# INTERSPECIFIC COMPETITION AND RELATIVE DISTRIBUTION OF THE CO-OCCURRING INVASIVE ANTS *PARATRECHINA LONGICORNIS* AND *SOLENOPSIS GEMINATA* (HYMENOPTERA: FORMICIDAE) ON MO'OREA, FRENCH POLYNESIA

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*Abstract.* The study of biological invasion is important for the preservation of biodiversity and other human interests. Ants (Hymenoptera: Formicidae) are some of the most harmful invasive organisms, and are frequently associated with human activity. On the remote islands of Polynesia, introduced ants form mosaic distribution patterns, supposedly through effects of competition, though this has been debated. The objective of this study is to use a simplified model with only two ant species, *Paratrechina longicornis* and *Solenopsis geminata*, to assess interspecific competition and its effects on relative distribution. I performed a survey of colony distribution and habitat preference, and conducted experiments to test resource partitioning and aggressive behavior. While no notable differences in distribution were observed, *P. longicornis* and *S. geminata* did show significant difference in primary habitat preference. Competition for food resources, as inferred from baiting and removal experiments and aggression assays, was present but rare among these species. Differences in distributions on larger scales may be affected by habitat preferences, or may be the result of stochastic processes. The effects of co-occurring invasive ant species on each other has important implications for ant community dynamics and for management of future biological invasions.

*Key words: competition, distribution,* Hymenoptera, *Moorea, French Polynesia*

## INTRODUCTION

Biological invasions, which may be defined as the relatively rapid spread of non-native organisms into new environments, are one of the most influential forces shaping global change (Vitousek et al. 1997). Purposeful or accidental human introductions pose major threats to global biodiversity, the effects of which are multiple and severe (Lodge 1993, Chapin et al. 2000). Invasive organisms can disrupt native or endemic communities, dramatically alter environments, and lead to reduced ecosystem resilience or complete collapse (Lodge 1993, Meyer and Florence 1996, Green et al. 1999). Invasions by disease vector organisms can have serious implications for public health (Lounibos 2002). Biological invasions also have great economic impact; it is estimated that non-native organisms cost the US $120 billion annually (Lodge et al. 2006). Especially vulnerable to invasion are islands, due to their low biotic resistance and ecological niche availability. Many islands are considered hotspots of global biodiversity, and with increasing traffic to and from these

islands biological invasion is a growing problem.

Among the most harmful groups of invading organisms are ants (Hymenoptera: Formicidae). For example, a recent invasion of the Yellow Crazy Ant, *Anoplolepis gracillipes*, on Christmas Island is leading to the decimation of the island's crab population (Green et al. 1999). Invasive ants disrupt native communities, cause vast economic impact, spread across great distances, and are difficult to control (Porter and Savignano 1990, Gillespie and Reimer 1993, Gotelli and Arnett 2000, Torres et al. 2007). Alien ants are very frequently established by accidental human introduction, and consequently are found in virtually all habitats around the globe, often with multiple ant species co-occurring (Holldobler and Wilson 1990). Tropical ant communities are often distributed in a "mosaic" pattern, with dominant species distributed in non-overlapping patches and subordinate species scattered in between (Room 1971, Lynch et al. 1980, Torres 1984, Morrison 1996a). These mosaics are supposedly established and maintained by deterministic factors such as interspecific

competition.

On the remote islands of Polynesia, ant fauna distribution is a product of relatively recent introductions. In the last century, the number of documented ant species on the island of Mo'orea, French Polynesia has climbed from 13 to 38 distinct species (Wheeler 1908, Biocode 2010), and although some portion of this apparent increase in species richness is probably due to innovation in effective sampling methods rather than actual introductions, more species continue to arrive (Morrison 1996b). These islands are too isolated for ants to arrive by natural colonization events and most species have been introduced within the last 400 years with the arrival of Europeans, or certainly within the last 1000 years with the arrival of ancient Polynesians (Wilson and Taylor 1967a). Ant species on Mo'orea and other tropical islands are distributed in a typical mosaic pattern, (Morrison 1996a). Wilson and Taylor argued that the ant fauna of these islands would attain quasi-equilibrium richness after a certain species richness was attained (1967b). However, it has been shown that many published ant mosaics are not significantly different from null models of distribution, and therefore not attributable to deterministic factors such as competition (Ribas and Schoereder 2002).

The objective of this study is to ask whether competition affects the distributions of ant communities on islands. Specifically, in a simplified model with only two species, is competition present and does it account for differences in distribution? In order to test the hypothesis that *Paratrechina longicornis* and *Solenopsis geminata*, two co-occurring invasive ants on Mo'orea, French Polynesia, compete for habitat and food resources, and that this competition affects the relative distribution of these species, I studied distribution and habitat preference, resource partitioning, and aggression. I predicted that if these species compete for habitat, then they should have similar habitat preferences. Furthermore, if these species compete for food resources, interference should be demonstrable in resource utilization. Additionally, in the case of direct competitive interactions aggressive behavior should be heightened between these species. Finally, the distributions of these species should be different relative to one another.

MATERIALS AND METHODS

*Study site*

Mo'orea is a high oceanic tropical island of the Society Archipelago in the southern Pacific Ocean (17º32' S, 149º 50' W) with total land area 134 km$^2$ and maximum elevation of 1207 m. All fieldwork was conducted from October 4 through November 19, during the hours of 8:00am to 3:00pm, at the Atitia Cultural Outreach Center, part of the Richard B. Gump Research Station, located on the northwest side of Cook's Bay. The Atitia center, which opened in 2009, is a recently disturbed habitat. In such recently disturbed habitats multiple co-occurring ant species will spread into and colonize the habitat simultaneously, forming a distribution pattern free of temporal confounding factors. This provides a miniature model of co-occurring invasion between ant species..

*Study organisms*

Two ant species were selected for this study. *Paratrechina longicornis* (Latreille) also known as the longhorn crazy ant is of Southeast Asian origin (Wetterer 2008). *P. longicornis* is one of the most widespread ants in the world, and thrives in disturbed or artificial habitats (Wetterer 2008). *Solenopsis geminata* (Fabricius) is a fire ant from North America (Trager 1991). It is found on most continents, and is well studied as both a pest and as an agent of biological control (Wetterer 2006, Way and Heong 2009). *S. geminata* is also associated with disturbed habitats, and is an aggressive species that is capable of displacing other ants (Risch and Carroll 1982). Both species were identified using the Pacific Invasive Ant online key.

*Distribution and habitat preference*

A survey of ant colonies was performed to assess micro-scale distribution and habitat preferences of *P. longicornis* and *S. geminata*. Colonies were found by manual searching, specifically disturbing patches of loose dirt, turning over leaf litter, rocks and logs, and following trails of foraging workers. Individuals were collected for identification from each colony found in this manner. Locations of colonies were marked by GPS using a Garmin GPSMAP-60CSX.

Obtained GPS coordinates were uploaded using DNR Garmin software, and ArcGIS software was used to create a distribution map. To assess differences in habitat preference the substrate of each colony, i.e. dirt rocks, hollow logs, sand, etc., was recorded. Differences in primary habitat preferences were analyzed using a Chi-square analysis.

### Resource partitioning

Food resources are important sites of competition. To assess resource partitioning, artificial tuna baits were placed in between colonies of *P. longicornis* and *S. geminata*. A total of 10 baiting trials were performed, at 10 sites where colonies of *P. longicornis* and *S. geminata* were separated by less than 3 m and both colonies had unobstructed access to baits. Approximately 100 g of tuna bait was placed in a Petri dish at time t=0. At 10-minute intervals for one hour, individuals from each species present at the bait were counted. Only individuals inside the dish, with access to the resource, were counted. After the prescribed hour, a removal experiment was conducted. All individuals of the species most abundant at the bait were removed by aspiration, and counts were recorded for the remaining species at 10-minute intervals for an additional 30 minutes. Baits were replenished as necessary.

### Aggression

Aggressive behavior was evaluated by on site arena experiments. During baiting experiments, 5-7 individuals from each colony were placed together in a Petri dish for 5 minutes. An aggressive encounter was recorded if more than one aggressive act such as biting, stinging, or extended chasing was observed during the 5-minute period. As a control, conspecific interaction was observed in the same manner using individuals from spatially separated colonies of each species. As a further control, colony mates were left alone in the dish for 5 minutes and observed for aggressive behavior. Ten replicates of each interaction were observed.

### Distribution and habitat preference

A total of 50 colonies, 32 for *P. longicornis* and 18 for *S. geminata*, were found. No notable difference in the distribution of these species was found (Fig 1). However, *P. longicornis* and *S. geminata* do show significant difference in choice of primary habitat type (Fig 2). 80.4% of all ant colonies are found in two primary habitat types: rock and dirt. The rock habitat type is characterized by the spaces between and underneath loose rocks, and the dirt habitat by subterranean excavations of soft, loose dirt. 81% of *P. longicornis* colonies were found in the rock habitat type, while 83% of *S. geminata* colonies were found in the dirt habitat type. The difference in occurrence frequency between *P. longicornis* and *S. geminata* within these two primary habitat types was shown to be significant by Chi-square analysis ($\chi^2 = 29.9$, $p < 0.0005$, df = 2).



FIG 1. Colony distribution map for *P. longicornis* (black) and *S. geminata* (red) at Atitia Center. No notable difference in distribution was observed. Basemap from GoogleEarth, photo by GeoEye.

### Resource partitioning

Artificially introduced resources tended to be exploited exclusively by either *P. longicornis* or *S. geminata* for the duration of the trial. Both species are capable of recruiting strongly, in excess of 100
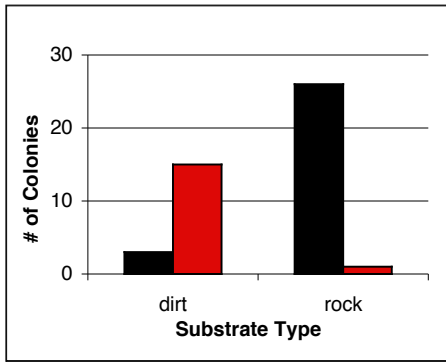
FIG 2. Primary Habitat Preferences of *P. longicornis* (black) and *S. geminata* (red). Occurrence of colonies in two primary habitat types, loose dirt and loose rock, was significant. ($\chi^2 = 29.9$, p < 0.0005, df = 2)

individuals, to nearby baits. However, *P. longicornis* and *S. geminata* were found to be present at the same bait during only 10% of trials. The remaining 90% of baits were exploited exclusively by either *P. longicornis* (50%) or by *S. geminata* (40%). In the case that both species exploited the same bait, the abundance of the first species to arrive, *S. geminata*, decreased after the arrival of the second species, *P. longicornis* (Fig 3).

Removal experiments resulted in a change in the abundance of the other species only in the case that both species were present at the bait before removal. In this case, removal of the more abundant ant species, *P. longicornis*, resulted in an increase in the abundance of *S. geminata* to the level observed before arrival of *P. longicornis* (Fig 3). At baits exploited exclusively by one species (90%), removal most often resulted in no change in abundance of the other
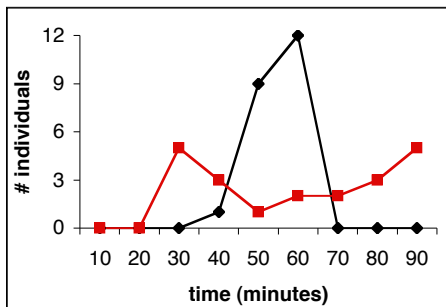


FIG 3. Numerical abundance of *P. longicornis* (black) and *S. geminata* (red) at an artificial tuna bait. Graph depicts one trial. Removal occurred after t=60.

species. Removal of the exploiting ant species at exclusive baits increased the

abundance of the other species in only one instance, and only at a single time point.

*Aggression*

Aggressive behavior was more common between *P. longicornis* and *S. geminata* than between conspecific colonies (Fig 4). For example, 80% of interactions between *P. longicornis* and *S. geminata* resulted in aggressive behavior, while only 40% of interactions between *S. geminata* conspecifics resulted in aggression. No aggressive behavior was observed between *P. longicornis* conspecifics, or among colony mates of *P. longicornis* or *S. geminata* alone.
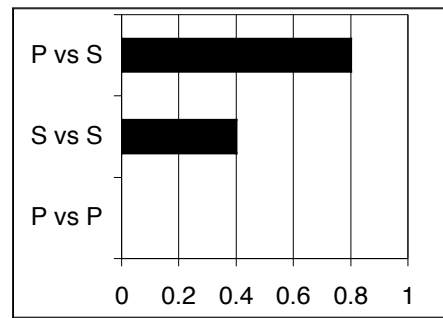


FIG 4. Frequency of aggressive encounters between colonies of *P. longicornis* and *S. geminata*. Heightened aggression in interspecific interaction compared to conspecific.

DISCUSSION

The principle findings of this study are 1) *Paratrechina longicornis* and *Solenopsis geminata* do not compete heavily for habitat or food resources, and 2) interspecific competition does not affect the relative distributions of these species. *P. longicornis* and *S. geminata* show some evidence of competition for food resources, and show increased aggression towards each other as a probable mechanism for direct displacement from resources. However, this competition is rare. In addition, *P. longicornis* and *S. geminata* do not compete over habitat resources as they have different primary habitat preferences. Therefore, I reject the first part of my hypothesis: These species do not compete for habitat and food resources. Though it has not been demonstrated here, the broader literature would certainly suggest that some level of competition would exist between ant species (Holldobler and Wilson 1990). In the

absence of demonstrable competition, and with no notable differences in distribution on a small scale, I also reject the second part of my hypothesis: Interspecific competition does not affect the relative distribution of these species.

Habitat preference appears to be the only factor that would influence distribution on a larger scale. For example, one might find higher densities of one species over another in regions with higher density of preferred habitat. To this author's knowledge, this has not been investigated. Most habitat surveys on Mo'orea have dealt with disturbed vs. undisturbed habitats, and not with microhabitat or substrate type (Morrison 1996a). The possibility that either of these species actually prefers living in either primary habitat type, but is simply excluded from one type by the other species is unlikely, as those colonies which were classified as being in the primary habitat of the other species were often located in a hybrid habitat type which was difficult to classify. These hybrid habitats may be places of competition as well, and would be an interesting avenue of further research, but they are uncommon and there exists an abundance of other, more clearly classifiable habitat.

*P. longicornis* and *S. geminata* show no notable differences in distribution, which is attributed to lack of competitive interaction. The slight differences and specific pattern of distribution is therefore likely the product of stochastic processes. This is in keeping with the arguments of Ribas and Schoereder (2002). Wilson and Taylor argued that competition would limit the number of species of ants present on an island (1967b). Although the results of this study would certainly suggest that competition is not responsible for affecting distributions, the scale of this study is too small to refute the claims Wilson and Taylor. However, their arguments have been addressed elsewhere in detail (Morrison 1997).

The lack of competition for food resources was not expected. The literature would suggest that between such ecologically similar species, some level of competition for food resources would exist (Holldobler and Wilson 1990). Perhaps the foraging strategies of these species are different enough to make interaction at artificially placed resources on a short timescale nearly undetectable. The use and partitioning of natural resources would be another productive avenue of further research. In a broader context, if *P. longicornis* and *S. geminata* do not compete heavily for resources with each other, it would be interesting to expand this study to include other co-occurring species pairs or community subsets.

Understanding the interactions between individual species is important to understanding the interactions of the entire community. This has implications not only for the study of ant community structure, but also for invasion management. The effects of different species on the success of others is important when considering a management plan for future introductions.

## CONCLUSIONS

The results of this study show that *Paratrechina longicornis* and *Solenopsis geminata* do not compete heavily for food or habitat resources, and that this low level of competitive interaction has no notable effect on their relative distribution on a local scale. On a larger scale, differences in distribution may be attributable to habitat preference or stochastic processes. The study of ant species interaction has important implications for both ant community research and for biological invasion management.

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