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Cover image - Patch reef near the wall off Grotto Beach (photo by Lee Florea).

KEYNOTE ADDRESS

Plant-animal interactions in the face of disturbance

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1. Abstract

A multitude of interactions among plants and animals are shaped by the environment and influenced by disturbance at different levels. Plant survival and reproduction are proximally influenced by edaphic conditions, which are transformed dramatically through natural and anthropogenic phenomena including fire, hurricanes, and environmental disasters, and ultimately via water management, deforestation, and sea level rise. A number of plants are now listed as threatened or endangered due to habitat transformation and loss; many places once full of native vegetation have been cleared for agriculture or urban development, and areas that were formerly seasonally inundated are now dry. Plants in habitats that experience recurring natural disturbances have been selected for adaptations to changing conditions, and display strategies of recovery such as resprouting and/or reseeding after devastation by fire, or regrowing from damaged or downed stems after hurricanes. Herbivory, pollination, and seed dispersal are three interactions affected by disturbance: the degree to which plants are eaten by herbivores, how they are protected by bodyguards, their flowers visited and pollen transported, and their fruits and seeds dispersed by a variety of biotic agents, may increase, decrease, or be changed in other ways. Disturbed habitats are more likely to be invaded by exotic pest species, which in turn may alter the interactions among plants and their native animal partners. As global climate change affects the planet, sea level rise is a major concern for many ecosystems. Some species endemic to Caribbean islands and coastal areas already require help in restoration of their habitats, and perhaps eventually will need assisted relocation for future survival.

2. Introduction

A number of plant/animal interactions are involved in plant reproductive success, including pollination, herbivory, and seed dispersal. Plant reproduction and survival may be influenced by disturbance at different levels. Proximal effects are those affected by nearby edaphic conditions, such as fire, hurricanes, and other natural disasters; ultimate effects are those that shape the landscape, such as water management, deforestation/development, and sea level rise.

Similarities between the biota of southern Florida and the Bahamas archipelago provide an interesting comparison and may allow us to apply lessons learned from one place to the other. The flora of the Bahamas is overall more species-rich than that of southern Florida (Correll and Correll 1982), but individual islands each contain only part of the diversity. In the Bahamas, pines occur only on the four larger islands (Grand Bahama, Abaco, New Providence, and Andros) that have a freshwater lens, providing the conditions suitable for the growth and survival of these glycophytic plants; on these, and all the other islands, coastal vegetation is present. Much of the Bahamas is south of Florida, with a much larger proportion of the flora of tropical origins than that of the northernmost islands (Correll and Correll 1982) and south Florida (Tomlinson 1980).

2.1. Ant/Plant mutualisms, plant defense, and fire

A substantial proportion of plants of Everglades upland habitats bear extrafloral nectaries (Koptur 1992a), glands outside of the flowers, generally not involved with pollination, but rather promoting visitation by ants and other benefi-

cial insects that may result in plant protection in facultative ant/plant mutualisms (Bentley 1977; Koptur 1992b; Rico-Gray and Oliveira 2007). Pine rocklands are fire-successional habitats that succeed to hardwood hammocks after 20 years or more without fire (Alexander 1967; Snyder et al. 1990). Ant activity at baits is greater in pine rocklands than in hardwood hammocks; baits are discovered more quickly, and recruitment is greater (Koptur 1992a). Cover of plants with extrafloral nectaries is higher in pine rocklands than in hardwood hammocks (ibid.), suggesting that ant/plant mutualisms are more likely to occur in pine rocklands. Similar studies in the Bahamas, on the pine island of Andros, similarly found greater ant abundance in pineyards than in coppice (equivalent to hardwood hammocks), and the cover of plants with extrafloral nectaries also greater in pineyards (Koptur et al. 2010). Comparing pineyards of different times since fire, there was greater ant activity with less time since fire; ants were abundant even in very recently burned sites (ibid.).

In pine forests of both south Florida and the Bahamas there are many understory plants adapted to fire; the majority of species resprout from underground parts after their above-ground plant bodies have been killed by fire (Maguire and Menges 2011), and some have contractile roots to protect meristems underground during fires (Fisher 2008). Fire promotes flowering in many species of Florida's pyrogenic ecosystems (Abrahamson 1984a; Platt et al. 1988; Slapcinsky et al. 2010). Post-fire, the understory is more open, a good time for seed germination and seedling establishment of understory plants (Abrahamson 1984b; Carrington 1999) and overstory pines as well (O'Brien et al. 2008).

2.2. Habitat fragmentation and pollination

Pine rocklands are an imperiled, fire-dependent habitat, unique to S. Florida and the Bahamas, where they are called pineyards. The diverse understory of Florida pine rocklands has more than 250 herbaceous species (Snyder et al. 1990), with a number of endemic species. Some of these species are federally and state listed as endangered or threatened due in large part to habitat loss; development in southern Florida took place on the higher, dryer ground upon which pine rocklands and hardwood hammocks historically occurred. In the Bahamas, as in much of south Florida, the original pine forests were logged as recently as the mid-20th century; only in very remote places (e.g. in Florida, Lostman's Pines in the Big Cypress National Preserve) are there pines of large diameter, an indication of their long lives, growing for years before the loggers harvested the rest of their kind.

We have been studying the effects of the disturbance of diminished habitat into small, separated patches (habitat fragmentation) on specialized vs. generalized pollination systems, with the prediction that plant species especially vulnerable to negative effects of fragmentation are those with either specialized pollination and/or obligate outcrossing. To test this hypothesis, we need to learn about the floral biology and breeding system of study species, and then collect evidence of pollination: visitor/pollinator activity at flowers; presence of pollen on visitors; and deposition of pollen on stigmas. The most telling data are those on fruit set from marked flowers, as those are evidence of successful pollination with compatible pollen.

Our methods are to collect comparative data from multiple sites that are different sizes and have different degrees of isolation from other pine rockland sites. For starters, we compared four types of sites: 1) intact pine rockland (in Everglades National Park); 2) fragments greater than 10 ha in size ("large fragments"); 3) fragments 3 – 10 ha in size ("medium"); and 4) fragments < 3 ha. ("small"). In Keys pine rockland, we studied multiple urban edge and forest sites.

Comparisons reveal fewer visitors to flowers for some plant species in fragments,

and fewer and some different animal taxa within guilds (Koptur 2006). Some plant species exhibit a shift in pollinators – in some species, native bees predominate in natural areas, butterflies in fragments (Geiger 2002). Fruit set is only affected in species that are pollinator-dependent, such as Fabaceae species *Amorpha herbacea* Walter var. *crenulata* (Rydb.) Isely (Linares and Koptur 2010), *Centrosema virginiana* (L.) Benth. (Cardel and Koptur 2010), *Chamaecrista lineata* (Sw.) Greene var. *keyensis* (Pennell) H.S.Irwin & Barneby (Liu and Koptur 2003), and *Senna mexicana* (Jacq.) H.S.Irwin & Barneby var. *chapmanii* (Isely) H.S.Irwin & Barneby (Jones, unpub. data), and most dramatically in those that are self-incompatible, e.g., *Byrsonima lucida* (Mill.) DC. (Malpighiaceae) (Downing and Liu 2013), *Ipomoea microdactyla* Griseb. (Convolvulaceae) (Geiger 2007), and *Angadenia berteroi* (A.DC.) Miers (Apocynaceae) (Barrios and Koptur 2011).

Not all pollinator-dependent plants suffer lower fruit set in fragments: pollinator and herbivore abundance are affected by surroundings. Perhaps this is because ornamental plants can support them (both pollinators and herbivores) between fragments. *Byrsonima lucida* planted in urban gardens prior to 1990s did not set fruit, even though its flowers were visited by oil-collecting bees that also visit ornamental Malpighiaceae such as *Malpighia coccigera* L.*, Malpighia emarginata* Sessé & Moç. ex DC., and *Stigmaphyllon littorale* A.Juss. Not until *Byrsonima lucida* became more frequently planted, did fruit form, when there were other genetic individuals providing some compatible pollen (pers. obs.).

Chamaecrista keyensis flowers are buzz-pollinated much more by *Xylocopa micans* Lepeletier 1841 (carpenter bee) pollinators in urban edge sites than in forest sites on Big Pine Key, where *Melissodes* spp. prevail (Liu and Koptur 2003). Numbers of both these solitary bees were diminished following aerial insecticide spraying for mosquito control. Other plants on Big Pine Key (*Linum*

arenicola (Small) H.J.P.Winkler (Linaceae), and *Pentalinon luteum* (L.) B.F.Hansen & Wunderlin (Apocynaceae)) also receive fewer pollinator visits and their flowers set less fruit when they open in the weeks following mosquito spray events (Harris 2016, and unpublished).

Angadenia berteroi receive many more visits from skipper butterflies than bees in habitat fragments, but it turns out that bees are much better pollinators (Barrios et al. 2016a). These plants are also subject to much greater damage from caterpillars of *Syntomeida epilais* Walker (the oleander moth) when there are ornamental plantings of oleander near the pine rockland fragment (Barrios Roque 2015). These caterpillars have a very large effect on plant reproduction, consuming not only leaves but flowers and entire stems of plants upon which their eggs are deposited.

2.3. Overall effects on plant existence and re-production

Quality of habitat is very important – less time since fire (more frequent fires, every 10 years or less) reduces litter depth and leaves the understory more open and sunny. Abundance of most pine rockland understory plants is greater in areas that are regularly burned; species disappear gradually with more years since fire, though their seeds may remain in the seed bank, as shown by Liu for *Chamaecrista keyensis* (Liu et al. 2005). Pine rockland endemics are often more abundant in larger habitat fragments maintained by fire (e.g. *Angadenia berteroi*, Barrios et al. 2011; *Chamaesyce* spp. and *Galactia* spp., O'Brien 1998).

Structural equation modeling was undertaken to explore the interactions between habitat fragmentation and quality with the reproductive fitness of *Angadenia berteroi* (Barrios Roque 2015; Barrios Roque et al. 2016b). Habitat fragment size was correlated with the density of *A. berteroi,* but did not much affect its reproductive success. However, habitat quality (represented by litter depth and

subcanopy cover) had strong negative effects on the reproductive fitness of *A. berteroi*, evidence that the increased light availability and low litter cover resulting from recent fires may favor reproduction.

2.4. Water management effects

As development in southern Florida proceeded, the landscape was transformed with canals to move water off the low-lying land so that people could build on or farm the areas considered "useless". Wet areas became dry, including the transverse glades that occurred throughout the Miami rock ridge, between the slightly higher areas where pine rocklands and hammocks were located.

The crenulate lead plant (*Amorpha herbacea* var. *crenulata*) occurred historically in pine rocklands on the edges of wet prairies throughout the transverse glades in the northern part of the Miami rock ridge, in the ecotonal transition from wet to dry. With the canals, the transverse glades disappeared; the species is now federally listed as endangered. A study of the floral biology and breeding system of the plants and pollinator observation in remnant locations (Linares and Koptur 2010) indicated that plants show self-incompatibility and may therefore exhibit suboptimal reproduction in their few remnant populations, despite visits to their flowers by generalist pollinators.

2.5. Hurricane effects

Polygala smallii R.R.Sm. & D.B.Ward (Polygalaceae), an endangered species, appears to disappear from certain sites, where it had been previously observed, until the site is disturbed. This tiny, monocarpic (or short-lived perennial) plant has seeds that remain in the seed bank, able to establish new plants when conditions are right and the site is disturbed by hurricane or canopy opening (Kennedy 1998).

Hurricanes are a frequent disturbance in the Caribbean, and the paths of many hurricanes have affected the vegetation of south Florida to a great extent. In August of 1992, Hurricane Andrew hit south Florida, affecting most of Everglades National Park as well as many areas near and north where pine rockland fragments remained. Ecologists studying plant/animal interactions prior to a hurricane have the opportunity to observe changes that result from that hurricane (Landry et al. 2014). Rathcke (2001) saw increased flowering after *Bourreria succulenta* Jacq. (Boraginaceae) plants were stripped of leaves by Hurricane Lili and Hurricane Floyd on San Salvador Island, Bahamas, but pollinators were much less abundant, limiting fruit set, and fruit production was further limited by intense predation; both these post-hurricane effects potentially limit recruitment of new individuals at those times of disturbance. Landry (2011) documented changes in pollination of white mangrove, *Laguncularia racemosa* (L.) C.F.Gaertn. (Combretaceae), following Hurricane Wilma, and also found that the change in pollinator assemblages affected the breeding system of that species (Landry 2013). The obligate wasp pollinators of native *Ficus* spp. (Moraceae) were absent after Hurricane Andrew, but returned to pollinate within five months of the storm (Bronstein and McKey 1995). Pascarella (1998) found the generalist pollinators of marlberry, *Ardisia escallonioides* Schltdl. & Cham. (Myrsinaceae), to be present equally before and after the hurricane, but the specialist flower-galling wasp disappeared for up to two years following Hurricane Andrew. Epiphytic Bromeliaceae in cypress domes showed losses in larger size-classes, dependent largely upon their strength of attachment to cypress trees (Oberbauer et al. 1996), but in most species, these losses were compensated by large numbers of new recruits in the year following Hurricane Andrew.

After a study of hurricane damage and post-hurricane recovery to woody plants of upland habitats in the Everglades after Hurricane Andrew (bayheads, cypress domes, hammocks,

pinelands), there was something unusual: silence in the middle of the wet season, a time normally full of mosquitoes in Everglades pine rocklands and other upland forests. Absence of those insects suggested that others might also be absent, so we monitored damage to leaves emerging at different times, as Hurricane Andrew had totally defoliated woody plants in Everglades upland habitats. Damage to leaves produced immediately after defoliation, was compared to damage on leaves produced several months later. There was little damage to the first cohort of leaves, and substantially less damage than to some of the same species that had been monitored before the storm, and to the second leaf cohort for all species studied (Koptur et al. 2002). In addition, leaves in the first cohort were substantially larger than those in the second cohort for five of seven species (*Ardisia escallonioides* (Myrsinaceae)*, Guettarda scabra* (L.)Vent. (Rubiaceae)*, Damburneya coriacea* (Sw.) Trofimov & Rohwer (Lauraceae)*, Psychotria nervosa* Sw. (Rubiaceae), *Myrsine cubana* A.DC. *(*Myrsinaceae), but not for *Exothea paniculata* (Juss.) Radlk. (Sapindaceae), where leaves were substantially larger in the second cohort, and *Miconia bicolor* (Mill.) Triana (Melastomataceae), where cohorts did not differ in size. Evidently, hurricanes affected different species differently, depending on the particular stage of the life cycle of the animal or plant at the time of the disturbance (Koptur et al. 2002).

Those leaf-size differences may have been the plant's response to balance the large discrepancy between remaining shoot and root area via compensatory growth. To test this hypothesis, experimental defoliations were conducted with the help of students in two offerings of Plant Ecology lab, one in the fall term (wet season), the other in the spring term (dry season), in Everglades field exercises exploring leaf size variation in different habitats, and leaf size before defoliation and after regrowth. Our assumptions were: whole-plant defoliation simulates hurricane damage,

and two months is long enough for new leaves to be produced and mature.

For these experiments, our hypotheses were: 1) total defoliation may funnel more resources into regrowth so that resprouting leaves will be larger; and 2) size of leaves regrowing may be influenced by season of defoliation. In four of five species, regrown leaves were smaller than original leaves (three of four significantly so) – in both wet and dry seasons (Koptur et al., in prep.). This was different from our earlier post-hurricane results. We found no obvious effects of season of defoliation on regrowth (as might have been predicted from phenology of growth and reproduction), and concluded that whole-plant defoliation may simulate hurricane damage, but not hurricane conditions.

Hurricanes may cause larger leaves to regrow because branches and stems broken or buds damaged may decrease the number of leaf buds on a plant overall; there would be fewer leaves to refoliate those remaining shorter branches and stems. Furthermore, additional resources due to the large input of nutrients from fallen vegetation and extra water brought by hurricane rains may support luxuriant growth. The open canopy after a hurricane would have no shading to interfere with sunlight so there would be no light limitation to the growth of understory plants. Future experiments should include greater plant damage and nutrient additions.

2.6. Habitat change and loss

Perhaps the most direct effect of disturbance on plant-animal interactions is the loss of habitat, rendering the interactions impossible in the affected area. Sea level rise will affect every low-lying coastal area, but none more than the island ecosystems of the Florida Keys. Pine rocklands occur on the Miami rock ridge on the southeast mainland of southern Florida, and also in the Lower Keys on islands large enough to have a freshwater lens below them. Ross, O'Brien, and Sternberg (1994) documented and explored the reasons for pine forest loss in the

lower Florida Keys. Their work followed earlier observations by Taylor Alexander (1953) of vegetation change on Key Largo, an area now without pine forests; Alexander (1976) hypothesized that sea-level rise was responsible for the loss of pine forest.

The physiography of the substrate determines the vegetation mosaic in the Florida Keys (Ross et al. 1992), with pine forests occurring only on islands with limestone outcroppings and the presence of a reservoir of fresh water underlying the islands, similar to the inland, slightly higher areas, on the larger islands of the Bahamas archipelago. Though the composition of the flora is slightly different in the Florida Keys than pine rocklands on the Florida mainland (Tomlinson 1980), they also have an overstory of *Pinus elliottii* Engelm. and a diverse understory of shrubs and herbs. Pine rocklands occur on Big Pine Key, No Name Key, and Sugarloaf Key, though historically they were also on Key Largo (Ross et al. 1994).

Ross and colleagues (1994) found evidence of environmental change on Sugarloaf Key, much like those reported by Taylor Alexander – pine snags (trunks of dead pine trees) in the salt-tolerant vegetation of buttonwood woodland. They documented the recession of Sugarloaf pine forest toward the interior of the island, toward higher elevations. Their sampling of the water underlying the various sites revealed that the freshwater lens underlying the island was shrinking, the reason they could see unhealthy pine trees around the edge of the remnant pine rocklands. They predicted that pine rockland habitat will continue to decline with sea level rise on Sugarloaf Key. Salt-tolerant plants (halophytes) are replacing those that need fresh water (glycophytes) throughout coastal regions in south Florida (Saha et al. 2011a), due to salinity negatively affecting transpiration of freshwater-dependent vegetation.

Sugarloaf Key and Big Pine Key were hit by Hurricane Wilma on the 24th of October 2005. A large windfield occurred when the hurricane hit the South Florida mainland; storm surge several hours later covered much of the coastal land in the lower Keys, including land supporting pine rocklands. Ross and colleagues documented substantial pine mortality that was attributed to salt-water inundation from Hurricane Wilma (Ross et al. 2009): on Sugarloaf Key, 70-100% of the pines were killed, and on Big Pine Key, mortality ranged from 10-90% depending on the location and elevation of the forest on this larger island (Saha et al. 2011b). It is evident that for management of these coastal refuges, both local and regional dimensions must be considered; these conclusions are applicable to the Bahamas as well as south Florida. Locally, managers must identify and defend the core areas of habitat of concern in existing refuges; and regionally, the conservation plan must be expanded outward in time and in space to preserve threatened communities in the future (Ross et al. 2009).

Recent efforts to characterize and enhance the habitat for the endangered Schaus' Swallowtail Butterfly (*Heraclides aristodemus ponceanus* (Schaus 1911), Papilionidae), has led to a realization that the current distribution of the species, in coastal hardwood hammocks (subtropical dry forest) on islands in the upper Florida Keys, is also threatened by sea level rise (Clayborn et al., in review). Torchwood (*Amyris elemifera* L., Rutaceae) is the main host plant of the butterfly (Minno and Emmel 1993), and a major effort to enhance habitat on Elliott Key involved planting more than 2400 torchwood seedlings in locations around the island, and monitoring their success in establishment and growth. The plants did not establish well in areas where the soil was salty, faring better in the slightly higher elevation locations in the center of the island. Clayborn and collaborators made sea level rise projections (Slow = 1.6 feet in the next century; Medium = 3.3 feet; Fast = 4.9 feet) and mapped the potential butterfly habitat remaining; the outlook is not good, in the best of scenarios, the habitat for torchwood and the Schaus swallowtail butterfly will shrink dramatically. For threatened endemic taxa, extraordinary measures will likely be needed to save them from these "sinking ships"

(Maschinski et al. 2011), perhaps more than just promoting awareness through schoolyard gardens and ecological schoolyards (Clayborn et al. in press).

Low-lying islands are liable to a double threat. Xeric conditions promote negative effects following saltwater inundation; the drier the island, especially those islands with depressions in the middle, the greater the danger of evapotranspiration accelerating aquifer salinization (Gulley et al. 2016), and subsequent negative impacts on plants and animals requiring fresh water.

2.7. Invasions by exotic plants and animals

Most of the areas chosen for habitat enhancement for Schaus swallowtail butterflies were overgrown with exotic pest plants, that were removed prior to planting the area with native plants (Clayborn et al. in review); native plants can inhibit the colonization of disturbed areas by invasive exotic plants (Pearson et al. 2016). More drastic measures, such as changing topography, may be required to control exotic pest plant establishment and spread. In south Florida, the rockland area within Everglades National Park was cleared for agriculture, and after farming was abandoned, became overgrown with a veritable monoculture of *Schinus terebinthifolia* Raddi (Anacardiaceae), known as Brazilian pepper. Nicknamed the "Hole in the Donut", this area has been the focus of major restoration efforts. Effective control of the invader has been made in parts of this area that were bulldozed and scraped to a lower elevation, so that it is inundated most of the year, preventing the regrowth of this pest plant despite dispersal of its propagules into the area, as they cannot establish under water. Rocklands were not restored, but the pest plant species was controlled and natural wetland vegetation grew (Smith et al. 2011).

Not only do invasive plants occupy space, competing with native plants for sunlight and other resources, but their flowers may attract pollinators, interfering with visitation to native plants (Liu et al. 2006), and their pollen can interfere with pollen tube growth (Bruckman and Campbell 2016) and effective pollination of native plants. Non-native pollinators may also promote pollination and fruit set of invasive plants (Liu and Pemberton 2009) and potentially interfere with pollination of native plants (Downing and Liu 2012). Predators on herbivores can moderate fluctuations in plant abundance and facilitate recovery after hurricanes, as *Anolis sagrei* lizards benefit *Sesuvium portulacastrum* (L.) L. (Aizoaceae) in the Exumas (Spiller et al. 2016).

Some exotics move to the Bahamas after they have become established in Florida, or have the same origin of introduction, such as *Melaleuca quinquenervia* (Cav.) S.T.Blake (Myrtaceae) (Pratt et al. 2007), lobate lac scale (*Paratachardina pseudolobata*, Coccoidea: Kerriidae) (Schroerer et al. 2008), and termites (*Nasutitermes corniger*, Termitidae) (Scheffran et al. 2016). While exotics can have significant negative effects on community structure, they can also help maintain natural systems. For example, grazing by exotic animals (goats) may facilitate the growth of host plants preferred by migratory birds, such as Kirtland's warbler wintering in the Bahamas (Fleming et al. 2016).

3. Conclusions

Plant-animal interactions are affected by many types of disturbance, and frequently more than one disturbance at a time. Hurricanes may reduce herbivory for a while, but may bring in propagules of invasive plants and animals that have subsequent effects on native organisms. It is easiest to measure the effects of disturbances that are proximal, as they happen within a shorter period of time; the effects of ultimate disturbances such as habitat fragmentation may incur an "extinction debt" (Tilman et al. 1994), where species may persist without reproducing for an indefinite period of time, but eventually disappear. Sea level rise may be seen historically, and projected into the future, but the continued existence of species in the affected

habitats depends upon their ability to adapt to changing edaphic conditions, and very likely will disappear without some assistance in re-location.

4. Acknowledgments

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