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Ants in the clouds: A preliminary checklist of the ant (Hymenoptera: Formicidae) fauna of a Honduran cloud forest ecosystem, featuring a key to country genera.

Frederik C. De Wint[1,2,3,*], Dominik Oorts[1], Michael G. Branstetter[4], Dario De Graaf[1], Wouter Dekoninck[5], Merlijn Jocque[1], Thomas E. Martin[6,7], Jennifer Sudworth[1], Ronja Van Osselaer[1], Matthew T. Hamer[1,8]

[1]Biodiversity Inventory for Conservation npo (BINCO), Walmersumstraat 44, 3380 Glabbeek, Belgium
[2]Department of Zoology, Faculty of Science, University of South Bohemia, Branisovska 1160/31, 37005 České Budějovice, Czech Republic
[3]Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Department of Ecology, Branisovska 1160/31, 37005 Ceske Budejovice, Czech Republic.
[4]U.S. Department of Agriculture, Agricultural Research Service, Pollinating Insects Research Unit, Utah State University, Logan, UT, U.S.A.
[5]Entomology Department, Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000 Brussels, Belgium
[6]School of Natural Sciences, College of Environmental Sciences and Engineering, Bangor University, Bangor, Gwynedd, LL57 2DG, UK
[7]Operation Wallacea Ltd, Wallace House, Old Bolingbroke, Lincolnshire PE23 4EX, UK
[8]School of Biological Sciences, The University of Hong Kong, Kadoorie Biological Sciences Building, Pok Fu Lam Road, Hong Kong SAR, China

* Corresponding author email: frederikdewint@hotmail.com

Abstract

Ant diversity in tropical montane rainforests is understudied globally. This is true in Cusuco National Park (CNP), a cloud forest ecosystem in northwestern Honduras which supports geographically isolated and threatened habitats. The current study represents the first comprehensive ant species checklist for CNP, which is also the first ant checklist for Honduras in over a century. Species records from several projects are combined and presented. Sampling occurred along an elevational range (mainly between 1170-2030m a.s.l.), with methodologies and intensities varying among projects and dates. Overall, 162f ant species, belonging to nine subfamilies and 60 genera are reported from CNP. Five species are recorded for the first time in Honduras (*Pheidole natalie* Longino, 2019; *Strumigenys* cf. *calamita*; *Solenopsis invicta* Buren, 1972; *Solenopsis texana/carolinensis*; *Pseudomyrmex pallens* Mayr, 1870). For the first time, male individuals are reported of *Pheidole balatro* Longino, 2019. For each species, we provide information on observed habitat preference, elevational range, and sampling technique. Species accumulation curves are provided for each sample technique, representing sampling intensity and community sample coverage. We also provide a key to the ant genera of Honduras to aid future taxonomic efforts in the country. Our research demonstrates that CNP harbours a surprising richness of ant species, despite its small area, similar to many other taxa in the park. The information provided here represents baseline information for future work on ants in CNP and other Honduran cloud forests, and will help guide research in these otherwise poorly explored yet highly threatened ecosystems.

Keywords

Biodiversity Hotspot, Cusuco National Park, Insects, Mesoamerica, Species diversity, Tropical montane forest

Introduction

Tropical montane cloud forests are located in the humid tropics within the zone of maximum cloud condensation (Ellenberg 1959). These forests are markedly different from those found at lower elevations, creating biogeographical isolation, and harbour abundant endemic flora and fauna as result (Long 1995, Anderson and Ashe 2000, Bubb et al. 2004, Martin et al. 2021). For instance, because of their precipitation patterns, many cloud forests show high abundances of epiphytic plant growth, which provide unique niches and microhabitats for other species (Stadtmuller 1986). Cloud forests are understudied globally, particularly in terms of insect fauna, with baseline inventories lacking for many sites (Jones et al. 2008, Sabu et al. 2011). Habitat loss and climate change significantly threaten these unique ecosystems and the species they support (Freeman et al. 2018, Hansen et al. 2020).

Cusuco National Park (CNP hereafter), situated within the Merendon mountain range in northwest Honduras, is one such tropical montane cloud forest. Located in the Mesoamerican biological hotspot (Myers et al. 2000), CNP has been designated as one of the 137 most irreplaceable protected areas in the world (Le Saout et al. 2013). Despite this, the park is under severe threat from deforestation and subsequent land conversion for subsistence agriculture (Martin et al. 2021). Honduras as a whole is one of the most severely impacted countries in terms of deforestation within protected areas (Hansen et al. 2020). Biodiversity in the park is therefore under significant anthropogenic pressure, particularly for regionally endemic species, of which the park harbours a high number across many floral and faunal groups (Martin et al. 2021). This forest is known for harbouring understudied taxa, with ongoing discoveries of multiple novel species, particularly within the arthropod class. (Mendes et al. 2011, Pinto and Jocque 2013, Damron et al. 2018, Santos-Silva et al. 2018, 2021, Longino 2019, Jocque and Garrison 2022).

The ecological impact of ants on most communities is hard to overstate. Ants (Formicidae) are ecologically dominant and ubiquitous in nearly all habitats across the globe. They are key components of many ecosystems, influencing communities as predators, seed dispersers (myrmecochory), and direct and indirect herbivory (Hölldobler and Wilson 1990, Del Toro et al. 2012). These socially organised insects are often closely associated with a variety of organisms, ranging from plants to arthropods (Hölldobler and Wilson 1990). Arthropod community patterns are significantly shaped by ants across montane landscapes (Rudgers et al. 2010) and even increase plant growth (Moreira et al. 2012). The diversity of ants is typically higher in lowland tropical regions (Dunn et al. 2009, Economo et al. 2018) with abundance and diversity decreasing at high elevations (Longino et al. 2014). In Mesoamerica, and other regions, a mid-elevation peak in ant diversity is generally observed, with montane specialist species from multiple subclades dominating the highest elevations (Longino and Branstetter 2019). In addition to natural diversity patterns, many species have also been anthropogenically redistributed across the globe, colonising areas that were previously inaccessible (Bertelsmeier 2021, Wong et al. 2023). Some of these species have had devastating ecological impacts in the ecosystems they have been introduced into (Tercel et al. 2023).

Although progress has been made towards understanding ant macrodiversity across biogeographical realms, continental and climatic scales (Janicki et al. 2016, Guénard et al. 2017), fundamental knowledge is still lacking on a local scale, especially in tropical regions (Kass et al. 2022). This is particularly true for higher elevations that have historically been difficult to access and survey (Guénard et al. 2017, Liu et al. 2020). One clear example is Honduras, located in Mesoamerica. Historical country records originate from Wheeler (1907) and Mann (1922) who both compiled short species lists from their brief visits to the country over a century ago. Taxonomic literature and implementation of database infrastructures have changed myrmecology substantially since (e.g. Bolton 1995, 2003; www.AntWeb.org; Janicki et al. 2016, Guénard et al. 2017); however the Honduran ant fauna has not been reassessed since the development of such resources. Recent collections of ants for both Honduras and CNP have been made; resulting in the description of multiple novel species: *Octostruma leptoceps* Longino, 2013; *Stenamma cusuco* Branstetter, 2013; *Stenamma atribellum* Branstetter, 2013; *Temnothorax altinodus* Prebus, 2021; *Pheidole cusuco* Longino, 2019. All but the latter species are considered restricted to CNP. However, most species records of these recent collections have not been published in comprehensive lists. One project in particular, the Leaf Litter Arthropods of MesoAmerica (LLAMA) project collected leaf litter arthropods, including ants, across various elevational gradients throughout Mesoamerican mountain ranges (Longino et al. 2014). Alongside other sites in Honduras, the LLAMA project visited CNP in 2010. Compiling accurate species checklists is of vital importance, not only for taxonomic studies but also for providing fundamental biogeographical knowledge (Kass et al. 2022), and thus essential data for conservation efforts (Guénard et al. 2017, Liu et al. 2020). This is of particular importance considering the broad consensus of the heightened threats to biodiversity in CNP specifically, and cloud forest ecosystems generally (Bubb et al. 2004, Martin et al. 2021).

Here, we produce the first ant checklist of CNP by combining new sampling efforts with existing data records from the LLAMA project (2010). This list, as far as we are aware, represents the first checklist of the ant fauna from any Honduran site in over a century. We include information on species known to be of restricted distribution to CNP and species considered to be exotic (non-native) in the park. Knowledge gaps are highlighted in terms of considered elevation range, sampling techniques and sampling intensity. Finally, we include an identification key for all ant genera of Honduras.

Methods

Study region

CNP (15°32′31″N; 88°15′49″W) encompasses approximately 23,440 ha, with an elevational range of 500-2242 m a.s.l. (ICF 2015) (Fig. 1). The park is divided between an inner core zone (7690 ha) where settlement and resource extraction are prohibited, and an encircling buffer zone (15,750 ha) where some of these practices are allowed. Closed canopy forest dominates the core zone, with a diverse community of broadleaf evergreen tree species present in the mid to upper elevational ranges (1300 - 1800 m a.s.l), interspersed with pine forest occurring mostly in the drier, eastern slopes of the park. Secondary forest, at various levels of succession, is also present below 1300 m a.s.l as a result of commercial logging during the mid-20th century (Martin et al. 2021). At higher elevations (>1800 m a.s.l.) upper montane rainforest - characterised by dense growth of mosses, liverworts, ferns and a high abundance of bromeliads - is present as a result of cool temperatures and comparatively higher rainfall. At the uppermost peak elevations (>2000 m a.s.l.) a combination of soil erosion and lack of decomposition results in stunted but densely interwoven vegetation known as elfin forest (Martin et al. 2021).

Sampling and specimen processing

Ant species observations from two different projects were pooled into a single dataset. Respective projects and methodologies are described below. Sampling techniques used for each project are summarised in Table 1 and Fig. 2. Sampling was completed mainly in the core zone of the park, between the elevations of 1170-2030 m a.s.l.

1. Leaf Litter Arthropods of Mesoamerica (LLAMA)

Project LLAMA, funded by the U.S. National Science Foundation, sampled leaf litter-dwelling arthropods across Mesoamerica from southern Mexico to Nicaragua, with a focus on ants and weevils (Curculionidae) (Longino et al. 2014). Specimens were collected in CNP from 29 May to 3 June 2010, during the transition from the dry season to the short wet season. Most collections were made between 1210-1360 m a.s.l., but additional non-quantitative samples were collected between 1580 and 2030 m a.s.l. (Fig. 2). A few additional leaf litter samples were collected earlier by R. Anderson on 24 August 1994 and included in this dataset.

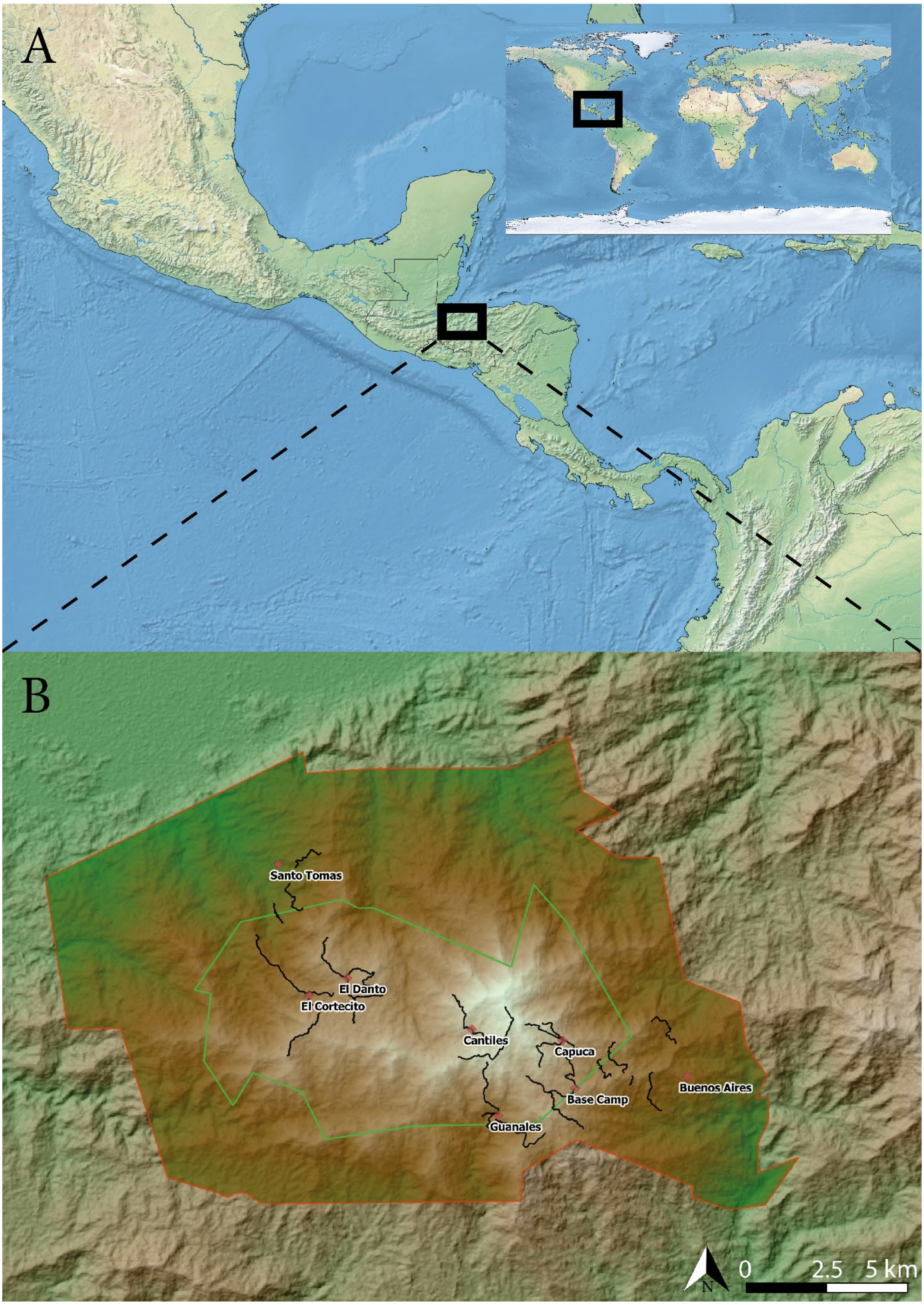

Figure ***1.*** *Map of Cusuco National Park. Buffer and core zone boundaries are shown (red and green respectively) with camps (red dots) and corresponding transects with sampling subsites (black lines). Cuscuo elevation data derived from Burdgis.org (accessed 16/09/2021). Continental relief map derived from SimpleMappr, Shorthouse, 2010.*

Sampling methods

Sampling was completed according to a standardised transect-based framework in mesophyll cloud forest. Arthropods were extracted from two transects of 50, 1 m² forest floor quadrats, using MiniWinklers following methods used in Fisher 1999. Other sampling techniques used included general collection by hand, cookie baiting, vegetation beating, MaxiWinkler extraction, Berlese extraction, and Malaise trapping. The samples collected in 1994 were those obtained by the Berlese extractions.

Specimen processing

Ants were sorted from the samples by project staff. For several reasons, only a subset of the ants present in samples were identified to species-level, with unidentified species designated a morphospecies code. Several taxa were only identified to genus level due to taxonomic impediments, particularly within genera presenting challenges in species classification: *Azteca* Forel 1878, *Brachymyrmex* Mayr 1868, *Nylanderia* Emery 1906, *Solenopsis* Westwood 1840, *Tapinoma* Foerster 1850. *Hypoponera* Santschi 1938 workers were classified at the genus level, except for two species that were readily distinguishable. *Pheidole* Westwood 1839 workers were predominantly identified to the species level, though the rarely isolated minor workers were identified only at the genus level.

Voucher specimens were stored in regional collections in Honduras, and temporarily in the Longino research collection at The University of Utah, as well as the Branstetter research collection. Comprehensive specimen data can be accessed on AntWeb (www.AntWeb.org). A full description of the LLAMA collection and processing methodology can be found in Longino et al. 2014.

2. BINCO - MyrmEcoDex (MED)

The Biodiversity Inventory for Conservation NPO (BINCO) project studies biodiversity in understudied regions globally. MyrmEcoDex (MED) is BINCO's ant workgroup. Samples were collected during Operation Wallacea (henceforth 'OpWall') biodiversity monitoring expeditions. OpWall has been conducting volunteer-funded biodiversity surveying and monitoring in CNP from June-August since 2006, operating from satellite camps distributed in the East and Western regions of CNP at different elevations. MyrmEcoDex members participated in OpWall expeditions during the 2018 and 2019 field seasons. A total of six camps were operational: one in the buffer zone (Buenos Aires) and five in the core zone of the park (Base Camp, Guanales, Cantiles, El Danto, El Cortecito) (Fig. 1). Each camp established three to four transects that extended into the park, which were used for surveying. Ant collections were made between 1170-2030 m a.s.l. Some opportunistic sampling was also completed at Santo Tomás in the lower elevational ranges of the park; a former camp that is no longer used for formal surveys.

Sampling methods

Surveys were carried out every 3-5 days at up to eight subsites distributed at least 200 m apart along transects (Hinchcliffe et al. 2017). Four baited (horse dung) pitfall traps were deployed at each subsite. Pitfall traps were placed in a 20 x 20 m grid, 10 m from one another and 5 m from grid edges to ensure compatibility with other plot sampling as well as to reduce interference between individual pitfalls. Ants were sorted from pitfalls in the field by MED members. During the 2019 field season, 61 out of 198 total pitfalls were screened for ants (31%). Ants extracted in 2018 only include six pitfall samples; other specimens were lost due to deterioration.

MyrmEcoDex members carried out additional sampling techniques. Ants were searched for and collected opportunistically by hand or aspirator from a variety of substrates: nests, soil, deadwood, leaves, tree bark, inside epiphytes and others. Additionally, MaxiWinkler extractors were used to sample ants in leaf litter with extraction times varying between 3-5 days (depending on time availability). Forty bromeliads from different sizes were also dissected leaf by leaf and ants were collected when a colony was present.

Additional specimens originating from previous OpWall expeditions were provided by Oxford University Museum of Natural History (OUMNH) and examined by the authors. The majority of such specimens originated from hand collection and pitfall trapping regimes as described above.

Specimen processing

Collected ants were stored in ethanol (70%). These specimens were sorted to morphospecies, point-mounted, and identified to the lowest taxonomic rank possible. Specimens which could not be assigned to species were given morphospecies codes. Identifications at species level were verified by experts to ensure accuracy. The latter was facilitated via specimen pictures, taken using a quick and easy to use photographic setup detailed within Mertens et al. (2017). Due to their taxonomic complexity, collected specimens of the genera *Nylanderia,* as well as part of the hyperdiverse *Pheidole*, were not considered for species level identification. Specimens were deposited at the Royal Belgian Institute for Natural Sciences (RBINS) collections after identification.

Images

A subset of species (43) were photographed and pictures are provided in Supplement 3. These photographs were taken using the following setups: (1) Canon 80D with a Venus Optics Laowa 25mm f/2.8 2.5-5X Ultra Macro Lens, or EF 100mm f/2.8L Macro IS USM with Raynox 250DCR macro attachment. Images were taken using a homemade diffuser system, and manual rail system. Images were stacked in Adobe Photoshop (Adobe inc.). (2) Canon-Cognisys set-up (Brecko et al. 2014).

Table 1. *Summary of the methods used in two ant collection projects in Cusuco National Park: LLAMA (Leaf Litter Arthropods of Mesoamerica) and MED (MyrmEcoDex* - *BINCO).*

Sampling method	**LLAMA**	**MED**
Baiting	✓	
Berlese extraction	✓	
Hand collection	✓	✓
Malaise	✓	
Pitfall		✓
Vegetation beating	✓	
Winkler extraction	✓	✓

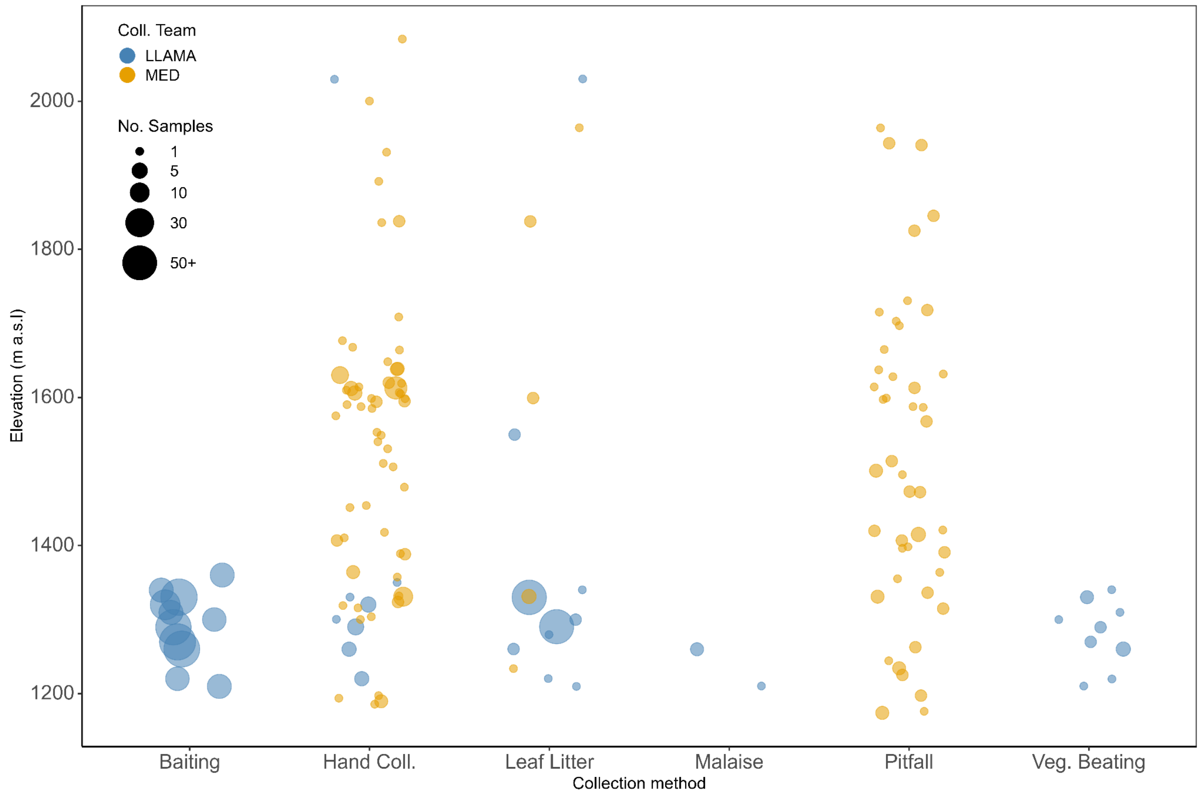

Figure 2. *Distribution of sampling effort across the elevation gradient of Cusuco National Park. For the Leaf litter Arthropods of Mesoamerica (LLAMA) and MyrmEcoDex (MED) collections. Circle size corresponds to the number of samples at a specific elevation. Leaf litter sampling includes MiniWinkler, MaxiWinkler and Berlese traps.*

Unconfirmed identifications

Some identifications could not be confirmed and are marked as cf. (Latin: *confer*) or by a summation in the species epithet. These specimens appear similar to the named species, but verification was not possible. Verification requires more specimens and comparison with morphologically similar species.

Spatial distribution status

An assessment of biogeographic distribution status was made for all recorded species in this study, using Antmaps (Janicki et al. 2016, Guénard et al. 2017). The following categories were applied: regionally restricted (to Honduras), exotic (to Honduras; i.e. non-native), and globally invasive species (showing wide global occurrence patterns). Species not previously reported in Honduras were also noted.

Species accumulation

Species accumulation curves were made to grant insight into sample completion and method efficiency. By assessing species richness cumulatively per additional sample we show the intensity of individual sampling techniques respectively to the potential for collecting additional species with additional sampling. Accumulated species richness was also compared with sampling coverage of the community, which is the probability that an individual of the entire ant community belongs to a species that has been sampled before. As sampling techniques each address a different subset of the total ant community, respective subset communities are considered. Species presence-absence matrices using unique sample code as individual sampling units, were built per collection methodology. Non-species level identified specimens and OUMNH material were excluded as a result of low taxonomic resolution and lack of collection codes respectively. Final accumulation curves and summary statistics were generated with the iNEXT R package using the first Hill number (species richness) (Chao et al. 2014, Hsieh et al. 2022).

Identification Key: Ant genera of Honduras

To improve accessibility of this work, and the Honduran ant fauna in general, a dichotomous identification key was constructed for ant genera for the whole of Honduras (Supplement 2). Genera occurring in Honduras were determined using records from Antweb (www.AntWeb.org). The identification key was constructed manually by combining multiple works and identification keys on relevant taxa (Ward 1985, Hölldobler and Wilson 1990, Shattuck 1992, Bolton 1995, Longino 2007, Wild 2007, Donoso 2012, Fayle et al. 2014, Schmidt and Shattuck 2014, Baccaro et al. 2015, 2015, Borowiec 2016, Ward and Fisher 2016, Ward et al. 2016, Williams and Lapolla 2016, Solomon et al. 2019, Prebus 2021b, Camacho et al. 2022, www.Antwiki.org), with respective citations provided (provided as supplementary material).

Results

Ant fauna of CNP

Across all sampling projects, a total of 5690 ants were collected in CNP, resulting in nine subfamilies comprising 60 genera and 162 species (Table 2). Appendix 1 provides a complete list of all ant species found in CNP, with the respective sampling method, recorded elevational distribution ranges, and habitat (data also in Supplement 1). Characteristic specimens from our collections are shown in Fig. 3.

In addition to the first 127 species collected by LLAMA (3445 specimens), the MED collections resulted in an additional 41 species for CNP. The latter yielded a total of 78 species and 2155 specimens; 894 in 2018 and 1261 in 2019. Of these, 286 and 419 were mounted respectively and added to the RBINS collections (together with the remaining specimens in ethanol). The checklist also includes 90 mounted specimens from the OUMNH, collected during earlier field surveys in CNP and identified by MED.

Some ant species in CNP have notable distributions (Table 3). Seven species are regionally restricted to Honduras and two species are exotic. Three species have global distributions (including the two exotic species) and five species were recorded for the first time in Honduras.

We report the first collection of male *Pheidole balatro* individuals (Fig. 4). Males of this species were previously unknown. Six male individuals were collected alongside minor and major workers of this species from a nest residing inside a bromeliad plant (Base Camp, 26 June 2019, 1613 m a.s.l.). The nest was basally located in the bromeliad between the leaves and was discovered by removing leaves from their basal attachment. All six specimens of *P. balatro* males were stored in the RBINS collections (three mounted, three preserved in ethanol; sample code: CNP-222).

Sampling elevation and methodology

Sampling effort across the elevation range varied between LLAMA and MED (Fig. 2). There were also differences in collection techniques used between the two datasets. LLAMA focussed on a more narrow elevation range between ~1210-1360 m a.s.l. (with the exception of three higher samples at ~1580m and ~2030 m a.s.l.), using thorough sampling in a standardised framework. A large part of ant diversity in CNP (127 species) was thus recorded in a narrower elevation range using four sampling techniques: leaf litter extraction, bait trapping, Malaise trapping and vegetation beating. Project MED considered a broader range of elevation from ~1170-1960 m a.s.l., employing less exhaustive sampling. A different set of sampling techniques was employed (pitfall traps and more hand collections) at wider elevation ranges, including higher elevations. This resulted in the collection of a different subset of the ant fauna (78 species total; 41 newly reported). Additional species were even collected at the same narrow elevation range just by a change of techniques (e.g. *Odontomachus yucatecus*).

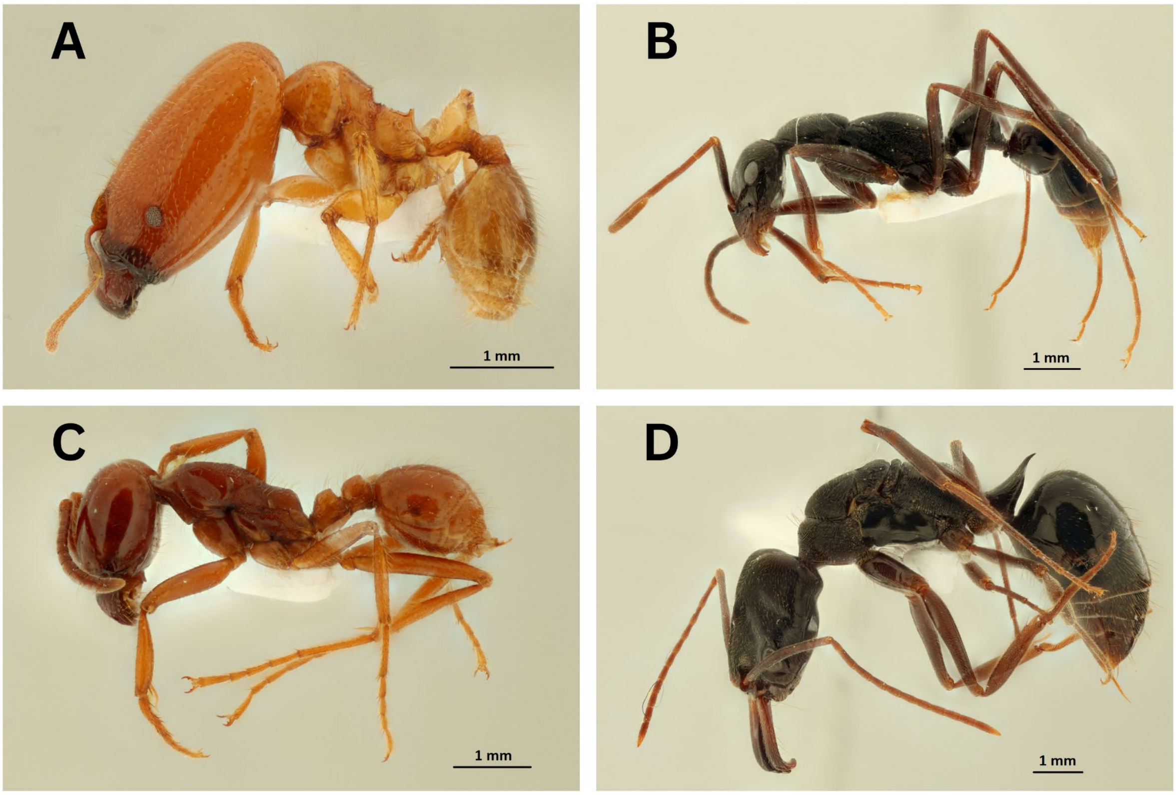

Figure ***3.*** *Select ant species collected in Cusuco National Park. Top:* Pheidole absurda *(**A** - major worker),* Leptogenys imperatrix *(**B** - worker); Bottom:* Labidus coecus *(**C** - major worker),* Odontomachus yucateus *(**D** - wingless female).*

Table 2. *Composition of genera and species per subfamily contributing to total species richness detected in Cusuco National Park.*

Subfamily	**Genera**	**Species**
Amblyoponinae	1 (2%)	1 (1%)
Dolichoderinae	5 (8%)	8 (5%)
Dorylinae	7 (12%)	14 (9%)
Ectatomminae	4 (7%)	9 (6%)
Formicinae	4 (7%)	10 (6%)
Myrmicinae	24 (40%)	88 (54%)
Ponerinae	12 (20%)	26 (16%)
Proceratiinae	2 (3%)	2 (1%)
Pseudomyrmecinae	1 (2%)	5 (3%)
Total	*60*	*162*

Table 3. *Ant species from Cusuco National Park with notable geographic distributions: known distribution restricted to Honduras (*P. cusuco *in CNP and just across the Guatemalan border), exotic to Honduras and/or globally invasive. First records for Honduras are also shown. *P. cusuco in CNP and just across the Guatemalan border.*

Species	**First Honduran record**	**Regionally restricted**	**Exotic**	**Globally invasive**
Leptogenys bifida Lattke, 2011		✓		
Leptogenys honduriana Mann, 1922		✓		
Monomorium pharaonis Linnaeus, 1758			✓	✓
Octostruma leptoceps Longino, 2013		✓		
*Pheidole cusuco** Longino, 2019		✓		
Pheidole natalie Longino, 2019	✓			
Pseudomyrmex pallens Mayr, 1870	✓			
Strumigenys cf. *calamita*	✓			
Solenopsis texana/carolinensis	✓			
Solenopsis invicta Buren, 1972	✓		✓	✓
Solenopsis geminata Fabricius, 1804				✓
Stenamma atribellum Branstetter, 2013		✓		
Stenamma cusuco Branstetter, 2013		✓		
Temnothorax altinodus Prebus, 2021		✓		

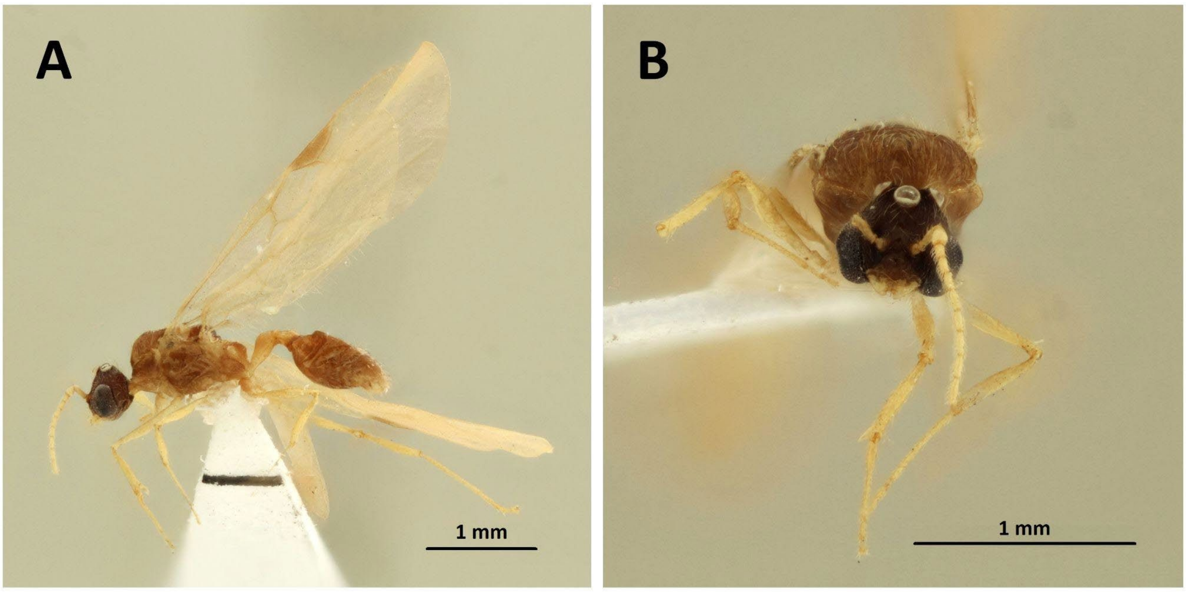

Figure *4.* Pheidole balatro *male specimen (Specimen code: CNP-222-3-3). **A** - Lateral and **B** - frontal view.*

Species richness - sampling effort and efficiency

Leaf litter extraction obtained the greatest proportion of genera (26%) and species (31%) compared to other methods, with hand collection also comprising a large proportion of genera (20%) and species (21%) (Table 4). Baiting, Malaise, leaf litter extraction and vegetation beating were predominantly conducted at relatively lower elevational ranges (Fig. 2.). Pitfall traps and hand collection events were distributed more evenly across the elevation range in contrast, with a concentration of hand collection events at 1600 m a. s. l. To reduce interpretation bias on efficiency of sampling techniques, Table 4 complements Fig. 2, illustrating sampling effort.

Fig. 5 presents species accumulation curves, showing the captured species richness and the sampling intensity (observed and extrapolated). Additional sampling for each individual sampling technique is expected to result in capture of more species, with a total asymptotic richness estimating 257 (95% confidence interval: 204–365) species when all sampling effort is combined. The maximum rate of increase in species richness seems not to have reached yet for vegetation beating and Malaise trapping. However for leaf litter extraction, hand collection, pitfall trapping and baiting it appears that the maximum rate has been reached.

The relation between species richness and community sample coverage is presented in Fig. 6. As stated before, sample coverage concerns the probability that an individual of the entire ant community addressed per sampling technique belongs to a species that has been sampled before. High values show low probability (1 - sample coverage) of sampling additional species for each technique; low values show high probabilities to find species that are yet unaccounted for. The total sampling considered in this study shows a high community sample coverage with a value of 0.978. There are however differences between individual sampling techniques. Leaf litter extraction, pitfall trapping and baiting show a community sample coverage of >0.9 (0.977, 0.916 and 0.978 respectively), whereas this value is lower for hand collection, vegetation beating and Malaise trapping (0.835, 0.815 and 0.44 respectively). The extrapolation shows the expected increase in species richness with greater sampling effort. The 95% confidence intervals are low for most techniques, except for Malaise trapping, which had considerably lower effort compared with other sampling methods.

Table 4. *Representation of Subfamilies, Genera and Species collected per respective sampling method (in respective elevational ranges), alongside asymptotic estimated species richness (with 95% confidence intervals). Percentage of total ant fauna collected by individual sampling methods, per taxonomic level. See* Fig. *2 for complementary data regarding sampling intensities across CNP elevation gradient.*

Sampling method	**Subfamily**	**Genera**	**Species**	**Estimated richness (95% CI)**	**Sample coverage**
Baiting	6 (67%)	20 (33%)	42 (26%)	71 (51–139)	0.978
Hand collection	7 (78%)	30 (50%)	62 (39%)	114 (75–225)	0.835
Leaf litter extraction	7 (78%)	39 (65%)	92 (56%)	127 (105–183)	0.977
Malaise	7 (78%)	22 (37%)	30 (18%)	62 (40–128)	0.440
Pitfall	6 (67%)	23 (38%)	38 (23%)	65 (47–354)	0.916
Vegetation Beating	7 (78%)	16 (27%)	29 (18%)	50 (40–88)	0.815

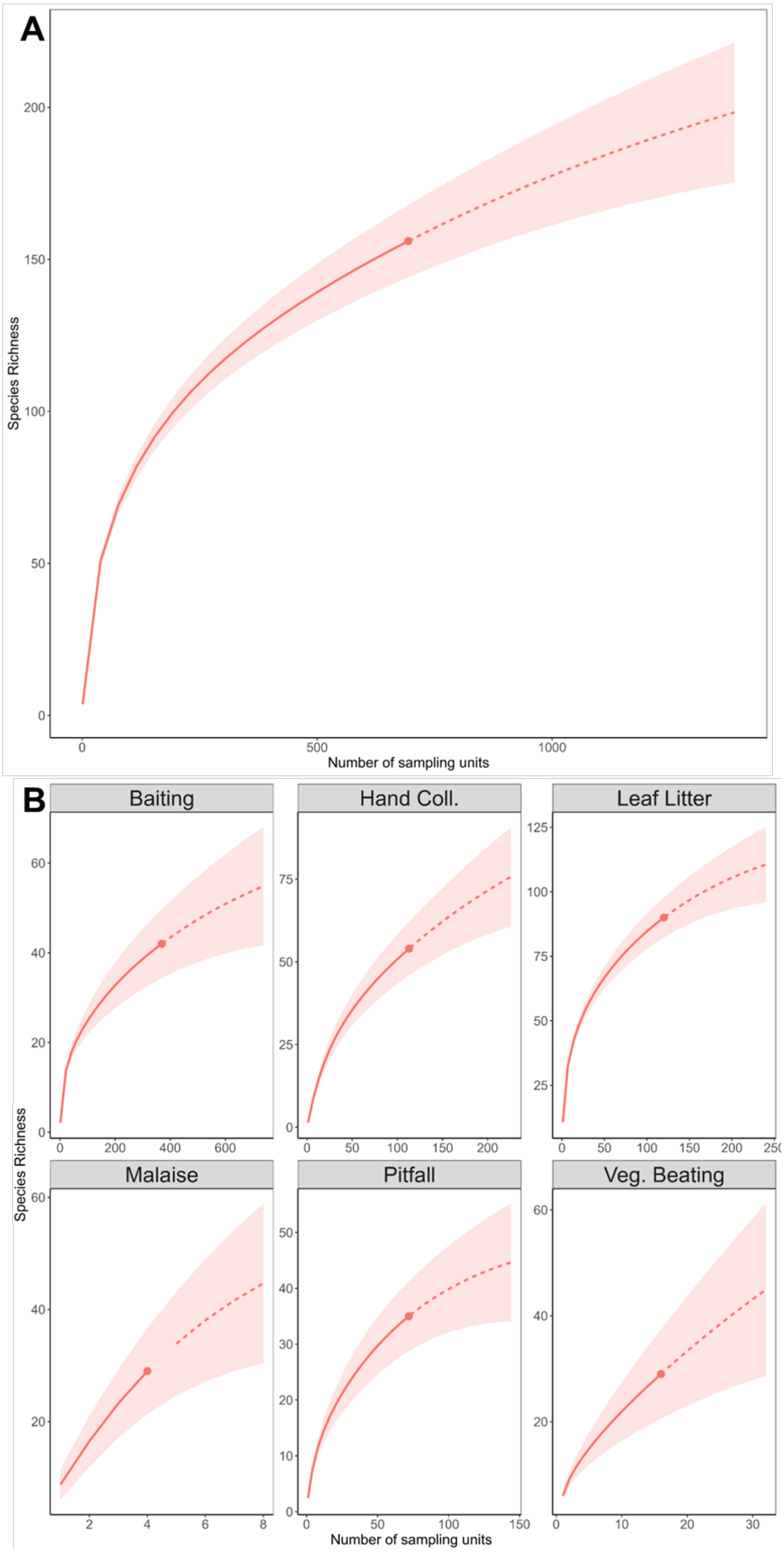

Figure 5. *Species accumulation curves according to the number of samples taken. Shaded regions represent 95% confidence intervals.* ***A*** *- Total species richness for number of samples taken;* ***B*** *- Species richness for number of samples taken, for each technique.*

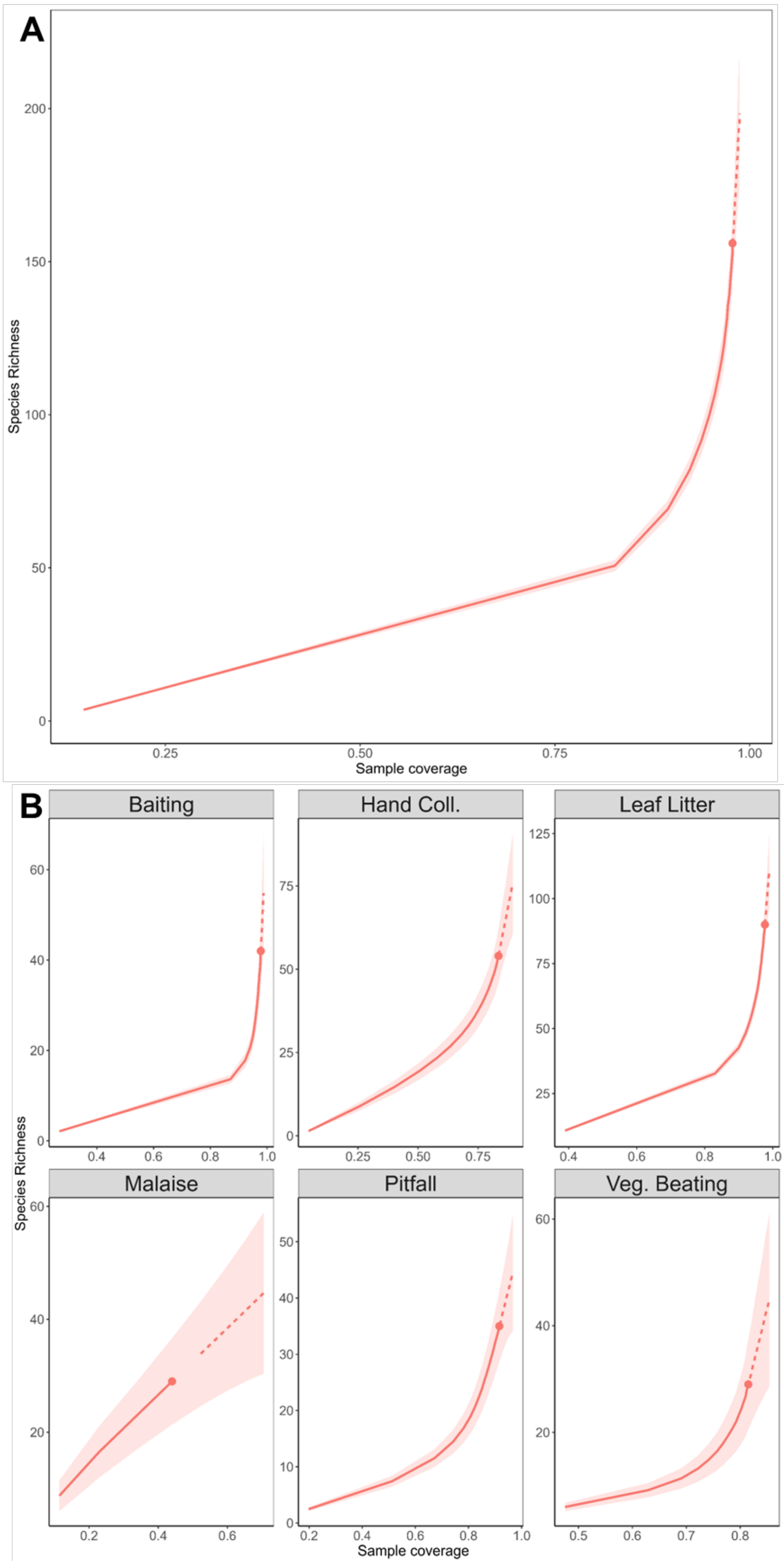

Figure 6. *Species accumulation curves according to community sample coverage. Sample coverage is the probability for an individual of the entire ant community to belong to a species that has been sampled before. Shaded regions represent 95% confidence intervals.* ***A*** *-* *Total species richness for sample coverage;* ***B*** *-* *Species richness for sample coverage, for each technique.*

Discussion

Ant fauna of CNP

Our research confirms that CNP supports a high richness of ant species, on par with many other taxa in the park (Martin et al. 2021). We present the first checklist for the ants of CNP, which is also the first species list published for ants in Honduras in over a century. With the inclusion of a genus-level identification key for all Honduran ant taxa (Supplement 2), we hope this work will stimulate further ant research in Honduras.

Ant species composition showed patterns consistent with other ant faunal inventories (Yanoviak and Kaspari 2000, Patrick et al. 2012, Donoso 2017) with Myrmicinae, Formicinae, Ponerinae and Dolichoderinae comprising over 80% of species collected (Table 2). Compared to other subfamilies, Dorylinae contributed a substantial number of genera (7) considering only 14 species were recorded.

Seven ant species recorded in CNP are spatially restricted to the region. According to current known occurrences, six species are regionally restricted to Honduras. Of these, four are restricted to CNP: *Octostruma leptoceps*, *Stenamma cusuco*, *S. atribellum* and *Temnothorax altinodus*. Two other species restricted to Honduras belong to the genus *Leptogenys*, previously reported from La Ceiba (*Leptogenys bifida*) and Lombardia (*Leptogenys honduriana*). *Pheidole cusuco* was originally described from CNP and has also been reported just across the Guatemalan border (Longino 2019). This indicates the importance of CNP as a potential refuge for these spatially restricted species, which has implications for their conservation. Conversely, two non-native ant species were recorded, *Monomorium pharaonis* (at edge of core zone) and *Solenopsis invicta* (in buffer zone, deforested area). Both species show globally invasive distribution patterns, as does *Solenopsis geminata* which is native to the region (recorded in both core and buffer zone). This suggests that the core zone of CNP remains largely unaffected by highly invasive ant species. Five species represent new records for Honduras: *Pheidole natalie, Strumigenys* cf. *calamita, Solenopsis invicta, Solenopsis texana/carolinensis* and *Pseudomyrmex pallens*. The relatively high number of new country records identified in a single protected area indicates the understudied nature of the region, confirming the need for more field surveys.

Discovery of *Pheidole balatro* males is another noteworthy find. Given the large diversity of *Pheidole* ants, it is common practice not to describe newly discovered males through extensive morphological description - which we have adopted here. The provided photograph and information in the results section could, however, provide a useful basis for comparison.

The genus *Procryptocerus* is understudied and requires greater taxonomic attention in order to better understand populations and species delimitations. Though we present *P. batesi* Forel, 1899 here, we were unable to exclude the possibility of *P. mayri* Forel, 1899 given they are very morphologically similar.

Species richness - sampling effort and efficiency

Results suggest that the recorded species richness (162) appears to be an underrepresentation of the actual species richness in CNP (asymptotic estimate 257; 95% CI: 204–365) (Figs 5–6). The observed and extrapolated patterns in Fig. 5 can be interpreted as the relative efficiency of techniques in capturing different ant species. Since a plateau of species richness is not reached for any of the sampling techniques, all show much potential to record additional species with additional sampling. However, the rate of increase for species richness appears to have reached a maximum for most all techniques, meaning that greater sampling will be required to keep finding additional species.

Community sample coverage is relatively high overall, suggesting that our sampling is rather representative of the ant community in CNP. This holds true for the communities addressed by leaf litter extraction, pitfall trapping and baiting (CSC >0.9). For these techniques probabilities of sampling additional species are relatively low. It seems that high community sample coverage only increases mildly with additional species. Species that have not been recorded yet at this point in the accumulation curve, seem to play only a small role in the ant community and are likely to be rare. However hand collection, vegetation beating and Malaise trapping still seem to show under representations of the community (CSC <0.9). Respective probabilities of sampling additional species are relatively higher when compared to the other three techniques. Hand collection and vegetation beating still show relatively high sample coverage (CSC = 0.8–0.9) with trends suggesting that some common species might still be added using these techniques. Malaise trapping shows a low sample coverage of <0.5, and thus might yield many more species, both common and rare. Sample coverage for hand collection might be lower because of a less consistent sampling along the elevation range. For vegetation beating and Malaise trapping, this is probably due to lower sampling numbers (N = 4 and 16 respectively). It is interesting to consider that just four Malaise traps captured a similar number of ant genera as extensive pitfall trapping, although collected genera are more typical of arboreal ant fauna such as *Procryptocerus*, *Pseudomyrmex* and *Crematogaster* indicating an alternative faunal community sampled.

The elevational range addressed with each technique is to be considered. The species accumulation rate of leaf litter extraction, baiting, vegetation beating and Malaise trapping are expected to increase when used along larger elevational ranges, especially when including higher altitudes which will likely collect altitude specialist species and subclades (e.g. *Stenamma*).

Knowledge gaps and research potential CNP

Despite the substantial species list accumulated from the two projects, there remains high potential to add more species. This study confirmed the presence of 162 ant species, however a total of 250+ species is predicted to be present in CNP. Knowledge gaps are presented below which could be considered in order to obtain a more complete ant species inventory for the park. First of all it is important to note that there is a lack of any specific canopy and subterranean sampling. Though Malaise trapping and leaf litter extraction may sample a subset of those communities, more species are likely present and have yet to be collected.

By expanding methodological approaches and sampling along a broader elevational range, we increased the number of ant species recorded from CNP. However, there are still some elevation zones that were not sampled using the primary survey methods (Fig. 2), and an unequal sampling effort was used along the elevation gradient. To address these sampling gaps we recommend employing a variety of sampling techniques along the full elevational gradient, with appropriate replication in order to ensure inclusion of less prevalent species.

The middle elevation ranges were sampled most intensely; however the higher (mountain peaks) and lower elevation ranges (e.g. buffer zone) remain undersampled. Leaf litter extraction results in the highest number of genera and species recorded, followed by hand collection and pitfall trapping. Although the hand collection and pitfall trapping were used along a broader elevational gradient than leaf litter extraction, the latter still shows a higher number of ant species captured. Sampling leaf litter at higher altitudes in particular should provide promising results. Baiting is still unexplored at higher altitudes. Additional Malaise trapping and vegetation beating are recommended in general, regardless of elevation range.

As a hotspot of biodiversity, numerous novel species have been previously described from CNP (Martin et al. 2021), including ants (Branstetter 2013, Longino 2013, 2019, Prebus 2021a). Further targeted surveys in CNP are expected to lead to the discovery of more ant species, especially at the higher, undersampled altitudes and buffer zones.

Sampling in a standardised framework would allow for a better understanding of species ecology and the taxonomy of the local ant fauna, which could then lead to improved knowledge of regional diversity and wider biogeographical patterns (especially for highly understudied groups, such as those in the genera *Apterostigma, Procryptocerus,* and *Temnothorax*). The effect of anthropogenic habitat change could also be examined, given persistent habitat alterations across both core and buffer zones.

Conclusion

CNP has a rich and diverse ant fauna with the potential as a study site for addressing a multitude of research questions concerning ants. Other tropical mountain cloud forests in Honduras could hold similar ant species richness, with most of these being even more understudied and lacking any survey data. The materials we provide here could form a baseline for future work related to ants in other Honduran cloud forests, helping to guide research in these otherwise poorly explored yet highly threatened localities.

Contributions

According to author order and the CRediT categories: Conceptualization (FCDW, MJ, MTH), Methodology (FCDW, DO, MTH), Validation (FCDW, MGB, WD, MTH), Formal analysis (FCDW, MTH), Investigation (FCDW, DO, DDG, JS, RVO, MTH), Resources (TEM, WD, MJ), Data Curation (FCDW, MTH), Writing - Original draft (FCDW, MTH), Writing - Review and Editing (FCDW, DO, MGB, DDG, WD, MJ, TEM, JS, RVO, MTH), Visualization (FCDW, WD, MTH), Supervision (FCDW, MJ), Project administration (FCDW).

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Appendix 1: Ant species collected within Cusuco National Park, northwestern Honduras. The list is broken down by subfamily, collection method (Winkler sampling relates to specimens obtained through leaf litter extraction via Mini- and MaxiWinkler), elevation range and project collectors. *Non-species level taxa; **Subspecies level (some specimens were not identified to subspecies level; if respective information for specimens with only species level identification deviates from that of the subspecies, it is shown between parentheses).

Species (per subfamily)	Collection	Elevation Range (m.a.s.l.)	Habitat	Project
Amblyoponinae				
Prionopelta antillana complex*	Winkler	1220	Mesophyll Forest	LLAMA
Dolichoderinae				
Azteca alfari (Emery, 1893)	Veg. Beating	1310	Mesophyll Forest	LLAMA
Azteca cf. *coeruleipennis*	Pitfall	1588	Mesophyll Forest	MED
Azteca constructor/instabilis	Hand Coll.	1546	Mesophyll Forest	MED
Bothriomyrmex paradoxus (Dubovikoff & Longino, 2004)	Beating, Baiting, Hand Coll.	1220-1340	Mesophyll Forest	LLAMA
Linepithema dispertitum (Forel, 1885)	Veg. Beating	1310	Mesophyll Forest	LLAMA
Tapinoma ramulorum	Baiting, Veg. Beating	1210-1340	Mesophyll Forest	LLAMA
Tapinoma JTL-003	Baiting	1330	Mesophyll Forest	LLAMA
Technomyrmex JTL-001	Pitfall, Baiting, Malaise	1260-1336	Mesophyll Forest	LLAMA, MED
Dorylinae				
Cheliomyrmex morosus (Smith, 1859)	Hand Coll.	1270	No-Data	MED
Cylindromyrmex meinerti (Forel, 1905)	Veg. Beating	1300	Mesophyll Forest	LLAMA
Eciton burchellii parvispinum (Forel, 1899) **	Winkler, Hand Coll. (Pitfall, Hand Coll.)	1220-1628 (1364-1964)	Mesophyll Forest	LLAMA, MED

Eciton mexicanum (Roger, 1863)	Pitfall, Hand Coll.	1364-1637	Mesophyll Forest	MED
Eciton vagans angustatum (Roger, 1863) **	Pitfall, Hand Coll. (Pitfall)	1174 - 1336 (1174-1415)	Mesophyll Forest, Deforested	MED
Labidus coecus (Latreille, 1802)	Winkler, Pitfall	1407-1964	Mesophyll Forest	MED
Labidus praedator (Smith, 1858)	Pitfall, Hand Coll.	1197-1941	Mesophyll Forest	MED
Leptanilloides gracilis (Borowiec & Longino, 2011)	Malaise	1260	Mesophyll Forest	LLAMA
Neivamyrmex halidaii (Shuckard, 1840)	Winkler	1290-1340	Mesophyll Forest	LLAMA
Neivamyrmex sumichrasti (Norton, 1868)	Pitfall, Hand Coll.	1197-1613	Mesophyll Forest	MED
Syscia JTL082	Winkler, Malaise	1260-2030	Cloud Forest, Mesophyll Forest, Pine-liquidambar Forest	LLAMA
*Syscia parietali*s (Longino & Branstetter, 2021)	Winkler, Malaise	1260-1330	Mesophyll Forest, Pine-liquidambar Forest	LLAMA
Syscia persimilis (Longino & Branstetter, 2021)	Winkler	1290-1300	Mesophyll Forest	LLAMA
Syscia tolteca (Forel, 1909)	Berlese	1550	Cloud Forest	LLAMA
Ectatomminae				
Alfaria minuta (Emery, 1896)	Winkler	1235-1340	Mesophyll Forest	LLAMA, MED
Alfaria simulans (Emery, 1896)	Winkler, Pitfall	1210-1599	Mesophyll Forest	LLAMA, MED
Gnamptogenys interrupta (Mayr, 1887)	Hand Coll.	1331	Mesophyll Forest	MED
Gnamptogenys JTL-010	Winkler	1260-1330	Mesophyll Forest	LLAMA
Gnamptogenys mordax (Smith, 1858)	Pitfall	1315	Mesophyll Forest	MED
Gnamptogenys sulcata (Smith, 1858)	Malaise	1260	Pine-liquidambar Forest	LLAMA
Holcoponera porcata (Emery, 1896)	Pitfall, Hand Coll.	1331-1718	Mesophyll Forest, Deforested	LLAMA, MED
Holcoponera strigata (Norton, 1868)	Winkler, Pitfall, Veg. Beating, Baiting, Hand Coll., Malaise	1174-1718	Mesophyll Forest, Pine-liquidambar Forest, Coffee Plantation, Deforested	LLAMA, MED

Typhlomyrmex indet.*	Malaise	1260	Pine-liquidambar Forest	LLAMA
Formicinae				
Acropyga exsanguis (Wheeler, 1909)	Winkler	1330-1340	Mesophyll Forest	LLAMA
Camponotus abscisus (Roger, 1863)	Winkler, Veg. Beating, Baiting, Hand Coll., Malaise	1260-1838	Mesophyll Forest, Pine-liquidambar Forest	LLAMA, MED
Camponotus albicoxis (Forel, 1899)	Veg. Beating, Pitfall, Hand Coll., Malaise	1234-1613	Mesophyll Forest	LLAMA, MED
Camponotus atriceps (Smith, 1858)	Veg. Beating, Pitfall, Baiting, Hand Coll.	1270-1639	Mesophyll Forest	LLAMA, MED
Camponotus cf. *senex*	Hand Coll.	1190	Deforested Village	MED
Camponotus cuneidorsus	Veg. Beating, Baiting, Hand Coll.	1270-1613	Mesophyll Forest	LLAMA, MED
Camponotus planatus (Roger, 1863)	Veg. Beating	1330	Mesophyll Forest	LLAMA
Camponotus sericeiventris (Guérin-Méneville, 1838)	Hand Coll.	1197	Mesophyll Forest	MED
Myrmelachista indet.*	Hand Coll.	1331	Mesophyll Forest	MED
Nylanderia indet.*	Veg. Beating, Baiting, Winkler, Malaise, Pitfall, Hand Coll.	1220-1613	Mesophyll Forest, Deforested	LLAMA, MED
Myrmicinae				
Acanthognathus ocellatus (Mayr, 1887)	Malaise	1210	Mesophyll Forest	LLAMA
Acromyrmex coronatus (Fabricius, 1804)	Veg. Beating, Pitfall, Hand Coll.	1260-1639	Mesophyll Forest	LLAMA, MED
Acromyrmex volcanus (Wheeler, 1937)	Hand Coll.	~500	NO-DATA	MED
Adelomyrmex JTL-024	Berlese	1550	Cloud Forest	LLAMA
Adelomyrmex silvestrii (Menozzi, 1931)	Winkler, Hand Coll.	1220-1613	Mesophyll Forest	LLAMA, MED
Apterostigma pilosum complex*	Winkler, Veg. Beating, Baiting	1210-1330	Mesophyll Forest	LLAMA
Atta cephalotes (Linnaeus, 1758)	Hand Coll.	498-1613	Mesophyll Forest, Deforested	MED

Carebara intermedia (Fernández, 2004)	Winkler, Baiting, Hand Coll.	1210-1330	Mesophyll Forest	LLAMA
Carebara urichi (Wheeler, 1922)	Winkler	1260-1340	Mesophyll Forest	LLAMA
Cephalotes cf. *multispinosus*	Hand Coll.	NA (lowland)	NO-DATA (forest)	MED
Crematogaster crinosa (Mayr, 1862)	Veg. Beating	1340	Mesophyll Forest	LLAMA
Crematogaster montezumia (Smith, 1858)	Malaise	1210	Mesophyll Forest	LLAMA
Cyphomyrmex rimosus s.l.	Malaise	1260	Pine-liquidambar Forest	LLAMA
Cyphomyrmex salvini (Forel, 1899)	Winkler, Pitfall, Baiting, Hand Coll.	1174-1340	Mesophyll Forest, Deforested	LLAMA, MED
Eurhopalothrix hunhau (Longino, 2013)	Berlese	1550	Cloud Forest	LLAMA
Eurhopalothrix zipacna (Longino, 2013)	Winkler, Baiting	1260-1340	Mesophyll Forest	LLAMA
Hylomyrma versuta (Kempf, 1973)	Winkler, Pitfall	1174-1340	Mesophyll Forest, Deforested	LLAMA, MED
Megalomyrmex megadrifti (Boudinot et al., 2013)	Winkler	1290-1330	Mesophyll Forest	LLAMA
Monomorium pharaonis (Linnaeus, 1758)	Hand Coll.	1613	Mesophyll Forest	MED
Mycetomoellerius squamulifer (Emery, 1896)	Baiting	1290	Mesophyll Forest	LLAMA
Mycetophylax andersoni (MacKay & Serna, 2010)	Winkler, Baiting	1220-1340	Mesophyll Forest	LLAMA
Octostruma balzani complex	Winkler, Baiting	1210-1340	Mesophyll Forest	LLAMA
Octostruma gymnogon (Longino, 2013)	Winkler, Baiting	1260-1330	Mesophyll Forest	LLAMA
Octostruma leptoceps (Longino, 2013)	Winkler	1290	Mesophyll Forest	LLAMA
Pheidole absurda (Forel, 1886)	Hand Coll.	1190	Deforested Village	MED
Pheidole balatro (Longino, 2019)	Winkler, Veg. Beating, Pitfall, Baiting, Hand Coll.	1270-1620	Mesophyll Forest	LLAMA, MED
Pheidole biconstricta (Mayr, 1870)	Winkler, Baiting	1234-1290	Mesophyll Forest	LLAMA, MED

Pheidole bilimeki (Mayr, 1870)	Winkler, Veg. Beating, Baiting	1260-1330	Mesophyll Forest	LLAMA
Pheidole branstetteri (Longino, 2009)	Veg. Beating, Malaise	1210-1330	Mesophyll Forest	LLAMA
Pheidole browni (Wilson, 2003)	Winkler, Pitfall, Baiting, Hand Coll.	1210-1415	Mesophyll Forest	LLAMA, MED
Pheidole cusuco (Longino, 2019)	Winkler, Veg. Beating, Pitfall, Baiting	1225-1421	Mesophyll Forest	LLAMA, MED
Pheidole deceptrix (Forel, 1899)	Winkler, Baiting, Hand Coll.	1260-1330	Mesophyll Forest	LLAMA
Pheidole guerrerana (Wilson, 2003)	Winkler, Veg. Beating	1260-1330	Mesophyll Forest	LLAMA
Pheidole gulo (Wilson, 2003)	Winkler, Veg. Beating, Pitfall, Baiting, Hand Coll., Malaise	1210-1697	Mesophyll Forest	LLAMA, MED
Pheidole harrisonfordi (Wilson, 2003)	Winkler, Baiting	1210-1360	Mesophyll Forest	LLAMA
Pheidole indagatrix (Wilson, 2003)	Winkler, Baiting, Malaise	1260-1320m	Mesophyll Forest	LLAMA
Pheidole insipida (Forel, 1899)	Winkler, Veg. Beating, Baiting, Hand Coll., Malaise	1210-1388	Mesophyll Forest	LLAMA, MED
Pheidole JTL-209	Malaise	1210-1260	Mesophyll Forest	LLAMA
Pheidole lagunculiminor (Longino, 2019)	Winkler, Baiting	1210-1360	Mesophyll Forest	LLAMA
Pheidole natalie (Longino, 2019)	Winkler, Baiting	1270-1340	Mesophyll Forest	LLAMA
Pheidole rectispina (Wilson, 2003)	Baiting	1290	Mesophyll Forest	LLAMA
Pheidole tschinkeli (Wilson, 2003)	Winkler, Veg. Beating, Baiting, Hand Coll., Malaise	1210-1360	Mesophyll Forest	LLAMA, MED
Pheidole ursus (Mayr, 1870)	Winkler, Veg. Beating, Pitfall, Baiting, Hand Coll.	1210-1594	Mesophyll Forest, Deforested	LLAMA, MED
Procryptocerus batesi (Forel, 1899)	Winkler, Veg. Beating, Hand Coll., Malaise	400-1648	Mesophyll Forest, Coffee Plantation	LLAMA, MED

Rhopalothrix andersoni (Longino & Boudinot, 2013)	Winkler	1300	Mesophyll Forest	LLAMA
Rogeria innotabilis (Kugler, 1994)	Winkler	1210-1340	Mesophyll Forest	LLAMA
Rogeria JTL-009	Malaise	1260	Pine-liquidambar Forest	LLAMA
Solenopsis geminata (Fabricius, 1804)	Hand Coll.	1190-1407	Mesophyll Forest, Deforested Village	MED
Solenopsis invicta (Buren, 1972)	Hand Coll.	1190	Deforested Village	MED
Solenopsis terricola (Menozzi, 1931)	Winkler, Pitfall	1331-1599	Mesophyll Forest	MED
Solenopsis texana/carolinensis	Hand Coll.	1668	Deforested	MED
Stenamma atribellum (Branstetter, 2013)	Hand Coll., Berlese	1550-2030	Cloud Forest	LLAMA, MED
Stenamma brujita (Branstetter, 2013)	Winkler, Baiting, Berlese	1210-1550	Cloud Forest, Mesophyll Forest	LLAMA
Stenamma crypticum (Branstetter, 2013)	Winkler	2030	Cloud Forest	LLAMA
Stenamma cusuco (Branstetter, 2013)	Winkler	1280-1330	Mesophyll Forest	LLAMA
Stenamma felixi (Mann, 1922)	Winkler, Baiting, Hand Coll., Malaise	1260-1613	Mesophyll Forest	LLAMA, MED
Stenamma hojarasca (Branstetter, 2013)	Winkler	1220-1340	Mesophyll Forest	LLAMA
Stenamma ignotum (Branstetter, 2013)	Winkler, Berlese	1300-1550	Cloud Forest, Mesophyll Forest	LLAMA
Stenamma manni (Wheeler, 1914)	Pitfall	1472-1845	Mesophyll Forest	LLAMA, MED
Stenamma muralla (Branstetter, 2013)	Hand Coll.	1677	Mesophyll Forest	MED
Stenamma ochrocnemis (Branstetter, 2013)	Winkler	2030	Cloud Forest	LLAMA
Stenamma pelophilum (Branstetter, 2013)	Baiting, Hand Coll.	1290-1320	Mesophyll Forest	LLAMA
Stenamma picopicucha (Branstetter, 2013)	Winkler	2030	Cloud Forest	LLAMA
Stenamma saenzae (Branstetter, 2013)	Winkler	1210-1340	Mesophyll Forest	LLAMA
Strumigenys biolleyi (Forel, 1908)	Winkler, Baiting, Hand Coll.	1260-1613	Mesophyll Forest	LLAMA, MED
Strumigenys brevicornis (Mann, 1922)	Winkler	1210-1340	Mesophyll Forest	LLAMA

Strumigenys cassicuspis (Bolton, 2000)	Winkler	1290	Mesophyll Forest	LLAMA
Strumigenys cf. *calamita*	Winkler	1599	Mesophyll Forest	MED
Strumigenys cf. *myllorhapha*	Winkler	1331	Mesophyll Forest	MED
Strumigenys elongata (Roger, 1863)	Winkler	1300	Mesophyll Forest	LLAMA
Strumigenys excisa (Weber, 1934)	Winkler	1220	Mesophyll Forest	LLAMA
Strumigenys gundlachi (Roger, 1862)	Winkler, Baiting, Malaise	1210-1340	Mesophyll Forest, Pine-liquidambar Forest	LLAMA, MED
Strumigenys humata (Lattke & Goitía, 1997)	Winkler	1220-1330	Mesophyll Forest	LLAMA
Strumigenys JTL-028	Winkler	1290-1300	Mesophyll Forest	LLAMA
Strumigenys JTL-pyr020	Winkler	1290	Mesophyll Forest	LLAMA
Strumigenys microthrix (Kempf, 1975)	Winkler	1280	Mesophyll Forest	LLAMA
Strumigenys paradoxa (Bolton, 2000)	Winkler	1290-1340	Mesophyll Forest	LLAMA
Strumigenys rogata (Bolton, 2000)	Winkler	1260-1290	Mesophyll Forest	LLAMA
Strumigenys subedentata (Mayr, 1887)	Pitfall, Malaise	1260-1263	Mesophyll Forest, Pine-liquidambar Forest	LLAMA, MED
Strumigenys timicala (Bolton, 2000)	Winkler	1330	Mesophyll Forest	LLAMA
Temnothorax altinodus (Prebus, 2021)	Veg. Beating	1290	Mesophyll Forest	LLAMA
Temnothorax aztecus (Wheeler, 1931)	Winkler, Veg. Beating	1220-1310	Mesophyll Forest	LLAMA
Temnothorax cf *longinoi*	Hand Coll.	1364	Mesophyll Forest	MED
Temnothorax med01	Hand Coll.	1838	Mesophyll Forest	MED
Temnothorax med02	Winkler	1838	Mesophyll Forest	MED
Temnothorax med03	Hand Coll.	1331	Mesophyll Forest	MED
Temnothorax terraztecus (Prebus, 2021)	Winkler	1220	Mesophyll Forest	LLAMA
Ponerinae				
Anochetus mayri (Emery, 1884)	Winkler	1300-1330	Mesophyll Forest	LLAMA
Belonopelta deletrix (Mann, 1922)	Winkler, Malaise	1260-1330	Mesophyll Forest, Pine-liquidambar Forest	LLAMA

Cryptopone gilva (Roger, 1863)	Winkler, Hand Coll.	1599-1838	Mesophyll Forest	MED
Hypoponera nitidula (Emery, 1890)	Winkler, Pitfall, Baiting	1210-1415	Mesophyll Forest	LLAMA, MED
Hypoponera parva (Forel, 1909)	Winkler	1210-1330	Mesophyll Forest	LLAMA
Leptogenys BEB003	Malaise	1210	Mesophyll Forest	LLAMA
Leptogenys bifida (Lattke, 2011)	Hand Coll.	1331	Mesophyll Forest	MED
Leptogenys cf. *foveonates*	Pitfall	1263	Mesophyll Forest	MED
Leptogenys honduriana Mann, 1922	Pitfall	1174-1501	Mesophyll Forest, Deforested	MED
Leptogenys imperatrix (Mann, 1922)	Pitfall, Hand Coll.	1197-1718	Mesophyll Forest	MED
Leptogenys JTL-023	Winkler	1290-1330	Mesophyll Forest	LLAMA
Leptogenys tiobil (Lattke, 2011)	Pitfall	1597	Mesophyll Forest	MED
Neoponera apicalis (Latreille, 1802)	Hand Coll.	498-1331	Mesophyll Forest	MED
Neoponera crenata (Roger, 1861)	Pitfall, Malaise	1197-1260	Mesophyll Forest	LLAMA, MED
Neoponera curvinodis (Forel, 1899)	NO-DATA	NO-DATA	NO-DATA	MED
Neoponera lineaticeps (Mayr, 1866)	Veg. Beating, Pitfall, Hand Coll., Malaise	1210-1630	Mesophyll Forest, Pine-liquidambar Forest	LLAMA, MED
Odontomachus haematodus (Linnaeus, 1758)	Pitfall, Hand Coll.	498-1639	Mesophyll Forest	MED
Odontomachus laticeps (Roger, 1861)	Winkler, Baiting	1290-1330	Mesophyll Forest	LLAMA
Odontomachus yucatecus (Brown, 1976)	Hand Coll.	1331-1639	Mesophyll Forest	MED
Pachycondyla harpax (Fabricius, 1804)	Winkler, Pitfall, Baiting, Hand Coll.	498-1612	Mesophyll Forest	LLAMA, MED
Pachycondyla purpurascens (Forel, 1899)	Winkler, Pitfall, Baiting, Hand Coll.	400-1613	Mesophyll Forest, Coffee Plantation, Deforested	LLAMA, MED
Platythyrea prizo (Kugler, 1977)	Malaise	1210-1260	Mesophyll Forest, Pine-liquidambar Forest	LLAMA
Ponera exotica (Smith, 1962)	Malaise	1260	Pine-liquidambar Forest	LLAMA

Rasopone mesoamericana (Longino & Branstetter, 2020)	Winkler, Pitfall	1220-1514	Mesophyll Forest	LLAMA, MED
Rasopone politognatha (Longino & Branstetter, 2020)	Winkler, Pitfall	1290-1514	Mesophyll Forest	LLAMA, MED
Thaumatomyrmex ferox complex*	Winkler, Hand Coll.	1210-1340	Mesophyll Forest	LLAMA
Proceratiinae				
Discothyrea horni complex*	Winkler	1210-2030	Cloud Forest, Mesophyll Forest	LLAMA
Proceratium mancum (Mann, 1922)	Winkler	1300	Mesophyll Forest	LLAMA
Pseudomyrmecinae				
Pseudomyrmex ejectus (Smith, 1858)	Malaise	1260	Mesophyll Forest	LLAMA
Pseudomyrmex elongatulus complex	Hand Coll.	1364-1838	Mesophyll Forest	MED
Pseudomyrmex pallens (Mayr, 1870)	Hand Coll.	1190	Deforested Village	MED
Pseudomyrmex PSW-159	Veg. Beating, Baiting	1220-1330	Mesophyll Forest	LLAMA
Pseudomyrmex PSW-53	Veg. Beating, Baiting	1210-1330	Mesophyll Forest	LLAMA