BioOne COMPLETE

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Abstract. Southern Florida's Everglades are at the front line of potential negative effects on aquatic ecosystems from climate change and associated sea-level rise. A diversity of aquatic habitats supports a rich assemblage of aquatic and terrestrial wildlife, including 36 vertebrates and 26 plant species federally listed as endangered, threatened, or candidate species. Anticipated climate-change trends for southern Florida include increased weather uncertainty with more droughts, higher temperatures, and an increased number of more intense storms. Hydrologic regimes, temperature, and CO_2 have been strongly correlated with plant community structure, coral and fish abundance and diversity, and higher trophic-level responses. Higher levels of variability in extreme climatic events, such as droughts, have the potential to destabilize aquatic communities. Sea-level rise is expected to be 0.8 to 2 m over the next century, a serious problem in a landscape that rises only 5 cm/km from Florida Bay inland. Wading birds and other wildlife species dependent on fresh water are likely to decline because of salt-water overwash and inundation. In addition to causing habitat loss, saltwater inundation of the peat substrate of Everglades freshwater wetlands may increase C emissions from sequestered C released as peat is destroyed and freshwater plant communities die. Identification of those species and habitats most at risk and ways to increase habitat and landscape resilience to large-scale environmental change will be critical for maintaining a diverse and productive Everglades.

Key words: Climate change, sea level rise, Everglades, ecology, management.

Southern Florida's Everglades are a wet grassland ecosystem in a broad depression filled with freshwater peat and, in some locations, calcitic mud deposits. Water flows slowly down a gentle gradient as sheetflow—a shallow, continuous expanse of water moving broadly across the wetland landscape, not restricted to channels or streambeds. Although >50% of the spatial extent of the Everglades has been lost to development and agriculture, the remaining Ever-

glades extend from the Arthur R. Marshall Loxahatchee National Wildlife Refuge south to Everglades National Park (ENP) (Fig. 1). The Everglades landscape rises gradually from Florida Bay inland at a gradient of ~5 cm/km. The depression is bounded by the limestone and quartz sand Atlantic Coastal Ridge to the east and the Big Cypress limestone ridge to the west. On the south and southwest, extensive natural berms in coastal areas protect the Everglades depression from saline intrusion. These berms are created by sediment deposition during storm surges and retention by mangrove prop roots.

The Everglades is an internationally recognized wetland and wilderness area. Included in this area

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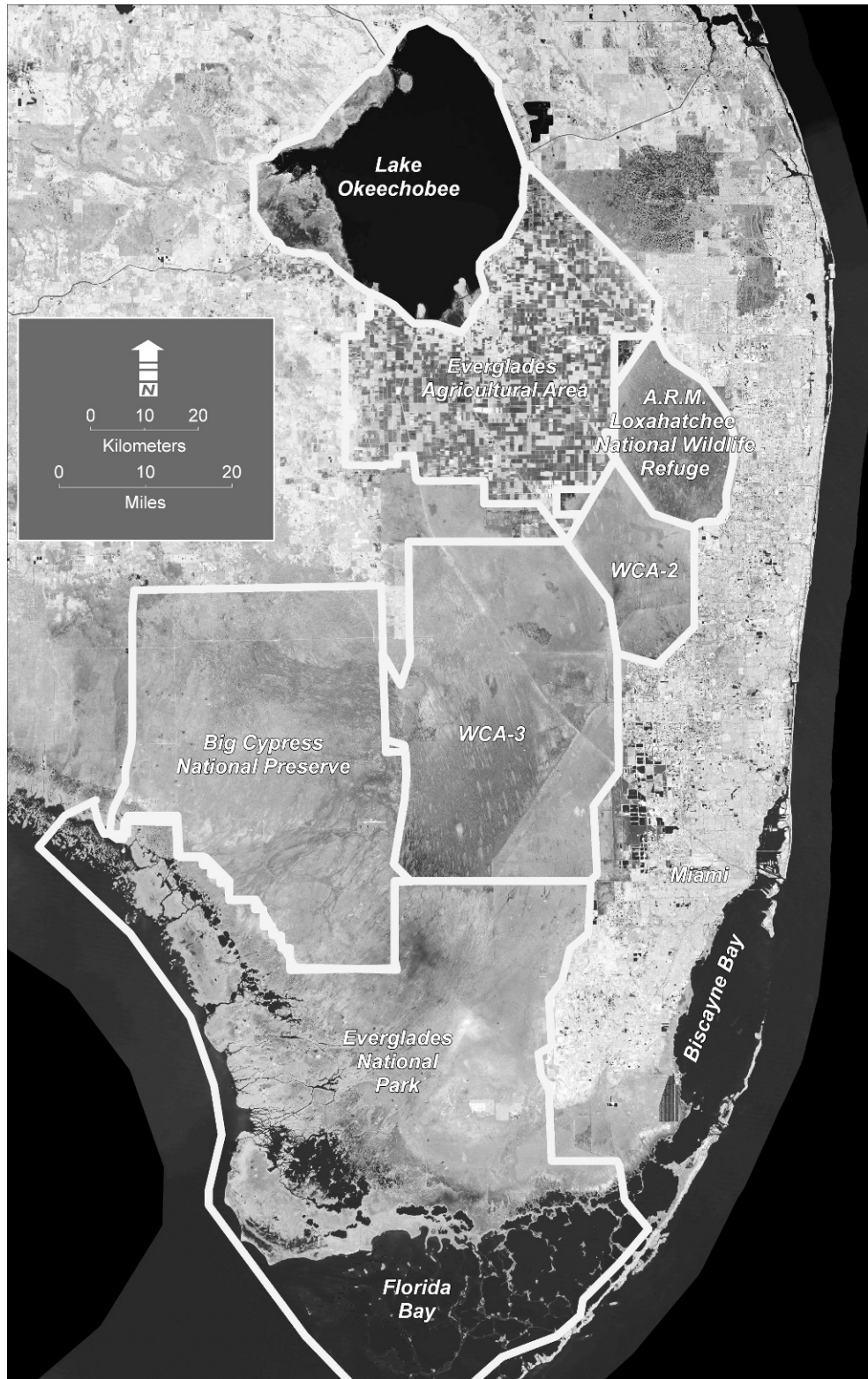
FIG. 1.   Physiographic map of southern Florida with conservation land boundaries and place names.

is the largest congressionally designated wilderness area east of the Rocky Mountains. Everglades National Park is a Wetland of International Importance under the Ramsar Convention of 1987, a United Nations Education, Scientific, and Cultural Organization (UNESCO) International Biosphere Reserve (1976), and a UNESCO World Heritage Site (1979). The unique position of the Everglades ecosystem at the interface of the temperate and subtropical regions and of fresh and brackish water creates a unique complex of habitats. These habitats include the largest sawgrass (*Cladium jamaicense*) freshwater prairies and mangrove ecosystems in North America, tree islands, ridge-and-slough habitat, and significant foraging and breeding grounds for wading birds. The Everglades also are habitat for a high diversity of threatened, endangered, candidate, and endemic species (IUCN 1979).

In this paper, we briefly examine known or anticipated effects of climate change on Everglades aquatic ecosystems and outline management options for aiding species resilience and adaptability to change. The larger Everglades landscape includes the estuarine habitats of Florida Bay and southwestern Florida and Biscayne Bay to the southeast. Near shore, and protecting Florida Bay, is the 3rd-largest living coral reef tract in the world (behind Australia and Belize). These adjacent estuarine and marine systems, although generally beyond the scope of our paper, are considered here in their context with the freshwater ecosystem. Climate-change effects on coral reefs are reviewed extensively elsewhere (e.g., Knowlton 2001, Orr et al. 2005, Hoegh-Guldberg et al. 2007, Munday et al. 2009).

The synthesis of literature in our review reinforces significant uncertainties about the extent of climate change, the extent and direction of climate-change effects for most natural communities, and the need for management to prepare for surprises. The literature addresses climate-related responses, and in some cases, adaptability of some species mostly to changes from single causes. Syntheses of multiple interactions and environmental variables that may have a high degree of variability and interaction are rare. The ecological consequences of climate change will most certainly result in unanticipated community responses, possibly as new species compositions not seen previously in southern Florida (e.g., Burkett et al. 2005). Anticipated southern Florida and Everglades-specific physical and biological modeling studies are the most likely source of information on multiple-variable interactions in the near future.

South Florida Climate-Change and Sea-Level Projections

The Intergovernmental Panel on Climate Change (IPCC), established by the World Meteorological Organization and by the United Nations Environment Programme, examined trends and variability among climate-simulation models from 18 modeling centers around the world (IPCC 2007). They estimated changes in temperature, precipitation, storms, ocean circulation, and sea level that are expected to occur over the next 100 y primarily as a result of rising atmospheric CO_2 and methane. Warming trends are being observed in southern Florida (Soule 2005), and estimates based on simulations of greenhouse-gas emission scenarios indicate that by 2100, temperatures in southern Florida will be 2 to 2.5°C higher than the 2000 annual average if emissions are moderate (IPCC 2007) or 5.5°C higher if emissions are higher (Stanton and Ackerman 2007). Most simulations indicate shifts in ocean circulation patterns (particularly the North Atlantic Oscillation [NAO]) that are associated with less precipitation in the Caribbean. The combined effects of even modest increases in temperatures and reductions in rainfall during the wet season (May–October) could be extended droughts and uncertain recharge of Everglades wetland ecosystems that may produce dramatic changes to the Everglades. Allan and Soden (2008) used satellite observations of precipitation and El Niño/La Niña events to suggest that tropical precipitation extremes of wet and dry are likely to be greater than predicted in the current models. Much uncertainty exists about predicted changes in the frequency and intensity of tropical storms and hurricanes (e.g., Oouchi et al. 2006, Vecchi et al. 2008, Wang and Lee 2008), but existing models consistently project a decrease in the globally averaged frequency of tropical cyclones, but with a substantial shift toward more intense cyclones and increases of ~20% in the precipitation rate within 100 km of storm centers (Knutson et al. 2010). Although annual average precipitation may change little because increased droughts will offset increased storms, these projected trends raise a concern because ecosystems respond to increased weather variability and extreme events, not to average conditions.

Salt water expands when heated. Simulated changes in ocean temperatures and salinity and projections of Antarctic and Greenland ice-mass loss from land shelves to the oceans can be used to forecast sea-level changes. Rahmstorf (2007) predicted a sea-level rise in 2100 of 0.5 to 1.4 m above the 1990 level but stated that these projections might be conservative because of uncertainties associated with ice-shelf modeling.

Pfeffer et al. (2008) considered the physical constraints on ice moving from land basins to the ocean and projected a range in sea-level rise of 0.8 to 2.0 m. However, they regarded the lower end of the range as more plausible than the upper end. These projections are global averages, but sea level will not rise uniformly. Sea level varies across the globe as a result of ocean circulation patterns, regional gravitation differences, deformation of the Earth's surface, and shifts in its rotation axis in response to ongoing changes in loading by glaciers and ice sheets, atmospheric pressure changes, and regional salinity changes (IPCC 2007, Mitrovica et al. 2009, Gomez et al. 2010). Models of West Antarctica ice-sheet melting suggest that sea level along US coastlines will be 25 to 30% higher than the global mean (Bamber et al. 2009, Gomez et al. 2010). Southern Florida is especially vulnerable given the low relief and gradual rise in elevation throughout the system. In general, species in southern Florida that are at the edge of their physiological range, that depend on environmental cues to synchronize life-history events, or that have limited dispersal capacity will be the most affected.

General Ecosystem Responses

A summary of potential ecological consequences of climate change for the freshwater Everglades and adjacent ecosystems is presented in Table 1. Both sea-level rise and a change in rainfall are likely to affect coastal and inland wetland communities through increased drought and fire, saltwater intrusion, loss of freshwater wetlands, soil subsidence, damage through intense storms, and changes in freshwater flow in Shark River Slough and Florida Bay. Higher surface-water temperatures, driven by a warming atmosphere, will result in decreased dissolved O_2 concentration and increased toxicity of pollutants. Rising CO_2 concentrations will result in lower pH with unknown effects on marine species. As species' ranges shift, community compositions will change, affecting native community interactions, distributions of exotic species, and the commercial fishing industry.

Whether species can adapt fast enough to survive a changing climate depends on the rate of environmental change and species' sensitivities to change (Fig. 2). Species that use environmental cues to synchronize life-history events may experience mismatches between cues and actual conditions. Uneven shifts in phenology have been illustrated for a variety of terrestrial species, such as caterpillars and their predators. These uneven shifts indicate that prey and predator might be responding to different environmental cues (Visser and Both 2005). Shifts in

phenology of marine pelagic communities also show mismatches between successive trophic levels (Visser and Both 2005). Similar patterns could occur in freshwater systems. Species are likely to respond in highly variable ways to similar climate-change trends because they differ in physiological tolerances, life-history strategies, population extinction and colonization likelihood, and dispersal abilities (Parmesan 2006). Tropical systems like the Everglades have been little studied. However, similar mismatched phenological changes are likely to occur there. Several butterfly species that occur in ENP are dependent on specific host plants that tie them to specific habitats. Both butterflies and hosts are sensitive to critical ranges of temperature, humidity, and light levels (Murphy et al. 1990). For example, the Florida leafwing (*Anaea troglodyte floridalis*) is a pine rocklands specialist that feeds on the pineland croton (*Croton linearis*). Bartram's hairstreak (*Strymon acis bartrami*) is a similar specialist in the larval stage, but it has a greater chance of survival should plant communities shift because it has a wider range of plant nectar sources (S. Perry, ENP, personal communication).

In addition, habitat might simply be lost through inundation or conversion to other habitat types (vegetation succession, fresh marsh to brackish, invasion of exotics) or damaged through fire or flooding. Plant communities will experience changes in phenology, possible range shifts, and altered hydropatterns caused by temperature increases. Negative effects on coral and coral reefs already are apparent and will continue. These effects include bleaching, disease, and coral death from increased temperature, sea-level rise, and decreases in pH. The unique habitats on the Florida Keys, the Dry Tortugas, and Ten Thousand Islands may well be lost to sea-level rise and through more intense storm events.

Vegetation Communities

Black Mangrove (*Avicennia germinans*), White Mangrove (*Laguncularia racemosa*), Red Mangrove (*Rhizophora mangle*), and buttonwood (*Conocarpus erectus*) communities line the western and southern coasts of most of ENP. Mangrove provides habitat and forms the base of the detritivore food web for 217 species of fish, 18 to 24 species of amphibians and reptiles, 180 species of birds, and 21 species of mammals (Odum et al. 1982, Meshaka et al. 2000). Increases in temperature and direct effects of increased CO_2 concentrations are expected to increase mangrove growth and change the timing of flowering and fruiting. However, decreased precipitation and rising sea level could lead to increased salinities, resulting in decreased

TABLE 1. Summary of potential effects of global climate change on Everglades and southern Florida biodiversity. Groups affected in each event may experience ≥ 1 of the possible effects.

Projected event	Possible effect	Taxa/group affected
Increased temperature	Changing phenology of vegetation and plant communities	Plant communities including graminoids
	Loss of species synchronization	Cyanobacteria
	Increased surface-water temperatures with decreased concentration of dissolved O_2 and increased toxicity of pollutants	Fish, coral, invertebrate herbivores
	Range shifts of fish and other vertebrates	Aquatic communities
	CO_2 concentrations reduce pH value	Amphibians
	Changing hydro-pattern	Insectivores, migrants—birds and butterflies, pollinators, seed-eaters, invasive species, species on the edge of their range (either northern or southern)
Weather uncertainty, more extreme storm events	Altered fire patterns and dynamics	Vegetation communities
	Increased wind strength and precipitation during storms	Marshes and wetlands
	More storms and higher intensity storms	Mangroves
	Droughts	Aquatic fauna
	Soil subsidence or accretion	Amphibians
	Disconnect between breeding patterns of birds and hydrologic events	Florida Bay species, wading birds, species that time nesting/breeding with hydrologic cycles, most wildlife species, colonial waterbirds
Precipitation changes	Decreased rainfall during dry season	Amphibians
	Decreased rainfall during wet season	Fish, especially small species
	Loss of dry season refugia	Plants and plant communities
Sea-level rise	Saltwater intrusion	Plant communities, especially mangrove, freshwater marsh, saltwater marsh, etc.
	Increased sea level in current coastal areas – loss of protective berms	Coastal tidal flats
	Increased inundation of Florida Keys and Ten Thousand Islands	Rare or endemic coastal plant species, sea turtles
	Habitat loss in low-lying areas in general, including coastal nurseries for important marine fish species	Wading birds, vertebrate species of the Florida Keys and other low-lying areas
Shift to more positive North Atlantic Oscillation	Extended droughts	Wetland vegetation communities
	Increased evaporation	Wetland-dependent wildlife species
	Reduction of recharge in Everglades wetlands and aquifers	General plant and wildlife impacts from changes in fire regime and droughts
	Changes in fire patterns	
Increased atmospheric CO_2 concentration	Reduced pH in oceanic waters	Coral, fishes
	Photosynthetic pathways	C3 vegetation

productivity and seedling survival and a net loss of peat as anaerobic decomposition increases (Snedaker 1995). At southwestern sites, tropical-storm surges have caused mangrove mortality and decreased ground elevation (Smith et al. 2009). These results suggest that mangroves might not recover from the effects of rapid sea-level rise. Presently, Everglades freshwater marshes are protected from saltwater intrusion by natural marl berms and extensive forests of mangrove and buttonwood. Rapid sea-level rise probably would overtop the natural berms like those in Cape Sable (Wanless et al. 1997), and freshwater wetlands would quickly be lost. Everglades National Park and the Institute for Regional Conservation have identified 27 rare plant species, some of which are critically imperiled, that are vulnerable to sea-level rise primarily within these mangrove and buttonwood forests (Gann et al. 2002, J. Sadle, ENP, personal communication).

Inland from the mangrove zone, Everglades wetland grass and sedge communities might change broadly in response to changing temperature, precip-
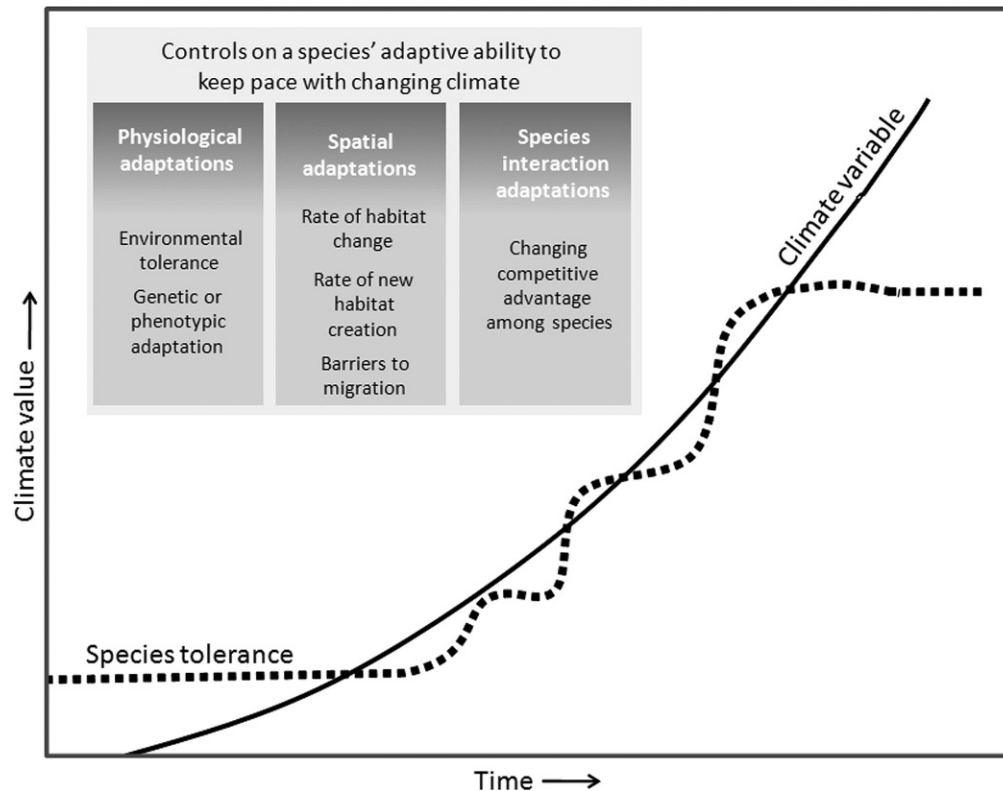
FIG. 2. Adaptations to a changing climate might be constrained by how quickly the environment is changing. The curves in this chart illustrate the concept of evolutionary adaptation to changing environmental conditions. The dotted line represents a species for which environmental tolerances initially are higher than climate conditions. As the climate variable (e.g., maximum annual temperatures, salinity, drought frequency) increases and crosses the species' tolerance threshold, the species is able to adapt over time to tolerate higher values of the climate variable. However, at some point the species is no longer able to maintain adaptations to changing conditions.

itation, drought, and floods. Plants will respond in different ways to the interacting effects of CO_2, water availability, nutrients, and temperature (Jifon and Wolfe 2005). Increased atmospheric CO_2 associated with climate change can alter seed germination (Thurig et al. 2003, Mohan et al. 2004), leaf development (Ainsworth et al. 2006), time of flowering (Springer and Ward 2007), mortality (Rae et al. 2006), and salinity tolerance for some wetland species (Rozema et al. 1991). Differential responses among species with different photosynthetic pathways increase the potential for alterations of community composition with climate change (Springer and Ward 2007). *Typha* spp., *Scirpus* spp., *Cladium jamaicense*, *Carex* spp., and *Phragmites australis* in Everglades marshes and prairies use the C3 photosynthetic pathway. *Schizachyrium rhizomatum* and *Paspalum monostachia* use the C4 photosynthetic pathway. Some genera, such as *Eleocharis* and *Rhynchospora*, can be either C3 or C4 depending on the species (Bruhl 1993, 1995, Vorster 1996, Soros and Bruhl 2000). Graminoids using the C3 photosynthetic pathway assimilate CO_2

at a greater rate than those using the C4 pathway (Kimbell 1983). However, species using the C4 pathway have a physiological advantage in hot environments (Bjorkman et al. 1974) and during droughts (Raven 2001). Long-term responses to elevated atmospheric CO_2 concentration also might differ substantially from short-term responses (Soussana and Lüscher 2007).

Many tropical and subtropical woody species indigenous to southern Florida might expand their ranges under climate-warming scenarios. Alternatively, increased periods of drought could restrict many species. Woody plant communities including tree islands, coastal hardwood hammocks, and pine rocklands are unique to the Everglades and are critical habitat for diverse wildlife species ranging from mammals seeking shelter to butterflies seeking nectar.

Peatlands and C Sequestration

Peat soils throughout the world store large amounts of C removed from the atmosphere. They are among

the largest organic C stores on Earth and hold up to 24% of global C (Jauhiainen et al. 2008, Vicca et al. 2009). Soil respiration, which includes CO_2 production by root and soil organisms and oxidation of C-containing materials, such as peat soil, contributes CO_2 to the atmosphere (Raich and Schlesinger 1992). The rate of soil CO_2 release to the atmosphere depends on the strength of the gradient between soil and atmosphere as well as soil pore size, air temperature, and wind speed (Raich and Schlesinger 1992). As a result of these factors, luxuriant plant growth, and ideal environmental conditions for decomposers, the highest soil respiration rates are found in the tropics (Schlesinger and Andrews 2000). Warm temperatures increase soil respiration, but mineral soils show acclimation leading to decreasing CO_2 production over time. Organic soils, such as peats, store enormous amounts of labile C and are a large source of released C. Increased CO_2 release from such soils consequent to warming might not reach a plateau and potentially could exhibit a ''sustained positive feedback to global warming'' (Vicca et al. 2009, p. 2014). No clear predictions exist for C sequestration and release from tropical peat soils (Schlesinger and Andrews 2000, Davidson and Janssens 2006). In addition, destruction of peat and freshwater plant communities from sea-level rise might increase CO_2 emissions (Henman and Poulter 2008).

Fishes

In addition to raising water temperatures, climate change is likely to alter the biogeochemistry and hydrologic regime of the freshwater Everglades. Decreased dissolved O_2 and increased toxicity of pollutants are likely to occur as a result of these changes (Loftus et al. 1990, Ficke et al. 2007). Furthermore, marine and estuarine habitats are likely to experience acidification and changes in salinity caused by changing rainfall and increased evaporation rates. In addition to these uniquely aquatic challenges, species range shifts probably will occur and alter community compositions. Many species might be unable to migrate or acclimate to temperature and other changes to the environment and, thus, will have to evolve, acclimate, or face local extinctions. Effects of increased water temperature already are being observed in freshwater and marine systems, especially at higher latitudes, with shifts in distribution and increases in invasive species and pathogens (Beaugrand et al. 2002, Brander 2007).

Fishing pressure, particularly in estuarine and marine areas adjacent to the Everglades, might interact with other climate-related stressors. Fishing is selective and changes distribution, age, and size structure of populations (Berkeley et al. 2004, Ottersen et al. 2006, Brander 2007). The Everglades system is expected to experience extended and more severe droughts with high potential for negative consequences to freshwater fishes. In 1-dimensional computer models simulating communities of small fish in the Everglades, hydroperiods <~6 mo result in negligible fish biomass (DeAngelis et al. 2005). Biomass increases with longer hydroperiods (Trexler et al. 2002). Karst solution holes provide critical refugia for small freshwater fishes during drydowns when groundwater is <46 cm below the ground surface (Kobza et al. 2004), but deeper solution holes might be dominated by predatory species (often nonnative), which would make survival difficult for native species, which are often small. The persistence of native fish populations in the Everglades depends on maintaining sites with longer hydroperiods and adequate refugia.

Amphibians and Reptiles

Amphibians appear to be among the most sensitive species to changes in temperature and precipitation (Corn 2005). Results of meta-analyses already have confirmed shifts in breeding for some species (Parmesan 2007). The matrix of upland hammocks and freshwater habitats characteristic of the Everglades are necessary for the life cycles of a diverse group of amphibians, including toads, treefrogs, frogs, sirens, newts, and amphiuma (Meshaka et al. 2000). Changes in temperature can adversely affect disease resistance because the amphibian immune system is highly temperature-dependent (Raffel et al. 2006). An example is the differing temperature-dependent interactions between the infectious *Batrachochytrium dendrobatidis* (a chytrid fungus that causes the amphibian disease chytridiomycosis) and various amphibian hosts (Woodhams et al. 2007). Increases in temperature and reduced precipitation in southern Florida also would reduce soil moisture, which would affect prey species and amphibian habitat (Corn 2005).

More than 50 kinds of reptiles inhabit ENP (Meshaka et al. 2000). Although related, the American alligator (*Alligator mississippiensis*) and American crocodile (*Crocodylus acutus*) are expected to respond differently to climate change. Alligators in the Everglades are at the southern end of their tolerance range and grow more slowly, take longer to reach sexual maturity, and have higher metabolic costs than alligators in other areas (Mazzotti and Brandt 1997). Temperature increases might decrease their physio-

logical well-being, but changes in hydropattern, habitat, and prey availability are likely to be just as, or more, important. Prolonged droughts that decrease aquatic faunal densities and biomass (Loftus et al. 1990) might further exaggerate the low growth and reproductive rates of Everglades alligator populations. In contrast, American crocodiles in southern Florida are at the northern end of their range. Temperature increases are not expected to be problematic for this subpopulation (Mazzotti and Cherkiss 2003). However, indirect adverse effects of global climate change on this species might result from potential rapid to complete loss of existing coastal wetland and shore habitat (Wanless et al. 1997) and increased salinities (Mazzotti and Cherkiss 2003). Habitat loss from saltwater transgression of coastal berms might be alleviated if nesting habitat shifts landward into the Everglades and berms suitable for nesting remain next to water with low salinity.

Sex in crocodilians, such as the American alligator and American crocodile, and other reptiles including sea turtles and mangrove terrapin (*Malaclemys terrapin*) is determined by temperature during incubation of the embryo (Ferguson and Joanen 1982, Janzen 1994, Lang and Andrews 1994), and patterns vary between species. Loss of sea-turtle nesting habitat is likely where beaches are inundated by rising seas and landward shifts of eroding beaches are blocked by hard structures and developed land uses (Klein and Nicholls 1999). Hobe Sound National Wildlife Refuge and Juno Beach on Florida's east coast have beaches with high densities of nesting sea turtles at risk from extensive coastal-zone development (Engeman et al. 2002, Stewart and Wyneken 2004). In the Ten Thousand Islands area of southwestern Florida, success of loggerhead sea turtle (*Caretta caretta*) hatchlings decreases as inundations, sand water content, and sand water salinity increase on low-relief mangrove islands (Foley et al. 2006).

Birds

Aquatic invertebrates and vertebrates provide food to support a large and varied avian population in the area. Timing and extent of flooding; droughts; increase or decrease in nutrients; integrity of freshwater, estuarine, and saline systems; disturbance from storms; and loss of habitat all can affect important prey species. Both resident and migratory wading birds and shorebirds are expected to lose habitat as sea levels rise, destroying coastal marshes and mangrove habitat. Breeding birds depend on hydrologic events during their reproductive cycle, which is timed so that suitable water conditions are available for nesting and for feeding (Frederick and Collopy 1989a). Successful breeding is tied especially to water-recession rates that occur during the dry season. As water recedes, smaller areas of wetlands and shallow water serve as refugia for fish. These areas of prey concentration provide important food resources for nesting birds that must feed young and for foraging fledglings. Sudden reversals can cause widespread nest abandonment in wading birds (Frederick and Collopy 1989b). Snail Kites (*Rostrhamus sociabilis*) are dependent on regular and moderate flooding and drying events to maintain their primary prey source, the Apple Snail (*Pomacea paludosa*). Snail Kites also depend on flooded sites for nest protection and experience increased predation and nest abandonment if water recedes from under nests (Sykes et al. 1995). Roseate Spoonbills (*Platalea ajaja*) depend on demersal fish populations in freshwater wetlands. Spoonbills already are experiencing food-resource stress from water management changes upstream from Florida Bay (Lorenz and Serafy 2006), and sea-level rise probably will exacerbate this problem. Availability of roosting areas adjacent to standing water and shallows in which fledglings can feed also is important (Dumas 2000). Wetland-dependent birds are likely to experience reproductive failure, population declines, colony abandonment, and local extinctions if aquatic prey species are negatively affected by climate change. Range shifts are possible only if suitable habitat exists elsewhere and is not occupied. For specialists like the Snail Kite, such range shifts are unlikely.

Evolutionary Adaptation

Adaptation can occur through genetic change or through phenotypic plasticity. Genetic variation in critical traits and localized evolutionary responses (Conover and Schultz 1995, Stockwell et al. 2003, Pelletier et al. 2007) allow some species or populations to mitigate effects of climate change by adapting to new conditions. Little information is available to inform estimates of whether species evolution is occurring at a rate sufficient to respond to climate change (Visser 2008). We present 3 examples from outside the Everglades to illustrate potential rates of genetic change in response to environmental change. Guppies (*Poecilia reticulata*) are present in southern Florida waters but are nonindigenous. However, they are similar to the ubiquitous mosquitofish (*Gambusia holbrooki*) (J. Trexler, Florida International University, personal communication). Guppies that were transplanted from low- to high-predator environments exhibited genetic change in life-history traits within

11 y—a rate much higher than predicted based on paleontological records but similar to rates during artificial-selection experiments (Reznick et al. 1997). Bluegills (*Lepomis macrochirus*) exposed to high temperatures in heated effluent water from a South Carolina nuclear reactor exhibited high thermal tolerance thought to be genetically based (Holland et al. 1974). The period of exposure to high temperatures was 13 y. The pitcher plant mosquito *Wyeomyia smithii* (in a continent-wide study including northern Florida) showed differentiation in a genetically controlled photoperiodic response (Bradshaw and Holzapfel 2001). Onset and maintenance of diapause in this mosquito is mediated by photoperiod, genetically based, and highly heritable. Bradshaw and Holzapfel (2001) concluded that *W. smithii* had a genetic response to changing seasonality and that the change occurred over a time period as short as 5 y.

However, for some species, time lags and limits on genetic variation are potential constraints to evolutionary response (Holt 1999, Schiedek et al. 2007). The endangered Florida Panther (*Puma concolor coryi*) is an example of a species that might have limited ability to adapt if climate change further restricts its environment. Hedrick et al. (2008) found microsatellite heterozygosity of contemporary Florida panthers that was only $0.3\times$ levels measured in museum samples from the 1890s. The estimated diversities in mitochondrial deoxyribonucleic acid (DNA) of the museum and contemporary Florida panther samples were 0.600 and 0.000, respectively.

Some species will not be able to respond quickly enough to changing conditions (Davis et al. 2005). Others might initially respond rapidly to changes but with a subsequent decay in the rate of evolution (Kinnison and Hendry 2001, Bradshaw and Holzapfel 2006) as habitat continues to change in response to climate (Fig. 2). In a broad study of adaptive evolution, Reznick and Ghalambor (2001) determined that a common feature of successful evolutionary response to directional selection is the presence of at least a short-term opportunity for population growth. This opportunity is important because directional selection also is likely to create the potential for population decline or extirpation. Bradshaw and Holzapfel (2008) did not observe a genetic shift in thermal optima or tolerance and suggested that the primary climate-change parameters that would lead to genetic change are seasonality and corresponding day-length cues. However, seasonality is likely to be less important in southern Florida than elsewhere because seasonal changes are more strongly associated with changes in precipitation than in temperature or day length. Instead, thermal tolerance and a shift

from fresh to salt water are more likely to be critical. Examination of the Pleistocene fossil record (glaciations and subsequent cooling) suggests that major evolution did not occur at the species level but, rather, that the distributions of existing species shifted. Thus, species tracked the changing climate rather than remaining stationary and adapting (Parmesan 2006). Evidence is lacking that species are capable of evolving to change their absolute climate tolerance. Thus, evolutionary change might be insufficient to prevent species extinctions (Parmesan 2006), especially where movement to more favorable climatic conditions is impossible.

Adaptive Conservation Strategies

Present and future climate-change scenarios in conjunction with irreversible human alteration of the landscape lead to the conclusion that restoration efforts will not return the Everglades to its past condition. The Department of Interior Task Force on Climate Change (DOI 2009) and the National Research Council (NRC 2008) agree that historic conditions are no longer adequate as the sole basis for decisions regarding future resource management. Multiple effects from climate change, sea-level rise, and human changes to the landscape will reduce land extent and resources available for natural systems, further fragment the landscape, and interact to produce ecological effects that cannot be fully predicted. Traditional management practices on public lands are based on the assumption of stable climatic conditions. Even if human interventions were to stabilize climate regimes, the new regimes would differ from recent historic climate regimes, and many species would not survive (Ruhl 2008). Nonetheless, restoration under climate change is more important than ever before and might be most properly defined in terms of reducing ecosystem vulnerability and promoting adaptation and resilience. If ecosystems and species are pushed beyond their ability to recover, managers might have to encompass transitions to new ecosystem states while managing for resilience (West et al. 2009). Examples of managing for resilience include reducing anthropogenic stressors, protecting key ecosystem features, identifying and protecting refugia, and implementing other practices intended to reduce ecosystem change in the face of disturbance (West et al. 2009).

Ferriter et al. (2008) identified 80 nonindigenous terrestrial vertebrates (amphibians, reptiles, birds, and mammals), 32 nonindigenous fishes, 81 nonindigenous invertebrates (including ants, bees, ticks, mussels, and others), and 25 nonindigenous priority plant species in

Florida south of Lake Okeechobee. Invasive plant and animal species typically are opportunistic over a range of environmental conditions (Qian and Ricklefs 2006). Changing climates are unlikely to affect current invasive species negatively and might increase successful colonization by and competitiveness of new species (Hellmann et al. 2008). For example, many of the 23 exotic freshwater fishes considered permanently established in Florida waters, including the banded cichlid (*Heros severus*) and spotfin spiny eel (*Macrognathus siamensis*), have been restricted by temperature to southern Florida (Shafland et al. 2008). Increasing minimum temperatures associated with climate change might facilitate their northward spread.

Southern Florida species most at risk are likely to be those dependent on isolated or fragmented changing habitats, on the edge of their climatic tolerance ranges, dependent on interspecies interactions, being displaced by opportunistic exotics, and unable to respond quickly to changing climate trends by migration or adaptation. Recommendations addressing climate change should include locally specific management options for conservation of species and habitats most at risk. Some species are likely to thrive under changing climate conditions, whereas others might survive only with assistance through a focused application of ecosystem-level management of habitat and other resources vital to sustainability (Ruhl 2008).

A number of active management strategies could be considered for focal species within a framework of scenario development and modeling (e.g., Mawdsley et al. 2009, Running and Mills 2009, West et al. 2009). These options are discussed below.

Restoration to maximize resilience

Restoration of characteristic habitats with the goal of improving their quality and native diversity would help sustain existing habitats and associated species that might otherwise be displaced by climate-change effects. Even if these refugia are likely to be nonsustainable in their historical or current status in the face of long-term climate change, restoration undertaken with climate change in mind could increase the probability that species could adapt or could buy time to implement other options (Hannah and Hansen 2005). Current Everglades restoration efforts to increase water flow to Shark River Slough, Taylor Slough, and Florida Bay might be particularly important in the coming decade to provide the freshwater head necessary to delay the rate at which salt water moves landward and to offset sea-level rises that would profoundly alter extensive areas of freshwater marsh and prairie.

Reduce local anthropogenic stressors

The negative effects of global climate change are compounded when local stressors reduce the ability of the biota to cope or adapt. For example, increased freshwater inflows to ENP sloughs are part of Everglades restoration plans and would help mitigate freshwater plant community loss from sea-level rise and saltwater intrusion. Increased flows would provide a freshwater head and promote peat sediment accumulation. However, nutrient loading from anthropogenic sources is a substantial stressor and could negate these restoration efforts.

Movement corridors, stepping stones, and multihabitat options

The Everglades is essentially a contained ecosystem surrounded by urban development, large agricultural development, the Atlantic Ocean, and the Gulf of Mexico. Southern Florida is fortunate to have multiple national and state wildlife refuges and parks, but with development at their borders, minimal opportunity exists to expand these conservation areas to accommodate habitat and species responding to climate change. Conservation of wildlife-movement corridors would provide a pathway for terrestrial wildlife to migrate from southern habitat northward along the Florida peninsula (e.g., Kautz et al. 2006). Wildlife, including migratory birds, would benefit from identification of habitat stepping stones between larger conservation areas and protection of multiple potential areas of refuge that would permit species to shift across the landscape depending on conditions in a given year. The Everglades is compartmentalized into water conservation areas surrounded by levees and canals. Removing these structural barriers (one of the goals of Everglades restoration) would provide movement corridors for aquatic species. Outright purchase of large expanses of additional land for conservation is becoming increasingly difficult and expensive, but alternative strategies, such as working with surrounding landowners for conservation easements and other conservation agreements, have been proposed and implemented in other areas (Main et al. 1999, Newburn et al. 2005, Hunt 2008, Attwood et al. 2009) and should be actively and resolutely pursued in the Everglades.

Assist propagation and adaptive breeding

Assisted propagation and adaptive breeding of native plants and animals span a range of interventions from captive breeding to artificial fertilization to directed evolution. Directed evolution refers to

identification of traits favorable for adapting to climate change in individuals from the field or in captive breeding programs and assisting differential reproductive success (Running and Mills 2009). A consortium of research groups is expanding a breeding program started by the Coral Restoration Foundation to restore staghorn coral (*Acropora cervicornis*) and other coral species to reefs off the coasts of the Florida Keys (Allen 2009). Selective breeding might produce staghorn and other coral that are better adapted to a changing climate (Vollmer and Kline 2008, Baums 2010). Everglades National Park has identified 27 rare plant species in coastal tropical hardwood habitats (Gann et al. 2002, J. Sadle, ENP, personal communication) that are on the front line of salinity and flooding effects from sea-level rise and that also might be stressed by increased drought and warming temperatures. Assisted propagation and breeding methods might be needed individually or in combination to conserve some of these species in or near their present habitats. Should conditions worsen, it might be necessary to move them to more suitable refugia. However, by assisting rare populations in the wild through such means as habitat restoration, time might be provided for species to adapt or other options to be implemented. Knowledge gained now in terrestrial environments might assist in conserving aquatic species.

Assist migration/translocation

Assisted colonization (Hunter 2007, McLachlan et al. 2007), also called assisted migration or translocation, should be considered where present habitat is no longer sustainable and species are unable to adapt or migrate unassisted. Species in patchy, isolated habitat are particular candidates for this high level of human intervention. Assisted colonization is one of the options of last resort, but an immediate need exists to plan for this option in a number of southern Florida communities. Sea-level rise and saline overwash from increasing storm surges would permanently or episodically inundate large proportions of habitat in the Florida Keys (Janetos et al. 2008) and are an imminent threat to wildlife and plant species endemic to these islands that have no options for unassisted migration to new habitats. Examples include small mammals, such as the Key deer (*Odocoileus virginianus clavium*), Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*), silver rice rat (*Oryzomys palustris natator*), and other federally endangered species (US Fish and Wildlife Service 1999). Plant species found exclusively in pine rocklands of the Florida Keys, such as Big Pine partridge pea (*Chamaechrista lineatea* var *keyensis*) and

wedge sandmat (*Chamaesyce deltoidea serpyllum*), rely on fresh groundwater and recurrent fire, both of which are increasingly affected by rising seas and storm surges (Ross et al. 2009). Ross et al. (2009) proposed a time-series of adaptive management events from intensive management of core sites to eventual translocation for the conservation of rare pine-rockland species.

However, the success of relocating populations is uncertain because our biological knowledge of most species has significant gaps regarding how to select a new optimal habitat site and because of unpredicted and novel species interactions and responses to the new location and its existing biological communities. Risk is increased under climate-change scenarios because of uncertainty associated with selecting emerging new habitat as conditions change and with the sustainability of new habitat in future climate conditions.

Captive populations (zoos, herbariums, seed banks)

Captive maintenance is a strategy that could be used to aid other approaches. It should be considered as a last resort when an endangered species must be removed from the wild because the only other choice is extinction. This approach is resource intensive (Kleiman et al. 1997) and may not be a viable long-term option for more than a few sustainable populations (Mawdsley et al. 2009).

Accept change

Natural resource managers also must be open to the potential for a rich, biodiverse, functioning Everglades ecosystem that will include a new mix of habitats and species. The Everglades can be characterized as a complex of systems that are self-organizing, adaptive, and heterogeneous (Casti 1997). The system is not closed and predictable, but open, evolving, and in constant change (Pahl-Wostl 2007).

Conclusions

Anticipated effects of climate change on the Everglades physical environment over the next century are: 1) a probable rise in sea level of ≥1 m, 2) reduced precipitation with increased drought punctuated by more intense storms resulting in greater climate variability and extremes, and 3) temperature increases that will be lower than in many other parts of the country but that could have substantial impacts to species already near the extremes of their temperature tolerances in southern

Florida subtropical environments. Sea-level rise is the most obvious of these changes and has ecological consequences to a large proportion of the coastal and near-shore Everglades. Potential consequences include loss of freshwater graminoid and mangrove wetlands, vegetation community shifts, lower light levels on coral reefs if sea-level rise occurs faster than reef formation, loss of sea turtle nesting habitat, and inundation of threatened, endangered, and rare wildlife and plant species and habitats on the Florida Keys and coastal Everglades. Southern Florida wildlife species are adapted to a cycle of wet and dry seasons, but heightened extremes between periods of heavy storm activity and more severe drought and fire will have unknown consequences to Everglades vegetation as a result of differing photosynthetic pathways, competition, interactions with affected nutrient dynamics, and other changes. Wildlife adapted to Everglades habitats, hydrologic timing and patterns, and timed synergistic interactions with other species also will be affected. Their responses could range from migration in response to shifting habitats and climate conditions to extirpation from a failure to adapt.

The Everglades are internationally recognized as unique and valuable ecosystems and habitats. That recognition is reflected in the willingness of the US Congress and the State of Florida to spend billions of dollars on restoration. Climate change reduces the justification for restoration only if it is thought that the environmental changes will completely degrade the system without a reasonable chance of mitigation or adaptation. Climate change and sea-level rise alone will not destroy the Everglades. The ecological consequences of climate change will reshuffle vegetation and wildlife composition, distributions, and abundance in unpredictable ways (Ruhl 2008).

Monitoring designed to support decision-making and rigorous ecosystem- and landscape-level adaptive management can promote resilience of Everglades' ecosystems to changing conditions and allow the Everglades to evolve as a healthy system. For example, sea-level rise will inundate large areas of the southern coastal Everglades. Saltwater encroachment into ground water and from higher storm surges already is changing species composition inland from inundation (J. Sadle, ENP, personal communication). Agreement is increasing that Everglades restoration is more important than ever because increased freshwater flow to the southern Everglades is needed to slow saltwater encroachment and to give species a chance to adapt (NRC 2008). A critical component of that adaptation might lie in the response of freshwater marsh peat. With adequate freshwater restoration,

peat can be maintained, will continue to accumulate, and can provide the substrate necessary for plants to establish. A slow transition to increasingly saline waters would allow submerged vegetation to become established and to contribute litter to peat formation. However, a sudden change from freshwater to saltwater conditions is likely to oxidize and remove the organic substrate rapidly, leaving large areas of thin substrate or bare limestone bedrock with a greatly reduced potential to shift to a healthy estuarine environment.

Identification of species and habitats most at risk, anticipation of potential ecological changes, strategies for increasing habitat and landscape resilience to change in climate, and preparation for surprises will be critical next steps for Everglades restoration. Climate change imposes long-term, continuous change on systems. Continuous changes make management goals a moving target and observable systems responses to actions under current conditions only a partial indicator of success. An adaptive-management strategy must include preparation for long-term, often gradual changes with potential for large abrupt changes. Successful use of this strategy will require ecological and physical modeling to develop hypotheses and goals (Füssel and Klein 2006). Integration of directed research, management, and research-focused monitoring, risk assessment, and database management among projects will be critical.

Anticipating ecological responses in the Everglades with reduced uncertainty will require a better understanding of short-term (decadal) climate trends, comparative studies, physiological studies, and modeling. Some key research needs include: 1) area and distributional shifts in estuarine and freshwater wetland habitats, 2) changing habitat and trophic linkages, 3) short- and long-term adaptive capacity of southern Florida species, 4) southern Florida species phenology and distribution shifts and disruptions in species interactions, 5) increased resolution in coastal topography and bathymetry mapping, 6) coastal hydrologic modeling, 7) increased understanding of environmental tolerances of coastal plants, 8) mechanisms and rates of peat collapse from saltwater intrusion, 9) relationships between soil C and greenhouse-gas production in tropical fresh and saltwater wetlands, and 10) understanding combined stressors of sea-level rise, climate change, and anthropogenic stressors, such as pollution and habitat fragmentation.

The Everglades ecosystem has changed continually over relatively short spans of geologic time, and its character will continue evolving to some yet unknown extent in response to climate change. With a

management emphasis on ecosystem viability and resilience, the Everglades can be restored to a region of high biodiversity and function.

Acknowledgements

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