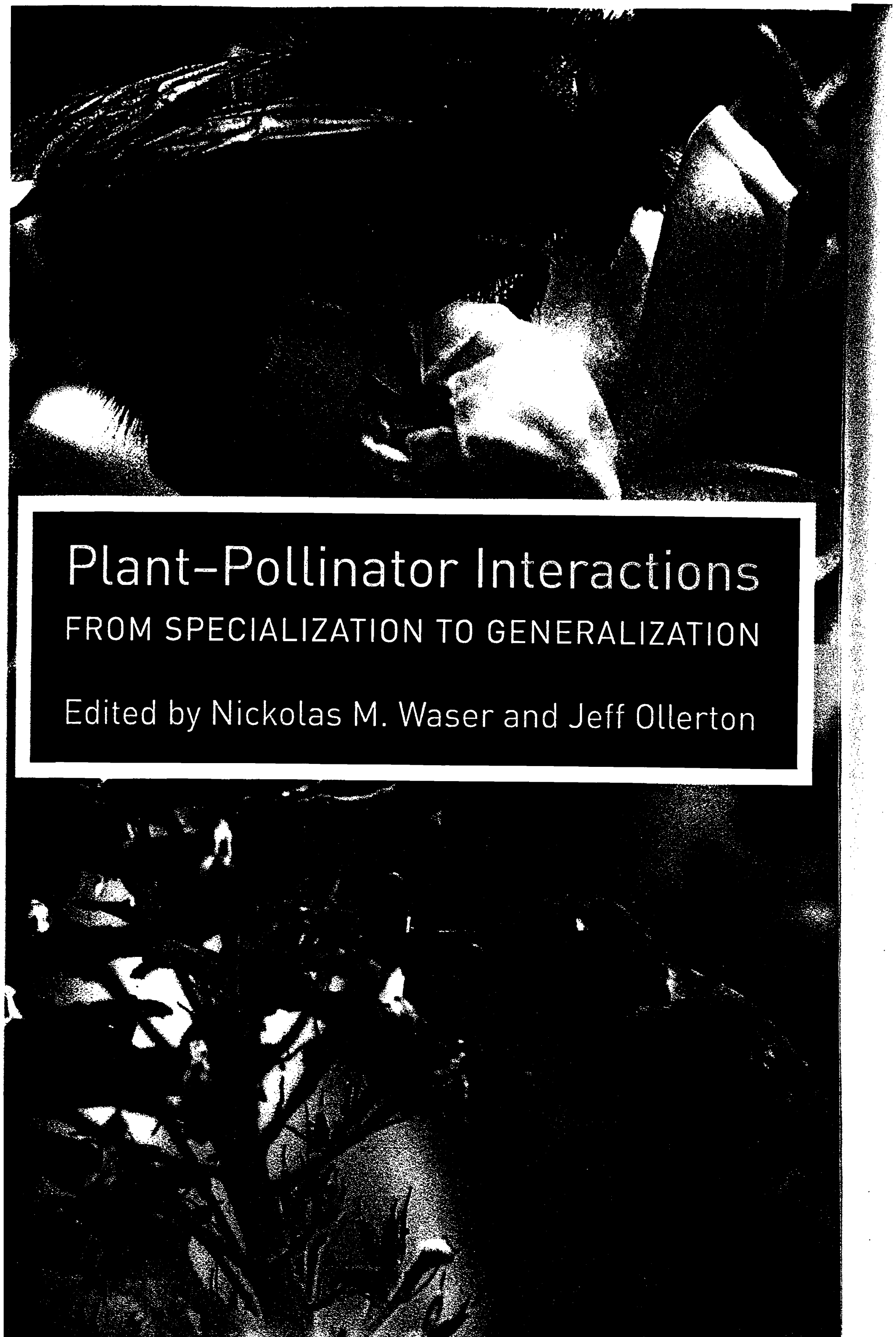

CHAPTER FIFTEEN

The Conservation of Specialized and Generalized Pollination Systems in Subtropical Ecosystems: A Case Study

Suzanne Koptur

They paved paradise and put up a parking lot
—Joni Mitchell

If one is lucky enough to hike in a pristine natural area and to come upon a display of native plants in bloom, one may see native visitors pollinating flowers and enjoying the floral rewards. These visitors may even have evolved over time to best exploit the rewards and the flowers, to best export their pollen for dispersal to another individual of the same plant species. Much important research has been conducted in natural areas with minimal disturbance, and from these studies a body of ecological and evolutionary theory has grown about these striking mutualisms. This idyllic scenario is becoming the exception, however because many parts of the planet now have a disproportionately large percentage of the fauna made up of one species, *Homo sapiens*. The earth's human population has doubled in the past 40 years (surpassing six billion in 2001). Humans are prone to taking the nicest places and transforming them into places where they will live and work, often in isolation from anything natural. Even areas that superficially seem to be "pristine" often or always show the imprint of humans (McKibbin 1989); for example, nonnative plants or pollinators are likely to join the natives in the idyllic scenario just described (Brown et al. 2002; Memmott and Waser 2002).

Habitat destruction and fragmentation often shift the balance of nature in remaining habitat patches so that native organisms can no longer persist. Large predatory animals that require large areas for their home range provide the most obvious indication when they disappear, and, with the demise of predators, cascading effects of increased herbivore abundance may affect plants (Anderson 1997; Malcolm 1997; Dicke and Vet 1999; Jeffries 1999; Terborgh et al. 2001; Dyer and Letourneau 2003). Smaller animals, including insects, may hold on longer in remaining habitat patches as long as their survival requirements are met, but many groups show increased species richness with larger fragment size

(Robinson et al. 1997; Steffan-Dewenter and Tscharntke 2002; Steffan-Dewenter et al., chap. 17 in this volume). Predators and parasitoids are more strongly affected by habitat fragmentation than are lower trophic groups (Gibb and Hochuli 2002). Various phenomena accompanying fragmentation may lead to the decline or disappearance of organisms, including negative consequences of inbreeding, which results from isolation of small populations (Holsinger 1993; Hastings and Harrison 1994), and stochastic extirpation without recolonization due to greater distances from other populations (Hanski 1997). Smaller animals may have even greater effects on plants, because many of them serve as pollinators (Steffan-Dewenter et al. 2002) and seed dispersers (Bierregaard and Stouffer 1997) as well as herbivores (Rao et al. 2001) and seed predators (Donoso et al. 2003). Animals disappear more quickly than plants from landscapes affected by humans, but plants without their mutualistic animal partners may not persist long into the future.

In many situations it is not possible to preserve wild habitats, especially in the vicinity of urban areas, where human population pressures are great. Forward-thinking governments may set aside preserves, but these are often smaller and fewer than what conservation biologists might deem optimal or desirable. Plant species may be preserved in protected and/or managed habitat remnants, but, if their pollinators are lost and they cannot reproduce sexually, they may be evolutionarily dead. Habitat destruction can incur an "extinction debt" that will not be realized for decades or centuries; this is the reasoning behind using successful pollination as a measure of ecosystem health (Aizen and Feinsinger 1994), although using pollination deficits to infer pollinator declines may not be entirely straightforward (Thomson 2001).

In conquering the natural world, we humans have been largely oblivious to our dependence on pollinators for much of what we eat and use (Nabhan and Buchmann 1997) and have "forgotten pollinators" (Buchmann and Nabhan 1996). For over a decade, there have been declines in pollinators and pollination disruption has been reported worldwide (Kearns et al. 1998), though there is less direct evidence than many have presumed and such conclusions may be premature (Cane and Tepedino 2001). Long-term data are needed to track changes (Kearns 2001; Roubik 2001), and it is difficult to tell if changes are truly declines, or just supra-annual fluctations (Roubik 2001; Williams et al. 2001) or statistical artifacts (Cane 2001; Kerr 2001).

Indeed, there are some anthropogenically fragmented habitats where many of the mutualistic plant–animal relationships remain fairly intact, and not all mutualistic interactions show negative effects of habitat fragmentation or land-use intensity (Klein et al. 2001). Humans may actually enhance their own habitats in ways that can attract and sustain pollinators—to the benefit of native plant species dependent on specialized and generalized pollinators. The quality of the matrix—the space between the habitat fragments—can play a role in reducing negative effects of fragmentation (Perfecto and Vandermeer 2001). In subtropical southern Florida, extensive plantings of nonnative ornamentals provide abundant floral rewards to sustain pollinators of native plants in the urban matrix between the remaining fragments of natural habitat. Native-plant enthusiasts have promoted gardening with indigenous species, further enhancing the seemingly inhospitable between-fragment spaces for pollinator attraction and survival.

For the past decade my students and I have been studying plant–animal interactions in the South Florida pine rocklands. In this chapter I will review the effects of habitat destruction and fragmentation on native plants that remain in the natural landscape, consider the role of the matrix in ameliorating some of the negative effects of habitat fragmentation on pollinators, and discuss some measures that are being taken to conserve pollinators in the human-dominated landscape of subtropical South Florida in the United States. My hope is that this example will serve to illustrate problems and possibilities for more general maintenance of pollination systems in human-dominated landscapes.

Effects of Habitat Destruction and Fragmentation in Pine Rocklands of South Florida

The basic result of habitat destruction is that less habitat is available in which native plants can persist. I will illustrate this point by using the pine rocklands habitat from the uplands of extreme southern peninsular Florida. Pine rocklands, a fire-maintained subclimax vegetation with many endemic taxa, used to be nearly continuous albeit divided occasionally by freshwater wetlands or "transverse glades" (Snyder et al. 1990). The area covered by the rocklands ecosystems was never large (fig. 15.1A) and shrank rapidly from the mid- to late 20th century because of economic development. Rockland sites were preferred areas for clearing, building, and (after the invention of the rock plow) vegetable fields. Today, less than 2% of the original habitat outside of Everglades National Park remains, composed of a highly fragmented patchwork throughout urban and suburban Dade County (fig. 15.1B). Many of these anthropogenic fragments are protected as parks, but only some are maintained with exotic-pest-plant control and periodic fires. Other fragments are in private ownership; most of these have management problems similar to those of the parks, or precarious preservation status.

Fragments of pine rocklands also dramatically illustrate the "edge effects" resulting from increased perimeter-to-interior ratio: greater invasion by exotic species (especially weedy pest plants) that crowd out natives. The edges are greatly influenced by the surrounding inhabitants in terms of fire suppression: without periodic fires, pine rocklands undergo succession to hardwood hammock forest, losing their diverse understory of herbs and shrubs (Snyder et al. 1990; DeCoster et al. 1999). Many of these understory plants are endemic to this

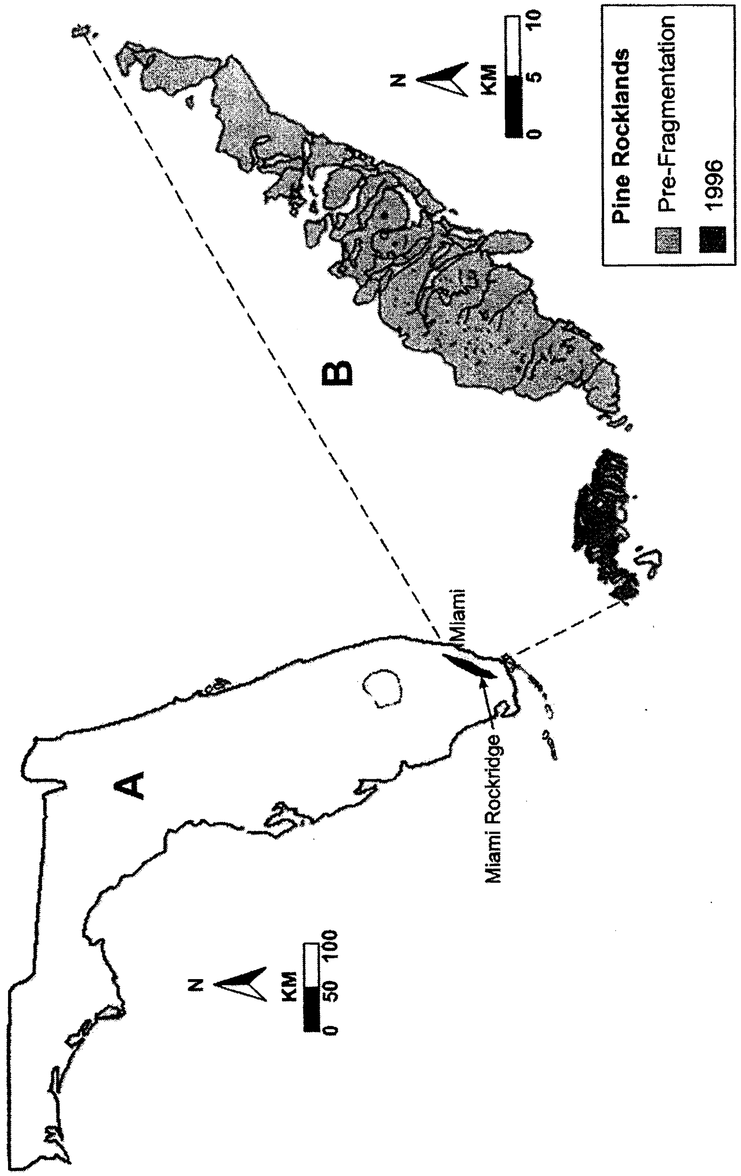

Figure 15.1 Original (*left*) and present-day (*right*) extent of pine rocklands in mainland southern Florida. There are also pine rocklands in the lower Florida Keys but they are not shown at the scale of the state map. (*Left*) Location and extent of Miami Rockridge is shown in black, and that same area is shown outlined at a much larger scale in the projection to the right. (*Right*) Prefragmentation extent (outlined) and extent in 1992 (black areas). Most remaining intact rocklands are protected within Everglades National Park; outside this park, less than 2% of the original rocklands remain.

habitat, and many are rare and becoming more so. Many former pine rocklands fragments have been degraded so completely that there is no longer a central core with native species, only a monoculture of Brazilian pepper (*Schinus terebinthifolius*) or a mixture of pest-plant species (Bradley and Gann 1999).

Exotic plants are not the only pests; exotic insects can compete with and eliminate native beneficial insect mutualists as well. Many areas in the southern United States (as well as Central America), formerly species-rich in native ants (and other insects), have become dominated by exotic ant species such as fire ants (*Solenopsis invicta*). Fire ants can limit the numbers of herbivores and pollinators with their aggressive, omnivorous foraging behavior (Fleet and Young 2000). Honeybees may be kept by beekeepers in groves adjacent to, and even in, some natural forest areas and may usurp floral resources that originally supported a diversity of native insects (Cairns 2002).

Animals kept as pets (or feral colonies maintained by kindhearted but misguided humans) can, in some cases, also have a profound impact on natural habitats. Many natural areas have networks of people who feed stray cats, capture them, neuter/spay them, and release the strays. Rather than controlling the populations, the presence of the colony serves as an "attractive nuisance," so that more cats are abandoned at the parks and populations continue to grow from the continual "immigration" of new individuals (Clarke and Pacin 2002; Castillo and Clarke 2003). The effects of domestic cats (Churcher and Lawton 1987; Schneider 2001) and other feral animals (Woodroffe et al. 1990; Schneider 2001) on wildlife are destructive and profound. Birds, lizards, and small mammals eat a variety of insects; when cats reduce their numbers, then insect populations can grow to levels that severely limit plant growth and reproduction. Some residents of Miami keep chickens that roam freely, which may travel through local parks in their search for food—eating seeds, seedlings, and small plants (and sometimes themselves providing food for resident foxes!). Goats and rabbits may similarly alter the landscape in their quest for forage and make "natural" areas less diverse and more barren, just as livestock does in midwestern U.S. forests (Dennis 1997).

Native animals may also be influenced by human interaction that in turn can affect their habitat. Sportsmen hunted the charismatic, endangered Key deer to near extinction as the Keys were exploited for tourism (Silvy 1975; Frank et al. 2003). Since their protection, Key deer have grown so numerous that populations have reached carrying capacity (Lopez 2001) and their grazing effects may have a larger impact than ever in the past (Folk et al. 1991; Koptur et al. 2002). Key deer herbivory, especially after fire, significantly reduces plant stem length and eliminates flowers on many preferred species (S. Koptur et al., unpublished data).

There is clearly need for management of pine rocklands fragments in the urbanized landscape of South Florida. County natural-areas managers prioritize activities in lands they manage and are fairly effective in controlling exotic plants via manual removal and herbicides. It is more difficult to use fire to manage fragments, especially those in close proximity to residential areas, but on occasion progress is made in this aspect of pine rocklands habitat conservation. Urban and suburban areas inhabited by humans are also managed for problem insects, especially mosquitoes, cockroaches, and ants. Pesticides that are used to control insects in adjacent areas can certainly affect survival of nontarget insects in natural area fragments in the urban landscape. Closer to humans, more pesticides are used: more than 20,000 pest control firms and 100,000 service personnel treat 12 million dwellings nationally, including most of the 280,000 retail food outlets, 480,000 commercial restaurants and kitchens, and 66,000 hotels and motels in the United States (National Pest Management Association 2001). In subtropical southern Florida, I estimate that more than 90% of homes use chemical pest control inside the dwelling, and more than 60% use some sort of chemical pest control in the yard. Termite control in dwellings is ubiquitous but usually has little broadcast effect. Certain pesticides (some used for fleas, ticks, and juvenile mosquitoes) are fairly specific; but broad-spectrum insecticides (such as those used for adult mosquito or fruit fly control) can certainly cause a decline of beneficial insects. The aerial application of pesticides to crops and forestry plantations has been shown to depress pollinator populations (Kevan 1975; Johansen 1977; Johansen et al. 1983; Kearns and Inouye 1997; Spira 2001). Coincident aerial insecticide spraying and flowering of endangered entomophilous plants puts those plants in peril (Bowlin et al. 1993; Sipes and Tepedino 1995). Even application of *Bacillus thuringensis* by organic gardeners can be detrimental to butterfly pollinators if *B. thurigensis* spores drift to weedy and native larval host plants adjacent to vegetable gardens.

Empirical Examples

Observations of pollinator–plant interactions in relatively pristine pine rocklands of the Everglades and lower Florida Keys provide a basis for comparison of the interactions of the same plants occurring in fragments of pine rocklands in suburban and urban Miami-Dade County and in the developed areas of Big Pine Key. We imagined that fragmentation of habitat would be detrimental to plant–pollinator interactions, and it seemed reasonable to hypothesize that species especially vulnerable to negative effects of fragmentation would include specialists and obligate outcrossers. Therefore, we selected to study native plant species that span a range of pollination systems, from specialized to generalized. I will choose examples from this research to illustrate that "all is not lost" for some plant species persisting in pine rocklands fragments.

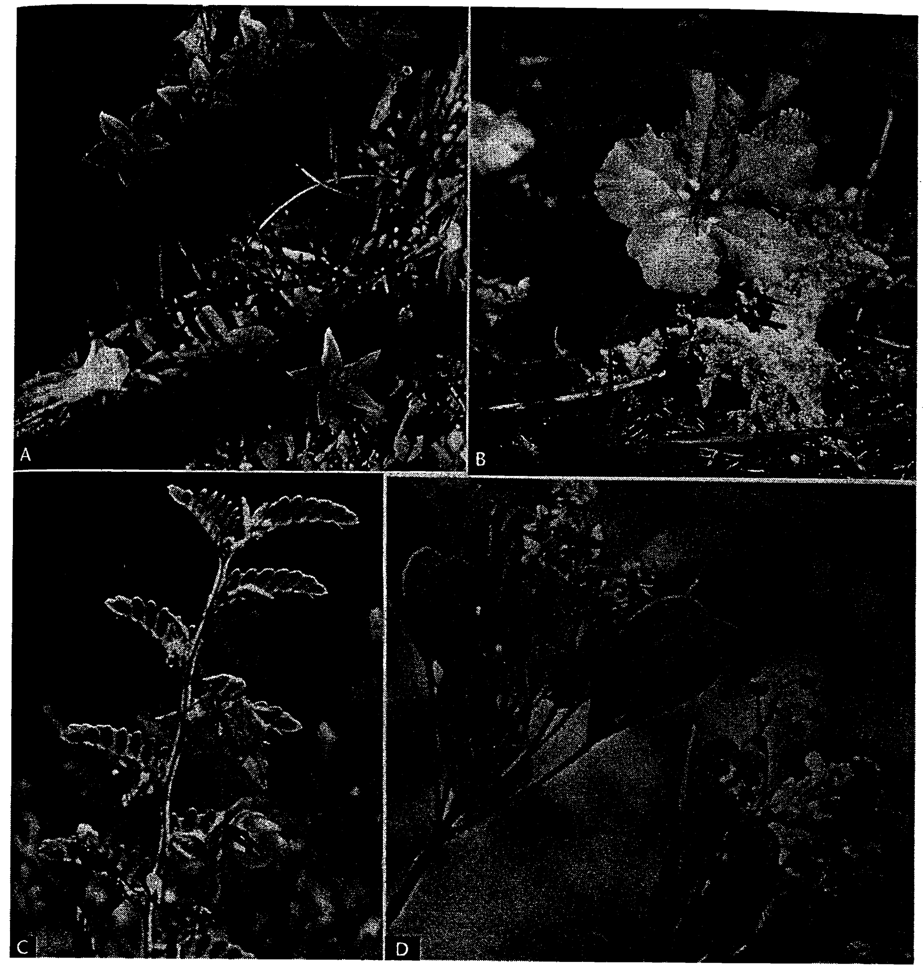

Figure 15.2 Flowers of pine rocklands plants: (A) flowering shoots of the pineland clustervine, *Jacquemontia curtissii;* (B) a small individual of the pineland petunia, *Ruellia succulenta,* in full bloom; (C) the Big Pine partridge pea, *Chamaecrista keyensis,* with flowers and developing fruit; and (D) fast-moving bee (*Centris errans*) collecting oil from flowers of locustberry, *Byrsonima lucida.*

Pollinator Fauna

There are certainly differences in the pollinator fauna between pristine habitat and habitat fragments. For most of the plant species we have examined, pollinator species richness is greater in pristine habitat and in larger fragments than in medium-sized and small fragments. The composition of the fauna varies as well, as illustrated by the following examples.

The pineland clustervine, *Jacquemontia curtissii* (Convolvulaceae), has numerous white flowers with rotate, open corollas about 2–3 cm in diameter, with nectar in the center of the flower available to a wide array of visitors (fig. 15.2A);

some flower visitors also collect its white pollen. Three pristine pine rocklands sites in Everglades National Park had a total of 22 species of flower visitors, of which 19 were probable pollinators (determined by size and activities on flowers): three large (greater that 10 ha) fragments had 12 probable pollinator species, medium (3–9 ha) fragments had 11 pollinator species, and small (less than 3 ha) fragments had 6 pollinator species (Koptur and Geiger 1999). We recorded 26 species of floral visitors and observed certain visitors only in fragments, indicating that the pollinator fauna of *J. curtissii* in fragments is not simply a subset of pollinators in the intact habitat.

The pineland petunia, *Ruellia succulenta* (Acanthaceae), has large, showy flowers with a lavender funnelform corolla (fig. 15.2B), suggesting that visits are limited to insects with long proboscises. Geiger (2002) found this was not the case because numerous bees, as well as Lepidoptera visitors, crawl down the corolla tube to reach the nectar and pollinate the flowers. There were highly significant differences in the proportions of Hymenoptera (bees) and Lepidoptera (butterflies and skippers) visitors by habitat size class; bees make up an increasing proportion of the total floral visitors as one moves from small to intact/pristine size classes, and Lepidoptera are more important in the smaller fragments (Geiger 2002).

The Big Pine partridge pea (*Chamaecrista keyensis,* Fabaceae: Caesalpinioideae) has large, showy, yellow flowers (fig. 15.2C) that are buzz-pollinated by carpenter bees (*Xylocopa micans*) and two species of *Melissodes* bees (Liu and Koptur 2003); they are also visited by other, nonbuzzing bees who pick up the pollen scattered on the petals by the buzzing bees but usually do not contact the stigma in the process. *Chamaecrista keyensis* flowers received substantially more visits by *X. micans,* but fewer visits from *Melissodes* spp., in urban edge versus forest sites in the Key Deer Refuge. Unexpectedly, the buzz-pollinators made up a substantially greater proportion of the bee visits in urban edge sites than in forest sites, where nonbuzzing visitors were more common (Liu and Koptur 2003). The numbers of buzz-pollinating bees at partridge pea flowers declined after repeated aerial mosquito spraying in Big Pine Key (Liu and Koptur 2003). This aerial spraying has been observed to depress Lepidoptera populations in the Keys as well (Salvato 2001; S. Carroll and J. Loye, unpublished data).

Byrsonima lucida, the sole member of the tropical plant family Malpighiaceae native to South Florida (fig. 15.2D), has a specialized pollination system: oil is secreted as a floral reward and is collected by andrenid bees in the genus *Centris,* of which only two species occur in this area (*Centris errans* = *C. versicolor,* and *C. lanosa*). Our hand-pollination experiments show that flowers need visitation to set fruit, and plants set substantially more fruit with cross- than self-pollination (Koptur and Geiger 2000). Copious fruit production in this species is, therefore, evidence of not only visitation, but also likely deposition of pollen from other individuals. Everglades plants fruit heavily, as do plants in or near some of the larger fragments, and it is common to see *C. errans* bees at these sites. Plants in smaller fragments also set fruit, though sometimes only modestly; even plants in gardens and planted landscapes set fruit. *Centris lanosa* is the more common visitor to these plants, although both *Centris* spp. have been observed in urban areas.

Pollinator Activity in Disturbed Habitats

Native plants do exist in the urban landscape, either persisting in fragmented or semideveloped land or planted back into the landscape as garden specimens or in landscaping projects of varying size. The native plants are visited by some of the same insect species that visit them in natural environments, and by some species that are more common in disturbed situations. Plants that are both generalists and specialists in their pollinator affinities have been observed to maintain pollinator relationships in urban situations in South Florida.

The endangered crenulate leadplant (*Amorpha herbacea* var. *crenulata,* Fabaceae: Papilionoideae) needs pollinator visits for fruit set, and cross-pollinations set considerably more fruit and seed than self-pollinations (Linares 2004). *Amorpha crenulata* survives in only a few small pine rocklands fragments in Miami-Dade County, but, wherever it grows, it receives visits from a variety of native solitary bees (such as *Dianthidium curvatum floridense*) and nonnative honeybees (*Apis mellifera*). Even in sporadically mowed lots, crenulate leadplant produced abundant fruit. Planted in gardens within its native range and beyond, its striking inflorescences of tiny white flowers tipped with orange-yellow anthers are visited by native and introduced insects (figs. 15.3A, 15.3B).

The purple flowers of pine rocklands milkpeas, *Galactia* spp., are visited by nectar-collecting halictid bees which get brushed by the anthers and pollinate them (personal observation). While conducting a study of the distribution of rare milkpeas of southern Florida pine rocklands, O'Brien (1988) observed native bee pollinators (*Augochlora pura* ssp. *mosieri*) visiting remnant milkpea individuals in manicured lawns of Coral Gables.

Role of the Matrix

The characteristics of the matrix—the space between habitat fragments in a fragmented landscape—are crucial to the maintenance of plant–pollinator interactions in fragments. Those fragments that are small and/or isolated from larger areas of intact habitat may depend in particular on the matrix for support of pollinators passing through or possibly even nesting and living in the matrix. A thorough comparison of ecology of species across fragmented landscapes must also consider matrix habitat (Jules and Shahani 2003). I will consider several types of matrix habitat found between pine rocklands fragments and their potential effects on plants and insects in remnant habitat.

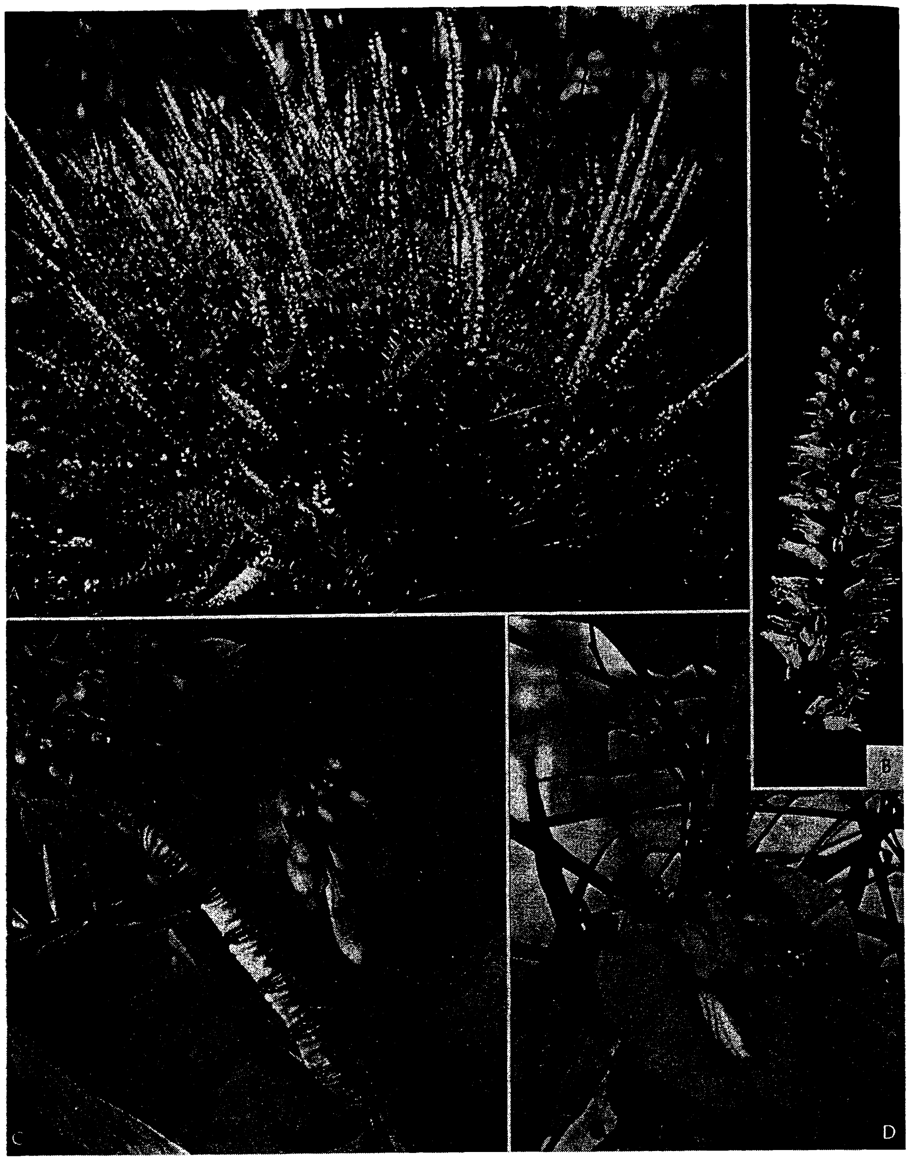

Figure 15.3 More pine rocklands plants and insects: (A) crenulate leadplant, *Amorpha herbacea* var. *crenulata*, plant habit; (B) inflorescence close-up of *A. herbacea;* (C) caterpillar of naturalized orange-barred sulfur (*Phoebis agarithe*) butterfly on native *Cassia bahamensis* (aka *Senna mexicana* var. *chapmanii*); and (D) flowering stem of the butterfly pea, *Centrosema virginiana.*

Concrete in the Big City

One aspect of urbanization (that is definitely not pollinator friendly) is the use of asphalt (tarmac) on roads and concrete on other horizontal surfaces to thwart the establishment and growth of any plant life. As the population of South Florida has grown, roads that were formerly unpaved became paved, then widened from two-lane, then four-lane roads, then to multilane expressways. Consequently, the area covered by asphalt has steadily increased over the past century. As areas have been developed for human habitation and other uses, more and more ground has been covered by concrete. Gardens have been eliminated from many lots for various reasons (they require care, attract unwanted animals, they look "too wild"). As in many parts of Latin America, a sign of success is a tidy, barren yard consisting of concrete (frequently painted) with a minimum of plants.

Suburban Lawns: A Golf-course Green in Every Yard?

As inhospitable as concrete is, matrix consisting of meticulously maintained lawns (turf grass) may be even more detrimental to the movements of pollinators. Turf grass science leads to the development of grass strains that are tough and easy to maintain; the goal is to make the lawn as uniform as possible. Extensive use of chemicals (fertilizers, herbicides, and pesticides/insecticides) is needed to maintain the ideal lawn. Pest control operators leave signs in lawns so that humans can avoid these areas for at least one day, but few pollinators (or pets or children) are able, or take the time, to read these signs.

Pollinator Relief in the Land of Flowers

Fortunately, a number of features of the matrix between natural habitat fragments exist that are improvements over concrete. The penchant many residents of Florida (dubbed by the Spaniards "the land of flowers") have for lush landscaping and beautiful flowers has led to an extensive array of cultivated ornamental plants that can provide pollinators with a variety of foods and shelter. Most pollinator foods are provided in flowers, usually in the forms of nectar and pollen, but certain species also provide oils (e.g., Malpighiaceae), resins (e.g., Clusiaceae), and extrafloral nectar (many families; Koptur 1992).

There are some spectacular sights involving animals and flowers to be seen on the streets of Miami. Brilliant yellow, black, and white spot-breasted orioles (*Icterus pectoralis*) visiting flowers of the sausage tree (*Kigelia pinnata,* Bignoniaceae) are the facultative pollinators of these bat-adapted flowers, the fruit of which resembles huge, pendant sausages. High up on the bare trunks of majestic Bombacaceae, squirrels drink nectar from the flowers of *Bombax malabaricus* and *Pseudobombax* sp. These visits rarely lead to fruit production because conspecific individuals of these species are few and far between. Fortunately, in big cities (especially in the subtropics), there are many opportunists who use floral rewards, sometimes, though not always, pollinating in the process.

Isolated individuals of *Byrsonima lucida* in urban garden plantings receive visits from their specialized *Centris* bee pollinators even though no other *B. lucida* are in sight. Those bees visit alternative oil sources found in frequent plantings of several ornamental species of Malpighiaceae: *Malpighia coccigera, Stigmaphyllon* spp., and *Thryallis glauca*. And when the neighbors decide to add native *B. lucida* to their gardens, fruit set is then possible for formerly isolated individuals. Perhaps this fruit set is of less fitness consequence than fruit set on individuals in native habitats, but it can serve to perpetuate this species in the matrix between natural habitat fragments.

Nonnative species cultivated for their useful fruit are readily pollinated in South Florida. Passion fruit (*Passiflora edulis*) are usually grown along fences and are most effectively pollinated by carpenter bees, but a group of honeybees working together can also effect pollination (Hardin 1987). Flower beetles visiting the purportedly wind-pollinated flowers of jackfruit (*Artocarpus heterophyllus*) growing in orchards or garden plantings may enhance fruit production and seed set in South Florida (El-Sawa 1998).

Ornamental, exotic congeners of native species can serve to attract and feed pollinators and can help pollinators make their way between fragments or between native species in the urban landscape. A very popular cultivated species, *Ruellia brittoniana,* has purple, pink, or white flowers that look very similar to the native *R. succulenta.* Ubiquitous plantings of this popular species ensure plentiful nectar for butterflies and bees, and maybe even larval food for specialist herbivore butterflies (Nymphalidae) such as the white peacock (*Anartia jatrophae*) and the malachite (*Siproeta stelenes*). Found throughout the tropics, *Lantana camara* volunteers readily as its seeds are dispersed by birds that eat the blue fruits; butterflies are nourished by its nectar and may contribute to its hybridization with native *L. depressa* in South Florida (Ramey 1999).

Even Weeds Serve a Purpose

Lantana camara is listed as a category I nonnative, invasive plant by the Florida Exotic Pest Plant Council and is one of the worst weeds in all the world (Holm 1977), forming dense thickets in 47 countries and a weed in many crops as well; yet it is frequently planted to attract butterflies in the United States and in South Florida is a well-used nectar plant for many butterfly species. Other pervasive weeds are nourishment mainstays for pollinators in the seminatural and disturbed landscape.

Devil's pitchfork (*Bidens pilosa,* Asteraceae) is a crop weed in the Old and New World tropics and a frequent resident of any disturbed ground or unmown lawn in South Florida. It is so favored by insects that one can obtain a good general collection of floral visitors for an area simply by observing its blossoms. A recent edition of a popular ecology textbook had a photo of a zebra butterfly (*Heliconius charitonius*) sipping nectar on this flower rather than any of the native plants in the area!

Brazilian pepper (*Schinus terebinthefolius,* Anacardiaceae) is a woody species with attractive red berries that facilitate its dispersal by birds into natural areas; it frequently colonizes disturbed ground to form a monospecific stand (as in the former agricultural area within Everglades National Park known as the "Hole in the Donut"). Honeybees and other insects consume the floral nectar of this pest tree, and honey production is greatly enhanced by its presence (Ewel 1982).

Another notorious pest plant, the paperbark tree (*Melaleuca quinquenervia*), has attractive white flowers full of nectar that is collected by a variety of insects, including butterflies, skippers, moths, wasps, bees, and flies. Honeybees are the most abundant pollinators (Vardaman 1994), and, although the flowers can automatically self-pollinate, seed set is enhanced by insect visitors (Vardaman 1994). The beekeeper practice of placing their bees in natural areas may therefore promote the spread of noxious pest trees (both paperbark and Brazilian pepper) that provide nectar for honeybees and in turn receive pollinator services.

Exotic Alternatives When Natives Are Absent: Benefits to Butterflies

Lepidoptera feed in different ways as either adults or larvae, and larval food plants are necessary to maintain butterflies, moths, and skippers in the landscape. Some of South Florida's rare butterflies use not only native but also exotic host plants. The Atala butterfly (*Eumaeus atala*), once thought to be extinct, lays its eggs on coontie, a native cycad (*Zamia pumila*), and the extensive coontie starch industry of the early 20th century may have led to the extirpation of this butterfly in South Florida prior to its subsequent recolonization (Smith 2000). A reintroduction program undertaken at Crandon Park utilized extensive cycad host plantings and larval relocations from colonies at Fairchild Tropical Garden (Smith 2002), where Atala larvae also feed on the cultivated cardboard palm (*Z. furfuracea*) and other cycads in the garden's extensive collection—the reason the garden is eager to farm out the larvae of this endangered butterfly species! Atala adults visit many flowers, including native palmettos, *Lantana involucrata,* and weedy *Bidens pilosa* (Smith 2000, 2002).

The Miami Blue (*Hemiargus thomasi bethunebakeri*) utilizes balloon vine (*Cardiospermum* spp.) hosts. The larvae feed on the plant and hide in the seedpods to avoid predators. Balloon vine occurs adjacent to hammocks in the lower Florida Keys (Loye and Carroll, in press), and these hammocks are often close to roads, resulting in the mowing of these areas to appease safety concerns. Consequently, the state's Department of Environmental Protection has requested that an area several feet wide be left unmown to allow the plants to fruit, to perpetuate suitable host plant for the Miami Blue.

Common butterflies also utilize both native and cultivated species for their rval hosts: the native cloudless sulfur (*Phoebis sennae*) and the naturalized range-barred sulfur (*Phoebis agarithe*) utilize native and cultivated *Cassia* spp. as ieir larval host plants (Glassberg et al. 2000). These butterflies visit a variety of owers for nectar, and their activity is greatest in areas with abundant host lants, in both natural areas and urban areas (fig. 15.3C).

ieneral Conclusions

Irban and Anthropogenic Landscapes and Pollinator Conservation

)ur results do not show a marked difference in the response of specialized versus ;eneralized pollination systems to habitat fragmentation (table 15.1). Aizen et l. (2002) surveyed the literature and concluded that the extent of specialization loes not necessarily correlate with the likelihood of a species experiencing negitive effects of habitat fragmentation. Ashworth et al. (2004) noted more re-:ently that, although pollinators are sensitive to habitat fragmentation, plants :hat are pollination specialists do not appear to suffer more from habitat fragnentation than do generalists, and they proposed that this is because of asymmetry in the degree of specialization of the plants and their pollinators (see also Vázquez and Aizen, chap. 9 in this volume; Petanidou and Potts, chap. 11 in this volume).

Thompson (1997) makes the case for conserving interaction biodiversity as well as species diversity. Although this may be most easily done with large preserves, there are "chronically fragmented" landscapes where this option does not exist and there is much value in small preserves (Schwartz and van Mantgem 1997). If small preserves can be managed in ways that tip the balance of nature in favor of native species (using exotic removal, fire management, and augmentation of resources in the matrix between preserves), many plant-animal interactions will also be maintained. Generalized interactions are more flexible, and it will take more care to ensure the persistence of extreme specialists; it will certainly not be possible in all cases. One way of increasing the chances of the persistence of these interactions is by "gardening for pollinators."

Gardening for Pollinators

Some naturalists have promoted butterfly gardening (e.g., Minno and Minno 1999; Glassberg et al. 2000), as have plant societies, public and private gardens, and plant-related businesses. The most important message for nonbiologists is that gardeners need to plant not only nectariferous plants but also larval food plants to encourage the butterflies to linger and proliferate. The beneficial effects on urban wildlife (specifically Lepidoptera) are noticeable. Little has yet been done, however, to promote the numbers of other pollinators. It is essential not only to include plants with floral rewards for the pollinators, but also to consider the pollinators' other needs (larval host plants and nesting sites).

The idea of gardening for pollinators was expressed in a popular article (Tasker 1996) by a newspaper columnist influenced by the "Forgotten Pollinators Campaign" (Buchman and Nabhan 1996); since that time, local interest in making pollinators welcome has been growing. The Forgotten Pollinators Campaign directed much attention to disappearing pollinators in the southwestern United States, and worldwide, and a booklet entitled *Gardening for Pollinators* was published by the Sonoran Desert Museum for guidance in the arid southwest. The humid, subtropical climate of South Florida is vastly different from the arid southwest, and some parts are considerably more urbanized; nonetheless, both areas share problems in disappearing species and declining pollinators. Although bee diversity of the desert southwestern United States dwarfs that of Florida, Florida's bee fauna is still fairly rich compared with that of the rest of the United States (Pascarella et al. 1999, 2001).

Table 15.1 Summary of fragmentation effects (FEs) on pine rockland plants (general conclusions from work in progress)

Species (family)	Specialist/ generalist	Principle pollinators	FEs on flowering	FEs on pollen deposition	FEs on pollinators at flowers	FEs on fruit set
Amorpha crenulata (Fabaceae)	Generalist	Bees	Negative	No info	None	None
Byrsonima lucida (Malpighiaceae)	Specialist	Centris bees	Positive	None	None	Slight negative
Centrosema virginiana (Fabaceae)	Specialist	Large and medium-sized bees	Mixed	None	Medium bees more common	None
Dyschoriste angusta (Acanthaceae)	Generalist	Bees and butterflies	Mixed	None	None	No info
Evolvulus sericeus (Convolvulaceae)	Generalist	Small bees and flies	Negative	—	None	No info
Galactia spp. (Fabaceae)	Specialist	Medium and small bees	Negative	—	None	None
Jacquemontia curtissii (Convolvulaceae)	Generalist	Bees, flies, wasps, butterflies	Negative	None	Fewer species	None
Ruellia succulenta (Acanthaceae)	Generalist	Bees and butterflies	Negative	None	Butterflies more common	None

Solitary bees may find it difficult to nest in gardens that are too neatly maintained: some of these bees nest in dead twigs, which they may stuff with pieces of leaves they cut; others nest in rocky crevices, or right in the ground in sandy patches. Carpenter bees nest in wood, including wooden structures, and are often more abundant in urban edge habitats (Liu and Koptur 2003). *Centrosema virginiana*, the butterfly pea (fig. 15.3D), is pollinated primarily by these large bees, and carpenter bee activity at flowers is much greater for plants near picnic tables and park visitor facilities than those farther from wooden structures (Cardel 2004). In the Redland agricultural area of South Florida, edible passionfruit (*Passiflora edulis*) grown on fences with wooden posts, or in areas with wooden structures, receive more visits from carpenter bees; *P. edulis* on chainlink fences with only concrete structures nearby receive more honeybee visits (Hardin 1987). Therefore, it is important to have some habitat heterogeneity in a garden to promote nesting by a variety of bee pollinators. Entomologists use pollinator nest traps to study bee diversity (Pascarella et al. 1999, 2001), but nest blocks/boxes have not been yet deployed in the South Florida landscape to attract pollinators. Wasps frequently colonize nest blocks (much more than bees) in South Florida studies (J. Pascarella, personal communication).

Importance of Education in Pollinator Restoration

Insects and Gardens (Grissell 2001) gives readers an appreciation of the diversity of insects maintained by plants in a garden. This innovative work not only educates about insect biology and natural history; it also guides gardeners to a coexistence in which humans and insects can share gardens, encouraging gardeners to tolerate many types of insects (such as bees, wasps, earwigs) that may at first seem undesirable—those that benefit garden plants not only by visiting and pollinating flowers but also by eating potential pests.

The most powerful conservation education starts with children, and many activities are aimed at young people. Butterflies are lovely, and butterfly gardening is the easiest hook for most people; once hooked, they are more likely to be open to appreciating the presence and activities of other insects in the garden, the home landscape, and in natural areas. Schoolyard ecology (Berkowitz 2000) brings students (and families) in touch with the natural environment, and students who are exposed to nature activities in school are more likely to care about nonhuman life in the future. Most organizations that have conservation of flora and/or fauna as part of their mission, therefore, have a substantial educational component, for example, botanical gardens, zoos, government agencies (federal, state, and county), and nongovernment organizations. Continuing to educate people after elementary school is perhaps the most important mission of many organizations if their goals of conservation are to be realized in our complex, modern world. One example is the North American Butterfly Association, whose Miami Blue chapter conducts semiannual butterfly counts, which increase public awareness of these insects. Adult education with public programs and special events displays and activities are ways to engage members of society who might otherwise never think about the importance of pollinators.

The Florida Native Plant Society and the Tropical Audubon Society regularly have plant sales to promote creation of a habitat for wildlife. As more native plants join the home landscape, the earlier planted individuals find mates, fruit and seed are produced, and, in some cases, new populations become self-sustaining. Admittedly, the genetic structure of remnant natural populations is very likely changed with these native plantings in the matrix between natural habitat fragments as pollinators move from fragment to oases of floral rewards (some from exotic plants, some from native plants). This is a dilemma in our irreversibly altered human-dominated landscapes.

Restoration of pollinator–plant interactions by gardening for pollinators can enhance plant and pollinator diversity and help rejuvenate landscapes in which plants have lost their partners. There are many examples of pollinators that have disappeared and are presumed extinct, from localized specialists to far-ranging generalists (Buchman and Nabhan 1996). Planting projects can serve to replace floral resources lost through development and may attract and support populations of floral visitors that would otherwise decline or disappear. These may be the only means that can conserve both generalist and specialist pollinators in the face of ever-growing human populations.

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