Can green iguanas compensate for vanishing seed dispersers in the Atlantic forest fragments of north-east Brazil?

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Abstract

The Atlantic forest of Brazil is a biodiversity hot spot, but is extremely fragmented. Local extinction of important seed dispersers, such as primates, threatens the maintenance of these fragments. It is important to evaluate the capacity of fragment-tolerant species to disperse seeds and help maintain plant communities within fragments. Green iguanas *Iguana iguana* are large, fragment-tolerant, canopy-dwelling lizards and have been noted to disperse seeds. We described the seed dispersal patterns produced by green iguanas in six urban forest fragments (1.2–8 ha in size) in the Atlantic forest of north-east Brazil, over 20 months. A total of 294 seeds were counted in 321 scats, and 12 plant species were dispersed. The largest seeds dispersed were 14.9 mm long and up to 9.2 mm wide. Iguanas deposited 86.9% of scats within latrines, which were used over a mean of at least 9 months. We show that iguanas can be effective seed dispersers and might partially replicate deposition patterns produced by howler monkeys in other studies. It is critical that we improve our understanding on the functional roles played by these cryptic, yet common, iguanas in order to determine whether they could buffer the negative effects caused by the local extinction of primates from forest fragments.

Introduction

High rates of deforestation throughout the world have resulted in extensive fragmentation of many native habitats, with associated losses of biodiversity (Pereira *et al*., 2010) and alterations of ecological interactions necessary to maintain ecosystems (Hooper *et al*., 2012; Naeem, Duffy & Zavaleta, 2012). Seed dispersal is a critical process in the maintenance and recovery of habitats, and is directly impacted by ecosystem disturbance (McConkey *et al*., 2012). Plant species with large-seeded fruits are most at threat from recruitment failure, because they are often dependent on large, fruit-eating animal species for dispersal (Silva & Tabarelli, 2000), and these animals are the most vulnerable to fragmentation (Peres & Palacios, 2007; Markl *et al*., 2012).

The Atlantic forest of Brazil has lost up to 84% of its original cover (Ribeiro *et al*., 2009) and coupled with the resulting fragmentation are dramatic losses of biodiversity (Coimbra-Filho & Câmara, 1996; Ribeiro *et al*., 2009). The north-eastern region is the most severely fragmented, with larger forest fragments (>8000 ha) almost non-existent (Ranta *et al*., 1998; Ribeiro *et al*., 2009) and all medium- and large-bodied mammals eradicated from most fragments (Silva & Pontes, 2008; Canale *et al*., 2012). The local extinction of fruit-eating primates (Coimbra-Filho & Câmara, 1996; Silva & Pontes, 2008) has negatively affected seed dispersal of zoochorous trees within fragments (Silva & Tabarelli, 2000; Markl *et al*., 2012), and this may initiate further declines in species diversity and changes in forest structure (Terborgh *et al*., 2008; McConkey *et al*., 2012). Only a few primate species can persist within the fragments, but even highly tolerant species are absent in most fragments (Canale *et al*., 2012). There is an urgent need to evaluate the capacity for less-specialized, but fragment-tolerant, fauna to compensate for the lost seed dispersal function of primates.

Lizards are considered to play significant roles in seed dispersal in some habitats (Godinez-Alvarez, 2004; Rodríguez-Perez, Wiegand & Santamaría, 2012), and the larger species can disperse large-seeded fruit (Swanson, 1950). Many lizard taxa inhabit tropical forests, and may have the capacity to partially compensate for functional losses of seed-dispersing primates, but there is a dearth of information on their functional roles in forests (Valido & Olesen, 2007). The green iguana *Iguana iguana* has the widest geographical

distribution among the neotropical lizards (Central America to southern Brazil and Paraguay) and occupies a variety of habitats (Vitt & Caldwell, 2009). *Iguana iguana* are arboreal, medium-sized lizards (6 kg; length: 1.7 m: Swanson, 1950), and, like most other species of Iguanines (Iguanidae, 8 genera, 29 species), feed on leaves, flowers and fruits (Lazell, 1973; Rand *et al.*, 1990; Campbell, 1998; Godinez-Alvarez, 2004; Govender *et al.*, 2012). Although *I. iguana* disperse seeds (Valido & Olesen, 2007; Govender *et al.*, 2012), available information is scant. Iguanas can endure high levels of disturbance and are very common in forested fragments immersed in an anthropic matrix (Ávila-Pires, 1995), particularly where predators have become locally extinct (Terborgh *et al.*, 2001). In the highly fragmented Atlantic forests, they have the potential to have a major influence on plant species persistence.

Here, we describe seed dispersal by iguanas inhabiting Atlantic forest fragments in North-east Brazil. We determine whether *I. iguana* disperses seeds within fragments, and evaluate how their fruit diet and basic dispersal pattern compares with patterns of dispersal exhibited by fragment-tolerant primates, as reported in published studies.

Methods

Our study was conducted in forest fragments located at the Universidade Federal da Paraiba (7°6′54″ S 34°51′40″ W), Joao Pessoa, Paraiba, north-east Brazil. Nine fragments of semi-deciduous Atlantic forest (1.2–8.0 ha in size) occur within the university's grounds (Fig. 1). These fragments were connected with the Mata do Buraquinho (515 ha) until the 1960s, but are now separated by about 500 m of roads and buildings. Annual rainfall in the area is around 1500–1700 mm and the average temperature is 25°C (Lima & Heckendorff, 1985). Barbosa (1996) reported 52 tree species for the fragments (0.5 ha sampled; only trees with Diameter at Breast Height ≥ 5 cm analysed).

Iguana iguana scats were collected from May 2011 to July 2012 and from October 2013 to February 2014 on 10 walking trails of different lengths along the edge of six forest fragments (1.2–8.0 ha in size; separated by 8–20 m) (Fig. 1, Table 1). Each trail was monitored between 3 and 20 months and the total sampled area was 0.28 ha. Difficulty in locating scats within the leaf litter prevented collections within fragments. However iguanas often dispersed seeds from tree species that are only available in the forest interior, suggesting they move between interior and edge depending on available resources. Previous studies on forest-dwelling iguanas indicate that forest interiors are used (Lazell, 1973; Terborgh *et al.*, 1997; Morales-Mávil, Vogt & Gadsden-Esparza, 2007), although we have no information on their preferences. It is possible that the iguanas use the forest edge as sleeping or basking sites. We surveyed all trails two to three times a week, in the morning or afternoon. All scats were collected, their location recorded and then immersed in alcohol in the lab to facilitate seed extraction. Seeds found in the scats were counted, identified by A.C. de A. Moura, photographed using a stereo microscope Leica M205C with an apochromatic 20.5:1 Zoom and fusion optics technology Leica (Leica Microsystem, Wetzlar, Germany) and deposited in the Herpetological collection of Universidade Federal da Paraiba (UFPB). Length and width of seeds were measured with digital callipers. Dispersal distances were not systematically measured because of the difficulty of observing feeding iguanas (Supporting information Fig. S1), but whenever possible, distance from the nearest fruiting conspecific tree to the scats was noted, providing conservative distance estimates. The trails were swept regularly during term time (at intervals of 1/2 days), which reduced the number of scats collected.

Results

Seeds were found in 18.1% of collected iguana scats (*n* = 321 scats; *n* = 294 seeds; Table 1). Of the 12 plant species dispersed by iguanas in our study, the most common species were the
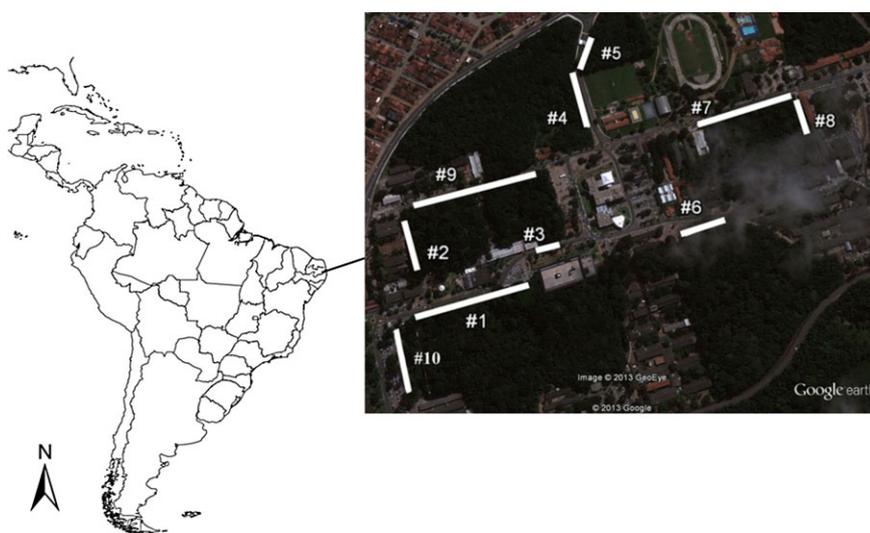
Table 1 Details of the trails surveyed for iguana scats, number of scats collected and latrines found

Fragment size (ha)	Trail No.	Length × width (m)	Sampling effort (months)	Number of scats with seeds (total # scats)	Number of latrines	Number of scats in latrines
8.0	#1	210.0 × 2.4	20	19 (96)	6	75
3.9	#2	94.0 × 2.1	15	0 (1)	0	0
3.9	#3	30.2 × 2.1	20	6 (19)	1	19
6.7	#4	130.0 × 2.4	20	0 (2)	0	0
1.2	#5	70.0 × 2.4	15	0 (0)	0	0
6.2	#6	72.8 × 2.4	20	13 (82)	1	76
3.8	#7	207.0 × 2.4	20	4 (34)	1	32
3.8	#8	75.5 × 2.0	3	4 (15)	1	14
3.9	#9	223.0 × 2.1	8	7 (57)	2	48
8.0	#10	135.0 × 2.0	5	5 (15)	1	15

Location of trails are indicated in Fig. 1.

Table 2 List of fruit species consumed by green iguanas and primates

Family	Species	Iguanas Number of seeds	Seed size[a] (mean ± SD) Length (mm)	Width (mm)	Number of scats	Ca	Ho	Ma	Source[b]
Anacardiaceae	*Tapirira guianensis*[a]	123	9.32 ± 0.92	6.58 ± 0.55	19	✓	✓	✓	1, 2, 3
Anacardiaceae	*Spondias sp.*	–	–	–	–		✓		1, 4
Annonaceae	*Annona spp.*	–	–	–	–	✓	✓		5, 6
Araliaceae	*Didymopanax morototoni*[a]	120	5.38 ± 0.69	1.57 ± 0.21	9		✓		6
Boraginaceae	*Cordia spp.*[a]	5	11.57 ± 1.78	6.29 ± 0. 67	2	✓	✓		7, 8
Burseraceae	*Protium spp.*[a]	2	13.31 ± 2.26	8.05 ± 1.23	2	✓	✓	✓	1, 2, 3
Cannabaceae	*Celtis sp*	–	–	–	–	✓	✓		6, 8, 9
Malpighiaceae	*Byrsonima sp*[a]	1	4.7	5	1		✓	✓	1, 2
Melastomataceae	*Miconia sp.*	–	–	–	–	✓	✓		4, 6, 8
Moraceae	*Ficus spp.*	–	–	–	–	✓	✓		1, 8, 10
Myrtaceae	*Eugenia sp.*	–	–	–	–	✓	✓		1, 3, 10
Polygonaceae	*Coccoloba sp*[a].	5	4.08 ± 0.7	4.06 ± 0.62	3			✓	2, 10
Rubiaceae	*Randia sp*	–	–	–	–	✓	✓		5, 6
Rubiaceae	*Genipa sp*	–	–	–	–		✓		5,6;
Sapotaceae	*Pouteria sp.*[a]	4	10.41 ± 2.2	6.7 ± 1.17	3	✓	✓		3, 11
Smilacaceae	*Smilax sp1*[a]	4	2.62 ± 0.09	2.77 ± 0.11	2				
Smilacaceae	*Smilax sp2*[a]	25	6.87 ± 0.51	7.03 ± 0.54	9				
Smilacaceae	cf. *Smilax*[a]	3	3.82 ± 0.09	3.62 ± 0.17	1				
Unknown	Unknown sp. 1[a]	1	10.5	6.76	1				
Unknown	Unknown sp. 2[a]	1	6.18	4.80	1				

[a]Data from this study.

[b](1) Bonvicino (1989); (2) Alonso & Langguth (1989); (3) Montenegro (2011); (4) Swanson (1950); (5) Rand *et al.* (1990); (6) Chaves & Bicca-Marques (2013); (7) van Marken Lichtenbelt (1993); (8) Galetti & Pedroni (1994); (9) Bergh & Dahlberg (2001); (10) Morales-Mávil *et al.* (2007); (11) Porfírio (2005).

For primates, only studies carried out in fragments of the Atlantic forest were considered. When more than one species of the same genus were ingested by Iguanas and monkeys, we indicate only genus.

Ca, capuchin; Ho, howler monkey; Ma, marmoset.

trees *Tapirira guianensis* (123 seeds) and *Didymopanax morototoni* (120 seeds) and the liana *Smilax* sp. 2 (25 seeds) (Supporting information Fig. S2). Dispersed seeds ranged up to 14.9 mm long, and seed width between 3.6 and 9.2 mm (Table 2); no destroyed seeds were found and 11 *T. guianensis* seeds were germinating.

Iguana-dispersed seeds were found 0 and 50 m [$n = 20$; mean 12 m ± 11.2 standard deviation (SD); one seed found under a conspecific canopy] from the nearest fruiting conspecific. The iguanas in our study repeatedly defecated in the same localities, forming at least 13 latrines and we believe these came from at least eight iguanas based on the number of separate trails on which these occurred and the distance between latrines (the nearest latrines were 30 m apart and each trail was at least 20 m apart, which is higher than the average daily travel distance for iguanas; Escobar, Besier & Hayes,

2010). This behaviour appears to be unique among herbivorous lizards. We found latrines along seven of the 10 studied trails, and 86.9% of scats (n = 321; Table 1; mean 63.7% ± 44.4 SD) on these trails were found in latrines. Latrine size was approximately 2 m² (Supporting information Fig. S3) and estimated latrine density was 46.4 latrines per ha; we were unable to calculate scat density within latrines as the trails were often cleaned between searches. Of the scats found in latrines, 28.9 ± 26.2% (mean ± SD; range = 0–100%) contained seeds (compared with 18.1% for all scats), indicating that iguanas deposited seeds regularly in the latrines. Latrines were used over 9.1 ± 4.8 months (mean ± SD; range = 2–14 months; period from May 2011 to July 2012), with five latrines being used for more than 14 months, and one for at least 25 months (A.C. de A. Moura, pers. obs.). Latrines were found beneath trees that usually had canopies covered with lianas.

Discussion

The proportion of scats with seeds (18.1%) and the total number of species (12) is similar to that reported for other iguanids of similar size and in studies of comparable duration (Traveset, 1990; van Marken Lichtenbelt, 1993.; Blázquez & Rodríguez-Estrella, 2007).

Passage through iguana guts has been shown to increase germination rates of seeds (e.g. Benítez-Malvido *et al*., 2003; Morales-Mávil, Sánchez-Marín & Domínguez, 2005). These data suggest that iguanas could provide effective seed dispersal in Atlantic forest fragments and could attenuate the negative effects caused by the loss of primates.

Marmosets, capuchins and howler monkeys are the primates most commonly found in Atlantic forest fragments, but only marmosets persist in the most heavily disturbed areas (Chiarello & de Mello, 2001; Bicca-Marques, 2003; Canale *et al*., 2012). Marmosets are primarily insectivorous, and while they consume some fruits, they rarely disperse seeds (two of nine fruit species consumed, Alonso & Langguth, 1989; Tables 2 and 3). In one of the UFPB fragments, marmosets ate two of the same plant species we recorded as iguana dispersed, but discarded the seeds (Alonso & Langguth, 1989). In contrast, howler monkeys and capuchins are important seed dispersers (Julliot, 1996; Andresen,

2002; Wehncke *et al*., 2003), but can only persist in small fragments when fragment connectivity and/or food supplies are adequate (Siemers, 2000; Freitas *et al*., 2008; Chaves & Bicca-Marques, 2013).

Iguanas in this study dispersed fewer seed species and fewer scats contained seeds, compared with what has been recorded for some howler monkey and capuchin populations from the Atlantic forest (Table 3). However, our study was conducted in small, urban fragments with impoverished tree diversity (52 species, of which 29 had zoochoric fruits). The iguanas dispersed 13.5% of the trees and at least 24% of the total zoochoric tree diversity, which is higher than that found for capuchins (12% of 130 tree and shrub species bearing zoochoric fruit during the study period; Galetti & Pedroni, 1994) and howler monkeys (11%; Galetti, Pedroni & Morellato, 1994) in larger, more floristically diverse Atlantic forest fragments (250 ha in size) and over much longer study periods (44 months) (Table 3). This low floristic diversity may also explain the high frequency of the two most consumed species (94% of seeds were of three species), although similar results were found in a study on howler monkeys in Mexico (89% of seeds in scats were of three species; Amato & Estrada, 2010). Iguanas are also large-bodied and can reach high densities in fragments, particularly where predators are absent (6.3–13.0 individuals per ha; Munoz *et al*., 2003; Smith, Golden & Meshaka, 2007). Hence, iguanas could disperse a similar diversity of species as howler monkeys and capuchins, and lower consumption rates of fruit can be offset by high iguana density within fragmented forest (Vazquez, Morris & Jordano, 2005). Further, there is potentially high overlap between iguanas and howler monkeys in the seed species ingested (Table 2), but the extent of this overlap will need to be researched in comparative studies. One could expect that in fragments where howlers and iguanas both occur, the abundance and diversity of seeds in iguana scat might be lower and the number of faeces without seeds would be much higher than what we report here. It is also possible that the absence of howlers in fragments could reduce competition for resources and favour increased density of iguanas.

Iguanas in this study swallowed seeds up to 9.2 mm wide, but fruits of up to 20 mm wide have been recorded being swallowed by green iguanas in previous studies (Swanson,

Table 3 Comparison between Iguanas and fragment-tolerant primates in the Atlantic forest. Values shown are only from studies conducted in the Atlantic forest, except when marked with a. Weights for primates are from Smith & Jungers (1997) and gut-passage time from Lambert (1998)

Species	Weight (kg)	Number of species dispersed	Percentage of scats with seeds	Gut-passage time	Dispersal distance (m)	Home range (ha)	Daily movement (range, m)	Source[b]
Green iguana	≤6	12	18.0	>4 d	≥50	0.66; 0.95	0.8–10	This study, 1, 2, 3, 4
Spine-tailed iguana		6; 22	25.3	>4 d	500	–	–	5, 6
Capuchin monkey	≤3.7	23	93.0[a]	3.5 h	216[a]	268	550–3000	7, 8, 9
Howlers	≤7.3	18; 33	64.0[a]	20–35 h	250[a]	4.75–9.5	80–650	10, 11, 12, 13
Marmoset	≤0.38	2		3.5 h	–	1–5	150–704	14, 15.

[a]Values were taken from studies in the Amazonian forest.
[b](1) Rand *et al*. (1989); (2) Morales-Mávil *et al*. (2007); (3) Escobar *et al*. (2010); (4) Troyer (1984); (5) Traveset (1990); (6) Blázquez & Rodríguez-Estrella (2007); (7) Galetti & Pedroni (1994); (8) Rímoli, Strier & Ferrari (2008); (9) Wehncke *et al*. (2003); (10) Julliot (1996); (11) Bonvicino (1989); (12) Galetti *et al*. (1994); (13) Andresen (2002); (14) Alonso & Langguth (1989); (15) Stevenson & Rylands (1988).

1950; Govender *et al.*, 2012). In fact, Swanson (1950) found up to 79 seeds of these fruits, *Spondias mombin*, in the gut of a single animal, indicating a significant capacity to consume many large seeds. These fruits are approximately the same size as the largest fruits dispersed by howler monkeys (18 mm wide, Andresen, 2002) and capuchins (30 mm long, Wehncke *et al.*, 2003), indicating that iguanas have the capacity to disperse seeds of similar size ranges as the primates. In our study site, only four zoochoric fruit species had seeds with widths of 20 mm or larger that may have been inaccessible to iguanas: the bat-dispersed *Andira* sp. (seed width = 23 mm), *Licania octandra* and *Sacoglottis mattogrossensis* (both about 20 mm wide) and *Pouteria grandiflora* (seed width ≥30 mm), which was probably dispersed by extinct megafauna (A.C. de A. Moura, pers. obs.).

Dispersal distances for iguanas have rarely been measured, but our results suggest that regular dispersal away from parent canopies occurs and distances of up to 500 m have been recorded for *Ctenosaura similis* (Traveset, 1990). This compares favourably to dispersal distances reported in howler monkeys and in capuchins (Table 3). However, seed dispersal distances more commonly achieved by iguanas are likely to be smaller, given their limited mobility. Home ranges of green iguanas vary between 0.65 and 0.95 ha (Rand *et al.*, 1989; Morales-Mávil *et al.*, 2007), with average daily movements from 0.8 to 10.0 m each day (Escobar *et al.*, 2010), and longer distances during nesting periods (Rodda & Grajal, 1990), or to use favoured resources (Fitch & Hackforth-Jones, 1983). This limited ranging behaviour will be partially offset by the much longer gut-passage time of iguanas (>4 days; Troyer, 1984) compared with howler monkeys (21 h, Julliot, 1996; Table 3).

The long gut-passage times of iguanas may also enhance seed germination for some plant species (Traveset, 1990; Mandujano, Gallina & Bullock, 1994; Morales-Mávil *et al.*, 2005). *Smilax* seeds have very low rates of germination even after chemical and mechanical treatment (Palhares *et al.*, 2009; Martins *et al.*, 2012), and this long dormancy could benefit from a long transit time (Traveset, 1990). Indeed, Morales-Mávil *et al.* (2005) compared germination rates of *S. mombin* after gut passage in captive spider monkey, green iguana and toucans, and germination success of seeds ingested by green iguana was almost twice as high as those ingested by spider monkey.

The use of latrines and consequent clumped deposition of dispersed seeds is particularly associated with seed shadows created by howler monkeys (Julliot, 1997; Bravo, 2012; González-Zamora *et al.*, 2012). Howlers deposit more than 65% of scats into latrines (usually 5 m in diameter) that are associated with sleeping and resting trees (Bravo, 2009). While iguana latrines may be smaller (2 m^2 for the disturbed latrines in this study), iguanas deposit most scats within them (87%), and seeds may face similar patterns of post-dispersal mortality and survival as in howler latrines. Regular seed deposition in the same site can promote a saturation of mortality factors, and cause high nutrient availability, which favours the recruitment of saplings and has direct impact on vegetation dynamics (Feeley, 2005; Bravo, 2012; González-Zamora *et al.*, 2012).

Further research is required to assess whether iguana latrines may also impact vegetation dynamics, but our initial results indicate that the deposition pattern produced by iguanas may partially replicate that of howler monkeys.

Green iguanas have the capacity to attenuate the seed dispersal function that is lost when primates disappear from heavily fragmented forests. While seed dispersal distances may be truncated under iguana seed dispersal, iguanas can consume seeds of a similar size range as primates and they can disperse a similar diversity of species. However, the extent to which green iguanas contribute to seed dispersal within forest fragments can only be fully evaluated following detailed studies of this cryptic, yet common, species. Our knowledge on frugivory, dietary diversity and seed deposition patterns remains extremely rudimentary and does not allow us to determine the extent to which iguanas may complement (Schupp, Jordano & Gómez, 2010) or overlap the role of other dispersers. Given the severe fragmentation and defaunation of Brazil's Atlantic forests, it is paramount that we improve our knowledge on functional roles played by fragment-tolerant species, such as the green iguana.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. An adult iguana feeding on unidentified liana.
Figure S2. Seeds found in the iguana scats: (a) *Tapirira guianensis*; (b) *Cordia* cf. *rufescens*; (c) *Smilax* sp.2; (d) Smilax sp.1; (e) *Didymopanax morototoni*; (f) *Pouteria* sp.
Figure S3. Latrine on trail # 7, the rule measure 15 cm. Note the stains on the trail from old iguana scats.