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INVASION NOTE

Effects of invasive Green Iguanas (*Iguana iguana*) on seed germination and seed dispersal potential in southeastern Puerto Rico

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Abstract Green Iguanas (*Iguana iguana*) are invasive in Puerto Rico due to a variety of negative economic effects, yet we know very little about their ecological impacts. Because they are herbivorous, defecate intact seeds, move through the forest, and have long gut-passage times, Green Iguanas may affect seed germination and seed dispersal. In summer 2013, a total of 258 Green Iguana scat samples were collected at the Humacao Natural Reserve in southeastern Puerto Rico. Seeds extracted from scat and collected from fruit were planted under common garden conditions using experimental treatments designed to tease apart the effects of feces, fruit, and ingestion on seed germination. Green Iguanas decreased the time for seeds to germinate in *Ficus* spp. by removing fruit pulp, but had no effect on germination of native *Annona glabra* seeds. For non-native *P. pterocarpus* and *Pterocarpus* spp., Green Iguanas produced conflicting results, decreasing the percentage of seeds germinating, but at the same time, reducing the time for seeds to germinate. Green Iguanas likely disperse most seeds beyond the canopies of parental tree at our site. Government and economic resources are being used to eradicate Green Iguana populations in Puerto Rico, but the lack of consistent effects of Green Iguanas on seed germination for the plant species consumed at our site complicates generalizing about their ecological effects and developing management plans that minimize negative effects for native plant communities. We recommend additional studies that target both species of particular concern, such as threatened native or invasive species, as well as studies of sensitive habitats in Puerto Rico.

Keywords *Annona glabra* · Introduced herbivore · Lizard · Mangrove forest · Non-native range · *Peltophorum pterocarpum* · Saurochory

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Introduction

The Green Iguana (*Iguana iguana*) has been introduced to Puerto Rico, Florida, and many islands in the Lesser Antilles and Pacific, primarily as a result of the exotic pet trade (Rivero 1998). Its native range extends from Mexico to tropical/subtropical South America (Rivero 1998). Green Iguanas are widespread and abundant in their introduced range with some studies estimating a threefold higher abundance compared to their native range (López-Torres et al. 2012; but see Arce-Nazario and Carlo 2012). Green Iguanas are sometimes associated with agricultural loss, commercial and residential landscape damage, erosion hazards, salmonella infection, and are a threat to aviation because they bask on runways (López-Torres et al. 2012; but see García-Quijano et al. 2011). Because of these negative impacts on the economy, the government of Puerto Rico has classified Green Iguanas as a nuisance pest. Despite these well-known economic costs, we know little about potential ecological effects of Green Iguanas. Introduction of this large herbivore might affect the diversity and abundance of native and non-native plant species through direct herbivory as well as its effect on seed dispersal and germination, which could influence community composition.

Some studies have characterized the distribution, diet, and reproduction patterns of Green Iguanas in Puerto Rico (García-Quijano et al. 2011; Govender et al. 2012; López-Torres et al. 2012), but no study has assessed effects on seed germination and the potential for seed dispersal by Green Iguanas. This species feeds primarily on vegetation, specifically leaves, flowers and fruits (Rand et al. 1990; Lara-López and González-Romero 2002; Figueiredo-de-Andrade et al. 2011; Govender et al. 2012). Green Iguanas have a number of characteristics that should make them successful seed dispersers, including consumption of fruits, relatively long passage times, microbial activity in the intestinal tract, and the ability to swallow food in large portions, which allows them to process seeds without destroying them by chewing (Troyer 1984a,b; van Marken 1992; Schupp 1993). Green Iguanas do not generally have extensive home ranges, varying between 0.65 and 0.95 ha (Rand et al. 1989), and daily movements can average 10 m or less (Escobar et al. 2010). However, their ability to move across the landscape creates the potential for seed dispersal to environments not otherwise easily accessed, such as upstream habitats or dense forests that limit dispersal through the air, and they make some longer-distance movements associated with seasonal reproduction.

Effects of digestion on seed germination are common in reptile, mammal, and bird seed dispersers, both enhancing and inhibiting seed germination (Traveset 1998). For example, frugivores potentially enhance germination by removing pulp from the seeds, which can contain germination inhibitors or support potentially infectious fungi and bacteria (Traveset 1998). Green Iguanas are known to decrease the time to germination under experimental conditions for some plant species in their native range (Morales-Mávil 1997; Benítez-Malvido et al. 2003). Whether Green Iguanas have a significant effect on seed germination in Puerto Rican plant communities composed of both native and non-native plant species is not known.

In this study, we assessed the potential for invasive Green Iguanas to effect seed germination and seed dispersal in a mesic, mangrove habitat in Puerto Rico. We experimentally tested for possible seed germination effects for several tropical plant species that are naturally consumed by Green Iguanas. We also quantified minimum dispersal distances for the most common seeds consumed by Green Iguanas. Because Green Iguanas are the largest and most abundant vertebrate frugivore in Puerto Rican mangrove forests, their impact on seed germination may be important for plant community structure (Iverson 1985). Previous studies of Green Iguana diet in Puerto Rico have found they consume plant material from both native and non-native species, including seeds of the highly invasive Brazilian pepper, *Schinus terebinthifolius* (Govender et al. 2012). If Green Iguanas promote the germination of non-native species compared to native species, then they could pose a threat to native communities by facilitating the spread of potentially invasive species.

Methods

We conducted this study at the Natural Reserve of Humacao (NRH) in southeastern Puerto Rico. Within the NRH, we concentrated our efforts near the Palmas Lagoon, a mangrove forest with white mangroves (*Laguncularia racemosa*) and successional vegetation on higher elevation substrate. We collected Green Iguana scat samples from mid-June through July 2013 in $\sim$0.15 km^2 of the 10.5 km^2 reserve, focusing primarily along hiking paths in the forest. Samples were found primarily on the ground, and locations of most scat samples were recorded using GPS. We were careful to collect all adjacent pellets as a single sample. We also recorded GPS coordinates for all mature trees of our focal species in the study area.

Green Iguana scat samples were stored out of the sun in plastic bags at room temperature, and dissected less than 1 week after collection. We used a dissecting microscope and magnifying glass to extract seeds from the scat sample; some small seeds may have been below detection limits using this method. No water was used because it could initiate the germination process prior to planting the seeds. We identified seeds in scat samples from four main tree species—*Annona glabra*, *Ficus* spp., *Peltophorum pterocarpum*, and *Pterocarpus* spp.—by comparing them to reference samples from fruits collected at our site (see details in the Supplementary Materials). For germination trials, we used these seeds and others collected from 3 to 10 individuals of each tree species for control treatments.

Our germination experiment consisted of four treatments under common growth conditions: (1) seeds that have not passed through the Green Iguana gastrointestinal tract without fruit pulp; (2) seeds that have not passed through the Green Iguana gastrointestinal tract with 0.5 g fruit pulp; (3) seeds that have passed through the Green Iguana gastrointestinal tract mixed with 0.5 g fecal material; and (4) seeds that have passed through the Green Iguana gastrointestinal tract without fecal material. These four treatments allow us to separate the effects of gut-passage, fruit pulp removal, and the presence of feces (Samuels and Levey 2005), giving us a robust way to evaluate the overall effect of Green Iguanas on seed germination.

Seeds were planted individually in clean commercial soil in plastic germination domes as they were found in scat samples, alternating treatments. Up to 14 seeds from each scat sample were planted with an equivalent number of control seeds. For *A. glabra*, individual unaltered seeds were used because this species produces discrete units of pulp with each seed. For treatments that included clean seeds, tissue paper was used to clean the seeds, but not water. All treatments were not possible for *Peltophorum pterocarpum* and *Pterocarpus* spp. because feces could not be completely cleaned from the seeds, so the treatment consisting of ingested seeds without feces was not possible. Additionally, the treatment of seeds with fruit pulp was not possible because both species have fruits that lack pulp. Domes were housed in a covered, well-lighted area near the University of Puerto Rico Rio Piedras, exposed to natural light cycles, and rotated daily to account for possible microclimate differences. Seeds were watered daily using a pressure sprayer for a period of 60 days and checked daily for germination. Successful germination was scored when shoots emerged from the soil.

To estimate the minimum dispersal distance of seeds, we calculated the difference between the mean overstory radius for a sample of trees from each focal species and the mean distance from scat samples containing seeds to the nearest seed-producing tree of the same species. We considered this a conservative estimate of seed dispersal distance by Green Iguanas at our study site (Moura et al. 2015).

We measured two responses in the germination experiment, germination percentage (i.e., the number of germinating seeds out of the total number planted) and time to germination (i.e., the number of days to germination). We used analysis of variance (ANOVA) to test for differences among the treatments for (log) time to germination, and Tukey's Honestly Significant Difference (HSD) tests to determine differences among treatment levels. We used a General Linear Model (GLM) to test for differences among the treatments for germination percentage, following Crawley (2007) but implemented in JMP v. 11 (SAS Institute, Inc 2014). Because germination percentage was calculated as a proportion, the results were bounded (0–1). We used a binomial distribution using a binomial denominator, which is a two-vector response that accounts for the number of germinated seeds versus the number of planted seeds. We used analysis of variance (ANOVA) to test for differences among the focal species in (log) minimum distance of scat samples from the nearest parental tree, and Tukey's HSD tests to determine differences among the four focal species. We used JMP v. 11 to conduct all statistical analysis (SAS Institute, Inc 2014).

Results

We collected a total of 258 Green Iguana scat samples, of which 122 (47 %) contained seeds. Most scat samples contained only one species of seed (68 %), but some contained two (27 %) or three (5 %) different species of seeds with an average of 8.2 seeds per scat (Table 1). *Annona glabra* was the most common species found in scat at 36 % of samples, followed by *Ficus* spp. at 21 %, an unidentified single species 'Unknown' at 21 %, *P. pterocarpum* at 13 %, and *Pterocarpus* spp. at 11 % (Table 1). In terms of the total numbers of seeds in scat, *A. glabra* seeds were most common at 49 %, followed by *Ficus* spp. at

Table 1 Seed contents from Green Iguana scat samples collected at the NRH in Puerto Rico in June and July 2013

Tree species	Scat samples containing seeds from this species	Percentage of scat samples containing seeds from this species %	Total number of seeds from this species	Percentage of the total number of seeds %	Seeds per scat sample (mean ± SD, range)
Annona glabra	44	36.1	490	48.7	17.3 ± 13.4 (1–69)
Ficus spp.	26	21.3	172	17.1	6.6 ± 9.1 (1–46)
Peltophorum pterocarpum	13	13.1	35	3.5	2.2 ± 2.3 (1–5)
Pterocarpus spp.	16	10.6	34	3.4	2.6 ± 2.2 (1–7)
Unknown	26	21.3	109	10.8	4.2 ± 3.6 (1–13)
Others	36	29.5	166	16.5	6.0 ± 7.0 (1–31)

We collected 258 scat samples, of these 122 samples contained seeds from one to three different tree species. Seeds of a single species 'Unknown' could not be identified. 'Others' indicates additional unidentifiable seeds from multiple species present in scat samples. A total of 1006 seeds were found in green iguana scat

17 %, *P. pterocarpum* at 4 %, and *Pterocarpus* spp. at 3 % (Table 1).

There were no significant differences in germination percentage among treatments for *A. glabra* ($X^2 = 1.09$, df $= 3$, $P = 0.77$) or *Ficus* spp. ($X^2 = 1.26$, df $= 3$, $P = 0.73$; Table 2). In contrast, a greater percentage of uningested seeds without fruit pulp than ingested seeds with feces germinated for *P. pterocarpum* ($X^2 = 4.90$, df $= 3$, $P = 0.03$) and *Pterocarpus* spp. ($X^2 = 6.97$, df $= 3$, $P = 0.008$; Table 2), but few total seeds germinated for these species. Time to germination did not differ among treatments for *A. glabra* ($F_{3,19} = 2.01$, $P = 0.48$; Table 2). In contrast, germination times differed among treatments for *Ficus* spp. ($F_{3,116} = 3.72$, $P = 0.01$), *P. pterocarpum* ($F_{1,16} = 9.68$, $P = 0.007$), and *Pterocarpus* spp. ($F_{1,17} = 10.6$, $P = 0.005$; Table 2; Fig. 1). Green Iguana effects on seed germination differed among the four focal plant species, decreasing the percentage of seeds germinating in some instances (*P. pterocarpum* and *Pterocarpus* spp.) and reducing the number of days to germination in others (*Ficus* spp., *P. pterocarpum*, and *Pterocarpus* spp.).

The minimum distance between Green Iguana scat samples containing seeds of a focal species and the nearest mature tree of the same species differed among the four focal species ($F_{3,50} = 6.84$, $P = 0.0006$). Tukey's HSD tests showed that *A. glabra* seeds (mean = 33.0 m) were found significantly farther from the nearest tree than *Ficus* spp. seeds (mean = 9.9 m; Fig. 2; Supplementary Table 1). For all species, the average minimum dispersal distance exceeded the mean canopy shadow as measured by the radius of the overstory canopy (Supplementary Table 1), suggesting a role for Green Iguanas in seed dispersal regardless of their effects on seed germination.

Discussion

Green Iguanas in Puerto Rico consumed fruits from both native and non-native plant species and these seeds were likely dispersed beyond the canopies of parent trees in most cases. Effects on seed germination varied among tree species as well as between measures of seed germination, which makes predicting the community-wide impacts of fruit consumption by invasive Green Iguanas difficult.

Ficus spp. can be a keystone species for herbivores due to their abundant year round fruit presence (Santinelo Pereira et al. 2007). Yet, native range studies have found no evidence of *Ficus* seed consumption by Green Iguanas (Rand et al. 1990; Lara-López and González-Romero 2002; Benítez-Malvido et al. 2003). In contrast, Green Iguanas in Puerto Rico had *Ficus* spp. seeds in 21 % of scat samples and fruit pulp removal led to a 24–35 % reduction in the number of days for *Ficus* spp. seeds to

Table 2 Summary of seeds planted under common garden conditions, and germination success in terms of the percentage of seeds germinating and time to germination (i.e., days to germination) for experimental treatments

Tree species	Treatment	Total no. of seeds planted	Seeds planted per scat (mean ± SD)	Total no. of seeds germinated	Germination percentage (mean ± SD)	Time to germination in days (mean ± SD)
Annona glabra	Ingested seeds without feces	139	3.2 ± 3.0	6	4.9 ± 2.4	46.0 ± 3.7
	Ingested seeds with feces	145	3.3 ± 3.0	8	7.4 ± 2.8	24.1 ± 17.7
	Uningested seeds without fruit	140	–	4	2.0 ± 2.0	28.8 ± 25.7
	Uningested seeds with fruit	146	–	6	6.1 ± 2.4	39.2 ± 19.7
Ficus spp.	Ingested seeds without feces	51	2.1 ± 1.8	25	49.8 ± 3.6	22.1 ± 6.9
	Ingested seeds with feces	60	2.5 ± 1.6	27	40.3 ± 3.9	20.6 ± 7.1
	Uningested seeds without fruit	52	–	30	51.8 ± 3.6	24.3 ± 12.8
	Uningested seeds with fruit	51	–	25	48.2 ± 3.6	31.9 ± 13.3*
Peltophorum pterocarpum	Ingested seeds with feces	29	2.1 ± 1.6	3	8.6 ± 1.6	15.0 ± 5.7
	Uningested seeds without fruit	28	–	11	41.0 ± 2.6*	31.6 ± 14.0*
Pterocarpus spp.	Ingested seeds with feces	31	2.4 ± 1.9	4	12.3 ± 1.9	12.3 ± 10.6
	Uningested seeds without fruit	30	–	14	36.7 ± 2.7*	32.8 ± 11.3*

Seeds were found in Green Iguana scat and fruit at the NRH in Puerto Rico in June and July 2013. *Ficus* spp. may include the native *Ficus citrifolia* and non-native *Ficus benjamina*. *Pterocarpus* spp. may include the native *Pterocarpus officinalis* and non-native *Pterocarpus indicus*. The mean and SD for germination percentage are based on germination trials with seeds from individual scat samples and are not the overall germination percentage. Dashes indicate no data when seeds were derived from fruit for the seeds planted per scat column. Asterisks indicate experimental levels that differ significantly for germination percentage and time to germination (see Results for statistical tests)

germinate. Whether these effects on seed germination and dispersal by Green Iguanas are positive or negative for native plant communities in Puerto Rico depends on whether seeds are from native *F. citrifolia* or non-native *F. benjamina*, which we were unable to differentiate after Green Iguanas consumption.

Our two measures of germination success differed for *P. pterocarpus* and *Pterocarpus* spp. Ingestion by Green Iguanas reduced the number of days to germination for *P. pterocarpum* by 53 % and for *Pterocarpus* spp. by 63 %, but also decreased the percentage of seeds germinating in both species. Consumption and dispersal of seeds from the year round fruiting, non-native *P. pterocarpum* could make this species a high risk to native plant communities. However, these potential negative effects are tempered in this case because *P. pterocarpum* seeds account for only 3.5 % of the total number of seeds in

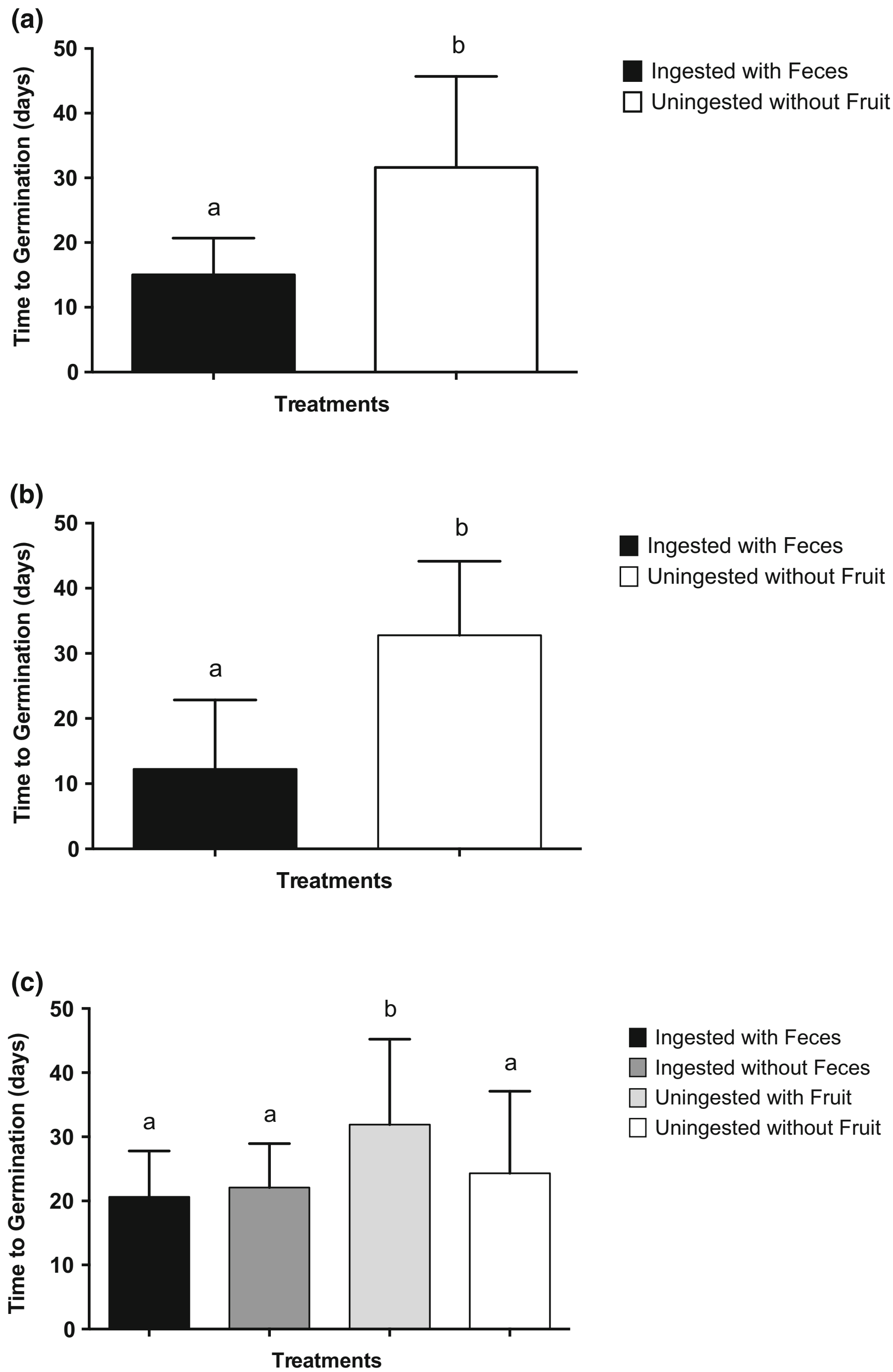

Fig. 1 Mean (±SD) for time to germination (i.e., the number of days to germination) of **a** *P. pterocarpum*, **b** *Pterocarpus* spp., and **c** *Ficus* spp. seeds ingested by Green Iguanas in Puerto Rico. Different letters above bars denote a significant difference between treatments based on Tukey's HDS post hoc tests

Green Iguana scat. The seeds of other non-natives, such as the invasive Brazilian pepper (*Schinus terebinthifolius*) may be also affected by Green Iguana ingestion and dispersal, however, we could not determine the effect on this species because it was not present at our study site.

For native *A. glabra*, ingestion of seeds by Green Iguanas does not appear to affect germination;

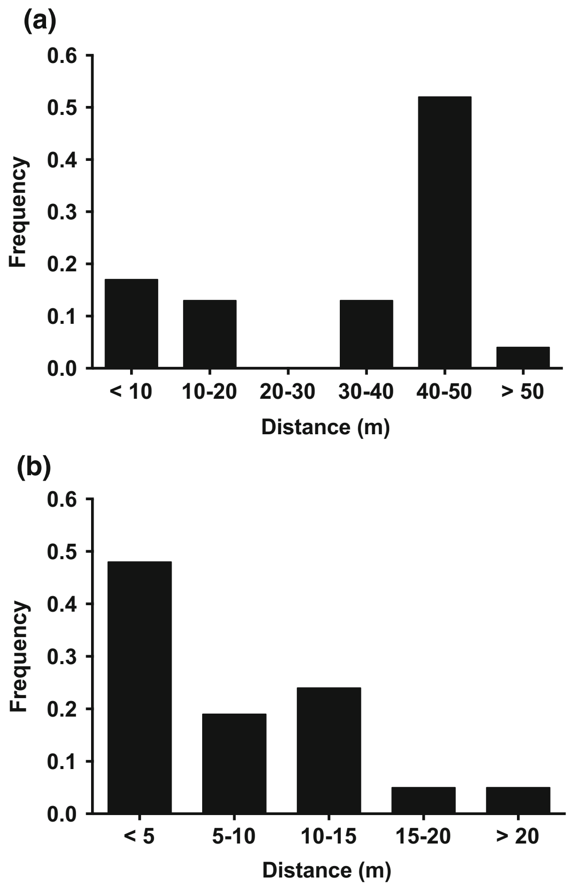

Fig. 2 Frequency of minimum distances of scat samples to seed-producing trees of the same species (m) for **a** *Annona glabra* (n = 23) and **b** *Ficus* spp. (n = 21) seeds found in Green Iguana scat samples. Minimum dispersal distances should be discounted by taking into account the overstory canopy radius for each tree species, which is on average 2.2 m for *Annona glabra* and 0.8 m for *Ficus* spp.

however, seed germination was overall very low for *A. glabra* as in previous studies (Infante Mata and Moreno-Casasola 2005; Table 2). Given that *A. glabra* seeds represented almost half of all seeds in feces (Table 1), Green Iguanas at our site may heavily use these fruits during summer months. This differs from previous studies in Puerto Rico and the native range where Green Iguanas occupy *A. glabra* trees, but have not been observed feeding on this species (Lara-López and González-Romero 2002; Figueiredo-de-Andrade et al. 2011). *Annona glabra* is a major component of the diet of the Puerto Rican slider turtle (*Trachemys stejnegeri stejnegeri*), which is a near threatened species that is listed as a critical element of Puerto Rico's fauna (Tortoise and Freshwater Turtle Specialist Group 1996). The Puerto Rican Department of Natural Resources (Departamento de Recursos Naturales y Ambientales 2009) lists the seasonally available fruit (from March to November) of *A. glabra* as an important component of the conservation of Puerto Rican sliders. Green Iguana consumption of *A. glabra* fruit might negatively affect Puerto Rican sliders by decreasing this food source. In contrast, Green Iguanas may have a positive effect by dispersing native *A. glabra* seeds, particularly to environments not otherwise easily accessed, such as upstream habitats and non-flooded inland habitats. However, whether these seeds are deposited in suitable microenvironments is unknown. Understanding the relative importance of positive and negative effects of Green Iguanas on *A. glabra* is an important area of future study.

Although eradication and control efforts of Green Iguanas to address potential economic loss and various hazards are already occurring in Puerto Rico, lack of information on specific negative ecological effects of this invasive species limit efforts to reduce ecological impacts. Our study shows that Green Iguanas effect seed germination and dispersal of both native and non-native plant species. Given these species-specific effects, it is difficult to predict the overall effects of Green Iguanas on mangrove forests and other communities in Puerto Rico. Therefore, future ecological research should target specific plant species and communities to assess the longer-term effects of Green Iguanas on seed germination and dispersal, particularly on plant species available at different times of the year.

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