Flower number and distance to neighbours affect the fecundity of *Goetzea elegans* (Solanaceae)

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Abstract: Pollinator visits to flowers of self-incompatible tropical trees are critical for plant fecundity. However, few studies have examined how much of the variance in tropical tree fecundity is explained by individual attributes of trees (e.g. number of flowers), and how much is due to contextual variables such as distances to nearest flowering neighbours. Using multiple regressions we examined the relative contributions of these factors to the pollination and fecundity of *Goetzea elegans*, a mainly self-incompatible tree endemic to Puerto Rico. We studied the largest wild population of the species during the peak flowering and collected data on the frequency of pollinator visits ($N = 25$ trees), and the fecundity of the whole population ($N = 105$), including the visitation rate of two pollinators (the honey bee *Apis mellifera* and the bananaquit *Coereba flaveola*), the total number of flowers produced by each tree, and the total fruit set and seed viability per tree. We also recorded the distance to flowering conspecifics and heterospecifics, and the height for each tree. Flower number had a strong positive effect on pollinator visitation, but distance to nearest neighbours was equally or more important than flower number in influencing fecundity. Also, competition for limited pollinators between *G. elegans* and other species has a stronger effect than the facilitation that conspecifics may provide. Our results suggest that pollinator visits and aspects of fecundity of *G. elegans* depend both on the attributes of individual plants, and on those of the community of other nearby plants.

Key Words: *Apis mellifera*, Caribbean, *Coereba flaveola*, fruit set, nearest neighbour distance, partial self-incompatibility, pollination, Puerto Rico, seed viability, tropical trees

INTRODUCTION

Relationships between plants and their animal pollinators are complex and mediated by factors that bridge scales across the properties of individuals, populations and species (Ghazoul 2005, Johnson *et al.* 2003). For example, most tropical tree species are characterized by having spatially sparse populations, by rejecting their own pollen to varying degrees (from total to partial self-incompatibility), and by being dependent on animal pollinators for outcrossing (Bawa *et al.* 1985, Ward *et al.* 2005). These characteristics make the fecundity of many tropical tree species an outcome contingent on interactions among the spatial structure of populations, the behaviour and availability of pollinators, and the community context in which individuals are embedded (Ghazoul 2005, Jones & Comita 2008).

Proximity among synchronously flowering plants is important for self-incompatible species because they require pollen from neighbours to set fruit and to produce viable seeds (Duncan *et al.* 2004, García-Camacho *et al.* 2009). The typically sparse population of tropical trees makes pollination difficult in many cases, and demands accounting for the effects of distance and density of conspecifics in order to fully understand variation in fecundity (Fukue *et al.* 2007, Ghazoul 2005). This is because pollinators tend to visit locations that maximize rewards while minimizing energetic expenditures in foraging (Pyke 1984). Therefore, at the level of individual trees, pollinators adjust visitation rates in response to the number of available flowers and/or visual cues (de Jong *et al.* 1992, Lázaro *et al.* 2009). Additional external

factors such as the presence of other flowering species that share the same pollinators can also affect fecundity by causing competition or facilitation (Takakura *et al.* 2009, Waser 1978). Thus, the availability of pollinators and the way they respond to plant spatial patterns are important elements that contribute to variance in the fecundity of tropical trees (Ghazoul 2005, Stacy *et al.* 1996).

Typically, low rates of flower visitation by pollinators translate into decreased seed set by causing pollen limitation (Burd 1994, Haddad & Tewksbury 2005). Low seed set due to pollen limitation is common in tropical trees, especially for self-incompatible species (Nayak & Davidar 2010, Sunnichan *et al.* 2004). Widespread degradation of tropical forests decreases tree population sizes and increases isolation, two conditions that further reduce pollen transfer among trees and thus lower fecundity (Schulke & Waser 2001, Wagenius & Lyon 2010). The combination of pollen limitation and habitat destruction is believed to be especially harmful for populations of uncommon self-incompatible trees in biodiversity hotspots where pollination services can be limited and high deforestation rates are prevalent (Vamosi *et al.* 2006).

In this study we examined the effects of plant characteristics and spatial aggregation on the pollinator visitation and fecundity in the mainly self-incompatible tropical tree *Goetzea elegans*, a rare endemic of the Caribbean Islands Biodiversity Hotspot (Myers *et al.* 2000). Specifically, we examined how the distance to the nearest reproductive conspecific tree (nearest neighbour distance; hereafter NND), the number of open flowers on a tree, and tree height influence pollinator visitation rates, fruit production and seed viability. We expected an increase in pollinator visits and fecundity (because of increased pollen outcrossing rates) for trees with many versus few flowers, as plants with many flowers have been found to be more attractive to pollinators, thus increasing their visitation rate (Klinkhamer *et al.* 1989, Mitchell & Waser 1992). We also expected a decrease in fecundity (i.e. fruit set and seed viability) with increasing NND, as greater isolation reduces the probability of outcrossing (Cascante *et al.* 2002, Mimura *et al.* 2009).

METHODS

Study species

The genus *Goetzea* is part of an ancient lineage in the nightshade family (Solanaceae). The genus contains two tree species, *G. elegans* Wydler and *G. ekmanii* O.E. Schulz, both endemic to the Caribbean (Santiago-Valentín & Olmstead 2003) and both endangered (IUCN Red List of Threatened Species (C2a version 2.3) available at http://www.iucnredlist.org, Peguero *et al.* 2003, USFWS

1987). *Goetzea elegans* is only known from several populations on the northern and eastern region of the island of Puerto Rico (including Vieques Island). Although *G. elegans* was once considered as critically endangered, with about 50 individuals in three populations (USFWS 1987), new populations have been discovered. The total number of trees is now estimated at about 820 individuals in 12 populations. In north-western Puerto Rico there are eight populations with over 550 individuals. Here, the trees are restricted to karstic ravines in the Municipalities of Isabela and Quebradillas. In north-eastern Puerto Rico there are over 20 individuals in one population in the Municipality of Fajardo, and Vieques Island has one fragmented population of about 300 individuals scattered in ravines in the western region of the island.

Goetzea elegans often grows to 10 m tall in the wild, and some trees reach 18 m. It produces flowers and fruits throughout the year, with peak flowering occurring between February and July (Little *et al.* 1974, Santiago-Valentín 1995). The flowers are perfect with no fragrance perceptible to humans. The pale yellow corolla is funnel-shaped, up to 2 cm long and 1.3 to 2 cm across, with six stamens and a single pistil. The fruits are orange drupes about 4 cm long covered by velvety hairs with a persistent calyx. The seeds are elliptical and about 0.7 cm in size (Little *et al.* 1974).

Although the flowers of *G. elegans* exhibit a bird pollination syndrome (Knapp 2010), they are visited by both birds and insects. The most frequent flower visitor is the native nectarivorous bananaquit *Coereba flaveola* Bryant (Coerebidae), which is the most abundant bird in Puerto Rico (Raffaele *et al.* 1998) and has been shown to be a pollinator of *G. elegans* (Caraballo-Ortiz & Santiago-Valentín 2011). Although *C. flaveola* robs nectar from flowers of other plant species (Kodric-Brown *et al.* 1984), in *G. elegans* it only visits flowers legitimately (Caraballo-Ortiz 2007). Another common visitor and pollinator is the honey bee *Apis mellifera* L. (Apidae; Caraballo-Ortiz & Santiago-Valentín 2011). This introduced bee is commonly found visiting flowers throughout the island and lives in both managed and wild colonies. Previous experiments of Caraballo-Ortiz & Santiago-Valentín (2011) demonstrated that both *C. flaveola* and *A. mellifera* pollinate *G. elegans* with similar efficiency. Infrequent visitors to flowers of *G. elegans* flowers are two native hummingbird species (*Anthracothorax dominicus aurulentus* Audebert & Vieillot and *Eulampis holosericeus holosericeus* L.; Santiago-Valentín 1995; M. A. Caraballo-Ortiz, pers. obs.).

Previous experiments on the breeding system of *G. elegans* indicate that the species is mainly self-incompatible, producing significantly higher fruit set, seed set and seed viability from outcrossed pollen than from pollen from the same plant (Caraballo-Ortiz & Santiago-Valentín 2011).

Study site

We worked in the largest continuous natural population of *G. elegans* (N = 197 trees) located at Quebrada Bellaca (18°28′30″N, 66°54′13″W) in the municipality of Quebradillas, in the karstic region of north-west Puerto Rico. Quebrada Bellaca is a wooded, seasonally dry ravine about 3.25 km long, with some segments forming small canyons, which drains north into the Atlantic Ocean. Altitude along the ravine ranges from 1 to 100 m asl. Climate at the site is classified within the subtropical moist life zone (Holdridge system: Ewel & Whitmore 1973).

Tree characterizations

All *G. elegans* individuals in the study site were mapped using a GPS (Trimble®, Sunnyvale, California) with an accuracy of ±2 m. Distances between trees were calculated using the 'Hawth's Analysis Tools for ArcGIS' extension (version 3.26, available at http://www. spatialecology.com/htools) from a digital map of all *G. elegans* trees at the study site generated in ARCGIS 9 (ARCMAP version 9.1, ESRI, Redlands, California). To examine the spatial aggregation pattern of *G. elegans* trees in the population, we performed a nearest neighbour analysis using Crime Stat III (version 3.3, Ned Levine & Associates, Houston, TX, and the National Institute of Justice, Washington, DC). We also recorded the height of all trees using a clinometer.

Pollinator visits

We recorded pollinator visits using systematic focal observation of 25 flowering trees selected at random during peak flowering in March and April 2005. Each tree was observed once during 4 h on the same day: in the morning from 08h00–10h00, and in the afternoon from 15h00–17h00. These time periods were selected based on preliminary observations to capture peaks of foraging activity for both *C. flaveola* and *A. mellifera*. For each sampled tree, we counted the total number of open flowers during the observation period (for large trees with many flowers, we counted all the open flowers and observed a randomly selected upper branch), the number of flowers visited by each pollinator, and the number of flowers of conspecifics and of other species (heterospecifics) present in a 20-m radius from the sample tree (modified from Saracco *et al.* 2005). For heterospecifics, we only selected trees with flowers visited by *C. flaveola* and/or *A. mellifera*, and for these we counted all the flowers in a randomly selected upper branch (or all the branches in trees with few flowers). For small-flowered trees, we estimated the total number of flowers on the branches based on the average number per inflorescence.

We used multiple regression to assess the effects of the total number of open flowers on the observed tree during the observation period, tree height and neighbourhood variables (NND and the total number of flowers of conspecifics and heterospecifics in the neighbourhood) of each tree on the frequency (total number of visits to the flowers of each observed trees during the 4 h of observations) of pollinator visits (i.e. *C. flaveola*, *A. mellifera*, pooled species). Visitation data for *C. flaveola* and *A. mellifera* were summed to obtain a total for pollinator visits, and then normalized using a logarithmic transformation. The flower number and NND data were also normalized using a logarithmic transformation. We entered all the variables and interaction terms in the model (standard least square) and used a stepwise backward procedure with probability to remove variables set to 0.10 (JMPIN software, version 4.0.2., SAS Institute, Cary, North Carolina).

Fecundity measures

We measured fecundity for each of the 105 that were reproductive during the peak of flowering in April 2005. On a weekly basis we counted the number of all aborted flowers and fruits that had fallen beneath each tree. We continued weekly counts of aborted flowers until the first week of May, and of fruits until June, since fruits require approximately 45 d after pollination to mature and abscise (Santiago-Valentín 1995). Aborted flowers in turn abscise an average (±SD) of 3.4 ±0.82 d after opening (Santiago-Valentín 1995). Aborted flowers and fruits could be assigned to the tree above them with confidence, because putative ancestral mammalian and reptilian seed dispersers are extinct, because the high walls of the ravine prevent movement by wind, and because strong rain events, which can lead to movement by water flowing down the ravine, did not occur during this dry month. We randomly selected up to 32 fruits per tree (minimum: one fruit; median: 15.5 fruits) to extract seeds for a test of their viability. Fruits not chosen were removed from beneath the parental tree and dispersed to the surrounding forest in places where other *G. elegans* trees were not present, so as not to include them in the next weekly count and so as to assist in dispersal of the species. To test for seed viability we germinated them in a humid peat bed with low sunlight conditions (to simulate natural germination conditions) from June to September 2005. All seeds collected from an individual tree were planted in a block, and all the blocks were positioned at random along the peat bed. Total flower number for the month of April was defined as the sum of aborted flowers and fruits collected under each tree. We also calculated the percentage of flowers set as fruit for each tree and the percentage of planted seeds that germinated.

Table 1. Descriptive statistics of flower number, fruit set, seed viability, nearest neighbour distance (NND), and height of focal *Goetzea elegans* trees used in observations of pollinator visits and for the whole population monitored during April 2005 in Quebradillas, Puerto Rico.

	Mean ± SD	Median	Range
Pollinator visits (N = 25 trees)			
Flower number	87 ± 155	23	3–700
Fruit set	115 ± 204	51	0–921
Seed viability (%)	68 ± 29	76	0–100
NND (m)	19 ± 30	8	1.3–116
Height (m)	9 ± 3	8	4–18
Fecundity measures (N = 105 trees)			
Flower number	314 ± 680	65	1–4855
Fruit set	112 ± 250	17	0–1516
Seed viability (%)	59 ± 35	72	0–100
NND (m)	14 ± 24	5	0.4–116
Height (m)	8 ± 3	7	3–18

We used multiple regression to assess the effects of the total number of flowers produced during the month of April, tree height, and NND on fruit set and seed viability, following the procedure described above. We also used regression to assess the effect of NND on the number of aborted flowers, and a *t*-test to compare abortion rate in trees with NND values above and below the mean for the population (14 m). Flower number, number of aborted flowers, tree height, and NND were normalized using a logarithmic transformation, while fruit set and seed viability were normalized using an arcsine transformation.

RESULTS

Pollinator visits

We recorded 7654 pollinator visits to *G. elegans* flowers, of which 95% were by *C. flaveola*. The remaining 5% of the visits were by *A. mellifera*. No other visitor was recorded visiting *G. elegans* flowers during the observation period. More than half (60%) of all *C. flaveola* visits were during afternoon hours. In contrast, 77% of all *A. mellifera* occurred during morning hours. The 25 *G. elegans* trees selected for quantifying pollinator visits produced a mean of 87 flowers during the observation period, with a mean tree height of 9 m and a mean NND of 19 m (Table 1).

The regression model identified significant effects of the total number of open flowers on the observed *G. elegans* trees, the number of flowers from heterospecific neighbours, the height of *G. elegans* trees, and the number of flowers on conspecific neighbours, on pollinator visits. The most important variable predicting pollinator visits was the flower number of focal trees, which accounted for 68.6% of the explained whole-model variance (Table 2). Important predictor variables with a

positive effect on pollinator visits included flower number, tree height, and the number of flowers on conspecific neighbours, while the number of flowers from heterospecific neighbours and the interaction between conspecific and heterospecific neighbours had a negative effect on visits (Table 2). The relationship between the number of open flowers and tree height on the number of pollinator visits is presented in Figure 1a and 1b.

Fecundity measures

Trees in the population were highly aggregated, with 75% growing within 15 m of their nearest conspecific neighbour. The mean NND was 13.8 m (± 27.8 m), with an expected NND of 80 m, a mean dispersed distance of 172 m, and a nearest neighbour index of 0.173 (Z = −16.2, SE = 4.08, P < 0.0001). The mean height of the trees was 8 m, and flower production ranged from 1 to 4855 (median: 65 flowers; Table 1). In the regression model the NND, the total number of flowers produced during the month of April, the height of *G. elegans* trees, and the interaction between tree height and NND were identified as significant predictors of fruit set. The most important variable predicting fruit set was NND, accounting for 19.8% of the explained whole-model variance (Table 2). The only important predictor variable with a positive effect on fruit set was the total number of flowers, while the NND, the height of *G. elegans* trees and the interaction between tree height and NND had a negative effect on fruit set (Table 2). The interactions between the number of flowers and the height of trees, and between the number of flowers and the NND were not identified as significant predictors of fruit set and were excluded from the model. In trees with a NND greater than 45 m, fruit set dropped below 50%. The relationship between the total number of flowers and NND on fruit set is presented in Figure 1c and 1d.

For seed viability, the regression model identified significant effects from the total number of flowers produced during the month of April, the NND and the height of *G. elegans* trees. The most important variable predicting seed viability was the total number of flowers, which accounted for 17.7% of the explained whole-model variance (Table 2). The only important predictor variable with a positive effect on pollinator visits was the total number of flowers of *G. elegans* trees, while the NND and the height of *G. elegans* trees had a negative effect on seed viability (Table 2). The interactions between the total number of flowers and the height of trees, and the NND and the height of trees were not identified as significant predictors of seed viability and were excluded from the model. Seeds from trees with NND within 20 m had the highest viability, and viability declined below 85% when NND was greater than 40 m. In fact, the only plants in

Table 2. Results of multiple regression models testing the effects of individual attributes of trees (flower number, tree height), contextual variables (nearest neighbour distance (NND), flower number of conspecific and heterospecific neighbours) and their interactions on pollinator visits, fruit set, seed viability and aborted flowers in *Goetzea elegans*.

Variable	Estimate	t-ratio	SE	F-Ratio	P
Pollinator visits (Whole model $R^2 = 0.95$, $F_{7, 17} = 44.6$)					
Flower number	1.21	13.1	0.09	172	<0.0001
Height	1.62	3.66	0.44	13.4	0.0019
Conspecific neighbours	0.45	3.54	0.13	12.5	0.0025
Heterospecific neighbours	−0.19	−5.00	0.04	25	0.0001
Conspecifics × Heterospecifics	−0.09	−3.21	0.03	10.3	0.0052
Height × Conspecifics	−0.64	−1.93	0.33	3.73	0.0703
Height × Heterospecifics	0.14	1.09	0.12	1.18	0.293
Fruit set (Whole model $R^2 = 0.38$, $F_{4, 100} = 15.2$)					
Flower number	0.10	4.62	0.02	21.3	<0.0001
NND	−0.19	−5.97	0.03	35.7	<0.0001
Height	−0.37	−2.54	0.15	6.44	0.0127
Height × NND	−0.24	−2.22	0.11	4.92	0.0288
Seed viability (Whole model $R^2 = 0.36$, $F_{4, 100} = 14.3$)					
Flower number	0.15	5.45	0.03	29.7	<0.0001
NND	−0.17	−4.67	0.04	21.8	<0.0001
Height	−0.42	−2.40	0.17	5.75	0.0184
Flower number × NND	0.03	1.74	0.02	3.03	0.0848
Aborted flowers (Whole model $R^2 = 0.09$, $F_{1, 103} = 10.1$)					
NND	0.23	3.17	0.07	10.1	0.0020
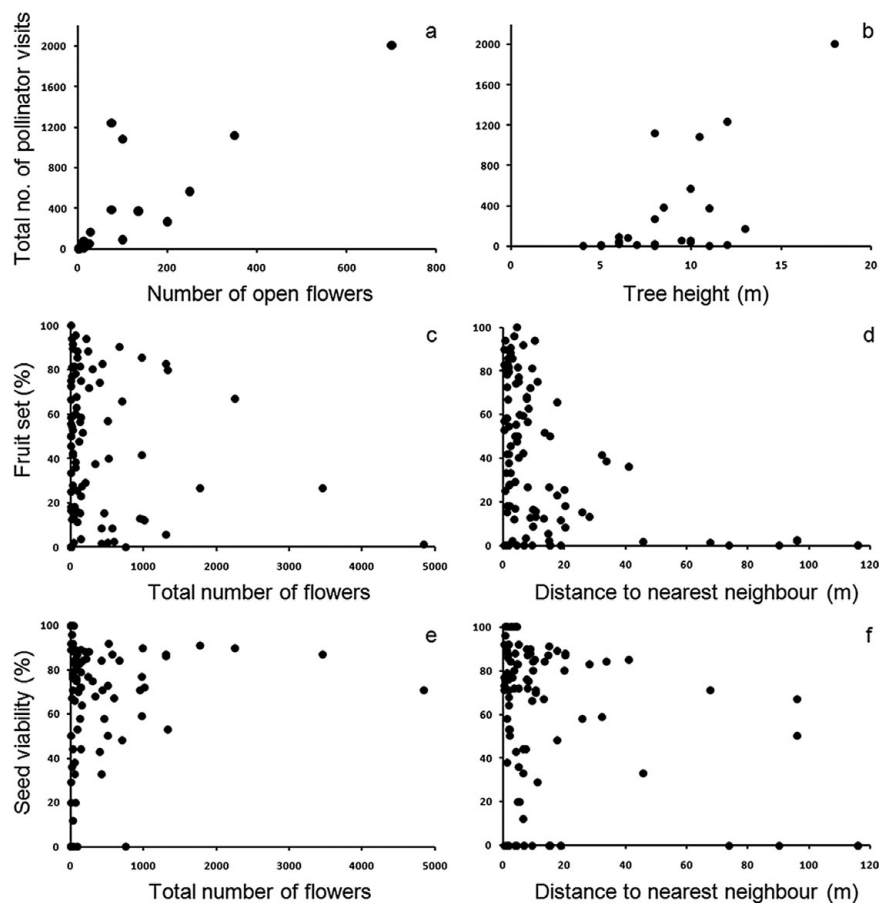
Figure 1. Relationships between the number of flowers, tree height, and distance to the nearest reproductive conspecific neighbour (nearest neighbour distance) on the pollinator visits, fruit set and seed viability in *Goetzea elegans* (Solanaceae). Total number of open flowers on the observed trees versus total number of pollinator visits (a). Tree height (m) versus total number of pollinator visits (b). Total number of flowers in April versus percentage of fruit set (c). Nearest neighbour distance (m) versus percentage of fruit set (d). Total number of flowers in April versus percentage of seed viability (e). Nearest neighbour distance (m) versus percentage of seed viability (f).

the sample that achieved germination values of 100% were individuals with flowering neighbours within 4.5 m. The relationship between the total number of flowers and NND on seed viability is presented in Figure 1e and 1f. Finally, the number of aborted flowers showed a positive correlation to the NND (Table 2). Trees with NND greater than the mean of 14 m experienced significantly more flower abortion than trees with NND below the mean ($t =$ 5.28; df $= 103$; P < 0.0001).

DISCUSSION

Although previous studies have recognized the importance of spatial and individual tree characteristics on fecundity metrics, ours is one of the few tropical studies that have accounted for all of these variables at once, estimating the relative contribution of each to the fecundity of an endangered and partially self-incompatible tree. Our results indicate that *G. elegans* requires highly clumped populations to optimize its reproductive investments, with effective NND of less than 15 m – a strikingly small scale over which to observe strong Allee effects (Groom 1998). On the other hand, heterospecific flowering neighbours appeared to compete with *G. elegans* by drawing away shared pollinators, which illustrates how a highly generalized island pollination network can limit plant fecundity (Olesen *et al.* 2002). Curiously, tree height increased visitation by pollinators, but also decreased fecundity, suggesting that an increment in flower number can increase geitonogamy, i.e. pollination among flowers of the same tree (de Jong *et al.* 1992).

Pollinator visits

A dependence of pollinators such as *C. flaveola* and *A. mellifera* on visual cues for attraction could explain the positive relationships we detected between both the total number of open flowers on the observed trees and tree height and rate of pollinator visits. Per-flower rates of pollinator visits often are positively related to the size of floral displays of individual plants (Feinsinger *et al.* 1991, Rodríguez-Robles *et al.* 1992, Willson & Price 1977). Another possibility is that pollinators learned and could recall the locations of larger and taller trees and returned to these preferentially due to their larger overall supplies of nectar reward (Pyke 1984, Sih & Baltus 1987). Although we did not detect any odour in the flowers of *G. elegans*, nor have floral fragrances been reported for any Antillean Goetzoideae (Santiago-Valentín & Olmstead 2003), we do not discard the possibility that pollinator visits in *G. elegans* might be also influenced by odour cues detected by pollinators but imperceptible for humans.

Aggregation of focal trees with other conspecifics and heterospecifics might also serve to attract more visits (Johnson *et al.* 2003). In general, pollinators appear to be more attracted to groups of flowering plants than to isolated individuals, probably because of richer resources (Pyke 1984, Wunderle & O'Brien 1985). However, in our system it appeared that competition for common pollinators between *G. elegans* and other species outweighed any facilitative effect of aggregation on rate of visits. In some cases, *G. elegans* appears to have been the preferred resource for *C. flaveola*, which was observed more frequently on *G. elegans* than on neighbouring species (M. A. Caraballo-Ortiz, unpubl. data). In contrast, visits of *A. mellifera* to *G. elegans* flowers were rare, perhaps because honey bees prefer flowers of other species. Indeed, we observed *A. mellifera* visiting blooming trees of *Andira inermis* (W. Wright) H. B. K. (Fabaceae), *Mangifera indica* L. (Anacardiaceae), *Spondias mombin* L. (Anacardiaceae), *Roystonea borinquena* O. F. Cook (Arecaceae) and other trees at the site, suggesting that honey bees were present but did not prefer *G. elegans*. We also observed that, when *C. flaveola* forages on *G. elegans*, it visits a few flowers and moves on to a different tree (even for trees with many flowers), this behaviour promoting pollen outcrossing. Unlike *C. flaveola*, *A. mellifera* usually foraged during long periods in single *G. elegans* trees with many flowers, this promoting selfing pollination (M. A. Caraballo-Ortiz, pers. obs.).

Fecundity measures

The decline in seed viability with increasing NND is suggestive of an increase in deposition of self pollen and resulting inbreeding depression. Previous work with *G. elegans* showed that seeds derived from selfing are less viable than those derived from outcrossing (Caraballo-Ortiz & Santiago-Valentín 2011). More isolated trees may suffer from higher rates of within-plant pollen movement, i.e. geitonogamy, if pollinators are more likely to visit larger numbers of flowers before leaving such trees. Lower viability of seeds from isolated trees has been documented with other tropical species (Cascante *et al.* 2002, Naito *et al.* 2008, Nason *et al.* 1997).

Although the positive correlation of fruit set and seed viability with the total number of flowers during April suggests that a large floral display contributes strongly to successful reproduction in *G. elegans*, complete germination was realized only for seeds from some individuals with small displays of fewer than 50 flowers. Such trees therefore were proportionately more successful than trees with more flowers. However, this remarkable result might be explained by the small NND values (< 4.5 m) of the most successful trees. Spatial aggregation may be of particular importance for young trees with few flowers.

Our results suggest that pollinator visits and aspects of fecundity of *G. elegans* depend both on the attributes of individual plants, and on those of the community of other nearby plants. To be sure, our approach was correlative, since it was impractical to manipulate individual and community-level factors, and we did not directly measure such things as genetic relatedness of conspecific trees as a function of their proximity (Jones & Comita 2008). Thus our conclusions about causation and about mechanism must remain somewhat speculative. Furthermore, final realized reproductive success in *G. elegans* may be influenced by both pre- and post-dispersal seed predation (DeMattia *et al.* 2004, Raghu *et al.* 2005). Conserving this rare endemic species for future generations requires not only protecting extant populations, but perhaps also intervention to increase fecundity. Possible examples are the planting of additional trees close to isolated trees and special effort to maintain large trees which can facilitate nearby smaller trees.

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