THE ANT (HYMENOPTERA: FORMICIDAE) FAUNA OF COCOS ISLAND, COSTA RICA

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ABSTRACT

Cocos Island, Costa Rica is a 24-square kilometer volcanic island in the tropical eastern Pacific Ocean, located approximately 480 kilometers from the mainland. Despite its biogeographic significance, much of the entomofauna have not been systematically surveyed. A detailed survey of the ant (Hymenoptera: Formicidae) fauna of this island was conducted over a three-week period. The results suggest that, despite the relatively minor presence of humans on Cocos, much of the ant fauna is dominated by non-native species. Furthermore, the current ant community is substantially different from that described by previous expeditions. One of the previously described endemics, *Camponotus biolleyi* Forel, was not found during the survey. A species known to be invasive, *Wasmannia auropunctata* Roger, was found in extremely high abundance near disturbed sites, but was not present in more pristine habitats. Furthermore, this population displays intraspecific aggression, which is uncommon among invasive ants, including other invasive populations of this species.

Key Words: invasion, non-native species, species richness, *Wasmannia auropunctata*

RESUMEN

La Isla del Coco, Costa Rica, es una isla volcánica de 24 kilómetros cuadrados y está ubicada en el oriente del Océano Pacífico tropical, 480 kilómetros de la costa del continente. A pesar de su relevancia biogeográfica, la mayor parte de la entomofauna de esta isla no ha sido examinada sistemáticamente. Un relevamiento detallado de las hormigas (Hymenoptera: Formicidae) de esta isla fue realizado durante tres semanas. Nuestros resultados sugieren que, a pesar de la escasa presencia humana en La Isla del Coco, la mayor parte de la fauna de hormigas está dominada por especies introducidas. Además, la fauna actual de hormigas es substancialmente diferente de la descrita por las expediciones anteriores. Una de las especies endemicas previamente descritas, *Camponotus biolleyi* Forel, no fue encontrada durante nuestro estudio. Una especie conocida como invasora, *Wasmannia auropunctata* Roger, fue encontrada con abundancia extremadamente alta en sitios disturbados, pero está ausente en habitats más prístinos. Además, esta población presenta signos de agresión intraespecífica, la cual es infrecuente en especies invasoras, incluyendo otras poblaciones invasoras de esta especie.

Translation provided by the authors.

Surveys of island faunas are a basic step for ecological and biogeographical studies, and are critical for conservation efforts. Surveys conducted over long periods are especially useful for the insight they can offer into the processes of community assembly, dispersal, competition, and extinction. Species invasion may affect all of these processes and has received increasing attention as a force threatening attempts at conservation. Species are defined as invasive if (1) they are non-native (or alien) to the ecosystem under consideration, and (2) their introduction causes or is likely to cause economic or environmental harm or harm to human health (Williams 1994). The patterns by which invasive species are spread and the impact that they have on the environment in which they are introduced are both of fundamental interest to ecologists and conservationists. Ants (Hymenoptera, Formicidae) are particularly common invasive species (McGlynn 1999) and their impact can be quite profound (Lubin 1984; Human & Gordon 1997; Vinson 1997).

Cocos Island, Costa Rica

Cocos Island (5°32'57"N, 86°59'17"W) is a relatively small (24 km^2), volcanic island in the tropical eastern Pacific Ocean. It is has been of particular interest to biogeographers (see Hertlein 1963) because it is the only island in this region that supports a lowland tropical forest, due to the warm climate (Montoya 1990), and heavy precipitation (Montoya 1990) which it receives. It is also relatively isolated, located approximately 480 km from the coast of Central America. Early surveys of the flora and fauna of Cocos Island, conducted in the late 19th and early 20th centuries (Hogue & Miller 1981), described a diverse community of or-

ganisms, with a relatively high rate of endemism (Hogue & Miller 1981; Montoya 2002). While ants were included in several surveys (Hogue & Miller 1981), we have reason to believe that the data from at least one of these was erroneous (see Discussion). Nevertheless, these surveys provide baseline data for the purpose of comparison.

Cocos Island is also unique in that it has had a minimal history of human influence (Weston-Knight 1990). Due mostly to the presence of fresh water, mariners have consistently used Cocos as a refueling point for excursions in the region. However, Cocos is an extremely rugged island, surrounded by steep cliffs; only 3 bays (Chatham, Wafer, and Yglesias) provide access to the interior of the island and have been used for anchorage by visitors to Cocos. Although no permanent human settlement has ever been established, several attempts were made in the late 19th century, including an agricultural colony (1884-1912) and a penal colony (1879-1881). These settlements were restricted to the areas around Chatham and Wafer Bays, which are in the extreme northern end of the island and are the most accessible, and today house the park guards who manage the island (Fig. 1). The presence of humans on Cocos Island, though minimal, warrants inquiry into their impact on the island environment, particularly that of invasive species brought by humans.

We conducted a detailed survey of the ant fauna of Cocos Island to answer the following questions: (1) what is the current species richness of ants, (2) how have the diversity and community composition changed since previous surveys, and (3) what is the impact, if any, of invasive ant species on Cocos Island?

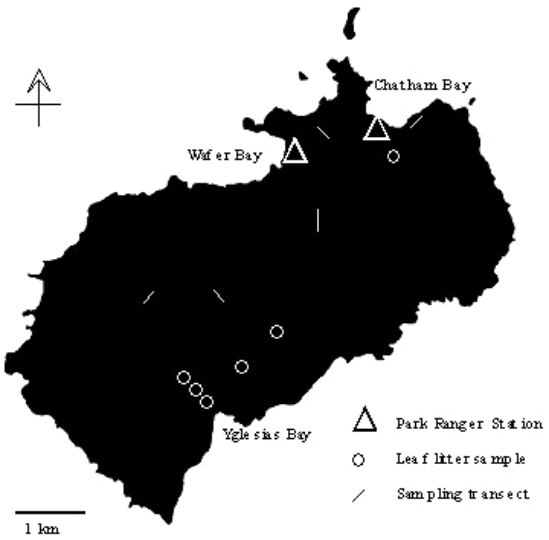

Fig. 1. Map of Cocos Island, Costa Rica, indicating sampling localities for leaflitter and pitfall transects, additional leaflitter samples, and the location of park stations.

Materials and Methods

Fieldwork was conducted on Cocos Island from 3-23 July 2003. Species richness was assessed by collection of ants and other invertebrates following the standardized "ants of the leaf litter" (ALL) collection protocol outlined in Agosti et al. (2000), except that transects were shortened from 200 m to 100 m due to the extremely rugged terrain of the island. Five 100-m transects were run on the island (Fig. 1), collecting moist leaflitter and other debris from a 1-m^2 quadrat every 10 m along the transect and placing a pitfall trap approximately 1 m from the site of leaflitter collection. Invertebrates were extracted from the leaf litter by sifting the litter to remove large particles, then use of Winkler traps. The moist leaflitter was allowed to dry for approximately 48 h. Pitfall traps consisted of plastic 60-mm diameter drinking cups (except for transect A, in which 30-mm-wide plastic tubes were used) containing approximately 25 milliliters of 100% ethanol covered by a plastic plate and were collected after 48 h. In addition to transects, six additional leaf litter samples (one square-meter each) were collected from various sites around the island (Fig. 1), in an attempt to sample as many regions and habitats on the island as time allowed. Baiting was conducted at human-inhabited Chatham and Wafer Bays, as well as at uninhabited Yglesias Bay with Pecan Sandies® cookie crumbs which were placed in 1.5-milliliter tubes and collected in two stages, at 10 and 30 min. General collecting techniques were also employed, in which foraging ants were found by visually searching and then collected by hand; ant nests were found by searching through leaflitter, rotting logs, recent treefalls, and under bark on living as well as decaying trees. Species accumulation curves were generated by EstimateS (Colwell 1997).

To assess the impact of an invasive ant species on the island, we chose to focus on *Wasmannia auropunctata* Roger, a species that has been shown to have profound impacts on native invertebrates in the nearby Galápagos Islands (Clark et al. 1982; Lubin 1984) and has been spreading rapidly to other sites worldwide (Wetterer & Porter 2003). A Kruskall-Wallis test was used to compare ant species richness in areas with *W. auropunctata* versus those without. Additionally, the effects of *W. auropunctata* density on ant species richness were analyzed by Spearman rank correlation. To measure intraspecific aggression (thought to correlate with competitive ability; (Holway et al. 1998; Tsutsui et al. 2003)) within the Cocos population of *W. auropunctata*, worker ants were baited to 45-ml tubes as described above. Aggression trials were conducted in a manner analogous

to Tschinkel et al. (1995) at four sites throughout the invaded range. After 10-30 min, when the bait tubes swarmed with several hundred (~200-500) *W. auropunctata* workers, they were sealed and transported to the lab, where the open ends of the tubes were joined. Aggression was scored as present or absent; when present, the number of overtly aggressive interactions (biting, grappling, and stinging) was noted over the next five min as the ants from the two tubes intermixed. Each trial was repeated no less than three times with replicate bait tubes. No more than an hour elapsed between the sealing of tubes in the field and the laboratory aggression trials.

Results

We discovered a total of 19 species of ants in 14 genera and 4 subfamilies during the survey (Table 1). Species identification was not possible for several taxa, because either the taxonomy is presently inadequate or because a nest series (i.e., the full range of worker castes) was not collected (S. Cover, MCZ: Harvard University, M. Deyrup, Archbold Biological Station, and J. T. Longino, Evergreen State College, pers. comm.). The observed species richness converges on that provided by estimators (Fig. 2), suggesting that our inventory of the leaf litter ants was thorough in the sites sampled.

Table 1. Species list of the ants of Cocos Island, July 2003.

Subfamily	Species
Dolichoderinae	*Tapinoma melanocephalum* F.[2]
Formicinae	*Brachymyrmex* sp.[5]
	Camponotus cocosensis Wheeler[1]
	Camponotus sp. 2[5]
	Paratrechina guatemalensis Forel[2]
	Paratrechina longicornis Latreille[2]
Myrmicinae	*Adelomyrmex* sp.[4]
	Monomorium floricola Jerdon[2]
	Pheidole moerens Wheeler[2]
	Pheidole sp. 2[5]
	Pheidole sp. 3[5]
	Pyramica nigrescens Wheeler[3]
	Solenopsis sp. (Diplorhoptrum)[4]
	Solenopsis geminata F.[2]
	Strumigenys louisianae Roger[3]
	Wasmannia auropunctata Roger[2]
Ponerinae	*Hypoponera opacior* Forel[3]
	Odontomachus ruginodis Smith[2]
	Pachycondyla stigma F.[2]

[1]Endemic.
[2]Tramp species.
[3]Unknown origin, likely tramp species.
[4]Unknown origin, likely native.
[5]Unknown origin.

The relative abundances of selected species, based on the number of 1-m^2 plots in which a species appears, are presented in Fig. 3. In general, more species were found at higher elevations (Fig. 4). Furthermore, the ant communities above approximately 200 meters elevation consisted of a higher proportion of native and potentially-native species. This pattern is exaggerated by the absence of some invasive species in higher elevation sites. In particular, three species (*Monomorium floricola* Jerdon, *Solenopsis geminata* F., and *Tapinoma melanocephalum* F.) were found exclusively in the human-modified habitats around Chatham and Wafer Bays. As a result, these species were never present in our leaflitter or pitfall samples. Other species that were absent from leaflitter and pitfall samples were found to nest in rotten logs (*Camponotus* sp. 2, *Pachycondyla stigma* F.) or were strictly arboreal (*Brachymyrmex* sp.).

The presence of *W. auropunctata* was uncorrelated with the number of other ant species in a quadrat (H = 0.29, df = 1, P = 0.59). Likewise, there was no significant effect of *W. auropunctata* density on the species richness of other ants (r_s = -0.19, n = 31, P = 0.30). There was no variance in the outcomes (presence or absence) of aggression assays among replicates, although when present, the levels of aggression (biting, grappling, and stinging) varied between sites on the island.

Discussion

Our survey of the ant fauna of Cocos Island revealed the presence of 19 species currently inhabiting the island. Several lines of evidence suggest that the majority of these are non-native, having likely arrived on the island via human transport. Of the species known to be common tramps (Deyrup et al. 2000), three were never found far from human habitation (*Monomorium floricola*, *Solenopsis geminata*, and *Tapinoma melanocephalum*). Likewise, the species that may be native (including the only species known to be endemic; see Appendix) were only collected away from human-disturbed regions of the island. Of the ten species we collected that are not known to be common tramp species, at least three of these (*Pyramica nigrescens* Wheeler, *Hypoponera opacior* Forel, *Strumigenys louisianae* Roger) may also be regularly transferred by human commerce (J. T. Longino, Evergreen State College, and M. Deyrup, Archbold Biological Station, pers. comm.). The remaining six species cannot be identified because the genus needs revision or because of insufficient material (S. Cover, MCZ: Harvard University, M. Deyrup, Archbold Biological Station, and J. T. Longino, Evergreen State College, pers. comm.). Therefore, a determination of their status as tramps is not possible. However, a conservative estimate would be that six of the nineteen ant species currently inhabiting Cocos Is-

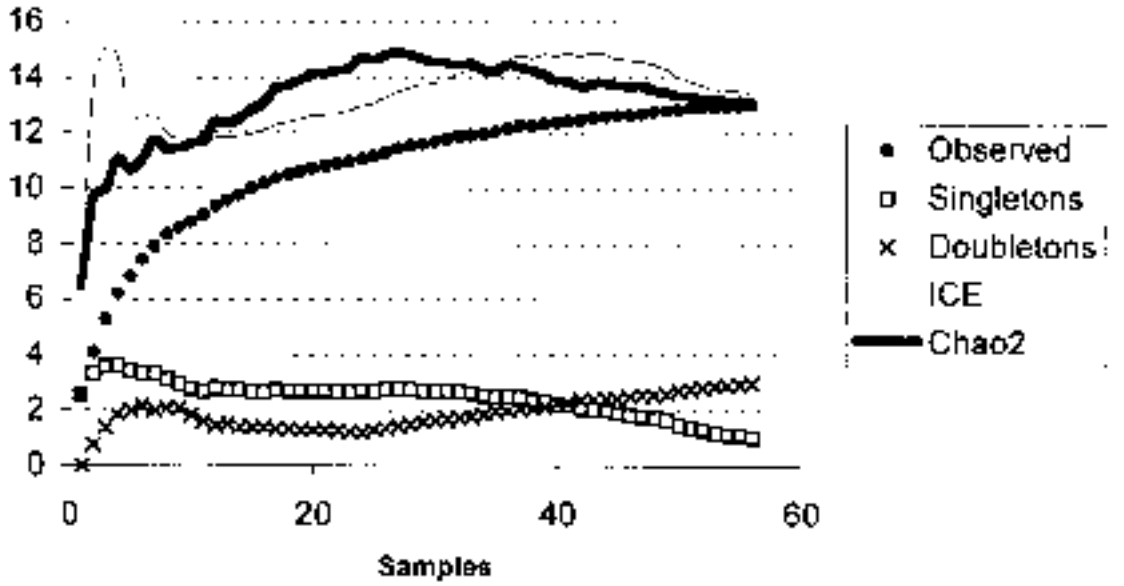

Fig. 2. Species accumulation curve for leaf litter ants collected using Winkler and pitfall traps. The accumulation curve does not include 6 additional species acquired by general collecting.

land are native (i.e., were not brought by humans). This leads us to the conclusion that most ants on Cocos Island are non-native species, an assertion reinforced by the apparent domination of a few species (e.g., *Wasmannia auropunctata*), especially near disturbed regions of the island.

The ant community currently inhabiting Cocos Island is substantially different than that reported from previous surveys (Hogue & Miller 1981; Table 2). Four prior expeditions collected ants on Cocos between 1898 and 1932, and the specimens from each of these were subsequently described by taxonomists who did not participate in the collection events (Forel 1902, 1908; Emery 1919; Wheeler 1919, 1933). Of these, the 1898 collections by Anastasio Alfaro (Forel 1908; Emery 1919), is closest to our survey in terms of the number of species collected (17), but the identities of the species in both surveys are quite different. In fact, we believe it is very likely that the reports from the 1898 surveys are erroneous for the following reasons. First, several of the species listed from this survey (e.g., *Atta cephalotes* L., *Nomamyrmex crassicornis* Smith) are unlikely to occur on a small oceanic island, and another, *Pseudomyrmex flavicornis*, an obligate acacia specialist is unlikely to be present on Cocos, from which no acacias have been reported (Fosberg & Klawe 1966). Second, the material from this expedition sent by Alfaro to Forel cannot be located (J. T. Longino, Evergreen State College, pers. comm.). Since Alfaro also sent a large amount of specimens from the mainland to both Emery and Forel, and since all of the species reported from the 1898 expedition also occur on mainland Costa Rica, it seems likely that there was some confusion between the Cocos Island and mainland material.

Further support for this hypothesis comes from three subsequent expeditions (1902 by Pablo Biolley; 1905 by Francis Williams; and 1932 by Maurice Willows, Jr.), none of which included the suspicious species mentioned above (Table 2). These surveys reported relatively few species (5, 7, and 1, respectively), but at least two have substantial overlap between the species reported: four of the five species (80%) reported from 1902 were also reported from 1905 (Wheeler 1919). Only a single species, *Camponotus cocosensis* Wheeler is mentioned from the 1932 expedition, (which also was reported from 1905) but it is not clear how extensive was the 1932 survey (Wheeler 1933). Thus the only surveys that seem both fairly extensive and reliable are the 1902 and 1905 surveys, which share 40% (2/5) and 57% (4/7) of species in common with our 2003 survey.

Our 2003 survey found fourteen species that have not been previously reported from Cocos Island. Of the remaining five species, four were reported by more than one previous survey. The differences in species composition between ours and previous surveys can be explained by one or more of the following non-mutually- exclusive hypotheses: (1) species turnover due to the arrival of new species and extinction of others; (2) insufficient or incomplete sampling by some expeditions; (3) misidentification of some species; or (4) mislabeling or confusion of specimens on expeditions that visited additional sites. As previously mentioned,

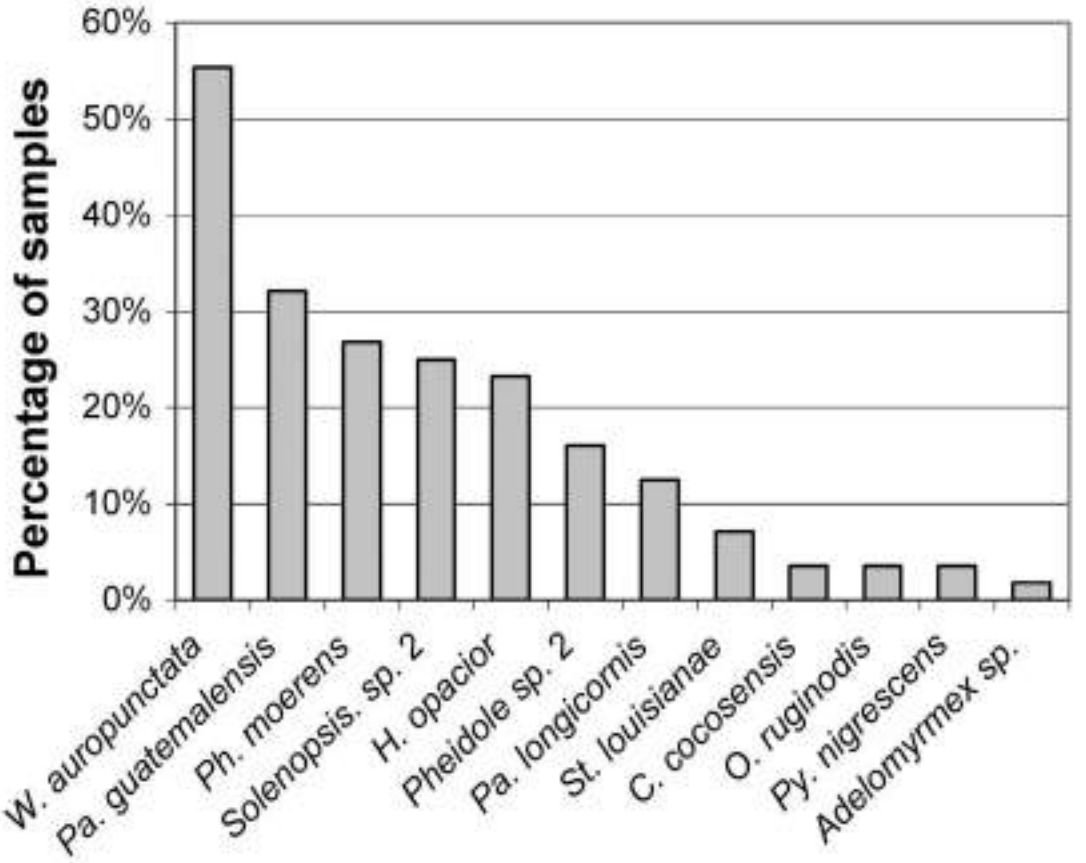

Fig. 3. The relative abundances of selected Cocos Island ant species in litter samples.

we believe that the report from the 1898 expedition can be discarded because hypothesis 4 (specimen mislabeling/confusion) likely applies. Hypothesis 2 (incomplete sampling) likely applies to the 1932 expedition. For the remaining two expeditions, we are unable to determine which hypotheses apply, although species turnover (hypothesis 1) and/or incomplete sampling (hypothesis 2) seem likely.

It is noteworthy that we were not able to locate any workers of *Camponotus biolleyi*, a species thought to have been endemic to Cocos Island and which was apparently quite abundant at the turn of the century, commonly seen foraging on understory ferns (Forel 1902, p. 178). This species was collected by two separate expeditions to Cocos Island, in 1902 and 1905. Because our intensive survey did not detect this species, it seems probable that *C. biolleyi* has either gone extinct or has greatly declined in abundance. The possibility that non-native species are displacing native ants on Cocos Island underscores the importance of conservation efforts on this and other oceanic islands, which may be more affected by human activity than is immediately apparent.

By far the most abundant ant species in our survey, based on the number of plots in which it occurred, is the little fire ant, *Wasmannia auropunctata*. This species is known to be highly invasive (Wetterer & Porter 2003) and to displace native arthropods, particularly other ant species, in areas in which it is introduced (Clark et al. 1982; Lubin 1984; Le Breton et al. 2003). To determine whether *W. auropunctata* has had a similar effect on the Cocos Island ant community, we made detailed observations on the distribution, abundance, and behavior of this species. Our results indicate that *W. auropunctata* appears to be restricted to the regions of the island near disturbed sites (Chatham and Wafer Bays); the 1902 expedition by Biolley observed the same distribution, which therefore appears not to have changed significantly for at least 100 years (Forel 1902, p. 177). Further support for this observation comes from the fact that *W. auropunctata* appears to be completely absent from Yglesias Bay, which was never settled by humans but possesses apparently suitable habitat (e.g., groves of *Hibiscus tiliaceus* L. [Malvaceae], which are densely patrolled by *W. auropunctata* in Wafer and Chatham Bays).

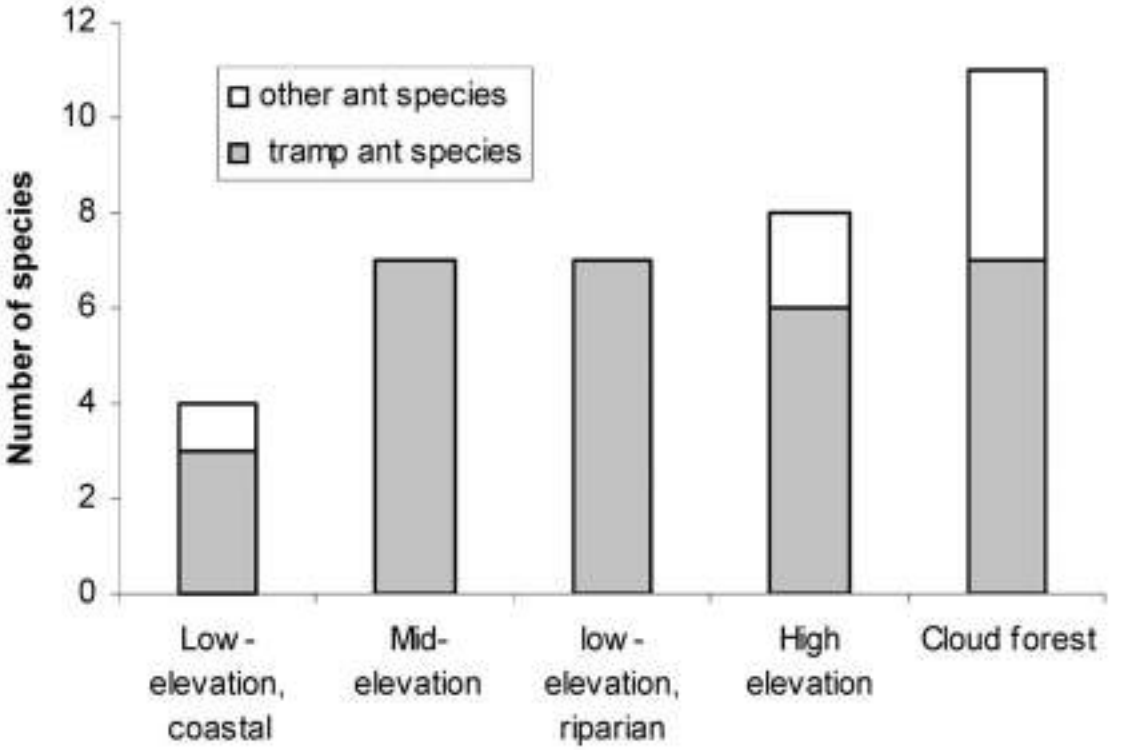

Fig. 4. Species composition among the sampling sites. Note that lower and middle elevations (also closer to shore) are occupied almost exclusively by tramp species.

This is surprising, considering the propensity of this species for colonizing new areas (Wetterer & Porter 2003) and suggests that the ants' dispersal may be limited by ecological factors, including possibly the absence of human-modified habitat.

The *W. auropunctata* population on Cocos Island appears not to be suppressing the richness of other ant species, as has been reported on other islands (Clark et al. 1982; Lubin 1984; Jourdan 1997). However, this may be partially due to the high proportion of non-native ant species comprising the Cocos ant fauna, because non-native species are often good competitors (lesser competitors may have already been competitively excluded). Alternatively, the Cocos population of *W. auropunctata* may be less competitive than other invasive populations of this species. The presence of intraspecific aggression within the Cocos population is in marked contrast with studies from other introduced populations of this species (Le Breton et al. 2003), and is consistent with the hypothesis that the Cocos population is not as competitively superior. Lack of intraspecific aggression is thought to contribute to the increased competitive abilities of many invasive ant species, by allowing them to effectively function as one enormous supercolony (Tsutsui et al. 2003). If lack of aggression is causally associated with competitive superiority, then the repeated presence of aggression between some colonies of *W. auropunctata* on Cocos may explain why this species has not spread as effectively across the island as it has in other introduced areas, and why it has not displaced other ants even in the areas in which it is abundant. Further study of this community is warranted to make generalizations about the patterns and processes involved in invasions of islands by non-native species.

In general, our survey revealed that Cocos Island appears to be dominated by non-native ant species, despite the minimal history of human habitation on the island. We are unable to make meaningful comparisons between our survey and previous surveys, because earlier collections were either incomplete, likely to have included mislabeled specimens, or both. Nevertheless, we are able to conclude that at least one non-native species, *Wasmannia auropunctata*, though abundant in some parts of the island, appears not to have a significant impact on the species richness of other ant species. However, the fact that such a high proportion of the ant species on Cocos are also non-native may indicate that some sort of competitive stalemate has been reached; follow-up surveys would help to test whether this equilibrium is stable or transient.

TABLE 2. SUMMARY OF THE HISTORY OF ANT COLLECTIONS ON COCOS ISLAND.

Ant species (outdated names in parentheses)	Year of expedition				
	1898[1]*	1902[2]	1905[3]	1932[4]	2003
Adelomyrmex sp.					X
Atta cephalotes L.	X				
Azteca constructor (*emmae*) Emery	X				
Brachymyrmex longicornis Forel	X				
Brachymyrmex sp.					X
Camponotus atriceps (*abdominalis*) Smith	X				
Camponotus biolleyi Forel		X	X		
Camponotus blandus Smith	X				
Camponotus cocosensis Wheeler			X	X	X
Camponotus mocsaryi Forel		X			
Camponotus sp.					X
Cyphomyrmex rimosus Spinola	X				
Hypoponera opacior Forel					X
Monomorium floricola Jerdon					X
Nomamyrmex (*Eciton*) *crassicornis* Smith	X				
Odontomachus haematodes L.	X		X		
Odontomachus ruginodis Smith					X
Pachycondyla stigma F.	X		X		X
Paratrechina guatemalensis Forel		X	X		X
Paratrechina longicornis Latreille					X
Pheidole biconstricta Mayr	X				
Pheidole moerens Wheeler					X
Pheidole punctatissima Mayr	X				
Pheidole subarmata Mayr	X				
Pheidole sp. 2					X
Pheidole sp. 3					X
Pseudomyrmex flavicornis (*belti*) Smith	X				
Pyramica nigrescens Wheeler					X
Solenopsis geminata F.	X				X
Solenopsis succinea Emery	X				
Solenopsis sp. (Diplorhoptrum)					X
Strumigenys louisianae Roger					X
Tapinoma melanocephalum F.					X
Tetramorium guineense Bernard		X	X		
Wasmannia auropunctata Roger	X	X	X		X
Zacryptocerus (*Cryptocerus*) *cristatus* Emery	X				
Total number of species collected	17	5	7	1	19

[1]Collections by Anastasio Alfaro described by Forel (1908) and Emery (1919).
*Species list for this expedition is unreliable; see Discussion for details.
[2]Collections by Pablo Biolley described by Forel (1902).
[3]Collections by Francis X. Williams described by Wheeler (1919).
[4]Collections by Maurice Willows, Jr. described by Wheeler (1933).

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Appendix

Miscellaneous Natural History and Taxonomy Notes

Adelomyrmex sp. This species is known only from a single leaflitter sample taken in the cloud forest transect (Transect E) on Cerro Pelón and therefore appears to be extremely rare. J. T. Longino has examined specimens of this morphotype and believes that it may be a new species, suggesting that it is likely a native and possibly an endemic species (J. T. Longino, Evergreen State College, pers. comm.).

Brachymyrmex sp. We found diffuse pockets of brood and workers scattered underneath the bark of a newly fallen tree, suggesting that this species may be arboreal.

Camponotus cocosensis Wheeler. This endemic species occurs in abundance throughout the island, nesting in trees. By examining new treefalls, we twice found single queens establishing nests in holes (which appear to have been made by bark-boring beetles) approximately 10 m up the tree. We once observed an entire nest underneath an epiphytic fern (10-15 m high).

Camponotus sp. 2. We found a single queen in a rotten log. The queen was different than that of *C. cocosensis* and that of *C. biolleyi* (B. MacKay, The University of Texas at El Paso, pers. comm.). We never found workers of this species, suggesting that it is either extremely rare or nocturnal.

Odontomachus ruginodis Smith. This may be the same species that previous expeditions collected, identified as *O. haematodes* L. by Forel (1908) and *O. haematoda insularis* Guérin by Wheeler (1919). *O. haematodes* is currently a valid species name, but *O. ruginodis* was previously known as *O. haematodes insularis* var. *ruginodis* (Wheeler 1905). Although Wheeler (1919) did not include the variety of the material he described from Cocos Island, he mentions (p. 303) that the specimens "agree . . . in all respects with specimens from Georgia, Florida, West Indies, and Central America in my collection."

Pheidole sp. 3. Though minor workers of this species were found in three pitfall traps scattered amongst two sites, it was never found in leaflitter samples or by general collecting. Consequently, it appears possible that this is a nocturnal species.

Wasmannia auropunctata Roger. Forel (1908) adds *W. auropunctata* var. *rugosa* to the list of species from Cocos Island based on the Alfaro collection in 1902. Subsequent authors list this variety (currently recognized as a subspecies) as part of the Cocos ant fauna, but no subsequent collections have included it. We found no morphological differences among the material we collected and therefore have no data to suggest that there is more than one type of *W. auropunctata* currently present on the island. Although this species is native to the Neotropics, its distribution on Cocos Island strongly suggests that it was introduced, despite its presence as early as 1902 (Forel 1902).