tobin 1991; Davidson and Patrell-Kim 1996; Floren et al. 2002; Davidson et al. 2003). Most studies of dominance within arboreal ant communities have emphasized the same definition and context: behavioral dominance in direct competitive interactions at food resources (e.g., Andersen 1992; Gibb and Hochuli 2004; Parr and Gibb 2012). Typically, this behavioral dominance has been assessed at seasonally variable food resources, like hemipteran aggregations and extra-floral nectaries, or at artificial food baits as a proxy of behavioral outcomes at natural food resources. The effects of behavioral dominance at food resources are then expected to scale to a community-wide influence on assembly.

Many observational studies have examined whether behavioral dominance over food is associated with a community-wide spatial structuring of ant species within the canopy (e.g., Room 1971; Greenslade 1971; Majer 1972; Jackson 1984; Leponce et al. 2019). More specifically, they have asked whether behaviourally and numerically dominant species establish mutually exclusive territories, and other species have positive and negative associations with these dominants (Leston 1978; Dejean and Corbara 2003; Dejean et al. 2007, 2010; Pfeiffer et al. 2008). The presence and strength of this proposed assembly process, known as the ant-mosaic hypothesis, is still being debated in the literature. The formation of mutually exclusive territories by a small number of behaviourally and numerically dominant species is not in question. Yet, support for the community-wide structuring of assembly that is hypothesized to follow from the formation of dominant territories is equivocal across managed and natural systems (Floren and Linsenmair 2000; Blüthgen and Stork 2007; Cerdá et al. 2013; Stuble et al. 2017). While this debate continues, it is important to consider that this may represent only one form of ecological dominance, and potential influence on assembly, within arboreal ant communities. Given the variety of ways in which species can assert ecological dominance in other taxa, examining the potential

contribution of other forms of dominance on assembly in arboreal ant communities may be beneficial. This may be especially true for forms of ecological dominance related to resources other than food.

Spanning diverse habitats worldwide, a high proportion of arboreal ant species nest primarily or exclusively in pre-existing cavities in tree wood. These cavities represent a critical resource base that contrasts food resources in its characteristics and associated species interactions, and over which species may still attain ecological dominance. Pre-existing wood cavities can be derived from a variety of processes, but many are the direct or indirect products of damage by wood-boring beetle larvae, and can be found in dead and live wood (Carroll 1979; Calderón-Cortés et al. 2011; Satoh et al. 2016). Unlike food resources, cavity resources are highly stable, because they can persist in location and properties (e.g., entrance size and volume) throughout the life of the tree. Nevertheless, availability may be limited at any given moment (reviewed in Blüthgen and Feldhaar 2010). Indeed, the ever-present competitive interactions over limited nesting cavities have been well supported by rapid colonization of supplemental cavities in diverse arboreal ant assemblages (Philpott and Foster 2005; Philpott 2010; Powell et al. 2011; Jiménez Soto and Philpott 2015; Philpott et al. 2018; Mottl et al. 2020) and by examining the process of cavity usurpation (Powell 2009; Powell et al. 2017). These community-level dynamics appear to be underpinned by established colonies constantly seeking out additional cavities with suitable properties that would allow colony expansion (Powell 2009; Powell and Dornhaus 2013; Powell et al. 2017), and the establishment of new colonies by founding queens (Powell et al. 2011).

Under conditions of limited resource availability, such as the limited cavity availability in arboreal ant communities, niche differentiation should help to maintain species diversity (Chesson 2000; Chase and Leibold 2003; Levine and HilleRisLambers 2009). In contrast, the presence of a dominant species may disrupt stable patterns of niche partitioning for a limited resource and reduce diversity (McNaughton and Wolf 1970). Cavity entrance size is now well established as an important axis of niche differentiation in arboreal ant communities, with greater entrance-size diversity promoting greater species richness (Powell et al. 2011; Jiménez Soto and Philpott 2015). Additionally, we know that the availability of specific entrance sizes can be critical for the process of colony growth and expansion for individual species (Powell 2009). Yet, it is not known whether any ant species exerts ecological dominance over cavity nesting resources, and, therefore, whether the presence of such a species can influence community assembly via a disruption of resource usage by other species.

Previous work has suggested that the turtle ant *Cephalotes pusillus* is potentially a dominant user of cavity nesting

resources in the diverse arboreal ant communities of the Neotropical Cerrado biome. Yet critically, *C. pusillus* does not meet the typical definition of a dominant arboreal ant, which are widely defined as being behaviourally dominant at food resources, living in large colonies, and territorial (Leston 1978; Dejean and Corbara 2003). While the tree-level incidence of *C. pusillus* species is high in the focal cerrado system (Ribas et al. 2010; Powell et al. 2011; Camacho and Vasconcelos 2015; Koch et al. 2015; Camarota et al. 2015; Costa et al. 2016; Vasconcelos et al. 2018), each tree is likely to have only one resident colony of *C. pusillus* (consistent with other turtle ants; Powell 2009; Powell et al. 2017; present study) that occupies multiple nests in different branches of the home tree. Even with this multi-nest colony structure, *C. pusillus* colonies reach reproductive maturity at less than a thousand ants (De Andrade and Urbani 1999; Powell 2016; Powell unpublished data). Concordant with this basic biology, *C. pusillus* is also not numerically abundant in the foraging arena compared to other ants, does not show behavioral dominance at food resources, and is not territorial (Camarota et al. 2016, 2018). These insights into the biology of *C. pusillus* suggest that while it is not typical of a dominant arboreal ant, it may still act as a dominant species within the community using a substantial proportion of the limited and essential nesting resources (following definition of dominant species by McNaughton and Wolf 1970; Price 1971).

In this study, we quantitatively assess the status of *C. pusillus* as a dominant species with respect to the usage of cavity nesting resources. We further test the hypothesis that *C. pusillus* meaningfully influences assembly via significantly altering the nesting ecology of other members of the arboreal ant community. We do this by first quantifying the natural nesting ecology of *C. pusillus*, to examine its breadth of resource usage, and using a set of observational and experimental studies to quantify the incidence of *C. pusillus* within the community and the proportional usage of new nesting cavities. Three experimental studies are then used to further test whether *C. pusillus* alters the nesting ecology of co-occurring species. In all experiments, the influence of *C. pusillus* was assessed at the level of species assemblages on individual trees (tree-level assemblages, hereafter). Each tree represents a colonizable patch of cavity resources within the overall arboreal ant community, so changes seen in tree-level assemblages necessarily scale to an influence at the level of the whole community. The first two experiments focused on the short-term response of established tree-level assemblages to newly available cavities, while the third experiment focused on cavity usage at the end of long-term reassembly on trees where the original resident ants had been removed. In tackling our overarching hypothesis that *C. pusillus* acts as a dominant user of cavity nesting resources, we addressed the following key questions: (1) Does the presence of *C.*

pusillus influence species diversity? (2) Does the presence of *C. pusillus* alter the cavity-occupation level by co-occurring species? and (3) Does *C. pusillus* change patterns of nest-entrance usage by co-occurring species?

Materials and methods

Study area

Initial characterization of the natural nesting ecology of *C. pusillus* was conducted at the cerrado reserve of Clube Caça e Pesca Itororó, Uberlândia, Brazil (19° 0' S, 48° 18' W), a 560-ha reserve located on the southern outskirts of Uberlândia, Minas Gerais, Brazil. Subsequent studies were conducted at the nearby Reserva Ecológica do Panga (19° 10' S, 48° 23' W), a 409-ha reserve located 35 km south of Uberlândia, Minas Gerais, Brazil and 20 km from the reserve of Clube Caça e Pesca Itororó. The region is characterized by a tropical climate with two well-defined seasons: a dry winter, from May to September, and a rainy summer, from October to April. The temperature and mean annual precipitation are 22 °C and 1650 mm, respectively. At both sites, survey data were collected across cerrado physiognomies that ranged from *cerrado ralo* (grassland with low connectivity between scattered, often isolated trees), through *cerrado sensu stricto* (30–50% crown cover) to *cerrado denso* (60–70% crown cover Oliveira-Filho and Ratter 2002), with canopy height of 3–8 m. The experiments at the Panga reserve were all conducted in the typical intermediate physiognomy of *cerrado sensu stricto* (30–50% crown cover).

Natural nesting ecology of *C. pusillus*

The discovery of *C. pusillus* colonies and nests followed the methods of Powell (2009). In brief, colonies were located initially by applying urine baits on all trees within 5 by 50 m transects haphazardly positioned throughout the study site and looking for recruits. Turtle ants feed naturally at patches of urine from arboreal mammals found within the canopy and recruit strongly to both natural and bait urine patches (Powell 2008). On each tree with *C. pusillus* recruitment to the baits, extensive baiting within the crown was then used to locate all nests and verify colony membership. To locate nests, recruits were visually tracked from a bait back to the nest which they originated from. *C. pusillus* workers from different colonies fight vigorously when in close contact, so the lack of aggression in natural and staged interactions among ants from different nearby nests was used to indicate membership to the same colony (following Powell 2009). Entrance area, stem diameter at the entrance, and wood type was also recorded for each nest. Nest-entrance area was measured by using a macro lens to photograph the entrance

with an in-shot scale for image calibration (following Powell 2008). Stem circumference was measured with a fiberglass tape measure at the midpoint of each entrance, and this was used to calculate stem diameter. The wood type for each nesting cavity was categorized as either a dead stem attached to a tree, or a live stem.

Survey studies of *C. pusillus* incidence

To assess the tree-level incidence of *C. pusillus* within our focal system, we used data from five different ant diversity surveys conducted at the Reserva Ecológica do Panga, each with a different design depending on the goals of the original project. All studies used the same basic sampling technique of many small, baited arboreal pitfall traps distributed throughout the crown of focal trees, with trap number per tree scaled from four to ten based on crown size (following Powell et al. 2011). Each trap consisted of a small plastic cup (measuring 6 cm high, 5 cm in diameter) wired to a tree limb, so that the mouth was horizontal and touching the tree. Human urine diluted 1:1 with water was used as the bait liquid, and in each trap, it was filled to the one-quarter mark with one drop of detergent added to increase the killing efficacy. Arboreal ants feed naturally at urine deposited by arboreal mammals, typically triggering strong recruitment. This sampling technique is highly effective at recording incidence of all species foraging on focal trees (Powell et al. 2011; Camarota et al. 2015), because it allows recruitment to the bait while reliably capturing a proportion of those recruits in the trap. Moreover, by using many small traps, sampling can be fully distributed throughout the crown and no one species dominates all traps (i.e., prevents “trap swamping” by large-colony, aggressive species). All traps across the different surveys remained in the field for 48 h. Previous work in the system has established that this is the ideal sampling period to reliably capture resident diurnal and nocturnal ants on focal trees. No tree was reused across studies, unless expressly identified as a repeated survey under different environmental conditions.

For Survey 1, a total of 60 trees of the abundant *Caryocar brasiliense* were sampled. Twenty trees were sampled in each of three distinct physiognomies (low, medium, and high connectivity), with matching stratified samples for tree size in each physiognomy (see full sampling details in Powell et al. (2011)). Survey 2 included 240 trees total, with 40 trees sampled for each of six common Cerrado tree species. Three tree species had extra-floral nectaries (*C. brasiliense*, *Qualea grandiflora*, and *Stryphnodendron polyphyllum*); three did not (*Kielmeyera coriacea*, *Machaerium opacum*, and *Tachigali aurea*). For each tree species, a stratified sample for tree size was used and the trees were evenly distributed across physiognomies [see full sampling details in Camarota et al. (2015)]. Survey 3 was a subsample of

survey 2, repeated when the extra-floral nectaries were at peak nectar production, including 17 *C. brasiliense* trees, 13 *Q. grandiflora*, 12 *S. polyphyllum*, 18 *K. coriacea*, 14 *M. opacum*, and 17 *T. aurea* for a total of 91 trees. Survey 4 consisted of 80 mid-sized trees, with 40 *C. brasiliense* trees and 40 *T. aurea* trees sampled as a baseline before an experimental manipulation [see full sampling details in Camarota et al. (2015)]. Survey 5 sampled 81 trees from three distinct ontogenetic stages of *C. brasiliense* trees (27 trees of each stage): juvenile, medium-size reproductive, and large-sized reproductive [see full sampling details in Koch et al. (2015)]. It is important to note that while all survey studies had differences in the specifics of the design, based on the goals of each original study, here, the data are being used solely to assess the consistency of high tree-level incidence of *C. pusillus* in the system.

Nest usage experiments

Short-term colonization experiments

The first two experiments aimed to test the effects of an increase in the number of available nesting cavities for assemblages already established on focal trees. Forty trees were used in each of the two experiments (80 total across the two experiments), with 20 mid-sized (20–25 cm of diameter at 10 cm from the base of the tree, DBT) *C. brasiliense* trees, and 20 mid-sized (18–23 cm DBT) *T. aurea* trees per experiment. The first experiment ran from February to May of 2011 and the second one from March to June of 2012. On each experimental tree, supplementary wooden cavities were wired to the branches, mimicking natural cavities produced by wood-boring beetles. The supplementary cavities consisted of wooden dowels 2.5 cm in diameter and 10 cm in length, in which a cavity was drilled 8 cm in length and 1 cm in diameter. A single entrance hole was drilled into each cavity from the side of the dowel at the closed end, and the open end was sealed with a latex stopper. Twenty supplementary cavities were added to each tree, with four cavities for each of five entrance hole sizes (2, 3, 4, 5, and 6 mm diameter). The diversity of entrance sizes allowed colonization by ant species with a wide spectrum of body sizes, and the entrance-size range is within the range used in nature by the focal species *C. pusillus* (see “Results”). In both experiments, half of the trees were assigned an artificial nectar supplementation treatment, with the addition of a mixture of sugar, water and the amino acid glutamine, while the others received a water control. Nectar supplementation was added to each tree by wiring cups containing the artificial nectar solutions to the tree. On each tree, we added 20 cups with either microcentrifuge (first experiment) or soaked toilet paper (second experiment). Both experiments ran for three months and all cavities were collected and censused at

the end (details below; see Camarota et al. (2015) for further study details). Again, it is important to note that while these two studies used different food supplement treatments, the emphasis here is on assessing consistency in cavity usage by *C. pusillus* and other resident ant species across the different experimental contexts.

Long-term reassembly experiment

The third experiment assessed the potential effects of *C. pusillus* on cavity usage during the reassembly of tree-level arboreal ant assemblages, allowing us to disentangle any effects of the prior presence of different species on nest usage (i.e., priority effects). This experiment used 40 medium-sized (13.9–27.1 cm DBT) *C. brasiliense* trees. It was set in the field in July of 2011 and lasted for 18 months to allow an extended period for succession in the tree-level ant assemblages and stabilization of cavity occupation. Before beginning this experiment, all focal trees were isolated from the surrounding canopy by cutting stems and other connections on adjacent trees (no damage to focal trees). This allowed us to contain the ant-removal process to the focal trees only and control canopy connections during the experiment. We removed the original ant species occupying focal trees by providing our standard urine bait (urine diluted 1:1 with water, minus the detergent killing agent) laced with the short-lived but potent insecticide Fipronil. To provide the ants on focal trees with continuous access to large quantities of the fipronil-laced bait, we used a modification of our standard pitfall-trapping procedure (above; Powell et al. 2011; Camarota et al. 2015). In each focal tree, trap cups were deployed in the same numbers used when censusing trees (above). However, in each cup, a tissue-paper platform was added, so that ants could feed freely from the Fipronil-laced bait liquid without being captured, and thus, most recruits could return to their home nest to distribute the poison via liquid food sharing (trophallaxis). Unlike our typical pitfall-trapping procedure, we also used cup lids with drilled holes of 10 mm diameter, which allowed full access by all foraging ant species, but prevented access by vertebrates. These feeding cups were deployed for 8 days, with the Fipronil-laced bait refilled after 4 days. No rain fell during this period, as is characteristic in the cerrado dry season. The concentration of Fipronil in our bait liquid was 0.001% (following Klimes et al. 2011) achieved via the dilution of Fipronil product KLAP[®] Insecticide (20% Fipronil) with prepared bait liquid.

After the 8-day period of offering the Fipronil-laced baits, we repeated our standard baited pitfall-trapping method for assessing tree-level incidence (above). These censuses were conducted at 30 and 60 days after providing the Fipronil-laced baits and they did not recover any ants in the traps. While we cannot confirm 100% removal of all living ants on

all focal trees, the previously confirmed high-level efficacy of our pitfall trap censusing technique, which recovered no ants after Fipronil application, suggests that our ant removal procedure was highly effective. At a minimum, our censuses after Fipronil application confirmed no active foraging by any resident ant colonies 1 month and 2 months after application. In addition to the removal of canopy connections prior to this treatment limiting the effects to the focal trees, it also increased the validity of our subsequent checks for effective removal.

After the removal and verification procedure, each tree was then reconnected to the surrounding canopy with four thick ropes (15 mm diameter), which served as effective connections between trees for arboreal ants [cf. Powell et al. (2011)]. Twenty-seven supplementary wooden cavities were placed on each focal tree; at the same time, the trees were reconnected to the surrounding canopy. On all experimental trees, the supplementary cavities had nine different entrance sizes (1.5, 2.0, 2.5, 3.0, 3.5, 4.0, 4.5, 5.0, and 5.5 mm in diameter), with three cavities per entrance size. These entrances were chosen to mimic the full range of sizes available on different tree species within the focal system, based on a prior study of stem dissection and quantification of beetle cavities at the same site (unpublished data). The smallest entrance was the only size outside the range of entrances used by *C. pusillus* naturally (below). At the end of the 18-month experiment, all cavities were collected and censused (details below).

Nest censusing

For all nests collected at the end of the experiments, the diameter of the entrance hole was recorded, and the contents censused. In the census, we recorded species identity of the ant occupants, the presence of brood, and the number of the following adult ant castes: workers, soldiers, queens (wingless female reproductive, assumed to be mated and active in ant production), winged female reproductives (unmated, pre-dispersal reproductive individuals), and males. A nest was considered occupied if it had either: (a) at least one queen, representing a newly founded colony; (b) one or more workers and brood; (c) or at least ten workers but no brood (following Camarota et al. 2015). In each nest, at least one ant was collected and mounted for subsequent identification to species or morphospecies. Non-ant inhabitants were identified to the level of order. Voucher specimens of all species/morphospecies were deposited at the Zoological Collection of the Federal University of Uberlândia in Brazil.

Statistical analyses

Ant diversity and nest colonization

The data from the two short-term colonization experiments were analyzed together, since they were similar in their

assessment of nest occupation in established assemblages, with the shared context of food supplementation and the same duration [details in Camarota et al. (2015)]. The full design of these two experiments incorporated the potential effects of nectar supplementation on supplementary cavity occupation between two different tree species [see Camarota et al. (2015)]. Thus, these two factors were accounted for in our statistical analyses. To evaluate the effect of the focal species on ant species richness and proportion of occupied nests, generalized linear mixed models (GLMM) were performed, with the presence/absence of *C. pusillus*, tree species, and presence/absence of artificial nectar supplementation as fixed factors and tree individuals as random effects. *C. pusillus* was included in the richness count for a focal tree when present. Four trees were excluded from the statistical analysis, because they had all their nests attacked by termites, and, therefore, did not have any nests colonized by ants.

For the long-term colonization experiment, a GLMM was also used to assess the effect of the focal species *C. pusillus* on ant species richness and proportion of nests occupied by other species. The presence/absence of *C. pusillus* was a fixed factor and tree individuals were assessed as random effects. To provide a species-level evaluation of whether the presence of *C. pusillus* altered the number of cavities occupied by other ants, we performed Chi-square tests for each ant species. We used the data from the long-term cavity colonization experiment and included only those species that had at least two nests in both the presence and absence of *C. pusillus*, giving a total of ten ant species. A PERMANOVA was also used to evaluate whether the presence of *C. pusillus* had an effect on ant species composition in the third experiment. The effect of *C. pusillus* on species composition was assessed only in the third experiment, since this experiment contained a broader range of resources and had a longer period for assembly and stabilization of the community. One tree was excluded from this analysis, because it had only *C. pusillus* occupying the supplementary nests. One tree was excluded from all statistical analyses for the long-term colonization experiment, because nests were heavily attacked by termites and so had no ant colonization. All statistical analyses were performed in R Software, version 3.5.1 (R Core Team 2018).

Nest-entrance usage and the focal species

To examine the role of *C. pusillus* as a dominant species that shifts resource-usage patterns in other species, we addressed whether the presence of *C. pusillus* changed entrance-size usage in other ant species. To do this, we first assessed the distribution of entrance sizes that were typically used by *C. pusillus* in the long-term colonization experiment, using a standard outlier boxplot. Those entrance sizes captured by

the box of the boxplot (i.e., interquartile range) were considered to be the ‘preferred’ entrance sizes of *C. pusillus*, while the remainder were designated as ‘non-preferred’. We then assessed how the other ant species would use these two entrance-size categories (‘preferred’ and ‘non-preferred’) in the presence or absence of *C. pusillus*. Prior to this analysis, we assessed the range of entrance sizes used by each of the other ant species and only considered those species that had at least two occupied nests in each treatment and used entrance sizes that overlapped with those used by *C. pusillus* (more than 50% of the occupied nests were within the ‘preferred’ range of *C. pusillus*). This sub-setting of our nest-occupation dataset established the relevant nest-usage comparison of how species with a nesting niche that overlaps with the preferred nesting resources of *C. pusillus* respond in the presence and absence of the focal species. A paired Student’s *t* test was performed to compare the proportional usage of the entrance-size categories (‘preferred’ and ‘non-preferred’) in the presence or absence of *C. pusillus*, with individual trees as replicates.

Results

Cephalotes pusillus as a dominant user of nesting resources

In the survey of natural *C. pusillus* nesting ecology, a total of 96 nests were located across 20 colonies. The number of nests per colony ranged from 1 to 12, and each tree contained only a single colony, based on aggression tests to assess colony boundaries. *C. pusillus* nesting ecology was very generalized, consistent with previous comparisons to other members of the genus *Cephalotes* (Powell et al. 2020). Specifically, 95 of the total 96 nests were in dead stems that spanned a broad range of diameters, from 7 to 240 mm. Entrance area spanned an equivalently broad range, from 2.8 to 57.5 mm² (calculated diameters 1.9–8.6 mm), with an interquartile range of 6.6–15.8 mm² (calculated diameters 2.9–4.5 mm; below for further examination of preferred entrance usage).

Concordant with the generalized nesting ecology of *C. pusillus*, the focal species also had high incidence in tree-level assemblages. Across the five surveys of the arboreal ant community within the focal system, totalling over 461 sampled trees and a combined richness of 90 species, *C. pusillus* was present on approximately one-half of the trees (Survey 1, *C. pusillus* on 29/60 trees; Survey 2, *C. pusillus* on 131/240 trees; Survey 3, *C. pusillus* on 53/91 trees; Survey 4, *C. pusillus* on 38/80; and Survey 5 on 55/81).

Consistent with the generalized nesting ecology and high tree-level incidence, *C. pusillus* also occupied experimental cavities with a high frequency in both our short-term and

long-term experiments (Fig. 1). In the short-term colonization experiments, 674 experimental cavities were occupied by a total of 18 species, with *C. pusillus* occupying at least one cavity on 33 of 80 trees. *C. pusillus* also occupied 270 of the 674 total occupied cavities across trees, which was the highest cavity-occupation prevalence of any species (Fig. 1b). Similarly, in our long-term reassembly experiment, 439 cavities were occupied by a total of 23 species of ants, and *C. pusillus* again dominated cavity usage by occupying at least one cavity on 19 of 39 experimental trees and 130 of all 439 occupied cavities across trees (Fig. 1b).

The influence of *C. pusillus* on assemblage diversity

In our two short-term colonization experiments, a total of 13 species occupied our experimental nests on trees without *C. pusillus*, whereas a total of only ten species occupied cavities on trees with *C. pusillus* (including *C. pusillus*; Table S1). Similarly, for our long-term assembly experiment, the total species richness in our experimental cavities on trees without *C. pusillus* was 21, whereas total richness on trees with *C. pusillus* was only 15 (including *C. pusillus*; Table S2). Concordantly, of the 23 species occupying cavities in this experiment, nine were never found nesting on trees with *C. pusillus* and one species was found only in its presence (Table S1; below for occupation levels in species that did cooccur). Importantly, substantial numbers of unoccupied nests remained on all

trees [short-term assembly experiments, 10.24 (SD \pm 5.02) unoccupied nests remaining per tree; long-term reassembly experiment, 14.07 (SD \pm 4.22) unoccupied nests remaining per tree], such that the responses were not simply due to resource saturation. The presence of *C. pusillus* on focal trees then appears to be associated with approximately a quarter fewer species colonizing available cavities and the absence of more than a third of the overall diversity of species colonizing experimental nests.

Nevertheless, in our colonization experiments, the presence of *C. pusillus* had a non-significant to weak effect on the species richness of the tree-level assemblages, with variable outcomes from including or excluding *C. pusillus* in the analysis. In the two short-term experiments, there was no effect including *C. pusillus* (*C. pusillus* presence, $t = 1.49$, $df = 22$, $P = 0.15$) and a negative effect excluding *C. pusillus* (*C. pusillus* presence, $t = -2.88$, $df = 22$, $P = 0.02$). In our long-term reassembly experiment, there was a positive effect including *C. pusillus* (*C. pusillus* presence, $t = 2.63$, $df = 36$, $P = 0.02$) and no effect excluding *C. pusillus* (*C. pusillus* presence, $t = -0.43$, $df = 36$, $P = 0.66$). The presence of *C. pusillus* had no significant effect on the composition of species occupying the experimental nests (*C. pusillus* presence, $F_{1,37} = 0.49$, $P = 0.81$) (Table S2). Thus, while the presence of *C. pusillus* appeared to have a cumulative reduction on overall species richness across all the trees which they occupy, a consistent tree-level effect was not detectable.

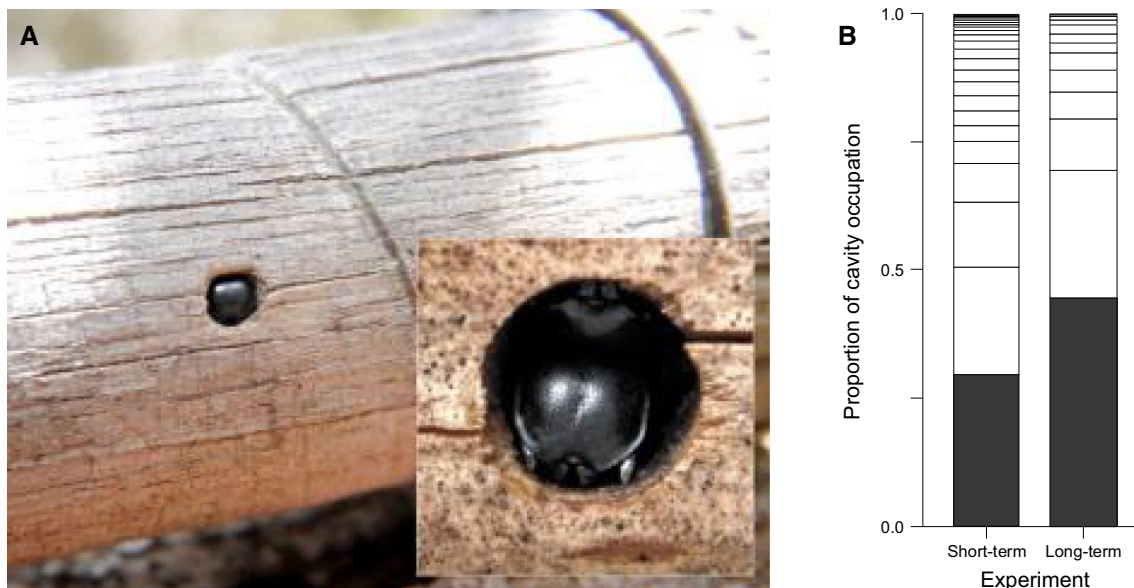


Fig. 1 Occupation of experimental nesting cavities by *C. pusillus*. **a** Photograph of an 18-month old experimental nest occupied by *C. pusillus*, with the entrance defended by soldiers in the main image and this behavior shown at greater magnification in the insert (photos Scott Powell). **b** Stacked proportion plot of the prevalence of cav-

ity use by *C. pusillus* (dark gray bar) and all other species (white bar for each additional species) in the short-term experiments (80 trees, $N = 674$ total occupied cavities) and the long-term experiment (39 trees, $N = 439$ total occupied cavities)

The influence of *C. pusillus* on prevalence of nest occupation

Contrasting the modest diversity results, nest-occupation levels by other ants were significantly lower on trees with *C. pusillus* in both the short-term assembly experiments (*C. pusillus* presence, $t = -4.89$, $df = 22$, $P < 0.001$; Fig. 2; no significant effects of nectar supplementation, tree species, or interactions) and the long-term reassembly experiment (*C. pusillus* presence, $t = -4.51$, $df = 24$, $P < 0.001$; Fig. 2). Again, it is important to note that substantial numbers of unoccupied nests remaining on all trees (14.07 ± 4.22 unoccupied nests remaining per tree across all trees in all experiments), including those occupied by *C. pusillus* (12.18 ± 3.57). The number of unoccupied nests suggests that the negative relationship between *C. pusillus* presence on cavity occupation by other ants was not simply due to resource saturation (see later for influence on nest-entrance selection).

For the long-term reassembly experiment, where nest occupation was tracked in more detail, we further identified differences in responses among those species that co-occurred on trees with *C. pusillus*. There were ten species that occupied nests in both the presence and absence of *C. pusillus*, and five of these occupied significantly fewer cavities when *C. pusillus* was present (*Camponotus arboreus*, $P = 0.004$; *Camponotus melanoticus*, $P = 0.03$; *Camponotus senex*, $P = 0.007$; *Pseudomyrmex curacaensis*, $P < 0.0001$, *Pseudomyrmex urbanus*, $P = 0.05$). Of the remaining five species, *Dolichoderus lutosus* occupied marginally significantly fewer nests in the presence of *C. pusillus*, ($P = 0.06$), while three did not differ in the number of nests which they occupied in the presence of

the dominant species (*Camponotus atriceps*, *Pseudomyrmex elongatus*, and *Tapinoma* sp. 1). One species occupied more nests in the presence of the dominant *C. pusillus* (*Camponotus bonariensis*, $P = 0.04$).

The influence of *C. pusillus* on nest-entrance usage

In the long-term reassembly experiment, where entrance-size data were recorded at the end of the experiment, we also identified a significant effect of the presence of *C. pusillus* on entrance-size usage by other ant species. Of all the nests used by *C. pusillus*, 81% were within the ‘preferred’ range (interquartile range of the boxplot for occupied nests, encompassing entrance diameters from 2.5 to 4.0 mm). This preferred entrance range from the experimental cavities corresponds tightly with the preferred entrance usage in the natural nesting data for *C. pusillus* (above; interquartile range diameter 2.9–4.5 mm). Five ant species (*C. senex*, *P. gracilis*, *C. melanoticus*, *C. bonariensis*, and *D. lutosus*) had a nesting niche that overlapped with the preferred nesting resources of the *C. pusillus* and occupied at least two nests in either the absence or presence of *C. pusillus*. In the presence of *C. pusillus*, nests with these preferred entrance sizes were used significantly less often by the other co-occurring species ($t = -3.91$, $P = 0.017$; Fig. 3a), while they were also using more of the ‘non-preferred’ sizes ($t = 3.94$, $P = 0.017$; Fig. 3b). Thus, while a diversity of entrance sizes was initially present on all trees, and some unoccupied cavities remained on all trees at the end, the presence of *C. pusillus* during the reassembly process was associated with significant changes in entrance-size usage among co-occurring species.

Fig. 2 Proportion (mean \pm SE) of occupied nests per tree (excluding the ones occupied by *C. pusillus*) in the presence/absence of the dominant species (*C. pusillus*)

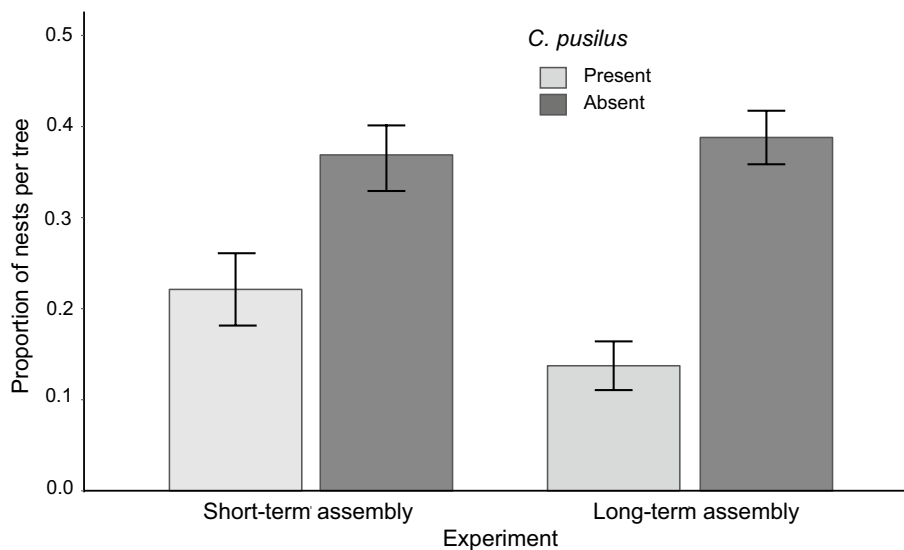
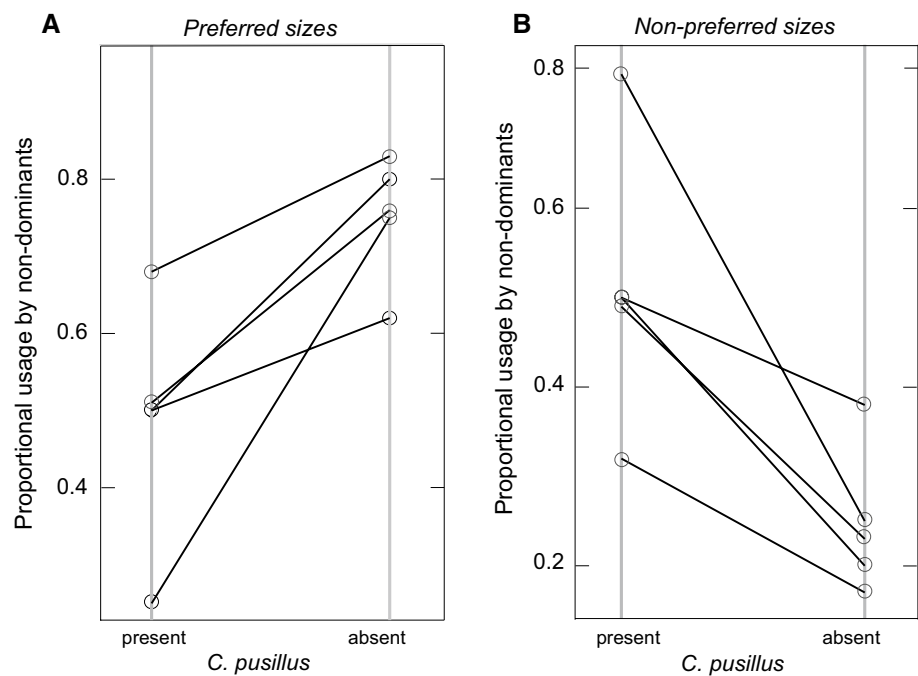


Fig. 3 Proportional usage by non-dominant ant species of **a** the preferred and **b** the non-preferred cavity entrance sizes of the dominant *C. pusillus* when the dominant is present versus absent



Discussion

In this study, combined survey and experimental data have revealed that *C. pusillus* is an ecologically dominant user of cavity nesting resources within the focal arboreal ant community, with cascading influences on assembly. More specifically, we have seen that *C. pusillus* can be defined as an ecologically dominant species based on generalized usage of nesting resources, high tree-level incidence, and its prevalence in using a wide range of experimental nesting resources (consistent with dominance definitions of McNaughton and Wolf 1970; Price 1971). It is noteworthy that while these data show that *C. pusillus* is a dominant user of nesting resources, this species did not meet the typical criteria used to define dominant arboreal ants, because it is not numerically and behaviourally dominant at food resources and is not territorial. The cascading influence of *C. pusillus* dominance over nesting resources was then examined at three distinct levels. First, the presence of the dominant ant appeared to have a detectable effect on overall assemblage diversity: the total number of species on trees with *C. pusillus* was reduced by about a quarter, and more than a third of the assemblage diversity never co-occurred with the focal species. Nevertheless, we did not detect a statistically significant effect of *C. pusillus* on average tree-level diversity. Second, the presence of the *C. pusillus* significantly reduced the number of experimental cavities used by other species, even though unoccupied cavities remained on experimental trees. This pattern is consistent with ongoing competitive exclusion of species using available nesting resources. Finally, *C. pusillus* also shifted the nest-entrance

usage of co-occurring species, which used fewer of the sizes preferred by the dominant ant and more of the non-preferred sizes when the dominant ant was present. This pattern is consistent with a process of competitive displacement of co-existing species from a specific resource range. Thus, a level of plasticity appears to be essential to facilitate coexistence with the dominant species. Broadly, our findings suggest that the heterogeneity of cavity resources and species' nesting preferences can often interact with ecological dominance, and together, these factors help shape the assembly of arboreal ant communities.

Ecological dominance has been recognized as a key feature of ecological communities for a long time (e.g., Connell 1961; MacArthur 1965; Whittaker 1965), and numerous theoretical models have been developed and tested over the years (e.g., McNaughton and Wolf 1970; Dayton 1975; McKane et al. 2002). However, despite the early efforts of MacArthur to understand the niche partitioning in birds and the particular 'importance' of some species and their impact on others (MacArthur 1957, 1958), the majority of studies assessing the impacts of ecologically dominant species involve sessile animals (e.g., Connell 1961; Paine 1971; Dayton 1975) and plants (e.g., Bazzaz 1975; Tilman 1984; Berendse 1998; Emery and Gross 2006; Sasaki and Lauenroth 2011). Moreover, within the body of work addressing the impact of dominant species in mobile animal communities (e.g., Valone and Brown 1995; Hoey and Bellwood 2009; Winfree et al. 2015), experimental studies in highly diverse communities have been scarce. Here, our data provide new insights into the interplay between dominance and niche differentiation in the assembly process. The dominant

ant appeared to be associated with an overall reduction in the number of species on trees which it occupied, but this influence was not detected at the level of average diversity on individual trees and so would need further examination. Nevertheless, of greater note is that the presence of the dominant ant significantly reduced both the prevalence of resource usage among species that co-exist on the same trees (reduction in nest-occupation levels) and significantly altered the specific nest properties that these species utilized (shifted nest-entrance usage). The presence of the dominant ant species then had a significant, multi-level influence on niche differentiation within the community.

Considered together, the multi-level effects of cavity dominance by *C. pusillus* are consistent with a mechanism of niche pre-emption, and a resulting priority effect within tree-level assemblages. First, we have seen that *C. pusillus* occupied newly available nesting cavities on approximately half of the trees and more than a third of all occupied nests across experiments. These patterns suggest that *C. pusillus* is capable of securing new nesting resources quickly and at high volume, likely diminishing availability of certain nesting niches for other species and setting the trajectory of assembly (Ashton et al. 2010). This may explain the absence of several species across trees when *C. pusillus* was present. Second, and providing further support for the ideas of niche pre-emption and priority effects, we also saw that the other species occupied fewer cavities and responded by switching to different entrance sizes in the presence of the dominant ant. Concordantly, direct competitive displacement via cavity usurpation may also be part of this pattern, because *C. pusillus* has been documented to take over occupied nests within this system (Powell 2009). The intraspecific plasticity in resource usage among different species in a community can be an important mechanism underlying multiple species coexistence in the presence of a superior competitor (Morse 1974; Turcotte and Levine 2016). Yet, experimental support for the role of plasticity in facilitating coexistence is mainly limited to sessile organisms [e.g., plants (Ashton et al. 2010)] or in simpler scenarios, like between species of the same genera [e.g., stickleback-fishes (Svanbäck and Bolnick 2007)]. Here, we provide evidence for this mechanism in a diverse tropical insect community.

With our dominant species seemingly altering the realized niche of other species in the community, it is worthwhile to note that non-dominant species are predicted to have a larger fundamental niche than dominant species (Morse 1974). While our experimental design does not allow us to determine the full niche breadth of each species directly, it is important to identify that it did provide a relatively high diversity and broad range of entrance sizes. An interaction between the availability of a variety of alternative resources and plasticity within a relatively large fundamental niche may then be critical for explaining the coexistence

which we saw in the presence of the dominant ant: a species can only adjust its entrance-size usage when it has a wide tolerance of, and access to, a diverse variety of resources. The natural diversity of these resources is promoted by the diversity of wood-boring beetles attacking the trees, which is high in the focal ecosystem (Powell 2008, 2016; Priest et al. unpublished data). More generally, the combination of resource heterogeneity and plasticity in entrance tolerance appears to be acting as a ‘stabilizing mechanism’, defined as any process that maintains diversity by reducing asymmetrical competition (Chesson 2000; Isbell et al. 2009). In this way, the diversity of resources can act as a buffer against the potential negative effects of dominant species. We, therefore, show two lines of evidence for niche-mediated coexistence within the focal community: first, we detected a degree of specialization in the use of nesting resources across situations in the most common species; second, there was a significant plastic shift in the range of nesting resources used by most community members in the presence of the dominant resource user.

Conclusions

Competition theory has generally outpaced experimental evidence, and field studies increasingly need to consider alternative or contributing mechanisms to explain the observed patterns of community assembly (Amarasekare 2003). In this way, community ecology benefits from moving away from a ‘single hypothesis approach’, to acquire a better assessment of the factors behind species diversity and community assembly (Amarasekare 2003). In the present work, we have shown how a species that dominates the usage of nesting resources, a form of ecological dominance that has not previously been a focus in arboreal ant communities, shapes community assembly at multiple levels. More specifically, we saw that the presence of the dominant ant had an overall influence on the number of co-existing species, and had significant influences on both the prevalence and properties of nesting resources used by co-existing species. Broadly, this interaction between a dominant species and the resource-usage patterns of other species shows that complex scenarios can shape assembly in diverse ecological communities. Further examination of these complexities, especially via experimental studies in diverse systems, will be necessary for developing a robust predictive framework for the process of community assembly.

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Author contribution statement FC, HLV, RJM, and SP conceived and designed the study. FC, HLV, RJM, and SP performed the data collection. FC, HLV, and SP analyzed the data. FC, HLV, RJM, and SP wrote the manuscript.

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