Disturbance and the rising tide: the challenge of biodiversity management on low-island ecosystems

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Sea-level rise presents an imminent threat to freshwater-dependent ecosystems on small oceanic islands, which often harbor rare and endemic taxa. Conservation of these assemblages is complicated by feedbacks between sea level and recurring pulse disturbances (eg hurricanes, fire). Once sea level reaches a critical level, the transition from a landscape characterized by mesophytic upland forests and freshwater wetlands to one dominated by mangroves can occur suddenly, following a single storm-surge event. We document such a trajectory, unfolding today in the Florida Keys. With sea level projected to rise substantially during the next century, ex-situ actions may be needed to conserve individual species of special concern. However, within existing public conservation units, managers have a responsibility to conserve extant biodiversity. We propose a strategy that combines the identification and intensive management of the most defensible core sites within a broader reserve system, in which refugia for biota facing local extirpation may be sought.

Front Ecol Environ 2009; 7(9): 471–478, doi:10.1890/070221 (published online 20 Aug 2008)

Disturbance is a powerful evolutionary force and a defining characteristic of terrestrial and aquatic ecosystems. In a world in which our own activity is an increasingly pervasive ecological driver, episodic events, such as fires, floods, and windstorms, still continue to shape our landscapes. However, the ecological impacts of these "pulse" disturbances (Bender *et al.* 1984; Glasby and Underwood 1996) may shift in response to changes in global climate, habitat fragmentation, or the spread of exotic species. These environmental changes alter the context in which pulse disturbances take place, and may themselves be viewed as "ramp" disturbances, defined as such in Lake's (2000) typology, because their impact increases steadily through time. The interactions of pulse and ramp disturbances sometimes result in sudden and unanticipated biotic responses, presenting resource managers with novel situations and difficult choices.

In a nutshell:

- Ecosystems on coastal islands face threats from sea-level rise that are distinct from those threatening continental margins
- Interactions between sea-level rise and pulse disturbances, such as storm surges or fire, can cause vegetation to change sooner than projected based on sea level alone
- Preservation of freshwater-dependent island biota requires the identification and management of the most defensible core sites, while planning for ex-situ conservation in the event that defense becomes impossible

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Here, we focus on the interactions of a ramp disturbance – sea-level rise – with hurricane and fire regimes, and its effects on the biota of low-lying coastal islands. Low oceanic islands present special problems for the design of refuge systems that facilitate species migration in a changing climate (Hannah *et al.* 2007). The maintenance of unique island communities and endemic taxa, especially those adapted to freshwater conditions, is made difficult by the progressive disappearance of suitable on-island habitat caused by rising seas, which also lengthen migration routes to similar environments on the mainland, or on higher islands.

We address this issue by using a case study from the Key Deer National Wildlife Refuge (Key Deer NWR) in the lower Florida Keys. Besides its direct effects on groundwater resources, sea-level rise, even at modest rates, amplifies the impacts of hurricane storm surges on the islands' terrestrial ecosystems, while decreasing the frequency and influence of fire. The result is that freshwater-dependent plant and animal assemblages, which comprise much of the biological diversity of the islands, will, in the future, disappear at rates faster than the historical average. The situation is made even more daunting by fragmentation of the existing habitat, caused by encroaching residential development at the wildland–urban interface.

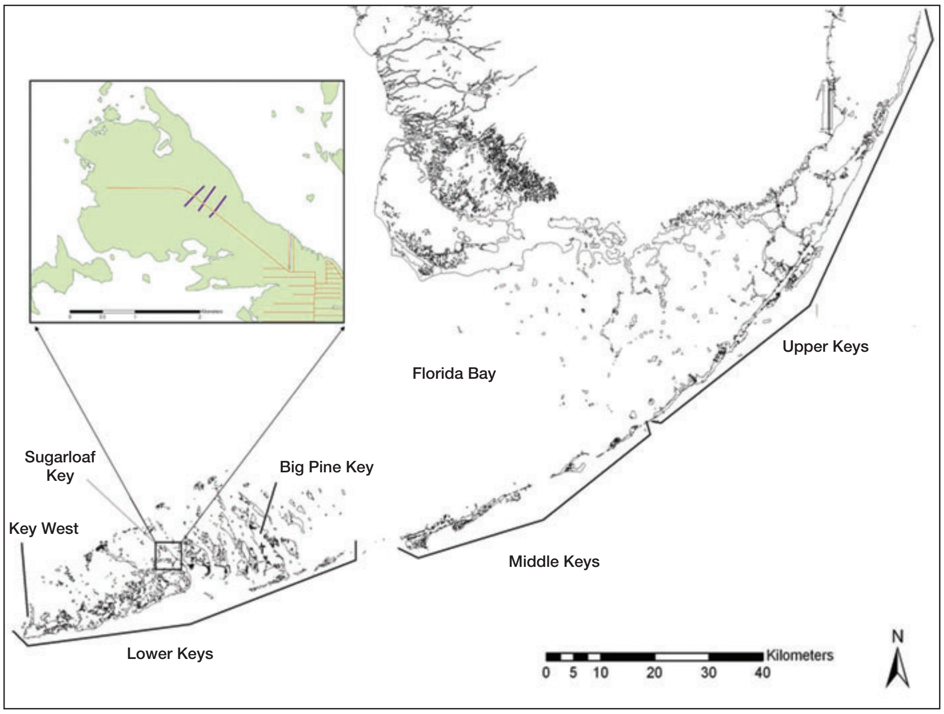

Figure 1. *The Florida Keys. Inset: study area on Sugarloaf Key.*

■ Holocene sea-level rise and Lower Keys ecosystems

The Florida Keys are built on a fossil coral reef, established during a period of higher sea level in the late Pleistocene, about 125 000 years ago. Above the high tide line on the east–west oriented upper and middle Keys islands (Figure 1), the coralline limestone is covered only by a thin (< 20 cm) organic soil, formed under broadleaf, "hardwood hammock" forests that occupy the highest elevations of 7 m or less (Ross *et al.* 2003). In the lower Keys (ie from Big Pine Key west), the surface limestone is an oolite (ie is comprised of spherical, sand-sized carbonate particles [ooids] formed in shallow marine waters). Cementation of the ooids causes this layer to be less permeable to water movement than the subtending coralline limestone, allowing retention of a fresh groundwater layer, or lens, which "floats" on the underlying salt water (Coniglio and Harrison 1983; Vacher *et al.* 1992). Until recently, most of the larger and more elevated (1–3 m maximum elevation) lower Keys islands supported freshwater wetlands and salt-intolerant slash pine (*Pinus elliottii* var *densa*) forests ("pine rocklands"); these are absent from the upper Keys (Ross *et al.* 1992).

The biodiversity of the freshwater-dependent communities is especially notable, with a high level of endemism in the pine forests (JJO unpublished). Today, two calcicolous (growing in lime-rich soils) plant taxa, Big Pine partridge pea (*Chamaechrista lineatea* var *keyensis*) and wedge sandmat (*Chamaesyce deltoidea serpyllum*), are found exclusively in pine rocklands on the Keys. The largest populations of sand flax (*Linum arenicola*), a third regional endemic, occurs there as well. Endemic animals closely associated with the pine forests and adjacent marshes include the federally endangered Key deer (*Odocoileus virginianus clavium*), lower Keys marsh rabbit (*Sylvilagus palustris hefneri*), and the Florida leafwing butterfly (*Anaea troglodyta floridalis*), a candidate for federal listing.

Two factors necessary for the maintenance of pine forests and herbaceous freshwater marshes on oceanic islands are (1) a persistent supply of fresh groundwater and (2) a recurrence of fire frequent enough to control invasion by hardwood trees and shrubs, which supplant herbaceous species and inhibit pine regeneration. Both factors have been greatly influenced by marine transgression (covering of previously exposed land) of the south Florida shelf since the last glacial maximum (18 000–21 000 years before present, ybp), when sea level in south Florida was approximately 120 m lower than at present (Lidz 2006). From that point, sea level rose rapidly, coming within 6 m of its current position by 5500 ybp. The discovery of pine cones and wood fragments (yellow pine group) dating to 8350–8600 ybp, buried beneath 1.5 m of bottom sediment in 12 m of water, 60 km west of Key West (C Malcom pers comm), suggests that pine forests were an important component of an extended south Florida land mass throughout most of this period.

In subsequent millennia, sea level rose more gradually, transforming the lower Keys from a continuous body of land to roughly its current configuration, a string of small islands, none more than a few thousand hectares in size (Lidz and Shinn 1991). As the islands became isolated, freshwater-dependent ecosystems would have become more vulnerable to saltwater intrusion from an enveloping marine environment, and fires ignited by lightning or human activity would no longer have had the capacity to spread across vast acreages, thereby reducing fire frequency across the landscape. Still, fires and freshwater resources were sufficient for substantial pine forest fragments to persist throughout the area in the early part of the 20th century (Small 1913).

■ The pine forest's 20th-century retreat

T Alexander of the University of Miami was the first scientist to document the decline of pine forests on the Florida Keys. Following up on local homesteaders' accounts of live slash pine trees bordering a remote mangrove swamp on the north end of Key Largo, Alexander and his students found only the remains of dead trees. He later attributed the forest's demise to salinization of the groundwater in response to sea-level rise (Alexander 1953, 1984). Between 1913 and 1999, the sea rose around

Key West at a rate of about 23 cm per century (NOAA 2001), about 1.4 times the global average for the 20th century (Meehl *et al.* 2007).

When two of us (MSR and JJO) observed dead stems far out in the supratidal wetlands of upper Sugarloaf Key in 1988–1989, we suspected that pine forests on the lower Keys were following the same trajectory as on Key Largo. To test this hypothesis, we searched for remnants of pine trees at the edges of the island, mapped changes in pine forest extent using sequential aerial photographs from 1935–1991, surveyed elevations throughout the island, measured groundwater salinity patterns, and assessed the level of physiological stress associated with the source water used by pine trees (Ross *et al.* 1994).

Our data showed that the area of pine forest on Sugarloaf Key declined from an initial 88 ha (furthest extent of pine remains) before 1935, to 30 ha by 1991 (Figure 2). The transformation of pine forest to more salt-tolerant vegetation types proceeded continuously, though at variable rates, and from low to high elevation. Live pine trees surviving in peripheral areas experienced diminished plant moisture potential and showed isotopic signs of physiological stress. The upslope recession in the pine forest border was generally consistent with a progressive salinization and rise in the groundwater associated with sea-level rise.

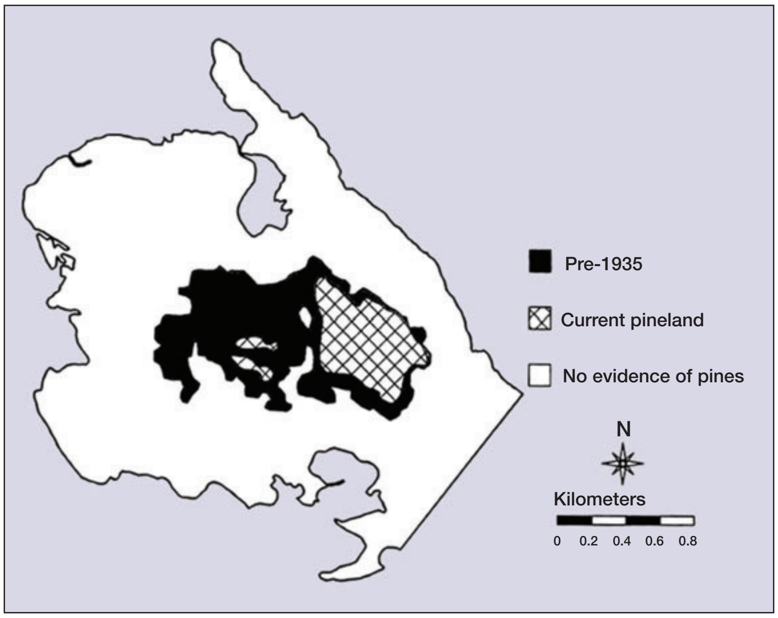

Figure 2. *Historical and current extent of pine forest on Sugarloaf Key.*

Prognosis for the pine forests: initial modeling effort

To better understand the historical changes in vegetation on Sugarloaf Key, and to project them into the future, we developed SeaChange, a spatially explicit simulation model of the habitat structure of Sugarloaf Key. This belongs to the general class of models referred to as "cellular automata", in which the state of a cell changes on the basis of the state of its neighbors. Each cell used in the model represents a specific 50-m x 50-m area assigned to a particular habitat type. The model assumes a fixed topography and steps in fixed increments of sea-level rise, simulating changes in habitat-type distribution. The habitat within each cell can change at each step, subject to the following constraints:

(1) The proportion of each community type within each 10-cm elevation band remains constant.
(2) The proportion of each habitat type directly adjacent to each of the other habitat types remains constant.
(3) The fractal index of the overall landscape, a measure of the "raggedness" of the edges of the habitat patches, remains constant.
(4) Unless prohibited by the above rules, habitats increase by adding cells at the edges of existing patches, rather than colonizing cells surrounded by another habitat type.

SeaChange is similar in some regards to the habitat-change model described by LaFever *et al.* (2007), but is designed to work on a much smaller scale and to take into account more detailed habitat relationships. In particular, it preserves the spatial relationships between habitat types (such as the tendency of one type to be surrounded by another), historical patch locations, and the "raggedness" (ie fractal index) of habitat patch boundaries.

We validated the model by comparing its prediction to the known habitat distribution in 1991, starting with our photographic interpretation of the distribution of three general habitat types (mangrove, transition, and upland) in 1935, and the historical sea-level rise rate of 2.3 mm yr^{-1}. Within the uplands, the model did not attempt to distinguish hammock from pineland, because of the importance of fire in their dynamics, and the complexity of the relationship between fire and topography. SeaChange accurately predicted an increase in mangrove habitat (a 42% increase predicted and a 47% increase observed) and upland habitat (a 33% decrease predicted and a 31% decrease observed), but performed less well with the transition habitat (17% decrease predicted, 6% decrease observed).

Model projections suggest that mangrove habitats will expand steadily at the expense of upland and transitional habitats as sea level rises (Figure 3). A rise of about 0.2 m will result in the loss of most of the upland and transitional habitat in the central portion of Sugarloaf Key. As sea-level rise approaches 0.5 m, about 95% of Sugarloaf will become mangrove forest and mudflat, leaving only a small amount of remnant upland habitat in the southeast portion of the Key. Based on the IPCC-projected range of sea-level rise (0.2 m to 0.6 m by 2100), this amount of change could occur by 2100. Since, at a given elevation, sea-level rise increases the likelihood of storm-surge flooding (a factor not included in the model), synergistic effects

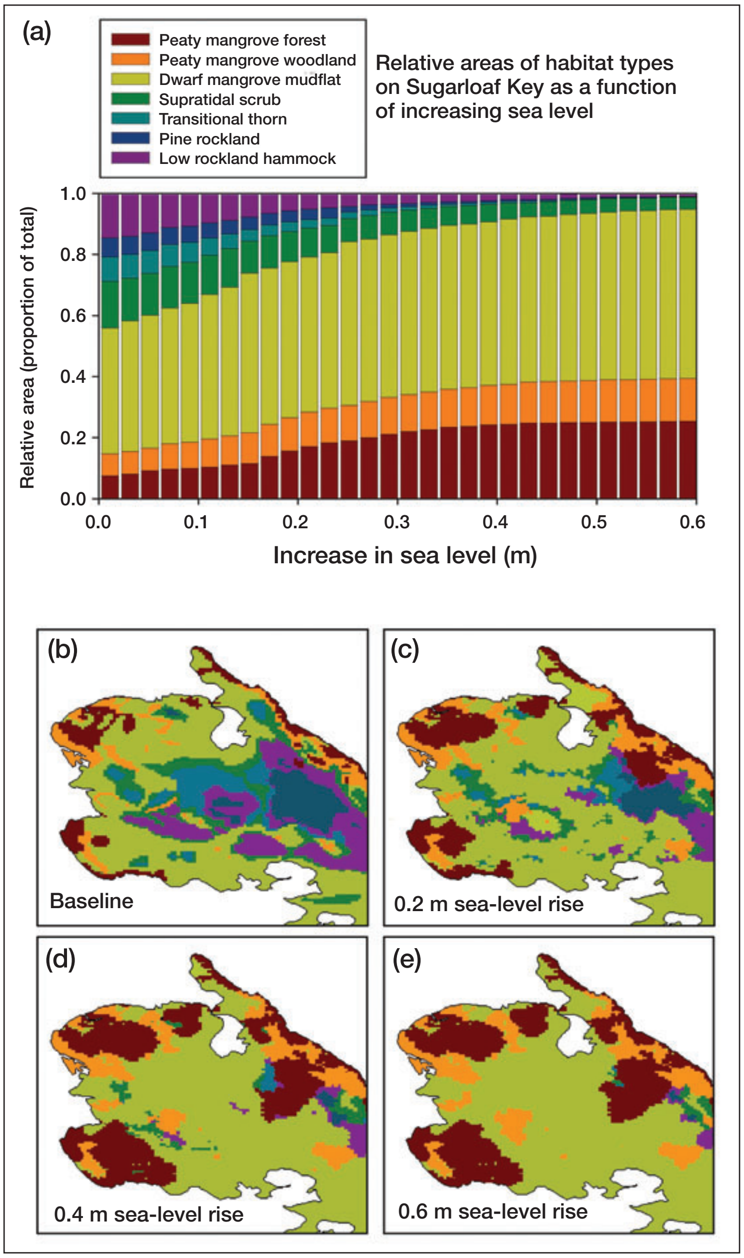

Figure 3. *Results of the SeaChange model, which predicts changes in habitat extent for Sugarloaf Key. (a) The relative extent of seven habitat types as a function of increasing sea level. (b–e) Model predictions of habitat configuration after different amounts of sea-level rise. Habitat colors on (b–e) correspond to those in (a).*

between these two variables could cause upland habitat to be reduced more rapidly than predicted.

Storm-associated complications: Hurricane Wilma, October 2005

Traveling on a northeast track, Hurricane Wilma made landfall as a Category 3 hurricane on the southwestern Florida coast on October 24, 2005 (NWS 2005). While wind effects in the Keys were minor, the westerly high winds arriving behind the eye wall drove water into the funnel-shaped Florida Bay from the Gulf of Mexico, producing a maximum storm surge of 1.8 to 2.4 m along the northern shores of many lower Keys islands, including Sugarloaf Key. The impact of Hurricane Wilma's storm surge was amplified by a long, nearly rainless winter and spring in the lower Keys. December–April rainfall at Key West was 2.67 cm, about 9% of the historical average for the period. Salinity in many Big Pine Key sinkholes that normally held fresh water remained brackish through June of 2006 (Ross *et al.* in prep), and salts that had collected after stormwaters receded remained visible on many islands. By the following fall, the catastrophic effects of Hurricane Wilma's storm surge on the pine forests of upper Sugarloaf Key were evident (Figure 4). Few pine trees survived on low surfaces north of a road that bisected the peninsula and may have impounded flood waters surging from the north. Survival was higher below the road and on relatively high ground above it, where about 30% of the trees persisted. Live pine seedlings were entirely absent throughout the area, and there was little evidence of characteristic pine-rockland herbs. On nearby Big Pine Key, a larger and higher island, the effects of the hurricane were more variable. At elevations > 1 m, two-thirds or more of the pine trees survived the first post-hurricane year, but survival in several low-elevation pine forests was less than 20% (Figure 5).

Disturbance interactions: storm surge, sea-level rise, and fire

The effects described above suggest that a prognosis for lower Florida Keys ecosystems should account not only for sea-level rise, but also for its interactions with disturbances associated with hurricanes and fire. Figure 6 conceptualizes how these interactions modify an inexorable succession, driven by sea-level rise. Fire inhibits the transition of pine to hammock forests and of herbaceous marshes to woody swamps. Hurricanes bring both wind damage and storm-surge impacts, but the latter appear to have the most persistent effects on coastal vegetation (Craighead and Gilbert 1962). In contrast to fire, storm surge accelerates the transition from freshwater-dependent ecosystems, by selective mortality of salt-sensitive vegetation (pines, herbaceous freshwater marsh species), which are also the major sources of fine fuels that carry fires. The consequent lack of fires then amplifies the vegetation transitions due to sea-level rise.

With the arrival of an active hurricane period due to decadal-scale variability (Goldenberg *et al.* 2001), the interaction between sea-level rise and storm surge will soon reach a tipping point with respect to the maintenance of local freshwater ecosystems. Possible acceleration in sea-level rise (Church and White 2006) and increase in hurricane intensity (Webster *et al.* 2005) due to global warming could bring this tipping point closer. Sea-level rise has rendered pine forests on the Keys more vulnerable, by reducing the area capable of capturing precipitation and recharging fresh groundwater supplies. As experienced after Hurricane Wilma, droughts that sometimes follow late-season hurricanes can further diminish the volume of freshwater available to dilute salts deposited by storm surge. A second mechanism that may have exacerbated the situation in the Keys was that sea-level rise brought the background level of the water table so close to the surface that drainage following storm-surge recession was reduced. In a study carried out in South Carolina, Gardner *et al.* (1992) found that hurricane-induced mortality in coastal bottomland hardwood forests was concentrated near depressions where the water table was close to the surface, causing saltwater to pool and evaporate in place. Salts may stress and kill trees directly or by causing large releases of nitrogen compounds that can be leached away prior to forest recovery (Blood *et al.* 1991).

The reduced incidence of fire due to sea-level rise may also have reached a critical point. Under steady-state conditions, a pine overstory supports a feedback loop in which fire-resistant pines are favored by recurrent fires carried by pine needles. Any interruption in the input of fine fuels (or a lack of fire) releases fire-sensitive species, leading to dominance by broad-leaved forests, an alternative stable state (Mitchell *et al.* 2006). Sea-level rise has certainly reduced fire frequency over millennia by fragmenting a continuous landmass and inhibiting fire spread from island to island. Moreover, within islands, the landscape has evolved into a patchwork of flammable uplands embedded within a relatively fire-resistant swamp matrix. Even within the upland patches, minor depressions intersect the shallow water table, raising fuel moisture, reducing fire intensity, and promoting hardwood shrub invasion. Once formed, hardwood patches burn with lower intensity than the surrounding pine forest (Sah *et al.* 2006). In the aftermath of a mortality event that causes extensive pine die-off in a mixed pine–hardwood forest, natural re-establishment of a pine-rockland ecosystem would be unlikely, due to the scarcity of nearby seed sources and unfavorable conditions for seedling establishment.

The management quandary

The Key Deer National Wildlife Refuge is part of a national network of lands set aside for the conservation of fish and wildlife. The National Wildlife Refuge System (NWRS) Improvement Act of 1997 directs the US Fish and Wildlife Service (FWS) to maintain the "biological integrity, diversity, and environmental health" of their refuges. Traditionally, these broad goals have been achieved by maintaining or restoring ecosystem functions so that they are comparable to historic conditions, that is, prior to the onset of substantial human-caused change. In light of the current rapidity and projected acceleration in rates of sea-level rise (Meehl *et al.* 2007), this Act provides scant guidance for the "no-analog future" (Overpeck *et al.* 1992; Williams and Jackson 2007) now facing managers of FWS's coastal refuges.

For protected-areas managers of coastal reserves inside and outside the US, the interaction of sea-level rise and other disturbances can cause unexpected and unwanted changes in vegetation. When pines are a substantial com-

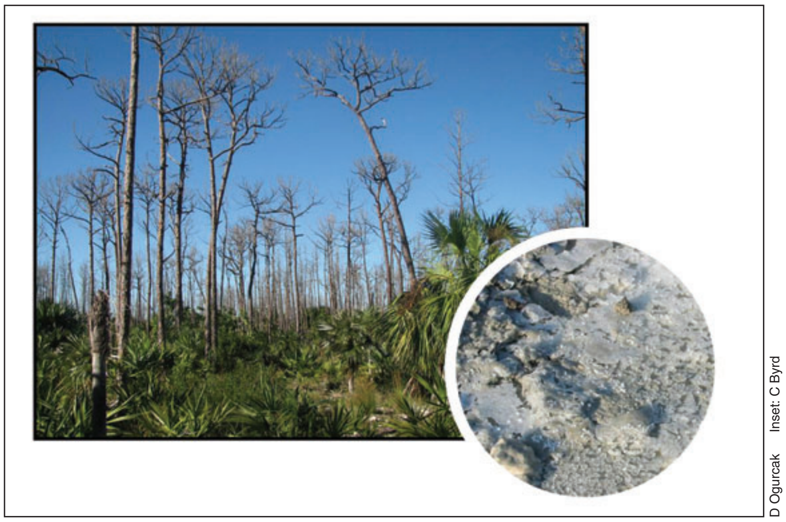

Figure 4. *A slash pine stand in the lower Florida Keys 2 years after Hurricane Wilma. Inset shows salt collected on the rockland surface a few weeks after the storm, with the imprint of a Key deer hoof.*

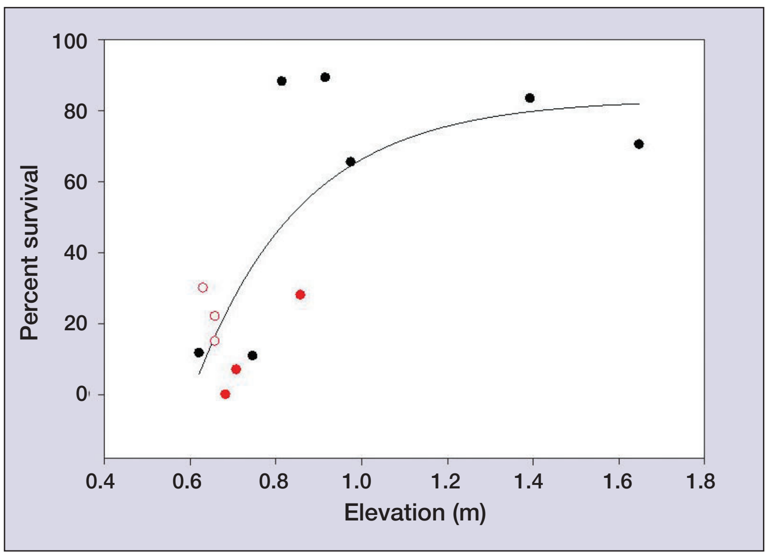

Figure 5. *The relationship between post-hurricane pine survival and elevation on Big Pine Key (solid black dots) and Sugarloaf Key, both north of the paved road (solid red dots) and south of the paved road (open red dots). The road acted as a drainage barrier, behind which saltwater pooled after the storm surge receded. The line represents the fit of an exponential rise-to-maximum equation with an* r^2 *of 0.60.*

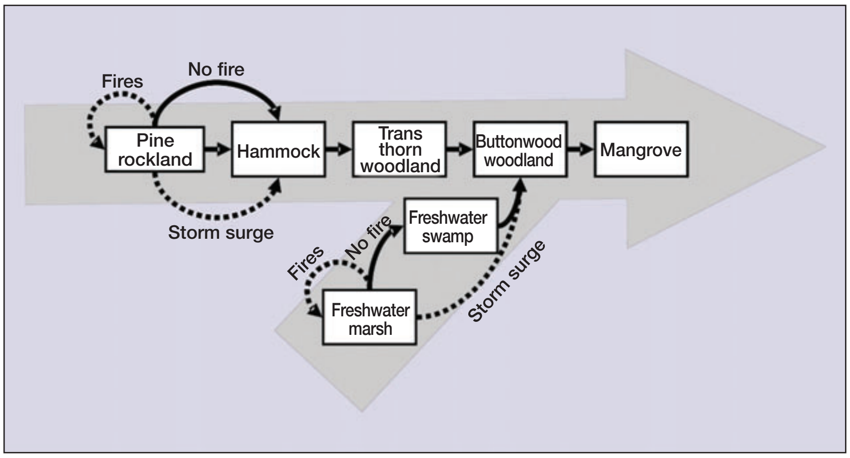

Figure 6. *Vegetation change in response to major ramp and pulse disturbances in the Florida Keys. The arrows represent transitions among vegetation types. Broken arrows represent rapid transitions driven by pulse disturbances; solid arrows indicate vegetation changes that occur over decades to centuries. The large gray arrow in the model background represents the overarching impact of sea-level rise as a ramp disturbance.*

ponent of the uplands in coastal areas, changes in fire regime can accelerate the impact of sea-level rise and result in a loss of fire-dependent ecosystems (eg Blackwater NWR on the Delmarva Peninsula [Kirwan *et al.* 2007], Swanquarter NWR in North Carolina [Poulter 2005]). In the Waccassa State Preserve in northern Florida, the synergism between periodic droughts and sea level drives unexpectedly rapid tree mortality (DeSantis *et al.* 2007). The impact of invasive species can also be exacerbated by chronic stress wrought by sea-level rise. Throughout the protected areas in the Turks and Caicos Islands of the Caribbean, the recently introduced pine tortoise scale (*Toumeyella parvicornis*) has caused catastrophic mortality in Caribbean pine (*Pinus caribaea* var *bahamensis*; Hamilton 2007), especially in low-lying areas, where pines are already stressed by rising sea level.

Development of management strategies for such complex interactions should begin immediately. We suggest an approach in which planning and implementation for concrete actions intended to slow the alteration of existing ecosystems, and longer-term activities intended to stabilize them in some future configuration, proceed in sequence. A brief synopsis of such a program for our Florida Keys case study is outlined below, along with a possible timeline for its implementation (Figure 7):

(1) *Identify sites with the best chances of persistence*. Current pine-rockland sites with the best prospects for persistence can be identified on the basis of surface topography, hydrogeology, forest and landscape structure, and adjacent land use. The SeaChange model (Figure 3) was a simple initial attempt to identify such core sites. More sophisticated models should be developed to identify core areas of at least 25 ha on individual lower Keys islands.

(2) *Manage core forests intensively*. Long-term maintenance of pine forests depends on periodic fire, which, in turn, requires the fuel continuity provided by needle fall from a full pine canopy. Where core sites currently lack such a canopy, it may be necessary to use prescribed fire to prepare the site, followed by augmentation of natural regeneration with seeded or planted pines. Once pines are established, management should focus on maintaining a high-diversity community that can serve as a seed source for adjacent areas following storm-surge events. Core-area management should include mitigation of hydrologic barriers that could compromise its effectiveness. Such activities might include (a) culverting of roads that impound tidal waters, causing salts to concentrate following flooding events, or (b) blocking or filling of canals and ditches that transport saltwater into freshwater ecosystems. In exceptional cases, establishment of physical defenses, such as levees, could provide some short-term (eg years to several decades) protection from storm surges. Management should also include the translocation to core areas of rare pine-rockland species surviving in marginal conditions elsewhere on the same or adjacent islands. This form of assisted migration (McLachlan *et al.* 2007) is an "inter-situ" conservation strategy, according to the terminology of Burney and Pigott Burney (2007).

(3) *Ex-situ conservation*. Given sufficient sea-level rise, an absence of suitable recipient areas nearby may necessitate the assisted migration of species outside of their historical ranges. In the case of lower Florida Keys pine forests, upper Keys sites are not suitable recipient areas because the highest elevations are occupied by broad-leaved, tropical hardwood hammocks that are unique in the US, and which host their own, extensive suite of fire-sensitive, protected species. Pine forests on the south Florida mainland are likewise inappropriate as refuges, due to their low elevation. However, the islands of the Bahamas could offer an alternative, as extensive areas of high-elevation pine rocklands occur there.

Among the 161 FWS-managed National Wildlife Refuges listed in the "Marine Managed Areas Inventory" (www3.mpa.gov/exploreinv/explore.aspx), 73 include vulnerable oceanic islands and 89 contain substantial expanses of low-lying upland communities embedded within freshwater or estuarine wetlands. As in the Florida Keys, the complex brew of sea-level rise and altered disturbance regimes threatens the future of many of these sites and limits FWS's ability to use historical conditions as a benchmark for success (Scott *et al.* 2008). At the same time, FWS's charge to implement the Endangered Species Act, including listing species, designating critical habitat, and developing recovery plans, becomes a great deal more complicated (Ruhl 2008). These looming difficulties can be made more tractable if strategic planning and adaptive management can effectively encompass, in a hierarchical manner, both the broad NWR system and individual, isolated refuges. Indeed, FWS's mandate to manage for biological integrity, diversity, and ecosystem health (FWS 2000) requires them to implement collaborative landscape-level planning as local habitat succession makes moving targets of coastal plant and animal assemblages. With its long history of actively managing a network of wintering, breeding, and staging sites for migratory birds, FWS is well positioned to carry out such system-wide management (Scott *et al.* 2008).

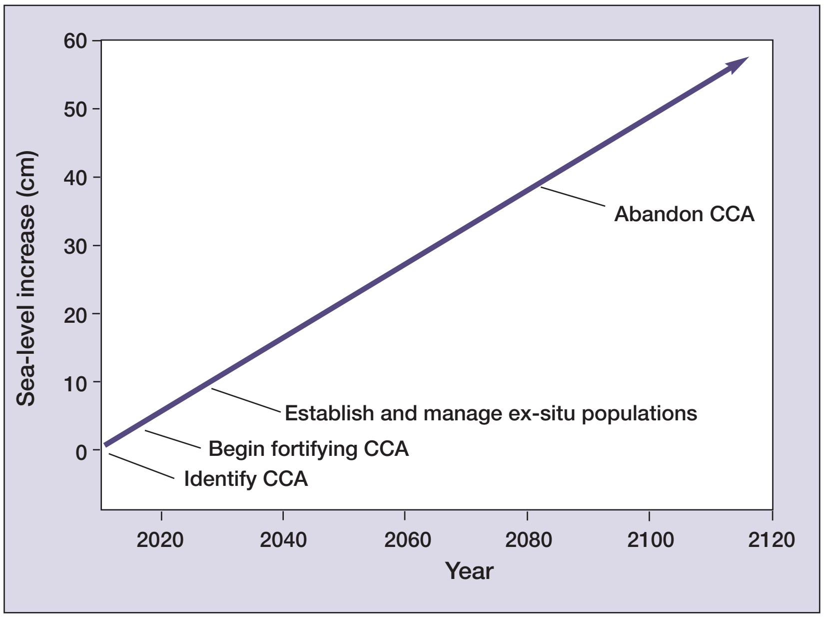

Figure 7. *Suggested plan of action for the establishment of Florida Keys pine rockland core conservation areas (CCA) and ex-situ conservation of endemic species. The timeline was developed based on estimates of sea-level rise and practical considerations (ie time needed to establish protocols and regulations for the transfer of species outside their historical ranges).*

Conclusions

Ecosystems of coastal islands face threats from sea-level rise that are distinct from those threatening ecosystems of continental margins (Mimura *et al.* 2007). When not blocked by development or other barriers, gradients in the flora and fauna of mainland coasts may shift inland in response to sea-level rise; however, with dispersal to adjacent islands limited by distance and habitat availability, rising sea level restricts freshwater communities on coastal islands to rapidly shrinking areas of suitable local habitat. Island ecosystems are also particularly vulnerable to changes in the regime of pulse disturbances, the impacts of which may be magnified by the slow rise in sea level. Here, we have presented an example from the Florida Keys, in which the decreasing influence of fire and the increasing effect of storm surges appear to be consequences of rising sea level. This combination of factors has compressed the time frame remaining for wildlife-refuge and other protected-area managers to secure the considerable biological resources of the area, whose value and uniqueness are, perhaps paradoxically, a result of the isolation brought on by sea-level rise over many centuries. Management has little choice now but to follow a strategy of adaptation, in which core sites within landscapes that retain some of their historical connectivity are identified, fortified, and defended, all the while planning for the day when species threatened with extinction due to submerging islands must be translocated to suitable recipient sites elsewhere, or, ultimately, maintained in captivity.

Acknowledgements

This research was supported by the US Department of Energy's Office of Science (Biological and Environmental Research) through the Coastal Center of the National Institute for Climatic Change Research at Tulane University. The analysis built on data collected with support from the Joint Fire Science Program. We also acknowledge The Nature Conservancy, Florida Keys Office, and the US Fish and Wildlife Service, Key Deer National Wildlife Refuge, for funding and logistical support. T Heinze, D Heinze, D Ogurcak, J Sah, S Stoffella, M Kline, J Espinar, E Hanan, and P Ruiz were instrumental in data collection or document preparation. This is SERC Contribution Number 391.

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