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Pollinator-mediated competition between two co-flowering Neotropical mangrove species, *Avicennia germinans* (Avicenniaceae) and *Laguncularia racemosa* (Combretaceae)

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• *Background and Aims* Three ecological relationships are possible between co-flowering plant species; they may have no effect on one another, compete for pollination services, or facilitate one another by attracting more pollinators to the area. In this study, the pollinator-mediated relationship between two mangrove species with overlapping flowering phenologies was investigated in one south Florida community.
• *Methods* Pollinator observations were recorded between 0900 h and 1700 h during June and July, 2008–2010. Insect visitation rates to *Avicennia germinans* and *Laguncularia racemosa* were estimated from 522 observation intervals of 10 min during three phenological time periods, when each species flowered alone and when they co-flowered. The number of timed intervals varied between years due to differences in flowering phenology, from four to 42 for *A. germinans* and from nine to 94 for *L. racemosa*.
• *Key Results Avicennia germinans* began flowering first in all years, and insect visitation rates were significantly greater to *A. germinans* than to *L. racemosa* ($P < 0.001$). Flowers of both species received visits from bees, wasps, flies and butterflies; *Apis mellifera* was the most common floral visitor to both species. Visitation rates to *L. racemosa* increased significantly when *A. germinans* stopped flowering ($P < 0.001$). However, there was no significant change in visitation rates to *A. germinans* after *L. racemosa* began flowering ($P = 0.628$).
• *Conclusions* When they co-flowered, *A. germinans* outcompeted *L. racemosa* for pollinators. *Laguncularia racemosa* hermaphrodites self-pollinate autogamously when not visited by insects, so reduced visitation to *L. racemosa* flowers reduced the frequency of outcrossing and increased the frequency of selfing. Reduced outcrossing limits male reproductive success in this androdioecious species, which could lead to changes in the breeding system. The degree of overlap in flowering phenologies varied between years, so the effect on the mating and breeding system may differ between years.

Key words: Androdioecy, *Apis mellifera*, *Avicennia germinans*, Florida, flowering phenology, insect visitation rate, *Laguncularia racemosa*, mixed mating system, pollinator-mediated interaction.

INTRODUCTION

Ecological studies concerned with the network of interactions between plants and pollinators in a community have long been recognized as important to our understanding of plant community dynamics (e.g. Rathcke, 1983; Kearns *et al.*, 1998; Mitchell *et al.*, 2009a). Many studies have investigated interactions between co-flowering species that are visited by the same pollinators, and collectively they demonstrate the breadth of potential outcomes for interactions, i.e. whether pollinator-mediated interactions have negative or positive effects on plant reproductive success, and under which conditions. For example, co-flowering species might compete for pollination services, which could lead to lowered reproductive success (e.g. Campbell, 1985; Brown and Mitchell, 2001; Bell *et al.*, 2005; Kandori *et al.*, 2009). Alternatively, each plant species may be more attractive at a different time of day, reducing the competitive effect of pollinator sharing by temporally partitioning pollination services (e.g. Koptur, 1983; Stone *et al.*, 1998; Raine *et al.*, 2007; Baldock *et al.*, 2011). Further, each plant species could be more attractive to a different sub-set of shared pollinators, partitioning the pollination services by having different 'major' and 'minor' pollinator species (e.g. Flanagan *et al.*, 2011; Oliveira-Rebouças and Gimenes, 2011). Finally, the plants could facilitate one another by increasing the attractiveness of the general area, thereby increasing the total number of pollinators in the area and increasing the reproductive success of both species, despite sharing pollinators (e.g. Schemske, 1981; Thomson, 1982; Rathcke, 1988; Moeller, 2004).

The community pollination dynamics of Neotropical mangrove species are not well understood, although mangrove communities have great ecological and economic importance. Mangroves provide significant ecosystem services; they stabilize coastal sediments (Kumara *et al.*, 2010; Laurance *et al.*, 2011), buffer adjacent inland communities against storm surge (Krauss *et al.*, 2009; Gedan *et al.*, 2011) and act as nurseries for marine fisheries (Beck *et al.*, 2001; Barbier *et al.*, 2011). Mangrove communities are vulnerable to a number of anthropogenic and natural disturbances, including human economic development (Ellison and Farnsworth, 1996; Dahdouh-Guebas *et al.*, 2004), sea level rise associated with climate change

(Krauss *et al.*, 2010; Kumara *et al.*, 2010), and hurricanes (Sherman *et al.*, 2001; Smith *et al.*, 2009), as well as interactions between disturbance types [e.g. sea level rise and hurricanes (Ross *et al.*, 2009); sea level rise and agriculture (Eslami-Andargoli *et al.*, 2010)]. Because effective management of these important plant communities requires knowledge of the reproductive ecologies of the species (Kearns *et al.*, 1998), including pollinator-mediated interactions between co-flowering plant species (Mitchell *et al.*, 2009*b*), studies of pollinator-mediated interactions are warranted.

In the Neotropics, mangrove communities include three principle species, *Avicennia germinans* (Avicenniaceae), *Laguncularia racemosa* (Combretaceae) and *Rhizophora mangle* (Rhizophoraceae), in addition to *Conocarpus erectus* (Combretaceae), which is a common mangrove associate (Tomlinson, 1994). This study is focused on *A. germinans* (black mangrove; Fig. 1A) and *L. racemosa* (white mangrove; Fig. 1B, C), which show seasonality and overlap in flower production. In black mangrove, flower production is initiated in response to water deficit and begins during the dry season, whereas flower production in white mangrove is initiated when water availability is higher, at the beginning of the wet season (Sánchez-Núñez and Mancera-Pineda, 2011). Tomlinson (2001) reports that the main flowering season for black mangrove in south Florida is May–July, and from April throughout early summer for white mangrove. However, variation in local precipitation patterns between years can lead to variation in the initiation and conclusion of flowering. Phenological observations recorded at the study site since 2001 indicate that black mangrove is usually finished flowering by the end of June, and that white mangrove does not usually begin flowering until early June and flowers throughout July (pers. obs.).

Investigation of pollinator-mediated interactions between black mangrove and white mangrove is warranted because the species are known to share insect pollinators (Rathcke *et al.*, 2001). Further, differences in flowering phenology between years due to variation in precipitation patterns can lead to differences in the amount of time that the species co-flower, and potentially to variation in the reproductive success of one or both species. Others have reported a correlation between climate change and differences in the species composition of co-flowering plants that could affect pollinator-mediated interactions (Forrest *et al.*, 2010). Trends in the current precipitation pattern and predictions for the future provide additional impetus for this study. In South Florida, precipitation has declined during summer months and has increased during winter months (Bates *et al.*, 2008), which could affect the flowering phenologies of both species.

In animal-pollinated plant species, pollen movement is determined exclusively by pollinator visitation patterns (Mitchell *et al.*, 2009*a*). Others have demonstrated that pollinator visitation rates (visitors per flower min^{-1}) can be used to determine the nature of pollinator-mediated interactions between co-flowering species (Vazquez *et al.*, 2005). If black mangrove and white mangrove compete for pollination services, then insect visitation rates to each species will be greater when flowering alone relative to when the species are co-flowering. If one plant species outcompetes the other for pollinators, then insect visitation rates will be greater to the
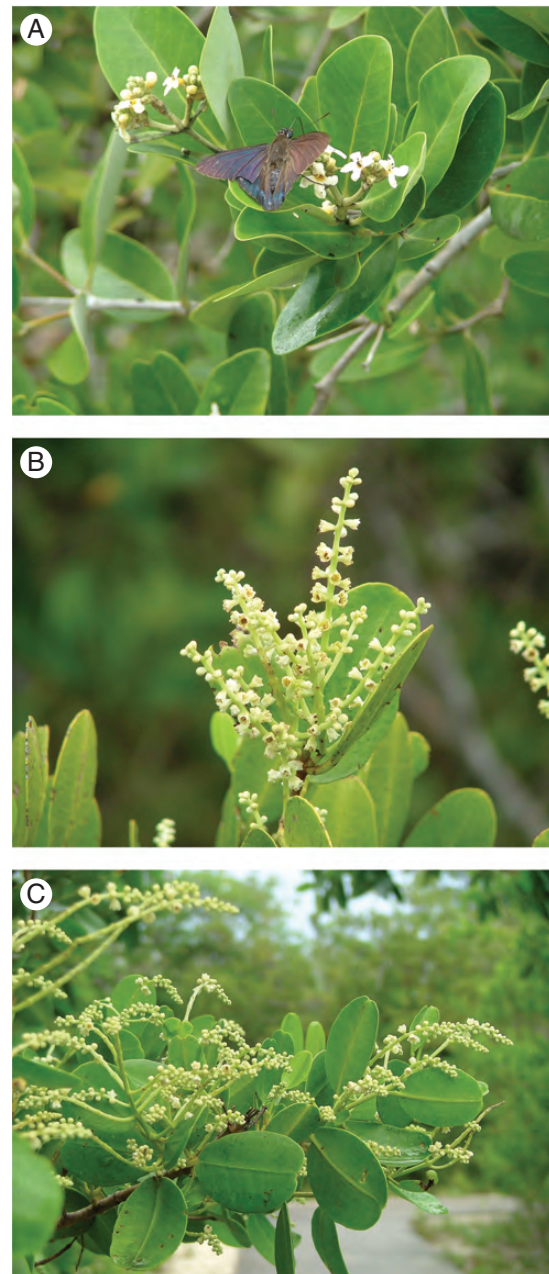

FIG. 1. Floral displays of hermaphroditic (A) *Avicennia germinans* (black mangrove, with *Phocides pigmalion*) and (B) *Laguncularia racemosa* (white mangrove) individuals, and (C) a white mangrove male.

superior competitor. Further, insect visitation rates to the lesser competitor will be significantly greater when flowering alone vs. when co-flowering with the other species. If black mangrove and white mangrove are partitioning pollination services by producing rewards at different times of day, then insect visitation rates to each species will peak at different times during the day. Finally, if black mangrove and white mangrove facilitate pollination of one another, then both species will have greater insect visitation rates when co-flowering vs. when either species flowers alone.

MATERIALS AND METHODS

Insects were observed and identified visiting flowers of black mangrove [*Avicennia germinans* (L.) L.] and white mangrove (*Laguncularia racemosa* (L.) C.F. Gaertn.) at West Lake County Park, Broward County Parks and Recreation, Hollywood, FL, USA during the following time periods: 31 May–8 June 2008, 9 July–12 July 2008, 27 June–12 July 2009 and 14 June–16 July 2010. The number of individual trees included in the study varied between years due to differences in the flowering strength of individual plants, but many trees were included in the study in all three years. In each year, insects were observed visiting flowers on 20–25 black mangrove hermaphroditic plants, 18–29 white mangrove hermaphroditic plants and 20–22 white mangrove male plants. The relative flowering strength of each species was categorized for each time period as 'strong', 'moderate' or 'weak' based on the number of inflorescences and the number of open flowers per inflorescence. Flowering strength was considered strong when most plants had many inflorescences, each with at least as many open flowers as buds or developing fruits. Flowering strength was considered weak when most plants had few inflorescences, each with many more buds and/or developing fruits than open flowers. Flowering strength was considered moderate if the number of inflorescences, the number of open flowers per inflorescence, or both were intermediate between strong and weak categories.

Insects were observed during 10 min intervals between 0900 h and 1700 h. Photographs of previously identified specimens (Landry, 2005; Landry and Rathcke, 2012) were used to confirm species identifications in the field when specimens could not be collected; voucher specimens were identified by Mark O'Brien of the University of Michigan Museum of Zoology (UMMZ) Insect Division, and are housed at the UMMZ. When possible, equal time was spent observing insects at black mangrove plants, hermaphroditic white mangrove plants and male white mangrove plants during time periods when each species flowered alone and when they were co-flowering. For each tree, a $0.5–2\ m^2$ watch zone was established each day. It was necessary to scale visitation rates by flower number in order to make direct comparisons between plants with different floral densities, as plants with larger floral displays are expected to attract more pollinators than plants with smaller floral displays. In most cases, multiple inflorescences were included in the watch zone.

Insect visitation rates were calculated for each timed interval using the following formula:

$$\text{Insect visitation rate} = (\text{number of insect visitors/number of flowers /10 min}).$$

Average insect visitation rates were calculated for each species and breeding type during each year for three time periods determined by flowering phenology: (1) when black mangrove flowered alone; (2) when the two species co-flowered; and (3) when white mangrove flowered alone. One-way analysis of variance (ANOVA) was performed with Systat 12 using data collected in 2008 to test for differences in insect visitation rates to black mangrove when co-flowering with white mangrove vs. when flowering alone. Three-way ANOVA was performed using data collected in 2008 and 2009 to test for differences in insect visitation rates to white mangrove between years, genders and when co-flowering with black mangrove vs. when flowering alone. Two-way ANOVA was performed using data collected when the species were co-flowering in 2008–2010 to test for differences in insect visitation rates to black mangrove individuals and white mangrove males and hermaphrodites between years and species or gender.

RESULTS

The flowering phenologies of the two species varied between years (Table 1), but black mangrove began flowering first in all years. Both species produced flowers for several months; flowering strength started out weak at the beginning of the flowering season, increased in strength and then stabilized for an extended time, and gradually weakened at the end of the flowering season. Large plants of both species produced more flowers than smaller conspecifics; large plants also produced new inflorescences throughout the season, so they flowered for longer periods of time (pers. obs.).

A total of 1173 insect visitors representing 26 species in four orders (Hymenoptera, Lepidoptera, Diptera and Coleoptera) were observed visiting flowers of the two plant species (Table 2). Eight species were considered common because at least ten individuals were observed during this study. Black mangrove and white mangrove shared 15 insect species (58 %), including all common species; nine species (approx. 34 %) were only observed visiting white mangrove flowers, while two species (approx. 8 %) were only observed visiting the flowers of black mangrove. *Apis mellifera* (honey-bee) was the most common floral visitor to both plant species in all categories during all years, representing approx. 75 % of all visitors to white mangrove and 87 % of all visitors to black mangrove.

The number of 10-min watch intervals in each phenological category varied between years; 4–42 watches were performed

TABLE 1. *Relative strength of flowering in* Avicennia germinans *(black mangrove) and* Laguncularia racemosa *(white mangrove) observed during work periods for 2008–2010*

Work period	*A. germinans*	*L. racemosa*
2008		
31 May–8 June	Strong	Weak (initiation)
9 July–12 July	NF	Strong
2009		
27 June–3 July	Weak (conclusion)	Strong
6 July–12 July	NF	Strong
2010		
14 June–15 June	Strong	NF
16 June–22 June	Strong	Weak (initiation)
24 June–16 July	Moderate	Weak–moderate

Key to flowering strength categories: strong, many inflorescences, all with at least as many open flowers as buds and/or developing fruits; weak, few inflorescences with open flowers, and many more buds and/or developing fruits than open flowers; moderate, intermediate between strong and weak categories due to the number of inflorescences and/or number of open flowers; NF, not in flower.

TABLE 2. *Taxonomic list and abundance data for insect species observed visiting flowers of* Avicennia germinans *(black mangrove) and* Laguncularia racemosa *(white mangrove) during the 2008–2010 flowering seasons*

Taxonomic group	Insect species	Avicennia germinans			Laguncularia racemosa		
		2008	2009	2010	2008	2009	2010
Hymenoptera							
Apidae	*Apis mellifera Linnaeus	(94)	(20)	344 (204)	134 (10)	336 (77)	(47)
Apidae	Bombus sp.	(1)	–	–	1 (0)	2	–
Apidae	**Xylocopa virginica Linnaeus**	–	–	–	–	–	(1)
Apidae	**Unknown species**	–	(2)	–	–	–	–
Halictidae	**Agapostemon sp.**	–	–	–	2	–	–
Halictidae	Augochlora sp.	(1)	–	–	3 (0)	–	–
Megachilidae	**Coelioxys sp.**	–	–	(3)	–	–	–
Megachilidae	*Megachile alleni Mitchell	(10)	–	–	(3)	–	(1)
Scoliidae	**Scolia nobilitata Fabricius**	–	–	–	(1)	–	(1)
Sphecidae	*Sphex jamaicensis (Drury)	(3)	–	(15)	9 (2)	6	(10)
Tiphiidae	**Myzinum sp.**	–	–	–	5	–	–
Vespidae	*Euodynerus sp.	(1)	–	2 (0)	4 (2)	3	(5)
Lepidoptera							
Hesperiidae	*Phocides pigmalion Cramer	(3)	(1)	12 (11)	3 (0)	2 (0)	(4)
Hesperiidae	**Unknown species**	–	–	–	1	–	–
Lycaenidae	Unknown species	(1)	–	–	1 (0)	–	(1)
Nymphalidae	**Heliconius charitonius (Linnaeus)**	–	–	–	2	–	–
Nymphalidae	*Junonia evarete Stall	–	–	8 (5)	2 (1)	1	–
Pyralidae	Unknown species	–	–	–	2	–	–
Arctiidae	**Empyreuma sp.**	–	–	–	–	1	–
Diptera							
Bombyliidae	Villa sp. 1	–	–	3 (1)	–	–	(1)
Bombyliidae	**Villa sp. 2**	–	–	–	–	–	(3)
Calliphoridae	*Unknown species	(1)	–	3 (1)	5 (0)	11 (3)	(1)
Syrphidae	Baccha sp.	–	–	5 (4)	1	1	–
Syrphidae	*Palpada albifrons (Wiedemann)	(1)	–	(7)	1 (0)	(3)	(8)
Syrphidae	Palpada sp.	(1)	–	–	(1)	–	–
Coleoptera							
Buprestidae	**Unknown species**	–	–	–	–	–	(1)
	Annual insect total	(117)	(23)	402 (251)	181 (20)	366 (83)	(84)
	Number of 10 min watch intervals	(32)	(4)	61 (42)	156 (76)	82 (19)	(187)

Insect species in bold were observed visiting flowers of only one plant species. Numbers in parentheses represent data collected when the plants were co-flowering; species with an asterisk (*) are considered common in this paper.

at black mangrove and 9–94 watches were performed at white mangrove males and hermaphrodites. Insect visitation rates differed significantly between years (Fig. 2), with greater numbers of insect visitors in 2009 relative to 2008 for black mangrove, and relative to 2008 and 2010 for white mangrove (F-ratio=14·070, d.f.=2, $P<0·001$). More insects visited black mangrove flowers than visited white mangrove hermaphroditic and male flowers in all years (Fig. 2; F-ratio=25·635, d.f.=2, $P<0·001$). Insect visitation rates to black mangrove were reduced when co-flowering with white mangrove vs. when flowering alone, but did not differ significantly (Fig. 2A; F-ratio=0·238, d.f.=1, $P=0·628$). In contrast, insect visitation rates to white mangrove hermaphrodites and males were significantly greater when white mangrove was flowering alone vs. when co-flowering with black mangrove (Fig. 2B, C; F-ratio=12·956, d.f.=1, $P<0·001$). Overall, white mangrove hermaphrodites received fewer visitors than male plants (F-ratio=8·208, d.f.=1, $P=0·005$), but insect visitation rates to plants of both genders responded similarly when black mangrove was co-flowering (F-ratio=0·996, d.f.=1, $P=0·319$).

DISCUSSION

Black mangrove outcompeted white mangrove for pollinators; at all times, the rate of insect visitation to black mangrove was significantly greater than to white mangrove, and insect visitation rates to white mangrove were significantly lower when co-flowering with black mangrove than when it flowered alone (Fig. 2). Vazquez and colleagues (2005) have demonstrated that differences in insect visitation rates can be used to determine the nature of pollinator-mediated interactions between co-flowering plant species. There was no difference in the time of day that visitors were observed at the flowers of the two species (data not shown), so the plants are not partitioning pollination services temporally. Floral preferences of honey-bees had the greatest effect on visitation rates to both species because they were far more abundant than any other insect species (Table 2). Honey-bees clearly preferred black mangrove over white mangrove when the plants were co-flowering in 2008 and 2010. White mangrove was favoured when co-flowering with black mangrove in 2009, but few flowers were found on black mangrove individuals at the time of observation, and few watches could be performed
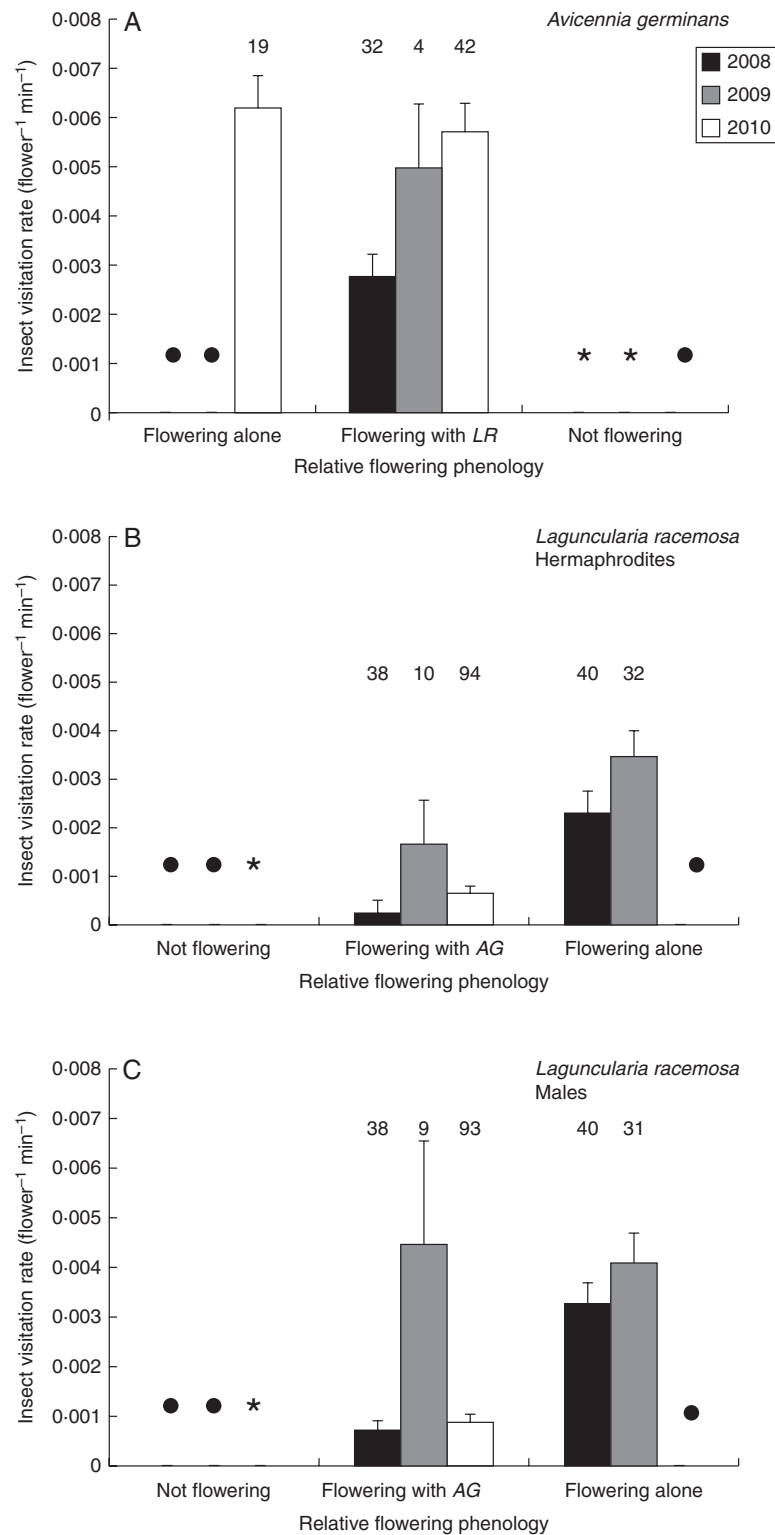
FIG. 2. Average number of insects visiting the flowers of (A) *Avicennia germinans* (black mangrove) and *Laguncularia racemosa* (white mangrove) (B) hermaphrodites, and (C) males. Visitation rates to black mangrove and white mangrove differ significantly (P<0·001), as do visitation rates to white mangrove when co-flowering with black mangrove vs. when flowering alone (P<0·001). The number of 10-min watch intervals is indicated above each column; *AG*, *Avicennia germinans*; *LR*, *Laguncularia racemosa*; dots indicate time periods when data were not collected; asterisks indicate collection time periods when the plants were not in flower.

because it was nearly finished flowering for the season. In contrast, most white mangrove individuals were in full flower during the observation period (Table 1), and were more attractive to insects because few black mangrove flowers were available. Honey-bees have not always been so influential in this community; the number of honey-bees visiting white mangrove flowers increased 433 % between 2001 and 2008 (Landry, 2011), possibly due to the effects of Hurricane Wilma in 2005. Honey-bees are regularly brought into the area to pollinate crops (Bureau of Plant and Apiary Inspection, 2008), so the rapid increase in honey-bees following the hurricane may be due to feral colonies that moved from nearby agricultural areas. Further, Africanized honey-bee colonies, which grow faster and swarm more frequently than European colonies (Schneider et al., 2004), were documented in the region in 2005 (USDA Agricultural Research Service, 2011). Native pollinators can be outcompeted for nectar and pollen resources (Goulson, 2003; Rivera-Marchand and Ackerman, 2006; Goulson and Sparrow, 2009), so rapid growth of the honey-bee population may have resulted in reduced resource availability for the other pollinator species, slowing the recovery of their populations.

Honey-bees were significantly more abundant than all other insect species and had the greatest influence on visitation rates, but the preferences of the other common species are important to consider as well. In addition to honey-bees, common species included: one bee species, *Megachile alleni* Mitchell; two wasp species, *Sphex jamaicensis* (Drury) and an unidentified *Euodynerus* sp.; two butterfly species, *Phocides pigmalion* Cramer and *Junonia evarete* Stall; and two fly species, *Palpada albifrons* (Wiedemann) and an unknown calliphorid species (Table 2). Of these, only *S. jamaicensis* and *P. albifrons* did not show a preference. All common species were previously observed visiting black mangrove and white mangrove flowers in this community (Landry, 2011; Landry and Rathcke, 2012) as well as other sites in Florida and the Bahamas (Rathcke et al., 2001; Landry et al., 2005; Landry and Rathcke, 2012).

The wasp *Euodynerus* and the calliphorid fly preferred white mangrove over black mangrove. Flies and wasps primarily seek nectar rewards from plants, so larger per flower nectar rewards reported for white mangrove (Rathcke et al., 1996) could explain the preference shown by these species. However, the preference displayed by *Euodynerus* individuals could also be due in part to the proximity of flowers to its larval prey. Many of the *Euodynerus* individuals that visited white mangrove flowers were also observed visiting rolled leaves and the undersides of leaves, a behaviour not observed during interactions between *Euodynerus* and black mangrove. All members of the genus *Euodynerus* are known to prey on lepidopteran caterpillars, which they use to provision their nests (Krombein et al., 1979). Several species of caterpillar have been observed on white mangrove vegetation and flowers, but not on black mangrove (pers. obs.). Unlike white mangrove, the leaves of black mangrove excrete salts, and salt crystals frequently cover one or both leaf surfaces (Tomlinson, 2001). The sharp-edged salt crystals may protect the plant from soft-bodied herbivores such as caterpillars, which could result in a reduction in *Euodynerus* visitors, if the wasps are visiting flowers that are located nearest to their lepidopteran prey.

Despite reports of greater nectar production in white mangrove flowers vs. black mangrove flowers in the Bahamas (Rathcke et al., 1996), the commonly observed species of bees and butterflies preferred black mangrove. Bee visitors could also be seeking pollen resources and are known to respond to pollen quality (Waddington et al., 1998), so they could be choosing black mangrove pollen if it is more nutritious. Other studies have shown that pollen grains from different species have different nutritional qualities (e.g. Human et al., 2007). The pollen grains of black mangrove are 40 % larger than those of white mangrove (Bertrand, 1983), but the relative nutritional value of pollen from the two species is not known. The butterflies, in contrast, may be more attracted to black mangrove due the architecture of the floral display, as has been found for other insect pollinators (Jordan and Harder, 2006; Ishii et al., 2008). Tight clusters of black mangrove inflorescences at the ends of the branches form a single cyme-like display with a relatively flat landing surface, from which many flowers can be probed (Fig. 1A). In contrast, white mangrove presents flowers in a raceme, an elongated inflorescence with flowers that open along the sides of the inflorescence, so insect visitors cannot probe multiple flowers from a single landing site (Fig. 1B, C).

The competitive effect of black mangrove influenced the mating system of white mangrove while the two species were co-flowering. White mangrove has a mixed mating system (Landry and Rathcke, 2007) and, in the absence of insect visitation, the plant self-pollinates autogamously (Landry, 2005). During this study, most white mangrove individuals had many flowers that were untouched by insects at the end of the day. Since the sticky pollen can only be transported between plants via insect pollinators, reductions in the frequency of floral visitors due to competition with black mangrove resulted in an increase in autogamously selfed white mangrove progeny. Inbreeding depression was weakly expressed in this population at the fruit set (Landry and Rathcke, 2007) and seedling emergence (C. Fliger and C. L. Landry, OSU, OH, USA, unpubl. res.) life history stages, but an accumulation of small fitness reductions between selfed and outcrossed progeny at multiple life history stages can result in a significant reduction in the overall success of selfed progeny (Affer and Thompson, 1997; Rojas-Sandoval and Meléndez-Ackerman, 2009; Grueber et al., 2010). White mangrove also has a mixed breeding system (Landry et al., 2009); some populations are androdioecious (Landry and Rathcke, 2007), a rare breeding system with plants that produce either male or hermaphroditic flowers (Darwin, 1888), while other populations lack male plants. According to Evolutionarily Stable Strategy models, male plants benefit from high outcrossing frequencies (Lloyd, 1975; Charlesworth, 1984), so reduced outcrossing due to pollinator-mediated interactions with black mangrove could also influence the maintenance of androdioecy. While hermaphrodites can produce progeny through autogamous selfing, males rely exclusively on pollinators for their reproductive success. If new precipitation patterns result in greater overlap of the flowering phenologies of white mangrove and black mangrove, then the frequency of white mangrove males could decline in this and other androdioecious populations.

Black mangrove outcompeted white mangrove for pollination services, but some insect species did show a preference for white mangrove. If these species become more frequent in the future, then the strength of competition on white mangrove will be reduced. Several insect species were more common before Hurricane Wilma, including the calliphorid fly that preferred white mangrove (Landry 2011). Their population sizes may eventually return to pre-hurricane numbers, although competition with rapidly growing honey-bee populations for floral resources could extend the time necessary for recovery or reduce the likelihood of full recovery. If the frequency of insect visitation does not increase, then the frequency of male plants, which depend completely on pollinators for reproductive success, will probably decline in this population over time. This study further demonstrates the need to investigate the effects of climate change on pollinator-mediated interactions, particularly in vulnerable communities that experience frequent disturbance.

ACKNOWLEDGEMENTS

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