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Diversity of commensals within nests of ants of the genus *Neoponera* (Hymenoptera: Formicidae: Ponerinae) in Bahia, Brazil

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Summary. Nests of ants in the Ponerinae subfamily harbor a rich diversity of invertebrate commensals that maintain a range of interactions which are still poorly known in the Neotropical Region. This study aims to investigate the diversity of these invertebrates in nests of several species of the genus *Neoponera* and search for possible differences in their commensal fauna composition in two distinct habitats: the understory and the ground level of cocoa tree plantations. From March to December, 2017, nests of *Neoponera* spp. were collected through inspection of different substrates in a cocoa tree plantation. We compared the composition of the assemblage of commensal invertebrates according to the environment stratum, the substrate of nesting and the species of *Neoponera*. Twenty-one nests of four species were collected: *N. apicalis* (1), *N. curvinodis* (1), *N. inversa* (3) and *N. verenae* (16). The invertebrates recorded in the nests of the ants belong to the following taxa – Mollusca: Gastropoda; Annelida: Haplotaxida; Arachnida: Acari, Araneae, Opiliones, Pseudoscorpionida; Chilopoda: Scolopendromorpha; Collembola: Entomobryomorpha, Poduromorpha; Hemiptera; Psocoptera; Hymenoptera; Diptera; and Coleoptera. Nests of *Neoponera* harbor a large variety of commensals, such as previously unknown species of Collembola in the genera *Cyphoderus*, *Friesea* and other Poduromorpha. Differences regarding the diversity of these invertebrates between the two strata were highlighted.

Résumé. Diversité des commensaux dans les nids de fourmis du genre *Neoponera* (Hymenoptera : Formicidae : Ponerinae) à Bahia, Brésil. Les nids des fourmis de la sous-famille des Ponerinae abritent une riche diversité de commensaux offrant différents types d'interactions, lesquelles sont encore mal connues dans la région Néotropicale. Vingt et un nids de fourmis de quatre espèces du genre *Neoponera* [*N. apicalis* (1), *N. curvinodis* (1), *N. inversa* (3) et *N. verenae* (16)] ont été récoltés de mars à décembre 2017 en inspectant différents substrats dans une cacaoyère, susceptibles d'abriter des colonies. Pour analyser les données, l'assemblage des invertébrés commensaux a été comparé en fonction de la strate et du substrat de nidification, ainsi que de l'espèce de *Neoponera* rencontrée. Les invertébrés recensés dans les nids de fourmis appartiennent aux taxons suivants : Mollusca : Gastropoda ; Annelida : Haplotaxida ; Arachnida : Acari, Araneae, Opiliones, Pseudoscorpionida ; Chilopoda : Scolopendromorpha ; Collembola : Entomobryomorpha, Poduromorpha ; Hemiptera ; Psocoptera ; Hymenoptera ; Diptera et Coleoptera. Les nids de *Neoponera* abritent une riche variété de commensaux, tels que quelques espèces des genres de Collembola *Cyphoderus* et *Friesea*, et d'autres Poduromorpha encore inconnus auparavant. Des différences quant à la diversité de ces invertébrés entre les deux strates étudiées sont mises en évidence.

Keywords: myrmecophily; ant nest; host–parasite interactions; Neotropical; agroforestry; Collembola

Ants are terrestrial organisms that are extremely successful and ecologically dominant in tropical regions and their nests can be found in a variety of habitats (Hölldobler & Wilson 1990). The ant nest is a structure that maintains the ideal conditions for the survival of the colony and meets the ecological needs of each species (Antonialli-Junior et al. 2015). Despite the high degree of sophistication which commonly exists among ants, there are groups of species that do not show elaborate strategies for the construction of their nests, occupying pre-existing spaces in the environment,

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such as branches, bark, or at the base of epiphytes (Delabie et al. 1997, 2008; Fernandes et al. 2013, 2014). Poorly structured nests provide a weak level of organization for facilities to keep the immatures and store the food; this situation is typical of ponerine ants, especially those of the genus *Neoponera* (Antonialli-Junior et al. 2015).

Species of this genus nest in different habitats (hypogeic, leaf-litter, undergrowth, epiphytes and canopy). Furthermore, the nest of these ants show structural differences according to the stratum in which they are found. The variations include diameter of the holes, branches or trunks, degree of humidity, exposure to sun light, and quantity of organic matter in the nest refuse (Arruda et al. 2015). Since these insects are predominantly predators, refuse can be deposited inside or outside the nest, enriching the environment with a range of nitrogenous components (Ngai & Srivastava 2006).

It follows that the nest also offers an ideal microhabitat for numerous organisms that seek shelter and food, and such organisms depend on host ants at some stage of their life cycle, being involved in different types of associations, including mutualism, inquilinism, parasitism, etc. (Hölldobler & Wilson 1990; Kronauer & Pierce 2011). In the Dorylinae subfamily and even without a permanent structure characterizing a nest, the nomadic ant *Eciton burchellii* (Westwood, 1842) is reported to maintain a diversity of at least 300 species of associated organisms (Rettenmeyer et al. 2011). These organisms have the collective names of commensals or myrmecophiles (Wilson 1971; Hölldobler & Wilson 1990). According to Glasier et al. (2018) commensals are organisms whose associations benefit themselves without profit or loss for their host ants, while myrmecophiles take advantage of the ant's social habits. Among the diverse invertebrates forming associations with ants, true myrmecophiles are found between mites (Acari), springtails (Collembola), and nematodes (Nematoda) (Rettenmeyer et al. 2011). Commensals reported within the ant nests or on the worker bodies include mites, beetles (Coleoptera), bugs (Hemiptera), and springtails (Hölldobler & Wilson 1990; Lapeva-Genova 2013), with mites being the most frequent (Lopes et al. 2015). Baltic amber records indicate that mites and ants have co-occurred for about 50 million years since Eocene (Shaw & Seeman 2009; Dunlop et al. 2014), and that the Rhizoecinae mealybugs lived in symbiosis in ant nests of the Formicinae *Acropyga* at least for the last 20 million years (Johnson et al. 2001). One group that possesses a large number of associations with the ants is the Coleoptera. A total of 121 species of beetles are known to live in ant nests. Of these, 71 are proven myrmecophilous, with the Staphylinidae family having the largest number of species that cohabit in ant nests and exhibiting the most diverse types of association (Parker 2016).

Although a few studies have focused on the diversity of springtails (Collembola) associated with ants, including ponerines, there are numerous other organisms present in *Neoponera* nests, sometimes in very high densities (Castaño-Meneses et al. 2014, 2015a). Several organisms within the Thysanura: Zygentoma (subfamily Atelurinae) (Mendes et al. 2011) and Araneae (families Linyphiidae and Oonopidae) (Cushing 2012) are known to live with ants, with which they can exhibit strong morphological convergence (myrmecomorphy, see Quicke 2017), suggesting an intimate specialization for integration and life within ant nests. Other ants also live within nests of Ponerinae, including members of the genus *Pheidole* Westwood, 1839, which are often found in nests of *Dinoponera quadriceps* Kempf, 1971 (Vasconcellos et al. 2004). *Pheidole rudigenis* Emery, 1906 and *Pheidole dinophila* Wilson, 2003 live exclusively in nests of *Dinoponera australis* Emery, 1901 (Wilson 2003). In addition to arthropods, one snail of the order Pulmonata (Mollusca), *Allopeas myrmekophilos* Janssen & White, 2002 (Gastropoda, Subulinidae), is strictly myrmecophilous, being only found within *Leptogenys* nests (Witte et al. 2002).

Extensive investigations on the fauna associated with ant nests are necessary and should give rise to a greater number of descriptions of new taxa and behaviors of commensals. We hypothesize that a greater diversity of commensals should be found in nests established in the leaf-litter of cocoa plantations, because of the expected availability of a range of resources and available preys in this environment compared to nests situated on vegetation. Thus, the aim of this study was to investigate the commensal invertebrate diversity in nests of species of the *Neoponera* genus living in cocoa tree (*Theobroma cacao* L., Malvaceae) plantations in southern Bahia, Brazil, as well as possible differences in the composition of this associated fauna living in two distinct habitats: the understory of the plantation (cocoa trees essentially) and on the ground (litter layer).

Materials and methods

Study area

The study was carried out in a cocoa plantation of the cabruca type (for details on this agroforestry system, see Delabie et al. 2007; Schroth et al. 2011) in the south of the state of Bahia, Brazil, from March to December, 2017. This cocoa plantation is located in the Private Reserve of Natural Heritage [Reserva Particular do Patrimônio Natural, RPPN] Fazenda Araraúna (15°18′S 39°09′W; 39 ha), in the municipality of Una, Bahia, Brazil. The biome that dominates the region is the Brazilian Atlantic Forest, characterized by a warm and humid climate of Af-type (Köppen 1936), with an annual temperature ranging between 24°C and 25°C, and an annual regional rainfall ranging from 1300 to 2000 mm (DaRocha et al. 2016).

With about 600 cocoa trees per hectare, the plantation is shaded by approximately 25 to 30 trees per hectare, and the canopy structure is discontinuous-open, reaching about 20–25 m in height. The shading trees are characteristic of the primary or secondary forest biome, such as *Cariniana legalis* Kuntze (Lecythidaceae), *Lecythis pisonis* Cambess. (Lecythidaceae), *Cecropia* sp. (Urticaceae) and *Inga* sp. (Fabaceae), or are exotic: *Spondias mombin* L. (Anacardiaceae); *Artocarpus heterophyllus* Lam. (Moraceae) and *Erythrina* sp. (Fabaceae) (DaRocha et al. 2016). The understory is essentially composed of cocoa trees.

Nest sampling

Ant nests were collected in two strata: understory and ground. The understory is shrubby vegetation that grows below the canopy. In this stratum, all nests are located in cocoa and tree trunks. The ground is characterized by different types of substrates present on the soil surface, including larger caliber decomposing plant material. In this stratum the nests were located in fallen bromeliad, fallen palm leaves and dry cocoa pods.

Ant foragers seen on the vegetation or on the ground were attracted with sardine baits or arthropod pieces (fragments of crickets and grasshoppers offered directly to the ants) and were then followed by the observer until the nest was located.

All imago and immature individuals were captured using entomological forceps and collecting vials. The entire nest structure was collected in large plastic sacks, labeled and carried to the Laboratory of Invertebrate Zoology of the State University of Santa Cruz (UESC), where the biological material was subsequently screened. Nests found in cocoa trees were collected by sawing the branches where the ants were present and taking them to the laboratory. Information on the nesting site and nest type for each colony was also recorded.

The nest substrate was placed in a modified Berlese-Tüllgren funnel (Palacios-Vargas et al. 2013) to extract the associated fauna. The material remained in the trap for 96 h, and the organisms were preserved in 70% alcohol for further analysis. Each colony was given its own identification number and all species of ants were identified to species level (keys and information available on 'Bolton World Catalogue' https://www.antweb.org/world.jsp, consulted in March 2019). Vouchers of the ants were mounted, labeled and kept in the Myrmecology Laboratory collection.

The individuals of the host population were numbered; specimens of mites and springtails were mounted on slides in Hoyer's medium for later identification (D.Z., G.C.-M); and identification of the commensal groups was done thanks to adequate identification keys up to the family level and, when possible, to the highest possible taxonomic level (Najt 2001; Kovác & Palacios-Vargas 2008; Zeppelini & Oliveira 2016; Oliveira et al. 2017).

In this study we used the word 'commensals' for whole organisms found associated within *Neoponera* nests, since in most cases, we do not have enough information about the exact nature of their dependency on the ant host.

Statistical analysis

The Shannon-Wiener diversity index (H′) was calculated according to the stratum, nest type and species. The H′ values were transformed into exponential aiming obtaining "true diversity" as suggested by Jost (2006), thus avoiding a possible bias of highly nonlinear entropy values. The Mann–Whitney test was used to verify possible differences in invertebrate species number and diversity between ground and understory. Jaccard's similarity index was used to compare the composition of invertebrate assemblages, according to the type of nest and host ant. In order to evaluate the composition of invertebrate assemblages according to the nest type and host species, we performed a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). In this analysis, the presence/absence of each invertebrate was the response variable, while the predictor variable was nest type and host ant. Statistical significance was obtained through comparisons with a null model (4999 permutations of the original matrix). These differences were illustrated by non-metric multidimensional scaling (NMDS) using the Jaccard's index. All analyses were carried out using the software R v. 3.5.0 (R Core Team 2018).

Results

We collected 21 nests of four species of the genus *Neoponera* [*N. apicalis* (Latreille, 1802) (1), *N. curvinodis* (Forel, 1899) (1), *N. inversa* (Smith, 1858) (3), *N. verenae* Forel, 1922 (16)] in the two environmental strata surveyed, the understory and the ground, and in different nesting substrates.

In the understory, a single nest of *N. curvinodis* and three nests of *N. inversa* were located in cocoa trees and the workers foraged on the vegetation and used the leaves to move from one plant to another. A nest of *N. verenae* was situated in a cocoa tree trunk cavity at 2 m above the ground and the workers used the soil surface to forage. On the ground, the ant nests belonged to *N. apicalis* (a single nest in a trunk lying on the ground) and *N. verenae* (fallen bromeliads [five nests], trunks fallen on the ground [six nests], dried palm leaves [four nests] and a dry cocoa pod [one nest]). These nests usually had a single entrance through which the ants brought the food resource and left again to forage; in some cases, the workers could also be seen foraging through the vegetation.

All the sampled ant colonies contained a fairly close number of workers. All of them had a single queen except one nest of *N. verenae* which contained up to eight wingless females. All colonies had immature individuals at some stage of development (Table 1).We recorded a total of 16 orders and 42 species/morphospecies of invertebrates associated to *Neoponera* nests (Table 2). These belonged to the taxa: Mollusca: Gastropoda; Annelida: Haplotaxida; Arachnida: Acari, Araneae, Opiliones, Pseudoscorpionida; Chilopoda: Scolopendromorpha; Collembola: Entomobryomorpha, Poduromorpha; Hemiptera; Psocoptera; Hymenoptera;

Table 1. Population structure of ant nests of *Neoponera* spp. recorded in a cocoa plantation. Una, Bahia, Brazil, 2018.

Ant species	Number of nests	Wingless gynes	Workers	Immature individuals	Winged gynes	Males
Neoponera apicalis	1	1	35	59	0	7
Neoponera curvinodis	1	1	7	6	5	2
Neoponera inversa	3	1	29.5 (2–56)	21 (0–45)	0	0
Neoponera verenae	16	1.7 (1–3)	26.3 (2–66)	44.2 (0–163)	0.7 (0–2)	0.6 (0–7)

Diptera; and Coleoptera. The average number of invertebrate species found associated to *Neoponera* nests differed significantly between the two layers (ground = 6.625 ± 3.94, understory = 3.2 ± 1.3; Mann–Whitney *U*-test: $U = 15.50$, $N_1 = 16$, $N_2 = 5$, $P = 0.043$, Figure 1A). However, the average diversity of invertebrates was not significantly different between strata (ground = 4.21 ± 2.43, understory = 3.1 ± 1.3; Mann–Whitney *U*-test: $U = 31.50$, $N_1 = 16$, $N_2 = 5$, $P = 0.482$, Figure 1B). There were also more invertebrate morphospecies associated with nests found in the leaf-litter (twice as many) than in the understory (Figure 1B). In the leaf-litter nests, we recognized 42 morphospecies of invertebrates: 24 in fallen bromeliads, 21 in dry leaves of palm, 14 in trunks laid on the ground and four in dried cocoa pods. Acari and Coleoptera were the orders that occurred on all nesting substrates. Only six species of invertebrates were found in nests located in cocoa trees (Table 2).

The species that presented the greatest diversity of invertebrates in its nests was *N. verenae* (Figure 2A). On average nests of *N. verenae* contained seven invertebrate morphospecies, whereas for the other ants, this value averaged three morphospecies per nest (Figure 2B).

The ant species that showed the highest similarity between their invertebrate assemblage compositions were *N. inversa* and *N. verenae*-understory (65%). *N. curvinodis* presented a similarity of 60% both with *N. inversa* and *N. verenae*-understory. The invertebrate fauna found in nests of *N. apicalis* presented a greater similarity to those found in understory nests (40%). The composition of the invertebrate fauna associated with nests of *N. verenae*-ground presented a low similarity to any of the other series of nests sampled (10% only) (Figure 3).

Nests located in fallen bromeliads, dried palm leaves and trunks laid on the ground housed a greater diversity and number of organisms. Diversity of invertebrates living in the nests of *Neoponera* varies according to the host species and microhabitats (Figure 4A). In general and independently of the habitat, nests of *N. verenae* shelter a larger amount of species of invertebrates than the other ants studied here (Figure 4B).

The composition of the invertebrate assemblage in *Neoponera* nests differed according to the strata where the nests were established ($F_{2,21} = 1.766$; $p = 0.004$) and also among nest types ($F_{6,17} = 1.3642$; $p = 0.009$). Invertebrates assemblages are organized in different manners according to the nest types (Figure 5). Most invertebrate morphospecies were most frequently found in nests sheltered by bromeliads and dry palm leaves. These nests were also those that presented a greater number of exclusive morphospecies. Only two species of Collembola were associated in nests in fallen trunks, whereas the single observed species of Psocoptera was found in a hanging pod (Figure 5).

Discussion

This study investigated the diversity of commensal invertebrate living in nests of *Neoponera* sp. collected in the understory and leaf-litter stratum of a cocoa cabruca plantation. Generally, nests found on the ground sheltered a high richness and diversity of associated invertebrates, particularly when situated in fallen bromeliads and dry palm leaves. The ant species that presented the highest diversity of fauna associated in this stratum was *N. verenae*. The understory nest showed a similar invertebrate composition, but sheltered the lowest numbers of commensals. The nests of the sampled species followed a similar pattern as those described in the literature (Delabie et al. 2008; Antonialli-Junior et al. 2015); they were opportunely located in cavities available in the habitat and generally exhibited unelaborated structures. It is well known that *Neoponera* species can nest in a range of habitats, either in the arboreal or in the soil strata.

The groups of invertebrates found in the ant nests were rather similar to those already described in previous studies (Witte et al. 2008; Castaño-Meneses et al. 2015a, 2019; Silva et al. 2018). The only exception was the phylum Nematoda (see Rettenmeyer et al. 2011), which has no representative in our nest series probably because they are too small and require a different extraction procedure than those we used. *Neoponera* nests are ideal places for a range of invertebrates for providing

Table 2. Abundance of invertebrates found in ant nests of *Neoponera* spp. recorded in a cocoa plantation. Una, Bahia, Brazil 2018.

					Ground		Understory			
Taxon	Order	Family	Morphospecies/species	Code	Fallen Bromeliad	Fallen Palm Leaf	Dry Cocoa Pod	Laid Trunk	Cocoa Tree	Tree Trunk
Mollusca	Gastropoda		Gastropoda sp.1	Gast1		3				1
Annelida	Haplotaxida		Annelida sp.1	Hapl1	3					
Arachnida – Acari	Mesostigmata		Mesostigmata sp.1	Meso1	48	107		36	3	1
	Sarcoptiformes		Astigmata sp.1	Astig1	36	3		11	4	1
	Sarcoptiformes		Oribatida sp.1	Sarc1	17	189		10	5	1
	Trombidiformes		Prostigmata sp.1	Trom1				1		
Arachnida – others	Araneae		Araneae sp.1	Aran1	1		1			
	Opiliones		Opiliones sp.1	Opil1	1	1				
	Pseudoscorpionida		Pseudoscorpionida sp.1	Pseu1	2					
Chilopoda	Scolopendromorpha		Scolopendromorpha sp.1	Scol1	2					
Collembola	Entomobryomorpha	Isotomidae	*Isotomiella nummulifer*	Ento1	2	1				
			Cryptopygus sp.1	Ento2		2	1			
			Proisotoma sp.1	Ento3		1				
		Lepidocyrtidae	*Cyphoderus agnotus*	Ento4		1	1			
			Cyphoderus ca. *innominatus*	Ento5				1		
			Lepidocyrtus sp.1	Ento6	4	1		1		
			Lepidocyrtus sp.2	Ento7	1					
	Poduromorpha	Brachystomellidae	*Brachystomella agrosa*	Podu1	1			1		
			Brachystomella sp.1	Podu2	1					
		Neanuridae	*Friesea* sp.1	Podu3		1				
			Poduromorpha sp.1	Coll2				1		
Hemiptera	Hemiptera	Cercopidae	Cercopidae sp.1	Hemi1		1				
		Cicadellidae	Cicadellidae sp.1	Hemi2		1				
		Reduviidae	Reduvidae sp.1	Hemi3	6					
Psocoptera	Psocoptera	Amphientomidae	Amphientomidae sp.1	Psco1					1	
Hymenoptera	Hymenoptera	Formicidae	*Azteca* sp.1	Hyme1		1		1		
			Camponotus sp.1	Hyme2	1					
			Eurhopalothrix sp.1	Hyme3		1				
			Nylanderia sp.1	Hyme4	1					
			Pheidole sp.1	Hyme4	2					
			Solenopsis sp.1	Hyme5		1				
			Solenopsis sp2	Hyme6	2		1	2		
			Strumigenys sp.1	Hyme7		2				
Diptera	Diptera	Cecidomyiidae	Cecidomiidae sp.1	Dipt1	3	6		1		
		Culicidae	Culicidae sp.1	Dipt2	1					
		Psychodidae	Psychodidae sp.1	Dipt3		1		1		
		Simuliidae	Simuliidae sp.1	Dipt4	1	1				
Coleoptera	Coleoptera	Elateridae	Elateridae sp.1	Cole1	1					
		Scolytinae	Scolytinae sp.1	Cole2	4	2		2	1	1
		Staphylinidae	Staphylinidae sp.1	Cole3	3					
Total					**144**	**327**	**4**	**70**	**14**	**5**

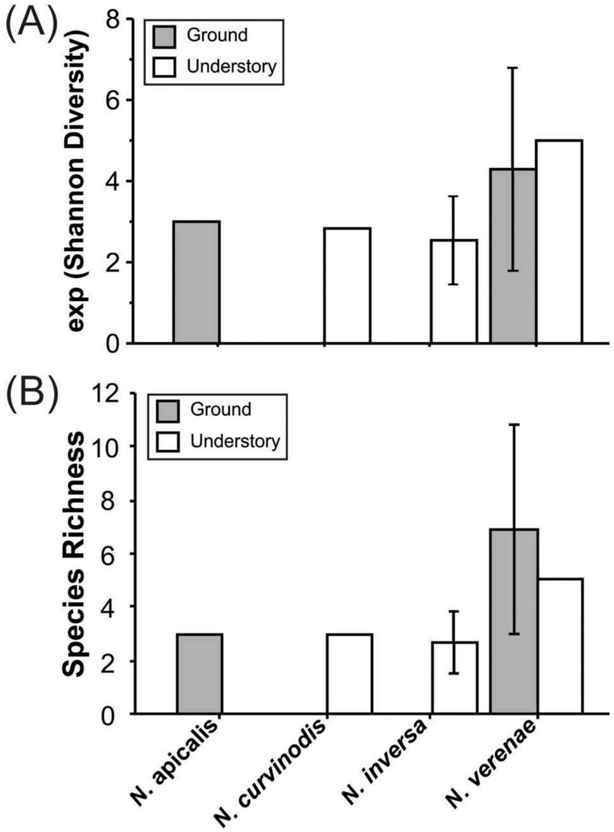

Figure 2. Diversity (A) and richness (B) of invertebrates associated with ant nests of the genus *Neoponera* recorded in the cocoa plantation. Una, Bahia, 2018. Bars represent the standard deviation (n = number of nests).

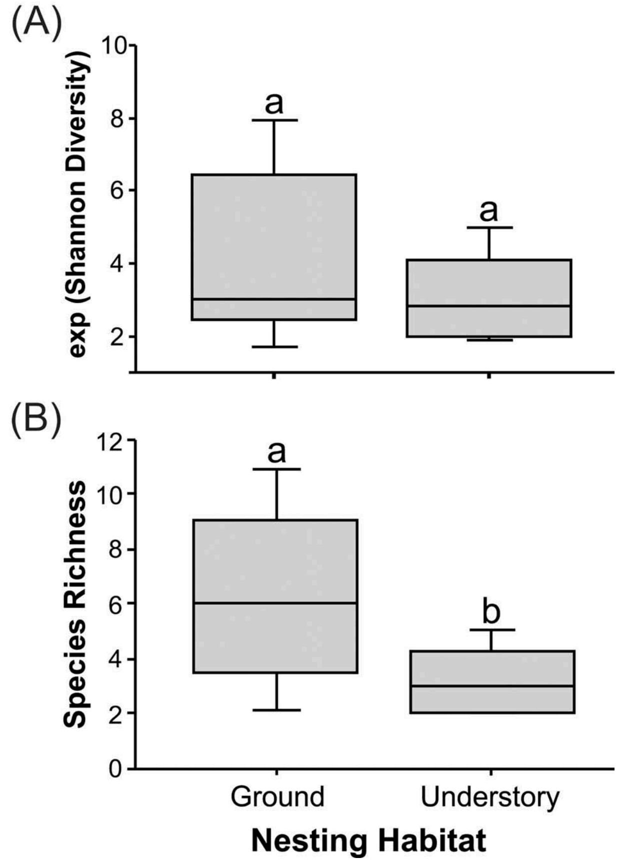

Figure 1. Diversity (A) and richness (B) of invertebrate species/morphospecies found in nests within the two strata in the cocoa plantation. Una, Bahia, 2018.

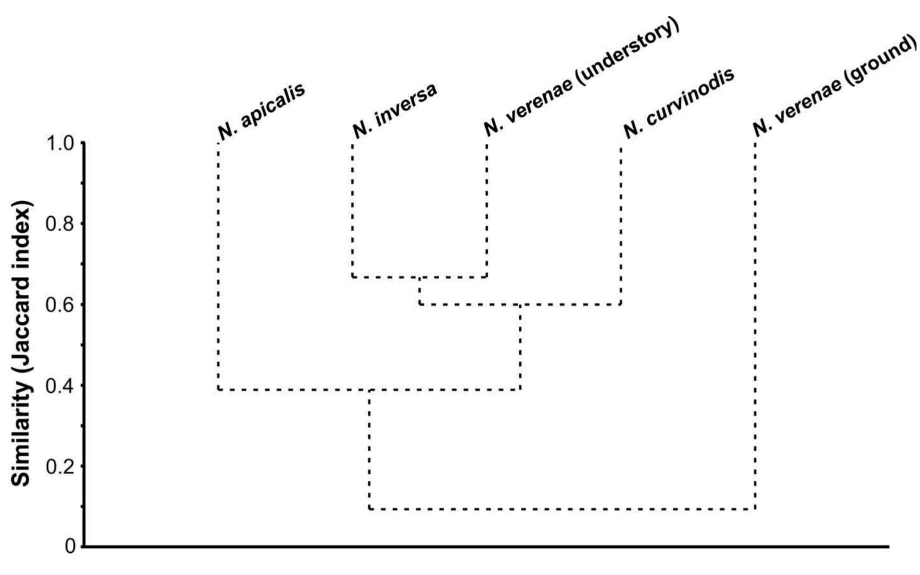

Figure 3. Similarity dendrogram (Ward's classification) of ant nest types of the genus *Neoponera* studied in a cocoa plantation according to the composition of their invertebrate assemblages found. Una, Bahia, 2018. In the case of *N. verenae*, the nests on the ground and understory were analyzed separately.

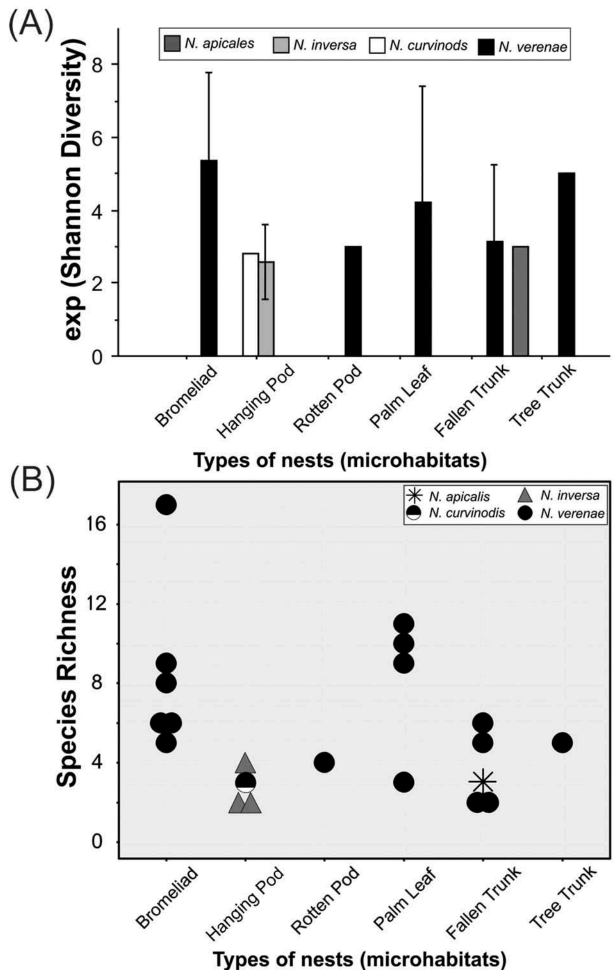

Figure 4. Diversity and richness of species of invertebrates found according to the substrate of the *Neoponera* ant nests, cocoa plantation, Una, state of Bahia, Brazil, 2018. Bromeliad: epiphytic Bromeliad fallen on the ground; Hanging Pod: dry cocoa pod on the tree; Rotten Pod: rotten cocoa pod fallen on the ground; Palm Leaf: palm leaf fallen on the ground; Fallen Trunk: piece of tree trunk laid on the ground; Tree Trunk: in a hollow *Erythrina* trunk.

protection and permanent availability and accessibility of food resources (Parmentier et al. 2014). They seem to be the main reasons for the abundance of these mutualisms (Kronauer & Pierce 2011). The entry of intruders into the colonies of *Neoponera* spp. is probably enhanced by the fact that many nesting sites used by the ants are transitory due to the rapid decomposition process, which increases the rate of seeking new spaces to inhabit (Byrne 1994).

Published studies on *Neoponera* nests located in cocoa plantations in southern Bahia have already pointed out the occurrence of springtails and mites living in the nests (Castaño-Meneses et al. 2014, 2015a, 2019; Silva et al. 2018), and despite their high frequency, these organisms remain poorly known (Castaño-Meneses et al. 2014, 2015a, 2015b). The listed species (Table 2) are new occurrences of these commensals with Ponerinae for the Neotropical Region.

Among the mites found in the ant nests the order Prostigmata includes phoretic species associated with *N. inversa, N. verenae* and *N. villosa* (Campbell et al. 2013). The order Oribatida, on the other hand, is a group of organisms frequent in ant nests (Ito & Takaku 1994). There is no record of species of this order in *Neoponera* ant colonies so far.

A greater number of invertebrates were found within *Neoponera* nests on the ground than those in the understory. Nests on trees are less predictable and more difficult to harvest, and consequently the fauna of associated organisms is possibly underestimated.

Nests located in the same microhabitat are subject to the same microclimatic, ecological and micro-environmental variations (Bihn et al. 2008). Therefore, it is to be expected that the invertebrate community living in *Neoponera* nests in a single stratum (understory) is more homogenous than when different strata are compared. *Neoponera verenae* was the only species that occurred in greater numbers of nests and in more types of substrates, and this may be one of the reasons for the rather large dissimilarity of the composition of the invertebrate fauna with the other ant species.

The comparison of the invertebrates associated with a particular substrate becomes difficult when the host species are generalists and opportunist in relation to nesting places. This could be associated with the fact that the nesting substrates occupied by *N. verenae* were more diverse than the other ants and it was also the most sampled species. Specimens of the following orders: Gastropoda, Haplotaxida, Opiliones, Entomobryomorpha, Poduromorpha and Pseudoscorpiones occurred only in these nests.

The nests of the species studied here were able to house a range of associated invertebrates, with some differences in their diversity according to the studied strata: ground and understory. Identifications at a more specific level could reveal a greater number of associations between ants and other invertebrates that have not yet been described, as has occurred for Collembola in other studies. It would also better inform us on the specificity between the host ants and the commensals, or the ecological role that these play within the ant nests. It should also be mentioned that *Neoponera*, like other genera of the subfamily Ponerinae, shows a strong preference for conserved or fragmented forest habitats (Campiolo et al. 2015), so the conservation of this environment is linked to the conservation of both ants and their associated fauna, especially those organisms that maintains intimate associations with their hosts.

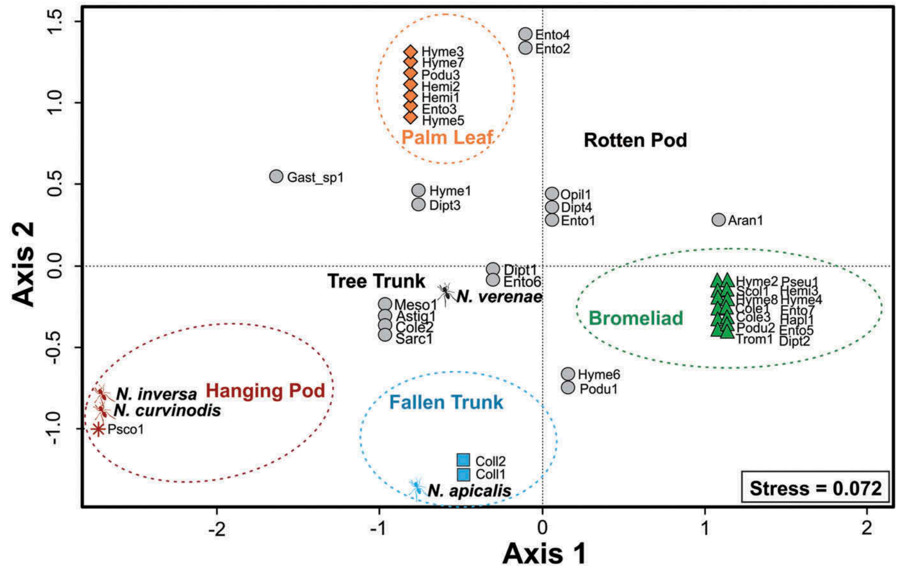

Figure 5. Non-metric multidimensional scaling (NMDS) of nests of *Neoponera* from different substrates, separated based on the composition of the invertebrate assemblages (presence/absence in each nest) found. Una, Bahia, 2018. Diamonds, star, squares and triangles surrounding a type of substrate and/or the code of an organism, corresponding to exclusive occurrences. The codes correspond to the invertebrates listed in Table 2.

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