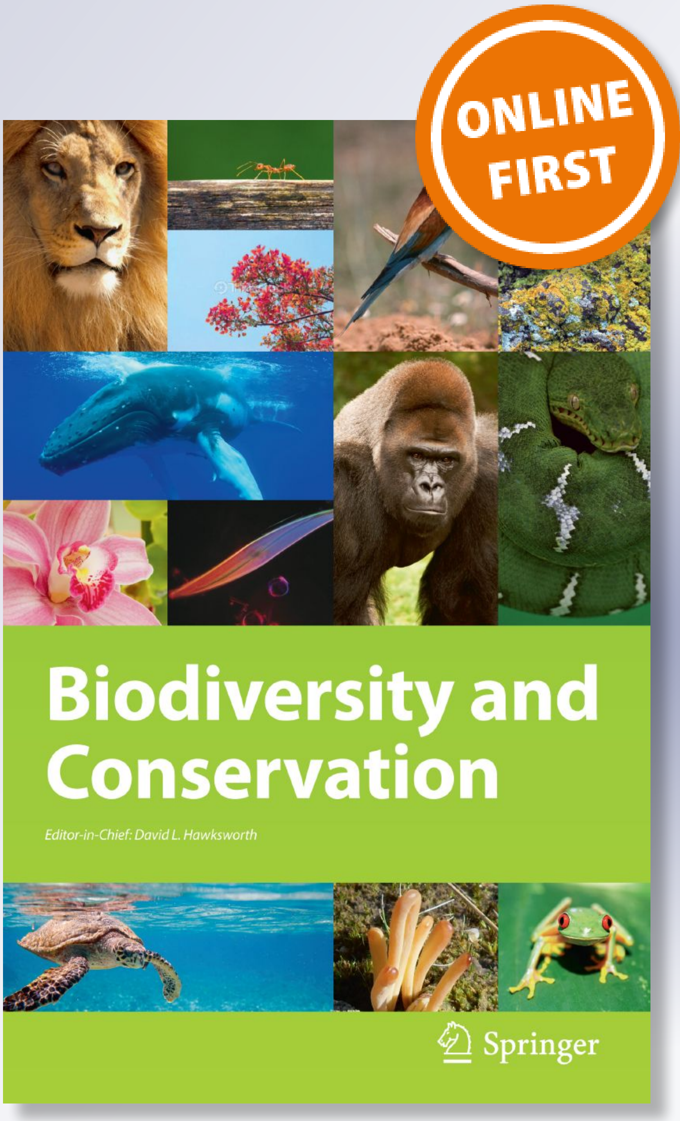
Dead land walking: the value of continued conservation efforts in South Florida's imperiled pine rocklands

Ian Matthew Jones & Suzanne Koptur

Biodiversity and Conservation

ISSN 0960-3115

Biodivers Conserv
DOI 10.1007/s10531-017-1433-6



Springer

Biodivers Conserv
DOI 10.1007/s10531-017-1433-6

REVIEW PAPER

Dead land walking: the value of continued conservation efforts in South Florida's imperiled pine rocklands

Ian Matthew Jones[1] · Suzanne Koptur[2,3,4]

Received: 26 May 2017 / Revised: 21 August 2017 / Accepted: 2 September 2017

Abstract Pine rocklands are deeply imperiled habitats restricted to South Florida and the Caribbean. In South Florida, more than 98% of pine rockland habitat has been destroyed in the past century (outside of Everglades National Park). Due to their proximity to human populations, management options in the remaining fragments are sometimes limited, and fires that are necessary to maintain healthy habitat structure are often excluded. Despite these pressures, conservation initiatives in pine rocklands have been surprisingly successful, and plant extinction has been avoided. In the coming decades, however, sea-level rise threatens to all but eliminate the pine rocklands, and efforts to preserve their many endemic species will likely fail. We synthesize the results of numerous ecological studies and review the successes and failures of conservation in South Florida's pine rocklands. Further, we illustrate the value of continued conservation efforts, and provide direction in the light of the habitats long-term fate. We advocate the increased use of prescribed fire and, as the effects of climate change become more apparent, the translocation of some endemic species. Finally, we acclaim pine rocklands as a model system for studying how plant communities respond to environmental change. South Florida's fragmented landscape, with shifting gradients of elevation, salinity, inundation and nutrient availability, should continue to inspire ecologists to address important questions, and better prepare the region, and the world, for the challenges of the coming decades.

Communicated by Frank Chambers.

✉ Ian Matthew Jones
ijone002@fiu.edu

1 USDA-ARS Invasive Plant Research Laboratory, 3225 College Avenue, Fort Lauderdale, FL 33314, USA

2 Department of Biological Sciences, Florida International University, Miami, USA

3 Agroecology Program, Florida International University, Miami, USA

4 International Center for Tropical Botany, Miami, USA

Published online: 16 September 2017

Keywords Community ecology · Conservation · Fire management · Pine rocklands · Sea level rise

Introduction

Pine rocklands are the most species-rich habitats in southern Florida, and occur in three distinct areas: the Miami Rock Ridge, the Florida Keys, and the Big Cypress area (Florida Natural Areas Inventory 2010). Similar pinelands occur in the Caribbean, particularly in the eastern Bahamas and the Caicos Islands (Correll and Correll 1982). Although these habitats are comparable to Florida pine rocklands physiognomically, they are dominated by the Caribbean pine, *Pinus caribaea*, and lack many species unique to South Florida (Correll and Correll 1982).

Pine rockland habitats are characterized by an open canopy of Florida slash pine (*Pinus elliottii* var. *densa*), a patchy subcanopy of palms and shrubs, and an extremely diverse herb layer (Florida Natural Areas Inventory 2010). The subcanopy layer alone is comprised of more than 100 species of palms and hardwoods (Gann et al. 2009), mostly derived from the tropical flora of the West Indies (Snyder et al. 1990). The herb layer, in particular, is home to a great many rare species, including 14 that are endemic to Florida pine rocklands (O'Brien 1998; Florida Natural Areas Inventory 2010) (Table 1). Within South Florida's pine rockland range, soils transition from acidic quartz sands in Big Cypress to basic calcareous soils in the Florida Keys (O'Brien 1998). For this reason many rare plant species have highly restricted ranges even within South Florida. Big Pine partridge pea, *Chamaecrista lineata* var. *keyensis*, for example, occurs only in the Florida Keys.

In addition to plants, pine rockland habitats support a host of federally listed and rare animals, including the Florida panther, *Puma concolor coryi*, the Key deer, *Odocoileus virginianus clavium*, the Miami tiger beetle *Cicindela floridana*, and two rare butterflies: the Florida leafwing, *Anaea troglodyta floridalis*, and Bartram's scrub-hairstreak, *Strymon*

Table 1 Plant species endemic to South Florida's pine rocklands

Family	Species	Common name
Asteraceae	*Brickellia mosieri*	Brickell bush
Euphorbiaceae	*Chamaesyce deltoidea* ssp. *adhaerens*	Goulds wedge sandmat
	Chamaesyce deltoidea ssp. *deltoidea*	Deltoid spurge
	Chamaesyce deltoidea ssp. *pinetorum*	None
	Chamaesyce deltoidea ssp. *serpyllum*	Keys wedge sandmat
	Poinsettia pinetorum	Pineland poinsettia
	Tragia saxicola	Pineland noseburn
Fabaceae	*Amorpha herbacea var. crenulata*	Crenulate lead plant
	Chamaecrista lineata var. keyensis	Keys partridge pea
	Galactia pinetorum	Pineland milkpea
	Galactia smallii	Small's milkpea
Linaceae	*Linum carteri var. carteri*	Carter's flax
Rubiaceae	*Hedyotis nigricans var. floridana*	Florida diamondflower
Verbenaceae	*Lantana depressa var. depressa*	Pineland lantana

acis bartrami (Florida Natural Areas Inventory 2010). Despite the importance and beauty of these imperiled habitats, and their charismatic mega and mesofauna, a host of anthropogenic and environmental factors threaten their integrity and, indeed, their very existence. Even today, some of the birds historically found in pine rocklands are no longer present such as the red-cockaded woodpecker, *Picoides borealis* (Lloyd and Slater 2012).

A habitat under threat

The relatively high elevation of pine rockland habitats in the South Florida landscape, between two and seven meters above sea level (Snyder et al. 1990), has led to its disproportionate targeting for cultivation and urban development. It is thought that of roughly 126,500 acres of habitat that originally existed in Miami Dade County, only around 2273 acres remain (2%) (Florida Natural Areas Inventory 2010). What remains of the pine rocklands outside of Everglades National Park has been severely fragmented, and is surrounded by a profoundly human influenced landscape (Possley et al. 2008). This fragmentation will inevitably affect plant species in a number of ways. As MacArthur and Wilson's theory of island biogeography would suggest, smaller fragments are likely to support fewer species, and those species are placed at a higher risk of extinction (MacArthur and Wilson 1967). Possley et al. (2008) monitored understory vascular plant presence and cover in 162 urban pine rockland plots, between 1995 and 2003, and found that species richness was highest in the largest fragments. Species richness in 1 m by 1 m plots ranged from 5.0 ± 0.4 to 18.1 ± 2.0 in 1995, and from 9.2 ± 0.1 to 26.9 ± 1.9 in 2003. A total of 182 and 189 native plant species were recorded in 1995 and 2003 respectively. In a separate study Barrios et al. (2011) investigated the influence of fragmentation on the threatened pineland trumpet, *Angadenia berteroi*, and found it to be significantly more abundant in larger pine rockland fragments.

The impact that habitat fragmentation has on each particular native plant will be strongly affected by the breeding system of that species. *Byrsonima lucida*, for example, is the only member of the tropical plant family Malpighiaceae that is native to North America. Studies of its reproductive biology have found it to be self-incompatible, and entirely dependent on a single genus of specialized bee pollinator, *Centris* spp. The small fragmented populations of *B. lucida* in South Florida are, therefore, highly vulnerable to extinction (Downing and Liu 2013). Plants need not be entirely self-incompatible, however, to be acutely affected by habitat fragmentation. The federally endangered crenulate leadplant, *Amorpha herbacea* var. *crenulata*, is a pine rockland endemic, restricted to the northern portion of the peninsular pine rocklands. While the plant is capable of some self-fertilization, it produces a greater percentage of seed, and sets significantly more fruit, when it is outcrossed. Predominantly self-incompatible species such as this are likely to suffer reduced reproductive fitness when isolated in remnant habitat fragments (Linares and Koptur 2010). Similar breeding systems, biased towards self-incompatibility, have been observed in several other pine rockland natives, including the pineland golden trumpet, *Angadenia berteroi* (Barrios and Koptur 2011), and man-in-the-ground, *Ipomoea microdactyla* (Geiger 2007). Some are self-compatible but require visitation, like the butterfly pea, *Centrosema virginianum* (Cardel and Koptur 2010), while others are self-compatible with mechanisms for automatic self-pollination if they are not visited, such as pineland petunia, *Ruellia caroliniana* var. *succulenta* (Geiger et al. 2010).

Chamaecrista keyensis and *Senna mexicana* var. *chapmanii* are perennial legumes endemic to the pine rocklands. Although both are self-compatible, they are not capable of automatic selfing. The flowers have poricidal anther dehiscence and require visitation from 'buzz' pollinating bees (Liu and Koptur 2003; Jones et al. 2016). In the case of *C. keyensis*, visitation rates by bees are lower in urban fragments compared to pristine pine rockland sites on Big Pine Key (Liu and Koptur 2003). Such pollinator limitation is likely to be exacerbated in smaller habitat fragments, and perhaps in areas subjected to aerial mosquito spraying (Liu and Koptur 2003; Harris unpublished data). While plants capable of self-pollination might be at less immediate risk in fragmented habitats, they may still suffer long term fitness costs through a loss of genetic diversity. Geiger et al. (2014) assessed the genetic diversity within populations of *Ipomoea microdactyla* in the Bahamas, Cuba, and in South Florida. Genetic diversity was lowest in Florida populations, possibly due to the extreme fragmentation of the plant's habitat in this area.

The open canopy structure of pine rockland habitats is maintained through regular fires (roughly every 6–9 years), that prevent the habitats from succeeding to rockland hammock. The proximity of the remaining pine rockland fragments to dense human habitation has led, in many cases, to the exclusion of these fires. Negative public perceptions, and issues relating to smoke management, can make it difficult for land managers to conduct prescribed burns (Florida Natural Areas Inventory 2010). In the absence of fire, trees and shrubs gradually dominate, and many plants in the herb layer are shaded out (Loope and Dunevitz 1981; Snyder et al. 1990). Given long enough, large palms and hardwood species rise to dominance, and most of the herbaceous pine rockland natives are lost (Possley et al. 2008) (Fig. 1). Even in shorter periods without fire, increased canopy cover can have serious negative effects on native species. *Senna chapmanii*, for example, produces extrafloral nectar and relies on ants for defense against herbivores (Jones et al. 2016). Exclusion experiments have shown that, in the presence of ants, *S. chapmanii* plants suffer significantly less herbivory and set significantly more seeds. These effects, however, only occur in open sunny microhabitats, and not in shaded microhabitats, where ant activity is reduced (Jones et al. 2016).

Another threat to the remaining pine rockland habitats is the encroachment of invasive plant species. The same fires that maintain the rocklands characteristic structure, create open niches that can be exploited by non-native species. In some cases, the presence non-native plants may then modify fire regimes to facilitate their further invasion. Stevens and Beckage (2009) found that prescribed burns caused significant mortality (30–45%) to Brazilian pepper, *Schinus terebinthifolius*, when it was found at low densities. At high

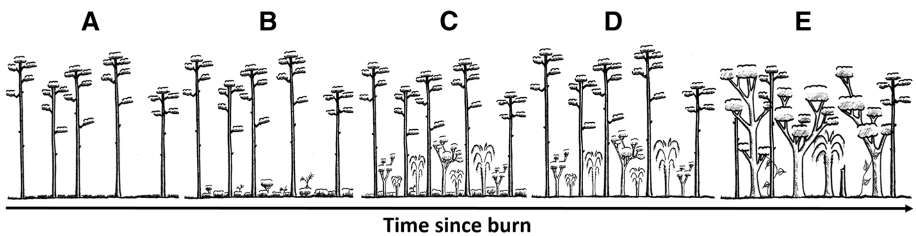


Fig. 1 A generalized depiction of pine rockland habitat succession post-fire. **a** Shortly after fire, most of the understory has been cleared, and only the canopy of slash pine remains intact. **b** Plants recolonize the diverse, and endemic rich, herb layer. **c** Large palms and broadleaf trees begin to form a sub-canopy. **d** The gradual domination of the sub-canopy leads to the shading out of many plants in the herb layer. **e** The habitat transitions to rockland hammock, as large palms and broadleaf trees dominate

densities, however, Brazilian pepper reduced fire temperatures by up to 200 °C, and suffered 80% less mortality. In areas where fires are infrequent, therefore, Brazilian pepper may reach sufficient densities to initiate positive feedbacks that further reduce the frequency of fires, transforming pine rocklands into invasive dominated forests (Stevens and Beckage 2009). As well as hardwood species, invasive grasses have also been observed displacing native understory plants. Possley and Maschinski (2006) monitored the spread of Natal grass, *Rhynchelytrum repens*, in urban pine rockland fragments. Increased *R. repens* density was strongly associated with a reduction in native understory plants, particularly graminoids.

The risk of extinction is very real for many plants in the pine rocklands, however, none more so than those plants adapted to the ecotone between habitats. The proximity of remaining pine rockland fragments to urban areas, along with the suppression of fire, has meant that pine rockland ecotone habitats have more or less ceased to exist. Plants like *Lantana canescens*, a rare tropical shrub native to the ecotone between pine rockland and hardwood forests, relies almost entirely on planned restoration sites for its continued existence (Possley et al. 2009).

The issues outlined above put many pine rockland plant species at high risk of extinction. Efforts to alleviate these issues have seen some success (see below); however, conservation efforts in the pine rocklands continue with the ominous backdrop of sea-level rise, which threatens South Florida as a whole. While pine rockland habitats occupy relatively high ground (by South Florida standards), even small variations in elevation have a marked impact on habitat structure. Big Pine Key and No Name Key are home to the largest remaining pine rockland fragments within the Florida Keys. Remotely sensed vegetation data, along with ground reconnaissance in these areas, have shown that elevation plays a crucial role in the longevity of *Pinus elliottii*, the foundation species of pine rocklands. Despite an elevation range of only 3 m, habitats at higher elevations contained older, larger trees. Pine rocklands at lower elevations contained more dead and downed trees, and were more susceptible to invasion by salt tolerant tropical hardwood hammock species (Harley et al. 2015). These results provide a stark reminder that long before the onset of actual inundation, sea-level rise will influence the species composition of coastal habitats through changes in groundwater salinity, or the overwash of seawater in the aftermath of hurricanes (Saha et al. 2011). Even the highest elevation habitats in South Florida are, therefore, being affected by sea-level rise now, not in the future, and the devastation of the pine rocklands will occur sooner, and faster than we thought.

Recent estimates indicate that sea-level rise could exceed 1 m by 2100 (Donoghue 2011). The long-term implications of sea-level rise for South Florida's pine rocklands are not difficult to ascertain, and we are forced to confront the question: How do you move forward with research and conservation in a habitat that likely cannot be conserved? While plant species extinctions in the pine rocklands have, thus far, been avoided, it is likely that the degree of habitat fragmentation and degradation has reached a threshold whereby some 'extinction debt' has already been incurred (Hanski and Ovaskainen 2002). Put more clearly, the remaining habitat is no longer sufficient to support some species populations in the long term and, as such, those species represent the living dead.

The role of fire

Fire plays an important role in shaping the characteristics of many habitats across the world. In the southern United States, fire-maintained ecosystems such as grasslands, prairies, and pine forests cover 90% of the land (Frost 1995). Systems such as this have been shaped largely by naturally occurring fires, most started by lightning. Peninsular Florida has one of the highest incidences of lightning strikes in the world (Slapcinsky et al. 2010), and lightning-caused fires occur mostly during convective storm events in the dry season. Going back thousands of years, these fires have been augmented by human-ignited fires, often set at times outside of the lightning fire season (Snyder 1991).

Because fire has been a consistent presence in the Florida landscape, around 70% of the state's terrestrial plant communities are considered to be fire dependent or fire adapted (Florida Natural Areas Inventory 1990; Menges and Kohfeldt 1995). Despite this, land managers are often restricted from using prescribed burns over concerns that fire may further threaten imperiled species (Slapcinsky et al. 2010). In 1926 it was estimated that 75% of pine rockland habitats in South Florida were burned (totaling 5,260,921 ha). In contrast, the average annual burn area of pine rocklands between 1995 and 2003 was 1% (76,486 ha) (Florida Division of Forestry 2005).

Concerns over the impacts of fire on threatened plant species are simply not backed by the literature. Slapcinsky et al. (2010) monitored the post fire response of 18 threatened species in South Florida pyrogenic habitats, four of which were pine rockland species (*Chamaecrista lineata* var. *keyensis*, *Chamaesyce deltoidea* subsp. *serpyllum*, *Linum arenicola*, and *Rhynchospora floridensis*). For a number of variables measured (frequency of occurrence, population density, flowering, and recruitment), nine of the species showed a significant positive response to fire over 3–6 years of post-burn monitoring. The other nine species exhibited a neutral response, and no species responded negatively, or was unable to recover. Koptur (2006) also observed increased flowering in many pine rockland plants the year after fire, presumably due to increased insolation and nutrient input.

Monitoring of urban pine rockland fragments has only highlighted the negative effects of fire exclusion, including increasing tree density, excessive accumulation of leaf litter, and a concurrent reduction in the coverage of native herbs and grasses (Possley et al. 2014). Possley et al. (2008) monitored the effects of burn frequency on understory plants in 16 publicly-owned pine rockland preserves. Plots were burned 0, 1, or >1 times during the study period, and more frequently burned sites supported significantly more native plant species (Possley et al. 2008). These results provide clear evidence that regular prescribed fires are necessary for the protection of native plant species in Miami-Dade's pine rockland preserves.

In the lower Florida Keys, a history of frequent fires followed by recent fire suppression is evident. Harley et al. (2013) used burn scars and dendrochronology to assess the impacts of fire history, over the past 150 years, on Big Pine Key and No Name Key. At both sites, fires were shown to have occurred at intervals of roughly 6–9 years on average, usually late in the dry season. In recent years, however, the frequency of natural fires has decreased. On Big Pine Key, several prescribed burns, conducted since 2000, have resulted in widespread pine recruitment. On No Name Key, however, no prescribed burning has taken place. As a result, pine recruitment since 2000 is almost absent, and loss of habitat has become inevitable (Harley et al. 2013).

In addition to establishing the importance of fire in maintaining pine rockland habitats, several studies have addressed the issue of when, and how often, pine rockland sites should be burned. In the lower Keys dendrochronology work, as mentioned above, has established a historical fire return rate of 6–9 years (Harley et al. 2013). Similar rates of burning have been shown to be effective for the conservation of some of South Florida's rare plants. Liu et al. (2005) modeled fire response using simulations for *Chamaecrista keyensis*, and found that extinction and population decline probabilities were lowest at burn frequencies of 5–7 years. While ideal fire return periods may be difficult to pinpoint, simple and inexpensive monitoring procedures, such as measuring leaf litter depth (Barrios et al. 2016), or estimating hardwood density, can also be employed to inform burn schedules (Possley et al. 2014).

In practice, ideal fire return rates will likely vary across the pine rocklands biogeographical range. Indeed, maintaining some variability in burn schedules across that range is important, as setting an overly narrow definition of target-habitat characteristics can harm species that occur at the extremes of this definition (Hiers et al. 2016). For example the red-cockaded woodpecker, no longer present in Florida pine rocklands, nested in old-growth cavity bearing trees that are characteristic of less frequently burned sites (Hiers et al. 2016). The ideal timing of burns, however, appears more clear-cut. Due to the historic climate of the region, most pine rockland endemics likely evolved under a fire regime that included anthropogenic winter burns, or lightning-caused early summer burns. Winter (dry season) burns have been shown to be particularly advantageous for *C. keyensis*. Liu and Menges (2005) compared vital rates of *C. keyensis* over a period of 3 years after burns. Both summer and winter burns stimulated increased vegetative growth, but winter-burn treatments produced greater seedling recruitment than the summer-burn or control treatments. Subsequent simulations have also shown that winter burns generated lower extinction risks and population decline probabilities than summer burns (Liu et al. 2005).

In addition to preserving native plants, improved fire management can have positive impacts on many threatened animals. Possley et al. (2016) assessed the ability of urban pine rockland fragments to support populations of two endangered butterflies, the Bartram's scrub-hairstreak, *Strymon acis bartrami*, and the Florida leafwing, *Anaea troglodyta floridalis*. The larval host plant for both species is pineland croton, *Croton linearis*. Populations of *C. linearis* were significantly more abundant in habitat patches that had experienced fire within the past decade.

While the conservation outcomes of fire management have been very positive, some authors have expressed caution. Populations of breeding and wintering birds, for example, have not been boosted by prescribed fires, although they have not suffered (Lloyd and Slater 2012). Perhaps more worryingly, fires may pose risks for some native reptiles. Enge et al. (2004) showed that pine rockland fragments support a higher proportion of native to non-native reptile species than do adjacent human modified habitats in Miami-Dade County. The standing and fallen dead slash pines that provide refugia for a number of native reptiles, however, are often consumed by fires.

Other species that might be negatively affected by prescribed burns include some seed dispersers of pine rockland plants (Liu et al. 2004), the Florida Box turtle, *Terrapene carolina*, and the Gopher tortoise, *Gopherus polyphemus*. Although population-level effects of burning on box turtles have never been quantified, Platt et al. (2010) measured turtle mortality after seven prescribed burns covering an area of 27.4 ha. A total of 14 fire-killed turtles were found after four wet season burns, while no turtle mortality was observed during dry season burns when turtles are dormant. This study, therefore, provides further reason to limit prescribed burns to the winter months, when impacts on turtle populations would be minimized. Gopher tortoises have also been killed by fires in pine rocklands (personal observation). Such deaths are, however, more likely to occur as a result of wild fires, than prescribed burns that can be limited to periods of turtle dormancy. While the weight of literature highlights the conservation benefits of fire in pine rockland habitats, it remains important to consider any possible negative impacts. In addition, the value of variability in disturbance regimes should be considered when approaching the management of proximal pine rockland fragments (Hiers et al. 2016).

Current initiatives and room for optimism

Despite the many threats faced by pine rockland habitats, and the limitations imposed by their human dominated surroundings, a number of successful conservation initiatives have offered encouragement, at least in the short term. In 1990, an extraordinary property tax was approved by voters in Miami-Dade County, to fund the Environmentally Endangered Lands (EEL) Acquisition program. The program has funded the acquisition, protection, and maintenance of over 9000 ha of natural areas within the urban and agricultural matrix of the county (Alonso and Heinen 2011). A related endeavor called the EEL Covenant Program has been in effect in Miami-Dade County since 1979. It aims to protect endangered habitats occurring on private land by offering financial incentives to land owners (a property tax reduction of 90%). The 85 participating properties encompass 173 ha of pine rockland, hardwood hammock, and wetland habitat, and many areas have been shown to support rare and endangered species (Giannini and Heinen 2014).

In addition to the preservation and restoration of pine rockland sites, a number of organizations and citizen science programs have highlighted the importance of using native species within the urban landscape. The Connect to Protect Network, for example, is an initiative of Fairchild Tropical Botanic Garden (FTBG) with initial support from the U.S. Fish and Wildlife Service (Maschinski et al. 2009). Plants are propagated from seed collected from remaining pine rockland sites, then shared with citizens who create plantings (gardens, landscapes, roadsides) that serve to create stepping stones or corridors to allow dispersal of plants and animals. One such effort is a project at West Miami Community Middle School, called PRIDE (Pine Rocklands in Dade Environments). A middle school teacher, Lisset Perez-Munoz, received a Toyota Tapestry Award, and with help from FTBG and Florida International University, planned and created several pine rockland habitat plantings on school grounds. Students, parents, and other volunteers cleared turf, planted young trees and understory plants, and maintained the areas with weeding and watering. After five years, a pine rockland habitat had been created that attracted insects, birds, and other native animals (Fig. 2). Such initiatives can enhance connectivity between the remaining habitat patches, alleviating problems such as pollinator limitation and inbreeding.

As pine rocklands at lower elevations begin to exhibit the effects of sea-level rise, attention has turned towards the translocation of imperiled species (Maschinski et al. 2011). While species translocations involving plants have historically seen little success (Falk et al. 1996), and are often considered a last resort of conservation biology, such projects involving rare plants in South Florida have shown some promise. In 2008, several key populations of the federally endangered Crenulate leadplant, *Amorpha herbacea* var. *crenulata*, occurred on unprotected land that had been slated for development. Wendelberger et al. (2008) rescued *A. crenulata* plants from an unprotected site and transplanted seedlings as well as 1, 2, and 7 year old plants into a restored pine rockland habitat along the Florida turnpike that had previously been dominated by Brazilian pepper. After 40 months, overall *A. crenulata* survival was 71%. In addition, the restored site supported 104 native plant species, including 17 state listed species that had been naturally recruited from the remnant seed bank and nearby pine rockland habitat fragments. Despite the initial

Fig. 2 Before and after pictures of the PRIDE project created by students, teachers, and parents at West Miami Community Middle School. Pictures **a** and **b** show the same site in 2008 and 2014 respectively

success of this project, rapid succession within the site lead to a sharp drop in *A. crenulata* survival, and plants that did not die were ultimately re-rescued. A subsequent re-introduction of *A. crenulata* was carried out by FTBG, in which plants were transplanted into Martinez Preserve, a 54 acre site comprised of protected pine rocklands and transverse glade (Roncal et al. 2012). This second project has seen longer term success, in part due to continued adaptive management. Introduced plants were monitored over two years to assess which microhabitats supported the greatest plant growth and survival. Selected plants were then re-transplanted from the least successful microhabitats, to those with the highest survival rates.

While the reduction of pine rockland habitats to small urban fragments has undoubtedly affected many native species, monitoring programs within these patches have yielded some surprisingly encouraging results. Possley et al. (2008) monitored understory vascular plant presence and cover in 162 nested urban plots. While more frequently burned sites supported significantly more native plant species than infrequently burned sites, no overall reduction in rare plant species was observed over the 8 year study period. Even infrequently burned sites maintained high native species diversity (Possley et al. 2008). Additionally, while natural ecotones between pine rockland and hardwood hammock are close to non-existent, dedicated restoration areas have proved effective for the establishment and recruitment of ecotone adapted species like *Lantana canescens* (Possley et al. 2009).

The importance of fires in remnant pine rockland fragments is increasingly being recognized by land managers, and implemented where practical. In addition, recent studies have indicated that where fire is impractical, manual thinning of trees and shrubs can significantly boost native species cover, without promoting invasive species (Maschinski et al. 2005). It should be noted however that, while sometimes effective, the cost and labor intensity of manual thinning are often prohibitive (Possley et al. 2014), and the process should seldom be used as a fire surrogate, but rather a fire pre-treatment in habitats that are too overgrown to be restored by fire alone (Menges and Gordon 2010).

Despite the extent of disturbance suffered by pine rockland habitats over the last century, even small habitat fragments continue to support a surprising diversity of plants. Some small fragments in Miami-Dade County retain higher levels of endemism than more pristine habitats in Long Pine Key (Possley et al. 2014). These fragments are also some of the highest in elevation, offering some hope that mainland endemics such as *A. crenulata* might persist for many years to come. Preservation of the highest elevation pine rocklands is also a priority as they might provide refuge for species of the coastal Keys pine rocklands, as conditions change there, via natural or assisted migration.

A look to the future

According to the Intergovernmental Panel on Climate Change, global warming in this century may be enough to condemn future generations to 6 m of sea-level rise (Solomon et al. 2007). Such a rise would engulf the lower half of the state of Florida, and eliminate the entire biogeographical range of pine rockland habitats. With this in mind, it is clear that while current efforts to conserve rare species within these habitat are imperative, they represent only short term solutions. In the long term, managed relocation of species, to areas outside of their historic range, may provide the only viable option. Such relocations have the potential to be a successful for a small number of species (Maschinski et al. 2011), however, the success rate, and safety of such relocations is a subject of intense debate (Davidson and Simkanin 2008; Minteer and Collins 2010).

The ex situ preservation of species in zoos, botanical gardens, and seed banks will also become increasingly important (Guerrant et al. 2004), but these are not permanent solutions either. Even cryogenically frozen seeds have a finite shelf life (Walters 2004), and living collections cannot be maintained indefinitely, especially where suitable habitat for their eventual repatriation does not exist (Snyder et al. 1996).

While the long term fate of the pine rocklands looks bleak, they have shown surprising resilience in the face of multiple environmental and anthropogenic pressures. The Miami tiger beetle, for example, was thought to be extinct until 2007, when two small populations were observed in small habitat fragments surrounded by urban development (Brzoska et al. 2011). This resilience is, in part, due to the work of conservationists and invested citizens, and the successful initiatives described above. The continued support for this work is proof of the intrinsic value of the pine rocklands for plants, humans, and other animals, and will hopefully preserve this natural heritage for many years to come.

The fragmentation of pine rockland habitats, along with influences such as invasive species and the disruption of fire regimes, have made them ideal testing grounds for a number of important ecological questions. For example, how does habitat fragmentation effect plant species with different breeding systems (Liu and Koptur 2003; Cardel and Koptur 2010; Linares and Koptur 2010; Downing and Liu 2013)? And how might species invasions affect fire regimes (Stevens and Beckage 2009)?

The migration of tree lines in montane regions have often been used as an indicator of climate change, and to track the ability of plant communities to keep pace with environmental change (Körner 1998; Jobbágy and Jackson 2000; Rehm and Feeley 2015). Sea-level rise, along with the acute influence of elevation on community characteristics in South Florida, provides an opportunity to address similar questions, and work is already being done to track shifts in mangrove communities in the Florida Bay area (Wendelberger unpublished data). To use a popular climate change metaphor, this could just be the tip of the iceberg. In South Florida's fragmented landscape, plant communities are faced with shifting gradients of elevation, salinity, inundation, and nutrient availability. As such the region should serve as an epicenter for research on the ability of species and communities to adapt and respond to environmental change.

The mangrove islands of the Florida Keys provided a setting for MacArthur and Wilson to develop their theory of Island biogeography, which continues to inform the decision making of ecologists and conservationists throughout the World (MacArthur and Wilson 1967). Continued research in Florida's imperiled habitats, can further enhance the scientific legacy of the region, and contribute knowledge that may be of use long after the pine rocklands have sunk beneath the waves.

Pine rockland habitats stand on the unenviable front line of sea-level rise. As such, their fate will depend not only on ecologists, but on economists, engineers, landscape architects, and politicians. South Florida should continue to set the example that scientists and practitioners must work together, along with governments and communities, in order to prepare for the environmental challenges of the coming decades.

Acknowledgements We are thankful for Jennifer Possley for providing valuable feedback throughout the development of this manuscript. We are also grateful to her for help with the list of endemic species, and for providing us with photographs of the PRIDE project.

References

Alonso A, Heinen JT (2011) Miami dade county's environmentally endangered lands program: local efforts for a global cause. Nat Areas J 31(2):183–189

Barrios B, Koptur S (2011) Floral biology and breeding system of *Angadenia berteroi* (Apocynaceae): why do flowers of the pineland golden trumpet produce few fruits? Int J Plant Sci 172:378–385

Barrios B, Arellano G, Koptur S (2011) The effects of fire and fragmentation on occurrence and flowering of a rare perennial plant. Plant Ecol 212:1057–1067

Barrios B, Koptur S, Sah JP (2016) The effects of habitat fragmentation on the reproduction and abundance of *Angadenia berteroi*. J Plant Ecol. doi:10.1093/jpe/rtw024

Brzoska D, Knisley B, Slotten J (2011) Rediscovery of *Cicindela scabrosa* floridana Cartwright (Coleoptera: Cicindelidae) and its elevation to species level. Insecta Mundi 693:1–7

Cardel YJ, Koptur S (2010) Effects of florivory on the pollination of flowers: an experimental field study with a perennial plant. Int J Plant Sci 171:283–292

Correll DS, Correll HB (1982) Flora of the Bahama archipelago. Gantner Verlag, Vaduz

Davidson I, Simkanin C (2008) Skeptical of assisted colonization. Science 322:1048–1049

Donoghue JF (2011) Sea level history of the northern Gulf of Mexico coast and sea level rise scenarios for the near future. Clim Change 107:17

Downing JL, Liu H (2013) Self-Incompatibility in *Byrsonima lucida* (Malpighiaceae), a threatened pine rockland specialist. Castanea 78(2):95–102

Enge KM, Robson MS, Krysko KL (2004) Reptile surveys of pine rockland habitat in six Miami-Dade County parks. Fla Sci 67:194–204

Falk DA, Millar CI, Olwell M (eds) (1996) Restoring diversity: strategies for reintroduction of endangered plants. Island Press, Washington DC

Florida Division of Forestry (2005) Florida's forest resources plan. Setting the course for 2030. Present condition of Florida's forest resources: an assessment. Florida Division of Forestry, Tallahassee

Florida Natural Areas Inventory (1990) A guide to the natural communities of Florida. Florida Natural Areas Inventory and Florida Department of Natural Resources, Tallahassee

Florida Natural Areas Inventory (2010) A guide to the natural communities of Florida. Florida Natural Areas Inventory and Florida Department of Natural Resources, Tallahassee

Frost CC (1995) Pre settlement fire regimes in southeastern marshes, peatlands, and swamps. Proc Tall Timb Fire Ecol Conf 19:39–60

Gann GD, Bradley KA, Woodmansee SW (2009) Floristic inventory of South Florida database. Institute for Regional Conservation, Delray Beach

Geiger JH (2007) Conservation implications of the reproductive biology of the endangered vine *Ipomoea microdactyla* Griseb. (Convolvulaceae). PhD dissertation, Florida International University, Miami, FL. p. 116

Geiger JH, Pratt P, Koptur S (2010) Breeding System of *Ruellia succulenta* Small (Acanthaceae). Castanea 4:454–460

Geiger JH, Meerow AW, Lewis C, Oviedo R, Francisco-Ortega J (2014) Genetic diversity and conservation of *Ipomoea microdactyla* (Convolvulaceae): an endemic vine from the Bahamas, Cuba, and southeastern Florida. Plant Spec Biol 29:2–15

Giannini HC, Heinen JT (2014) Miami-dade county's environmentally endangered lands covenant program: creating protected areas on private lands via financial incentives. Nat Areas J 34(3):338–345

Guerrant EO Jr, Havens K, Maunder M (2004) Ex situ plant conservation: supporting species survival in the wild. Island Press, Washington

Hanski I, Ovaskainen O (2002) Extinction debt at extinction threshold. Conserv Biol 16(3):666–673

Harley GL, Grissino-Mayer HD, Horn SP (2013) Fire history and forest structure of an endangered subtropical ecosystem in the Florida Keys, USA. Int J Wildl Fire 22:394–404

Harley GL, Maxwell JT, Raber GT (2015) Elevation promotes long-term survival of *Pinus elliottii* var. *densa*, a foundation species of the endangered pine rockland ecosystem in the Florida Keys. Endanger Species Res 29(2):117–130

Hiers JK, Jackson ST, Hobbs RJ, Bernhardt ES, Valentine LE (2016) The precision problem in conservation and restoration. Trends Ecol Evol 31:820–830

Jobbágy EG, Jackson RB (2000) Global controls of forest line elevation in the Northern and Southern Hemispheres. Global Ecol Biogeog 9:253–268

Jones IM, Koptur S, Gallegos HR, Tardanico JP, Trainer PA, Pena JE (2016) Changing light conditions in pine rockland habitats may affect the intensity and outcome of ant-plant interactions. Biotropica 49:83–91

Koptur S (2006) The conservation of specialized and generalized pollination systems in subtropical ecosystems: a case study. In: Waser N, Ollerton J (eds) Plant–pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago

Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. Oecologia 115:445–459

Linares LJ, Koptur S (2010) Floral biology and breeding system of the crenulate leadplant, *Amorpha herbacea* var. *crenulata*, an endangered South Florida pine rockland endemic. Nat Areas J 30(2):138–147

Liu H, Koptur S (2003) Breeding system and pollination of a narrowly endemic herb of the lower Florida keys: impacts of the urban-wildland interface. Am J Bot 90(8):1180–1187

Liu H, Menges ES (2005) Winter fires promote greater vital rates in the Florida Keys than summer fires. Ecology 86:1483–1495

Liu H, Platt SG, Borg CK (2004) Seed dispersal by the Florida box turtle (Terrapene carolina bauri) in pine rockland forests of the lower Florida Keys, United States. Oecologia 138:539

Liu H, Menges ES, Quintana-Ascencio PF (2005) Population viability analyses of *Chamaecrista keyensis*: effects of fire season and frequency. Ecol Appl 15(1):210–221

Lloyd JD, Slater GL (2012) Fire history and the structure of pine-rockland bird assemblages. Nat Areas J 32(3):247–259

Loope LL, Dunevitz VL (1981) Impact of fire exclusion and invasion of *Schinus terebinthifolius* on limestone rockland pine forests of southeastern Florida. Report T-645. South Florida Research Center, Everglades National Park, Homestead, Florida

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton

Maschinski J, Possley J, Fellows MQN, Lane C, Muir A, Wendelberger K, Wright S, Thornton H (2005) Using thinning as a fire surrogate to improve native plant diversity in a South Florida pine rockland habitat. Restor Ecol 23(2):116–117

Maschinski J, Lewis S, Walters D, Possley J, Wright SJ, Roncal J, Lewis C (2009) The Connect to Protect Network: botanical gardens working to restore habitats and conserve rare species. Bot Gardens Conserv Int 6(1):6–9

Maschinski J, Ross MS, Liu H, O'Brien J, von Wettberg EJ, Haskins KE (2011) Sinking ships: conservation options for endemic taxa threatened by sea level rise. Clim Change 107:147–167

Menges ES, Gordon DR (2010) Should mechanical treatments and herbicides be used as fire surrogates to manage Florida's uplands? a review. Fla Sci 73:147–174

Menges ES, Kohfeldt N (1995) Life history strategies of Florida scrub plants in relation to fire. Bull Torrey Bot Club 122:282–297

Minteer BA, Collins JP (2010) Move it or lose it? The ecological ethics of relocating species under climate change. Ecol Appl 20:1801–1804

O'Brien JJ (1998) The distribution and habitat preferences of rare Galactia species (Fabaceae) and *Chamaesyse deltoidea* subspecies (Euphorbiaceae) native to southern Florida pine rockland. Nat Areas J 18:208–222

Platt SG, Liu H, Borg CK (2010) Fire ecology of the Florida boxturtle (*Terrapene carolina bauri*) in the pine rockland forests of the Lower Florida Keys. Nat Areas J 30:254–260

Possley J, Maschinski J (2006) Competitive effects of the invasive grass *Rhynchelytrum repens* (Willd) on pine rockland vegetation. Nat Areas J 26:391–395

Possley J, Woodmansee SW, Maschinski J (2008) Patterns of plant composition in fragments of globally imperiled pine rockland forest: effects of soil type, recent fire frequency, and fragment size. Nat Areas J 28:379–394

Possley J, Maschinski J, Rodriguez C, Dozier JG (2009) Alternatives for reintroducing a rare ecotone species: manually thinned forest edge versus restored habitat remnant. Restor Ecol 17:668–677

Possley J, Maschinski J, Maguire J, Guerra C (2014) Vegetation monitoring to guide management decisions in Miami's urban pine rockland preserves. Nat Areas J 34:154–165

Possley J, Hodges S, Magnaghi E, Maschinski J (2016) Distribution of *Croton linearis* in miami-dade county preserves with potential for supporting the federally endangered butterflies *Strymon acis bartrami* and *Anaea troglodyta floridalis*. Nat Areas J 36(1):81–87

Rehm EM, Feeley KJ (2015) The inability of tropical cloud forest species to invade grasslands above treeline during climate change: potential explanations and consequences. Ecography 38:1167–1175

Roncal J, Maschinski J, Schaffer B, Gutierrez SM, Walters D (2012) Testing appropriate habitat outside of historic range: the case of *Amorpha herbacea* var. *crenulata* (Fabaceae). J Nature Conserv 20:109–116

Saha AK, Saha S, Sadle J, Jiang J, Ross MS, Price RM, Sternberg L, Wendelberger K (2011) Sea level rise and South Florida coastal forests. Clim Change 107(1):81–108

Slapcinsky JL, Gordon DR, Menges ES (2010) Responses of rare plant species to fire in Florida's pyrogenic communities. Nat Areas J 30(1):4–19

Snyder JR (1991) Fire regimes in subtropical South Florida. Proc Tall Timb Fire Ecol Conf 17:303–319

Snyder JR, Herndon A, Robertson WB Jr (1990) South Florida rockland. In: Myers RL, Ewel JJ (eds) Ecosystems of Florida. University of Central Florida Press, Orlando, pp 230–280

Snyder NFR, Derrickson SR, Beissinger SR (1996) Limitations of captive breeding in endangered species recovery. Conserv Biol 10:338–348

Solomon S (ed) (2007) Climate change 2007: The physical science basis. contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Stevens JT, Beckage B (2009) Fire feedbacks facilitate invasion of pine savannas by Brazilian pepper (*Schinus terebinthifolius*). New Phytol 184:365–375

Walters C (2004) Principles for preserving germplasm in gene banks. In: Guerrant EO Jr, Havens K, Maunder M (eds) Ex situ plant conservation: supporting species survival in the wild. Island Press, Washington, pp 113–138

Wendelberger KS, Fellows MQN, Maschinski J (2008) Rescue and restoration: experimental translocation of *Amorpha herbacea* Walter var. crenulata (Rybd.) Isley into a novel urban habitat. Restorat Ecol 16:542–552