

Hangin' by a coastal strand: breeding system of a federally endangered morning-glory of the south-eastern Florida coast, *Jacquemontia reclinata*

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Received: 14 May 2009 Returned for revision: 25 June 2009 Accepted: 18 August 2009

- **Background and Aims** Coastal development has led to extensive habitat destruction and the near extinction of the beach clustervine, *Jacquemontia reclinata* (Convolvulaceae), an endangered, perennial vine endemic to dune and coastal strand communities in south-eastern Florida. We examined the breeding system of this rare species, and observed visitors to its flowers, as part of a larger effort to document its status and facilitate its recovery.
- **Methods** Reproductively mature experimental plants were grown from seed collected from wild plants in two of the largest remaining populations. Controlled hand pollinations on potted plants were conducted to determine the level of compatibility of the species and to investigate compatibility within and between populations. Seeds from the hand pollinations were planted in soil, and they were monitored individually, recording time to seed germination (cotyledon emergence). Wild plants were observed in several of the remaining populations to determine which species visited the flowers.
- **Key Results** Hand pollination and seed planting experiments indicate that *J. reclinata* has a mixed mating system: flowers are able to set fruit with viable seeds with self-pollen, but outcross pollen produces significantly greater fruit and seed set than self-pollen ($\geq 50\%$ for crosses vs. $< 25\%$ for self-pollinations). Visitors included a wide array of insect species, primarily of the orders Diptera, Hymenoptera and Lepidoptera. All visitors captured and examined carried *J. reclinata* pollen, and usually several other types of pollen.
- **Conclusions** Remnant populations of beach clustervine will have greater reproductive success not only if floral visitor populations are maintained, but also if movement of either pollen or seed takes place between populations. Restoration efforts should include provisions for the establishment and maintenance of pollinator populations.

Key words: Breeding system, conservation, beach clustervine, *Jacquemontia reclinata*, Convolvulaceae, endangered species, floral visitors, coastal dunes, pollination, reproductive biology, Florida, Caribbean, bees, butterflies.

INTRODUCTION

Although many factors other than breeding system can contribute to a species' rarity and vulnerability to extinction (Rabinowitz, 1981; Weller, 1994; Cadotte and Lovett-Doust, 2002; Carlsen *et al.*, 2002; Murray *et al.*, 2002), the combination of breeding system limitations and habitat degradation may exacerbate species rarity, and thereby cause a species to become threatened or endangered (Schemske *et al.*, 1994; Weller, 1994; Sakai *et al.*, 2002). Habitat fragmentation may also disrupt pollination systems and lead to declines of certain types of pollinators (Jennersten, 1988; Aizen and Feinsinger, 1994a; Buchmann and Nabhan, 1996; Kearns *et al.*, 1998; Cunningham, 2000a; Liow *et al.*, 2001; Spira, 2001). When urbanization, intensive agricultural and forest management practices, pesticide use, and introductions of non-native species reduce relatively continuous natural habitats to isolated pockets of original flora and fauna in altered landscapes, adverse effects occur on pollination dynamics and plant–pollinator mutualisms (Jennersten, 1988; Aizen and Feinsinger, 1994a, b; Bond, 1994; Kearns and Inouye, 1997; Cunningham, 2000a, b; Liu and Koptur, 2003). The consequences for

pollination systems can range from increased spatial isolation and edge effects, inbreeding depression, increased genetic drift, and increased risk of extinction from demographic stochasticity (Fischer and Matthies, 1997; Hendrix and Khyl, 2000; Severns, 2003). Knowledge of the breeding system and pollination biology of a threatened or endangered plant species may be critical to its survival (Hamrick *et al.*, 1991; DeMauro, 1993; Sipes and Tepedino, 1995; Brzosko *et al.*, 2002; Pitts-Singer *et al.*, 2002; Weekley *et al.*, 2002).

Even naturally patchy plant species may be sensitive to human-caused habitat fragmentation in ways we may not be able to detect easily or predict (Wolf and Harrison, 2001). Within habitat remnants, plant reproduction may be affected as fragmentation changes the availability of potential mates, as well as resources, the microclimate, and the community of pollinators and their natural enemies (Aizen and Feinsinger, 1994a, b; Steffan-Dewenter and Tschardt, 1999; Cunningham, 2000b; Fuchs *et al.*, 2003). Effects of habitat destruction on pollinators may be greater than those on the plants they visit, as higher trophic levels may be more sensitive to habitat fragmentation than lower trophic levels (Didham *et al.*, 1996; Steffan-Dewenter, 2003). These effects, however, may also be difficult to predict (Cane, 2001).

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Plant species vary in their vulnerability to pollinator loss or limitation. Most vulnerable may be plants that are self-incompatible, those that have highly specialized pollination relationships, and those that propagate only by seeds and not vegetatively (Kearns and Inouye, 1997). Plant population size, density and location can also increase vulnerability to pollinator loss, as some plant populations may be too small, sparse, or isolated to receive sufficient pollinator services to replace themselves (Lamont *et al.*, 1993; Groom, 1998; Forsyth, 2003). However, the effects of inbreeding on seed set, germination, survival, and stress resistance also may be particularly pronounced in small, isolated populations of self-compatible plant species, especially when pollinator service is restricted (Weller, 1994; Weekley and Race, 2001).

In 1993, the Florida endemic species *Jacquemontia reclinata* was given federal endangered species status under the United States Endangered Species Act of 1973 (58 FR 62046). Habitat loss and modification throughout its range threaten to drive the species to extinction (USFWS, 1999; Lane *et al.*, 2001; Maschinski *et al.*, 2003). Urbanization has destroyed most of the species' primary habitat, and that which remains has been fragmented and modified. Most populations are separated by several kilometres of primarily urbanized land. A 1990 inventory of all tracts of coastal vegetation in southeast Florida showed that most *J. reclinata* populations occur on publicly owned land, most of which is public multiuse parkland (Johnson *et al.*, 1990). Coastal erosion, invasive plant species, recreation, and development, both within and around these parks, continue to threaten the remaining populations. The estimated total number of plants in 2002 was <900 in ten populations, and approx. 40% of all known individuals were in the two largest populations. The average number of plants per population was 75, with <10 individuals in the smallest three populations and approx. 245 in the largest population (Maschinski *et al.*, 2003). While the smallest populations are particularly vulnerable to chance events such as heavy storms or inadvertent trampling, even the largest populations may be victims of major disturbance. In 1996 more than a tenth of the plants were heavily impacted by a wildfire at the site of one of the larger populations (Kernan, 1998).

Our objective in this study was to determine the breeding and pollination systems of *J. reclinata* in an effort to develop an effective strategy for conservation and recovery of the species in remaining natural and restored habitat fragments. Significant differences appear between its historic and current ranges, where both disturbances (anthropogenic and natural) and changes to its habitat may have significantly altered pollen flow within and between populations. Also, although wild adult plants in some of the larger populations appear to flower and fruit prolifically, few seedlings or young plants have been observed. We wanted to determine whether or not this low rate of recruitment was due to self-incompatibility or some form of inbreeding depression that might affect seed production, seed germinability, or seedling establishment.

We sought to understand how these plants may be interacting with each other and their insect visitors by conducting a controlled study of the breeding system in a greenhouse environment and observing flowers in the wild. First, we determined the compatibility relationships of individuals within and

between populations and subsequently studied the seed produced by various pollinations. We hypothesized that crosses between flowers of distantly related plants (inferred from inter-individual geographic distance) would outperform all other crosses, as measured by fruit set, seed set, seed mass and germination success. Secondly, to begin to understand the pollination biology of *J. reclinata*, we observed wild plants in several populations for floral visitor activity, and caught and determined the identity of visitor species. We hoped the results of these studies would help to determine whether the rarity of *J. reclinata* is due to biological as well as anthropogenic factors, and contribute to the successful management and recovery of the species.

METHODS

Study species

Jacquemontia reclinata House ex Small is a coastal perennial vine endemic to south-eastern Florida. Mature *J. reclinata* plants spread numerous lateral stems in all directions from a stout, woody rootstock (Robertson, 1971; Austin, 1979). Plants generally occur on the crest and lee sides of stable coastal sand dunes in open, sunny areas of coastal strand vegetation, but they are also occasionally found on the foredune and in disturbed areas behind the dunes. The white, hermaphroditic, entomophilous flowers occur alone or in clusters in the leaf axils, and the five petals form a broad, funnel-shaped corolla, 2.5–3 cm in diameter (Garvue, 1999) (Fig. 1). The flowers last 1 d; the corollas open at sunrise and close by late afternoon (Maschinski *et al.*, 2003). Nectar, secreted into a hypogynous disc (Govil, 1975) and presented in the centre of the flower, and pollen (presented on the anthers) are available to flower visitors. The mature fruit is a brown capsule about 4–5 mm long, which opens by eight valves to release up to four seeds, which are 2.5–3 mm long and 0.1–0.2 mm wide (Robertson, 1971).

Study area

The species' range extends along Florida's south-eastern coast on barrier islands from Jupiter Inlet south to Key



FIG. 1 Flowers of *Jacquemontia reclinata* (corolla diameter is ~2.5 cm). Photograph by D. Monteith.

Biscayne, a distance of about 138 km (85 miles). Florida's south-eastern barrier islands are linear islands of quartz and calcium carbonate sand that parallel the coastline. Dunes are built as stems of grasses increase the deposition of sand grains by wind, and are eroded gradually by constant wave action or rapidly during storm events. Dwarfed sea grape (*Coccoloba uvifera*), poisonwood (*Metopium toxiferum*) and trema (*Trema micrantha*) trees dominate the canopy of coastal strand vegetation, and the herbaceous layer is dominated by beach sunflower (*Helianthus debilis*), sand spur (*Cenchrus incertus*), and stinging nettle (*Cnidioscolus stimulosus*) (Johnson and Barbour, 1990). *Jacquemontia reclinata* also shares habitat with two other endangered species: beach star (*Remirea maritima*, Cyperaceae) and beach peanut (*Okenia hypogaea*, Nyctaginaceae).

Field studies were conducted at six sites distributed across the range of *J. reclinata* (Fig. 2): Crandon Park and Bill Baggs State Recreation Area at the southernmost end of the range; Red Reef Park and South Beach Park near the centre of the range; and Carlin Park and Loggerhead Park in the northern part of the range. All of these sites are surrounded by heavily developed areas. One of the populations, at Bill

Baggs State Recreation Area, consists of introduced plants that are part of a separate restoration study conducted by researchers at Fairchild Tropical Garden in Miami, Florida (Maschinski and Wright, 2006).

Breeding system

To assess whether *J. reclinata* is capable of setting seed through self-pollination, a hand pollination experiment was performed with potted plants. Sixty-five reproductively mature experimental plants were grown from seed collected in 2000 from 16 wild plants at two sites, Bear Cut Preserve at Crandon Park on Key Biscayne, Florida, and South Beach Park in Boca Raton, Florida (Fig. 2). These two populations, which together contain approx. 40% of all individuals of the species, are separated by 86.4 km (54 miles). Between January and June 2002, hand pollination treatments were performed on the 65 experimental plants in a shade house at Fairchild Tropical Garden. All wild plants at these sites were mapped and numbered, so their position with respect to one another was used to determine if they were near or far neighbours. Using potted plants kept at the same location facilitated

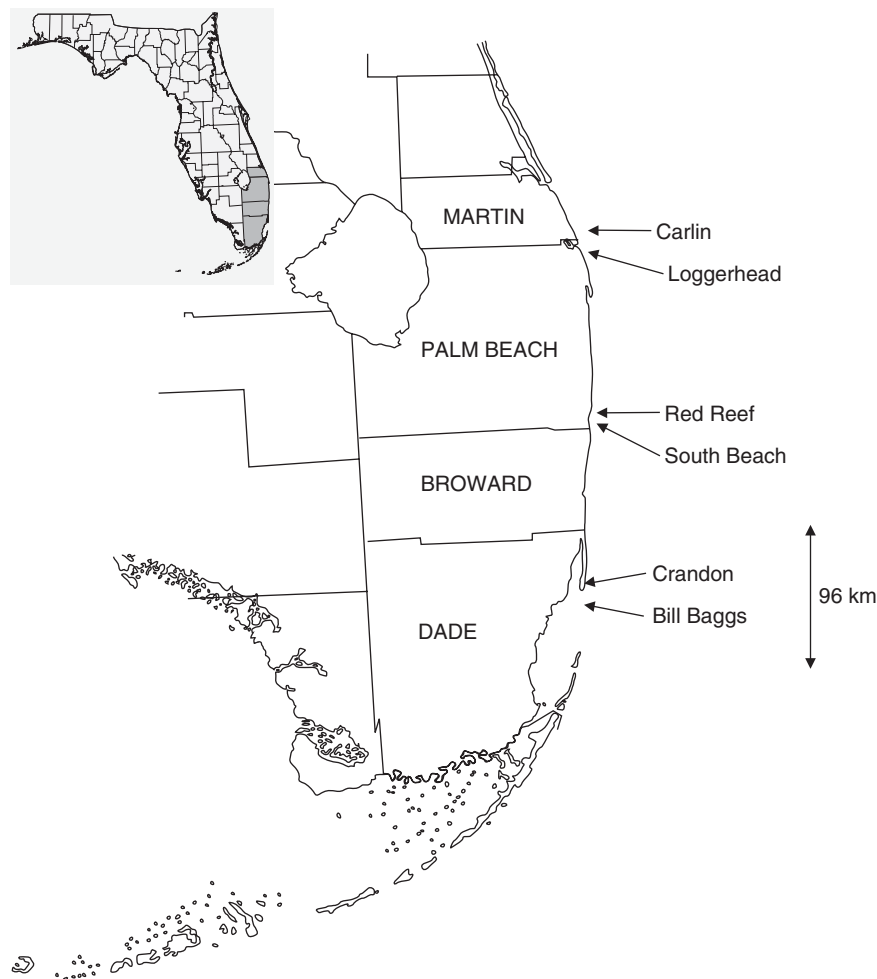


FIG. 2 Range and selected populations of *Jacquemontia reclinata* in south-eastern Florida, USA. From North to South: Carlin, Carlin Park, Jupiter; Loggerhead, Loggerhead Park, Juno Beach; Red Reef, Red Reef Park, Boca Raton; South Beach, South Beach Park, Boca Raton; Crandon, Crandon Park, Key Biscayne; Bill Baggs, Bill Baggs Cape Florida State Park.

making numerous pollinations between close and distant relatives, obviating problems with moving pollen between sites. To investigate autogamy, self-compatibility, and varying degrees of cross-compatibility, the following six treatments were conducted, based on protocols outlined by Dafni (1992) and Kearns and Inouye (1993): control, self-pollination, and cross-pollination with half-sibling (plants grown from seed from the same maternal parent), near-neighbour, far-neighbour (same population), and non-neighbour (other population) plants (Table 1).

All six treatments were bagged using fine tulle (mesh size <1 mm) to exclude insects, which was necessary because the study was performed in an open-sided shade house. The bags were held in place with twist ties, which helped keep ants from getting to flowers via stems and allowed easy access for manipulations. The control treatment involved tagging and bagging the flower, but doing nothing else. In all the other treatments, pollen was deposited on the stigma of each flower by direct contact with the surface of a dehisced anther held with clean fine forceps. Used anthers were discarded, and a new anther was used for each repetition. Paper jeweller's tags noting the treatment, date, and pollen source were attached to the floral pedicels.

Both pollen recipients and pollen donors (flowers) were bagged at least 1 d before opening, and pollen recipients were rebagged after hand pollination. The clustering of flowers and buds in axillary cymes along the length of the stems and the non-sequential opening of flower buds made it difficult to isolate inflorescences for a non-manipulated bagged treatment. Consequently, all flowers were handled at least for labelling (tagging) purposes. Experimental flowers on the same plant were selected to prevent position effects (non-random fruit production with respect to flower position), and to ensure that at least several repetitions of each treatment were performed on as many stems as possible on the same plant. A total of 665 hand pollinations were performed, with at least 30 repetitions per treatment.

Mature fruits resulting from the hand pollinations were collected before they opened to release seeds, and were individually stored in glassine or paper envelopes indoors, in a dry, air-conditioned environment. Fruit set and seed set were

recorded for each hand pollination. Each seed was individually weighed on an electronic balance to the nearest 0.1 mg.

Cotyledon emergence of planted seed

To explore hand pollination treatment success, a study of seed viability and seedling survival was conducted using the seeds resulting from the hand pollinations. After being weighed, each of the 833 seeds was placed into its own labelled well in a plastic tray, and a few drops of distilled water were added to each well for hydration. Though seeds of some Convolvulaceae require scarification, *Jacquemontia* is in a group of Convolvulaceae that have physical dormancy that can be broken by soaking as they have a 'water gap' (Jayasuriya *et al.*, 2009), and our previous germination attempts suggested that pre-soaking treatment was sufficient. The next day, seeds were planted individually in 6-celled plastic starter pots filled with a mixture of seedling potting soil and sand. Pots were arranged in trays, and trays were placed on a bench in a seedling germination greenhouse, where they were automatically misted every 5 min for 2 s throughout the day. After 2 weeks pots were moved to an area in the same greenhouse that was misted once a day. Every week, pots received an extra soaking of water, and trays were rotated on the bench to avoid position-related effects. The temperature of the greenhouse varied from 30.5 to 32.2 °C (87 to 90 °F).

Planted seeds were monitored weekly for germination as indicated by cotyledon emergence, and mortality. These observations were made for a 65 d period following the planting of the seeds.

Flower visitors

To determine the identity and behaviour of potential pollinators, flower visitor behaviour was observed during 69 ten-minute watches at five sites: Crandon Park, Bill Baggs Park, Red Reef Park, Carlin Park and Loggerhead Park (Fig. 2). These observations were made on 15 mostly sunny days between November 2000 and June 2003. Because diurnal insect activity was greatest before noon and tapered off by mid-afternoon, more watches were completed during the earlier part of the day; a total of 58 watches were made between 0700 h and 1200 h, and 11 were made between 1200 h and 1800 h. Flower visitors were captured for determination of genus and species with the help of several entomologists and their collections, and later identified by sight whenever possible. Voucher specimens are in the Florida International University collection. We also examined visitor specimens for *J. reclinata* and other pollen, using a dissecting microscope to remove pollen to fuchsin gel mounted on slides that were later examined under a compound microscope. We determined if they carried *J. reclinata* pollen and also the total number of types of pollen they carried.

Statistical analysis

We performed cross-tabulation analysis (χ^2 tests with Bonferroni *post hoc* tests) on fruit set from the hand pollination experiment (SPSS Inc., 2002). To test for differences in

TABLE 1. Experimental protocol of hand pollination study to determine the breeding system of *Jacquemontia reclinata*

Treatment	Pollen applied	Pollen source*	Test
Control	No	n/a	Facultative autogamy
Self	Yes	a	Geitonogamy
Sibling	Yes	b	Cross-compatibility
Near-neighbour	Yes	c	Cross-compatibility
Far-neighbour	Yes	d	Cross-compatibility
Other site	Yes	e	Cross-compatibility

* All treatments were bagged. Pollen source designated as: a, different bagged flower on the same plant; b, bagged flower on an offspring of the same maternal wild parent (half sibling); c, bagged flower on an offspring of a maternal wild parent <20 m away from the pollen recipient's maternal wild parent (same population); d, bagged flower on an offspring of a maternal wild parent >20 m away from the pollen recipient's maternal wild parent (same population); e, bagged flower on an offspring of a maternal plant from another population.

mean number of seeds per fruit, mean total seed mass per fruit, and mean seed mass among the treatments, one-way analyses of variance (ANOVAs) were performed with appropriate transformations, with pollination treatment as the main effect. *Post hoc* analyses were conducted using Tukey's procedure if Levene's test of equal variances was not significant, and Dunnett's C procedure was used if Levene's test was significant. Tests were significant if $P < 0.05$.

χ^2 tests with Bonferroni *post hoc* tests were performed to test the effect of pollination treatment on seed germination [indicated by seedling emergence (%)]. For germination time, one-way ANOVA with Tukey's *post hoc* procedure was used.

RESULTS

Fruit set

Mean percentage fruit set differed significantly among the six hand pollination treatments [$\chi^2_{(5,n=637)} = 143$, $P < 0.05$]. Cross-tabulation *post hoc* tests using the Bonferroni adjustment found that the control treatment (11.6 ± 3.9 % s.e.) was significantly different from all other treatments except the self treatment (26 ± 4.5 % s.e., $P < 0.0033$). The offsite treatment (74.3 ± 3.6 % s.e.) was significantly different from the control, self, sibling (47.5 ± 4.4 % s.e.) and near-neighbour (38.7 ± 7.9 % s.e.) treatments, but not from the far-neighbour (64.2 ± 3.8 % s.e.) treatment (Fig. 3A). Individual plants differed in self-incompatibility: of 65 plants studied, 17 set some fruit after hand pollination with self-pollen or with no manipulation controls.

Seed set

Mean seed set (mean number of seeds per flower) differed significantly among treatments [$\chi^2_{(5,n=637)} = 157$, $P < 0.001$]. The offsite treatment produced the most seed, followed by the far-neighbour and sibling treatments, which were indistinguishable from each other. The offsite, far-neighbour and sibling treatments set significantly more seed than the control and self treatments (Fig. 3B).

Significant differences occurred in the mean seed set per fruit for the hand pollination treatments that yielded fruit. Maximum seed set is four seeds per fruit; in all treatments the average seed set in fruits was > 2 seeds per fruit, but treatments differed overall, with seed set greatest in offsite and other cross-pollination treatments [$F_{(5,283)} = 4.39$, $P < 0.001$]. A Kruskal–Wallis non-parametric test performed on untransformed seed set data grouped by treatment confirmed significance ($P < 0.001$). Tukey's *post hoc* procedure showed significant differences between the offsite and all other treatments except sibling and near-neighbour (Fig. 3C).

Seed mass

Total seed mass per fruit differed significantly among treatments [$F_{(5,250)} = 5.83$, $P < 0.001$], and *post hoc* analyses revealed significant differences between control, self and offsite treatments (offsite pollen sources sired fruits with greater seed mass), and between near-neighbour and self

treatments (near-neighbour pollen sources yielded greater seed mass than self pollen, Fig. 3D). However, one-way ANOVA of mean individual seed mass by treatment did not show significant differences among treatments [$F_{(5,250)} = 1.86$, $P < 0.2$].

Seedling emergence

Significant differences in seed germination (seedling emergence) were found among treatments, [$\chi^2_{(5, n=830)} = 47.95$, $P < 0.001$]. Germination percentages of seeds resulting from near-neighbour crosses (10 %) were significantly lower than those from all other treatments (Fig. 3E). The emergence percentage for sibling-derived seeds (72 %) was significantly different from percentages for near-neighbour, far-neighbour (48 %) and offsite (51 %) treatments (Fig. 3E). Significant differences in days from planting to cotyledon emergence were found among treatments [$F_{(5,397)} = 3.91$, $P < 0.01$], with seeds from self-pollinations taking longer than seeds from most cross-pollination treatments to germinate (significantly different only from offsite and sibling treatments, Fig. 3F).

Flower visitors

While the majority of the 10 min watches were performed at Crandon Park, visitors to flowers of *J. reclinata* were observed at sites throughout the species' current range. During the watches, flower visitors were observed at four of the five study sites; no flower visitors were seen at Loggerhead Park. *Jacquemontia reclinata* flowers were visited by a wide array of insects (Table 2), primarily of the orders Hymenoptera (94 % of 377 visits observed), Diptera (4 %) and Lepidoptera (2 %). In general, species richness of visitors was greatest at Crandon Park, where the majority of individual plants are found. Visitor activity was highest during the early to middle morning and dropped off later in the day, except on cool or rainy mornings, when flying insect activity was low until the temperature increased or the rain stopped.

Flower visitors were often observed visiting every open flower in a patch, especially in smaller patches or in patches with relatively few flowers open and close together. Some of the larger-bodied visitors, especially megachilid bees, methodically visited flowers in a mostly linear sequence, while Lepidoptera and the apparently territorial halictid bees visited in a more haphazard sequence. Several individuals of one of the most frequently observed halictid visitor species, *Agapostemon splendens*, would often monopolize a flowering patch, patrolling the area in flight and chasing off potential competitors of the same species, then resting on bare sand nearby or within the patch. Time spent in each flower varied widely among species, but not as much within species; *Dialictus* bees spent up to 2 min per visit, while most other visitors spent from 1 to 15 s per visit.

Most flower visitors landed on the petals and crawled into the corolla, past the stigma and anthers if they were small enough, and down toward the nectary in the base of the corolla. Some of the larger bees (Megachilidae and Apidae) were too large to crawl all the way into the flowers, but grasped the outer corolla with their hind legs while moving

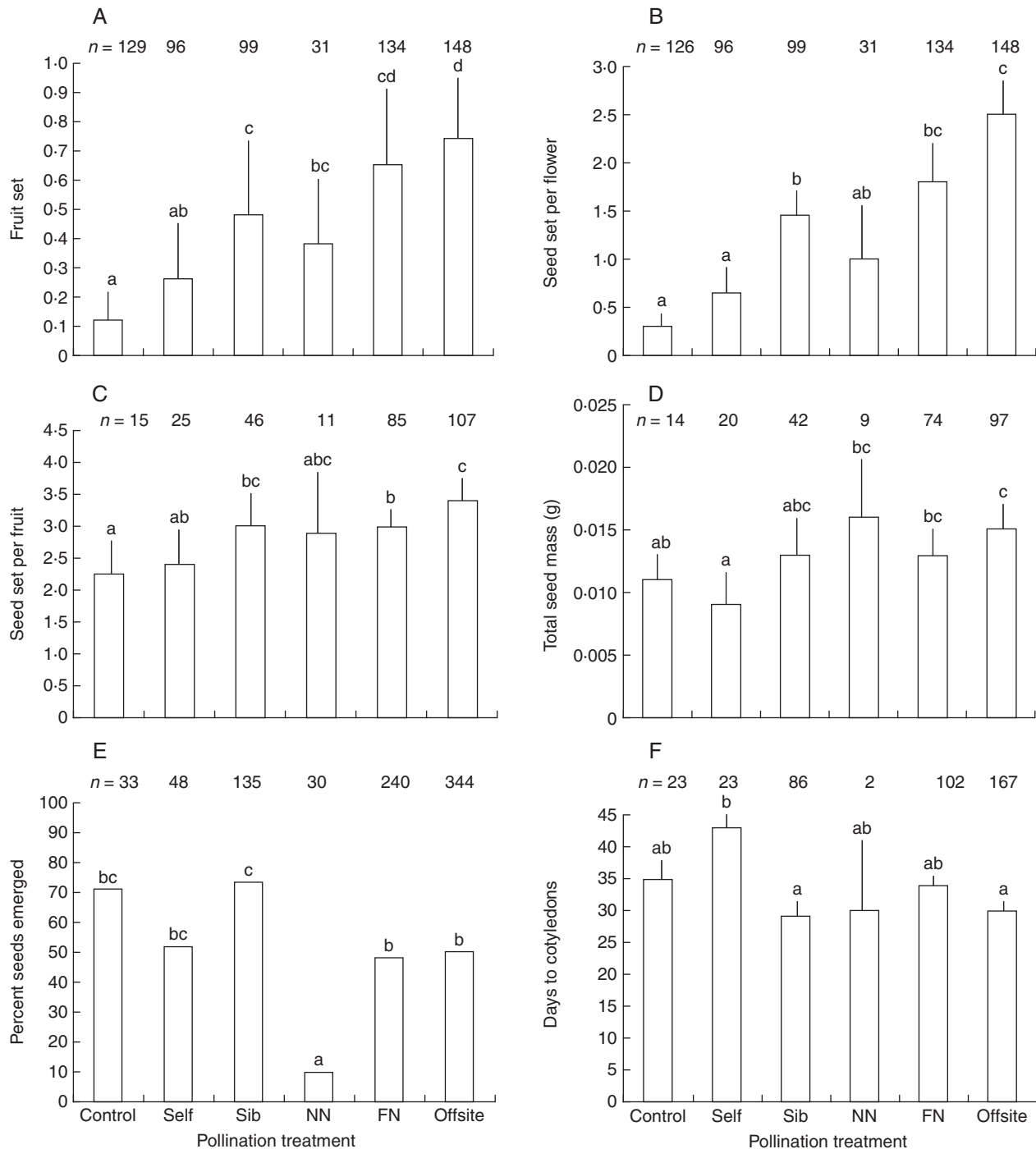


FIG. 3 Hand pollination experiments with six controlled treatments: Control, no pollen applied; Self, self-pollen applied; Sib, sibling pollen applied; NN, near-neighbour pollen applied; FN, far-neighbour pollen applied; Offsite, pollen of plant from a different population applied. Treatments with the same letter do not differ significantly from each other ($P < 0.05$). From upper left (A) to lower right (E): (A) Mean (+ s.e.) proportion of flowers producing fruits following treatment. (B) Mean seed set + 2 s.e. (mean number of seeds per flower) per treatment. These data include zeros, and full seed set is four seeds per fruit. (C) Mean number of seeds per fruit + s.e. resulting from hand pollination treatments. These results are only from flowers that set fruit. Full seed set is four seeds. (D) Mean total seed mass (g) per fruit + 2 s.e. (E) Percentage of seeds of each treatment type with cotyledons emerged after 65 d. Sample sizes varied because of differential fruit set among treatments. n = number of seeds. (F) Mean number of days + s.e. from planting to emergence of cotyledons for seeds resulting from different hand pollination treatments. n = total germinated.

the filaments aside to reach the nectar, and were covered with pollen in the process. Butterflies and skippers remained mostly outside of the corolla, with only the proboscis entering the

funnel, though this sometimes took several attempts during which pollen was picked up. Most of the visitors seemed only interested in nectar and were not actively collecting

TABLE 2. Insect visitors to flowers of *Jacquemontia reclinata*, and pollen on bodies of collected individuals of certain species

Taxon	Family	Range and number of pollen types (no. of specimens examined)
HYMENOPTERA		
<i>Melissodes bimaculata</i>	Anthophoridae*	–
<i>bimaculata</i> Lepeletier		
<i>Melissodes communis</i>	Anthophoridae	3–4 (2)
Cresson		
<i>Apis mellifera</i> L.	Apidae [†]	–
<i>Ceratina cockerelli</i> Smith	Apidae	3 (1)
<i>Agapostemon splendens</i>	Halictidae	3–4 (2)
Lepeletier		
<i>Augochlora pura</i>	Halictidae [†]	–
Cockerell		
<i>Augochlorella striata</i>	Halictidae [‡]	–
Provancher		
<i>Augochloropsis anonyma</i>	Halictidae	1–4 (3)
Cockerell		
<i>Dialictus (Evylaeus) nelombensis</i>	Halictidae [‡]	–
<i>Dialictus tegularis</i>	Halictidae	3 (1)
Robertson		
<i>Dialictus</i> sp.	Halictidae*	–
<i>Lasioglossum</i> sp.	Halictidae [‡]	–
<i>Nomia</i> cf. <i>maneei</i>	Halictidae [‡]	–
<i>Megachile brevis</i>	Megachilidae	2 (1)
<i>pseudobrevis</i> Mitchell		
<i>Megachile</i> sp. **	Megachilidae	–
<i>Campsomeris</i> sp.	Scoliidae [†]	–
<i>Scolia nobilitata</i> Fabricius	Scoliidae	5 (1)
Unidentified	Vespidae [‡]	–
DIPTERA		
<i>Chrysanthrax cypris</i>	Bombyliidae	1 (1)
Meigen		
Unidentified	Bombyliidae [‡]	–
<i>Palpada vinetorum</i>	Syrphidae	4 (1)
Fabricius		
<i>Euaesta</i> sp.	Tephritidae	–
<i>Litolinga</i> sp.	Therevidae	1 (1)
LEPIDOPTERA		
Unidentified skippers	Hesperiidae	–
<i>Agraulis vanilla</i> L.	Nymphalidae	–
COLEOPTERA		
<i>Acanthocelides</i> sp.	Bruchidae	–

Taxa verified with voucher specimens using the reference collections of Keith Waddington (University of Miami) and Mark Deyrup (Archbold Biological Station), who helped with determinations. Our collections were made in Dade County (at Crandon Park and Bill Baggs State Recreation Area). Dan Austin's records of collections (probably made in Palm Beach County) were communicated to us prior to our studies and are included with his permission. John Pascarella (Georgia Southern University) also shared his observations made at sites throughout the range of *J. reclinata* and these are included herein.

* Reported by J. Pascarella; † also reported by D. Austin; ‡ only reported by D. Austin.

pollen; however, we often observed *Dialictus* bees crawling around on the anthers, apparently collecting pollen, and crawling as well into the flower funnel, presumably to drink nectar.

Ants frequently were observed crawling into flowers and drinking nectar, but we do not include them as potential pollinators because of the relatively high frequency of 'visitation'; many *J. reclinata* plants have ant colonies at their rootstocks,

and ants are often seen on stems and leaves. Also, because of their small size (they did not usually touch anthers or stigmas) and their potentially negative effect on pollen viability (Beattie *et al.*, 1984; Wagner, 2000), we do not expect that they are effective pollinators. We did not observe ants driving away or otherwise deterring other potential flower visitors, and we did not observe any other nectar-robbers, as all visitors (except for ants) which took nectar also contacted stamens and stigma and carried *J. reclinata* pollen on their bodies (Table 2).

DISCUSSION

Breeding system

As *J. reclinata* is capable of both selfing and outcrossing, the species has a mixed mating system, with pollen flow both within and between plants. It is, however, largely self-incompatible (Bawa, 1974; Brown, 1990; Dafni, 1992; Kearns and Inouye, 1993). Self-incompatibility also has been established in several other members of the Convolvulaceae (Devall and Thien, 1992; Ushimaru and Kikuzawa, 1999), and in a local congeneric, *J. curtisii* (Koptur, 2006). Although fruit set for self-pollination was low (12%), clearly plants may set seed with their own pollen, especially, perhaps, when outcross pollen is unavailable or scarce but pollinators are not limited. This ability could be a form of bet-hedging, with the optimal method for full seed set being outcrossing. Limited fruit and seed set resulting from the control treatment suggest that late autogamy may also provide reproductive assurance, especially when plants are isolated and pollinator visitation is low.

The lack of highly significant differences among treatments in seed set per fruit (Fig. 3C) contrasts with the dramatic differences in percentage seed set among treatments. The lack of significant differences among treatments in mean seed mass may be explained by the possibility that once a flower receives compatible pollen, resources are directed toward seed development regardless of the pollen source. When treatments were compared by total seed mass per fruit (Fig. 3D), significant differences were due to differences in seed set, or total number of seeds per fruit.

A relationship is apparent between plant relatedness and pollination success. Crosses between plants from different populations had the greatest likelihood of setting fruit. They also had the greatest probability of achieving the maximum seed set of four seeds per fruit. Crosses between distant neighbours came in second for pollination success as measured by fruit and seed set. Because pollen dispersal in *J. reclinata*, and possibly seed dispersal (Maschinski *et al.*, 2003), are leptokurtic, near plants are more likely to be closely related than plants further apart. These patterns imply that the population has a spatial structure, with a general decrease in relatedness between plants following an increase in distance between plants. Flower visitors are important for the reproductive success of wild plants, which may need to exchange pollen over substantial distances to produce viable offspring. Visitor foraging patterns may also affect this relationship between physical distance and genetic similarity, as well as many

other factors such as modes of seed dispersal and the distribution of safe sites for germination and survival.

Flower visitors

Although the observed lack of wild seedling recruitment appears to be due to causes other than lack of pollinator visitation in the largest population, smaller, more isolated populations may experience low visitation rates and lower pollen quality (due to decreased deposition of outcrossed pollen) as both the pollinator species assemblage and behaviour change in response to patch size and isolation (Sih and Baltus, 1987; Kunin, 1997; Cunningham, 2000a; Smith and Gross, 2002), and the habitat quality of the surrounding matrix (Klein *et al.*, 2003). Also, non-synchronized flowering may cause temporal variations in pollen flow within populations (Torres *et al.*, 2002; Forsyth, 2003). As a result, pollen flow between individuals may therefore not only be determined by pollinator visitation, but by flower availability, and may vary significantly over even short periods (Webb and Bawa, 1983).

The experimental evidence that the species is somewhat self-compatible indicates that if the flowers available at a given time are closely related, some fruit set and seed set can still occur. However, the fact that selfing leads to lower reproductive success in *J. reclinata* implies that it benefits the reproductive fitness of a given plant to attract pollinators more likely to deposit outcross pollen, and to carry away and deposit pollen on as many other compatible flowers as possible (Barrett and Harder, 1996). If pollinators are visiting flowers sequentially and thoroughly in a patch, there is a greater likelihood of their depositing pollen from more closely related plants, or from flowers of the same plant.

Jacquemontia reclinata flowers are visited by at least 20 species of insects from diverse groups; most visitors examined also had pollen of 1–4 other flowering plant species on their bodies, supporting the description of the pollination system as ‘generalist’. The apparently generalized pollination system of this endangered species may be beneficial to its persistence in small or isolated populations (Waser *et al.*, 1996). Compared with specialized systems with one or few pollinator species, a species-rich pollinator assemblage can have complementary effects when there is temporal and spatial variability in flowering (Ornduff, 1975; Klein *et al.*, 2003), as there appears to be in the case of *J. reclinata* (Maschinski *et al.*, 2003). Furthermore, a generalized pollination system may be especially important in coastal dune systems, where large-scale disturbances such as fire and hurricanes can significantly affect pollinator populations (Cane, 1997; Rathcke, 2000). However, though generalized pollination systems may have greater resilience to linked extinctions when compared with specialized systems (Mawdsley *et al.*, 1998), there is also the possibility that introduced generalists will displace native pollinators with a net loss of species diversity (Waser *et al.*, 1996). It is also important to note that the apparent generalization of the pollination system of *J. reclinata* may be an oversimplification, as specialization can sometimes be masked when the relative effectiveness of pollinator species is not considered (Lindsey, 1984). Clearly, more work is needed in this system.

The size of the floral visitor foraging area may also affect pollen flow. For instance, if the most common flower visitors are territorial and tend to move pollen within a sub-population or patch of flowering plants, outcrossing may be dependent on those relatively rare visitors that move between populations, such as butterflies (Schmitt, 1980; Webb and Bawa, 1983). However, it is unlikely that any pollinators actually do move between populations except perhaps between Red Reef and South Beach, which are adjacent, because the distance between most populations is > 10 km. Butterflies and skippers, relatively long-distance fliers among the insect visitors we observed, may occasionally travel between *J. reclinata* populations. The search for mates and suitable oviposition sites, as well as predator avoidance, may influence the foraging behaviour of Lepidoptera, whose energy needs are relatively low (Watt *et al.*, 1974). Hence, they may visit only a small fraction of the flowers available at a given time and move frequently between plants (Webb and Bawa, 1983).

Those pollinators that are willing or able to travel relatively long distances to small, isolated populations may be ineffective in transferring pollen among flowers, either because of the way they handle pollen or because they are generalists and ‘clog up’ stigmas with pollen from other species of flowering plants (Fishbein and Venable, 1996; Caruso, 1999; Rathcke, 2000). Though visitors were observed only on *J. reclinata* during our timed watches, pollen on their bodies and informal observations indicate that many of them frequent flowers of other species as well. Pollen loads on individual flower visitors collected in this study and for other purposes included several kinds of pollen other than that of *J. reclinata*. Though deposition of the pollen of other species may be problematic at the level of the single flower or plant, an effective mutualism may occur between sequentially flowering species, as sympatric species support native pollinator communities to the advantage of those species flowering at different times (Waser and Real, 1979). Rare plant species may benefit from more common plants supporting their pollinators (Gibson *et al.*, 2006), even attracting them to be closer to and perhaps notice the rarer plants (Laverty, 1992); these other plants can also be important in supporting pollinators of rare species at times when the rare plants are not in flower. When *J. reclinata* was not in bloom, many of the same visitor species were observed on a diversity of sympatric species at the study sites. Many of the same insect species observed visiting *J. reclinata* flowers also have been observed visiting flowers of other species in and near Everglades National Park (Pascarella, 1997; Pascarella *et al.*, 1999, 2001) and elsewhere in southern Florida (Liu and Koptur, 2003).

Since this work was undertaken, we have learned much about the taxonomic and genetic relationships of this species. *Jacquemontia reclinata* is the most closely related to three species, *J. cayensis*, *J. curtisii* and *J. havanensis*, occurring in southern Florida and the Caribbean (Namoff *et al.*, 2007). There is substantially more genetic diversity within the larger populations of this species than between populations throughout its present range, with the exception of one distinct population that occurs in a unique habitat and which was not one of the sites in this study (see Thornton *et al.*, 2008). The variability of all the other smaller populations is encompassed

within the diversity of the larger populations, so that new populations for restoration or individuals for augmentation could be taken from the larger populations. Evidently, either pollinators are able to move between populations, or individuals are moved by other natural disturbance events such as strong winds or rains (since seeds would not move far with normal dispersal), maintaining genetic diversity within and among the remnant populations. It could also be that plants in nature are very long-lived, and the genetic diversity we see today is left over from when the range of the species was continuous along the coastline.

Conservation biology

Allee effects have been shown to limit reproductive success in small populations of a number of rare plants (Lamont *et al.*, 1993; Utelli and Roy, 2000; Colling *et al.*, 2004; Willi *et al.*, 2005; Wagenius, 2006; LeCadre *et al.*, 2008). Evidence of inbreeding depression can be seen either in lack of seed produced, or seedlings being less fit if produced from parents in small populations. The fact that *J. reclinata* has a predominantly outcrossing breeding system may mean that effective conservation and management of the species will require augmentation of remaining populations with genetically less related individuals to ensure adequate reproduction (genetic rescue, Holmes *et al.*, 2008), with careful consideration of interplant spacing. While partial self-compatibility may enable small, isolated populations to persist despite low pollinator visitation rates or a high degree of relatedness among plants, inbreeding depression may occur in some of these populations if selfed progeny have low fitness relative to outcrossed individuals (Barrett and Harder, 1996), as is the case with *J. reclinata*, or if selfed seeds do not germinate at all (Karron, 1991; Keller and Waller, 2002). More research is needed to determine whether inbreeding depression is occurring in some populations, especially those with very low levels of flowering and fruit set. Also, the possibility that individual genotypes may not be cross-compatible with certain others will need to be addressed (Weekley and Race, 2001). Generalized pollination in *J. reclinata* indicates that effective management of remaining and restored populations should also include plans for maximizing visitation by the most effective available pollinators. Provided the foraging and nesting needs of pollinators are incorporated into management plans, it may be possible to sustain *J. reclinata* and its pollinators with networks of small habitat reserves (Cane, 1997, 2001; Klein *et al.*, 2003).

Jacquemontia reclinata is one of the many endemic plant species that occur in the highly fragmented and rapidly vanishing dune and coastal strand communities of south-eastern Florida. Most of these species persist in habitat remnants within public parks and preserves, where they have the good fortune of being in the care of interested and enthusiastic land managers. However, in order to develop appropriate plans and protocols for the management of these habitat remnants, we need to know more about their ecological structure and functioning (Schemske *et al.*, 1994). Future work that deepens our understanding of the biology of *J. reclinata* is essential for effective conservation and restoration of this species and the web of interactions that keep the imperiled southern Florida coastal dunes alive.

ACKNOWLEDGEMENTS

We thank the US Fish and Wildlife Service (USFWS) Grant Agreement 1448-40181-99-G-173 cooperators Jack Fisher, Javier Francisco-Ortega, Cynthia Lane, Joyce Maschinski, Susan Carrara, Hannah Thornton, Sam Wright, and David LaPuma for their interaction and support during the project; Ken Neugent and Karen Griffin for greenhouse support; Yuria Cardel, Heather Gamper, John Geiger, Phil Gonsiska, Hong Liu, Jed Redwine, and Jennifer Richards for their constructive comments on earlier versions of the manuscript; Francisco, Lynda, and Sonia Pinto-Torres for technical assistance and feedback; Dwight Monteith for field, photographic and editorial assistance; Dan Austin for observations of visitors at northern sites; Mark Deyrup, Keith Waddington, and John Pascarella for insect determinations; and Paulette Johnson for statistical advice. This research was supported by funding from the USFWS, Florida Native Plant Society, FIU Tropical Biology Program and a Catherine H. Beattie Fellowship in Conservation Horticulture. This is contribution number 171 to the Florida International University Program in Tropical Biology.

LITERATURE CITED

- Aizen MA, Feinsinger P. 1994a. Habitat fragmentation, native insect pollinators, feral honey bees in Argentine 'Chaco Serrano'. *Ecological Applications* 4: 378–392.
- Aizen MA, Feinsinger P. 1994b. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology* 75: 330–351.
- Austin DF. 1979. Beach jacquemontia, *Jacquemontia reclinata*. In: Ward DB. ed. *Rare and endangered biota of Florida*, vol. 5: *Plants*. Gainesville, FL: University Presses of Florida, 36–37.
- Baker HG. 1963. Evolutionary mechanisms in pollination biology. *Science* 139: 877–883.
- Barrett SCH, Harder LD. 1996. Ecology and evolution of plant mating. *Trends in Ecology and Evolution* 11: 73–79.
- Bawa KS. 1974. Breeding systems of tree species of a lowland tropical community. *Evolution* 28: 85–92.
- Beattie AJ, Knox RB, Williams EG. 1984. Ant inhibition of pollen function: a possible reason why ant pollination is rare. *American Journal of Botany* 71: 421–426.
- Bond WJ. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions of the Royal Society B: Biological Science* 344: 83–90.
- Brown AHD. 1990. Genetic characterization of plant mating systems. In: Brown AHD, Clegg MT, Kahler AL, Weir BS eds. *Plant population genetics, breeding, and genetic resources*. Sunderland, MA: Sinauer Associates, 145–162.
- Brzosko E, Wroblewska A, Ratkiewicz M. 2002. Spatial genetic structure and clonal diversity of island populations of lady's slipper (*Cypripedium calceolus*) from the Biebrza National Park (northeast Poland). *Molecular Ecology* 11: 2499–2509.
- Buchmann SL, Nabhan GP. 1996. *The forgotten pollinators*. Washington, DC: Island Press.
- Cadotte MW, Lovett-Doust J. 2002. Ecological and taxonomic differences between rare and common plants of southwestern Ontario. *Ecoscience* 9: 397–406.
- Cane JH. 1997. Violent weather and bees: populations of the barrier island endemic, *Hesperapis oraria* (Hymenoptera: Melittidae) survive a category 3 hurricane. *Journal of the Kansas Entomological Society* 70: 73–75.
- Cane JH. 2001. Habitat fragmentation and native bees: a premature verdict? *Conservation Ecology* 5(1): 3 [online] <http://www.consecol.org/Journal/vol5/iss1/art3>.
- Carlsen TM, Espeland EK, Pavlik BM. 2002. Reproductive ecology and the persistence of an endangered plant. *Biodiversity and Conservation* 11: 1247–1268.

- Caruso CM. 1999. Pollination of *Ipomopsis aggregata* (Polemoniaceae): effects of intra- vs. interspecific competition. *American Journal of Botany* **86**: 663–668.
- Colling G, Reckinger C, Matthies D. 2004. Effects of pollen quantity and quality on reproduction and offspring vigor in the rare plant *Scorzonera humilis* (Asteraceae). *American Journal of Botany* **91**: 1774–1782.
- Cunningham SA. 2000a. Effects of habitat fragmentation on the reproductive ecology of four plant species in Mallee woodland. *Conservation Biology* **14**: 758–768.
- Cunningham SA. 2000b. Depressed pollination in habitat fragments causes low fruit set. *Proceedings of the Royal Society B: Biological Sciences* **267**: 1149–1152.
- Dafni A. 1992. *Pollination ecology, a practical approach*. New York: Oxford University Press.
- DeMauro MM. 1993. Relationship of breeding system to rarity in the Lakeside daisy (*Hymenoxys acaulis* var. *glabra*). *Conservation Biology* **7**: 542–550.
- Devall MS, Thien LB. 1992. Self-incompatibility in *Ipomoea pes-caprae* (Convolvulaceae). *American Midland Naturalist* **128**: 22–29.
- Didham RK, Ghazoul J, Stork NE, Davis A. 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution* **11**: 255–260.
- Fischer M, Matthies D. 1997. Mating structure and inbreeding and outbreeding depression in the rare plant *Gentianella germanica* (Gentianaceae). *American Journal of Botany* **84**: 1685–1692.
- Fishbein M, Venable DL. 1996. Diversity and temporal change in the effective pollinators of *Asclepias tuberosa*. *Ecology* **77**: 1061–1073.
- Forsyth SA. 2003. Density-dependent seed set in the Haleakala silversword: evidence for an Allee effect. *Oecologia* **136**: 551–557.
- Fuchs EJ, Lobo JA, Quesada M. 2003. Effects of forest fragmentation and flowering phenology on the reproductive success and mating patterns of the tropical dry forest tree *Pachira quinata*. *Conservation Biology* **17**: 149–157.
- Garvue D. 1999. Endangered species profile: beach jacquemontia. *Fairchild Tropical Garden News*, March 1999: 11.
- Gibson RH, Nelson IL, Hopkins GW, Hamlett BJ, Memmott J. 2006. Pollinator webs, plant communities and the conservation of rare plants: arable weeds as a case study. *Journal of Applied Ecology* **43**: 246–257.
- Govil CM. 1975. Phylogeny of floral nectary in Convolvulaceae. *Current Science* **44**: 518–519.
- Groom MJ. 1998. Allee effects limit population viability of an annual plant. *American Naturalist* **151**: 487–496.
- Hamrick JL, Godt MJW, Murawski DA, Loveless MD. 1991. Correlations between species traits and allozyme diversity: implications for conservation biology. In: Falk DA, Holsinger KE. eds. *Genetics and conservation of rare plants*. New York: Oxford University Press, 75–86.
- Hendrix SD, Khyl JF. 2000. Population size and reproduction in *Phlox pilosa*. *Conservation Biology* **14**: 304–313.
- Holmes GD, James EA, Hoffman AA. 2008. Limitations to reproductive output and genetic rescue in populations of the rare shrub *Grevillea repens* (Proteaceae). *Annals of Botany* **102**: 1031–1041.
- Jayasuriya KMG, Baskin JM, Geneve RL, Baskin CC. 2009. Phylogeny of seed dormancy in Convolvulaceae, subfamily Convolvuloideae (Solanales). *Annals of Botany* **103**: 45–63.
- Jennersten O. 1988. Pollination in *Dianthus deltooides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conservation Biology* **2**: 359–366.
- Johnson AF, Barbour MG. 1990. Dunes and maritime forests. In: Myers RL, Ewel JJ. eds. *Ecosystems of Florida*. Orlando, FL: University of Central Florida Press, 429–480.
- Johnson AF, Muller JW, Bettinger KA. 1990. *An assessment of Florida's remaining coastal upland natural communities: southeast Florida*. Report to Florida Natural Areas Inventory.
- Karron JD. 1991. Patterns of genetic variation and breeding systems in rare plant species. In: Falk DE, Holsinger KE. eds. *Genetics and conservation of rare plants*. New York: Oxford University Press, 87–98.
- Kearns CA, Inouye DW. 1993. *Techniques for pollination biologists*. Niwot: University Press of Colorado.
- Kearns CA, Inouye DW. 1997. Pollinators, flowering plants, and conservation biology: much remains to be learned about pollinators and plants. *BioScience* **47**: 297–307.
- Kearns CA, Inouye DW, Waser NM. 1998. Endangered mutualisms: the conservation of plant–pollinator interactions. *Annual Review of Ecology and Systematics* **29**: 83–112.
- Keller LF, Waller DM. 2002. Inbreeding effects in wild populations. *Trends in Ecology and Evolution* **17**: 230–241.
- Kernan C. 1998. *Restoration of Jacquemontia reclinata to the south Florida ecosystem*. Proposal submitted to US Fish and Wildlife Service, South Florida Ecosystem Office.
- Klein A, Steffan-Dewenter I, Tschardt T. 2003. Fruit set of highland coffee increases with diversity of pollinating bees. *Proceedings of the Royal Society B: Biological Science* **270**: 955–961.
- Koptur S. 2006. The conservation of specialized and generalized pollination systems in subtropical ecosystems: a case study. In: Waser N, Ollerton J. eds. *Plant–pollinator interactions: from specialization to generalization*. Chicago: University of Chicago Press, 341–361.
- Kunin WE. 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. *Journal of Ecology* **85**: 225–234.
- Lamont BB, Klinkhamer PGL, Witowski ETF. 1993. Population fragmentation may reduce fertility to zero in *Banksia goodii* – a demonstration of the Allee effect. *Oecologia* **94**: 446–450.
- Lane C, Pinto-Torres E, Thornton H, LaPuma D. 2001. *Restoration of Jacquemontia reclinata to the south Florida coastline*. Final year one report to the United States Fish and Wildlife Service for grant agreement 1448-40181-99-G-173.
- Lavery TM. 1992. Plant interactions for pollinator visits: a test of the magnet species effect. *Oecologia* **89**: 502–508.
- LeCadre S, Tully T, Mazer SJ, Ferdyn JB, Moret J, Machon N. 2008. Allee effects within small populations of *Aconitum napellus* ssp. *lusitanicum*, a protected subspecies in northern France. *New Phytologist* **179**: 1171–1182.
- Lindsey AH. 1984. Reproductive biology of Apiaceae. I. Floral visitors to *Thaspium* and *Zizia* and their importance in pollination. *American Journal of Botany* **71**: 375–384.
- Liow LH, Sodhi NS, Elmqvist T. 2001. 2001. Bee diversity along a disturbance gradient in lowland tropical forests of south-east Asia. *Journal of Applied Ecology* **38**: 180–192.
- Liu H, Koptur S. 2003. Breeding system and pollination of a narrowly endemic herb of the lower Florida Keys: impacts of the urban–wildland interface. *American Journal of Botany* **90**: 1180–1187.
- Maschinski J, Wright SJ. 2006. Using ecological theory to plan restorations of the endangered Beach jacquemontia (Convolvulaceae) in fragmented habitats. *Journal for Nature Conservation* **14**: 180–189.
- Maschinski J, Fisher J, Pascarella J, et al. 2003. *Restoration of Jacquemontia reclinata to the south Florida ecosystem*. Final report to the United States Fish and Wildlife Service for grant agreement 1448-40181-99-G-173.
- Mawdsley NA, Compton SG, Whittaker RJ. 1998. Population persistence, pollination mutualisms, and figs in tropical landscapes. *Conservation Biology* **12**: 1416–1420.
- Murray BR, Thrall PH, Gill AM, Nicotra AB. 2002. How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Austral Ecology* **27**: 291–310.
- Namoff S, Thornton HEB, Lewis CE, Oviedo R, Francisco-Ortega J. 2007. Molecular evidence for phylogenetic relationships of *Jacquemontia reclinata* House (Convolvulaceae) – a critically endangered species from south Florida. *Botanical Journal of the Linnean Society* **154**: 443–434.
- Ornduff R. 1975. Complementary roles of halictids and syrphids in the pollination of *Jepsonia heterandra* (Saxifragaceae). *Evolution* **29**: 371–373.
- Pascarella JB. 1997. Pollination ecology of *Ardisia escallonioides* (Myrsinaceae). *Castanea* **62**: 1–7.
- Pascarella JB, Waddington KD, Neal PR. 1999. The bee fauna (Hymenoptera: Apoidea) of Everglades National Park, Florida and adjacent areas: distribution, phenology, and biogeography. *Journal of the Kansas Entomological Society* **72**: 32–45.
- Pascarella JB, Waddington KD, Neal PR. 2001. Non-apoid flower-visiting fauna of Everglades National Park, Florida. *Biodiversity and Conservation* **10**: 551–566.
- Pitts-Singer TL, Hanula JL, Walker JL. 2002. Insect pollinators of three rare plants in a Florida longleaf pine forest. *Florida Entomologist* **85**: 308–316.

- Rabinowitz D. 1981.** Seven forms of rarity. In: Syngé H. ed. *The biological aspects of rare plant conservation*. Chichester, UK: John Wiley and Sons, 205–207.
- Rathcke BJ. 2000.** Birds, pollination reliability, and green flowers in an endemic island shrub, *Pavonia bahamensis* (Malvaceae). *Rhodora* **102**: 392–414.
- Robertson KR. 1971.** A revision of the genus *Jacquemontia* (Convolvulaceae) in North and Central America and the West Indies. PhD dissertation, Washington University, St Louis.
- Sakai AK, Wagner WL, Merhoff LA. 2002.** Patterns of endangerment in the Hawaiian flora. *Systematic Biology* **51**: 276–302.
- Schemske DW, Husband BC, Ruckelshaus MH, Goodwillie C, Parker IM, Bishop JG. 1994.** Evaluating approaches to the conservation of rare and endangered plants. *Ecology* **75**: 584–606.
- Schmitt J. 1980.** Pollinator foraging behavior and gene dispersal in *Senecio* (Compositae). *Evolution* **34**: 934–943.
- Severns P. 2003.** Inbreeding and small population size reduce seed set in a threatened and fragmented plant species, *Lupinus sulphureus* ssp. *kincaidii* (Fabaceae). *Biological Conservation* **110**: 221–229.
- Sih A, Baltus M. 1987.** Patch size, pollinator behavior, and pollinator limitation in catnip. *Ecology* **68**: 1679–1690.
- Sipes SD, Tepedino VJ. 1995.** Reproductive biology of the rare orchid, *Spiranthes diluvialis*: breeding system, pollination, and implications for conservation. *Conservation Biology* **9**: 929–938.
- Smith JA, Gross CL. 2002.** The pollination ecology of *Grevillea beadleana* McGillivray, an endangered shrub from northern New South Wales, Australia. *Annals of Botany* **89**: 97–108.
- Spira TP. 2001.** Plant–pollinator interactions: a threatened mutualism with implications for the ecology and management of rare plants. *Natural Areas Journal* **21**: 78–88.
- SPSS Inc. 2002.** *SPSS 11.5 for Windows*. Chicago: SPSS Inc.
- Steffan-Dewenter I. 2003.** Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology* **17**: 1036–1044.
- Steffan-Dewenter I, Tschardt T. 1999.** Effects of habitat isolation on pollinator communities and seed set. *Oecologia* **121**: 432–440.
- Thornton HEB, Roncal J, Lewis CE, Maschinski J, Francisco-Ortega J. 2008.** Conservation genetics of *Jacquemontia reclinata* (Convolvulaceae), an endangered species from southern Florida: implications for restoration management. *Biotropica* **40**: 507–514.
- Torres E, Iriando JM, Perez C. 2002.** Vulnerability and determinants of reproductive success in the narrow endemic *Antirrhinum microphyllum* (Scrophulariaceae). *American Journal of Botany* **89**: 1171–1179.
- United States Fish and Wildlife Service (USFWS). 1999.** *Beach Jacquemontia: Jacquemontia reclinata* House in south Florida. Multi-species recovery plan. Atlanta, GA: USFWS.
- Ushimaru A, Kikuzawa K. 1999.** Variation of breeding system, floral rewards, and reproductive success in clonal *Calystegia* species (Convolvulaceae). *American Journal of Botany* **86**: 436–446.
- Utelli AB, Roy BA. 2000.** Pollinator abundance and behavior on *Aconitum lycoctonum* (Ranunculaceae): an analysis of the quantity and quality components of pollination. *Oikos* **89**: 461–470.
- Wagenius S. 2006.** Scale dependence of reproductive failure in fragmented *Echinacea* populations. *Ecology* **87**: 931–941.
- Wagner D. 2000.** Pollen viability reduction as a potential cost of ant association for *Acacia constricta* (Fabaceae). *American Journal of Botany* **87**: 711–715.
- Waser NM, Real LA. 1979.** Effective mutualism between sequentially flowering plant species. *Nature* **281**: 670–672.
- Waser NM, Chittka L, Price MV, Williams NM, Ollerton J. 1996.** Generalization in pollination systems, and why it matters. *Ecology* **77**: 1043–1060.
- Watt WB, Hoch DC, Mills SG. 1974.** Nectar resource use by *Colias* butterflies. Chemical and visual aspects. *Oecologia* **14**: 353–374.
- Webb CJ, Bawa KS. 1983.** Pollen dispersal by hummingbirds and butterflies: a comparative study of two lowland tropical plants. *Evolution* **37**: 1258–1270.
- Weekley CW, Race T. 2001.** The breeding system of *Zizyphus celata* Judd & D. W. Hall (Rhamnaceae), a rare endemic plant of the Lake Wales Ridge, Florida, USA: implications for recovery. *Biological Conservation* **100**: 207–213.
- Weekley CW, Kubisiak TL, Race TM. 2002.** Genetic impoverishment and cross-compatibility in remnant genotypes of *Zizyphus celata* (Rhamnaceae), a rare shrub endemic to the Lake Wales Ridge, Florida. *Biodiversity and Conservation* **11**: 2027–2046.
- Weller SG. 1994.** The relationship of rarity to plant reproductive biology. In: Bowles ML, Whelan CJ. eds. *Restoration of endangered species*. Cambridge: Cambridge University Press, 90–117.
- Willi Y, Van Buskirk J, Fischer M. 2005.** A threefold genetic Allee effect: population size affects cross-compatibility, inbreeding depression and drift load in the self-incompatible *Ranunculus reptans*. *Genetics* **169**: 2255–2265.
- Wolf AT, Harrison SP. 2001.** Effects of habitat size and patch isolation on reproductive success of the serpentine morning glory. *Conservation Biology* **15**: 111–121.