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EFFECTS OF INTRODUCED GREEN IGUANAS (*IGUANA IGUANA*) ON TROPICAL PLANT COMMUNITIES THROUGH SEED DISPERSAL AND GERMINATION

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ON TROPICAL PLANT COMMUNITIES THROUGH SEED DISPERSAL

AND GERMINATION

BY

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ABSTRACT

Despite the importance of dispersal and germination for plant life cycles and population dynamics, the effects of reptiles are often overlooked because herbivory is relatively rare in reptiles. Green Iguanas (*Iguana iguana*) enhance seed germination in some plant species in xeric habitats in its native range, but no studies have been conducted on introduced populations, such as in Puerto Rico. Because Green Iguanas can be abundant where they have been introduced, they have the potential to affect plant communities by dispersing and germinating seeds. In summer 2013, a total of 258 Green Iguana scat samples were collected in the Humacao Natural Reserve in southeastern Puerto Rico. An additional 53 scat samples were collected from captive Green Iguanas fed non-native *C. papaya*. To determine the percentage of seeds that germinated and the number of days to germination, seeds were extracted from scat and collected from fruit, and then planted under common garden conditions using four experimental treatments: 1) Digested seeds planted with feces, 2) Digested seeds planted without feces, 3) Undigested seeds planted with fruit, and 4) Undigested seeds planted without fruit. Four main species were identified from seeds in wild Green Iguana scat: native *Anona glabra, Ficus* sp., non-native *Peltophorum pterocarpum,* and *Pterocarpus sp.* Since multiple species in the genus *Ficus* and *Pterocarpus* were present at our study site and produce similar seeds, we could not identify seeds from these genera to the species level. Nonetheless, these seeds are either native *Ficus citrifolia* or non-native *Ficus benjamina*, and either native *Pterocarpus officinalis* or non-native *Pterocarpus indica* because these are the only species present at our study site. Seeds that passed through Green Iguanas exhibited reduced germination

percentage in non-native *P. pterocarpum*, *Pterocarpus* sp., and non-native *C. papaya* seeds. In contrast to previous studies conducted in native habitats, Green Iguanas did not increase the germination percentage of any species in Puerto Rico, where Green Iguanas have been introduced. Passage through Green Iguanas reduced the days to germination of *Ficus* sp., non-native *P. pterocarpum,* and *Pterocarpus* sp., and increased the days to germination of non-native *C. papaya*. These results suggest the effect of Green Iguanas outside of their native range on germination percentage and days to germination depends on the species. Germination percentage and days to germination were both reduced for the dry seeds of *P. pterocarpum* and *Pterocarpus* sp. after passing through the Green Iguana gut. To assess seed dispersal potential by Green Iguanas, we collected GPS coordinates for scat samples and surrounding mature trees of the four main seed species found in scat samples (i.e., native *Anona glabra*, *Ficus* sp., non-native *Peltophorum pterocarpum,* and *Pterocarpus* sp.). Using these coordinates, we calculated the minimum distance between scat containing a specific seed species and the nearest tree of that species. Green Iguanas dispersed seeds throughout the habitats they used, but no trend or patterns was detected in dispersal of native and non-native plants, seed dispersal strategies, or types of seeds dispersed. Although minimum dispersal distances were relatively short for some species, mean distances were large enough for seeds of all species to be transported beyond the canopy of parent trees. Green Iguanas do not have consistent effects on seed germination among different plant species in introduced habitats, but because Green Iguanas have long retention time, defecate seeds that are relatively intact, and can move to dense forest and areas upstream where air and water seed dispersion cannot reach (e.g., *A. glabra*, *P. pterocarpum* and *Pterocarpus* sp.*),* Green Iguanas may be important seed dispersers in mesic habitats where they have been introduced. Further evaluation of Green Iguana effects on germination and dispersal are needed to determine how this species might influence specific species in plant communities outside of their native range.

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PREFACE

This thesis is being submitted in manuscript format. There is one chapter of this thesis. The title of the manuscript is, "Effect of introduced Green Iguanas (*Iguana iguana*) on tropical plant communities through seed dispersal and germination". This manuscript will be submitted to *Biological Invasions*.

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MANUSCRIPT

Effect of introduced Green Iguanas (*Iguana iguana*) on tropical plant communities through seed dispersal and germination

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INTRODUCTION

Mangrove forests cover eight percent of the world coastlines (Lugo *et al.* 1999). They are important ecologically as they build terrain, prevent erosion, protect against common tidal and cyclonic events, filter pollution, export organic matter to surrounding aquatic ecosystems, and are biodiversity hotspots (Lugo *et al*. 1999). Mangrove forest restoration and maintenance depends on seedling recruitment. Similarly, seedling recruitment depends on seed dispersal and germination. Birds and mammals are known to aid in dispersal and germination of many plants, reptiles have been overlooked in studies of this phenomenon, likely because only 34 species of reptiles are known to consume reproductive parts of plants (Abrahansom 1989; Olensen and Valido 2003; Godinez-Alvarez 2004).

The Green Iguana (*Iguana iguana*) was introduced to Puerto Rico, Florida, and the Lesser Antilles as a result of the exotic pet trade (Rivero 1998). The Green Iguanas' native range extends from Mexico to mid-South America (Rand 1989). This species is listed in the Convention on International Trade in Endangered Species II in its native range; however, due to the absence of natural predators and competitors it has become widespread and abundant in its introduced range (Lara-Lopez and Gonzalez-Romero 2002; Lopez-Torres *et al*. 2011). Green Iguanas are associated with agricultural loss, salmonellosis infection, commercial and residential landscape damage, and because they bask on runways, Green Iguanas have been categorized as a threat to aviation on par with ducks, pelicans, and eagles (Engeman *et al*. 2005; Lopez-Torres *et al*. 2011). Some studies have estimated that Green Iguana abundance in introduced habitats can be threefold higher than in its native range (Lopez *et al.* 2012). Furthermore, the most heavily occupy habitats are mature mangrove forests, where Green Iguanas have opportunities to feed and bask in the absence of significant predation risk (Lopez-Torres *et al*. 2012). The introduction of this large herbivore might affect the diversity and abundance of native and non-native plant species, causing changes in community composition and ecosystem function, including the capacity for plant communities to stabilize after ecological perturbation.

Some descriptive studies have characterized the distribution and reproduction patterns of Green Iguanas in Puerto Rico (Lopez-Torres *et al.* 2012), but no study has evaluated the effects of Green Iguanas on native communities and ecosystems, thus quantifying the ecological impacts of this introduced species. Green Iguanas are one of the few lizard species that feed strictly on vegetation, specifically leaves, flowers, and fruits (Rand 1978, Iverson 1982, Troyer 1984, White 1985, van Marken 1992). They have low metabolic rates and high gut passage times compared to mammals and birds (van Marken 1992). Retention of microbes and nematodes in the intestinal tract allows Green Iguanas to degrade plant cell walls, achieving a digestibility as high as 54% of biomass consumed (Bjorndal 1979, Iverson 1980, Troyer 1984). Reptiles are also known to swallow large portions of food whole instead of chewing food items into small pieces (Bjorndal *et al.* 1990). This characteristic allows reptiles to process seeds without destroying them by chewing. Consumption of fruits, relatively long passage times, microbial activity in the intestinal tract, and the ability to swallow food whole or in large portions are characteristic of successful seed dispersers (Schupp 1993), suggesting that Green Iguanas may be performing this ecosystem function.

Seed dispersal and germination facilitation by Green Iguanas has been studied in the species' native range (van Marken 1992, Morales-Malvin 1997, Benitez-Malvido 2003), but not in its introduced range. Native-range studies may not be representative of Green Iguanas in Puerto Rican mangrove forests because of differences in plant species composition and habitat structure. Green Iguanas have been studied in xeric habitats (Morales-Malvin 1997, Benitez-Malvido 2003) with a distinctive plant community, which requires them to maintain a diet composed of plants and structures with high-water content (van Marken 1992). In germination experiments, captive juvenile Green Iguanas were fed fruit and then seeds were removed from their feces and germinated in Petri dishes (Morales-Malvin 1997, Benitez-Malvido 2003). Results from these experiments examining only juveniles may not apply to adults since their intestinal tract may not be developed completely. Juvenile Green Iguanas need to consume adult feces to acquire intestinal microbes (Troyer 1982) and it is not clear from the publications of these studies whether this had occurred. Similarly, seed germination might be affected by feeding preference (Traveset 1998), such that feeding captive Green Iguanas only one plant species may not accurately reflect their natural diet. Finally, these germination experiments were conducted using Petri dishes under laboratory conditions rather than in a more representative common garden experiment using natural soil and field conditions (i.e., natural variation in temperature, humidity, and precipitation).

Seeds passing through the gut of Green Iguanas can exhibit enhanced germination, inhibited germination, or be unaffected (Traveset 1998). A review of the literature indicates that effects of digestion on seed germination are common: 50% of reptiles, mammals, and bird seed-dispersers either enhance or inhibit seed germination percentage and germination rate (Traveset 1998). Seed germination percentage reflects how many seeds germinate and germination rate reflects how fast a seed germinates after passage. Green Iguanas can potentially enhance germination by removing pulp from the seeds, which can contain germination inhibitors or support potentially infectious fungi and bacteria (Traveset 1998). Microflora and pH changes in Green Iguanas' intestinal tract may also kill infesting parasitic larvae (Fragoso 1997). Another way germination can be enhanced is by the abrasive effect of teeth or abrasive effect of food or other items during the ingestion process. This physical abrasion can disrupt the seed coat allowing a more rapid absorption of water (imbibition) and nutrients. Similarly, chemicals in the digestive tract can disrupt the seed coat, also allowing more rapid imbibition and nutrient uptake. A review of reptile effects on germination shows that reptiles enhanced germination percentage in 28% of studies, inhibited germination percentage in 16% of studies, and had no effect on germination percentage in 56% of studies (Traveset 1998). Furthermore, reptiles enhanced germination rate in 47% of studies, inhibited germination rate in 16% of studies, and had no effect on germination rate in 37% of studies (Traveset 1998). Overall, reptiles affected seed germination percentage in 44% of studies and germination rate in 63% of studies. Although facilitation of seed germination likely varies among reptile species, the trend for reptiles to facilitate seed germination suggests that Green Iguanas may have a significant effect on seed germination in novel Puerto Rican plant communities.

This study quantifies the effects of Green Iguana digestion on seed germination rate and germination percentage for several tropical plant species. Because Green Iguanas are the largest and most abundant vertebrate herbivore in Puerto Rican mangrove forests, their impact on seed germination may be critical for plant community structure. Dispersal can lead to a higher probability of establishment, survival, and germination because seeds are released from predation and interspecific competition, and can colonize new sites with better germination conditions (Janzen 1970, Connel 1978, Thompson and Wilson 1978, Clark and Clark 1984, Dirzo and Dominguez 1986, Andresen 2000). Enhanced germination can lead to faster absorption of nutrients, water, light, and predator avoidance (Sarukhan *et al.* 1984, Andersen 1999). If Green Iguanas feed on particular species and enhance their germination, then they may facilitate the spread of these species. Previous studies of Green Iguana diet in Puerto Rico have found plant material of both native and non-native plants in the stomachs of Green Iguanas (Govender *et al*. 2012). Furthermore, seeds of the highly invasive Brazilian Pepper (*Schinus terebinthifolius*) have been found in the stomachs of Green Iguanas living in mangrove forests (Govender *et al*. 2012). If Green Iguanas promote the germination of non-native species more than native species, then they could pose a severe threat to mangrove communities by facilitating the spread of invasive species.

Our study differs from previous studies in multiple ways. Previous studies focusing on Green Iguana germination effects were conducted in xeric habitats within the species' native range. This may not be representative of relationships outside of the native range where vegetation may differ because of differences in climate and patterns of species introductions. Second, previous studies used juvenile Green Iguanas, which could limit the effect on germination since their digestive tracts may not be fully developed. Furthermore, juvenile size limits the size of fruit that can be consumed, which may exclude some plant species. Third, previous studies held Green Iguanas in captivity and offered a limited selection of fruits; this may also influence results of germination experiments since food selection might affect digestive processes. Finally, previous studies used Petri dishes to germinate seeds using only two treatments: digested seeds without feces and undigested seeds without fruit residues. Restricting experiments to these two treatments may limit the interpretation of germination results because the effects of the presence of feces and fruit on seed germination are not taken into account. Seeds with associated feces and fruits may be more representative of conditions in natural systems.

Recognizing these limitations, our study builds on the work of previous studies in several important ways. First, the study was conducted in mesic habitat in Puerto Rico, where Green Iguanas have been introduced. This broadens the scope for understanding germination effects of Green Iguanas and the possible ecological effects of widespread introduction of Green Iguanas to tropical habitats. Second, our study uses scat from adult Green Iguanas with completely developed digestive tracts, thus eliminating possible effects on germination related to undeveloped juvenile digestive tracts. Third, with the exception of one fruit species fed to captive Green Iguanas, all scat samples were collected from Green Iguanas that fed freely in the environment. Fourth, we used soil for our germination experiment and included four treatments: digested seeds with feces, digested seeds without feces, undigested seeds with fruit, and undigested seeds without fruits.

Results from previous studies using only two treatments, undigested seeds without fruit and digested seeds without feces, provide information on chemical and mechanical effects of the gut on seed germination, but not on the effect of seeds being separated from fruit pulp (Samuels & Levey 2005). Using only these two treatments may limit interpretation of the results because seeds removed from the fruit pulp are more likely to germinate, regardless of gut treatment (Samuels & Levey 2005). Removing the pulp from the fruit may enhance germination by reducing high osmotic pressure caused by sugar levels and eliminating germination inhibitors such as lipids, glycoalkaloids, coumarin, abscisic acid, hydrogen cyanide, ammonia, and light-blocking pigments (Eveneri 1949, Cipollini and Levey 1997). Including the treatment of undigested seeds with fruit provides information on the effect of seed passage and the effect of the seed being removed from the fruit pulp (Samuels & Levey 2005). Similarly, including the treatment of digested seeds with feces may help interpret if Green Iguanas are altering germination by providing nutrient-rich microenvironment in scat. The effect of scat on germination may be independent from either removing pulp or the effects of gut passage. Including these four treatments is a robust way to evaluate the overall effect of Green Iguana gut passage on seed germination.

METHODOLOGY

I. Field Sampling

1. Study Site

We conducted this experiment on the Caribbean Island of Puerto Rico (18.25° North, 66.50° West). Puerto Rico is characterized by a humid subtropical climate (Etwel & Witmore 1973) and is divided in three major geographical areas, a central montane interior, “mogotes” or karst hills, and the sandy coastlines (Holdrige 1967). Our study site was located on the Natural Reserve of Humacao (NRH). This reserve is located on the southeastern part of the island (65.46^0 North, 18.10^0 West). The NRH is protected land and managed by the Puerto Rico Department of Natural Resource and the Environment (DRNA using the Spanish acronym). NRH has a total area of 10.5 km^2, with most of this area being covered by wetland environments (Fig. 1). The closest meteorological station to NRH records annual precipitation of 1,000-2,000 ml and daily annual maxima and minima temperature of 30.7^0C and 20.7^0C, respectively (NOAA & DRNA 1986). Before becoming a natural reserve in 1986, the NRH was used for agriculture at the beginning of the 21^{st} century followed by urbanization starting about mid-century (DRNA 2009, Cowardyn *et al.* 1976). This transition from agricultural landscape to residential landscape is characteristic of most of Puerto Rico’s forest. The NRH is characterized by six main habitat types: 1) coastal lagoons, 2) mangrove forest, 3) herbaceous swamps, 4) *Pterocarpus* forest, 5) secondary coastal forest, and 6) coastal grasslands. A total of 187 plant species, 188 vertebrate species, and 47 invertebrate species have been identified for the NRH (Negron *et al*. 1983, DRNA 1986, Vilella-Gray 1997, Lopez 2005, Cruz 2005 and Montero 2005, DRNA 2008, DRNA 2010). Within the NRH, we concentrated our efforts near the Palmas Lagoon. This area is characterized by an abundance of white mangroves (*Laguncularia racemosa*) as well as secondary vegetation on higher elevation substrates that avoid flooding, including *Pterocarpus* sp., *Peltophorum pterocarpum, Albizia procera, Andira inermis, Ceiba pentandra, Gliricidia sepium, Ficus citrifolia,* and *Terminalia catappa*, and others. The NRH sponsors a community-run ecotourism project that brings many visitors to the reserve annually.

2. Study Species

We identified four main species of plants in Green Iguana scat samples collected in the field: *Annona glabra*, *Ficus* sp., *Pterocarpus* sp., and *Peltophorum pterocarpum*. Species like *A. glabra*, *P. officinalis* and *F. citrifolia* are often found in association with periodically flooded coastal wetlands throughout the neotropics (Weaver 1997). *Annona glabra* (or Pond Apple) is a deciduous tree native to Puerto Rico and Central America. Common to coastal swamps, *A. glabra* can reach 8-10 m high with aggregate fleshy fruit containing more than 100 large seeds (Infante-Mata and Moreno Casasola 2005). *Pterocarpus* sp. refers to two possible species present at our study site: *P. indicus* and *P. officinalis*. Since both species contain similar dry, winged seeds, it was not possible to determine which species was found in Green Iguana scat samples. Both species are evergreen trees. One is native to Puerto Rico (*P. officinalis*) and the other (*P. indicus*) has been introduced and is native to Southeast Asia (Little *et al.* 1974). Both species can reach over 15 m in height and grow mainly in, but are not restricted to, coastal wetlands including freshwater and brackish swamps, the landward side of mangroves, and along stream banks (Little *et al* 1974; Weaver 1997). The number of seeds per frutescence differs between these species with *P. officinalis* having one dry, winged seed and *P. indicus* having two seeds per winged frutescence (Little *et al* 1974). *Ficus* sp. refers to two possible species present at our study site: *Ficus citrifolia* and *F. benjamina*. Because both species contain similar fleshy seeds, it is not possible to identify which species was found in Green Iguana scat samples. Both species are evergreen trees, one native to Puerto Rico (*F. citrifolia*) and the other non-native (*F. benjamina*) has been introduced and is native to Southeast Asia (Little *et al.* 1974; Bonstein and Patel 1992; Veneklaas *et al.* 2002). Both species can reach over 18 m in height and produce fleshy fruit with one seed. Yellow Flamboyant (*Peltophorum pterocarpum*) is an evergreen tree that is not native to Puerto Rico, but native to Southeast Asia (Salah *et al* 2005). *Peltophorum pterocarpum* can grow in different habitats ranging from mangrove tidal forests to tropical highlands (Mail-Hong *et al.* 2003). *Peltophorum pterocarpum* can reach 19 m in height and has dry winged frutescence with 1–2 seeds inside (Little *et al.* 1974).

3. Time Budget

We documented behavioral observations of 47 Green Iguanas over five days in January 2013. The amount of time spent in the following categories was scored: basking, movement within vegetation, feeding, reproduction, movement, intraspecific aggressive behavior, head bobbing, and swimming. Individuals were not observed for more than three hours each (<1 min to 175 min). In addition to behavior, we determined the sex of each Green Iguana and the species of tree it occupied, if possible. If Green Iguanas occupied vegetation, then we recorded if the plant had flowers, fruits, or both.

4. Vegetation Assessment

To help identify to species the seeds found in Green Iguana scat, we developed a seed catalog for the most common plant species at our field site. The Staff at the University of Puerto Rico Herbarium advised us on plant collection methods and provided the necessary materials. Branches were cut from each species and placed between layers of cardboard, desiccant paper, and newspaper. During May 2013, we collected 50 plant species and prepared specimens for identification. Specimens were deposited at the University of Puerto Rico Herbarium and DNRA Herbarium staff will identify each specimen to species level. At the same time, we collected seeds from 17 species, which were peeled, cleaned, and placed in plastic bags. From these seeds, we developed a seed catalog, which was used as a reference to identify seeds found in Green Iguana scat. At the end of our field season, we recorded the locations using a GPS unit of all trees of the four focal species within our primary study area.

5. Sample Collection

Scat sample collection started in mid-June and continued through the end of July 2013. We collected Green Iguana scat primarily along paths constructed for hiking and bike riding. Two to four researchers covered the same area to minimize the risk of missing a sample. Samples were found primarily on the ground, but also on anthropogenic structures, such as kiosks, machinery, and abandoned irrigation systems. When a sample was located, we recorded its location using a GPS unit. As we have seen Green Iguanas defecate one or more pellets at a time, we were careful to collect all adjacent pellets as a single sample to avoid pseudoreplication. When considering whether multiple pellets were from the same sample or not, we evaluated proximity, moisture content, structure, and composition. Scat pellets from a single defecation event are likely close to each other, and similar in moisture content, color, texture, and plant material. Canopy structure above a scat sample was also examined because branch arrangement provided information on the potential trajectory for defecated feces. Using plastic gloves to handle the scat, each sample was placed individually in a plastic bag for transportation. When looking for samples in the field, we paid special attention to areas around *Pterocarpus officinialis* because we often found large concentrations of Green Iguana scat around this tree species. Pilot field observations indicated up to five Green Iguanas on a single *P. officinialis* tree. Preliminary searches for scat under coconut trees fields had little success, so we did not search this area. To avoid collection of scat from other species, we avoided sampling in areas with feral cats and dogs because some scat might look similar to a single pellet of Green Iguana scat.

6. Dispersal

Global positioning system coordinates were taken for most scat samples collected at the HNR during summer 2013. GPS points were also taken for trees of our focal species, *A. glabra*, *Ficus* sp., *P. pterocarpum*, and *Pterocarpus* sp. at the HNR during winter 2014. We calculated the distance between scat samples containing seeds from each focal species and the nearest seed-producing tree of that species using the Near Distance Tool in ArcGIS (ESRI 2001). Mean dispersal distances were calculated from individual minimum distances. This minimum distance is a conservative estimate of dispersal distance by Green Iguanas at our study site. We created maps of Green Iguana scat locations and focal tree species locations using Quantum GIS.

II. Captive feeding experiment

We used a captive feeding experiment designed to quantify the effect of Green Iguana ingestion on seed germination of a specific plant species. We housed Green Iguanas in individually in metal mesh cages (24 x 36 x 24 inches) with cardboard put between the cages to limit aggressive behavior and reduce captivity stress. We mounted the cages on a wheeled platform to facilitate scat collection, cage transportation, and cage cleaning. We used a total of

13 Green Iguanas, one individual captured at the Humacao Natural Reserve and 12 lizards donated by the Best Iguana Puerto Rico Meat Company. This company is located on the northeast part of the island approximately 44 km from our field side. Captive Green Iguanas had been held in captivity for approximately two years in an outdoor enclosure with an artificial pond. We collected and transported Green Iguanas in well-ventilated 50-gallon plastic bins. We housed Green Iguanas individually and fed them on the second day. Although we tried to feed Green Iguanas multiple types of vegetation (e.g., mangoes, breadfruit leaves, breadfruit, and ripe plantains), the Green Iguanas ate only papayas (*Carica papaya*). Each iguana was fed one standard-sized papaya ring every morning. Papayas were cut into similar size rings. To simulate natural condition, seeds were left attached to the pulp. Therefore, we were not able to quantify the seeds on the papaya ring because the fruit contained inner seeds. Green Iguanas were allowed to bask under direct sun for one hour, two times per day at 11:00 h and 16:00 h. Scat was collected in the morning and placed in labeled plastic bags. These samples were used for germination experiments described below. All procedures in this study were approved by the University of Rhode Island Institutional Animal Care and Use Committee, protocol AN 13-03-011.

III. Laboratory Work

1. Sample Processing

We dissected Green Iguana scat less than one week after collection from the field or from captive lizards with the exception of samples S1–S17, which were dissected two weeks after collection. Scat sample dissection consisted of fracturing the scat sample with tweezers to extract the seeds. A dissecting microscope and a magnifying glass were used to locate seeds and separate them from the scat sample, although in some instances seeds were visible to the naked eye. No water was used to separate the scat samples because water could initiate the germination process prior to planting the seeds. Seeds separated from scat were placed in a separate plastic bag and labeled accordingly. We referenced our seed catalog to identify seeds. Some seeds found in the scat samples were not present in our seed catalog and remained unidentified.

2. Germination

We used seeds collected from the field or from captive lizards for the seed germination experiment, which consisted of four treatments under common growth conditions: 1) seeds that have not passed through the Green Iguana's gastrointestinal tract without fruit; 2) seeds that have not passed through the Green Iguana's gastrointestinal tract with fruit pulp; 3) seeds that have passed through the gastrointestinal tract of a Green Iguana mixed with fecal material; and 4) seeds that have passed through the gastrointestinal tract of a Green Iguana without fecal material. The treatments with fruit and feces were added to provide a more accurate representation of natural germination conditions because seeds ingested by Green Iguanas are covered in feces and undigested seeds are covered by fruit residue.

Plastic germination domes with 72 individual cells were used. Domes were given a letter and cells were numbered. Soil was placed on each individual cell initially and seeds were then covered with soil. Clean commercial soil from a nearby area was used for our experiment. For treatments that included seeds and fruit, 0.5 g of fruit was added for all species except the Pond Apple (*Annona glabra*). For *A. glabra,* individual unaltered seeds were used because this species produces discrete units of pulp with each seed. This better represents the natural conditions for this species compared to adding 0.5 g of fruit. For treatments that included seeds and feces, 0.5 g of feces was added. For treatments that included clean seeds, tissue paper was used to clean the seeds. No water was used to clean any of the seeds in any treatment. We identified seeds in scat samples from four main tree species: 1) Pond Apple (*Annona glabra*), 2) *Ficus* sp., 3) Yellow flamboyant (*Peltophorum pterocarpum*) and 4) *Pterocarpus* sp. As the multiple species of *Ficus* and *Pterocarpus* present at our study site produce similar seeds, we could not identify these seeds to the species level. Nonetheless, these seeds are either *Ficus citrifolia* or *Ficus benjamina,* and either *Pterocarpus officinalis* or *Pterocarpus indica,* as these species are present at our study site (DRNA 2009). We collected seeds for the control treatments in the field at NRH from multiple individuals of each tree species. Seeds of *C. papaya* for the control treatment of our captive lizards were purchased at a grocery store. All four treatments were not possible for each species. Only *A. glabra*, *Ficus* sp., and *C. papaya* received all four treatments. In the case of *Peltophorum* sp., we were not able to completely clean the feces from the seeds so the treatment consisting of digested seeds without feces was not possible. Additionally, the treatment of seeds with fruit was not possible because *Peltophorum* sp. have fruits that lack pulp. *Pterocarpus* sp. seeds had to be cut on the sides to fit the germination cells. Seeds were watered daily using a pressure sprayer for a period of 60 days. Wells were checked daily for seed germination. Successful germination was recorded when seedling was first visible at the soil surface. If a seed had germinated, it was recorded, identified, and marked to avoid over counting. To ensure similar environmental conditions for all seeds, germination domes were rotated daily.

IV. Statistical Analyses

For the germination experiment, we measured two responses, days to germination and germination percentage, for both the experimental (seeds consumed by Green Iguanas) and control (seeds found in the environment) treatments. The statistical program JMP Pro was used to conduct all statistical analysis. We used analysis of variance (ANOVA) to test for differences among the four treatments for days to germination. Days to germination for *A. glabra*, *Ficus* sp., and *P. pterocarpum* were log transformed to address unequal variances among groups. A *post hoc* Tukey's Honestly Significant Difference (HSD) test was used to determine differences among the four treatments when an overall significant effect was found. Following Crawley (2007), we use a General Linear Model (GLM) to test for differences among the four treatments for days to germination. Because germination percentage was calculated as a proportion, the results were bounded from 0-1. We used a GLM with a binomial distribution and a logit-link function. The binomial denominator incorporated in the model is a two-vector response that accounts for the number of germinated seeds versus the number of planted seeds. Establishing the binomial denominator is important because it takes into consideration sample sizes (Crawley 2007).

RESULTS

I. Time Budget

In a period of five days, we observed 47 Green Iguanas. Green Iguanas spent most of their time basking, followed by reproduction, movement within vegetation, other movement, intraspecific aggression, head bobbing, feeding, and swimming (Fig. 2). Green Iguanas most commonly selected white mangrove (*Laguncularia racemosa*) trees, followed by almond trees (*Terminalia catappa*), *Pterocarpus* sp., coconut palms (*Coccos nucifera*), flamboyant (*Delonix regia*), *Albizia procera*, and *Thespesia populnea*. Green Iguanas were also found on the ground and on unidentified trees (Fig. 3).

II. Scat Samples

We collected 258 Green Iguana scat samples (Table 1). Out of these, almost half (n = 122) contained seeds. Green Iguana scat differed in the composition of seeds from various plant species. Most scat samples contained only one species of seed, followed by scat samples with two species of seeds, and the remaining scat samples had three species of seeds (Table 1). Seeds of five main species were found in Green Iguana scat; however, only four of these species could be identified: *Annona glabra*, *Ficus* sp., *Pterocarpus* sp., and *Peltophorum pterocarpum* (Table 1). Of these four species, *A. glabra* was the most abundant species found in Green Iguana scat samples, followed by *Ficus* sp., *P. pterocarpum*, and *Pterocarpus* sp. (Table 2). The unidentified abundant seed was present in 30% of the Green Iguanas scat samples. Numbers of seeds found on Green Iguana scat by species differed among plant species (Table 2). Of these four species, *A. glabra* was the most abundant with almost half of the seeds, followed by *Ficus* sp., *P. pterocarpum*, and *Pterocarpus* sp. (Table 2). No animal material was found in Green Iguana scat.

III. Germination

The effect of Green Iguanas on germination percentage and days to germination differed among the four focal plant species: *Annona glabra*, *Ficus* sp., *Pterocarpus* sp., and *Peltophorum pterocarpum* (Table 3). For *A. glabra*, there was no significant difference in the percentage of seeds that germinated among treatments (P = 0.77) (Fig. 4, Tables 3 & 4). Moreover, no significant difference was found among treatments for days to germination for *A. glabra* ($F_{3,19}$ = 2.01, P = 0.48) (Table 6, Fig. 5). Thus, Green Iguana effects on seed germination of native *A. glabra* were neutral, meaning they did not enhance or inhibit germination in this species.

Germination percentage differed among treatments for *C. papaya* (P = 0.05; Table 4) with digested seeds with feces having higher germination percentage than other treatments (Fig. 6). Mean days to germination differed among treatments for *C. papaya* ($F_{3,275}$ = 4.8, P = 0.003; Tables 5 & 6) with digested seeds without feces taking longer than other treatments to germinate (Table 6, Fig. 7).

For *Ficus* sp., there was no significant difference among treatments for germination percentage (P = 0.73; Tables 3 & 4). In contrast, the mean days to germination differed among treatments for *Ficus* sp. ($F_{3,116}$ = 3.72, P = 0.01; Tables 5 & 6) where digested seeds with feces, digested seeds without feces, and undigested seeds without fruit had shorter days than undigested seeds with fruit (Table 6, Fig. 9).

Mean germination percentage for *P. pterocarpum* was higher for undigested seeds with fruit than digested seeds with feces (P = 0.003; Tables 3 & 4, Fig.10). For *P. pterocarpum*, the mean days to germination was half as long ($F_{1,16}$ = 9.68, P = 0.007; Table 6, Fig. 11) for digested seeds with feces than undigested seeds with fruit (Table 5).

Mean germination percentage for *Pterocarpus* sp. was higher for undigested seeds with fruit than digested seeds with feces (P = 0.008; Table 4, Fig. 12). For *Pterocarpus* sp., the mean days to germination was shorter ($F_{1,17}$ = 10.6, P = 0.005; Table 6, Fig. 13) for digested seeds with feces than undigested seeds with fruit (Table 5).

IV. Dispersal

Minimum distance of Green Iguana scat (Fig. 14) containing seeds of the focal species to the nearest mature tree of the same species differed among the four species: *Annona glabra*, *Ficus* sp., *Pterocarpus* sp., and *Peltophorum pterocarpum* (Table 7). Seeds of *A. glabra* were dispersed the farthest (Fig. 15), followed by *Pterocarpus* sp. (Fig. 16), then *Ficus* sp. (Fig. 17), and finally *P. pterocarpum* (Fig. 18). For *A. glabra,* most seeds were dispersed between 40-50 m from the nearest *A. glabra* tree (Fig. 19). In contrast, most seeds of *Ficus* sp. were not transported far, nearly 50% of seeds were found within 5 m of a mature tree (Fig. 20).

DISCUSSION

During January, Green Iguanas spent the vast majority of their time basking, and feeding made up less than 1% of their time budget (Fig. 2). In contrast, during March and April in mangroves and freshwater swamps in Puerto Rico, Green Iguanas spent about 18% of the time foraging (Figueiredo de Andrade *et al.* 2011). Time spent feeding by Green Iguanas in the winter in Puerto Rico is similar to the native range, where Green Iguanas are 96% inactive and spend only 1% of their time foraging (Dugan 1982, Rand *et al.* 1990; Lara-Lopez and Gonzalez-Romero 2002). Although Green Iguanas were most often observed on mangrove (*Laguncularia racemosa*), they also occupied other trees including *Thespesia populnea*, *Albizia procera*, almond tree (*Terminalis catappa*), coconut palm (*Coccos nucifera*), *Pterocarpus* sp., and flamboyant (*Delonix regia*) (Fig. 3). Of all plant species that Green Iguanas occupied during winter, only *Pterocarpus* sp. seeds where found in scat during the summer.

Since Green Iguanas have been observed on dead mangroves, it has been suggested that occupancy and feeding of abundant Green Iguanas on mangroves leads to mangrove mortality (Lopez-Torres *et al*. 2011). Nonetheless no study has demonstrated the connection between Green Iguanas and mangrove mortality. These observations have three possible explanations: (1) Green Iguanas may have a direct negative effect on mangroves, causing mortality through herbivory; (2) they may preferentially occupy dead mangroves to bask; or (3) they may be more easily observed when mangroves are dead (Lopez-Torres *et al.* 2011; Garcia-Quijano *et al.* 2011). If Green Iguanas spend little time feeding (Fig. 3) on mangrove and use other tree species to bask and feed (Fig. 4), then little evidence exists for negative impacts on mangroves in introduced habitats (but see Lopez-Torres *et al.* 2011; Carlo and Garcia-Quijano 2008). This is consistent with reports of Green Iguanas not being detrimental to mangrove communities in their native habitat (Henderson 1974, Lara-Lopez and Gonzalez-Romero 2002).

Whether Green Iguanas are strict herbivores has been debated for many years (Swanson 1950; Rand *et al*. 1990; van Marken 1993; Townsend *et al*. 2005; Lopez-Torres *et al.*2011; Garcia-Quijano *et al.*2011; Govender *et al.* 2012). It has been reported that Green Iguanas consume carrion (Loftin and Tyson 1965), juveniles consume insects (Swanson 1950), and in recent years consumption of tree snails *Drymaeus multilineatus* and crabs *Uca* sp. has been reported (Townsend *et al.* 2005, Govender *et al.* 2012). Nonetheless, lack of stomach content information and the anecdotal nature of most observations questions the validity of these reports. Scat samples of Green Iguanas collected in our study revealed no evidence of animal material, suggesting that Green Iguanas are strict herbivores at this site in Puerto Rico. This is consistent with feeding studies in the native range (Rand *et al.* 1990; Lara-Lopez and Gonzalez-Romero 2002). Seeds found in Green Iguana scat samples belong to native and non-native tree species, including species with both fleshy and dried fruits. For most species, the physical appearance of seeds after ingestion and gut passage was different than that of undigested seeds. Seeds of *A. glabra* that passed through the gut of Green Iguanas were darker and lacked pulp, whereas *Ficus* sp. seeds also lacked pulp, *Pterocarpus* sp. lacked wings, and *P. pterocarpum* seeds became softer, but remained inside the frutescence. Lack of pulp and loss of wings suggest mechanical processes (e.g., chewing and abrasive effects of gut passage), whereas changes in color and texture suggest chemical processes during gut passage. Thus, regardless of the effect on germination, Green Iguanas change the chemical and physical properties of seeds in some species in their introduced range by means of ingestion and gut passage.

At our study site, almost half of samples contained seeds (Table 1). In contrast, fewer than 7% of scat samples from within its native range contained seeds (Rand *et al.* 1990, Lara-Lopez and Gonzalez-Romero 2002). Scat samples also differed in the number of plant species per scat sample between native and non-native sites. In their native range, scat of Green Iguanas contain one plant species 52% of the time, two species 23% of the time, three species 23% of the time, and four species 3% of the time (Rand *et al*. 1990). At our study site, scat contained one plant species 69% of the time, two species 27% of the time, and three species 3% of the time (Table 1). This suggests that Green Iguanas may have a more diverse diet in native compared to non-native sites. However, we were unable to identify all seeds to species in scat samples from our site, and Green Iguanas also eat other plant structures, such as leaves and flowers, which were not quantified in our study. Furthermore, we did not assess the availability of plant species, which would allow us to determine the extent to which Green Iguanas selectively feed on particular plant species. Nonetheless, we predict that Green Iguanas will feed on a wider variety of plant species in their introduced range because predation pressure is lower compared to their native range (Morales-Mavil *et al*. 2007). Reduced predation pressure could result in increased foraging times and distances from refugia.

Coastal wetlands throughout the neotropics exhibit associations with particular plant species, such as *P. officinalis* and *A. glabra* (Weaver 1997). In Puerto Rico, this association exists and also includes other species, such as *Andira inermis*, *Bucida buceras*, *Calophyllum brasiliense, Ficus citrifolia*, *Roystonea borinquena,* and *Cordia borinquena.* Non-native *P. pterocarpum* is also associated with mangrove communities in Southeast Asia in areas with infrequent flooding; nonetheless, they are not mentioned as a tree species associated with mangroves in Puerto Rico (Weaver 1997). Given the species associated with coastal wetlands and also present at our study site, we found that Green Iguanas consumed fruits of three species: *A. glabra*, *Ficus* sp. (could be *Ficus citrifolia*) and *Pterocarpus* sp. (could be *Pterocarpus officinalis)* (Table 2). Thus, Green Iguanas may influence the maintenance of these associations when introduced outside of their native range. This differs from studies in native range where feeding on *A. glabra* and *Ficus* sp. fruit has not been observed (Lara-Lopez and Gonzalez-Romero 2002; Benitez-Malvido *et al* 2003). In Mexico, *A. glabra* was very abundant and preferred as habitat by Green Iguanas, but Green Iguanas were not observed consuming *A. glabra* (Lara-Lopez and Gonzalez-Romero 2002). Furthermore, observational studies in Puerto Rico documented Green Iguanas occupying *A. glabra* trees, but they were not observed feeding on this species (Figueiredo de Andrade *et al.* 2011). In the case of *Ficus* sp., vegetative material of this species was found in stomach contents of Green Iguanas in its native range, but no seeds were present (Rand *et al.* 1990; Lara-Lopez and Gonzalez-Romero 2002). These differences in consumption between the native and non-native range suggest that food selectivity may differ between habitats. Any shift in Green Iguana diet in non-native range could be associated with preferences for certain plant species, lack of competitors feeding on the same species, or changes in foraging patterns associated with lack of predation. The latter could be particularly true for *A. glabra* because Green Iguanas likely need to handle this large fruit on the ground for longer periods of time to feed on it as compared to other species (J. Burgos-Rodriguez, *pers. obs.*). In native habitats, such exposure could increase risk of predation.

Green Iguanas may prefer *A. glabra* fruit compared to other species since seeds from *A. glabra* represented almost have of all seeds found in scat (Table 2). The Puerto Rican slider turtle (*Trachemys stejnegeri stejnegeri*), listed as a critical element of Puerto Rico's fauna, consumes *A. glabra* as a major component of its diet (DRNA 2009; Vilella and Gray 1997). *Annona glabra* has been categorized as a critical element for the conservation of this species under the Puerto Rico Department of Natural Resources Program of Natural Patrimonies (DRNA

2009). High levels of consumption of *A. glabra* by the abundant Green Iguanas might have direct effects on the Puerto Rican slider by limiting the amount of *A. glabra* fruit available.

Green Iguanas introduced to Puerto Rico have the potential to affect seed germination, specifically the percentage of seeds that germinate and the number of days it takes seeds to germinate (Table 4 & 6). The effect on germination of passing through a Green Iguana's gut was not constant across plant species, suggesting that the effects of Green Iguanas on seed germination are species specific (Table 4 & 6). Species-specific effects are consistent with studies in native habitats (Benitez-Malvido *et al* 2003), but our study is the first to record that Green Iguanas reduce seed germination percentage in some plants (Table 4 & 6). Germination effects of Green Iguanas in Puerto Rico did not consistently differ between native and non-native plant species. Germination percentage was not enhanced for any species, was neutral for native *A. glabra* (Fig. 4) and *Ficus* sp. (Fig. 8), but was inhibitory by reducing germination percentage in *C. papaya* (Fig. 6), non-native *P. pterocarpus* (Fig. 10), and *Pterocarpus* sp. (Fig. 11). Germination was enhanced by reducing the number of days to germination in *Ficus* sp. (Fig. 9), non-native *P. pterocarpum* (Fig. 11), and *Pterocarpus* sp. (Fig. 13). However, the number of days to germination did not differ among treatments for native *A. glabra* (Fig. 5) and was inhibited by increasing days to germination for non-native *C. papaya* (Fig. 7). On the other hand, we found differences in germination between fleshy and dry fruits. Dry fruits of non-native *P. pterocarpum* and *Pterocarpus* sp. exhibited the same effect on germination. When ingested these species showed both a decrease in the percentage of seeds that germinated and an increase in the number of days to germination. This suggests the type of seed may influence the effects of ingestion on germination. Seeds of non-native *P. pterocarpum* and *Pterocarpus* sp. are both dry, winged and indehiscent, meaning they cannot split open on their own (Little *et al* 1974). Green

Iguanas may eliminate wings and facilitate the opening of such indehiscent seeds, thus enhancing germination. However, some seeds may be damaged by mechanical or chemical processes, and can be destroyed by digestion (Traveset 1998).

Seed germination can be altered by either removal of fruit pulp, providing nutrient-rich, moist microhabitats in scat, or by mechanical or chemical processes (Samuels and Levey 2005). Our study showed that Green Iguanas affect this process in multiple ways. For native *A. glabra*, ingestion of seeds does not appear to effect germination. However, seed germination was overall very low for *A. glabra* (Table 3). This could be attributed to limitations in the experimental design related to watering patterns and the observation period. Although previous studies of *A. glabra* show low germination in general, they watered seeds daily until the soil was saturated and observed germination for 120 days (Infante and Moreno-Casasola 2005). Our experimental design did not account for the tendency of *A. glabra* to germinate in flooded soils and the extended time needed for germination. For non-native *C. papaya*, germination percentage was lower for digested seeds with feces (Table 4, Fig. 6). On the other hand, *C. papaya* seeds digested with no feces took longer on average to germinate compared to seeds undigested with no fruit (Fig. 7, Table 4). We can conclude that the mechanical or chemical action of gut passage in Green Iguanas may slightly inhibit seed germination in *C. papaya*, but only when their feces is not present. For *Ficus* sp., the percentage of seeds germinating did not differ among treatments, thus we can conclude that ingestion of seeds is not important for this aspect of germination. On the other hand, undigested *Ficus* sp. seeds planted with fruit took longer to germination compared to undigested seeds with no fruit (Fig. 9, Table 7). This suggests the separation of seeds from fruit pulp enhances germination. This may be accomplished by ingestion by Green Iguanas, but this is confounded with the mechanical and chemical action of ingestion. Previous studies attempted to determine the effect of Green Iguanas on germination percentage and days of germination for *Ficus* sp. in native habitats, but juveniles Green Iguanas were unable to consume large *Ficus* sp. seeds (Benitez-Malvido *et al.* 2003). Such a comparison could be important because *Ficus* sp. have been categorized as keystone species for herbivores due to abundant year round fruit presence (Santinelo *et al.* 2007). Because *P. pterocarpum* and *Pterocarpus* sp. lack pulp and we could not clean fecal material from the seeds, we examined only undigested seeds with fruit and digested with feces. We were not able to determine whether Green Iguanas were important for removing pulp from seeds, have mechanical or chemical effects that alter germination, or whether scat microhabitat presence affects germination. As the effect of Green Iguanas on germination percentage and days to germination was inconsistent among plant species (e.g., *C. papaya*, *P. pterocarpum*, *Ficus* sp., and *Pterocarpus* sp.), it was difficult to summarize the overall effect on germination. Days to germination has been suggested as a better measure because seeds that germinate faster avoid predation and produce more vigorous seedlings with greater survival probabilities compared to late recruitment of conspecifics (Sarukhán *et al.* 1984; Andersen 1999). Also germination percentage could be inconsequential when plant species produce an overabundance of seeds. Green Iguanas could have an overall negative effect on germination of *C. papaya* since digested seeds with feces inhibit germination. On the other hand, Green Iguanas may have an overall positive effect on germination of *P. pterocarpum* and *Pterocarpus* sp. because digested seeds with feces germinate faster.

Minimum distances between mature trees and scat samples containing seeds of the same species indicate the patterns by which seeds are dispersed. Dispersal distance varied considerably among species. Although minimum dispersal distances may appear to be low for some species (e.g., 8 m for *P. pterocarpum*), distances were large enough that seeds of all species would be dispersed beyond the canopy of parent trees. Minimum distances showed no trend for dispersal of fleshy versus dry fruits. The potential for dispersal appears to be greater for *A. glabra* compared to other species in our study because of the large number of seeds of *A. glabra* per scat sample and the higher frequencies of relatively large dispersal distances for this species (Fig. 19; Tables 2 & 5). The Escape Hypothesis suggest that *A. glabra* will benefit from distant dispersal away from the source tree because proximity to the parent tree increases mortality due to density dependent effects such as increased predation, pathogen attacks, or seedling competition (Janzen 1970, Collins 1973). Similarly, this hypothesis suggests that dispersal of *Ficus* sp. may not be as effective as most seeds are dispersed closer to the parent *Ficus* sp. tree (Fig. 20; Table 2 & 5). Frequency distributions for dispersal distances between scat and the nearest parental tree could not be constructed for *P. pterocarpum* and *Pterocarpu* sp. species because of low number of these seeds in Green Iguanas scat samples.

When considering our focal species, *A. glabra* is primarily dispersed by water, *Ficus sp.* is dispersed by herbivores, and *P. pterocarpum* and *Pterocarpus* sp. are dispersed by air (Little *et al*. 1976; Weaver 1997). The ability of Green Iguanas to disperse these species may be beneficial not only for species dependent on animal-mediated dispersal like *Ficus* sp., but also for species dispersed by air and water. Although Green Iguanas do not have extensive home ranges (Dugan 1982; Morales-Mavil *et al.* 2007), their ability to move across the landscape creates the potential for seeds of these species to reach environments not otherwise easily accessed, such as upstream habitats, inland habitats that do not get flooded, and the interiors of dense forests where air dispersal may not be successful. Another aspect of Green Iguanas that could facilitate dispersal is the long retention time of seeds in the gut. Adult Green Iguanas have an average retention time of 5.5 days (Troyer 1984). Retention times of this length may allow Green Iguanas to move from feeding sites and disperse seeds away from the parent plants. Moreover, seeds ingested by Green Iguanas were defecated mostly intact, which is a good indicator of an effective disperser (Schuppe 1993).

To assess the effect of Green Iguanas on these plant species and their communities, it is important to integrate effects of germination percentage, days to germination, dispersal potential, and the life history. Green Iguanas feed on non-native species where they have been introduced in Puerto Rico (Govender *et al.* 2012). This study also demonstrates that Green Iguanas consume non-native *P. pterocarpum* in Puerto Rico. A potential negative effect could result from Green Iguanas enhancing germination and dispersal of non-native species. This may be the case for non-native *P. pterocarpum*. On the other hand, inhibition of non-native species may benefit ecosystems. Green Iguanas inhibit germination and increase the numbers of days to germination for non-native *C. papaya* under some conditions (Figs. 6 & 7). Because this non-native species is important for the agricultural industry, consumption and inhibition of germination might be perceived as negative economic effects. Negative effects on *C. papaya* on germination could be extrapolated to Green Iguanas in their native range where crops of *C. papaya* have important economical value (Teixeira da Silva *et al.* 2007). As fruits and seeds have similar appearances in native *P. officinalis* or non-native *P. indicus* as well as native *F. citrifolia* or non-native *F. benjamina*, it was not possible to differentiate between these species when Green Iguanas fed on them. Although this is a limitation of our experiment, it is reasonable to assume that if Green Iguanas prefer native (*P. officinalis* and *F. citrifolia)* over non-native (*P. indicus* and *F. benjamina*) plants, then Green Iguanas may facilitate germination of native species by decreasing the days to germination and dispersing seeds. On the other hand, if Green Iguanas prefer non-native (*P. indicus* and *F. benjamina*) as opposed to native (*P. officinalis* and *F. citrifolia)* plants, then Green Iguanas may have detrimental effects on the ecosystem by decreasing the days to germination and dispersing a non-native species. If Green Iguanas consume both the native and non-native related species, they can cause both detrimental and beneficial effects for the ecosystem. Even though the consumption of *A. glabra* by Green Iguanas may represent direct competition with the Puerto Rican slider turtle (DRNA 2009) and germination information is inconclusive, we suggest that Green Iguanas may have a positive effect on the ecosystem, in this case, by dispersing native *A. glabra* seeds. This is consistent with some studies that suggest dispersal to microhabitats is more important than the effect of gut passage on seeds (Rey and Alcántara 2000; Traveset *et al*. 2003).

Effects of Green Iguanas on the ecosystem through seed germination and dispersal may be influenced by fruit availability. Of our four focal species, *P. pterocarpum* and *Ficus* sp. fruit year round, and *A. glabra* and *Pterocarpus* sp. fruit between March-November (Little *et al.* 1976). Because *P. pterocapum* is non-native and fruits almost year round, Green Iguanas disperse them and enhance their seed germination, and their role in mangroves communities in Puerto Rico has not been studied, *P. pterocarpum* represents the highest potential risk of the species at our study site in Puerto Rico. Although Lugo (2009) suggested that mangrove forest succession is not threatened by the presence of non-native plant species, because they are intolerant of saline conditions, in some locations of our study area non-native *P. pterocarpum* was growing near to white mangroves (*Laguncularia racemosa*). If non-native *P. pterocarpum* are competing with white mangroves and Green Iguanas are facilitating their dispersal and germination, then Green Iguanas may represent a serious threat to long-term stability of mangrove communities. Although the effects of enhancing the establishment of non-native *P.*

pterocarpum are unclear, we have established that Green Iguanas have the potential to affect germination and aid in the dispersal of non-natives. The seeds of non-natives, such as the invasive Brazilian pepper (*Schinus terebinthifolius*), may be also affected by Green Iguana ingestion and dispersal.

Because Green Iguanas are known to have a negative impact on the economy (Egeman *et al.* 2005; Lopez-Torres *et al.* 2011), the government of Puerto Rico has classified this species as a nuisance pest. Nonetheless, no information is available on the effects of Green Iguanas in Puerto Rican ecosystems. Our study shows that Green Iguanas have the potential to change plant communities in Puerto Rico by seed dispersal and germination of both native and non-native plant species. However, classifying Green Iguanas as beneficial or detrimental to mangrove forest ecosystems in Puerto Rico would be premature. Further studies are needed to assess the long-term effect of seed germination and dispersal by Green Iguanas in Puerto Rican mangrove forest communities. Although current eradication efforts of Green Iguanas are needed to address economic loss, more ecological research is needed to justify allocation of funds, resources, and management to non-economic scenarios where the effect of this species is still unknown.

Figure 1. Humacao Natural Reserve. Shaded areas are part of the Humacao Natural Reserve, Humacao, Puerto Rico. The box delimits our study site in the Santa Teresa Unit.

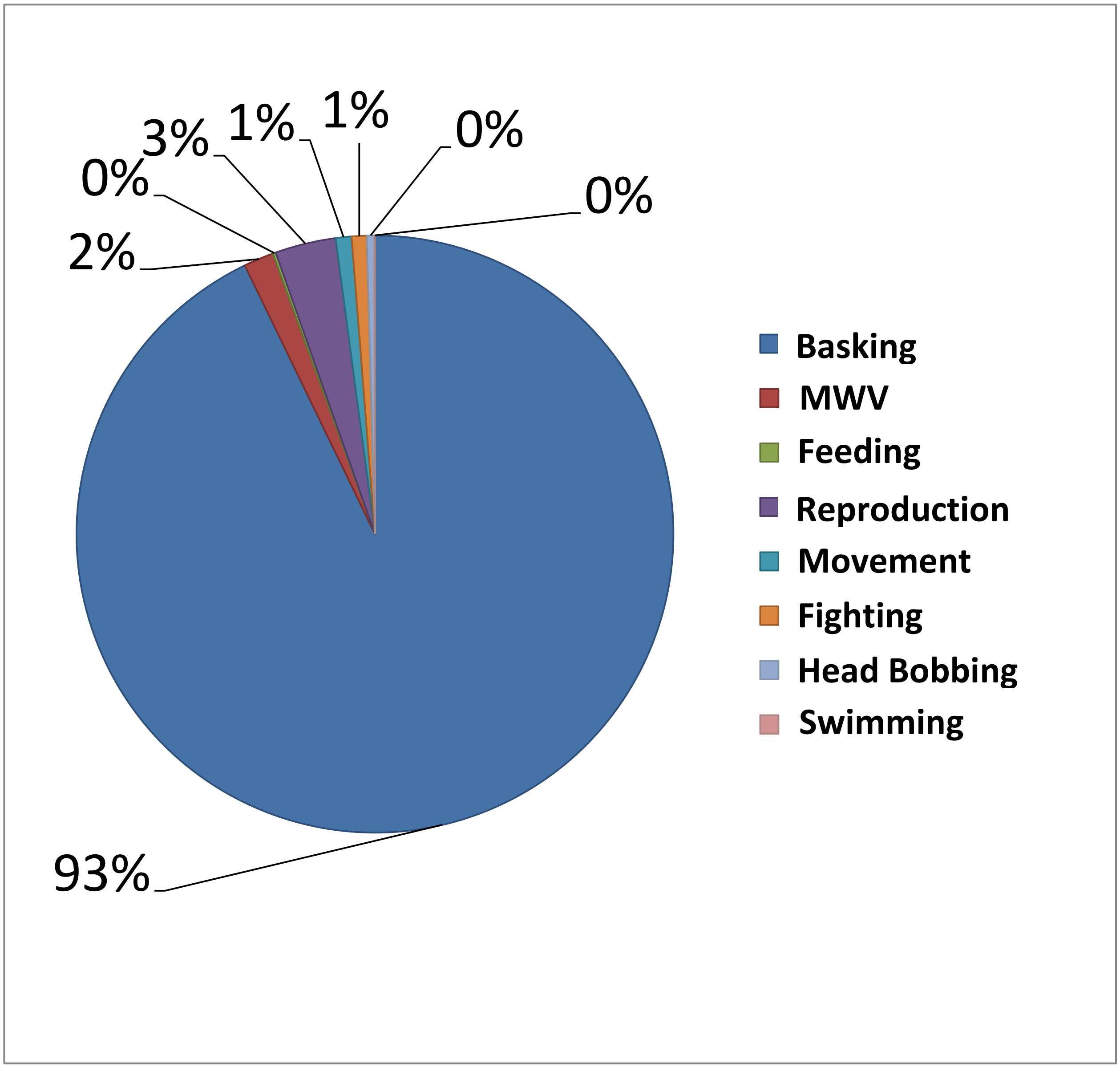

Figure 2. Time budget for Green Iguanas (*Iguana iguana*) at the Humacao Natural Reserve in Puerto Rico in January 2013 (n=47). MWV stands for movement within vegetation.

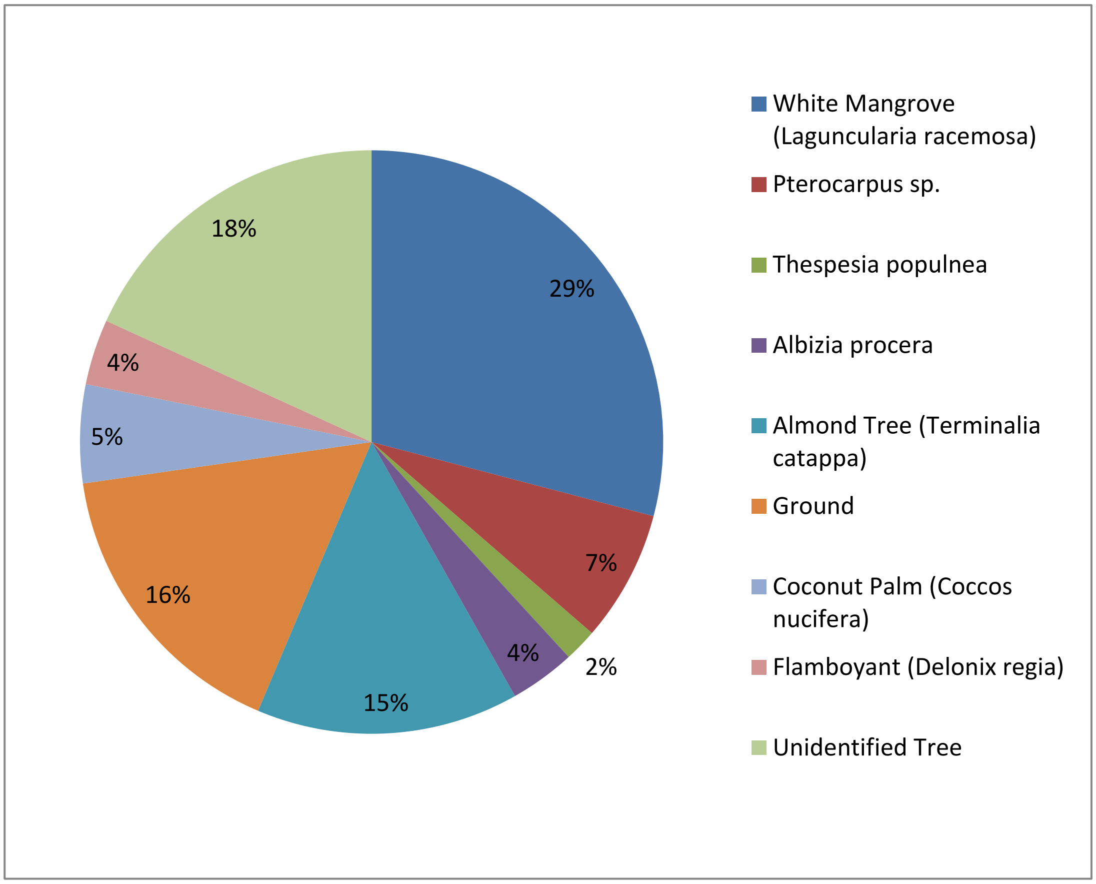

Figure 3. Habitats occupied by Green Iguanas (*Iguana iguana*) at the Humacao Natural Reserve in Puerto Rico in January 2013 (n=47).

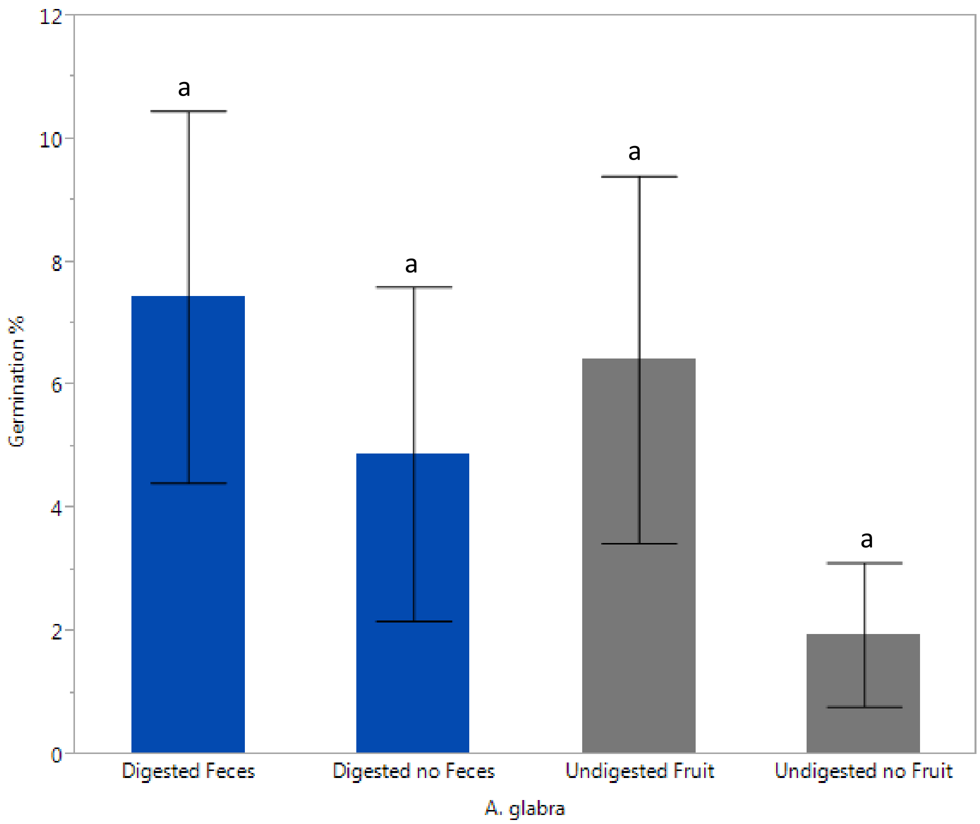

Figure 4. Mean and standard error for germination percentage of native *Annona glabra* seeds ingested by Green Iguanas (*Iguana iguana*) in Puerto Rico, June and July 2013. Germination percentage is calculated from mean germination percentage of individual samples. Same letters above bars denote no significant difference among the four treatments.

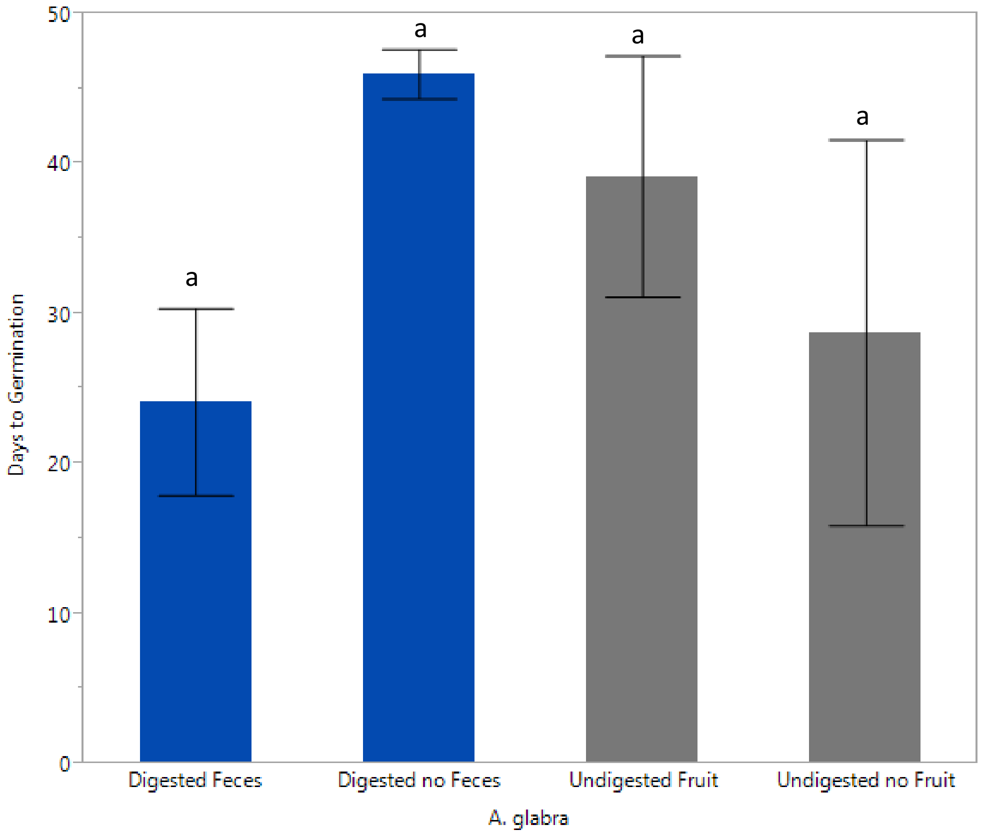

Figure 5. Mean and standard error for days to germination of native *Annona glabra* seeds ingested by Green Iguanas (*Iguana iguana*) in Puerto Rico, June and July 2013. Same letters above bars denote no significant difference among treatments.

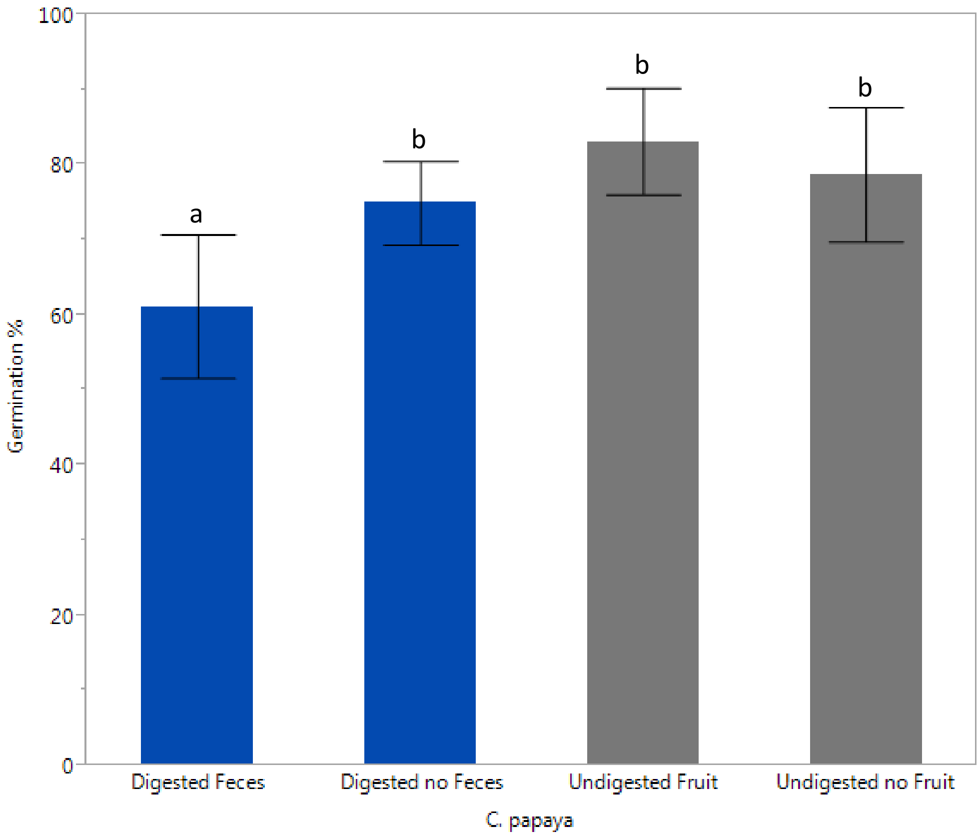

Figure 6. Mean and standard error for germination percentage of non-native *Carica papaya* seeds ingested by Green Iguanas (*Iguana iguana*) in Puerto Rico, June and July 2013. Germination percentage is calculated from mean germination percentage of individual samples. Same letters above bars denote no significant difference among the four treatments.

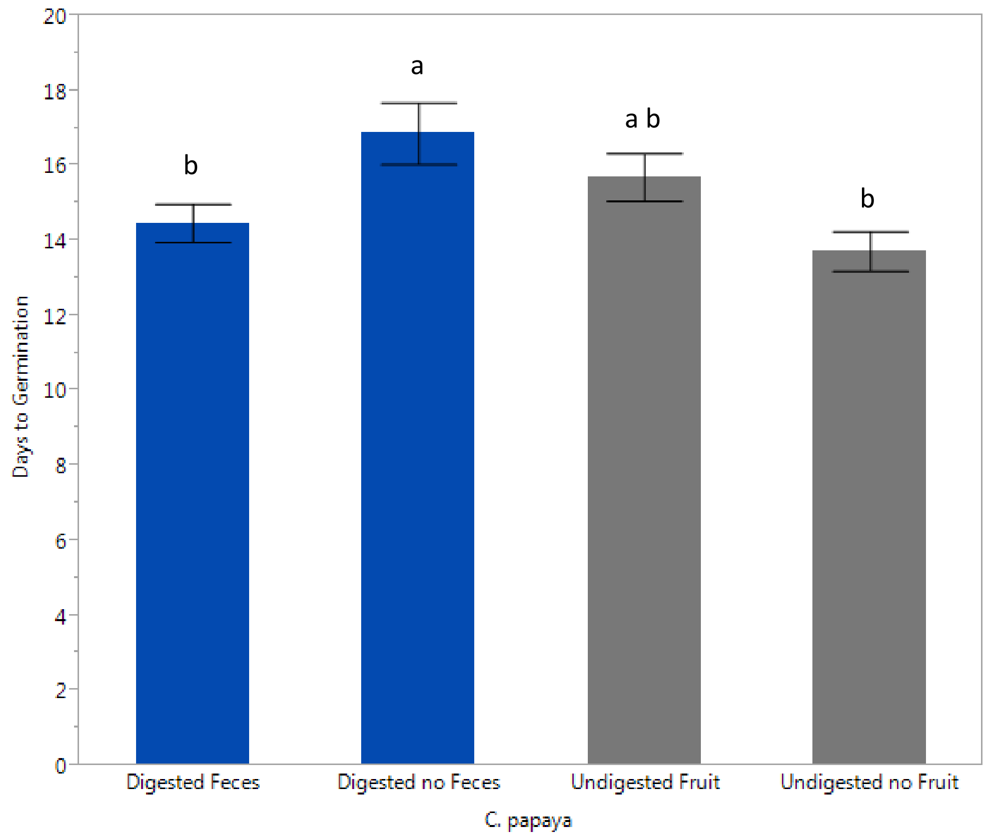

Figure 7. Mean and standard error for days to germination of non-native *Carica papaya* seeds ingested by Green Iguanas (*Iguana iguana*) in Puerto Rico, June and July 2013. Same letters above bar denote no significant difference among treatments.

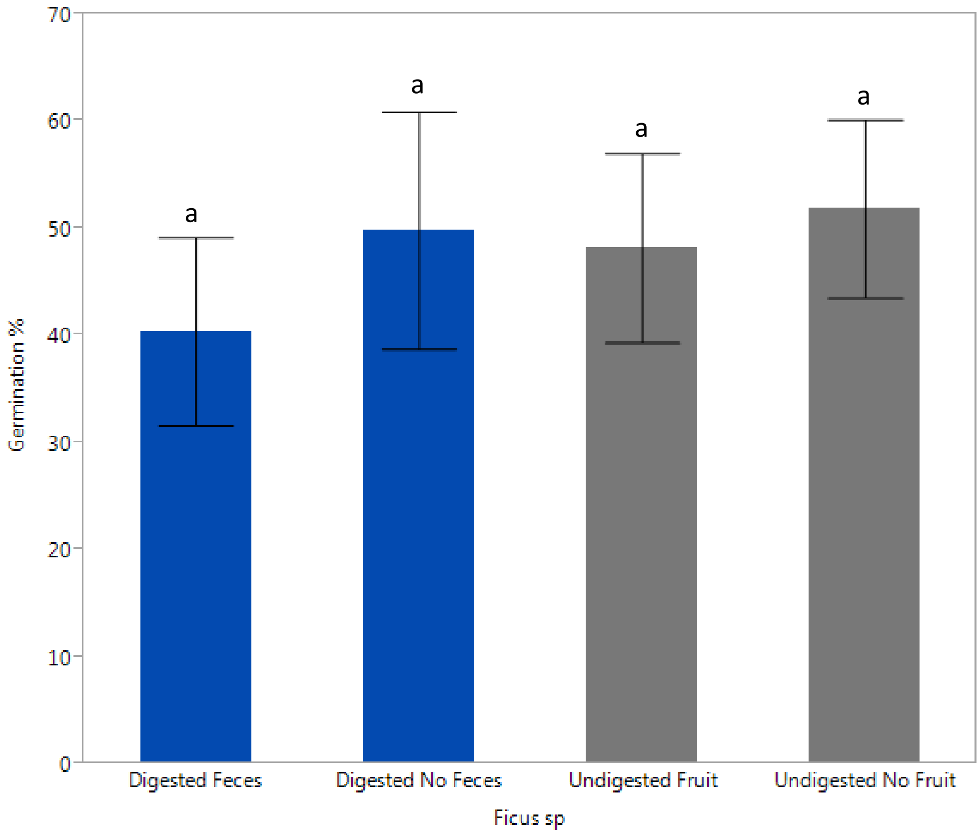

Figure 8. Mean and standard error for germination percentage of *Ficus* sp. seeds ingested by Green Iguanas (*Iguana iguana*) in Puerto Rico, June and July 2013. Germination percentage is calculated from mean germination percentage of individual samples. *Ficus* sp. includes native *Ficus citrifolia* and non-native *Ficus benjamina*. Same letters above bars denote no significant difference among the four treatments.

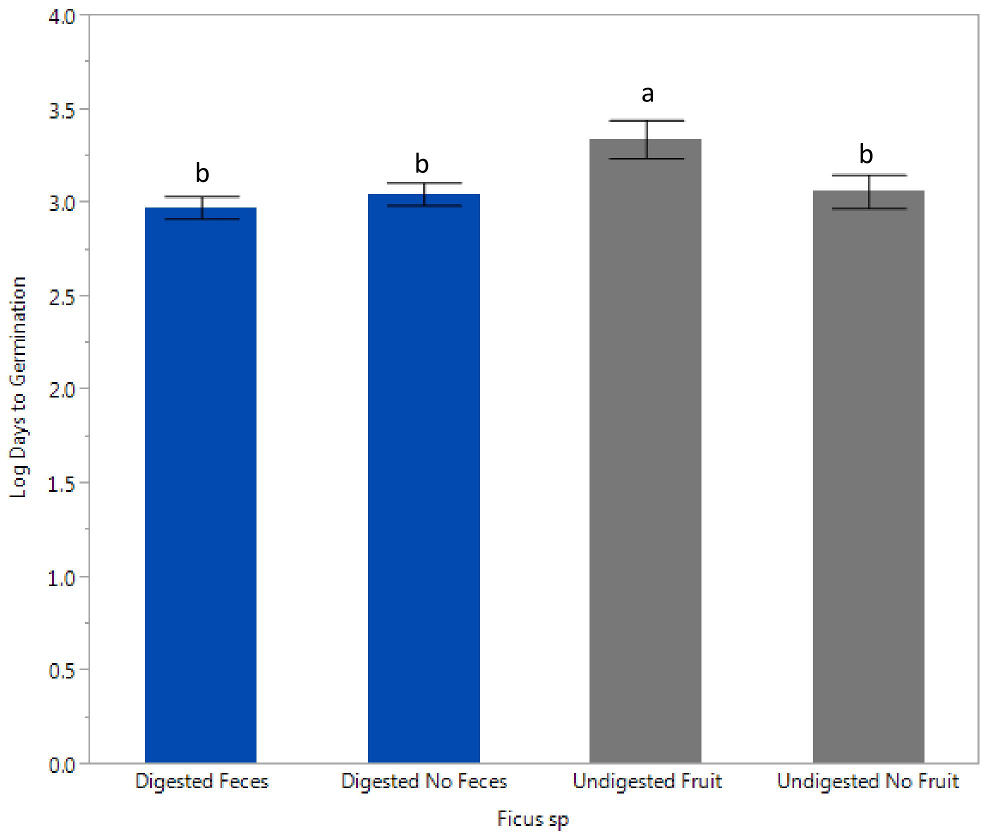

Figure 9. Mean and standard error for days to germination of *Ficus* sp. seeds ingested by Green Iguanas (*Iguana iguana*) in Puerto Rico, June and July 2013. *Ficus* sp. includes native *Ficus citrifolia* and non-native *Ficus benjamina*. Day to germination has been log transformed. Same letters above bar denote no significant difference among treatments.

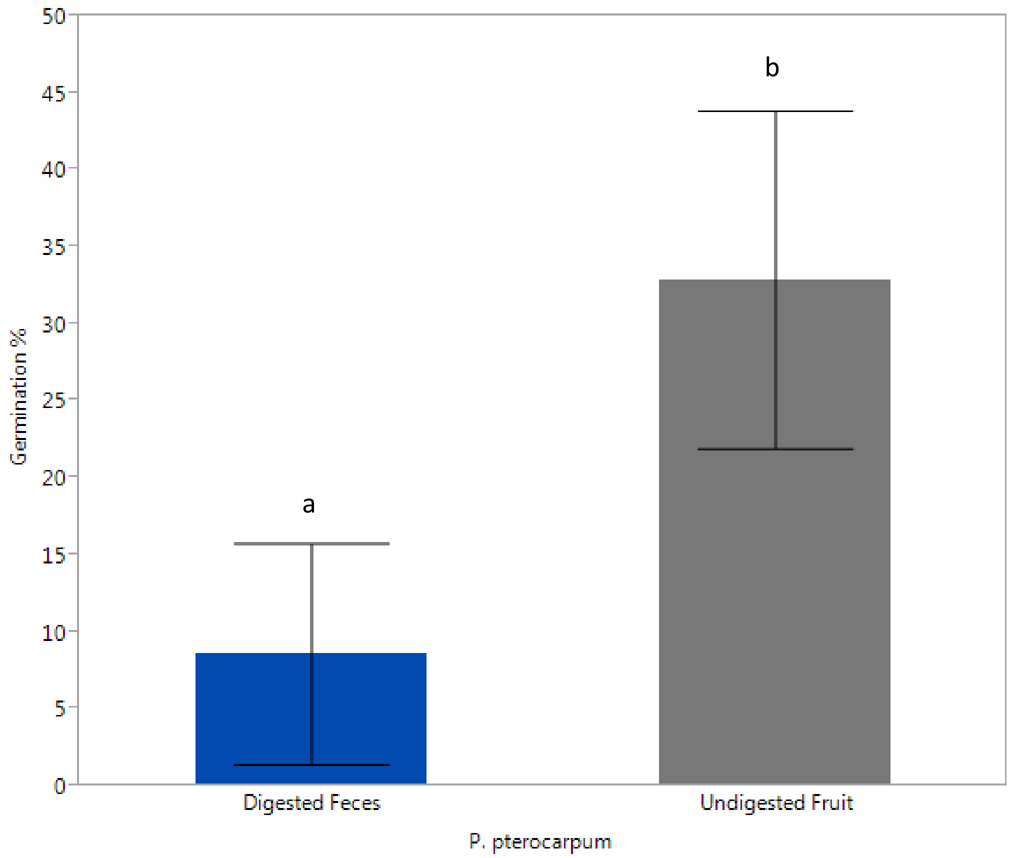

Figure 10. Mean and standard error for germination percentage of non-native *Peltophorum pterocarpum* seeds ingested by Green Iguanas (*Iguana iguana*) in Puerto Rico, June and July 2013. Germination percentage is calculated from mean germination percentage of individual samples. Same letters above bar denote no significant difference among treatments.

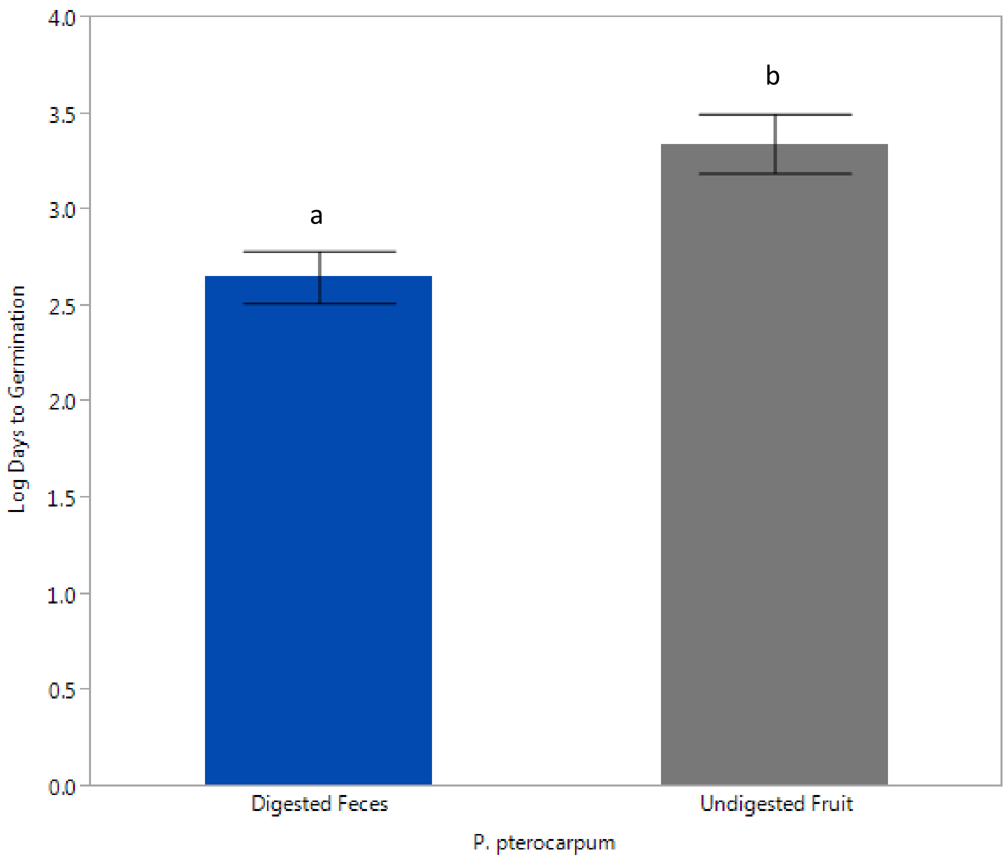

Figure 11. Mean and standard error for days to germination of non-native *Peltophorum pterocarpum* seeds ingested by Green Iguanas (*Iguana iguana*) in Puerto Rico, June and July 2013. Same letters above bar denote no significant difference between treatments

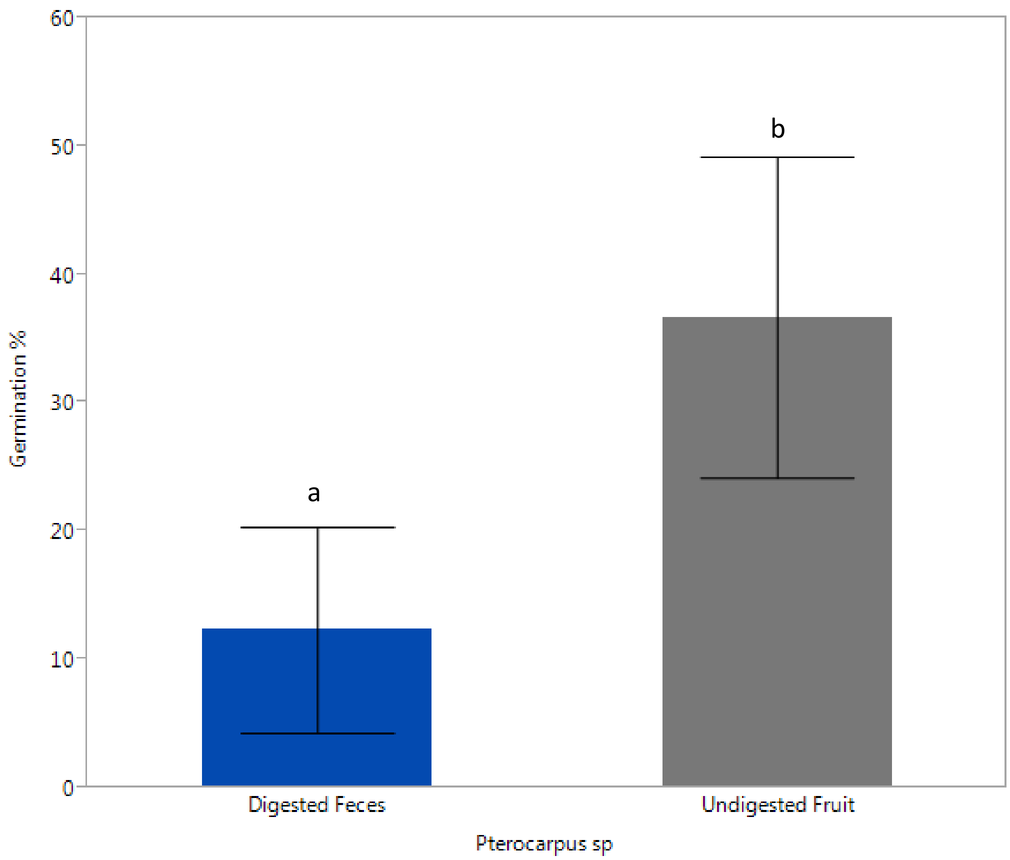

Figure 12. Mean and standard error for germination percentage of *Pterocarpus* sp. seeds ingested by Green Iguanas (*Iguana iguana*) in Puerto Rico, June and July 2013. Germination percentage is calculated from mean germination percentage of individual samples. *Pterocarpus* sp. includes native *Pterocarpus officinalis* and non-*native Pterocarpus indicus*. Same letters above bar denote no significant difference between treatments.

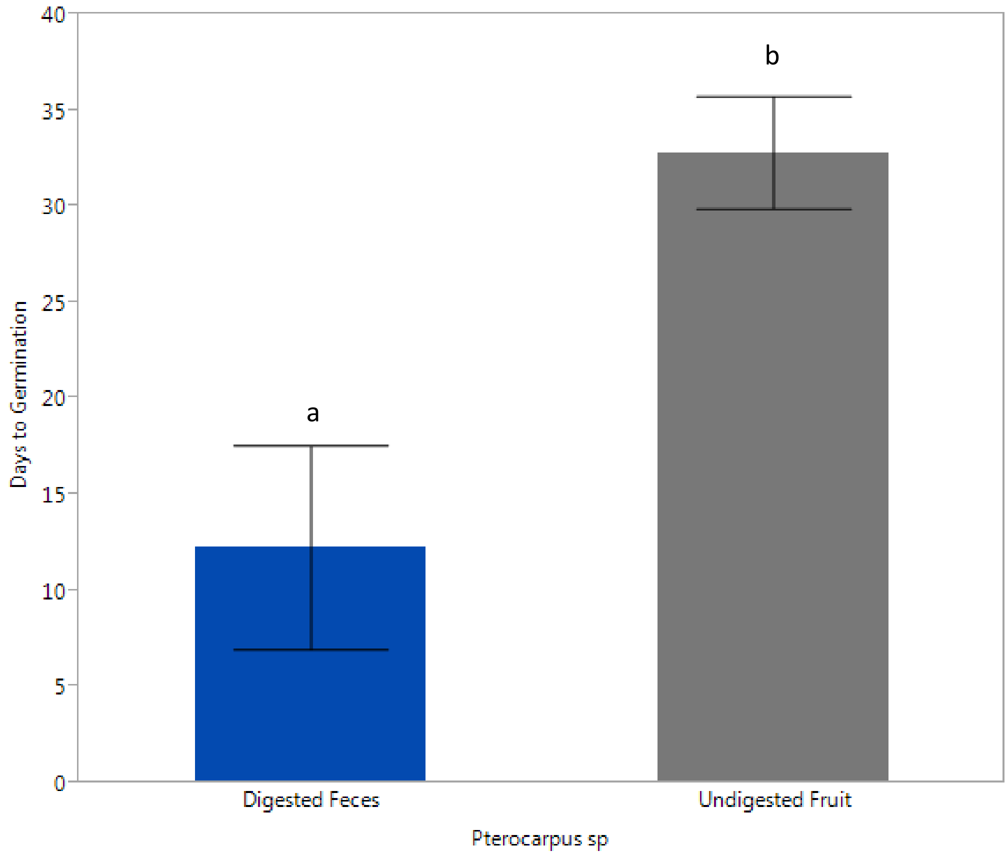

Figure 13. Mean and standard error for days to germination of *Pterocarpus* sp. seeds ingested by Green Iguanas (*Iguana iguana*) in Puerto Rico, June and July 2013. *Pterocarpus* sp. includes native *Pterocarpus officinalis* and non-*native Pterocarpus indicus*. Same letters above bar denote no significant difference between treatments.

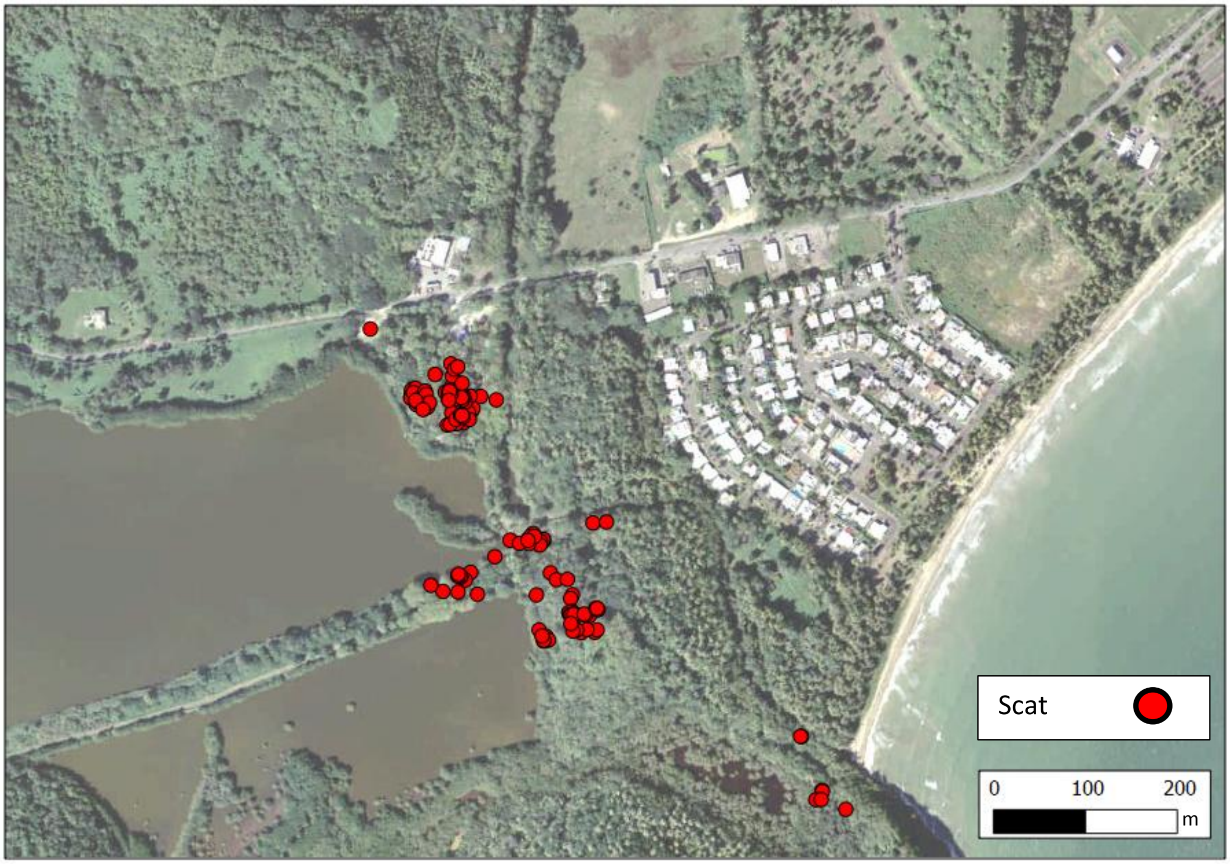

Figure 14. Location of Green Iguana scat samples collected at the Humacao Natural Reserve, Puerto Rico in June and July 2013. Circles indicate independent scat samples.

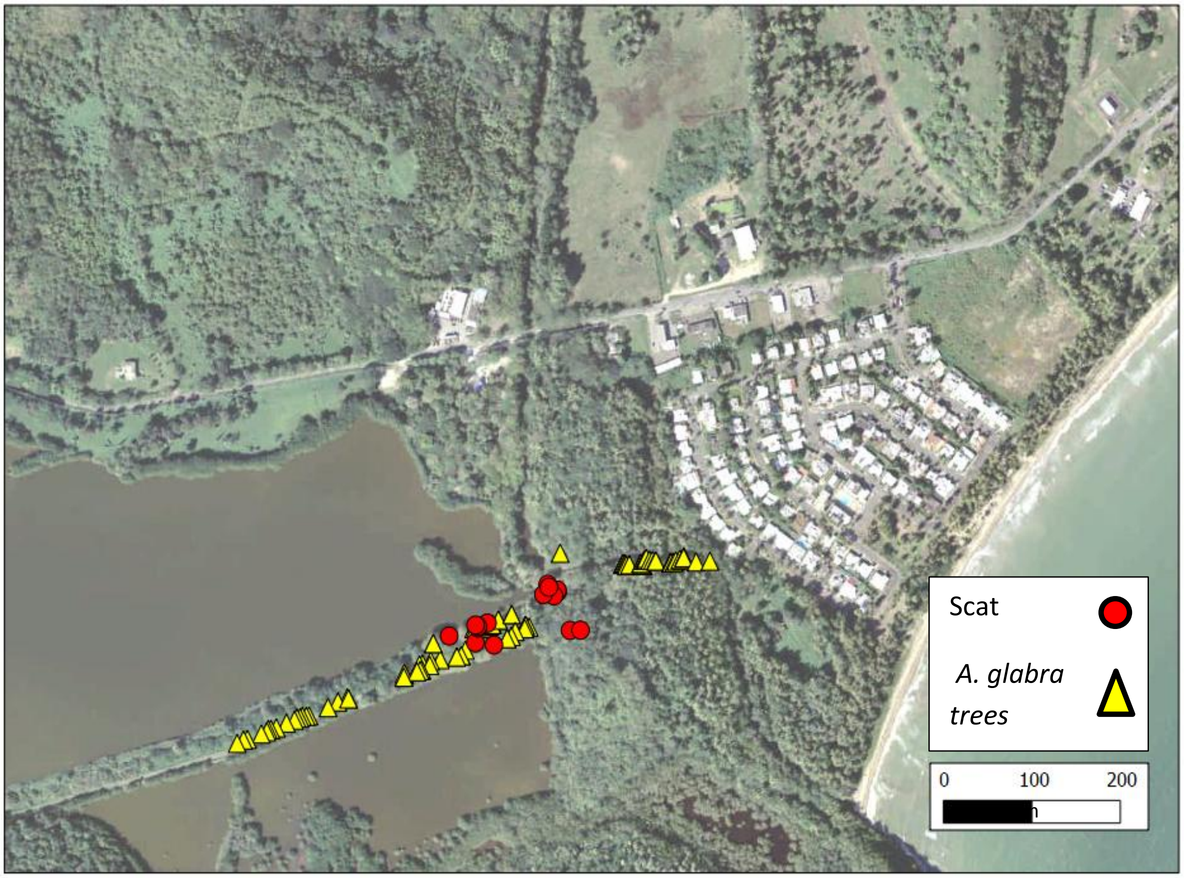

Figure 15. Location of Green Iguana scat samples containing native *Annona glabra* seeds and *Annona glabra* trees at the Humacao Natural Reserve, Puerto Rico in June and July 2013. Circles indicate scat samples containing *Annona glagra* seeds. Triangles indicate *Annona glabra* trees.

Figure 16. Location of Green Iguana scat samples containing *Pterocarpus* sp. seeds and *Pterocarpus* sp. trees at the Humacao Natural Reserve, Puerto Rico in June and July 2013. *Pterocarpus* sp. includes native *Pterocarpus officinalis* and non-native *Pterocarpus indicus*. Circles indicate scat samples containing *Pterocarpus* sp. seeds. Triangles indicate *Pterocarpus* sp. trees.

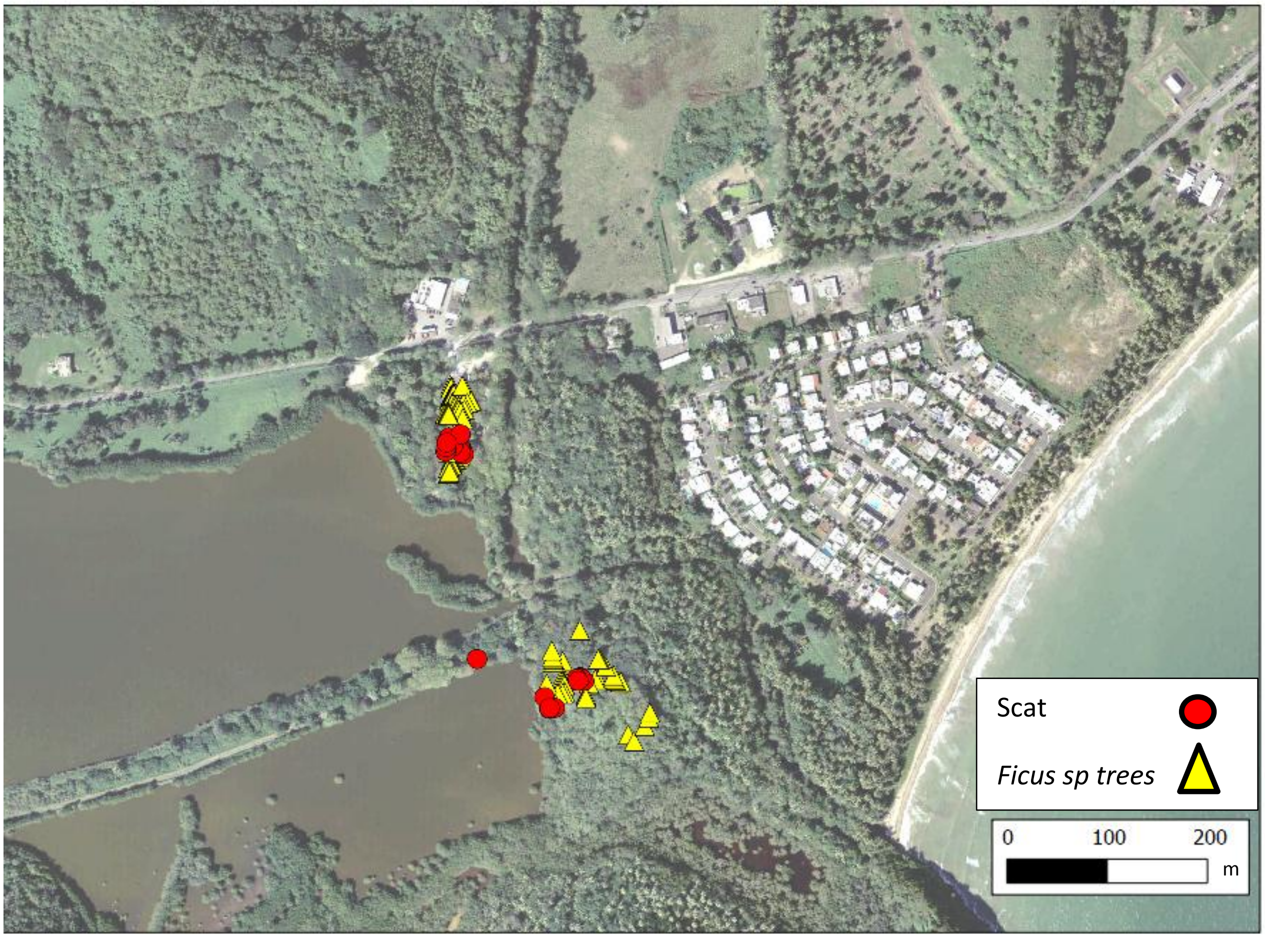

Figure 17. Location of Green Iguana scat samples containing *Ficus* sp. seeds and *Ficus* sp. trees at the Humacao Natural Reserve, Puerto Rico in June and July 2013. *Ficus* sp. includes native *Ficus citrifolia* and non-native *Ficus benjamina*. Circles indicate scat samples containing *Ficus* sp. seeds. Triangles indicate *Ficus* sp. trees.

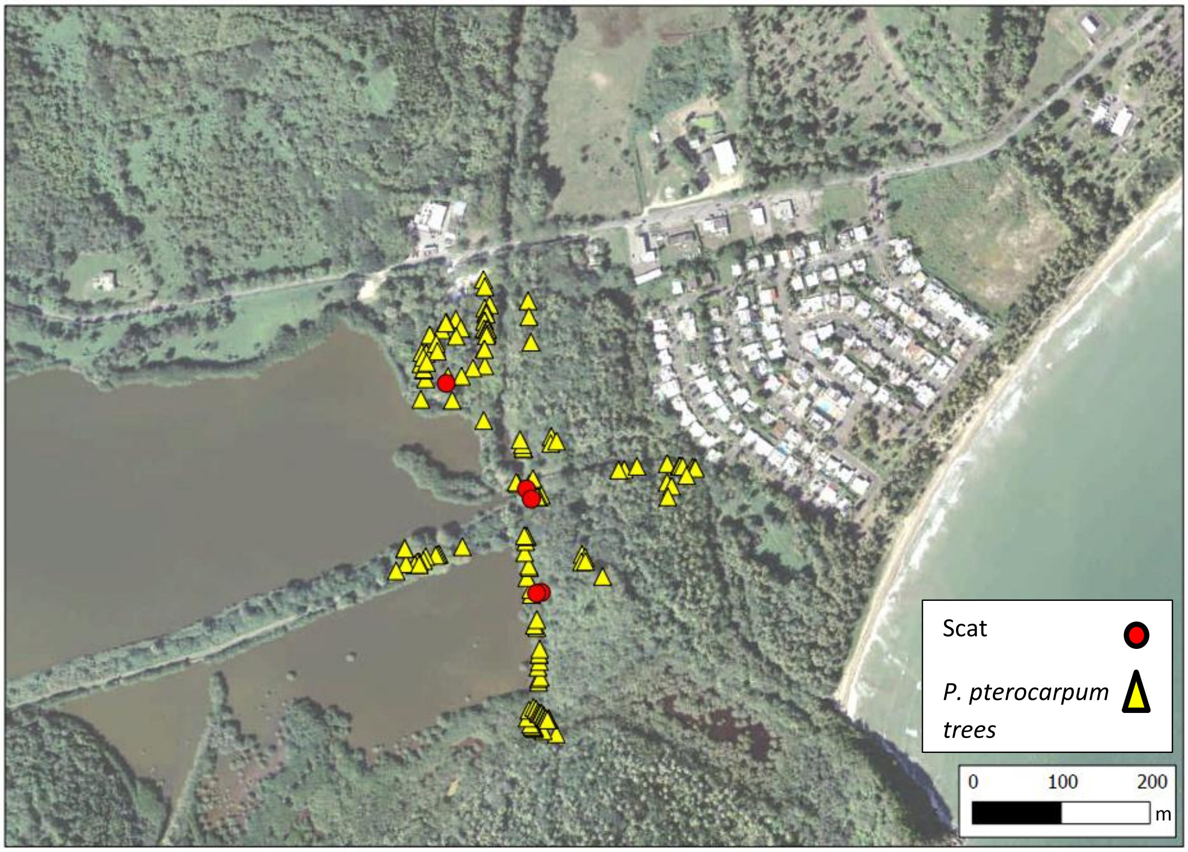

Figure 18. Location of Green Iguana scat samples containing non-native *P. pterocarpum* seeds and *P. pterocarpum* trees at the Humacao Natural Reserve, Puerto Rico in June and July 2013. Circles indicate scat samples containing *P. pterocarpum* seeds. Triangles indicate *P. ptercarpum* trees.

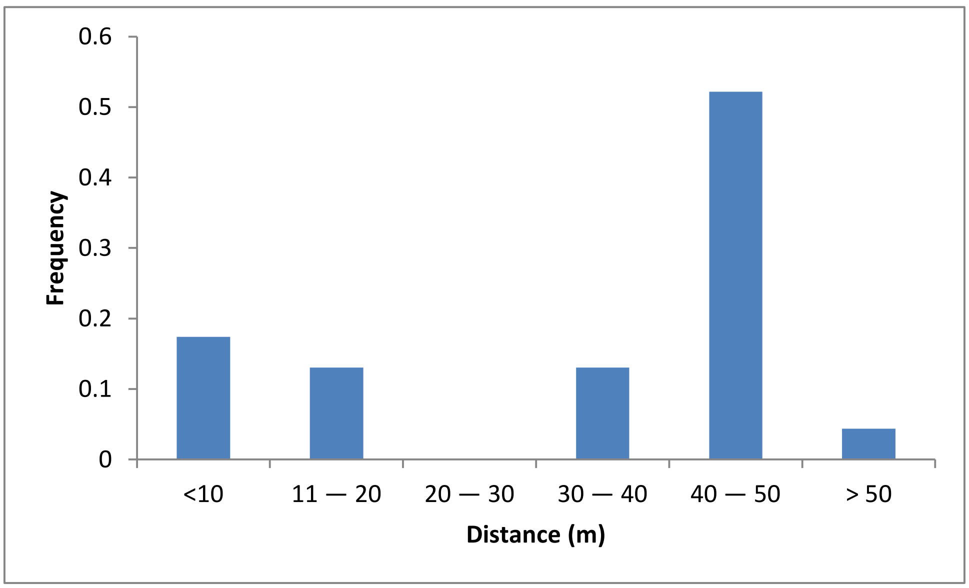

Figure 19. Frequency of minimum dispersal distances (m) for native *Annona glabra* seeds found in Green Iguana (*Iguana iguana*) scat samples in Puerto Rico, June and July 2013.

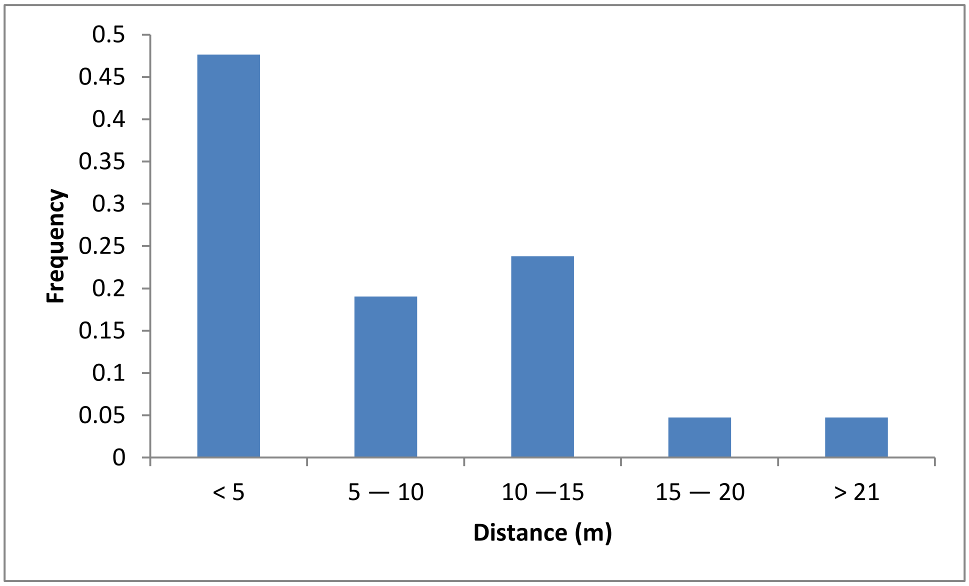

Figure 20. Frequency of minimum dispersal distances (m) for *Ficus* sp. seeds found in Green Iguana (*Iguana iguana*) scat samples in Puerto Rico, June and July 2013. *Ficus* sp. includes native *Ficus citrifolia* and non-native *Ficus benjamina*.

Table 1. Number of plant species represented by seeds and the total number of seeds found in Green Iguana scat samples in Puerto Rico, June and July 2013.

# Of plant species represented by seeds	Total # of Samples	Total Seeds	Mean # of Seeds by Sample	SD	Range
0	136	—	—	—	—
1	84	511	6.08	8.08	1 — 39
2	34	413	12.15	15.01	2 — 70
3	4	82	20.50	5.41	12 — 27
Total	258	1006	3.90	8.59	1 — 70

Table 2. Content of Green Iguana scat samples from Puerto Rico in June and July 2013. Unknown 1 could not be identified to the species level.

Species	**# of scat samples containing seeds from this species (n=122)**	**% scat samples containing seeds from this species (n=1006)**	**Total # of seeds from this species**	**% of seed from total seed**	**Mean # of seeds per scat sample (SD, Range)**
A. glabra	44	36.06	490	48.7	17.3 (13.45, 1-69)
Ficus sp.	26	21.31	172	17.09	6.62 (9.11, 1-46)
P. pterocarpum	13	13.11	35	3.48	2.18 (2.25, 1-5)
Pterocarpus sp.	16	10.65	34	3.38	2.65 (2.2, 1-7)
Unknown 1	26	21.31	109	10.83	4.19 (3.64, 1-13)
Others	36	29.5	166	16.5	6 (7.03, 1-31)

Table 3. Germination percentage for seeds digested by Green Iguanas and undigested seeds of *A. glabra*, *C. papaya*, *Ficus* sp., *P. pterocarpum*, and *Pterocarpus* sp. in Puerto Rico, June and July 2013.

Species	Treatment	Total # of seeds planted	Mean # Seeds planted per scat (SD)	Total # of seed germinated	Mean # of germinated seeds per unit (SD)	Germination percentage (SD)
Annona glabar	Digested seeds without feces	139	3.23 (2.9)	6	0.13 (0.3)	4.31 (0.17)
	Digested seeds with feces	145	3.37 (2.9)	8	0.18 (0.3)	5.51 (0.1)
	Undigested seeds without fruit	140	—	4	0.09 (0.07)	2.85 (0.07)
	Undigested seeds with fruit	146	—	6	0.14 (0.3)	4.10 (0.1)
Carica papaya	Digested seeds without feces	89	5.56 (4.4)	67	4.18 (3.8)	75.28 (0.2)
	Digested seeds with feces	91	5.68 (4.7)	61	3.81 (4.5)	67.03 (0.3)
	Undigested seeds without fruit	90	—	81	4.8 (4.5)	90 (0.3)
	Undigested seeds with fruit	92	—	77	4.41 (3.7)	83.69 (0.3)
Ficus sp.	Digested seeds without feces	51	2.12 (1.8)	25	1.04 (1.4)	49.01 (0.4)
	Digested seeds with feces	60	2.5 (1.6)	27	1.12 (1.5)	45 (0.4)
	Undigested seeds without fruit	52	—	30	1.5 (1.4)	57.69 (0.3)
	Undigested seeds with fruit	51	—	25	1.27 (1.2)	49.01 (0.4)
Peltophorum pterocarpum	Digested seeds without feces	–	–	–	–	–
	Digested seeds with feces	29	2.07 (1.6)	3	0.21 (0.5)	10.34 (0.2)
	Undigested seeds without fruit	–	–	–	–	–
	Undigested seeds with fruit	28	—	11	0.78 (1.1)	39.28 (0.4)
Pterocarpus sp.	Digested seeds without feces	–	–	–	–	–
	Digested seeds with feces	31	2.38 (1.8)	4	0.31 (0.6)	12.90 (0.2)
	Undigested seeds without fruit	–	–	–	–	–
	Undigested seeds with fruit	30	—	14	1.07 (1.5)	46.66 (0.4)

Table 4. Comparison of germination percentage for *A. glabra*, *C. papaya*, *Ficus* sp., *P.pterocarpum*, and *Ptercocarpus* sp. Asterisks denote significant differences at the P < 0.05 level.

	A. glabra				*C. papaya*				*Ficus sp.*				*P. pterocarpum*				*Pterocarpus sp.*			
Model	**–Log Likelihood**	**Chi-square**	**Df**	**P**	**–Log Likelihood**	**Chi-square**	**Df**	**P**	**–Log Likelihood**	**Chi-square**	**Df**	**P**	**–Log Likelihood**	**Chi-square**	**Df**	**P**	**–Log Likelihood**	**Chi-square**	**Df**	**P**
Difference	0.54	1.09	3	0.77	3.85	7.712	3	0.05*	0.63	1.26	3	0.73	2.45	4.896	1	0.0269*	3.5	6.973	1	0.0083*
Full	58.36				44.65				70.85				15.61				17.3			
Reduce	58.91				48.5				71.49				18.06				20.8			

* significant

Table 5. Days to germination for seeds digested by Green Iguanas and undigested seeds of *A. glabra*, *C. papaya*, *Ficus* sp., *P. pterocarpum*, and *Pterocarpus* sp. in Puerto Rico, June and July 2013.

Species	Treatment	# Planted	Mean Days to Germination
Annona glabar	Digested seeds without feces	5	46 (3.6)
	Digested seeds with feces	8	24.12 (17.6)
	Undigested seeds without fruit	4	28.75 (25.7)
	Undigested seeds with fruit	6	39.16 (19.7)
Carica papaya	Digested seeds without feces	66	16.61 (6.4)
	Digested seeds with feces	66	14.46 (4.1)
	Undigested seeds without fruit	77	13.98 (5.1)
	Undigested seeds with fruit	70	15.70 (5.2)
Ficus sp.	Digested seeds without feces	25	22.08 (6.8)
	Digested seeds with feces	28	20.64 (7.1)
	Undigested seeds without fruit	36	24.31 (12.7)
	Undigested seeds with fruit	31	31.91 (13.3)
Peltophorum pterocarpum	Digested seeds without feces	–	–
	Digested seeds with feces	7	15.0 (5.6)
	Undigested seeds without fruit	–	–
	Undigested seeds with fruit	11	31.63 (14.0)
Pterocarpus sp.	Digested seeds without feces	–	–
	Digested seeds with feces	4	12.25 (10.6)
	Undigested seeds without fruit	–	–
	Undigested seeds with fruit	15	32.8 (11.3)

Table 6. (A) Comparison of days to germination of *A. glabra*, *C. papaya*, Ficus sp., *P. pterocarpum*, and *Ptercocarpus* sp. in Puerto Rico, June and July 2013. (B) Pairwise comparisons of treatments. Asterisks denote significant differences at the P < 0.05 level.

A	*A. glabra*				*C. papaya*				*Ficus sp.*				*P. pterocarpum*				*Pterocarpus sp.*			
Source	**DF**	**MS**	**F-Ratio**	**P**	**DF**	**MS**	**F-Ratio**	**P**	**DF**	**MS**	**F-Ratio**	**P**	**DF**	**MS**	**F-Ratio**	**P**	**DF**	**MS**	**F-Ratio**	**P**
Treatment	3	1.04	2.01	0.48	3	134.5	4.8	0.0027*	3	0.78	3.72	0.0134*	1	2.06	9.68	0.0067*	1	1333.6	10.6	0.0047*
Error	19	0.52			275	27.8			116	0.21			16	0.213			17	125.8		
C. Total	22				278				119				17				18			

* significant

B	*Ficus sp.*				*C. papaya*			
	Digested without Feces	Digested with Feces	Undigested without Fruit	Undigested with Fruit	Digested without Feces	Digested with Feces	Undigested without Fruit	Undigested with Fruit
Digested without Feces	—	0.94	0.99	0.08	—	0.045*	0.0025*	0.56
Digested with Feces	0.94	—	0.88	0.0146*	0.045*	—	0.83	0.52
Undigested without Fruit	0.99	0.88	—	0.06	0.0025*	0.83	—	0.11
Undigested with Fruit	0.08	0.0146*	0.06	—	0.56	0.52	0.11	—

* significant

Table 7. Mean minimum dispersal distance (m) for seeds of native *A. glabra*, *Ficus sp*., *Pterocarpus sp*., and non-native *P. pterocarpum* in Puerto Rico, June and July 2013.

Vegetative Species	Mean Minimum Dispersal (m)	N	SD	Range (m)
A. glabra	33	23	18	1 — 59
Ficus sp	10	21	16	1 — 74
P. pterocarpum	8	5	3	6 — 12
Pterocarpus sp	20	5	32	4 — 76

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