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Research article

Ants of the Islas Murciélago: an inventory of the ants on tropical dry forest islands in northwest Costa Rica

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ABSTRACT

We conducted the first inventory of ants on the Islas Murciélago, Área de Conservación Guanacaste (ACG) of Costa Rica. We conducted this study on a chain of seven islands and a nearby mainland site, southwest of the Santa Elena Peninsula, northwestern Costa Rica. We collected ants during three different seasons throughout one year, using three techniques; pitfall traps, Winkler sacks, and opportunistic collecting by hand. We determined ant species richness and composition for all islands and the mainland site. We also evaluated the relationship between island area, distance from the mainland, and relative vegetation cover with the number of ant species recorded on each island. We found a total of 50 species of ants on the Islas Murciélago and 34 species on the mainland (combining results from standardized and non-standardized sampling). Thirteen species of ants found on the mainland were not recorded from the Islands. Distance and area did not explain ant species richness on the Islands. Ant species composition varied for each island, and we documented fluctuations in ant presence throughout different seasons. We found two exotic species on the Islands, but in relatively low abundances and coexisting with other species. Considering the extreme seasonality of the Islas Murciélago and the desert-like environment in the dry season, we found a higher number of ant species than we expected. It is unclear what factors best explain patterns of species richness and composition on the Islands, though human impacts likely contribute.

Keywords: ants; Costa Rica; islands; tropical dry forest; invasive species

RESUMEN

Realizamos el primer inventario de hormigas en las Islas Murciélago, Área de Conservación Guanacaste (ACG), Costa Rica. Llevamos a cabo este estudio en un archipiélago compuesto por siete islas y en un sitio de tierra firme adyacente, al sureste de la Península de Santa Elena, noroeste de Costa Rica. Colectamos hormigas durante tres estaciones diferentes a lo largo de un año, utilizando tres técnicas: trampas de caída, bolsas de Winkler y colecta manual oportunista. Determinamos la riqueza y composición de especies de hormigas en todas las islas y el sitio de tierra firme. También evaluamos la relación entre el área de la isla, la distancia hacia la tierra firme, la cobertura de vegetación y el número de especies de hormigas registradas en cada isla. Encontramos un total de 50 especies de hormigas en las Islas Murciélago y 34 especies en la tierra firme (combinando resultados de muestreos estandarizados y no estandarizados). Trece especies de hormigas encontradas en la tierra firme no fueron registradas en las Islas. La distancia y el área no explicaron la riqueza de especies de hormigas en las Islas. La composición de especies varió en cada isla y documentamos fluctuaciones en la presencia de hormigas en diferentes estaciones. Encontramos dos especies invasoras en las Islas, pero en abundancias relativamente bajas y coexistiendo con otras especies. Tomando en cuenta la estacionalidad extrema en las Islas Murciélago y las condiciones ambientales desérticas durante la estación seca, encontramos un número de especies de hormigas más alto que el originalmente esperado. No es claro qué factores explican la mayor parte de los patrones de riqueza y composición de especies en las Islas, pero es probable que los impactos humanos sean importantes.

Palabras Claves: hormigas; Costa Rica; islas; bosque seco tropical; especies invasoras

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Introduction

Tropical dry forests are one of the most threatened ecosystems in Central America, primarily due to their easy conversion to agricultural land and human settlements [1-2]. Tropical dry forests, bordering the pacific coast from Mexico to Panama, accounted for almost 50% of all forested areas in the region [2-3] though less than 2% of intact dry forest remains in Central America and Mexico [1-2]. The Santa Elena Peninsula and the nearby Islas Murciélago, in the western portion of the Area de Conservación Guanacaste (ACG) in northwest Costa Rica, contain one of the largest tracts of intact tropical dry forest left in Central America [1]. Given that the remaining undisturbed dry forests exhibit unique biological communities that face multiple threats, it is important to understand and document their biodiversity. To date few studies have been conducted in the western portion of the ACG that includes the Santa Elena Peninsula and the Islas Murciélago.

Islands, such as the Islas Murciélago archipelago, containing pacific tropical dry forest are ecologically and geographically unique and uncommon [4]. The Islas Murciélago and nearby mainland on the Santa Elena Peninsula belong to the tropical dry forest life zone [1] and experience drought conditions in the dry season and abundant rain in the wet season. Although a list of flora for Islas Murciélago has not been published, informal studies have recorded the presence of drought-adapted plants, many of which are also found on the Santa Elena Peninsula and mainland Costa Rica. Dauphin & Grayum found a small number of rare species of bryophytes on the Islands, notably one species who's only other locality is in Brazil [5]. Diversity patterns of invertebrates, which are often thought to be correlated with plant diversity and composition [6] have not been studied on the Islas Murciélago and nearby Santa Elena Peninsula.

Patterns of species richness on islands, oceanic and terrestrial, have traditionally been explained by island size and distance from the mainland [7-8]. However, other factors may be equally or more important in explaining these patterns, such as habitat structure, climatic conditions, and especially now, human impacts and disturbance [9-11]. The extreme fluctuations of rainfall and wind between the dry and wet seasons may also play a role in determining the existence of many species on the Santa Elena Peninsula and nearby Islas Murciélago as no rain falls between December and April but strong trade winds blow across the islands during these months.

Conducting an inventory is a way to assess the biodiversity of a particular area, on a local or regional scale. Biological inventories document species occurrences and provide baseline information for habitats where little is known [12]. Invertebrates are good candidates for biological inventories because of their high diversity and presence in nearly all ecosystems [13]. Additionally, invertebrates have many characteristics that make them useful study subjects for biological inventories, and their presence or absence in surveyed regions often serves as an indicator of ecosystem health [14-15]. Ants are an especially good taxon to use in such studies because they occur almost everywhere, are diverse in many habitats, taxonomically well-known, relatively easy to collect, and have stationary nesting sites that allow them to be re-sampled over time [16]. Additionally, ants are sensitive to environmental change and to the impact of invasive species [17-18].

Though the Islas Murciélagos occur in a protected area, they are not immune from human threats such as fire, logging, and the effects of invasive species. The ACG currently protects the islands from extractive activities by humans but fishermen have long used at least some of these Islands and continue to do so illegally. Fishermen have historically camped on these Islands and there is ample evidence of runaway camp fires that have burned and eliminated portions of forest (in one case, all of the forest) on some of the Islands. Due to the pattern of strong trade winds, and the difficulty of plant reestablishment in the dry season, many of the burned portions of the Islands have not regenerated native vegetation and are covered by invasive grasses [4].

Invasive species introductions can also negatively affect island biotas [19-20]. For example, islands in the Galapagos and Hawaiian archipelagos have suffered extinctions of native ants due to the introduction of a non-native ant, *Wasmania auropunctata* and *Pheidole megacephala*, respectively [19]. The exotic Argentine ant, *Linepithema humile*, is displacing native ants in California and South Africa which has been shown to negatively affect ecosystem processes and organisms in higher trophic levels [21-22]. Because the Islas Murciélagos have experienced human disturbance and alteration, this may have facilitated the establishment of non-native species [23]. Norway rats have also been documented on all but one island (Joyce and McCauley, unpub. data) but nothing on other invasive species has been studied on the Islands.

In this study we addressed the following questions: (1) What is the relative species richness among the islands of the Islas Murciélagos archipelago? (2) Which species of ants are on each Island and adjacent mainland site? (3) What factors best explain patterns of ant species richness and composition on the Islands and mainland? (4) Are there invasive ants on the Islands? And (5) how does seasonality and trapping method affect our ability to capture ants? Information from this study will increase our knowledge of tropical dry forest ant fauna, and our general understanding of the biogeography and natural history of tropical dry forest islands. This inventory serves as a foundation for additional biological surveys and research on the Islas Murciélagos, and provides information that will be useful in the future management and conservation plans within the ACG.

Methods

Study site

The study sites include seven islands and the mainland peninsula, the latter representing a potential source of ant species. The Islas Murciélago are located within the Sector Santa Elena of the Area de Conservación Guanacaste (ACG), Guanacaste Province, Costa Rica. The Islands vary in size and habitat composition, and the distance from each island to the mainland ranges from 1 to 4 km. The Islands are relatively close to each other, which likely facilitates movement of species between islands (Fig. 1)

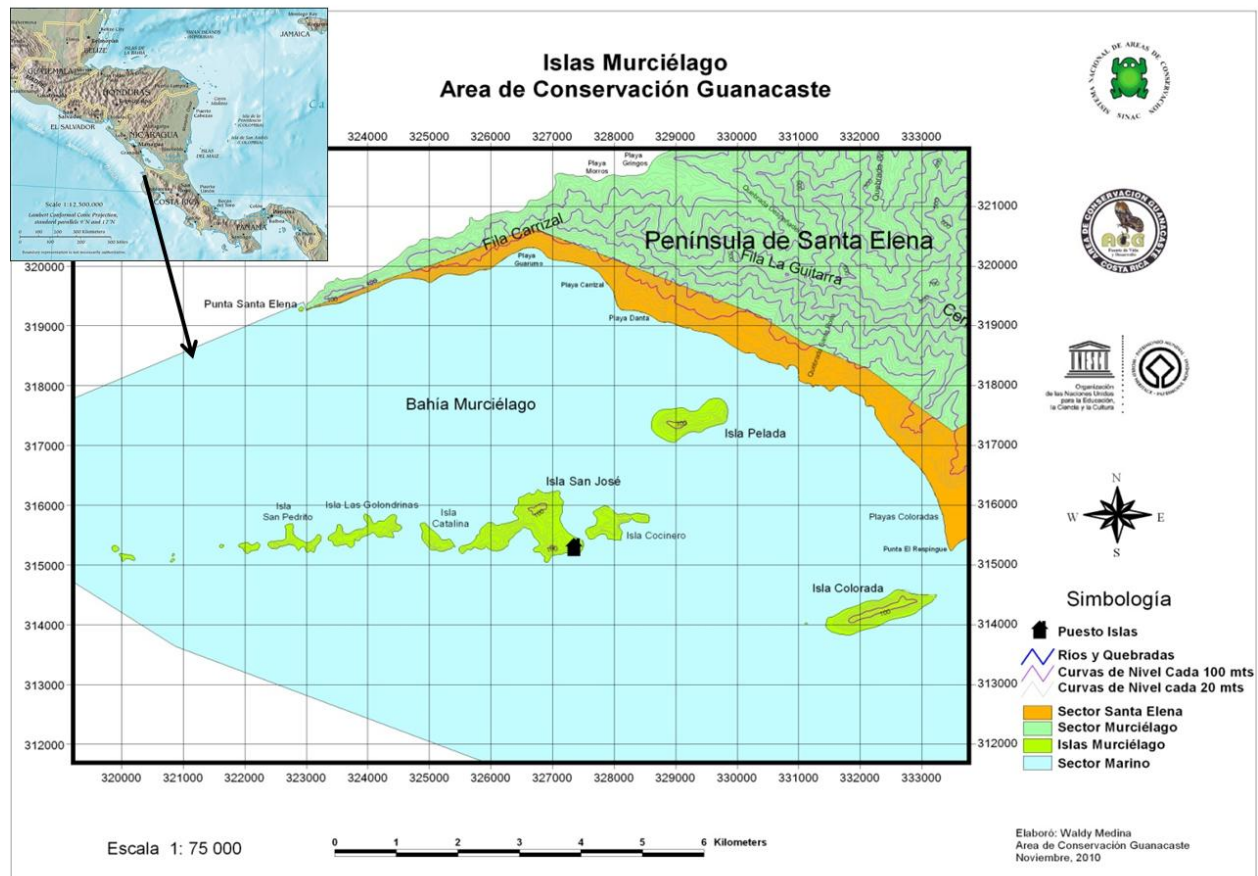


Fig.1. Map of study site (created by Wally Medina). Inset map of Central America sourced from http://commons.wikimedia.org/wiki/File:Central_america.jpg, accessed on 18 May, 2011. Obtained with permission under the terms of the GNU Free Documentation License.

The Islas Murciélagos and the Santa Elena Peninsula belong to the tropical dry forest life zone, characterized by wet and extremely dry seasons (see photos in Fig. 2). The wet season begins late May/early June and tapers off in late October/early November. The rainfall, recorded from the closest weather station in Santa Rosa National Park, averages 1530 mm per year. However, there is a higher incidence of deciduous vegetation and relatively more xerophytic plant species on the mainland peninsula compared to Santa Rosa, indicating that actual rainfall on the Islands and mainland peninsula is less than in Santa Rosa National Park [1]. The mainland peninsula has dense forest that runs from the mountaintops (ca. 700 m elevation) to the coastline [1]. In contrast, the Islands are covered by a mosaic of forest, grassland, shrubs, and scattered cacti and succulents. (For specific site descriptions and locations, see Table 1). Isla Catalina and Isla San José are the only islands that have forest canopy reaching ca. 15 m, most closely resembling forest on the mainland. Forests on the remaining islands have a maximum height of 6m, with the exception of Isla Cocinero that has no forest cover.



Fig.2. Photos of the wet season in June, 2009 (a) and dry season in October 2009 (b) on Isla San José with the mainland, Santa Elena Peninsula, in the background (far right).

The Islands are derived from mantle or volcanic extrusion. Isla Colorada and Isla Pelada (closest to the mainland) are derived from mantle and are primarily composed of serpentine, whereas the remaining westernmost islands are derived volcanically and are basaltic (Percy Denyer, pers. comm.). Plants associated with serpentine soils have been found growing only on Isla Pelada and Isla Colorada, while a common shrub (*Amphipterygium adstringens*) growing on the basaltic islands has not been found on the serpentine islands [5].

Isla Cocinero, San José, and Pelada have probably experienced the greatest degree of direct human impact (fire, hunting, and logging) though only part of Isla San José has been heavily disturbed and this area occurs around the small field station on the eastern end of the island. Isla San José is the only island with a building and is the only island with a relatively large freshwater source throughout the year. The other Islands, except Isla Colorada, which has no forest, have experienced spreading fires that have destroyed portions of their forest (Jaimie Lara, pers. comm.). However, we do not have clear and concise records of the historical vegetation cover on the Islands and it is difficult to know exactly how much, and how many of the Islands were burned. For all of the Islands, the majority of human disturbance, other than fire, has occurred near the shoreline. Most of the forest along the southern

portion of the Santa Elena peninsula (mainland forest nearest the islands) has suffered little human impact and is relatively pristine [1, 4].

Table 1. Characteristics of the study sites. Habitats include grassland, patches of shrubs, and forest. (*) Denotes high-canopy forest, ca. 15m, in contrast to the low-canopy forest, ca. 6m, at the other sites). Percent forest cover is an estimate of the area of forest at each site based on a topographical map of the region that was created with aerial photos. Forest cover was also confirmed with field observations. (This percentage reflects current forest cover.) Distance from mainland was determined by measuring the closest point on each Island to the mainland from a topographical map.

| Site | Size (ha) | Distance From Mainland (km) | Habitat Type | Habitat Sampled | Estimated Percent Forest Cover |
|-------------|-----------|-----------------------------|------------------------------------|------------------|--------------------------------|
| San Pedrito | 14.2 | 3.9 | Grassland, shrubs | Grassland/shrubs | 0 |
| Golondrinas | 29.1 | 3.75 | Grassland, shrubs, forest | Forest/grassland | 20% |
| Catalina | 14.5 | 4.5 | Grassland, shrubs, forest* | Forest | 50% |
| San José | 107.1 | 3.35 | Grassland, shrubs, forest* | Forest | 75% |
| Cocinero | 32 | 3.25 | Grassland, shrubs, scattered trees | Grassland | 1% |
| Pelada | 59.1 | 0.85 | Grassland, shrubs, forest | Forest | 25% |
| Colorada | 74.1 | 0.85 | Shrubs, forest | Forest | 75% |
| Mainland | N/a | N/a | Forest* | Forest | 100% |
| | | | | | |

Collection methods

In November 2001, and May and June 2002, we used pitfall traps and Winkler extraction for standardized collecting at each site (Table 2). We focused on terrestrial ants because we were able to standardize collecting at all sites. Not all of the Islands have forest, and of those that have forest, the canopies and species composition of the forests vary – making arboreal ant comparisons difficult (Table 1). We chose to collect ants in November, May and June based on the seasonality of these months, and specifically rainfall and wind patterns. The landscape is extremely dry until approximately the end of May or beginning of June when the first rains of the wet season come and the trade winds cease. In dry and hot climates, ants often exhibit reproductive activity with the first rains and we were interested in sampling at the time of potentially heightened activity [24]. Our May sampling event occurred at the very end of the dry season and our June sampling event occurred immediately after the first rains of the wet season. The sampling event in November occurred soon after the dry season started, and served as an intermediate sampling period between extremely dry and wet conditions.

For pitfall trap sampling, we used plastic tubes approximately 5 cm in diameter and 15 cm in height, filled halfway with 70% ethanol, placed flush with soil, and left for approximately 48 hours. In the November sampling we set out pitfall traps every 20 m, along a haphazardly selected transect

approximately 100 m long. We increased the number of pitfall traps in May and June, and spaced the traps 10 m apart. We collected in approximately the same locations (same transect) during November, May and June. The standardized collecting was primarily done by JMJ.

For leaf-litter sampling, we followed the Winkler extraction method as described in Agosti et al. [16]. Litter samples were taken every 10 m, 1-2 m parallel to the pitfall transect. We measured a 1 m² quadrat at each sampling point and collected all leaf litter filling that quadrat. After collecting the litter, we immediately sifted the litter in the field into an individual sack. The sifted leaf litter was hung in Winkler bags for approximately 48 hours under a roof at the field station on Isla San José.

In addition to standardized collecting, we carried out non-quantitative collection of ants during the preliminary phase of the study (September 2001, October 2001) to become familiar with collecting sites and to test collecting methods. We primarily used pitfall traps during the initial phase but also used Winkler extraction and baiting at some sites. We did not use bait traps in the standardized collecting regime because our preliminary results showed that baiting was redundant with Winkler and pitfall sampling. Ants were collected opportunistically by hand throughout the entire study. In general, we collected by hand when we were setting out pitfall traps or collecting leaf litter. Hand collecting was biased toward ants that we had not previously collected at a specific site or toward ants that we did not recognize.

Species collected solely by non-standardized collecting are included in the complete species lists for each site but are excluded from the quantitative analyses. Preliminary collecting was done by J.M.J and F.J.J. Samples were processed by J.M.J and all ants were identified by J.T.L. Only ant workers were included in the quantitative analysis. All material was deposited and databased at INBIO, Costa Rica and all locality information is available online through INBIO (<http://www.inbio.ac.cr/es/default.html>).

Table 2. Standardized sampling regime. (*) Isla Colorada lacks pitfall samples for November 2001 because we were unable to access the collecting site due to unfavorable ocean conditions. (**) slightly <1 x 1 m² sifted material was collected at sites where litter and topsoil was sparse.

| Method | Sample Unit | No. Samples | Sampling Period |
|---------|---|-------------|---------------------|
| Pitfall | 11.5 x 3.5cm tube | 5* | 20-25 November 2001 |
| | | 10 | 6-15 May 2002 |
| | | 10 | 17-23 June 2002 |
| Winkler | 1x1m ² sifted litter/topsoil** | 5 | 20-25 November 2001 |
| | | 5 | 6-15 May 2002 |
| | | 5 | 17-23 June 2002 |

Statistical analysis

The primary analyses in this study are based on data from the three standardized collections in November 2001, May 2002, and June 2002. All data are incidence data. Because ants are colonial, we did not base abundance measures on numbers of individuals, but rather on the presence of a particular species of worker in a sample, regardless of the number of individuals. [18].

We first created sample-based rarefaction curves scaled to number of species occurrences for each Island and the mainland. We used sample-based rarefaction to avoid problems with heterogeneity of species richness across samples [25]. We scaled to species occurrences rather than samples in order to focus on species richness rather than species density. We initially tested a variety of biodiversity estimators to gain a general sense of the pattern of species richness at each site and to determine the thoroughness of our sampling. We chose three estimators, first-order Jack-knife (Jack 1), Bootstrap, and Michaelis Menten Means, in which to compare with our observed number of species. We chose these estimators because they performed the most consistently for all sites. Other estimators, like the Chao2 and Jack 2, performed erratically for some islands possibly due to relatively extreme ratios of the number of “uniques” and duplicates in the dataset. We used Colwell’s program EstimateS, version 7.5 to produce all curves [26].

To test the hypotheses that island size, distance from mainland, and forest cover determine the number of ant species present on islands, we tested the effect of each of the independent variables – log distance from the mainland, log area of the island, and percent forest cover – on the dependent variable, ant species richness. Percent forest cover was calculated by estimating the area of forest at each site using a topographical map of the region (which was created with aerial photos). We used Spearman Rank Correlation as a non-parametric alternative to linear regression to examine the relationship between the independent variables and the dependent variable as our data did not meet the assumptions of regression analyses.

We created a cluster diagram to visualize the relationship of ant community structure across the Islands and mainland, using the Bray–Curtis similarity measure based on presence-absence data. The Bray-Curtis similarity measure provides a degree of similarity between pairs of sites and can be placed on a scale of 1-100. This analysis was carried out with Primer-E, version 6.0 [27].

We were additionally interested in the effects of seasonality, trapping methods and the combination of both, on ant species richness. To test the significance of trap type, for pitfall traps and Winkler traps, on the mean number of ant species at each site for different months of sampling (seasons), we used a non-parametric version of the paired t-test (Wilcoxon test). For pitfall traps, we were only able to compare two months, May and June, because we used fewer traps in November. For Winkler samples, we had an equal number of samples for all three months and used the non-parametric equivalent to a paired ANOVA, the Friedman test, to analyze the effect of season on ant species richness.

Results

We found 50 species of ants from 28 genera on the Islas Murciélago when combining numbers of species recorded from standardized and non-standardized collecting. When we included species collected from the mainland, we found a total of 63 species. Thus, mainland collecting added 13 additional species. The number of species documented with standardized sampling only was 41 on the Islands and 54 on the Islands plus the mainland. (See Appendix 1 for a complete list of every species occurrence at each site). We found 29 species on one or more Islands that were not found on the

mainland. Seventeen of these species have been documented in Santa Rosa National Park (J.T.L. unpublished data), and some of them are likely to occur on the Santa Elena Peninsula, though we did not record them. In total, we documented 685 species occurrences in 312 samples (Winkler and pitfall combined) during the standardized collecting events in November 2001, and May and June 2002. (For photos of many ant genera and species we collected, refer to:

<http://academic.evergreen.edu/projects/ants/AntsofCostaRica.html> and <http://www.antweb.org/>).

We found three species that appeared on only one Island, but in multiple samples. Two of these species, *Gnamptogenys curtula* and *Hypoponera parva*, were found on Isla Colorada and one species, *Ectatomma ruidum*, on Isla Cocinero. Though we did not collect these species at the mainland sampling site, they have been documented from mainland Costa Rica. Four species, *Cephalotes minutus*, *Pheidole cf. laselva*, *Nesomyrmex echinatinodis*, and *Paratrechina longicornis*, were collected on only two Islands, in multiple samples, and were not found at our mainland site (though have been documented on mainland Costa Rica). We found six “unique” species (species only occurring in one trap) and 12 singletons (species represented by one individual throughout all sampling). Many of the species that were collected on the Islands, but not mainland site, have been reported in Santa Rosa National Park – the closest comparable collecting site with intensive sampling. However, the complete range and identification of some species have not yet been determined.

When comparing sample-based rarefaction curves for all sites, scaled to the number of species occurrences (Fig. 3), diversity on the mainland was higher than any Island. Isla Cocinero exhibited the lowest number of species and the approximate rank of all other islands remained the same in terms of species richness. Species richness estimators showed relatively similar values of expected number of species per site but estimated a higher number of species for all sites compared to the observed species richness values (Fig. 4).

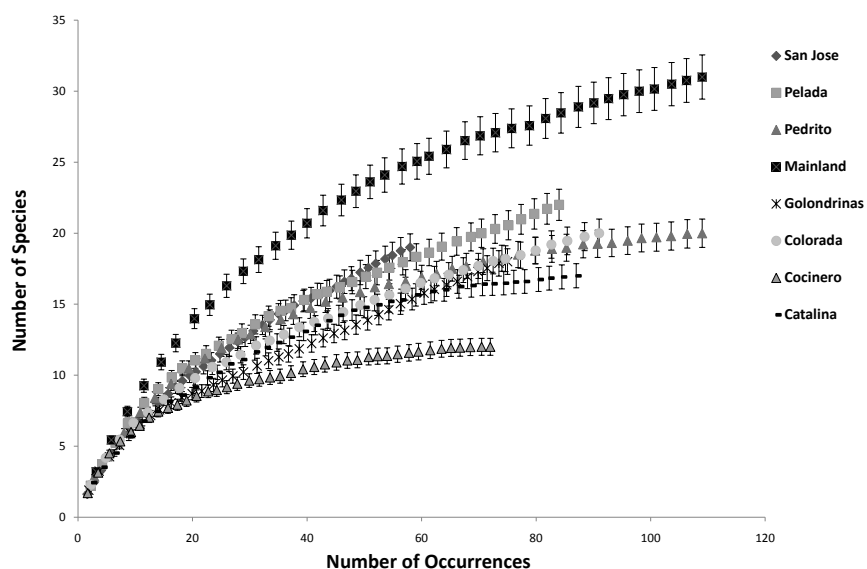


Fig.3. Sample-based rarefaction curves (Sobs) for all sites scaled to number of individuals, which in the case of incidence data, is represented by number of species occurrences. The thin black lines above and below the curves for each site indicate upper and lower 95% confidence intervals.

Distance and area did not explain a significant portion of the variation in species richness on the Islands. We found no correlation between the log number of species and the log distance from the mainland, between log number of species and the log area of each Island, or between log number of species and the percent forest cover on each Island. (Spearman correlation, $p > 0.05$ for all three correlations).

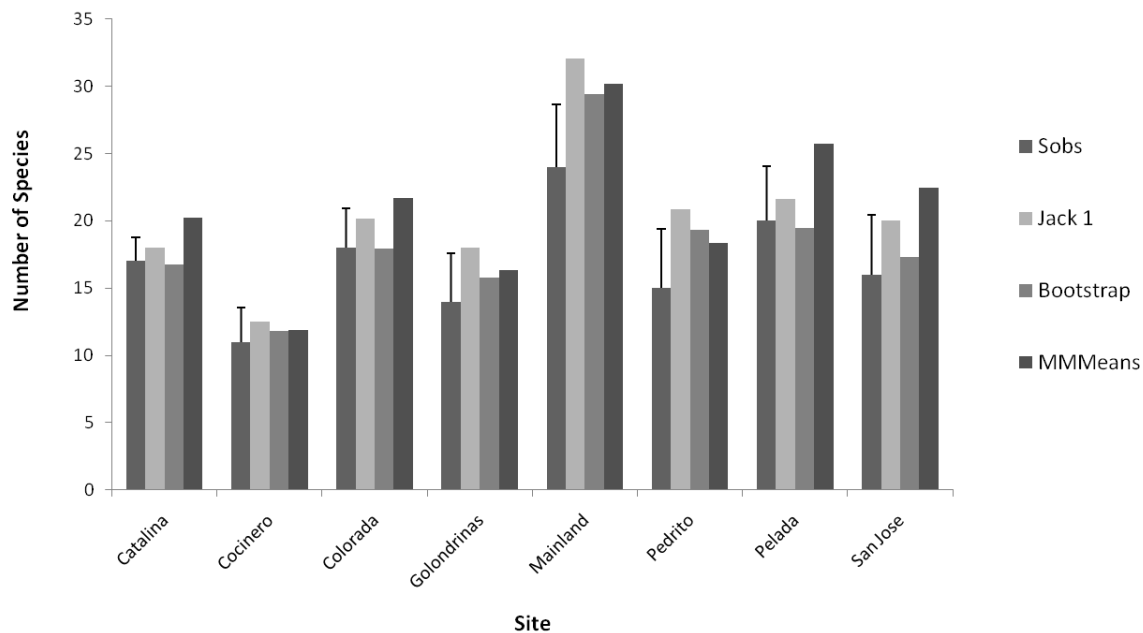


Fig. 4. Estimates of species richness compared to observed number of species (Sobs) for each site. Confidence intervals are placed on the column representing observed number of species (Sobs) to determine if this number falls within the ranges of the estimators.

The Island pairs that were most similar to each other in ant species composition, using the Bray-Curtis similarity measure on a scale of 0-100, were Isla Golondrinas with Isla San Pedrito (70%), Isla Cocinero with Isla Golondrinas (67%), Isla Catalina with Isla San José (63%), and Isla Colorada with Isla Pelada (62%). This pattern is illustrated in the cluster diagram (Fig. 5). Particular ant species distributions on all sites can be found in Appendix 1. Each island was most similar to a neighboring island in terms of species composition.

We collected two or three (depending on future identification and classification) commonly known invasive ant species, *Monomorium floricola*, *Paratrechina longicornis*, and another *Paratrechina* sp. that is not yet identified. *Monomorium floricola* was collected in November and June in both pitfall and Winkler traps at all sites except Isla Golondrinas and Cocinero, though in low densities. *P. longicornis* was collected in all seasons, only with pitfall traps, and only on Isla Pelada and Isla San José. *Paratrechina* sp was collected in November and May, with pitfall and Winkler traps, on Isla Pelada, San Pedrito, San José, and Catalina, though in relatively low numbers.

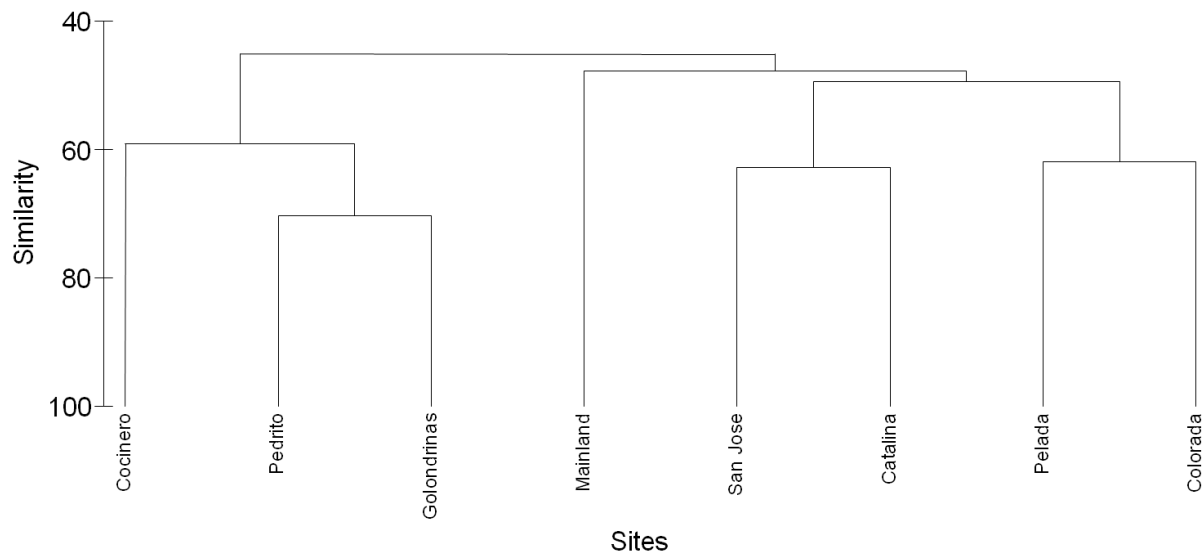


Fig. 5. Cluster diagram illustrating patterns of ant species composition across all Island and mainland sites based on a Bray-Curtis similarity matrix of presence-absence data. The sites are clustered according to similarities in their ant species composition.

We found that the number of species occurrences and composition on the Islands and mainland, in the standardized collection, differed among sampling dates, which corresponded to different seasons. We found 29 species in November 2001, 23 species in May 2002, and 41 species in June 2002. With the exception of Isla Cocinero, we found the greatest number of species on all Islands in June. Isla Cocinero appears to primarily contain ants that are tolerant of heat and dry conditions because we found the greatest number of heat/dry-tolerant species [16, 28] on Isla Cocinero in May (e.g. *Camponotus* spp., *Pheidole* spp., *Leptothorax* spp., (Appendix 2). Our sampling yielded a much lower number of cryptic litter ants in May versus June on all of the Islands, excluding Isla Cocinero. Isla Cocinero lacked cryptic litter ants that were found on the other Islands and mainland (e.g. *Mycetosoritis* sp, *Octostruma* sp, *Cyphomyrmex* sp, (Appendix 2).

We found a significant difference in mean number of species captured with Winkler traps (at all sites) between the three sampling periods ($\chi^2 = 12.289$, $df = 2$, $n = 24$, $p < 0.002$). We collected a higher number of ant species in Winkler traps during June (wet season) compared to November or May (Fig. 6). Interestingly, we did not find a similar pattern in ant species richness between seasons with the pitfall trapping method (Fig. 6). However, while we did not observe a significant change in species richness collected in pitfall traps between the dry and wet season, there were differences in species composition between the dry and wet season (see Appendix 2).

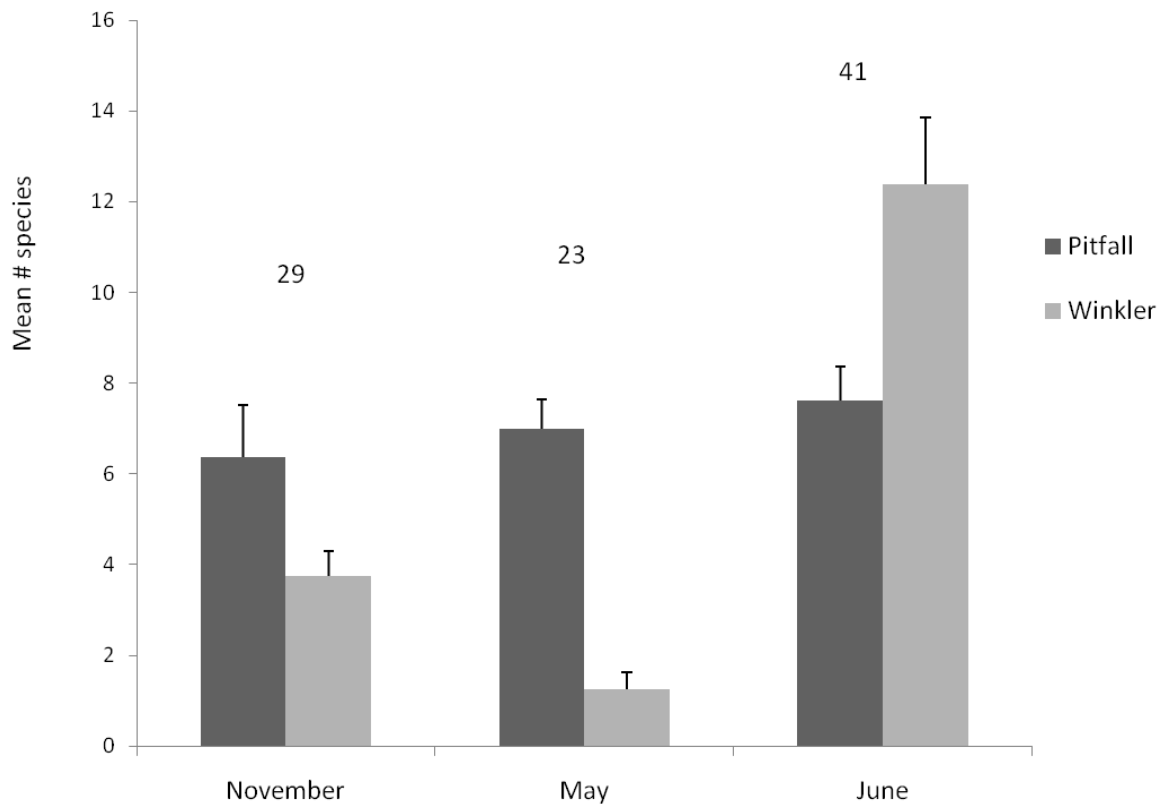


Fig. 6. The mean number of species for all sites pooled during each of three sampling periods (also representing different seasons) for both standardized trapping techniques (Pitfall and Winkler methods). The numbers above each group of bars represent the total number of species recorded during that month. (We collected 29 ant species in November 2001, 23 species in May 2002 and 41 species in June 2002).

Discussion

In this study, the first quantitative assessment of insects of the Islas Murciélagos, we compare the ant species of the Islas Murciélagos. Though we sampled quantitatively, we acknowledge that this is a preliminary, baseline study. We found what seems to be a relatively intact native fauna, despite a long history of human presence and disturbance. We recorded two exotic species on the Islands, *Monomorium floricola* and *Paratrechina longicornis* and possibly a third unknown exotic species, *Paratrechina* sp., but these species were only collected on some islands and appeared to occur at medium to low densities compared to native species' occurrence records. Even with the extremely dry conditions that occur during at least half of the year, low diversity of vegetation, and human disturbance, we found a greater number of ant species than expected on the Islas Murciélagos.

The mainland site had the greatest number of ant species compared to any Island site, which conforms to the general expectation as the mainland is assumed to be the source of colonizers to the islands [7]. Rarefaction curves, based on samples and species occurrences, and a variety of richness estimators, supported this pattern (Figs. 3, 4). However, 29 species that were collected on the Islands were not collected on the mainland. Seventeen of these 29 species have been collected farther east on the mainland in Santa Rosa National Park (JTL, pers. obs.). This pattern suggests that we have likely underestimated the species richness of the mainland. Our conclusion is supported by the steepness of the mainland Sobs curves (Fig.1), the estimations of mainland richness compared to that of the Islands (Fig.3), and that the mainland curves do not reach an asymptote. Though rarefied accumulation curves for some Islands came close to approaching an asymptote (Fig. 1), it is likely that several additional species will be recorded on each Island. Isla Cocinero appears to be the only site that was thoroughly sampled, as it practically reached an asymptote relatively early as illustrated by the Sobs curve (Fig.3).

Island area and distance from the mainland did not explain the patterns of ant species richness on the Islas Murciélago. The lack of correlation between distance and ant species richness is not surprising because the islands are very close to the mainland (between 0 and 4 km away). Over time, dispersing, reproductive ants from the mainland have probably had an equal likelihood of arriving at all Islands because distance from the nearest point on the mainland to any Island only differs by a maximum of 4 km. Although the Islands vary in size, ranging from 14.2 ha to 107.1 ha (Table 1), island area did not explain the pattern of observed species richness in the Islands. Based on area alone, one would expect to find a higher number of ant species on Isla San José compared to that on Isla San Pedrito [6], though we found approximately the same number of species with standardized sampling (18 and 19, respectively). However, when looking at total numbers of ants collected with standardized and haphazard sampling, we found 30 species on ants on Isla San José and 25 species on Isla San Pedrito (Appendix 2). Because we did not perform proportional sampling, it is likely that we have underestimated the ant species richness on the larger Isla San José versus smaller Isla San Pedrito [29]. To address why such a high number of ant species collected on the Islands (50) were not collected on the adjacent mainland (29) we would need to increase sampling effort and sample in a manner that is proportional to area [29].

Factors such as vegetation, fire history, human disturbance, and abiotic factors may better explain ant species richness than area or distance from mainland [30], though these factors are more difficult to quantify and were not evaluated during our study (with the exception of vegetation cover). Some Islands are more heavily forested, with varying heights of forest canopy (Table 1) which probably favors the persistence of additional ant species in comparison to Islands with no forest. It is also unclear as to what was the historical forest coverage on all of the Islands prior to recent heavy human use and fire disturbance, and unfortunately there are no reliable paleontological data. Isla Cocinero and part of Isla San José were burned frequently for 30 years prior to this study (Frank Lara, pers. comm.) and the vegetation that at one time covered the burned areas has not regenerated. Seedling establishment and regeneration on the Islands is difficult because the seed source of the Islands is relatively far away (mainland) and there are few riparian areas with remnant vegetation that, on mainland areas, often serve as seed sources for burned habitat [4]. The strong trade winds that blow throughout half of the year intensely dry the Islands' vegetation, also making seedling regeneration difficult [4]. Interestingly, it is possible that these trade winds actually facilitate the arrival of reproductive ants coming from mainland regions of Costa Rica. Further studies are needed to evaluate colonization patterns and processes on the Islands, particularly during months in which most ant species reproduce and disperse.

In addition, the presence and absence of invasive species on the Islands may affect ant species richness and native ant distributions.

We observed contrasting patterns of ant species composition on the Islands and the mainland. Although the mainland has the greatest number of species, many species found on the Islands were not found on the mainland. The most probable explanation for this pattern is our insufficient sampling of the mainland, and increased mainland sampling might reveal the presence of many ant species that were only collected on the Islands. However, every Island has a different composition to that of every other Island (Fig. 5, Appendix 1). It is also possible that each Island has its own unique assemblage. When looking only at the Islands, we observed that the maximum similarity in ant species composition for each island pair was only 70%. Throughout time, various species of ants may have dispersed and colonized each Island, and thereby assembled different sets of species. We observed queens of one species, never collected in our samples, blowing in with a storm and landing on the highest peak of Isla San José. Moreover, the introduction of invasive species and fire may have altered what were once more similar ant communities across the Islands [31].

Interestingly, Isla Colorada and Isla Pelada were most similar to each other in terms of ant species composition, possibly because they are neighboring islands and/or both similar in terms of their geologic origins. They are both comprised largely of serpentine rock, which makes them of particular interest because of the high endemism often associated with serpentine soils [32]. In the case of these two Islands, more detailed research is needed to better understand the relationship of geology, vegetation, and insect species richness and composition.

Ant diversity on Isla Cocinero stands apart from the other Islands in its relatively low ant species richness and noticeably disparate composition. On Isla Cocinero, we captured and often observed the presence of *Ectatomma ruidum*, a large dominant ponerine ant. This species, which is a common ant from mainland Costa Rica, was frequently captured in pitfall traps but never with Winkler traps (Appendix 2). In addition, we did not capture any cryptic leaf litter ants on Isla Cocinero that were found on all other Islands and mainland (Appendix 1). The pattern of observed ant diversity on Isla Cocinero probably reflects the history and effects of fire on the Island. The Island is reported to have had more vegetation and forest cover, similar to that of the other Islands (Frank Lara pers. comm.). Isla Cocinero is now only covered with grass, and very few trees or shrubs have regenerated. The leaf litter and its invertebrate inhabitants were most likely destroyed in the fires and the original ant community has not returned. With the presence of a dominant and abundant ant it is possible that other small native ants cannot re-establish on the Island.

None of the invasive ant species that we captured (*Monomorium floricola*, *Paratrechina longicornis*, and *Paratrechina* sp.) appeared numerically dominant, as we collected many additional, native species along with the invasive species, in the same traps. The invasive species we are most concerned about is *P. longicornis* because we observed this ant in high density near the field station on Isla San José and on Isla Pelada which, until recently, has been used as a resting point/campground by fishermen. This ant species is extremely hardy, has the ability to exclude native species, travels long distances and, if it migrates to the other islands and adjacent mainland, it could potentially disrupt native ant flora (<http://www.issg.org/database/>). Surprisingly, and fortunately, we did not collect *Wasmmania auropunctata* or *Pheidole megacephala*. These ant species are two of the world's most pernicious invasive ant species, are known to displace native ants in disturbed or introduced locations, and have negative impacts on local biodiversity [33-36]. Though there are few studies of ants from tropical dry

forests, researchers working in Columbian dry forest fragments have found that the presence of *W. auropunctata* was significantly and negatively correlated with native ant species richness [37].

The results from this study illustrate the importance of sampling in several seasons in tropical dry forest as many ant species were only present in one season (Appendix 2), and a far lower number of species overall were captured during the dry season (Fig. 6). Though we sampled in two consecutive months (May and June), our sampling detected large changes in ant activity with the onset of the rainy season. We captured 23 species in May and only four weeks later in June, we captured 41 species. In addition, we did not collect the majority of the cryptic litter ants (e.g. *Octostruma JTL-008*, *Strumigenys elongate*, *Pyramica rogata*) in the dry season which suggests their decreasing activity and potential movement deeper into the litter and soil as the environment dries out [24]. Thus, seasonality plays an important role in ant activity on the Islands and mainland, and potentially influences which species are able to survive on the Islands (though further experiments and regional comparisons are necessary to determine this). Researchers working in other dry forest sites have found that seasonality has a strong effect on animal activity and observed relative abundance of many taxa [38-40]. It is also possible that extreme conditions during the dry season prevent other invasive ants from establishing and persisting on the Islands and adjacent mainland.

Our study additionally revealed that sampling methods have a significant effect on the ability to detect species, especially in seasonal environments. In general, Winkler traps are best at capturing small, cryptic litter ants and pitfall traps do well with larger, ground foragers [41]. During the wet season, Winkler traps were more effective as we captured more ant species using this method than with any other method at all sites. However, because the leaf litter on the Islands and mainland dried out considerably in the dry season (Fig. 2), Winkler traps proved ineffective at capturing ants during the dry season; on average, we captured two species using Winkler traps during the dry season (May) whereas we captured 12 species at the onset of the wet season (June) (Fig. 6., Appendix 2). The efficacy of pitfall traps remained approximately the same across all seasons, with a slight increase in captures in June. Our results show that it is important to test the efficiency of each trap method for specific habitats and climates, especially when performing large-scale inventories or monitoring programs where time and money are considerably limited.

Implications for conservation

The Islas Murciélagos represents a globally unique and highly threatened habitat, as uninhabited tropical dry forest islands are uncommon. The protection of these Islands is important for marine and terrestrial biodiversity, and though the Islands and their surrounding waters have not been thoroughly inventoried, unique floral and faunal assemblages have been documented in the region [4-5]. In addition, sea turtles use the relatively protected beaches of the Islas and nearby mainland for nesting sites [4]. Studies like ours, and that carried out by Dauphin and Grayum, documenting the bryophyte species of the region [5], provide important baseline information that will aid future research and monitoring programs on the Islands and mainland. Because the Islas Murciélagos are part of the larger Area de Conservación de Guanacaste (ACG), their conservation will contribute to the region's overall biodiversity and ecosystem services.

Insects, as well as bryophytes, are sensitive to environmental changes, and studies and inventories involving these organisms are invaluable tools when attempting to gauge the health and endurance of a habitat or ecosystem [42-43]. Given that we found an invasive ant species (*Paratrechina longicornis*) on two Islands (Pelada and San José), it is important to continue monitoring for the presence and

absence of invasive ants because of their ability to disrupt trophic webs and ecosystem functioning [44]. Additionally, complexes of native species that are part of ant “functional groups” [16], such as cryptic litter ants, may also provide important information about whether the habitat or ecosystem in question is relatively intact or if it has been affected by (natural or anthropogenic) disturbance. Our ant data corroborate that Isla Cocinero was denuded of almost all vegetation because it has neither leaf litter nor the associated cryptic litter ant fauna, and has a relatively low number of ant species compared to other Islands.

Because we identified all ants to species, and properly curated, stored, and electronically databased all specimens in INBIO, the entire collection from the Islas Murciélago is an accessible tool that park employees from the ACG or any interested person are free to use for a comparative study. With minimal funding, it would be relatively straightforward to repeat our study in the future in order to monitor the ecosystem health of the Islands and determine changes in the ant community. We recommend more extensive sampling for the entire region to complete the list of ant species for the Islas Murciélago and Santa Elena Peninsula, adding to our baseline data. We suggest that a re-evaluation of the Island and mainland ant fauna should be done using proportional sampling effort scaled to area and, in addition to the methods used in our study, include methods to sample arboreal ant species such as fogging and beating [45].

Overall, the Islas Murciélago represent a model system with which to monitor population dynamics of organisms over time. Because of the modest number of species, monitoring all ant species will produce tractable datasets on which to assess the potential effect of change in local weather patterns, fire disturbance, invasive ants, etc. The Islands are ideal for all-fauna/all-flora inventories with which baseline data could be created because they are not inhabited by humans (except for one field station that sporadically receives visitors) and cover a relatively small area. Monitoring studies of thoroughly-inventoried areas are especially important with regard to climate change. Current models predict sea level rises and changes in temperature and rainfall, and recent research has already shown that these abiotic changes will impact many species – especially invertebrates in tropical areas [46].

Though much of the region is protected by law, the long-term conservation of the lands of the ACG is challenging and complex. We seek to bring awareness to the fragile and fascinating biology of the Islas Murciélago, call for further studies of the region including continued monitoring over time, and additionally recommend regulation and supervision of human activities near and on the Islands.

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Appendix 1: Species composition by site (column names) Mainland, Pelada, Colorada, San Pedrito, San José, Golondrinas, Catalina, Cocinero. White = present in standardized collecting, Black = absent, White with * = present in hand collecting and/or preliminary observations in standardized collecting.

| SPECIES | Main | Pel | Col | Ped | SJ | Gol | Cat | Coc |
|--------------------------------------|------|-----|-----|-----|----|-----|-----|-----|
| <i>Azteca sp</i> | * | | | | | | | |
| <i>Azteca velox group</i> | | | | | * | | | |
| <i>Dorymyrmex sp</i> | | * | | | * | | | |
| <i>Forelius pruinosus</i> | | | | * | * | | | |
| <i>Forelius damiani</i> | | | | | | | | |
| <i>Eciton sp</i> | | | | | | | | |
| <i>Labidus coecus</i> | * | | | | | | | |
| <i>Brachymyrmex depilis</i> | | * | | | | | | |
| <i>Brachymyrmex 2set</i> | | | | | | | | |
| <i>Brachymyrmex 4set</i> | | | | | | | | |
| <i>Camponotus atriceps</i> | | | | * | | | | |
| <i>Camponotus blandus</i> | | * | | * | * | * | | |
| <i>Camponotus brevis</i> | | | | | * | | | |
| <i>Camponotus coloratus</i> | | | | | * | | * | |
| <i>Camponotus rectangularis</i> | | | * | | * | | | |
| <i>Camponotus zonatus</i> | | * | | | | | | |
| <i>Paratrechina longicornis</i> | | | | | | | | |
| <i>Paratrechina sp</i> | | | | | * | | * | |
| <i>Crematogaster sp</i> | | * | | | | | | |
| <i>Leptothorax augusti</i> | | | | | | | | |
| <i>Nesomyrmex echinatinodis</i> | | | | | | | | |
| <i>Megalomyrmex silvestrii</i> | | | | | | | | |
| <i>Monomorium floricola</i> | | | | | * | | | |
| <i>Pheidole cocciphaga</i> | * | | | | | | | |
| <i>Pheidole gouldi</i> | | | | | | | | |
| <i>Pheidole angusticeps</i> | | | | | | | | |
| <i>Pheidole cf. laselva</i> | | | | | | | | |
| <i>Pheidole nebulosa</i> | | | | | | | | |
| <i>Pheidole punctatissima</i> | | | | | * | | * | |
| <i>Pheidole bilimeki</i> | | | | | | | | |
| <i>Pheidole radoszkowskii subsp</i> | | | * | | | | | |
| <i>Pheidole cf. ruida</i> | | | | | | | | |
| <i>Pheidole "shine"</i> | | | | | | * | | |
| <i>Pheidole suzannae</i> | | | | | | | | |
| <i>Rogeria leptotana</i> | | | | | | | | |
| <i>Solenopsis "Diplorhoptrum"</i> | | | | | | | | |
| <i>Solenopsis Globularia complex</i> | | | | * | * | | | |
| <i>Acromyrmex octospinosus</i> | | | * | | | * | | |
| <i>Cyphomyrmex costatus</i> | | | | | | | | |

| SPECIES | Main | Pel | Col | Ped | SJ | Gol | Cat | Coc |
|-----------------------------------|------|-----|-----|-----|----|-----|-----|-----|
| <i>Cyphomyrmex rimosus s.l.</i> | | | * | | | | * | |
| <i>Mycetosoritus vinsoni</i> | | | | | | | | |
| <i>Mycocepurus smithii</i> | | | | | | | | |
| <i>Myrmicocrypta cf. ednaella</i> | | | | | | | | |
| <i>Eurhopalothrix JTL-005</i> | | | | | | | | |
| <i>Octostruma JTL-001</i> | | | | | | | | |
| <i>Octostruma JTL-008</i> | | | | | | | | |
| <i>Rhopalothrix weberi</i> | | | | | | | | |
| <i>Cephalotes minutus</i> | | | | | | | | |
| <i>Pyramica eggersi</i> | | | | | | | | |
| <i>Pyramica rogata</i> | | | | | | | | |
| <i>Strumigenys dubitata</i> | | | * | | | | | |
| <i>Strumigenys elongata</i> | | | | | | | | |
| <i>Ectatomma ruidum</i> | | | | | | | | |
| <i>Gnamptogenys curtula</i> | | | | | | | | |
| <i>Gnamptogenys hartmani</i> | | | | * | | | | |
| <i>Hypoponera distinguenda</i> | | | | | | | | |
| <i>Hypoponera opacior</i> | | | | * | | * | | |
| <i>Hypoponera parva</i> | | | | | | | | |
| <i>Leptogenys JTL-004</i> | | | * | | | | | |
| <i>Odontomachus bauri</i> | | | | | * | | | |
| <i>Pachycondyla harpax</i> | | | | | | | | |
| <i>Pseudomyrmex cretus</i> | | * | * | | | | | |
| <i>Pseudomyrmex sp</i> | | * | | | | | | |
| Total: Standardized 54 | 31 | 22 | 20 | 19 | 18 | 18 | 17 | 12 |
| Total: All Collecting 63 | 34 | 29 | 27 | 25 | 30 | 22 | 21 | 12 |

Appendix 2: This table illustrates in which season and by which method each species was captured. November represents the transition of dry and wet seasons, May represents the end of the dry season, and June represents the beginning of the wet season. For seasons, a “1” represents presence. For trapping method, an “x” indicates whether a species was trapped by pitfalls and/or Winkler traps.

| | Nov. | May | June | Total | Pitfall | Winkler |
|--------------------------------------|------|-----|------|-------|---------|---------|
| Species | | | | | | |
| <i>Forelius big orange</i> | 0 | 1 | 1 | 2 | x | x |
| <i>Forelius small black</i> | 0 | 1 | 0 | 1 | x | 0 |
| <i>Eciton</i> | 0 | 1 | 0 | 1 | x | 0 |
| <i>Brachymyrmex depilis</i> | 0 | 1 | 1 | 2 | x | x |
| <i>Brachymyrmex 2set</i> | 0 | 0 | 1 | 1 | 0 | x |
| <i>Brachymyrmex 4set</i> | 1 | 1 | 1 | 3 | x | x |
| <i>Camponotus atriceps</i> | 1 | 1 | 1 | 3 | x | 0 |
| <i>Camponotus blandus</i> | 0 | 0 | 1 | 1 | x | 0 |
| <i>Camponotus brevis</i> | 1 | 0 | 1 | 2 | x | x |
| <i>Camponotus coloratus</i> | 1 | 1 | 1 | 3 | x | x |
| <i>Camponotus rectangularis</i> | 1 | 0 | 0 | 1 | x | x |
| <i>Camponotus zonatus</i> | 1 | 1 | 0 | 2 | x | x |
| <i>Paratrechina longicornis</i> | 1 | 1 | 1 | 3 | x | 0 |
| <i>Paratrechina spp.</i> | 1 | 1 | 0 | 2 | x | x |
| <i>Leptothorax augusti</i> | 1 | 1 | 1 | 3 | x | x |
| <i>Nesomyrmex echinatotus</i> | 0 | 1 | 0 | 1 | x | x |
| <i>Megalomyrmex silvestrii</i> | 0 | 0 | 1 | 1 | 0 | x |
| <i>Monomorium floricola</i> | 1 | 0 | 1 | 2 | x | x |
| <i>Pheidole gouldi</i> | 1 | 1 | 1 | 3 | x | x |
| <i>Pheidole gradifer</i> | 0 | 0 | 1 | 1 | x | x |
| <i>Pheidole cf. laselva</i> | 0 | 0 | 1 | 1 | x | x |
| <i>Pheidole nebulosa</i> | 0 | 0 | 1 | 1 | 0 | x |
| <i>Pheidole punctatissima</i> | 1 | 1 | 1 | 3 | x | x |
| <i>Pheidole punctatissima</i> | 1 | 1 | 1 | 3 | x | x |
| <i>Pheidole radoszkowskii subsp</i> | 1 | 1 | 1 | 3 | x | 0 |
| <i>Pheidole cf. ruida</i> | 1 | 0 | 1 | 2 | x | x |
| <i>Pheidole suzanne</i> | 0 | 1 | 0 | 1 | x | 0 |
| <i>Rogeria leptotana</i> | 0 | 0 | 1 | 1 | x | x |
| <i>Solenopsis Globularis complex</i> | 1 | 1 | 1 | 3 | x | x |
| <i>Solenopsis diplocephalum</i> | 1 | 1 | 1 | 3 | x | x |
| <i>Acromyrmex octospinosus</i> | 1 | 0 | 1 | 2 | x | x |
| <i>Cyphomyrmex rimosus s.l.</i> | 1 | 0 | 1 | 2 | x | x |
| <i>Cyphomyrmex costatus</i> | 1 | 0 | 1 | 2 | x | x |
| <i>Mycetosoritus vinsoni</i> | 1 | 1 | 1 | 3 | x | x |
| <i>Mycocepurus smithii</i> | 1 | 0 | 1 | 2 | x | x |

| | | | | | | |
|-----------------------------------|---|---|---|---|---|---|
| <i>Myrmicocrypta cf. ednaella</i> | 0 | 0 | 1 | 1 | 0 | x |
| <i>EurhopalothrixJTL-005</i> | 0 | 0 | 1 | 1 | 0 | x |
| <i>Octostruma JTL-001</i> | 0 | 0 | 1 | 1 | 0 | x |
| <i>Octostruma JTL-008</i> | 1 | 0 | 1 | 2 | 0 | x |
| <i>Rhopalothrix weberi</i> | 1 | 0 | 0 | 1 | 0 | x |
| <i>Cephalotes minutus</i> | 1 | 0 | 0 | 1 | x | x |
| <i>Pyramica eggersi</i> | 0 | 0 | 1 | 1 | 0 | x |
| <i>Pyramica rogata</i> | 0 | 0 | 1 | 1 | 0 | x |
| <i>Strumigenys dubitata</i> | 1 | 0 | 1 | 2 | x | x |
| <i>Strumigenys elongata</i> | 0 | 0 | 1 | 1 | 0 | x |
| <i>Ectatomma ruidum</i> | 0 | 1 | 1 | 2 | x | 0 |
| <i>Gnamptogenys curtula</i> | 1 | 1 | 0 | 2 | x | x |
| <i>Hypoponera distinguenda</i> | 0 | 0 | 1 | 1 | 0 | x |
| <i>Hypoponera opacior</i> | 1 | 0 | 0 | 1 | 0 | x |
| <i>Hypoponera parva</i> | 1 | 0 | 0 | 1 | 0 | x |
| <i>LeptogenysJTL-004</i> | 0 | 0 | 1 | 1 | 0 | x |
| <i>Odontomachus bauri</i> | 1 | 1 | 1 | 3 | x | x |
| <i>Pachycondyla harpax</i> | 0 | 0 | 1 | 1 | 0 | x |
| <i>Pseudomyrmex cretus</i> | 1 | 0 | 0 | 1 | x | 0 |