Out of place: a study of the mangrove crab *Cardisoma carnifex* on Mo'orea, French Polynesia

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Background. Invasive plant species pose a significant threat to island biodiversity and ecosystems. Invasive mangrove trees in particular have been shown to be devastating to the shorelines of islands across the Pacific. Previous studies have assumed that the mangrove crab, *Cardisoma carnifex*, plays a significant role in controlling *Rhizophora stylosa* mangrove populations on Mo'orea, French Polynesia. Found across East Africa, Indonesia, and the Pacific, *C. carnifex's* behavior can change drastically depending on the environment it's found in.

Methods. From October-November 2016, a field study was conducted on Mo'orea to assess *C. carnifex* habitat and food preferences. A series of 30 meter transects were done to determine the population density of crabs in mangrove and non-mangrove sites. In addition, a set of food preference experiments were run to determine if *C. carnifex* preferred to eat *R. stylosa* leaves, propagules, *Hibiscus tiliaceus* leaves, flowers, and *Paspalum vaginatum* marsh grass.

Results. *Cardisoma carnifex* was found to be more prevalent in mangrove sites although the results were not statistically significant. There were no food preferences found regardless of habitat and the flow of food through both habitats was the same.

Discussion. Results do not give a clear indication of *C. carnifex's* ability to impact *R. stylosa* populations. However, results do demonstrate *C. carnifex's* opportunistic nature, suggesting that they are extremely adaptable and do not rely on one habitat or food source for survival. *Cardisoma carnifex's* role in its habitat is still poorly understood and needs to be studied in more detail in the future.

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Abstract

Background. Invasive plant species pose a significant threat to island biodiversity and ecosystems. Invasive mangrove trees in particular have been shown to be devastating to the shorelines of islands across the Pacific. Previous studies have assumed that the mangrove crab, *Cardisoma carnifex*, plays a significant role in controlling *Rhizophora stylosa* mangrove populations on Mo'orea, French Polynesia. Found across East Africa, Indonesia, and the Pacific, *C. carnifex's* behavior can change drastically depending on the environment it's found in. **Methods.** From October-November 2016, a field study was conducted on Mo'orea to assess *C. carnifex* habitat and food preferences. A series of 30 meter transects were done to determine the population density of crabs in mangrove and non-mangrove sites. In addition, a set of food preference experiments were run to determine if *C. carnifex* preferred to eat *R. stylosa* leaves, propagules, *Hibiscus tiliaceus* leaves, flowers, and *Paspalum vaginatum* marsh grass. **Results.** *Cardisoma carnifex* was found to be more prevalent in mangrove sites although the results were not statistically significant. There were no food preferences found regardless of habitat and the flow of food through both habitats was the same. **Discussion.** Results do not give a clear indication of *C. carnifex's* ability to impact *R. stylosa* populations. However, results do demonstrate *C. carnifex's* opportunistic nature, suggesting that they are extremely adaptable and do not rely on one habitat or food source for survival. *Cardisoma carnifex's* role in its habitat is still poorly understood and needs to be studied in more detail in the future.

Introduction

Invasive alien species are considered the second most significant threat, after habitat loss, to biodiversity (International Union for the Conservation of Nature, 2016). Invasive species are defined by the Convention on Biological Diversity as "*a species that is established outside of its natural past or present distribution, whose introduction and/or spread threaten biological diversity.*" Invasive species pose a unique threat to island habitats, since island natives tend to be poor competitors and lack natural defenses, making them particularly susceptible to invaders from the mainland (Loope & Mueller-Dombois, 1989). Despite their rapid spread and their ecological impact, invasive plants have been studied less than invasive animals. As a result, plant invasions are poorly understood. Attempts at control and eradication of invasive plants have been less successful than efforts with invasive animals (Meyer, 2014).

Mangrove trees are an example of an invasive species that has been introduced on multiple Pacific islands. Purposely introduced, these trees have caused serious damage to the environments they establish in (Demopoulos & Smith, 2010). On Hawaii, the red mangrove *Rhizophora mangle* is an invasive species that has significantly altered ecosystems on the coastlines, despite being an important key species in threatened habitats around the globe. A 2010 study found that *R. mangle* was responsible for increasing hard substrata, higher porewater salinity, and reducing light levels and water flow (Demopoulos & Smith, 2010). Mangrove trees' extensive root systems trap fine and organic rich sediments increasing the sedimentation of the shoreline. It is thought that because these mangrove trees are substantially ecologically underutilized that they have the potential to offer footholds to invading animal species (Demopoulos & Smith, 2010).

The stilted mangrove, *Rhizophora stylosa,* was purposely introduced to Mo'orea, French Polynesia in 1930 to aid oyster cultivation (Grenier, 1994). By 1987, *R. stylosa* had established itself on more than a fourth of the coastline. Since then these trees have caused numerous problems, including increasing mosquito abundance, replacing salt marsh grass habitats, altering the diversity and abundance of intertidal gastropods, and accumulating sediments (Acutt, 1995; Gershman, 1997; Hestir, 2004). Accumulated sediments can lead to increased densities of deposit-feeding animals, while the resulting reduced water flow depresses the feeding rates and densities of suspension feeders (Demopoulos & Smith, 2010). Those negative traits led to a removal of mangrove stands. Today mangroves are mostly clustered in a few places on the northern and western sides of the island, areas cultivated by fishermen because of the habitat they create for fish.

This study focuses on the terrestrial burrowing land crab *Cardisoma carnifex*. *Cardisoma carnifex* is widespread across coastlines from East Africa to the Indo-West Pacific islands (Hartnoll, 1988). Known as tupa by Tahitians in French Polynesia, *C. carnifex* has lived on Mo'orea long before *R. stylosa* was introduced in the 1930's. However, in other parts of the world *C.* carnifex is known as a mangrove crab (Micheli, Gherardi, & Vannini, 1991). In Kenya, for instance, they live in mangrove forests and eat a significant amount of mangrove leaves and propagules and have the ability to influence forest tree species composition (Micheli et al., 1991). On Mo'orea, however, *C. carnifex* lives in both mangrove forests and shoreline habitats free of mangroves. This was a unique opportunity to look at an invasive species' interactions with a native species where the two coexist elsewhere in the world.

Cardisoma carnifex has played an important role in controlling plant numbers through seed predation on other islands such as Aldabra (Lee, 1988). One study looking at *R. stylosa* stand distribution around Mo'orea suggested that seedling consumption by *C. carnifex* played a definitive role in limiting and reducing the distribution of mangroves around the island (Kramer, 1992). However, the author of this study never directly observed *C. carnifex* eating *R. stylosa* seedlings. After observing unexplained herbivory on *R. stylosa* propagules, the author attributed it to *C. carnifex* by simply citing studies from other regions of the world. On Tabuaran Island, *C. carnifex* preferred to eat *Pandanus tectorius* in addition to a diet of leaves and other fruits which is very different from the behavior shown in Kenya (Lee, 1988). This is problematic because multiple studies done on *C. carnifex* feeding preferences suggest that it varies wildly depending on where the study was carried out. This indicates that *C. carnifex* behavior and food preferences exhibit high plasticity and cannot be predicted in new locations based on previous studies from elsewhere. There have been no studies on *C. carnifex* diet preferences on Mo'orea.

The goal of this field study is to determine the diet and habitat preferences of *C. carnifex* on Mo'orea, French Polynesia. *Cardisoma carnifex* scavenges a range of organic material but is generally herbivorous and known to eat *Hibiscus tiliaceus* and *Paspalum vaginatum* (Cheng, 2000; Woo, 1996). Both species are common in the sandflat habitats that *C. carnifex* inhabits and are the most likely alternative food choices the crabs have to *R. stylosa.* This study characterizes (1) the prevalence of *C. carnifex* populations in mangrove versus non-mangrove habitats, (2) *C. carnifex* diet preferences when offered *R. stylosa* leaves and propagules, *H. tiliaceus* leaves and flowers, and *P. vaginatum* salt marsh grass, (3) any differences in diet preference between habitats, and (4) the flow of food in both habitats.

Materials & Methods

Study sites

The study was conducted on Mo'orea, French Polynesia. Four sites were chosen to conduct food preference trials with *C. carnifex*, two with mangroves and two without mangroves. Four sites in addition to the four food preference sites were surveyed for *C. carnifex* population density (Fig. 1). These sites were along the northern and western sides of the island. Mangrove sites were chosen for stands of mangroves that were established in the water, not above the water line as occurs in some areas. Non-mangrove sites were chosen simply for the presence of *C. carnifex* and lack of mangroves. Non-mangrove sites were all open beaches.

Population density sampling

At each of the eight study locations, a 30m transect was completed during which a 1 x 1m quadrat was placed and its contents analyzed every 2m. Thus, 10 quadrats would be analyzed in total for each transect. The distance of the transect was determined by a transect tape and the direction was always parallel to the shore. The number of burrows within each quadrat were counted and used as a one to one proxy for the number of crabs. *C. carnifex* is very territorial, individuals occupy and defend separate burrows and often adjacent areas (Cheng, 2000). Therefore it is unlikely that using this method will result in double counting of crabs.

Food preference study

The diet preferences of different populations of crabs in mangrove sites versus non-mangrove sites were examined. To do this, *R. stylosa* leaves and propagules as well as *P. vaginatum* were collected at mangrove sites in order to run comparison food preference tests at treatment and control sites. Each day that a food preference test was run, freshly fallen *H. tiliaceus* flowers were collected and *H. tiliaceus* leaves were picked off the tree. The leaves were green and had minimal damage prior to use. After sundown when crabs are most active, 10 1 x 1m quadrats were placed around the site at least one meter apart and with roughly the same number of crab burrows in each. While crabs do leave their burrow in search of food, it is unusual for them to venture far if they are able to find food in the near vicinity of their burrow (Lee, 1988). Therefore risk of cross contamination where crabs visit other quadrats is low. Each quadrat had a unique combination of food pairings, four items of each food (Table 1). The preference experiment was left to run for an hour, at which point the number of plant pieces eaten in each quadrat was recorded. This experiment was run a minimum of three times at each site.

Statistical analysis

All statistical tests and graphs were made in the program RStudio (RStudio Team, 2015). Because population density data was not normally distributed, a Wilcoxon Rank Sum Test was used to compare the differences in the mean population density between mangrove sites and non-mangrove sites. A chi-squared test of independence was used to test each of the food preference combinations to see if there were differences in preference for a particular combination within mangrove sites and non-mangrove sites. Then the same test was run again to see if there was a difference in the total volume of a particular food consumed between habitats. The observations of choices were all independent and continuous. The data was normalized by population density and then compared by another Wilcoxon Rank Sum Test to compare the mean amount of food a single mangrove crab would consume versus a single non-mangrove crab.

Results

Population density study

A total of 286 *C. carnifex* individuals were counted in the field survey. Although crab populations were higher in mangrove sites (5 crabs/m^2) than in non-mangrove sites (2.15 crabs/m^2) these values were not statistically different (Fig. 2, Wilcox rank sum test, $P > 0.05$).

Food preference study

Regardless of habitat or food combination, *C. carnifex* showed no preference for any type of food when they were directly compared against each other (Chi-squared test of independence, $P > 0.05$). However, when comparing the total amounts of food consumed for each food type, *C. carnifex* populations in mangroves did consume much higher numbers of *H. tiliaceus* flowers than non-mangrove populations (Fig. 3, Chi-squared test of independence, $P < 0.05$). But when normalized by population density, the mean amount of food consumed by mangrove crabs was the same as non-mangrove crabs for all food types (Wilcox Rank Sum Test, $P > 0.05$).

Discussion

The results of the population density transects suggest that there may be a difference between mangrove and non-mangrove sites, although they were not statistically significant (*P-value*=0.057). Sampling a larger number of sites might have been able to demonstrate that *C. carnifex* populations are indeed higher in mangrove sites. However, due to a small number of accessible mangrove forests around Mo'orea, it was impossible to gather more transects. In spite of this, the results illustrate that *C. carnifex* is able to live in non-mangrove habitats successfully, but still thrives better in mangrove forests.

Cardisoma carnifex did not exhibit a preference for any type of food. This was true for both habitats. *Cardisoma carnifex* was observed taking *H. tiliaceus* leaves and flowers first, but the study did not have a time dimension of what food was chosen first. This evidence suggests that *C. carnifex* are opportunists. They are extremely adaptable, eating whatever food is available to them regardless of the habitat they are used to living in. Despite being herbivores, there was even an instance where a crab grabbed an unfortunate gecko and dragged it into its burrow.

The flow of food going through ecosystems did not differ between mangrove and non-mangrove habitats. A mangrove crab ate the same amounts as a crab in a non-mangrove site despite the increased availability of food and protective cover. This behavior may be an example of one attribute that is consistent across habitats for *C. carnifex.*

It is possible that the reason why *C. carnifex* thrives better in mangrove forests is due to the increased sedimentation and protective cover that the trees offer. A future study may want to look into whether or not the defining factor for good *C. carnifex* habitat is canopy cover itself, regardless of the type of plant. *Hibiscus tiliaceus* trees have a dense root structure similar to *R. stylosa,* and *C. carnifex* populations seemed to be thriving in dense *H. tiliaceus* areas. The non-mangrove sites in this study were almost entirely open beach areas with little cover. Further investigation should look at mangrove forests versus hibiscus forests and open beaches.

Although previous studies thought that *C. carnifex* played a role in limiting and reducing *R. stylosa* population numbers, it is unclear how much of an impact it actually has. While *C. carnifex* does consume *R. stylosa* propagules, it is just as likely to eat something else nearby. Even in dense *R. stylosa* mangrove stands, it was never the only plant in the area and *C. carnifex* was observed eating the range of food available. A future study wanting to quantify the impact of *C. carnifex* should directly study their herbivory of *R. stylosa* seedlings and seedling survival rates.

Cardisoma carnifex's role in its habitat is still not well understood. In various places like Tanzania and Polynesia, researchers have demonstrated that *C. carnifex* burrows serve as a breeding ground for mosquitos and a vector for disease (Irish & Kirby, 2013; Riviere et al., 1998). Some have suggested that the solution is to control or completely remove *C. carnifex* populations. Without fully understanding how *C. carnifex* interacts within the sandflat habitat food web, such actions could prove disastrous. Species diversity on small islands is especially vulnerable to disruption due to the lack of opportunities for species to shift their ranges (Ferreira et al., 2016; Harter et al., 2015). Island species are already at high risk of extinction as a result of the predicted effects of climate change: higher temperatures, altered rainfall patterns and sea level rise (Averett, 2016). But combined with the consequences of human intervention, *C. carnifex* and other sandflat habitat species could be at risk.

However, the overwhelming evidence indicates that *C. carnifex* will be able to survive drastic changes resulting from climate change. They scavenge whatever organic material they can, their survival is not tied to any one food source. Previous studies have also found that *C. carnifex* burrows are extremely resistant to disturbance. They can rebuild and recover their burrow entrances within a week even in the face of intensive blockage, resisting low-level surface development by humans (Hurley, 2012). This opportunistic adaptable nature will help them survive and thrive major disturbances.

It is interesting to note that, while this paper treated *R. stylosa* as an invasive species, some local Tahitian people do not view them as such. While many mangroves have been removed from Mo'orean shorelines, in some places they are purposely planted and cultivated for the nursery habitat they create for marine creatures and *C. carnifex*. *Cardisoma carnifex* in turn, is considered a pest by some because of how it invades and eats plants in backyard gardens. Future studies should take these viewpoints into account and work with local peoples to understand the best ways to aid their livelihoods and preserve the ecosystem.

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Figure 1

Site Map

Study sites around Mo’orea. Triangles indicate non-mangrove sites; stars indicate mangrove sites. Red markers indicate sites used in food preference and population density studies; blue markers were sites only used for population density transects.

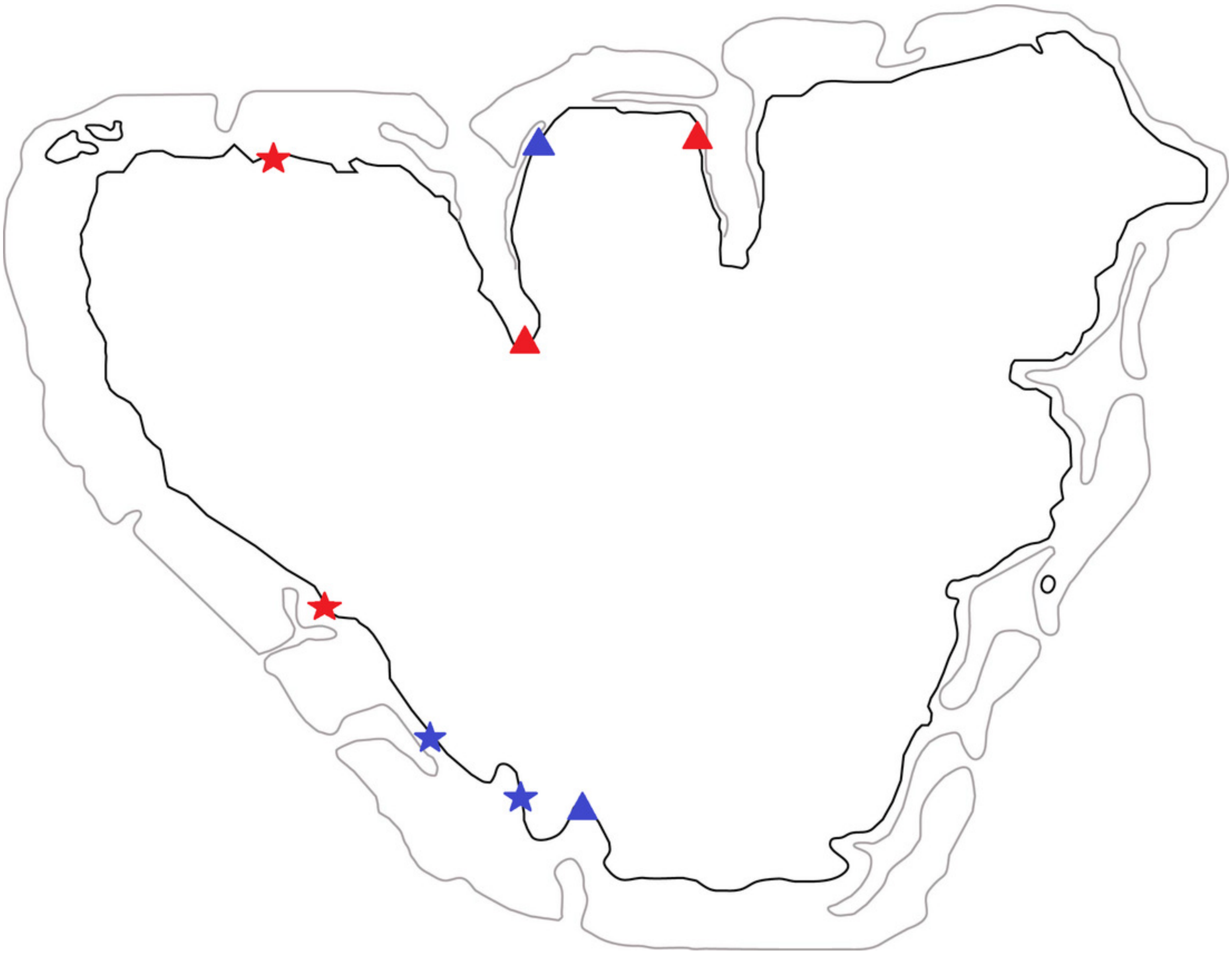

Figure 2(on next page)

Population density by habitat

Population density by habitat. Mean for non-mangrove sites = 2.15 crabs/m^2 (n=4) Mean for mangrove sites = 5 crabs/m^2 (n=4). Results not statistically significant (Wilcoxon rank sum test, *P-value* > 0.05).

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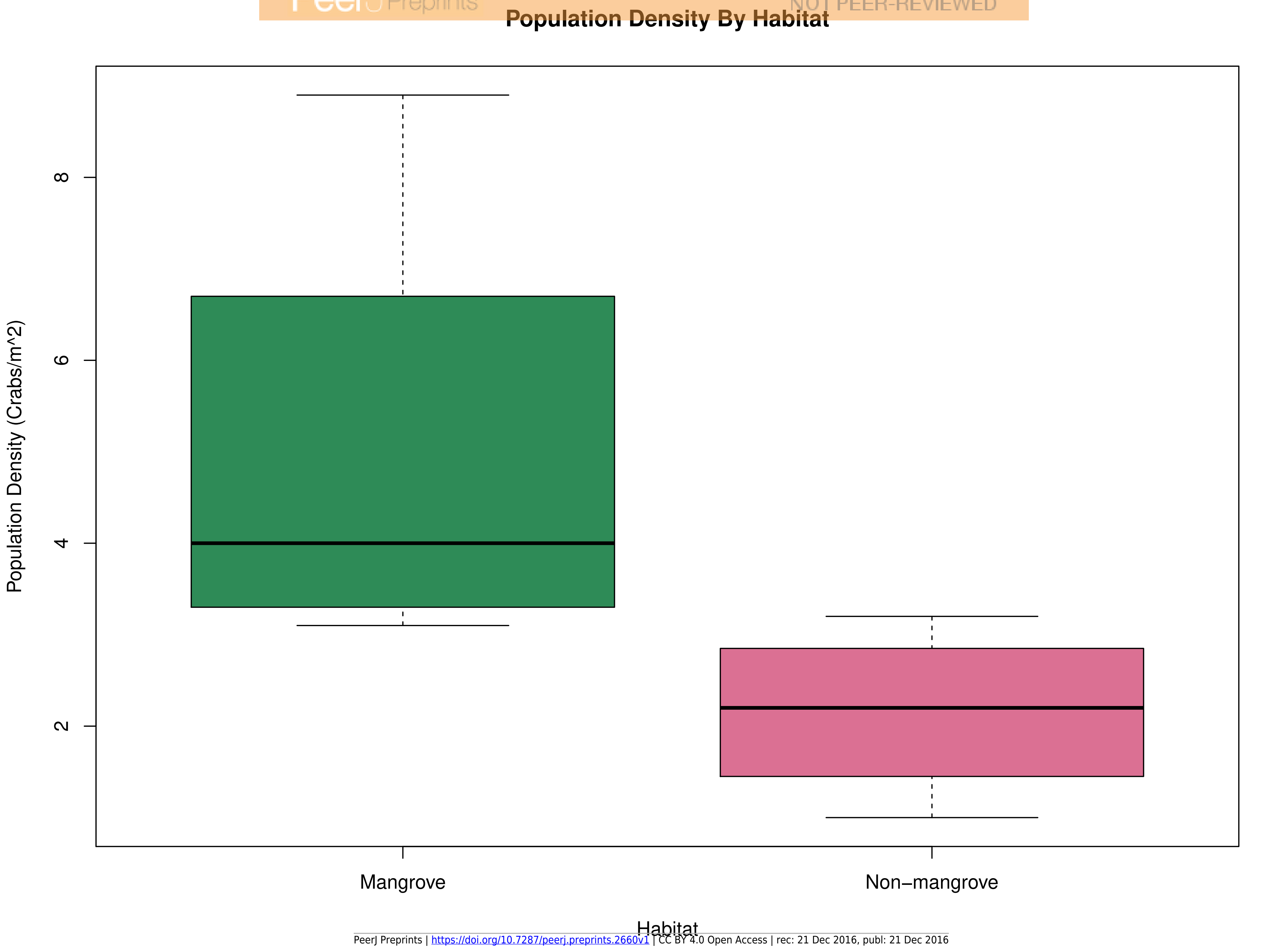
Population Density By Habitat
Population Density (Crabs/m^2)
2
4
6
8
Mangrove
Non−mangrove
Habitat

Figure 3(on next page)

Hibiscus Flower Habitat Food Preference

H. tiliaceus flowers eaten in mangrove (n=2) versus non-mangrove (n=2) habitats (Chi-squared test of independence, *P-value* < 0.05).

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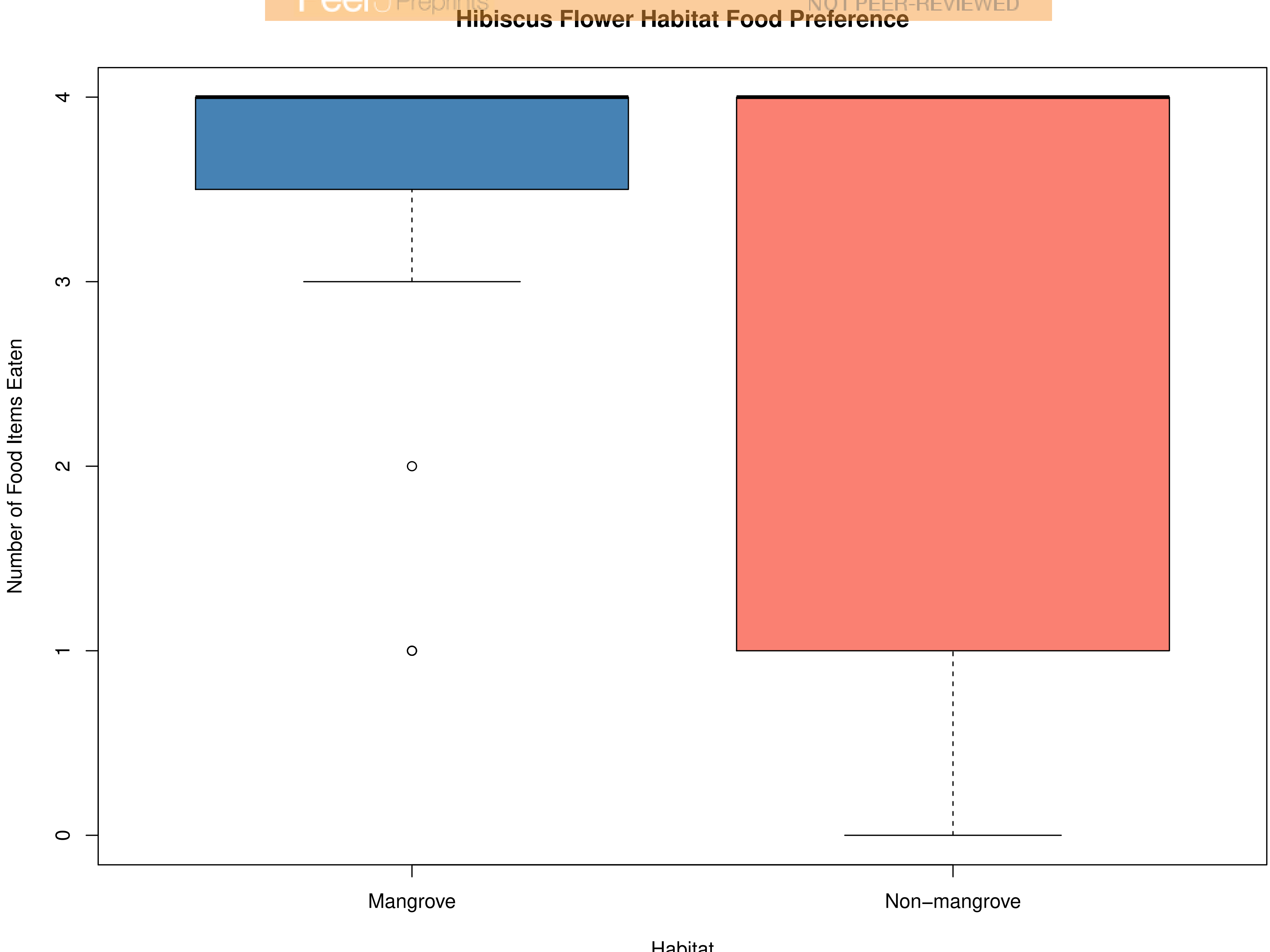
Hibiscus Flower Habitat Food Preference
Number of Food Items Eaten
0
1
2
3
4
Mangrove
Non−mangrove
Habitat

Table 1 (on next page)

Food Pairings by Quadrat

Specific food couplings used in quadrat for a food preference study of *C. carnifex*.

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Quadrat	Food Pairing
1	*R. stylosa* leaves/ *R. stylosa* propagules
2	*H. tiliaceus* leaves/*H. tiliaceus* flowers
3	*R. stylosa* leaves/*H. tiliaceus* leaves
4	*R. stylosa* leaves/*H. tiliaceus* flowers
5	*R. stylosa* propagules/*H. tiliaceus* leaves
6	*R. stylosa* propagules/*H. tiliaceus* flowers
7	*R. stylosa* leaves/*P. vaginatum*
8	*R. stylosa* propagules/*P. vaginatum*
9	*H. tiliaceus* leaves/*P. vaginatum*
10	*H. tiliaceus* flowers/*P. vaginatum*

Table 1. Specific food couplings used in quadrat for a food preference study of *C. carnifex*.