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Natural history and nest architecture of the fungus-farming ant genus *Sericomyrmex* (Hymenoptera: Formicidae)

Ana Ješovnik, Júlio Chaul & Ted Schultz

Abstract

The fungus-farming ant genus *Sericomyrmex* (Formicidae: Myrmicinae: Attini) contains 11 species distributed from northern Mexico to southern Brazil. Within their nests, all *Sericomyrmex* species grow highly specialized, obligately symbiotic fungi, which they use for food. *Sericomyrmex* is the youngest fungus-farming ant genus, the product of a recent, rapid radiation, with a crown-group age estimate of 4.3 million years.

We review the literature and report newly acquired data on the natural history of *Sericomyrmex*, with a focus on nesting biology. We present data for 19 collected nests (16 complete and three partial excavations) of seven different *Sericomyrmex* species from Mexico, Costa Rica, Guyana, Peru, and Brazil. The nests of *Sericomyrmex* are subterranean and consist of subelliptical to subspherical chambers connected by narrow tunnels, similar to those in most other attine ant genera. Chambers of the collected nests were 5 - 17 cm wide and 3.5 - 15 cm high, with average volumes of 96 - 1435 cm³. Total nest volume varied from 193 - 7179 cm³. Chambers occurred from 3 to 35 cm from the surface, but nests of *S. parvulus* Forel, 1912 were likely more than one meter deep at two localities where we were unable to finish excavations. In 18 out of 19 collected nests, at least some of the chambers were either directly underneath the nest entrance or offset by up to 10 cm, while in one *S. bondari* Borgmeier, 1937 nest they were displaced horizontally > 2 m from the nest entrance. Indirect evidence suggests that such lateral displacement may be common in *Sericomyrmex*. We document the presence of an external waste midden in a nest of *S. mayri* Forel, 1912 in Guyana, the first such record for the genus. Based on 904 habitat records in our *Sericomyrmex* database, *Sericomyrmex* species inhabit a wide variety of habitats, but nine out of 11 species are more commonly collected in forested areas and are less often collected in very dry or open areas. Two species, *S. scrobifer* Forel, 1911 and *S. maravalhas* Ješovnik & Schultz, 2017, are distributed almost exclusively in Brazilian savanna habitats, that is, cerrado.

Key words: Attine ants, Neotropics, nesting biology.

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Introduction

The nest of an ant, or of any animal, is considered to be part of its extended phenotype (Turner 2002), and nest architecture and nest-building behavior have been studied in an evolutionary framework in many organisms, especially social insects (Schmidt 1955, Wenzel 1998, Zyskowski & Prum 1999, Rasmussen & Camargo 2008). Aside from brood care and foraging for food, nest construction constitutes the largest energy investment for the colonies of many ant species (Sudd & Franks 1987). Most subterranean ant nests consist of two basic nest modules: tunnels or shafts, which connect different parts of the nest, and chambers, where the ants live, raise brood, and store food. The variation in size, shape, number, and arrangement of these basic nest modules is species-typical in many ants, and it is preserved as the colony grows (Cerquera & Tschinkel 2010, Tschinkel 2010). Many factors influence the structure of the ant nest, both biotic and abiotic. The volume of a nest, for example, is correlated with individual ant size and with number of individuals in the colony, i.e., with colony size (Tschinkel 2014), whereas the vertical distribution of brood and workers within the nest is influenced by the temperature of the soil (Tschinkel 1999). The depth of the nest is correlated with colony size as well (Clémencet & Doums 2007, Ramos-Lacau & al. 2012), but it is addition-
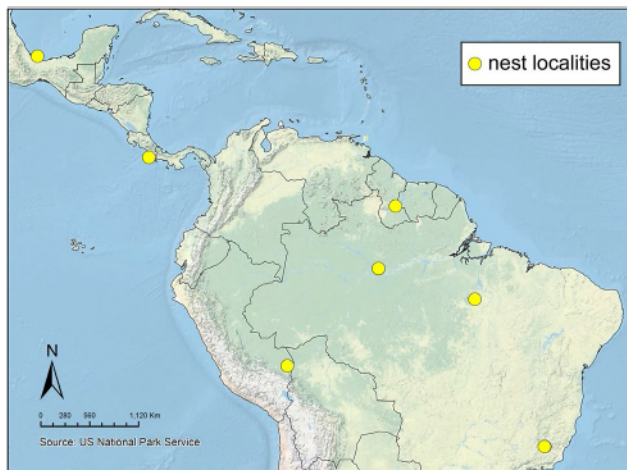
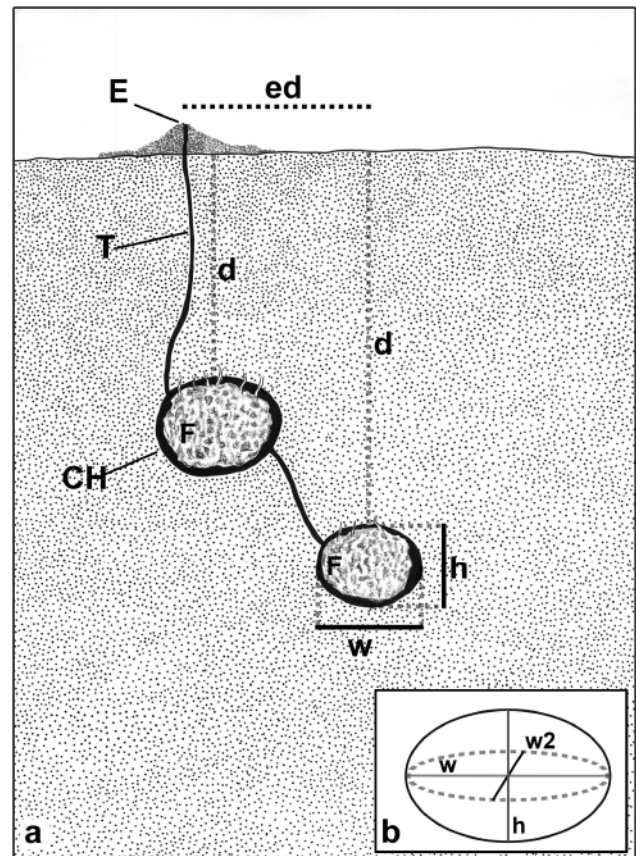Fig. 1: Localities from which *Sericomyrmex* nests were collected.

Fig. 2: Nest measurements. (a) Cutaway view of a fungus-farming ant nest indicating standardized measurements: E nest entrance; T tunnel; CH chamber; F fungus garden; d chamber depth; w chamber width; h chamber height; ed offset distance from the entrance; (b) schematic representation of a single chamber, with measurements indicated w chamber width; w2 chamber width 2, h chamber height (adapted from SOSA-CALVO & al. 2015).

ally constrained by environmental factors such as the water table (LAPOINTE & al. 1998, MIKHEYEV & TSCHINKEL 2004, CLÉMENCET & DOUMS 2007).

In the fungus-farming ants (Formicidae: Myrmicinae: Attini: *Atta* genus group; hereafter "attine" ants), a New World clade that contains over 250 species that are all obligately symbiotic with fungi that they farm for food, underground nests need to accommodate the mass of the fungus gardens. This requirement influences nest architecture: The nest chambers of most fungus-farming ants are subspherical, subovate, or subelliptical, rather than horizontally flattened as in many other ant species with subterranean nests, which only need to house brood and food (TSCHINKEL 2003, TSCHINKEL 2015). Further, in addition to an optimal environment for brood development, attine ant nests need to optimize temperature, humidity, and CO_2 concentrations for the growth of the fungi (ROCES & KLEINEIDAM 2000, BOLLAZZI & ROCES 2002, BOLLAZZI 2008, PIELSTRÖM & ROCES 2014). The importance of nesting biology for fungus-farming ants has been recognized by many researchers and nest architecture data have been recorded at least partially for the majority of the genera (WHEELER 1925, WEBER 1967, WEBER 1969a, WEBER 1976, JONKMAN 1980, MUELLER & WCISLO 1998, SCHULTZ & al. 2002, MOREIRA & al. 2004, MAYHÉ-NUNES & BRANDÃO 2006, DIEHL-FLEIG & DIEHL 2007, KLINGENBERG & al. 2007, RABE-LING & al. 2007, VERZA & al. 2007, KLINGENBERG & BRANDÃO 2009, MEHDIABADI & SCHULTZ 2010, CAMARGO & al. 2011, SOLOMON & al. 2011, JEŠOVNIK & al. 2013, SOSA-CALVO & al. 2013, PIELSTRÖM & ROCES 2014, SOSA-CALVO & al. 2017a, b).

Sericomyrmex, an ant genus with a broad Neotropical distribution, belongs to the so-called "higher" attine ants, a clade of ant species that grow a clade of highly coevolved, obligately symbiotic, polyploid fungal species (SCHULTZ & BRADY 2008, KOOIJ & al. 2015). The closest relatives of *Sericomyrmex*, the other higher attine ants, include the genus *Trachymyrmex*, the leaf-cutting genera *Atta* and *Acromyrmex*, and the rare and enigmatic species *Mycetosoritis explicatus* KEMPF, 1968, the sister species of *Sericomyrmex* (BRAN-STETTER & al. 2017). A few *Sericomyrmex* natural-history studies have been published (URICH 1895, WEBER 1967, 1976, FELDMANN & al. 2000), as well as a number of ecological or behavioral studies that included one or more *Sericomyrmex* species (KASPARI 1996, FERNÁNDEZ-MARÍN & al. 2004, 2006, VASCONCELOS & al. 2008, LEAL & al. 2011, BRUNER & al. 2014).

Until recently, however, reliable species identifications for *Sericomyrmex* were impossible. The last key was published 100 years ago and is incomplete (WHEELER 1916), so most studies including *Sericomyrmex* species did not identify or wrongly identified the species. For these reasons our knowledge of *Sericomyrmex* species distributions, as well as basic ecological data such as colony size, queen number, and timing of mating flights, is incomplete. Recently the phylogeny of *Sericomyrmex* was reconstructed based on genome-scale data (JEŠOVNIK & al. 2017) and a taxonomic revision (JEŠOVNIK & SCHULTZ 2017) based on molecular data and morphology was published. This work shows that *Sericomyrmex* consists of 11 species sharing a most-recent common ancestor only 4.3 million years ago, and a most recent common ancestor with its sister, *M. explicatus*, 15 million years ago, making *Sericomyrmex* the youngest attine ant genus.

Here, we use this new understanding of species boundaries in *Sericomyrmex* to review the natural history of *Sericomyrmex*, with a focus on nesting biology, and summarize previous work for each species. We present results of our nest excavations for a total of 19 *Sericomyrmex* nests belonging to seven different species, and report the first record of an external waste midden for the genus. For each of the

Tab. 1: Nest collection localities.

Country	Locality	Coordinates	Collection codes	Collectors	Collection date	Species collected
Brazil	Amazonas, Manaus, Reserva Ducke	-2.932, -59.972	AJ120926-02	A. Ješovnik, M. Rajković	26 Oct 2012	*S. bondari*
Brazil	Amazonas, Manaus, Reserva Ducke	-2.917, -59.983	TRS920809-15	T.R. Schultz	9 Aug 1992	*S. mayri*
Brazil	Pará, Parauapebas, FL Nacional de Carajás	-6.063, -50.057	AJ141001-05 AJ141002-01 AJ141004-01	A. Ješovnik, T.R. Schultz	Oct 2014	*S. mayri* *S. bondari*
Brazil	Minas Gerais, Viçosa, UFV, Mata de Biologia	-20.758, -42.864	JCMC002	J. Chaul, S. Epifânio	10 Oct 2015	*S. saussurei*
Brazil	Minas Gerais, Viçosa	-20.755, -42.887	JCMC001	J. Chaul	27 Sep 2015	*S. parvulus*
Costa Rica	Puntarenas, Corcovado, Sirena Station	8.50, -83.617	TRS920531-03 TRS920602-08 TRS920606-05	T.R. Schultz	May - Jun 1992	*S. amabilis* *S. opacus*
Guyana	Upper Takutu-Upper Essequibo, CI concesion, base camp	3.513, -58.235	JSC111119-04 AJ111125-08 JSC111122-13	A. Ješovnik, J. Sosa-Calvo	Nov 2011	*S. mayri*
Mexico	Veracruz, Catemaco, Tuxtla	18.587, -95.078	AJ131005-01	A. Ješovnik, M. Rajković	5 Oct 2013	*S. amabilis*
Peru	Madre de Dios, Tambopata Reserve	-12.819, -69.364	AJ120729-03 AJ120726-03 AJ120801-03 AJ120803-03 AJ120728-10	A. Ješovnik	Jul - Aug 2012	*S. mayri* *S. saramama* *S. parvulus*

colonies collected we report demographics and summarize *Sericomyrmex* species distributions and habitat occurrences.

Methods and materials

We conducted field work in Mexico, Costa Rica, Guyana, Peru, and three localities in Brazil (Fig. 1). Localities and collecting data are summarized in Table 1. In addition to our collections, we acquired > 1500 *Sericomyrmex* specimens from the entire geographic range of the genus from museum collections and colleagues. We constructed a data set containing the collecting information (locality, habitat, elevation, collection date) of those specimens. When analyzing these data to estimate habitat occurrences, we included only one data point for single specimens of the same species collected at the same locality in order to avoid collecting bias. If, for example, multiple individuals of the same species occurred in 20 leaf-litter samples taken at the same locality and in the same habitat, we recorded it as one occurrence of that species for that locality and habitat. Specimens were identified to species using a MZ16 Leica stereomicroscope and the most recent key (Ješovnik & Schultz 2017) and by molecular data (Ješovnik & al. 2017). The voucher specimens for each nest are deposited in the National Museum of Natural History (USNM) in Washington D.C., USA (see Table S1e for voucher specimen codes), and the collection data are deposited on AntWeb (www.antweb.org).

In the field, we located nests of *Sericomyrmex* by visually searching for nest entrances and by baiting. For bait we used Cream of Rice cereal, which is loved by all non-leaf-cutter attine ants, and which, due to its white color, is easy to track as it is carried by foragers across the dark forest floor. After locating a nest, we photographed the nest entrance and, if a mound was present, we measured its height and diameter. We cleared an area with a radius of 1 - 2 meters around the nest entrance of any debris and interfering vegetation in order to detect the presence of any additional nest en-

trances or external waste middens. For one nest for which we found a waste midden, we measured the distance from the midden to the nest and observed the behavior of the workers transporting debris to the midden. Following these observations, we collected the midden, including associated arthropods, into 95% ethanol. We started nest excavations 0.5 - 1 meter away from the entrance on the side that was easiest for digging. Nest excavations followed Sosa-Calvo & al. (2015). In short, we attempted to excavate a trench deep enough to facilitate exposing the nest chambers from the side rather than from above, enabling careful collection of the chamber contents and accurate measurements of chamber dimensions. For each chamber we recorded distance from the surface (d), horizontal distance from the nest entrance (ed) (if applicable), height (h), and two measures of width (w, w2) (width and "chamber depth" sensu Ješovnik & al. 2013, Sosa-Calvo & al. 2015), as indicated in Figure 2. Whenever possible we collected the fungus garden and workers from different chambers separately. We stopped the digging after we found the queen and / or after we had been digging for approximately half a meter without finding any new chambers. Also, we left the digging pit open until the following day. If there were no new tunnel openings or ant activity the following day, we refilled the pit. If we found new ant activity, we continued excavation. After returning to the lab, we counted all of the ants and the brood to obtain a colony census. Two colonies of *S. mayri* were maintained alive in the Smithsonian Ant Lab in Washington, D.C. (for live lab nest methods see Sosa-Calvo & al. 2015). We calculated the volumes of chambers following the formula for the volume of an ellipsoid shape (Sun & Liu 2003), which is $V = \pi / 6 \times a \times b \times h$, where a, b, and h are height (h), width (w), and width 2 (w2) of the chamber (Fig. 3b), respectively. To test correlations between the variables we used R (R Development Core Team 2014). We created a data set with total nest volume, individual chamber volume, nest census

(number of individual ants in the nest), and worker size for all collected nests, log-transformed it, and calculated correlation using the *stats* package function *cor.test*. For worker size we used mean head width of the species, based on 25 - 103 specimens measured per species (Ješovnik & Schultz 2017), with the exceptions of *S. lutzi* Wheeler, 1916 and *S. radioheadi* Ješovnik & Schultz, 2017, for which only eight and nine workers were available, respectively.

We also analyzed species-distribution data and a dated phylogeny (Ješovnik & al. 2017) to infer the biogeographic history of the genus and species, but because the results were ambiguous we summarize those analyses only in the supplemental material (File S1, Fig. S1 as digital supplementary material to this article, at the journal's web pages).

Review of *Sericomyrmex* natural history
Distribution

Like most other attine genera, *Sericomyrmex* has a wide Neotropical distribution. The northernmost record for *Sericomyrmex* in the literature is *Sericomyrmex* "*aztecus*" (either *S. opacus* Mayr, 1865 or *S. amabilis* Wheeler, 1925) in Cuesta de los Cedros, 36 km E of Ciudad del Maíz, in the state of San Luis Potosí, in Mexico [21.8025, -99.1803] (Sánchez-Peña 2010). The southernmost records are of *S. parvulus* Forel, 1912 and *S. saussurei* Emery, 1894 in Cananéia, Ilha do Cardoso, southern São Paulo state, Brazil [-25.0968, -47.9298] and, further west, *S. scrobifer* Forel, 1911 in Reserva Mbaracayú, Aguara Ñu, in Canindeyú, southeast Paraguay [-24.1833, -55.2833] (Ješovnik & Schultz 2017). Also, *Sericomyrmex opacus* is present on the Caribbean islands: on Dominica [15.4857, -61.424] and Guadeloupe [16.11735, -61.74291] (Ješovnik & Schultz 2017). In some areas *Sericomyrmex* nests can be very densely distributed, whereas in other areas they can be sparsely distributed, often with a patchy distribution, even if the habitat appears uniform (Weber 1972a). Where abundant, nest entrances may be very close to each other. For example, during a one-year attine-ant study in Trinidad, 67 *Sericomyrmex* nest entrances were observed in an 18 × 77 meter area (0.04 nests per square meter) (Weber 1972a). An attine-ant nest study in cerrado, a central Brazilian savanna biome, reported 17 to 26 nests per 160 m² (0.1 to 0.2 nests per square meter) for *S.* cf. *scrobifer* (Vasconcelos & al. 2008).

Sericomyrmex nests

Beginning at the end of the 19th century, several researchers published observations of *Sericomyrmex* natural history, most notably N.A. Weber (Weber 1937, 1967, 1969a, b, 1972b) and W. M. Wheeler (Wheeler 1916, 1925), the former reporting the first demographic study based on a colony of *Sericomyrmex* maintained alive in the lab for 10 years (Weber 1976). Early naturalists often at least partially excavated ant nests, noting the depths of the nests and the sizes of the chambers, and describing the fungus gardens (Urich 1895, Forel 1912, Weber 1969a, 1972a). More recently, different aspects of attine-ant nesting biology were studied in Panama (Fernández-Marín & al. 2004, Bruner & al. 2014) and in Brazil (Leal & Oliveira 1998, 2000, Vasconcelos & al. 2008, Leal & al. 2011), providing data on the nesting biology of *Sericomyrmex* as well as of other attine genera. Historical natural history data are summarized by species in Table 2 (where they are combined with the new data from this study) and in more detail in Table S1a.

Nest entrances: Early researchers reported that the nest entrances of *Sericomyrmex mayri* Forel, 1912, *S. amabilis*, and *S. opacus* have raised cylindrical craters, up to 2.5 cm high and 7.5 cm wide, made of excavated soil particles (Urich 1895, Wheeler 1925, Weber 1972a). For *S. opacus* (described at the time as *S. zacapanus* Wheeler, 1925) collected in Zacapa, Guatemala, W.M. Wheeler additionally noted that, apart from the soil particles, craters sometimes contain particles of exhausted fungus (Wheeler 1925). In a study of the nesting biology of cerrado attine ants, Leal and colleagues reported that nest-mound volume in *S.* cf. *scrobifer* is a good predictor of colony size (Leal & al. 2011). This is consistent with an earlier finding that the weight of nest tumuli is a good predictor of the amount of fungus garden for *Trachymyrmex septentrionalis* (McCook, 1881) (see Seal & Tschinkel 2006) and with the reported correlation between nest-ring size and colony size in harvester ants (Tschinkel 2014). This correlation between nest-mound volume and colony size in *Sericomyrmex* may, however, depend on the season because during the rainy season the amount of soil outside the nest entrance varies from day to day (Figs. 3c, d).

Nest architecture: Several authors have noted the presence of a vertical, straight tunnel connecting the nest entrance to the uppermost chamber in *Sericomyrmex* species, and Urich reports a small antechamber, common in other attine ants as well (Urich 1895, Fernández-Marín & al. 2004, Sosa-Calvo & al. 2015). Historically, the shallowest reported nest depth records were 8 cm for *S. mayri* in Guyana (Weber 1937) and *S. saussurei* (described at the time as *S. urichi maracas*) in Trinidad and Tobago (Weber 1937), and the deepest reported nest depth was 79 cm for *S.* cf. *scrobifer* in the cerrado of Minas Gerais, Brazil (Leal & al. 2011). The number of nest chambers recorded in the literature for *Sericomyrmex* species varies from 1 to 7 (Tab. 2, Tab. S1a), including the single species *S. mayri*, reported to encompass the full range of this variation (Urich 1895, Weber 1969a). The only nest chamber dimensions recorded in the literature are those of *S. mayri*, in which the width varies from 5 to 15 cm and the height from 3 to 12 cm (Urich 1895, Weber 1937, Weber 1969a), and for *S. saussurei*, for which chambers were recorded as 6 cm wide (Weber 1937). The only living laboratory nest of *Sericomyrmex* reported in the literature was a single *S. mayri* nest, which produced more than 55,000 individuals during its nearly 11-year life span, including ~2500 alate females, ~16,300 males, and the rest workers. This colony contained ~1600 individuals when it was collected in the field (Weber 1967).

Fungus gardens: *Sericomyrmex* fungi belong to one of two sister clades in the larger clade of higher-attine fungi, a derived clade of obligately symbiotic, polyploid species in the family Agaricaceae cultivated by *Trachymyrmex*, *Sericomyrmex*, *Acromyrmex*, and *Atta* ant species. The other sister clade of higher-attine fungi is represented by the single species *Leucocoprinus gongylophorus*. The majority of *Sericomyrmex* species grows a single, very recently diverged, higher-attine fungal species, the "*amabilis-mayri*" fungus, across the entire geographic range of the genus (Ješovnik & al. 2017). Most gardens are suspended from small rootlets in the roof of the chamber, but less frequently they can also be found sessile on the chamber floor (Wheeler 1925, Leal & al. 2011). If rootlets are not present the fungus can be suspended from rocks in the chamber ceiling (Fernández-Marín & al. 2004). *Sericomyrmex* fungus gardens have a firm texture and can reach a size of three liters in the lab (Weber 1976).

Fig. 3: Nest entrances of *Sericomyrmex*. (a) *Sericomyrmex amabilis* nest mound (AJ131005-01), Mexico; (b) *S. mayri* (JSC111119-04) nest mound, Guyana; (c) *S. bondari* (AJ141001-05) nest entrance, Brazil; (d) *S. bondari* (AJ141001-05) nest entrance after rain, Brazil; (e) *S. bondari* (AJ120926-02) nest entrance, Brazil; (f) *S. parvulus* (JCMC001) nest entrances, Brazil; (g) *S. mayri* (JSC111122-13) nest entrance, Guyana; (h) *S. parvulus* (AJ120728-10) nest entrance with bait (Cream of Rice) accumulated around it, Peru. White arrows point to nest entrance holes.

Tab. 2: Species summary. Distribution, habitat, elevation, total nest volume, number of chambers, number of workers, and number of queens, summarized by species. Country codes: BR Brazil, CR Costa Rica, HN Honduras, EC Ecuador, GY Guyana, GF French Guiana, GP Guadeloupe, GT Guatemala, MX Mexico, NI Nicaragua, PA Panamá, PE Peru, SR Suriname, TT Trinidad and Tobago, VE Venezuela. a.s.l. above sea level. 1° primary, 2° secondary. * Live nests not included.

Species	Distribution	Habitat	Elevation (m a.s.l.)	Nest					
				Entrance	Volume	Depth	No. of chambers	No. of workers	No. of queens
S. amabilis	CR, HN, GT, MX, NI, PA, CO, EC	1° and 2° rainforest, dry forest, xeric open habitat, coffee plantation, disturbed habitat, forest edge (N = 53)	333 (5 - 1009) (N = 36)	soil mound (16 × 30 cm), entrance opening 2.5 - 3 mm	214.11 (194 - 234)	11.75 (2 - 25)	1 - 5	482 (45 - 2569)	1 - 2
S. bondari	BR, PE, CO, EC, GY	1° and 2° rainforest, mountain forest, restinga forest, forest edge, semi-open habitats, cacao plantation (N = 48)	325 (5 - 779) (N = 21)	soil mound (23 × 18 cm), nest entrance opening 0.5 - 1.5 cm	866.4 (857 - 875)	17.65 (10 - 23)	2 - 3	845 (826 - 864)	1 - 3
S. lutzi	GY	1° rainforest (N = 2)	732 (N = 1)						
S. maravalhas	BR	Cerrado: cerradão, galery forest & cerrado sensu stricto (N = 6)	535 (532 - 539) (N = 2)						
S. mayri	CO, EC, BR, PE, GY, SU, GF, TT,	1° and 2° rainforest, dry, Atlantic and riparian forest, cerrado, cerradão, agricultural habitat, pasture (N = 75)	341 (5 - 1033) (N = 31)	soil mound, about 2.5 cm in height	2706.8 (402 - 6609)	18.6 (10 - 32)	1 - 18	2102 (817 - 5165)	1 - 3
S. opacus	CR, HN, GT, GP, MX, NI, PA, CO, EC, BR	1° and 2° rainforest, mountain forest, pasture, scrub vegetation, coffee plantation (N = 29)	338 (50 - 800) (N = 19)	excavated soil, no mound, 3 - 7.6 cm in diameter	103.6 (94 - 113)	12.3 (5-20)	1	173 (105 - 231)	1
S. parvulus	CO, PE, BR, GY, TT, SU	1° and 2° rainforest, Atlantic forest, gallery forest, cerrado, cerradão, cacao plantation, urban habitat (N = 59)	325 (45 - 813) (N = 26)	small hole in the ground	484.9 (222 - 904.5)	6.6 (2.5 - 13)	2 - 5	258 (190 - 312)	1 - 2
S. radioheadi	VE	1° rainforest (N = 1)							
S.saramama	PE, EC, CO	1° rainforest (N = 3)	187 (150 - 224) (N = 2)	small hole in the ground	465.00	10.5	1	51	1
S. saussurei	GY, SU, GF, BR	1° and 2° rainforest, Atlantic forest, gallery forest, cerrado, cacao plantation, open habitats (N = 60)	282 (39 - 789) (N = 19)	soil mound	7179.22	31 - 35	5	1249	4
S. scrobifer	BR, PY	Cerrado: campo cerrado, cerrado sensu stricto, cerradão (N = 9)	666 (240 - 910) (N = 5)	soil mound	2918	61 - 79	1 - 2	573	2

Foraging material and behavior

As a substrate for the fungus garden, *Sericomyrmex* ants collect mostly fresh plant material consisting of fallen flowers and leaves and, less frequently, depending on the season, moss, grass, seeds, seed husks, dry leaves, insect frass, and fruit pulp (LEAL & OLIVEIRA 1998, DE FINE LICHT & BOOMSMA 2010). Cerrado species of *Sericomyrmex* prefer pieces of fallen flowers and fruit during the wet season and turn to vegetative parts of plants and moss during the dry season, depending on availability (LEAL & OLIVEIRA 2000). *Sericomyrmex* are known to cut leaves and fruit in a manner similar to leaf-cutter ants. They do not climb vegetation like leaf-cutters and they cut more slowly and produce smaller fragments, up to 2 mm in diameter (WEBER 1967, 1969b, 1976, LEAL & OLIVEIRA 2000). In a study of seed-size selection by ants in a tropical forest in Costa Rica, *Sericomyrmex* workers (either *S. amabilis* or *S. opacus*) removed more than half of the total bait (milled barley), more than any other ant species studied (KASPARI 1996). This seed removal suggests that *Sericomyrmex* ants were taking the bait back to the nest as a fungus substrate. In contrast, in a study of cerrado attine ants, *Sericomyrmex* visited plant, fruit, and seed baits less frequently than other attine ants in the study, and most of the baits were consumed on the spot instead of taken to the nest (LEAL & OLIVEIRA 1998). Similarly, in a seed-dispersal study of the plant *Parkia panurensis* in Peru, Feldmann and colleagues observed *Parkia* seed predation by *Sericomyrmex* workers, which appeared in groups of 2 - 6 individuals, chewed on seeds slowly, and did not attempt to transport the seeds (FELDMANN & al. 2000). Foragers of *Sericomyrmex* cf. *scrobifer* have been recorded up to 7.2 meters away from the nest (LEAL & OLIVEIRA 1998) and they are active during day and night, but peak activity is in the afternoon, whereas in the morning there is usually no activity at all.

In a study of attine trail pheromones that investigated whether attine ants follow the trail pheromones of other attine and non-attine species and genera, it was found that

Tab. 3: Nest architecture data per nest. Chamber measurements: d nest depth, h chamber height, and w and w2 chamber widths (mean and range values). Asterisks* indicate incomplete excavations.

Species	Nest collection code	No. of chambers	Nest volume	Average chamber volume	Chamber measurements			
					d	h	w	w2
S. amabilis	TRS920531-03	1	234.5	234.5	3.0	7.0	8.0	8.0
	AJ131005-01	2	193.8	96.9	6.0 (2.0 - 10.0)	4.5 (3.5 - 5.5)	6.0 (6.0 - 6.0)	6.3 (3.5 - 9.0)
S. bondari	AJ120926-02	3	857.3	285.8	18.3 (10.0 - 23.0)	6.3 (5.0 - 8.5)	8.8 (8.5 - 9.0)	9.7 (8.0 - 11.0)
	AJ141001-05	2	875.5	437.8	17.0 (14.0 - 20.0)	8.5 (8.0 - 9.0)	11.0 (10.0 - 12.0)	9.0
S. saramama	AJ120729-03	1	466.0	466.0	10.5	9.0	11.0	9.0
S. mayri	TRS920809-15*	2	1041.0	520.5	10.5 (10.0 - 11.0)	9.5 (9.0 - 10.0)	10.0 (9.0 - 11.0)	10.0 (9.0 - 11.0)
	JSC111119-04	18	6608.7	367.2	22.3 (15.0 - 29.0)	6.9 (5.0 - 8.0)	8.5 (5.5 - 14.0)	11.4 (6.0 - 18.0)
	AJ111125-08	10	3249.3	324.9	22.9 (16.0 - 32.0)	7.4 (6.0 - 8.0)	7.7 (7.0 - 9.0)	10.7 (8.0 - 13.0)
	JSC111122-13	5	1592.8	318.6	14.7 (10.0 - 18.0)	7.0 (6.0 - 7.5)	8.2 (7.0 - 10.0)	10.5 (9.0 - 12.5)
	AJ120726-03	4	2231.4	557.8	18.6 (10.5 - 25.0)	9.8 (9.0 - 11.0)	9.6 (8.0 - 11.0)	11.0 (8.0 - 13.0)
	AJ120801-03	4	2547.3	626.8	21.8 (13.0 - 26.0)	9.3 (8.0 - 10.0)	9.8 (7.5 - 11.0)	12.9 (10.5 - 17.0)
	AJ141002-01*	2	2316.4	1158.2	20.0 (13.0 - 27.0)	10.0 (7.0 - 13.0)	16.5 (16.0 - 17.0)	11.5 (6.0 - 17.0)
	AJ141004-01*	1	401.7	401.7	10.0	6.0	16.0	8.0
S. opacus	TRS920602-08	1	113.0	113.0	5.0	6.0	6.0	6.0
	TRS920606-05	1	94.2	94.2	12.0	5.0	6.0	6.0
S. parvulus	AJ120728-10	5	904.5	180.9	3.9 (2.5 - 6.0)	6.1 (3.5 - 9.0)	6.9 (5.5 - 8.5)	7.8 (7.5 - 8.5)
	AJ120803-03	3	328.3	109.4	4.2 (2.5 - 6.0)	4.7 (4.5 - 5.0)	5.8 (5.5 - 6.0)	7.7 (7.0 - 8.5)
	JCMC 001	2	221.8	135.3	11.7 (9.0 - 13.0)	5.2 (4.5 - 5.5)	6.7 (4.0 - 8.0)	NA
S. saussurei	JCMC 002	5	7179.2	1435.9	33.8 (31.0 - 35.0)	10.0 (8.0 - 15.0)	13.0 (8.0 - 20.0)	14.8 (6.0 - 27.0)

Sericomyrmex foragers will not follow artificial trails prepared from glandular extracts of other genera, including the non-fungus-farming *Daceton armigerum* (Latreille, 1802) and fungus-farming *Trachymyrmex* and *Atta* species, indicating that their trail pheromones differ from those of the other ants (Blum & Portocarrero 1966). In the same study, *Atta* and *Trachymyrmex* species workers followed each other's trails, as well as the trails of *Daceton armigerum*, but not those of *Sericomyrmex*, whereas *Sericomyrmex* ants followed only their own trails.

Association with other ants

At least some *Sericomyrmex* and *Trachymyrmex* species, including *S. amabilis*, can be attacked by the agropredator ant species *Gnamptogenys hartmani* (Wheeler, 1915) (see Dijkstra & Boomsma 2003), which forces the host ants to retreat from the nest, eats the fungus garden, and, once the garden is consumed, moves on to raid a new nest. *Sericomyrmex amabilis* is also the host of *Megalomyrmex symmetochus* Wheeler, 1925, which has long been known as a social parasite of *Sericomyrmex* (Wheeler 1925). Interestingly, recent studies have shown that *Megalomyrmex* protects *Sericomyrmex* from *Gnamptogenys* ants (Adams & al. 2013). *Megalomyrmex* ants repel and kill *Gnamptogenys* much more effectively than *Sericomyrmex* because they possess alkaloid venom. In addition, *Gnamptogenys* foragers recognize the odor of *Sericomyrmex* colonies that are hosting *Megalomyrmex* and avoid them. This renders *M. symmetochus* colonies a functional soldier caste of a *Sericomyrmex* colony. A *M. symmetochus* colony spends its entire life in a single *Sericomyrmex* colony, so protection of that colony is a shared mutual interest (Adams & al. 2013).

Additional details can be found in Wheeler (1925), Adams & al. (2012), Adams & al. (2013), Bruner & al. (2014), and Liberti & al. (2015).

Queen numbers

Villesen & al. (2002) studied two *Sericomyrmex* species that occur in Panama, *S. amabilis* and *S. opacus*, and overturned the conclusion of multiple mating (polyandry) previously proposed by Murakami & al. (2000). Instead, they found evidence for single mating with occasional polygyny (Villesen & al. 2002). Single-queen colonies appear to be the general rule in *Sericomyrmex* species, but multiple queens are occasionally encountered. A study of nest founding in attine ants found that 40 out of 44 nests of *S. amabilis* had a single foundress queen, and that 4 nests had more than one queen (Fernández-Marín & al. 2004), while a study of Brazilian cerrado species reports 1 - 2 queens for *S. scrobifer* (see Leal & al. 2011).

Results
Distribution and habitat

When redundant records are removed, our habitat data set contains 904 habitat records. *Sericomyrmex* species can be found in dry open areas, dry forest, cerrado, open urban grassy areas, agricultural land (e.g., cacao plantations), and primary and secondary rainforest (Tab. 2). Nine out of eleven species are either exclusively or most commonly found in forested habitats. The species that are mostly, but not exclusively, found in forest are *S. amabilis* (82.7% occurrences are in forest habitats), *S. bondari* (91.7%), *S. mayri* (80.0%), *S. parvulus* (88.13%), *S. saussurei* (88.9%), and *S. opacus* (75.8%). The forest habitats where these

Tab. 4: Nest demography data per nest. * incomplete excavations.

Species	Nest collection code	Nest volume	Number of						
			Workers	Larvae	Pupae	Males	Queens	Alate queens	Total
S. amabilis	AJ131005-01	234.45	455	42	37	0	1	0	535
	TRS920531-03	193.77	487	40	37	0	1	0	565
S. bondari	AJ120926-02	857.3	826	5	85	0	1	0	917
	AJ141001-05	875.5	864	28	74	0	1	2	969
S. saramama	AJ120729-03	466.0	51	2	5	0	1	0	59
S. mayri	TRS920809-15*	1041.0	540	16	1	0	0	32	589
	JSC111119-04	6608.7	5165	532	869	74	2	0	6642
	AJ111125-08	3249.3	2266	416	445	1	1	0	3129
	JSC111122-13	1592.8	1202	155	207	0	1	0	1565
	AJ120726-03	2231.4	817	124	125	0	1	0	1067
	AJ120801-03	2547.3	1062	203	303	0	3	0	1571
	AJ141002-01*	2316.4	181	25	27	0	1	0	234
	AJ141004-01*	401.7	1409	107	129	0	3	0	1648
S. opacus	TRS920602-08	113.0	105	3	4	0	0	0	112
	TRS920606-05	94.2	231	0	0	8	1	3	243
S. parvulus	AJ120728-10	904.5	312	30	60	0	1	0	403
	AJ120803-03	328.3	271	31	65	0	1	0	368
	JCMC 001	221.8	190	60	0	0	2	0	252
S. saussurei	JCMC 002	7179.2	1249	3	0	235	1	81	1565

species are collected are diverse: primary and secondary wet tropical rainforest, Atlantic forest, dry forest, riparian forest, and gallery forest. These species are also found in open and semi-open habitats such as cacao, banana, and coffee plantations; savanna; pastures; orchards; and disturbed urban habitats such as yards and parks. Of the species that mostly prefer forest habitats, *S. bondari* is apparently the most specialized; it was found in forested habitats 91.7% of the time and it was never collected in cerrado (Fig. S2 *S. bondari* distribution map). This is interesting because *S. bondari* has a broad South American distribution and is found in forest habitats bordering cerrado areas, and because species with similar distributions, *S. mayri*, *S. parvulus*, and *S. saussurei* (Fig. S2), have all been collected in cerrado habitats. It is possible, but not likely, that this is caused by undersampling. *Sericomyrmex bondari* is large and easy to notice and our sampling of cerrado habitats is thorough.

Three species that occur only in forest, *Sericomyrmex lutzi*, *S. radioheadi*, and *S. saramama* Ješovnik & Schultz, 2017, have all been collected in primary rainforest only. However, these species are rarely collected in general, so this could be an effect of undersampling. Two species, *S. scrobifer* and *S. maravalhas*, occur almost exclusively in the cerrado, but within the cerrado they have been more often collected in forested cerrado than in open areas (Vasconcelos & al. 2008). About 400 records in our data set contain elevation data. The mean and range of elevation records for each species can be found in Table 2. In general, most species were found at mean elevations of 300 to 400 meters (*S. amabilis*, *S. bondari*, *S. mayri*, *S. parvulus*, *S. saussurei*, and *S. opacus*), with wide ranges (widest range in *S. mayri*, 5-1033 m). Two cerrado-specialist species had

narrower ranges and higher means, 240 - 900 m (mean 666.2) for *S. scrobifer* and 532 - 539 m (mean 535) for *S. maravalhas*. The only elevation record for *S. lutzi* is 732 m. This species is known from the mountain plateaus (tepuis) of the Pakaraima Mountains on the border of Guyana, Venezuela, and Brazil (Fig. S2), and is most likely endemic to Guiana tepuis, known for high levels of endemic flora and fauna (Brown 1975, Steyermark 1987, Berry & al. 1995, LaPolla & al. 2007).

Nest architecture

We collected nest data for seven different species: *Sericomyrmex amabilis* (2 nests), *S. bondari* (3 nests), *S. saramama* (1 nest), *S. mayri* (8 nests), *S. opacus* (2 nests), *S. parvulus* (3 nests), and *S. saussurei* (1 nest). These data, including locality, nest measurements, and colony demography, are summarized by species in Table 2. The nest architecture data are summarized in Table 3 and demography data of each collected nest in Table 4.

Nest-entrance morphology (Fig. 3) varied between two main forms, with and without a soil mound. *Sericomyrmex parvulus*, *S. opacus*, and *S. saramama* nest entrances consisted of either a simple, small hole in the ground (*S. parvulus*, *S. saramama*, Fig. 3g) or two such holes (*S. parvulus*, Fig. 3f), with a small amount of excavated soil around it / them, but without an accompanying soil mound. The nests of *S. amabilis*, *S. bondari*, *S. mayri*, and *S. saussurei* all had irregular soil mounds around the entrances (Fig. 3a, b). The size of the entrance varied from 0.5 cm to 1.5 centimeters. The largest soil mound we recorded was for a *S. bondari* nest in Brazil (AJ141001-05) which measured 33 × 18 cm in area and 2 - 3 cm tall.

Fig. 4: Subterranean *Sericomyrmex* nests. (a) *Sericomyrmex bondari* (AJ120926-02) underground chamber after the fungus garden and ants have been removed; (b) *S. bondari* (AJ120926-02) chamber immediately after opening, with the fungus garden visible; (c) chambers of *S. mayri* (JSC111119-04) after garden removal; (d) *S. mayri* (JSC111119-04) chamber immediately after opening, with the fungus garden visible; (e) *S. bondari* (AJ141001-05) entrance and entrance tunnel side view; (f) plastic nest box with part of a *S. amabilis* (AJ131005-01) colony one day after excavation: the fungus garden has been re-assembled and soil particles introduced during excavation have been removed by the ants; (g) *S. parvulus* (AJ120728-09) carrying bait (Cream of Rice) into its nest (arrow indicates nest entrance).
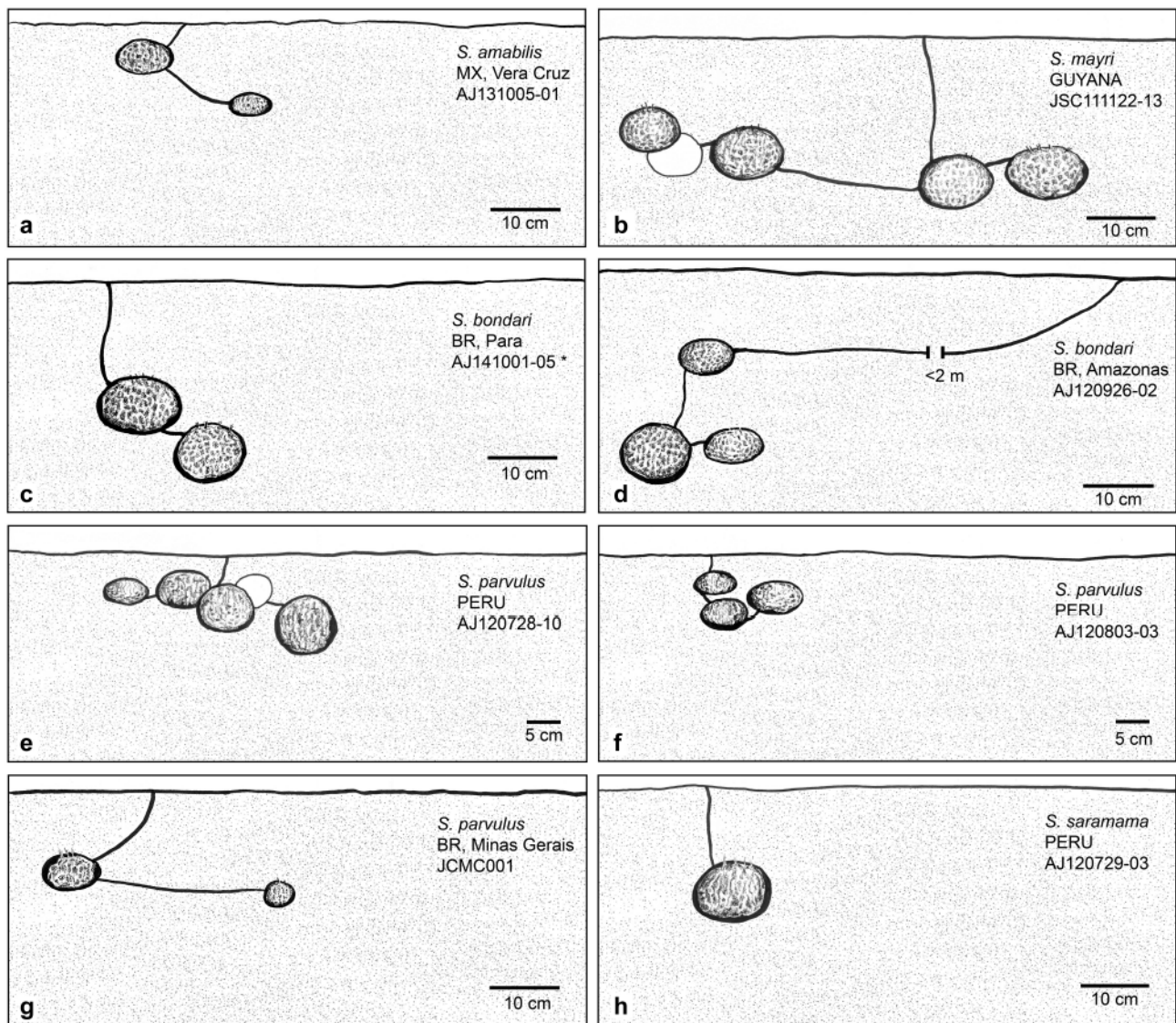
Fig. 5: Nest drawings 1. (a) *Sericomyrmex amabilis* (AJ131005-01), Mexico; (b) *S. mayri* (JSC111122-13), Guyana; (c) *S. bondari* (AJ141001-05), Brazil; (d) *S. bondari* (AJ120926-02), Brazil; (e) *S. parvulus* (AJ120728-10), Peru; (f) *S. parvulus* (AJ120803-03), Peru; (g) *S. parvulus* (JCMC001), Brazil; (h) *S. saramama* (AJ120729-03), Peru. White, unfilled chambers on the drawing indicate chambers that are behind other chambers.

In four nests, belonging to the larger species *Sericomyrmex bondari* and *S. mayri*, we observed one to two short foraging paths in the immediate vicinities of the nest entrances (Fig. 3c), usually radiating out from the entrance. These short paths were from 0.5 to 1 cm wide, were slightly impressed into the surrounding forest floor, and were most visible when the nest was surrounded with a mound of freshly excavated soil. There were a large number of openings in the soil mound of one *S. bondari* nest (AJ141001-05) immediately after an afternoon rain (Fig. 3d), probably consisting of temporary additional nest openings that were used by workers for faster removal of soil that was washed into the nest during the rain. In previous days, when no strong rains occurred, this nest had a single opening (Fig. 3c).

In 18 out of 19 nests excavated for this study, the tunnel leading from the nest entrance to the uppermost chamber was either vertical or deviated from vertical by a small angle. The tunnel was sometimes observed while digging (Fig. 4e), but more often its position and orientation were inferred based on the location of the nest entrance and the uppermost chamber because the majority of the nests had chambers either more or less directly beneath the nest entrance, or offset by no more than 10 cm. In contrast to this general rule, however, in a nest of *Sericomyrmex bondari* (AJ120926-02) collected in Reserva Ducke (Amazonas, Brazil), one of two nest entrances was horizontally displaced by more than 2 meters from the nest chambers (Fig. 5d), whereas a second nest entrance was positioned more or less immediately above the uppermost chamber.

In our excavations, an antechamber was found only in one nest of *Sericomyrmex mayri* (AJ141002-01); it was smaller in size than the other chambers and did not contain any fungus garden. This was a large nest, with a large fungus chamber beneath the antechamber, so the antechamber was probably a remnant of the first chamber created by the queen when founding the nest (FERNÁNDEZ-MARÍN & al. 2004).

Nests of *Sericomyrmex opacus* and *S. saramama* had a single chamber each, nests of *S. amabilis*, *S. saussurei*, and
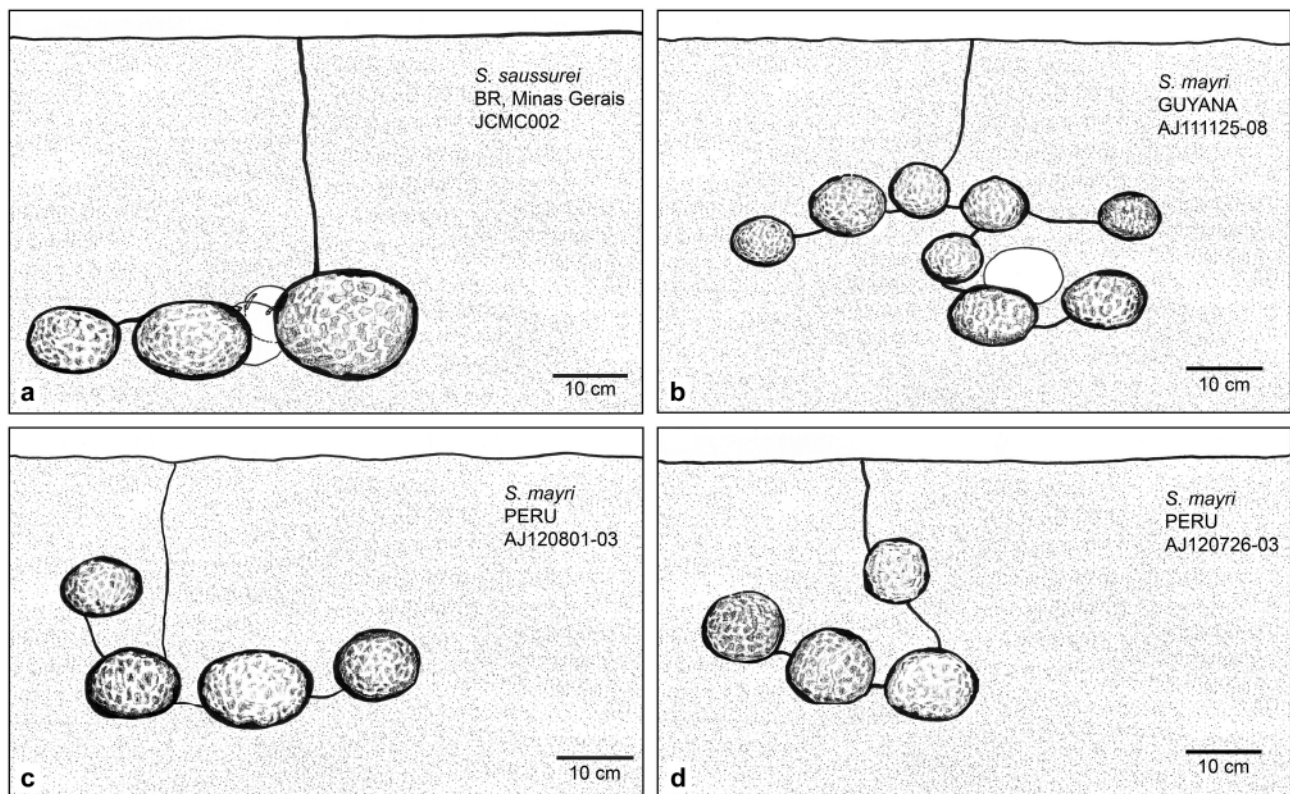
Fig. 6: Nest drawings 2. (a) *Sericomyrmex saussurei* (JCMC002), Brazil; (b) *S. mayri* (AJ111125-08), Guyana; (c) *S. mayri* (AJ120801-03), Peru; (d) *S. mayri* (AJ120726-03), Peru. White, unfilled chambers on the drawing indicate chambers that are behind the other chambers.

S. parvulus up to 5 chambers, and *S. bondari* nests had 2 to 3 chambers. The number of chambers in *S. mayri* nests varied the most, from 1 to 18, with two large nests collected in Guyana with 10 and 18 chambers.

Nest volume is usually related to ant body size, so that small species have smaller nests than larger species, even when the number of individuals in a colony is the same (TSCHINKEL 2015). Another factor that influences nest volume is the number of workers in the colony; for nests of ants with similar body sizes, the number of individuals in the colony (nest census) is a good predictor of nest volume (TSCHINKEL 2015). Our findings generally agree with these rules. Nest volumes varied from ~ 200 to ~ 7000 cm³ (Tab. 3) and the colony census varied from 59 to 6642 individual ants (Tab. 4). Ant size and colony size are correlated (r = 0.61, p = 0.004608) and both variables are correlated with nest volume. Colony size and nest volume are somewhat more strongly correlated (r = 0.68, p = 0.0012) than ant size and nest volume (r = 0.61, p = 0.0051). Average chamber size was also correlated with ant size (r = 0.64, p = 0.0033) and strongly correlated with total nest size (r = 0.79, p = 5.362e-05). The largest species, *Sericomyrmex mayri*, had some of the largest nests, while the small species *S. parvulus* and *S. opacus* had some of the smallest nests (Tab. 3). However, exceptions exist; the single examined nest of *S. saussurei* had the largest nest volume of all the species collected, even though it didn't have the highest colony census (1565 individuals, in comparison to large *S. mayri* nests with ~ 3000 and ~ 6000 individuals) and even though it is a medium-sized ant (smaller than both *S. bondari* and *S. mayri*). Another exception is S. *amabilis*, which is almost identical in size to *S. saussurei*, and

in which colony census is relatively high (550 ants) given its surprisingly small nest volumes (165.7 cm³) (Tab. 3). In contrast, *S. saramama*, a smaller species with a lower colony census (59 ants), has a larger nest volume (466 cm³). Before drawing any conclusions, however, it is important to note that our sample sizes are generally very low (19 nests) and particularly so for the species *S. saramama*, *S. saussurei* (a single nest for each species), and *S. amabilis* (two nests). Also, for most *Sericomyrmex* species we lack data that span different habitats and different seasons, which are essential for understanding the environmental factors that influence nest characteristics.

The spacing of underground nest chambers varied within a single nest: Some neighboring chambers were very closely positioned (1 - 5 cm) (Figs. 5c, e, f; 6a), whereas other neighboring chambers were separated by 10 - 30 cm (Figs. 5b, g). In some nests, both conditions applied, with clusters of closely spaced chambers separated from other such clusters by 10 - 20 cm (Fig. 5b). This pattern is at least partly explained by heterogeneity of the soil and the presence of large roots. We noticed that if a large tree root was present, chambers were often adjacent to it, incorporating the root to form at least part of the chamber wall (Fig. 4c).

In addition to the 19 successful nest excavations reported above, we attempted to excavate an additional seven nests for which we located the nest entrances and followed the tunnel for 1 - 3 days but ultimately did not find the chambers. These unsuccessful attempts also offer some insights. The uppermost chamber of the deepest *Sericomyrmex* nest we excavated was 35 cm below the surface (*S. saussurei* in Minas Gerais, Brazil), and the deepest record known

from the literature, for *S.* cf. *scrobifer*, was 79 cm from the surface (LEAL & al. 2011). During the 3-day excavation of an *S. parvulus* nest in the cerrado habitat of the Panga Ecological Reserve in Minas Gerais, Brazil, we created a pit more than 180 cm deep but still did not reach the chambers. The chambers were certainly deeper rather than displaced laterally because we observed ants emerging from a tunnel opening at the bottom of the pit. Similarly, during two attempted nest excavations of *S. parvulus* in Carajas in Para, Brazil, we excavated to greater than 1 meter in depth without encountering chambers, but observed the entrance tunnel continuing straight down.

Aside from depth, a separate cause of unsuccessful excavations was horizontal displacement of chambers from the nest entrance. In these cases, rather than descending vertically, the tunnel diverged from the nest entrance slightly below and almost parallel to the surface of the ground. We observed such horizontal entrance tunnels in two nests of *Sericomyrmex mayri* in Peru, one nest of *S. amabilis* in Mexico, and one nest of *S. mayri* in Minas Gerais, Brazil. We were invariably able to determine the direction of the chambers (directly below or horizontally displaced) by following the tunnel, or, when the tunnel was temporarily lost, by waiting for the ants to re-excavate the tunnel opening.

Fungus garden

In general, *Sericomyrmex* gardens are large, almost always completely filling the chamber (Fig. 4b, d). Garden color depends on the substrate collected by the ants; in the field the garden is yellow-brown to grey. Following field collection, fungus gardens are usually broken into fragments and littered with particles of soil, but once stabilized in a nest container the ants clean and rebuild the garden within a single day (Fig. 4f).

Arthropods associated with an external waste midden

We observed an external waste midden outside of a nest of *Sericomyrmex mayri* in primary forest habitat in the Upper Essequibo region of Guyana. Located 50 cm from the nest entrance, the midden consisted mostly of exhausted fungus garden. During 30 minutes of observation, workers visited the midden every one to two minutes. Workers invariably approached the midden from the direction of the nest entrance carrying a fragment of what looked like exhausted fungus substrate in their mandibles, which they deposited on the midden. In addition to exhausted garden, the midden contained two dead *Sericomyrmex* ants as well as many living organisms. A total of 57 organisms were collected from the midden: 41 live Diptera larvae, 12 live Coleoptera larvae, 2 live mites, and 2 dead *Sericomyrmex* workers (Tab. S1d).

Foraging material and behavior

In most of our field observations *Sericomyrmex* workers foraged on our bait, Cream of Rice cereal. We observed workers of *S. mayri* and *S. bondari* carrying small flowers, small pieces of fresh leaves, and dry leaves. We did not observe them cutting vegetation. *Sericomyrmex* workers move relatively slowly, and when disturbed they react like most other attine ants: They curl into a ball and become immobile. Based on our observations, the only species that does not behave like this is *S. mayri*. When disturbed, workers of *S. mayri* immediately try to escape, a behavior similar to that of larger *Trachymyrmex* species and leaf-cutter ants.

Sericomyrmex foragers recruit nestmates when bait (Cream of Rice, fruit) is encountered. They do not form heavily populated foraging columns as in leaf-cutter ants, but we observed *S. mayri* and *S. bondari* forming short foraging columns close to the nest entrance. When large amounts of bait were present, we observed *S. parvulus* workers depositing it around the nest entrance (Fig. 3h) before taking it into the nest. We observed crepuscular and nocturnal activity in *S. mayri* and diurnal activity of all other species collected in this study.

A colony of *Sericomyrmex amabilis* we collected in Costa Rica (TRS920531-03) contained 75 workers, 16 queens, and 23 pupae of *Megalomyrmex symmetochus*. None of the other 18 nests collected for this study contained *Megalomyrmex* symbionts.

Queen numbers

The majority of colonies (15 out of 19) and species (5 out of 7) we excavated had a single queen. Three colonies of *Sericomyrmex mayri* and one *S. parvulus* colony had 2 - 4 queens each (Tab. 4). It should be noted that we counted as a "queen" any dealate gyne. Because we did not further investigate the reproductive status (i.e., ovary development, insemination) of dealate gynes, it remains possible that, rather than inseminated colony co-foundresses, some of the observed dealate gynes were instead uninseminated daughters that had shed their wings and remained within the parent colony as functional workers, a condition that has been observed frequently in the colonies of multiple attine genera and species (e.g., WEBER 1941). The queen specimens are deposited at the USNM, but most of them are mounted on pins. However, for three nests queens are preserved in EtOH and are thus available for future dissections (for *S. bondari* AJ141001-05; *S. mayri* AJ111125-08 and JSC111122-13).

Discussion

We report nest architecture data for seven species of the attine-ant genus *Sericomyrmex* based on 19 excavated nests. With regard to the number of species represented, this represents one of the larger data sets for non-leafcutter attine-ant nest architecture. We also provide an overview of *Sericomyrmex* natural history, based on the literature and on our field research.

Our data on nest architecture, together with data culled from the literature, is in agreement with previous studies with regard to the relationships of nest, ant, and colony size (TSCHINKEL 2015). *Sericomyrmex* nest volume is correlated both with ant size and colony census: In general, smaller-bodied species have smaller chamber and nest volumes, larger-bodied species have larger chamber and nest volumes, larger nests contain larger colonies, and smaller nests contain smaller colonies. Exceptions exist, and not all of the observed variations in chamber size and number can be explained by body or nest size. They are likely also influenced by additional ecological and phylogenetic factors, which we are unable to further explore because of the small size of our data set.

The presence of very deep nests, e.g., in *Sericomyrmex parvulus* at two different localities, is intriguing. Nest depth in *Sericomyrmex* could vary by season, since it is known that at least some species of fungus-farming ants move their nests deeper during the dry season as a response to temperature and humidity requirements of their fungal cultivars (WEBER 1957, NAVARRO & JAFFE 1985, LAPOINTE & al. 1998, SEAL &

TSCHINKEL 2006, MUELLER 2011). However, in Carajas, Para, Brazil, we excavated three nests of *S. mayri* and *S. bondari* at the same place and at the same time that we excavated a *S. parvulus* nest, and the *S. mayri* and *S. bondari* nests occurred at much shallower depths (14 - 27 cm) than the *S. parvulus* nest (more than 1 m). Why did *S. parvulus* have such a deep nest in the same habitat and locality and during the same season in which other *Sericomyrmex* species had shallower nests, especially considering that at other localities we located and excavated *S. parvulus* nests at only 5 - 20 cm depth? Growing a different species of fungus with different ecological requirements is one of a number of possible explanations that need to be tested.

A nest of *Sericomyrmex bondari* had long horizontal tunnels connecting one nest entrance with the uppermost nest chamber almost two meters away, as well as a second nest entrance directly above the chamber. Similarly, the leaf-cutting ant species *Atta laevigata* (SMITH, 1858) and *A. vollenweideri* FOREL, 1893 have long underground tunnels leading from the nest to openings several meters away, possibly to protect foragers from predators or the sun (MEHDIABADI & SCHULTZ 2010). Protection from the sun is unlikely to be important for *S. bondari*, since this is a forest-dwelling species, but protection from predators remains a possible explanation. If a predator were to attack the main nest entrance, an additional nest entrance some distance away from the attacked entrance would offer an alternative escape route. Predator-avoidance behavior is well documented as a response to above-ground and underground army ant attacks in many ants, including attine ants, and it usually involves nest evacuation and frequent nest moving (FOWLER 1977, TOPOFF & al. 1980, LAPOLLA & al. 2002, SMITH & HAIGHT 2008, SOUZA & MOURA 2008). Also, heterogeneous ("clumped") local distributions of *Sericomyrmex* nests are reported in the literature (WEBER 1972a) and such observations, including our own, could be explained by army ant predation. Such clumping could also be explained by foundress bias (KING & TSCHINKEL 2016), i.e., foundress queens could prefer one microsite vs. another based on subtle microhabitat differences (e.g., soil type or humidity) that cannot be detected by the naked human eye, as has been shown for other attine ants (LAPOINTE & al. 1998). But, if such foundress bias is absent, or if foundress queens actually avoid founding colonies too near to existing, older colonies, e.g., to avoid competition, then localized army-ant predation could secondarily eradicate some nests and create the patchy distributions we observe in seemingly ecologically homogeneous habitats. At least one species of army ant, *Nomamyrmex esenbecki* (WESTWOOD, 1842), is known to prey on *Sericomyrmex* species (P. Hönle, pers. comm.). Both theories are speculation and require experimental testing in future field studies.

Interestingly, in most cases in which we encountered nests with two entrances, such as the Amazonian *Sericomyrmex bondari* nest, we also observed and in some cases excavated nests of that same species, sometimes only 10 - 20 meters away, with a single typical entrance located more or less directly above the uppermost chamber. This polymorphism in nest architecture within the same species and at the same locality could be caused by microhabitat differences that we were not able to detect. It is also possible that the presence of a second tunnel and a second entrance is more common than our data suggest, but that we only infrequently noticed the second entrance, perhaps because it was infrequently

used by foragers. Such features as the presence or absence of horizontal entrance tunnels and chamber depths may be influenced by multiple environmental factors. Explaining these features will require future studies that collect ecological data, including data for multiple nests of the same species from different habitats, and the excavation and study of nests during both the dry and wet seasons.

The presence of developing larvae from multiple insect orders in the waste midden of a *Sericomyrmex mayri* nest from Guyana suggests that the midden is a stable feature of the nest of this species, consistent with previous studies of attine waste-midden commensals (AUTUORI 1942, MOSER 1963, NAVARRETE-HEREDIA 2001, SANCHEZ-PENA & al. 2003, STEINER 2004). Waste disposal is important for colony hygiene (HART & al. 1998, BOT & al. 2001, BALLARI & al. 2007) because exhausted fungus garden becomes contaminated by numerous microorganisms and parasites that can threaten the health of the growing garden (BOT & al. 2001). Some leaf-cutter ants dispose of waste in specialized underground chambers, whereas others use external refuse dumps, a difference apparently driven by environmental factors (FARJI-BRENER & al. 2016). Prior to this study the only mention of *Sericomyrmex* waste management was made by WEBER (1976), who observed *Sericomyrmex mayri* workers carrying their dead, as well as fragments of exhausted fungus garden, to one corner of a captive colony. We observed this same behavior in our lab colony of *Sericomyrmex mayri* in the Smithsonian Institution NMNH Ant Lab (Fig. S3). Weber did not, however, report observations of waste middens in nature. In non-leaf-cutting higher-attine ants, external waste dumps have been described in *Trachymyrmex arizonensis* (LAPOLLA & al. 2002) and *Trachymyrmex* sp. (WHEELER, 1907) (see HART & RATNIEKS 2001).

Our results indicate that *Sericomyrmex* is a good candidate for more detailed studies of nest architecture in an evolutionary-ecological framework. *Sericomyrmex* is a moderately speciose ant genus, containing 11 closely related species with broad distributions across multiple habitats. Nest architecture differs across species with regard to chamber depth, chamber position with regard to the nest entrance, and morphology, and colony sizes vary from several hundred to almost 7,000 ants. Now that we have a resolved taxonomy and phylogeny for the genus, comparative studies of nest architecture across different environments and species can both account for the effects of phylogeny and accurately identify species, thereby improving our ability to isolate the effects of various environmental and genetic factors. It is our hope that this study will encourage further research on *Sericomyrmex* nest architecture.

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