CLIMATE CHANGE, HURRICANES AND TROPICAL STORMS, AND RISING SEA LEVEL IN COASTAL WETLANDS

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Abstract. Global climate change is expected to affect temperature and precipitation patterns, oceanic and atmospheric circulation, rate of rising sea level, and the frequency, intensity, timing, and distribution of hurricanes and tropical storms. The magnitude of these projected physical changes and their subsequent impacts on coastal wetlands will vary regionally. Coastal wetlands in the southeastern United States have naturally evolved under a regime of rising sea level and specific patterns of hurricane frequency, intensity, and timing. A review of known ecological effects of tropical storms and hurricanes indicates that storm timing, frequency, and intensity can alter coastal wetland hydrology, geomorphology, biotic structure, energetics, and nutrient cycling. Research conducted to examine the impacts of Hurricane Hugo on colonial waterbirds highlights the importance of long-term studies for identifying complex interactions that may otherwise be dismissed as stochastic processes.

Rising sea level and even modest changes in the frequency, intensity, timing, and distribution of tropical storms and hurricanes are expected to have substantial impacts on coastal wetland patterns and processes. Persistence of coastal wetlands will be determined by the interactions of climate and anthropogenic effects, especially how humans respond to rising sea level and how further human encroachment on coastal wetlands affects resource exploitation, pollution, and water use. Long-term changes in the frequency, intensity, timing, and distribution of hurricanes and tropical storms will likely affect biotic functions (e.g., community structure, natural selection, extinction rates, and biodiversity) as well as underlying processes such as nutrient cycling and primary and secondary productivity.

Reliable predictions of global-change impacts on coastal wetlands will require better understanding of the linkages among terrestrial, aquatic, wetland, atmospheric, oceanic, and human components. Developing this comprehensive understanding of the ecological ramifications of global change will necessitate close coordination among scientists from multiple disciplines and a balanced mixture of appropriate scientific approaches. For example, insights may be gained through the careful design and implementation of broad-scale comparative studies that incorporate salient patterns and processes, including treatment of anthropogenic influences. Well-designed, broad-scale comparative studies could serve as the scientific framework for developing relevant and focused long-term ecological research, monitoring programs, experiments, and modeling studies. Two conceptual models of broad-scale comparative research for assessing ecological responses to climate change are presented: utilizing space-for-time substitution coupled with long-term studies to assess impacts of rising sea level and disturbance on coastal wetlands, and utilizing the moisture-continuum model for assessing the effects of global change and associated shifts in moisture regimes on wetland ecosystems. Increased understanding of climate change will require concerted scientific efforts aimed at facilitating interdisciplinary research, enhancing data and information management, and developing new funding strategies.

Key words: climate change; coastal wetlands in southeastern United States; colonial waterbirds and hurricanes; comparative studies, conceptual models of; hurricanes; moisture-continuum model; sea level rise; space-for-time substitution; tropical storms.

INTRODUCTION

Coastal wetlands include a complex and diverse assemblage of freshwater swamps and marshes, mangrove swamps, salt marshes, mud flats, sandbars, hypersaline lagoons, sandy beaches, rocky shorelines, and seagrass beds. Although coastal wetlands comprise <5% of the world's terrestrial land mass (cf. Tiner 1984), the combination of high secondary productivity (Mitsch and Gosselink 1993) and accessibility to humans via land and water has made coastal wetlands attractive sites for human settlement for millennia (Bildstein et al. 1991). As a result, many of the world's largest cities are located in coastal areas (Day et al. 1989). Fifty-two percent of the United States' population resides within 80 km of the U.S. coast (Southworth 1989), and some estimates place 70% of the world's human population in the coastal zone (cf. Cherfas 1990).

Coastal wetlands rank among the most productive (Whittaker and Likens 1971, Odum 1979, Day et al. 1989) of all natural ecosystems. However, because of prolonged human contact, coastal and interior wetlands have been modified by humans in numerous ways. Since 1900, for example, ≈50% of the world's wetlands have been converted to other uses (Tiner 1984). Furthermore, continued human alteration of the physical structure of wetlands, the introduction of toxic materials, enrichment with excessive levels of nutrients, sediments, and heat, the harvest of native species, and the introduction of exotic species (Tiner 1984, Carter 1988, Day et al. 1989), are likely to exacerbate impacts projected to accompany global climate change (Tiner 1984) and rising sea level (Barth and Titus 1984, Warrick et al. 1993).

Increasing levels of carbon dioxide and other greenhouse gases are well documented, and are expected to affect numerous atmospheric and oceanic processes that will directly and indirectly affect coastal wetlands (Edgerton 1991). During the next half century, average global temperature is projected to rise by 2–5°C, sea level to increase by 80 cm or more, global precipitation and evapotranspiration to increase by 7–15% and 5–10%, respectively, runoff to increase, and average summertime soil moisture to decrease globally (Manabe and Wetherald 1986, Schneider et al. 1992). Although considerable scientific uncertainty remains (Houghton et al. 1992), current warming scenarios may result in changes in the geographic range, frequency, timing, and intensity of hurricanes, as well as in the duration of the hurricane season (Emanuel 1987, Broccoli and Manabe 1990, Mitchell et al. 1990, Haarsma et al. 1993). These projected alterations of climate and sea level are, however, expected to vary significantly in direction and magnitude on a regional basis, and the level of confidence for regional projections is much lower than that for global projections (Schneider et al. 1992).

Cumulative changes in temperature and precipitation, sea level, and storm frequency, intensity, timing, and distribution will have both direct and indirect effects on coastal and interior wetlands. Direct effects, for example, may include those relatively short-term population and ecosystem responses (e.g., mortality, nutrient pulses, etc.) to excess precipitation, flooding, and high winds, whereas indirect effects may include long-term or delayed population and ecosystem responses to disease and insects, salt stress, habitat modification, fire, and other secondary factors. In this paper, we primarily focus on how coastal freshwater, brackish, and high-salinity wetlands are likely to respond to rising sea level and, especially, to climate-change-induced modification of the frequency, intensity, timing, and distribution of hurricanes and tropical storms. For several reasons, most of our examples are drawn from research conducted in the southeastern United States. First, from a geological perspective, coastal wetlands in this region are the result of a dynamic synergism among riverine inflow (as mediated by droughts and human modifications), rising sea level, and natural disturbances. Second, coastal wetlands in this region cover a large areal extent and are well-studied systems whose economic values and ecological functions are well documented. Third, detailed investigations of the impacts of recent Caribbean hurricanes and tropical storms on coastal wetlands have yielded important insights into the ecological repercussions of natural disturbances in these systems.

In this paper we first examine how coastal wetlands have naturally evolved under a regime of rising sea level and recurring hurricanes and tropical storms. Projected changes in rising sea level and in the frequency, intensity, and extent of hurricanes and tropical storms are identified. A review of the literature and a detailed example from studies conducted to examine the impacts of a category 4 hurricane (sensu Gray 1990) on colonial waterbirds (Order Ciconiiformes) are used to examine the complex nature of ecosystem and population responses to hurricanes and tropical storms. We also address the following questions: (1) What can we infer about the impacts of global climate change and changes in hurricanes and tropical storms based on our current understanding of how ecological patterns and processes in coastal wetlands respond to natural disturbances?; (2) What types of data, information, and assessments are required to facilitate our understanding of climate-change impacts?; and (3) How do we acquire this necessary knowledge?

HISTORICAL DEVELOPMENT OF COASTAL WETLANDS AND PROJECTED CHANGES IN RISING SEA LEVEL, AND IN HURRICANES AND TROPICAL STORMS

Coastal wetland evolution and geomorphology

The marshes and associated barrier islands of the Atlantic Coastal Plain and Gulf Coast formed during

FIG. 1. Sources of coastal marsh sediments and processes of delivery: (a) resuspension of offshore shelf or lagoonal muds with landward transport during storms; (b) erosion of Pleistocene headlands or abandoned deltas with transport to marsh via longshore currents; (c) wave attack of Holocene marsh muds exposed in lower shore face with transport to the marsh via longshore currents (c′); (d) riverine input; and (e) overwash redistribution. (Note: eolian inputs are not shown.)
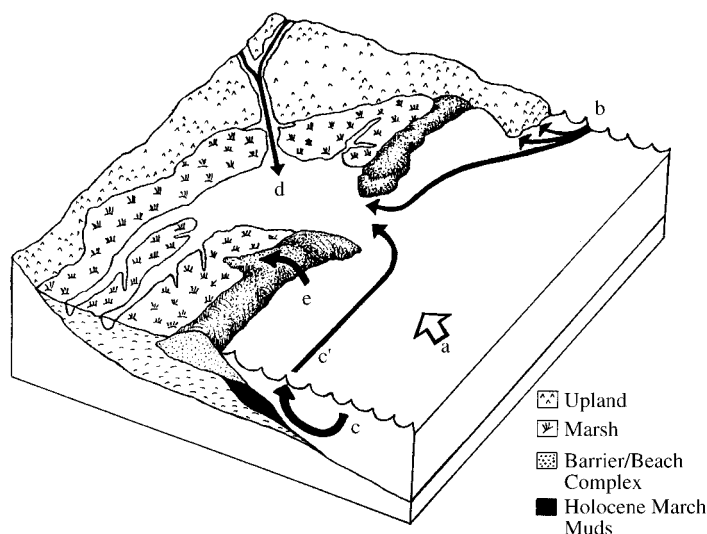
the Late Holocene under a regime of slowly rising sea level (Belknap and Kraft 1977, Colquhoun and Brooks 1986, Fletcher et al. 1993). This transgressive regime began at the end of the Wisconsin ice age and appears to be continuing today. In order to persist under a regime of rising sea level, coastal wetlands must accumulate sediment at a rate that is at least equal to the apparent rate of sea-level rise (DeLaune et al. 1983). Wetlands that fail to do so will become open bodies of water. Tide gauge records from the Atlantic coast indicate relative sea-level rise rates of 1.6–4.0 mm/yr over the past century (Stevenson et al. 1986). A higher rate of increase (9.0–10.0 mm/yr) occurs along portions of the Gulf coast. An important question is whether coastal wetlands will be able to persist amidst increases in the rate of rising sea level and changes in the frequency and intensity of coastal storms. Our current state of knowledge is inadequate to resolve this issue conclusively. Here, we outline the nature of the problem and the factors that should be considered.

The sediment that accumulates in coastal wetlands may be derived from in situ (autochthonous) processes, such as primary production or oyster reef growth (carbonate shell fragments), and imported from external sources (allochthonous), primarily as inorganic mineral grains in the clay–silt size range. The relative magnitudes of the allochthonous supply and the excess of in situ primary production over decomposition determines whether a particular wetland soil is dominated by autochthonous organic matter or allochthonous mineral sediments.

Soils dominated by autochthonous organic material produced in situ by the excess of primary production over decomposition are quite rich in organic matter, although they rarely conform to the more stringent definition of peat established by the American Society for Testing and Materials (1993). Throughout much of the

Coastal Plain of the southeastern United States, for example, these ''peats'' are most commonly found in hardwood swamps along ''blackwater'' rivers upstream from the limits of salt-water penetration, but not at equivalent locations along more sediment-laden rivers that drain the Piedmont. Extensive, low-lying peatlands also occur on the Pamlico–Albemarle peninsula of North Carolina, an area similarly characterized by low allochthonous input and minimal tidal influence (Moorehead and Brinson 1995). These observations suggest that peats in coastal wetlands do not form in the most hydrodynamically active areas where inputs of allochthonous mineral sediment are high and tidal currents are strong enough to transport this material to marshes.

Marshes that fringe estuaries at the mouths of Piedmont–draining rivers or lie behind barrier islands are commonly dominated by allochthonous silt and clay. This inorganic allochthonous material is most likely supplied ultimately by Piedmont rivers, but other sources and processes may also play a role (Fig. 1). These could include (1) wave erosion of Pleistocene headlands or abandoned deltas, followed by sediment transport to marshes via longshore currents; (2) resuspension and landward transport of shelf sediments during storms; and (3) eolian inputs and overwash redistribution. Non-riverine sources are difficult to quantify. It is possible, however, to compare riverine inputs of sediment to the coastal environment with that required by marshes to keep pace with rising sea level. Sediment in salt marshes in South Carolina, for example, has an organic carbon content of 5–10% by mass, a porosity of 70–80%, and a dry mass bulk density of 0.4–0.5 g/cm^3. For a typical rate of sea-level rise (0.2–0.3 cm/yr), the amount of allochthonous sediment required to keep pace with sea level is about 600–1300 g·m^{-2}·yr^{-1}. Based on U.S. Geological Survey mea-

surements of discharge and suspended-sediment loads for South Carolina rivers and the areal extent of salt marshes (1500–1800 km²; South Carolina Water Resources Commission 1970, Ringold and Clark 1980), this amount is about equivalent to the average annual delivery of riverine sediment to the coastal environment. Thus, sediment requirements for marsh maintenance appear to be about equal to those currently available (see also Meade 1972). The sediment yield of rivers in this region today is thought to be about an order of magnitude greater than that which occurred under the pristine conditions of pre-Colonial times (Meade and Trimble 1974). How marshes managed to keep pace with sea level under pre-settlement conditions of greatly reduced riverine supply is not known.

Perhaps the non-riverine processes were and still are important. Available measurements of dust fallout in this region (Smith et al. 1970), however, suggest that eolian inputs are too small to be important. The magnitude and importance of headland erosion remains unresolved. In this regard, however, a mechanism that is analogous to headland erosion should be noted. Many lagoonal and mainland marshes occur on Pleistocene surfaces that have been intercepted recently by rising sea level (Oertel et al. 1989a). Their continued existence depends on vertical sediment accretion, regardless of source, at rates approximating that of rising sea level (Oertel et al. 1989b). A number of other sources of sediment can serve as supplies for depositional environments (Heron et al. 1984). These include shoreface erosion of materials beneath barrier island sands. Two groups of materials serve as sources: (1) Pleistocene surfaces outcropping on the shoreface as islands migrate landward, and (2) outcropping Holocene marsh muds, peats, and flood-tide deltas stranded by migrating inlets. For example, as barrier islands retreat landward in response to rising sea level and wave attack, outcropping Holocene marsh muds are eroded and some of this material may be flushed back through inlets, via flood-tide deltas, to supply the modern marsh (Hackney and Cleary 1987). Thus some of the sediment required to keep pace with sea-level rise may be supplied by recycling or ''cannibalizing'' older marsh sediments. Also, evidence from clay composition suggests that landward transport from marine sources can make substantial contributions to estuarine sediments (Benninger and Wells 1993).

Along the western Gulf coast, the supply of sediment by the Mississippi River far exceeds that required for marsh survival (Meade 1972), despite the large area of coastal wetlands and their rapid rate of subsidence. Here, the failure of marshes to keep pace with rising sea level can be attributed in part to human interference in the distribution of the river's sediment along the coast. Nearly continuous levees along the river focus the delivery of sediment to the continental shelf. Natural shifting of the Delta and the formation of new distributary channels have been largely curtailed so that marshes on inactive deltas only receive sediment after it has dispersed into the Gulf and has been transported along shore by wind-driven and tidal currents. Delivery of this sediment to marshes on inactive deltas is further impeded by artificial levees and spoil banks along the many canals that have been dredged in these areas (Day et al. 1993).

Projected changes

Rising sea level.—A major concern related to climate change is rising sea level associated with ice-sheet melting and calving (Webb et al. 1993), the melting of small alpine glaciers and other forms of land ice, and thermal expansion of the ocean (Wigley and Raper 1993). Thermal expansion, a steric effect induced by changes in the density of sea water, results from the fact that as temperature rises seawater density decreases (Wigley and Raper 1993). Freshwater melt both contributes to additional ocean volume and decreases seawater salinity and density, thereby supplementing the effects of thermal expansion. The thermal inertia of the ocean results in a warming commitment, which means that even after climate forcing ceases, sea levels will continue to rise. Indeed, the impact of thermal expansion associated with current climate forcing will manifest itself more fully in the latter part of the 21st century than in the immediate future (Wigley and Raper 1993). Except for the larger range of values, recent projections of sea-level rise, in general, confirm earlier Intergovernmental Panel on Climate Change (Warrick and Oerlemans 1990) estimates, ranging from 3 to 124 cm over the course of the next 110 yr. Sea levels have risen by 10–20 cm during the past century and recent projections suggest rates of rise of about 4 cm per decade, two to four times the rate of the past 100 yr (Wigley and Raper 1993).

Sea levels have fluctuated by an order of 100 m over the past 18 000 yr, offering a ''natural background'' against which to compare projected anthropogenic effects. Studies of historical changes suggest that sea-level rises are not necessarily associated with marsh erosion, and that declines in sea level are not necessarily associated with marsh accretion. If greenhouse forcing is stabilized, surface ocean temperatures quickly equilibrate, but sea level continues to increase for decades as heat propagates into lower ocean layers and they expand. This contribution of greenhouse forcing is reasonably well modeled and estimated (Wigley and Raper 1987, 1993, Warrick and Oerlemans 1990, Woodworth 1993). Even if greenhouse forcing is assumed to increase only up until 2050, thermal expansion would result in a 31-cm increase in sea level (Woodworth 1993). Although there are uncertainties in these calculations, its seems reasonable to conclude that sea level will rise by several decimeters over the next 100 yr. However, discoveries of deformations in

FIG. 2.   Number of hurricanes making landfall in individual states along the Atlantic and Gulf coasts, 1899–1992 (adapted from Neumann et al. 1993). The numbers given for each state are, first, the total and then the number of major hurricanes, where ''major'' = categories 3–5 according to the Saffir-Simpson hurricane scale (see Table 1 footnote).
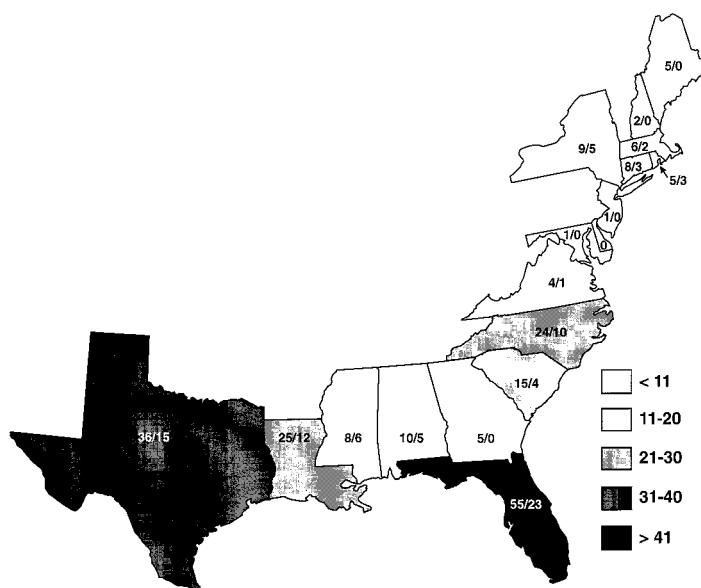
geoid relief and the nonrandom distributions of density of earth materials, together with evidence indicating that the world's oceans are regionally divisible with regard to historic fluctuations in sea level, suggest that the notion of uniform, eustatic changes in sea levels is outmoded and that the magnitude of greenhouse-gas-forced changes in sea levels will vary regionally (Tooley 1993).

Hurricanes and tropical storms.—Hurricanes characterize most equatorial waters (e.g., Muller 1977), including coastal regions of North, Central, and South America, the Indian subcontinent, Southeast Asia and Africa, Indo-Malaysia, and northern Australia (Gray 1975). Within the world's six hurricane belts, cyclonic storms are typical, synoptic weather patterns. The Florida Keys, for example, have been buffeted by >200 000 hurricanes during the past 2×10^6 yr (Ball et al. 1967), while the entire Atlantic Basin—including the Caribbean and Gulf of Mexico—has been struck by more than five hurricanes annually since the middle of this century (Gray 1990). Between 1899 and 1992, states along the Atlantic and Gulf coasts were affected by 219 direct hits, including 89 major hurricanes that reached category 3 or higher on the Saffir-Simpson hurricane scale (Neumann et al. 1993: Fig. 2). Every state except Delaware experienced at least one direct hit during this period.

Six principal factors are related to the formation of hurricanes and typhoons including subsurface ocean-water temperatures, distance from the equator, high air-temperature gradients, low values of vertical shear, high relative humidity in the middle troposphere, and previous levels of cyclone activity (Gray 1979). For example, ocean-water temperatures of at least 26°C to a depth of 60 m are essential to the formation of tropical cyclones, which are fueled by the warm waters (Raper

1993). Although the relationship between subsurface ocean temperatures and cyclonic frequency varies regionally, consistent positive correlations exist in three of six hurricane belts (North Atlantic, eastern North Pacific, and Australian) (Raper 1993). Because evaporation increases exponentially with rising surface-water temperatures, it has been inferred that global-warming-induced changes in ocean temperatures and circulation could increase the frequency and intensity of hurricanes, and increase the size of the regions affected by such events (Emanuel 1987, O'Brien et al. 1992, Raper 1993). Emanuel (1987) has further suggested that potential damage from hurricanes may increase by 40–50% with a doubling of atmospheric CO_2.

Recent global-climate modeling efforts have produced mixed results related to future hurricane and tropical-storm activity. With global warming, tropical storms and hurricanes are predicted to increase in intensity or remain relatively unchanged, and to either increase or decrease in frequency (Broccoli and Manabe 1990, Haarsma et al. 1993, Lighthill 1994). Haarsma et al. (1993), for example, reported an increase in the number of simulated tropical storms, but no changes in intensity, with a doubling of CO_2. Global climate models appear to be especially sensitive to cloud radiative feedback. Broccoli and Manabe (1990) observed an increase in tropical storms when clouds were ignored, but a decrease in the number of tropical storms when cloud cover could be generated within the model.

The utility of models for examining how global climate change may affect hurricanes and tropical storms has recently been challenged. Mitchell et al. (1990), for example, suggest that although climate change may result in an increase in the maximum intensity of tropical storms, current climate models do not adequately

simulate tropical circulation and thus cannot be utilized for predicting changes in storm distribution and frequency. Specifically, global-climate models have been run at too coarse a resolution (300 km and greater) to adequately resolve tropical storms and associated winds and yield data relevant to actual tropical-storm formation (Gates et al. 1990, Lighthill et al. 1994).

Currently, there is no evidence that the frequency and intensity of tropical storms has increased as the globe has warmed over the past century, although critical thresholds may not yet have been reached (Folland et al. 1990). The question of whether global climate change will affect tropical-cyclone frequency or intensity was recently addressed at a symposium cosponsored by the World Meteorological Union and the International Council of Scientific Unions (Lighthill et al. 1994). Participants concluded that any responses to increasing sea-surface temperatures may be limited because of physical constraints on the other five conditions necessary for tropical storm formation and because of increased spray evaporation and sea-surface cooling (Lighthill et al. 1994). Although indirect effects of global warming on the frequency and intensity of tropical storms and hurricanes were not excluded, it was concluded that such effects would likely be overshadowed by large natural variability (Lighthill et al. 1994).

Clearly, it is not yet possible to reliably predict how global climate change will affect hurricane and tropical-storm characteristics, nor is it apparent that we would be able to statistically detect any changes that might occur given the large natural variability and the relatively short historical record of meteorological observations. Nevertheless, some of the observed natural variability in tropical-storm and hurricane frequency and intensity has been related to long-term meteorological cycles including the multidecadal Sahel rainfall cycle (Landsea and Gray 1992), the quasi-biennial oscillation (Gray 1984), and the El Niño-Southern Oscillation cycle (Gray 1984, Wu and Lau 1992). Thus, regardless of any effects of global climate change, we can expect changes in tropical-storm and hurricane activity as atmospheric and oceanic conditions respond to these long-term meteorological cycles. Furthermore, projected rising sea level alone will amplify the impacts of hurricane-attendant storm surges (Raper 1993).

Coastal wetlands exist within a narrow margin between land and ocean and have naturally evolved in response to specific ranges and rates of sea-level changes, variations in sources and amounts of sediment supply, and specific patterns of storm frequency, intensity, and timing. Our current level of knowledge is inadequate to accurately predict how coastal wetlands will respond to increased rates of rising sea level, changes in hurricanes and tropical storms, and land-use changes that will accompany population growth in coastal areas. Although coastal wetlands continue to persist, critical thresholds may have yet to be reached, and departures from past patterns and historic rates of change may lead to significant changes in coastal ecosystems.

ECOLOGICAL RESPONSES OF COASTAL WETLANDS TO HURRICANES AND TROPICAL STORMS

Although there is little evidence that hurricanes produce "long-term detrimental impacts to unmodified coastal systems" (Conner et al. 1989:45), such storms are capable of accelerating, disrupting, and reversing numerous geomorphic events and ecological processes, and devastating human settlements in coastal areas (Tanner 1961, Hayes 1978, Lugo et al. 1983, Conner et al. 1989). In many tropical and subtropical coastal regions, hurricanes shape community structure and function in much the same way as do coastal upwelling in nearshore waters, fire in semiarid regions, and snow melt in montane ecosystems (Odum and Pigeon 1970, Lugo 1988, Harte et al. 1992). Indeed, tropical cyclones may be the most environmentally significant abiotic disturbance force in coastal tropical and subtropical ecosystems (Lugo et al. 1983, Raper 1993).

In this section, we examine the impacts of hurricanes and tropical storms on hydrology and physical structure, nutrient cycling and biogeochemistry, vegetation, and animal populations. Specific examples are drawn from ecological studies associated with 10 hurricanes (categories 1–5) that have affected the United States (including Puerto Rico), Jamaica, and Nicaragua (Table 1). Finally, an avian population example is used to highlight the importance of complex interactions and indirect effects.

Hydrology and physical structure

High winds, excessive rainfall, storm surges, and salt spray are frequently associated with hurricanes and tropical storms. Storm impacts vary among coastal and inland ecosystems and may include direct, indirect, and delayed effects. Impacts may be positive or negative, and frequently the severity of effects is not directly related to the magnitude of the hurricane or tropical storm. For example, in the Caribbean and along the coast of the southeastern United States, a single hurricane or tropical storm may account for 5–40% of the annual precipitation a site receives (Michener et al. 1990, Scatena and Larson 1991). Many such areas are dependent upon these episodic events for maintaining a positive annual net water balance (Michener et al. 1990), and would otherwise experience drought conditions more frequently. Excessive precipitation can result also in flooding, landslides, erosion, sediment deposition, and extensive valley or channel modification. For example, Hurricane Agnes (1972), although only a category 1 storm, had record-breaking rainfall (127 mm greater than the 24-h maximum rainfall in 100 yr for Baltimore County, Maryland), generated the

TABLE 1. Characteristics of 10 hurricanes discussed in this study (Walker et al. 1991, Neumann et al. 1993).

Hurricane	Date	Category†	Points of landfall
Agnes	1972 (June)	1	Florida, New York, Connecticut
Andrew	1992 (August)	4	Florida, Louisiana
Audrey	1957 (June)	4	Texas, Louisiana
Betsy	1965 (September)	3	Florida, Louisiana
Camille	1969 (August)	5	Louisiana, Mississippi
David	1979 (September)	2	Florida, Georgia, South Carolina
Donna	1960 (September)	4	Mississippi
Gilbert	1988 (September)	5	Jamaica, Mexico (Quintana Roo)
Hugo	1989 (September)	4	Puerto Rico, South Carolina
Joan	1988 (October)	5	Nicaragua

† The Saffir-Simpson hurricane scale: Category 1, wind speed 74–95 miles/h and/or storm surge 4–5 feet above normal; Category 2, 96–110 miles/h and/or 6–8 feet above normal; Category 3, 111–130 miles/h and/or 9–12 feet above normal; Category 4, 131–155 miles/h and/or 13–18 feet above normal; Category 5, >155 miles/h and/or >18 feet above normal (Neumann et al. 1993). Note: 1 mile = 1.609×10^3 m; 1 foot = 3.048×10^{-1} m.

largest floods on record for north-central Maryland, and resulted in the Western Run River being widened by 10–20% for >50% of its length, thereby reducing the effective riparian zone (Costa 1974).

In the southeastern United States, most hurricanes occur in the early fall, before water tables are fully recharged and soils are still relatively dry (Duever et al. 1994). Hurricanes can recharge the water table locally or prolong a high wet-season watertable. Terrestrial systems may experience a rapid flush of low-ionic-strength water, and inundation and saturation of soils in low-lying areas. If wetlands are dependent on shallow groundwater or rainwater, recharge can occur quickly. Excessive precipitation can result in order-of-magnitude increases in riverine discharge, which can significantly alter currents and salinity regimes in downstream reaches (Anderson et al. 1973, Van Dolah and Anderson 1991, NOAA 1993), increase non-point-source inputs of sediments, nutrients and organic material (Anderson et al. 1973, Van Dolah and Anderson 1991), and cause failure of wastewater treatment plants. Riverine flooding can result in above-normal inundation of riparian zones. The higher river volume and velocity can transport sediment and nutrients into the flood plain. Retreating flood waters subsequently may export materials from the flood plain. High-organic loads transported with flood waters and salinity stratification contribute to the anoxic conditions observed in estuaries following hurricanes and tropical storms (Tabb and Jones 1962, Jordan 1974, Van Dolah and Anderson 1991).

Wind and rainfall are responsible for most of the damage observed in non-coastal systems (Duever et al. 1994). In coastal areas, however, significant impacts may also be associated with oceanic storm surges, which may reach several meters above mean sea level (NOAA 1993). Hurricanes along the Atlantic Coast and Gulf Coast can result in substantial storm-surge impacts due to the relatively flat terrain (Chabreck and Palmisano 1973, Drennan 1991, NOAA 1993, Wanless et al. 1994). For example, Hurricane Donna's (1960) storm surge at Cape Sable, Florida, extended 2 km inland and converted mangrove forests into unvegetated marine subtidal environments (Wanless et al. 1994).

Hurricane-induced storm surges transport salt water, sediments, and particulate organic material inland to freshwater and brackish wetlands and low-lying terrestrial areas. Salinities may remain elevated in terrestrial soils and freshwater marshes for >1 yr (Chabreck and Palmisano 1973, Blood et al. 1991), causing significant long-term changes in plant communities (Hook et al. 1991).

Nutrient cycling and biogeochemistry

Hurricanes alter the timing, amount, and quality of nutrient input to terrestrial and wetland ecosystems. In forested ecosystems, hurricanes generate a large pulse of litterfall containing above-average concentrations of nutrients and labile organic carbon (Blood et al. 1991, Frangi and Lugo 1991, Lodge and McDowell 1991, Lodge et al. 1991, Whigham et al. 1991). Litterfall nutrient inputs associated with a single storm may range from 2 to 5 times the average annual input (Blood et al. 1991, Lodge and McDowell 1991, Lodge et al. 1991, Whigham et al. 1991). Increased nutrient inputs are associated both with the magnitude of litterfall and the timing of the event. Plants normally translocate many of the nutrients contained in needles and leaves prior to normal litterfall. Thus, storm-induced litterfall, particularly when it occurs prior to normal litterfall, may contain up to 3 to 5 times more nitrogen, phosphorus, magnesium, and potassium than average litter (Blood et al. 1991, Frangi and Lugo 1991, Lodge and McDowell 1991, Whigham et al. 1991).

Following Hurricane Hugo, for example, nitrogen inputs were approximately double those associated with average annual litterfall inputs in both a Puerto Rican tropical forest (Lodge et al. 1991) and a South Carolina coastal forest (Blood et al. 1991). Labile nu-

trients contained in the litterfall were rapidly transferred to soil pools. Soil ammonium pools rapidly increased five-fold in Puerto Rico and 10–1500 times pre-hurricane concentrations in South Carolina (Blood et al. 1991, Stuedler et al. 1991). Nutrient transfer from the litter may be enhanced by post-hurricane fires, which can consume all surface necromass and much of the soil organic matter (Whigham et al. 1991). Such fires are frequently associated with the large fuel build-up resulting from widespread forest damage.

The fate of available nutrients varied with the type and magnitude of storm damage to the terrestrial ecosystems. At forests in both Puerto Rico and South Carolina, soil nutrient pools increased rapidly and were projected to remain elevated years after the storm (Blood et al. 1991, Sanford et al. 1991). The highest concentrations of nitrate coincided with peak ammonium concentrations in the Puerto Rican forests. Peak net nitrogen mineralization and nitrification rates were directly correlated with peak concentrations of nitrate and ammonium in soil solution. Soil ammonium concentrations increased dramatically in the South Carolina coastal forest while soil nitrate concentrations declined to undetectable levels. High soil salinities associated with the seawater inundation increased ammonium concentrations through cation displacement by sodium ions (Blood et al. 1991). In both South Carolina and Puerto Rico, nutrients were not immediately sequestered by vegetation (Blood et al. 1991, Lodge et al. 1991) because root damage associated with physical stress (tree swaying, partial uprooting) and decreased water potential of the soil solution may have hindered uptake of nitrogen by plant roots. Reduced microbial immobilization of nitrogen occurred immediately after the hurricane. Reducing soil conditions resulted from large labile organic-matter inputs (Lodge and McDowell 1991), and additional inhibition of microbial processes occurred due to salt stress (Blood et al. 1991). In South Carolina, chloride concentrations were sufficiently high and pH sufficiently low to inhibit the conversion of ammonium to nitrate (Roseberg et al. 1986). Recovery of soil processes was more rapid at the Puerto Rico site, and soil microbial biomass increased within months and played a significant role in immobilizing phosphorus and nitrifying ammonium.

Hurricane Hugo altered nitrogen and carbon trace-gas fluxes from the Puerto Rican tabonuco forest (Lodge and McDowell 1991). One month after the storm, rates of N_2O fluxes were 15 times higher in heavily damaged sites than in control sites and remained elevated for >7 mo. Peak N_2O fluxes coincided with maximum soil pools of ammonium and nitrate. Forest methane uptake and CO_2 emissions were significantly reduced for >1 yr after the storm (Stuedler et al. 1991). For the year following the storm, N_2O flux increased three-fold, and CO_2 and methane fluxes were reduced by ≈50%. The large carbon input from litter

and roots may have lowered oxygen tension as the organic material decomposed and changed soil redox. Lower oxygen pressure may have inhibited oxidation of methane and CO_2 formation (potentially shifting to anaerobic metabolism), and may have enhanced denitrification rates.

Few studies have documented the hurricane-induced material transfer across the landscape, the magnitude of which can be substantial. Frangi and Lugo (1991), for example, observed significant exports of biomass and nutrients from montane forests to adjacent floodplain forests. Similarly, studies have noted the transfer of marsh muds, sediments, *Spartina* detritus, and mangrove litter from coastal marshes to adjacent coastal forests (Chabreck and Palmisano 1973, Gardner et al. 1991a, Wanless et al. 1994), but no quantitative measures of biomass or nutrients were reported.

Vegetation

Upland forests, riparian zones, mangrove swamps, hardwood hammocks, bottomland hardwoods, and isolated forested wetlands often sustain substantial damage from winds, which can snap boles, uproot trees, and completely defoliate vegetation (Gunter and Eleuterius 1973, Weaver 1986, Gable et al. 1990, Brokaw and Walker 1991, Ogden 1992, Wunderle et al. 1992, Duever et al. 1994). In South Carolina, for example, 1.8×10^6 ha of coastal forest lands were damaged by wind and water associated with Hurricane Hugo (Hook et al. 1991, Putz and Sharitz 1991). The hurricane downed 70% of all sawtimber on the 100,000-ha Francis Marion National Forest and damaged over 6×10^9 board feet of pine and hardwood sawtimber statewide (Cely 1991). Similarly, Hurricane Andrew damaged up to 80–95% of the mangroves in the Everglades National Park by trunk snapping and uprooting (Smith et al. 1994).

The extent of damage to coastal forest ecosystems is influenced by species composition, age structure, and geomorphic characteristics as well as by hurricane characteristics. In coastal environments, additional damage can result from oceanic storm surges that carry high-ionic-strength water and organic-rich sediments several kilometers inland, and become trapped in low-lying wetland areas (Chabreck and Palmisano 1973, Michener et al. 1991, Cablk et al. 1994, Duever et al. 1994). Salt spray associated with winds can have local effects on vegetation through desiccation and salt stress (Hook et al. 1991). Tree mortality in a South Carolina coastal forest, as a result of soil salinization by the Hurricane Hugo storm surge and subsequent pine bark beetle infestation, approximated tree mortality associated with the hurricane's high winds (Cablk et al. 1994).

Although tree species exhibit variable responses to hurricane-force winds (Boucher et al. 1990), several general trends are evident. Coastal trees in South Car-

olina were less damaged by Hurricane Hugo than those trees with wider geographic ranges, and larger trees were more heavily damaged than smaller trees (Gresham et al. 1991). Similarly, hurricanes usually inflict the greatest damage in mangrove forests on the largest trees (Roth 1992, Wunderle et al. 1992, Smith et al. 1994), and large trees in tropical ecosystems have been observed to be uprooted more frequently than smaller trees (Lugo et al. 1983). Hurricanes have been suggested to be a major selective force in coastal forest structure in South Carolina (Gresham et al. 1991).

Direct and indirect damage from hurricanes initially reduces primary production and may increase translocation of photosynthate. However, through the creation of gaps and increased nutrient turnover and availability, hurricanes ultimately stimulate net primary production. The increased growth comes from production of new leaves, seedling generation, stump sprouting, and a flush of understory vegetation (Bellingham 1991, Brokaw and Grear 1991, Walker 1991, Whigham et al. 1991). The appearance of new leaves, sprouting, and seedling regeneration were generally rapid following Hurricane Hugo. For example, Walker (1991) observed new leaves and stems sprouting within 7 wk at the Puerto Rican study site. Similarly, Whigham et al. (1991) observed a rapid increase in leaf-area index within 17 mo following Hurricane Gilbert and higher relative growth of all tree species in the 5 yr following Hurricane Gilbert than in the 5 yr prior to the hurricane.

Wetland marsh communities are differentially affected by hurricanes and tropical storms. Saltmarsh cordgrass (*Spartina alterniflora*), black needlerush (*Juncus roemerianus*), and common reed (*Phragmites communis*) were minimally affected by Hurricane Camille in the Mississippi River Delta (Chabreck and Palmisano 1973). Turtle grass (*Thalassia testidinum*) beds in south Florida appeared undisturbed after Hurricane Andrew (Ogden 1992). Emergent macrophytes are frequently damaged, but there is generally no long-term effect in natural brackish-water marshes (Conner et al. 1989). Woody vegetation is likely to be more damaged than herbaceous vegetation (Craighead and Gilbert 1962). Altered marshes are generally more heavily affected than natural sites (Conner et al. 1989), and emergent macrophytes present in impounded freshwater wetlands can experience high mortality as a result of saltwater inundation (Chabreck and Palmisano 1973).

Animal populations

Hurricanes are capable of differentially affecting resident organisms, and can cause substantial ecological disturbance (Lugo et al. 1983, Sousa 1984, Boucher et al. 1990). Hurricanes can disrupt estuarine and riverine salt wedges, causing widespread mortality in numerous stenohaline vertebrates (Robins 1957) and invertebrates (Stone and Reish 1965, May 1972, Andrews 1973). For example, following Hurricane Hugo in

South Carolina, water quality upriver in the Ashley River was affected as a result of hypoxia (due to debris and resuspension of highly reducing bottom sediments) and salinity changes. Fish and decapod crustacean populations were significantly reduced, but increased densities were observed downstream, suggesting that populations had moved in response to the altered water quality (Knott and Martore 1991). Water quality recovered within 2 mo of the storm, even in the most heavily affected areas (Knott and Martore 1991). Overall, effects on secondary producers were immediate and severe, but of limited duration (Knott and Martore 1991). Hurricane Andrew in south Florida removed detritus and organic materials needed as a nutrient source by mangroves and lowered oxygen levels to lethal minimums for several species of fish, creating plumes of hydrogen sulfide gas (Ogden 1992).

Many invertebrate and vertebrate populations are minimally affected by hurricanes and tropical storms or are highly resilient to such disturbances. Freshwater shrimp (*Atya lanipes*) were washed out of higher elevation streams in Puerto Rico due to Hurricane Hugo, but not from middle- and lower elevation streams where abundant food resources (decomposing leaves and algae) allowed this generalist consumer to increase to the highest population density ever recorded. Debris dams in headwater streams create good environments for such consumers, making them somewhat resilient after disturbance (Covich et al. 1991). Alligators were also displaced, but not killed, in coastal Louisiana following Hurricane Audrey (Ensminger and Nichols 1958). Similarly, Hurricane Hugo did not affect adult populations of the most common leptodactylid frog (*Eleutherodactylus coqui*) in Puerto Rico, which increased after the storm because of an increase in retreat sites made available by increased litter, and a decrease in predation (Woodbright 1991); but juveniles suffered high mortality as a result of the storm, possibly because of desiccation.

Insects may also survive storms relatively well because of the persistence of their larvae and pupae (Waide 1991b). However, walking stick (*Lamponius portoricensis* and *Agamemnon iphimedeia*) and most snail populations (*Caracolus caracolla, Nenia tridens,* and *Gaeotis nigrolineata*) were drastically reduced after Hurricane Hugo because of flooding during the storm, and increased temperatures and decreased humidity that likely affected early growth forms of these organisms (Willig and Camilo 1991). The low mobility of these species coupled with widespread habitat damage may result in low recruitment into affected areas and slow long-term recovery of these populations (Willig and Camilo 1991).

Hurricane Andrew's immediate effects on terrestrial vertebrate populations appeared to be minimal (Ogden 1992). However, flooding can drown terrestrial vertebrates, including mammals, especially when they are

raising young. For example, storms leading to increased inundation of coastal wetlands increase muskrat mortality, especially juveniles flooded in lodges (Kinler et al. 1990). Approximately 25% of loggerhead turtle (*Caretta caretta*) nests not hatched were destroyed by Hurricane Hugo in South Carolina (Cely 1991). Furthermore, Hurricane Hugo's storm surge appeared to significantly reduce whitetail deer (*Odocoileus virginianus*) and squirrel (*Sciurus* spp.) populations in selected areas (Cely 1991). Nutria, muskrat, raccoon, rabbit, and deer populations were significantly reduced in coastal Louisiana following Hurricane Audrey (Ensminger and Nichols 1958). Gunter and Eleuterius (1971) reported widespread mortality among harvest mice (*Reithrodontomys humulis*) and raccoons in the wake of Hurricane Betty in Mississippi.

Despite the immediate acute effects observed for many terrestrial vertebrate species, high population densities in adjacent unaffected areas and relatively high mobility of the individual species likely result in rapid recovery of populations in affected areas. Exceptions would include those species that already have declining populations or are severely restricted in habitat. For example, gopher tortoise (*Gopherus polyphemus*; Kushlan and Mazzotti 1984) and American Crocodile (*Crocodylus acutus*; Ogden 1978) populations may be limited in size and distribution by storms in south Florida.

Avian populations

Many coastal wetland birds are easily monitored, and the impact of hurricanes on their distribution and abundance is better known than that of other wetland fauna. Hurricanes affect wetland avifauna in numerous ways (Table 2). Most studies of storm effects have been short-term investigations documenting population responses to such perturbations, and the subsequent recovery of populations to pre-storm levels (e.g., Askins and Ewert 1991, Cely 1991, Covich et al. 1991, Waide 1991*a*, *b*, Wunderle et al. 1992, and references therein). Detailed studies of the processes governing species responses (e.g., Pérez-Rivera 1991, Shepherd et al. 1991, Wunderle et al. 1992), as well as those investigating the relative vulnerability of different species to storms (Wunderle et al. 1992, Bildstein 1993) are less common. Patterns emerging from such studies offer insights into how global-warming-induced changes in hurricane and tropical-storm activity can affect coastal-wetland ecosystems.

Avian communities inhabiting coastal wetlands are characterized by their high population densities and considerable species richness (Bildstein et al. 1991). Many are numerically dominated by waterfowl (Anseriformes), long-legged wading birds (Ciconiiformes), and gulls, terns, and shorebirds (Charadriiformes) (Bildstein et al. 1982). At many sites, numbers of birds increase substantially during fall and spring migration,

when some localities host significant portions of entire species' populations (Spaans and de Jong 1982, Hicklin 1987, Myers et al. 1987, Morrison and Ross 1989).

Many birds appear to be resilient to disturbances (Glynn et al. 1964, Holliman 1981, Milan 1989, Powell et al. 1989). Other birds are not resilient to disturbances, including populations of local endemic (Raffaele 1977) and endangered species (Cely 1991), for which hurricanes present a real and present danger (Ewens et al. 1987).

Hurricanes kill birds directly, both as a result of excessive wind and rain (Kennedy 1970), and by drowning (cf. Sutton 1945, Robertson and Paulson 1961, Glynn et al. 1964, Marsh and Wilkinson 1991). Storm-induced mortality appears to be greatest when hurricanes strike during the breeding season. Birds nesting on beaches and on dunes may be especially disturbed by hurricanes, because most nest directly on the ground, and because these habitats are likely to be severely affected by wind and wave action during such storms (Gardner et al. 1991*b*). Brackish and freshwater marsh-nesting birds fare somewhat better than dune- and beach-nesting species, because marshes are often buffered from tropical storms by dune ridges, and because many of the species nest above the ground in herbaceous and woody vegetation (Shepherd et al. 1991).

Species are affected by the extent to which the vegetation they nest in is damaged by the storm, as well as by their ability to reconstruct destroyed nests. Those nesting in or near the canopy are vulnerable to wind damage. Hurricanes often inflict the greatest damage in forested wetlands on the largest trees (Roth 1992, Wunderle et al. 1992). Birds that nest and roost in such vegetation, especially primary cavity-nesters, are affected more than those nesting lower in the canopy. A case in point is the Red-cockaded Woodpecker (*Picoides borealis*), a southeastern United States endemic that excavates its own cavities and is dependent upon mature pine–oak forests (Mengel and Jackson 1977). When Hurricane Hugo struck South Carolina in September of 1989, winds damaged 90% of the 470 known colony sites used by Red-cockaded Woodpeckers in the Francis Marion National Forest (LeGrand 1990*b*). Similarly, 24% of the Red-cockaded Woodpecker cavity trees on an 80-ha study site in southern Georgia were killed by Hurricanes Elena and Kate and tropical storm Juan in late 1985 (Engstrom and Evans 1990). Many Red-cockaded Woodpecker cavity trees (which are infected with a fungal disease and have rotten heartwood, and are further weakened by the woodpeckers' activities) snap at the cavity site itself (Engstrom and Evans 1990). Other canopy-nesting species such as Bald Eagles (*Haliaeetus leucocephalus*), which build more easily reconstructed platform nests, can recover more quickly so long as at least some trees remain available for renesting. For example, while Hurricane Hugo de-

TABLE 2. Synopsis of hurricane impacts on avian populations, and their ecological implications.

Hurricane impact	Ecological implications
Direct effects	
1) Long distance transport of individual birds (Darwin 1859, Pettingill 1970, Fussell and Allen-Grimes 1980, Le Grand 1990*a, b,* Cely 1991)	a) Reduced secondary productivity in hurricane impact zone
	b) Reduced biodiversity, including extinction, if the numbers of individuals transported is substantial
	c) Genetic restructuring of the species, if transported individuals survive and breed with local members of the same species
	d) Range expansion, if transported individuals establish themselves outside of their historic range
	e) Introduction of plant or animal propagules, parasites, and pathogens, carried on or in transported individuals
2) Death of individual birds (Sutton 1945, Robertson and Paulson 1961, Glynn et al. 1964, Kennedy 1970, Raffaele 1977, Holliman 1981, Powell et al. 1989, Cely 1991, Marsh and Wilkinson 1991)	a) Same as 1a
	b) Same as 1b
	f) Reduced secondary productivity outside of hurricane impact zone, if mortality includes migratory species
Indirect effects	
3) Destruction of nesting habitat and nest sites, leading to reduced reproductive effort and success (Marsh and Wilkinson 1991, Shepherd et al. 1991, Bildstein 1993)	a) Same as 1a
	b) Same as 1b
4) Destruction of protective cover, leading to increased predation (Engstrom and Evans 1990, Cely 1991)	a) Same as 1a
	b) Same as 1b
5) Destruction of forest habitat, leading to increased brood parasitism (Cely 1991)	a) Same as 1a
	b) Same as 1b
6) Habitat destruction, leading to physiological stress resulting in outbreaks of epizootics (Anonymous 1989)	a) Same as 1a
	b) Same as 1b
7) Destruction of vegetation, invertebrate, or vertebrate prey populations, leading to reduced food availability (nectarivorous, frugivorous, some insectivorous birds, etc.) (Boucher 1990, LeGrand 1990*b,* Lynch 1991, Shepherd et al. 1991, Varty 1991, Waide 1991*a,* Wunderle et al. 1992)	a) Same as 1a
	b) Same as 1b
8) Destruction of vegetation, invertebrate, or vertebrate prey populations, leading to increased food availability (insectivorous birds feeding on detritivorous insects) (Tanner et al. 1991)	g) Increased secondary productivity
	h) Increased or decreased biodiversity, depending upon the impact of population increases on species evenness
9) Destruction of vegetation, invertebrate, or vertebrate prey populations, leading to changes in diet (Johnson and Baldasarre 1988, Dunning and Watts 1991, Lynch 1991, Pérez-Rivera 1991)	i) Trophic-web restructuring if the species stays in its original habitat and changes prey type, or localized shifts in secondary productivity if the species shifts habitats to retain the prey type fed upon
10) Flooding, leading to dispersal of concentrated piscivorous prey (cf. Kushlan 1976)	a) Same as 1a
	b) Same as 1b

stroyed 44% of the eagle nests in coastal South Carolina in the fall of 1989, 21 of 24 nests had been rebuilt by the following spring (Cely 1991).

Hurricanes transport birds in the eye of the storm, carrying them far beyond their normal range (Darwin 1859, Pettingill 1970, Fussell and Allen-Grimes 1980, LeGrand 1990*a, b,* Cely 1991). Many North American neotropical birds migrate along or across the Caribbean Sea and Gulf of Mexico at the height of the region's hurricane season (Hagan and Johnston 1992). Included among these species are the endangered Kirtland's Warbler (*Dendroica discolor*), and the possibly extinct Bachman's Warbler (*Vermivora bachmanii*) (Cely 1991). Species can expand their ranges as a result of being blown off course, thereby altering community structure in the newly invaded areas (Thurber 1980). Island endemics may be transported either to extinction

(Raffaele 1977), or to new areas of settlement (Raffaele and Roby 1977). Aside from direct transport during the event, hurricanes may move birds indirectly afterward by creating new habitats for displaced and invading species (Johnson and Baldasarre 1988, Dunning and Watts 1991, Waide 1991*b*).

Hurricane damage to vegetation also alters feeding opportunities of birds. Flooding can affect species whose prey base is directly destroyed by the flood, either from drowning or osmotic stress, or whose prey base is dispersed by flooding and is no longer readily available as a food resource (cf. Kushlan 1976). Herbivorous birds tend to be affected moreso than insectivorous species. Waterfowl overwintering in impounded freshwater wetlands along the Santee River in coastal South Carolina, for example, were severely affected by saltwater intrusion of the area that lead to the de-

struction of their food resource (LeGrand 1990*b*). In wooded areas, frugivores and nectarivores appear to be especially vulnerable (Boucher 1990, Lynch 1991, Varty 1991, Waide 1991*a*, Wunderle et al. 1992; but see Pérez-Rivera 1991). Insectivores, granivores, and carnivorous wading birds display mixed responses, with some species exhibiting increases, and others, declines (Shepherd et al. 1991, Waide 1991*b*). Many insectivorous species benefit from increases in the numbers of detritivorous insects (Tanner et al. 1991) feeding on downed vegetation.

In many instances, observed population declines appear to represent the displacement of individuals rather than mortality, with populations rebounding soon after their food resources reappear (cf. Bénito-Espinal and Bénito-Espinal 1991). For example, Hurricane Joan, which left fewer than 20% of the trees standing in an Atlantic Coast rain forest in Nicaragua, resulted in the virtual absence of birds for several months. Within a year and a half, however, neither species richness nor overall avian density appeared to have been affected by the storm, suggesting that displaced birds returned when food resources became available (Will 1991).

Birds are well-known vectors of plant propagules, and those propagules transported by birds during storms may seed the areas in which they finally settle (Darwin 1859). Hurricane-induced damage to vegetation can affect competitive dynamics within the avian community (Waide 1991*b*), as well as increase vulnerability to natural predation (Engstrom and Evans 1990, Cely 1991), human persecution (Thompson 1900), water- and airborne epizootic diseases (Anonymous 1989), and brood parasitism (Cely 1991), the last by opening up forested wetlands to Brown-headed Cowbirds (*Molothrus ater*).

Many birds inhabiting coastal wetlands breed in large assemblages at traditional colony sites, and many exhibit considerable breeding-site tenacity (Bildstein et al. 1991). Avian responses to flooding indicate that site tenacity may play a major role in determining where birds breed in subsequent years (cf. Wiens et al. 1986). Recolonization of areas following flooding may be slow, since birds that breed elsewhere during adverse conditions will continue doing so until conditions in the new area become deleterious (Knopf and Sedgwick 1987). Hurricane damage to individual coastal wetlands can severely disrupt subsequent breeding efforts of substantial proportions of regional populations of coastal avifauna, affecting both overall abundance and species richness (Marsh and Wilkinson 1991, Shepherd et al. 1991, Bildstein 1993).

Hurricane effects may be spatially disjunct if affected populations are migratory. In 1990 in New Jersey, for example, the Clapper Rail (*Rallus longirostris*) breeding populations dropped by 78% to their lowest levels in 40 yr (Ferrigno 1990). Many New Jersey rails overwinter in southeastern coastal marshes (Bildstein

et al. 1982, Root 1988), and would have been present there the previous fall when Hurricane Hugo passed through that region (Marsh and Wilkinson 1991).

*Complex interactions and indirect effects:
An avian example*

The benefits of long-term studies in assessing the relative importance of aperiodic disturbances on ecological patterns and processes are well documented (Ehrlich et al. 1980, Callahan 1984, Coull 1985, Grant and Grant 1987, Likens 1988, Mooney 1991). The extended example that follows illustrates the value of such studies in understanding the complex and far-reaching consequences of climate change on coastal-wetland ecosystems.

In 1981, Bildstein began studying the feeding and breeding ecology of White Ibises (*Eudocimus albus*), the most abundant wading bird in coastal South Carolina (Bildstein and Brisbin 1990, Bildstein 1993). White Ibises are an important avian consumer at the 7805-ha North Inlet Estuary near Georgetown, South Carolina, where they breed on Pumpkinseed Island, a 9-ha, low-elevation, tidally inundated, marsh island at the southern edge of the site. Pumpkinseed Island annually hosts one of the largest traditional mixed-species wading-bird (order Ciconiiformes) breeding colonies on the eastern seaboard of North America (Parnell 1968, Osborn and Custer 1978). In most years, ≈10 000 pairs of wading birds nest on the island (Bildstein 1993). Although nine species of wading birds have been recorded breeding at the site, the colony is dominated by White Ibises, Tricolored Herons (*Egretta tricolor*), Great Egrets (*Casmerodius albus*), Snowy Egrets (*E. thula*), and Glossy Ibises (*Plegadis falcinellus*) (Bildstein 1993).

Hurricane Hugo made landfall 80 km southwest of Pumpkinseed Island on 22 September 1989 as a category 4 storm (Hook et al. 1991). At the time of the storm, winds in the area were estimated at 87 km/hr, with gusts of 138 km/hr (Gresham et al. 1991). Eroded bark and marsh-grass detritus clinging to trees in maritime forests in the area indicated the accompanying storm surge reached 2–3 m above mean high tide. Salt water penetrated up to 5 km into the nearby coastal pine (*Pinus* spp.) forest (Gardner et al. 1991*a*). Despite its destructive nature, the hurricane had only a modest impact on the North Inlet salt marsh (Gardner et al. 1991*a*). Pumpkinseed Island was little damaged, with erosion limited to losses typical of annual winter storms.

Although an estimated 60–75% of the aboveground woody biomass of marsh elder (*Iva frutescens,* a salt-tolerant shrub used as a nesting substrate by breeding Great and Snowy Egrets) had been stripped from its roots, most of the island's herbaceous vegetation, which is used for nesting by breeding White and Glossy Ibises and Tricolored Herons, was little disturbed. Al-
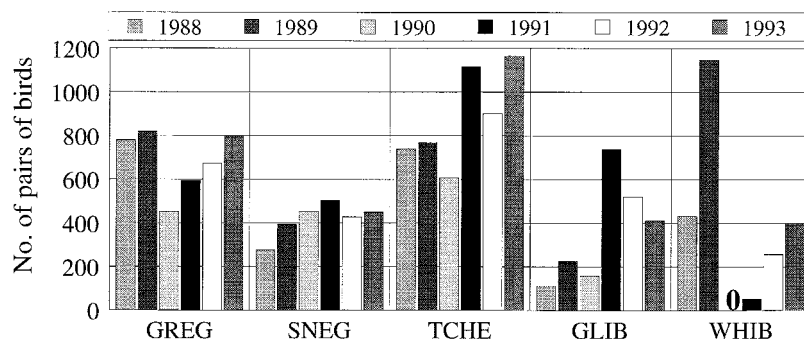
FIG. 3. Numbers of pairs of Great Egrets (GREG), Snowy Egrets (SNEG), Tricolored Herons (TCHE), Glossy Ibises (GLIB), and White Ibises (WHIB) at Pumpkinseed Island, South Carolina, in 1988 and 1989, before the passage of Hurricane Hugo, and in 1990–1993, after the storm. Note that White Ibis numbers are actually 10 times those indicated on the figure.

most all of the >2-m culms of giant cordgrass (*Spartina cynosuroides*) at the site remained upright after the storm. A 40-cm-thick layer of wrack covered much of the site's remaining elder, and some of the bird-manure-rich peat that had accrued beneath the elder was heaped over nearby herbaceous vegetation.

Most of the site's migratory wading-bird population had already migrated out of the region by late September (Shepherd et al. 1991), and so the storm's impact on the colony site was delayed by almost a year. Population densities of two of the five principal breeding species at the site, Great Egrets and White Ibises, declined substantially during the two breeding seasons following the storm from what they had been during the two years prior to the event. Population densities of the other three species either declined less substantially, increased, or remained similar (Fig. 3).

Almost certainly, the decline in Great Egrets was related to the destruction of nesting substrate. Unlike other species nesting at the site, Great Egrets nest almost exclusively in marsh elder (Shepherd et al. 1991), most of which was eliminated by the storm. This notion is supported by the fact that much of the woody vegetation that remained after the storm was quickly colonized the following spring by returning Great Egrets, and that a few late arrivals nested on the surrounding detrital wrack and even on the ground where elder had been growing a year earlier, while other late nesters

apparently recolonized a previously abandoned colony site 7 km away (T. Murphy, *personal communication*). Regeneration of the marsh elder stand to pre-storm levels by spring of 1993 (K. L. Bildstein, *unpublished data*), occurred coincidentally with the reestablishment of pre-storm populations of breeding Great Egrets (Fig. 3). The more substantial disruption of White Ibis breeding ecology at the site merits the following more complicated, but equally substantiated explanation (Bildstein 1993).

White Ibises have been the most numerous breeding bird at Pumpkinseed Island at least since the mid-1970s (Osborn and Custer 1978, Bildstein 1993). Since 1979, when detailed annual records were initiated for the species (Bildstein et al. 1990), the numbers of White Ibises breeding at the site fluctuated from just under 2000 to just over 20 000 pairs prior to the hurricane (8761 ± 4922 pairs [mean ± 1 SD]; Fig. 4) (Bildstein 1993). Indeed, for most of the last 25 yr White Ibises have been the most abundant wading bird in coastal North and South Carolina, and until the passage of Hurricane Hugo, Pumpkinseed Island had served as the largest and most consistently used Atlantic Coast breeding site for the species. Although a few late-nesting White Ibises on Pumpkinseed traditionally nest in marsh elder, >90% of the population nests in herbaceous vegetation at the site, especially black needlerush (*Juncus roe-*
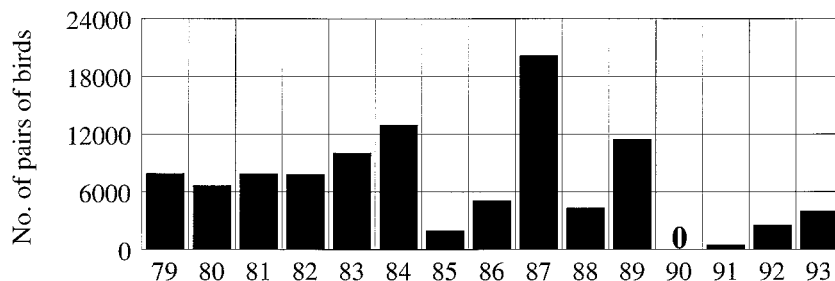

FIG. 4. Numbers of pairs of White Ibises breeding at Pumpkinseed Island, South Carolina, 1979–1993. Hurricane Hugo passed through the area in the fall of 1989, after that year's breeding season.

merianus) and saltmarsh bulrush (*Scirpus robustus*), two species that were little affected by the storm.

Unlike the egrets mentioned previously, however, White Ibis activity at the site was not directly affected by Hurricane Hugo's impact on the ibis colony, but rather by the storm's impact on the species' freshwater feeding habitats. Throughout their range, White Ibises customarily feed in large flocks on invertebrate and vertebrate prey (Kushlan and Bildstein 1992). Outside of the nesting season the species often feeds in coastal mangrove swamps and *Spartina* marshes, where it specializes in fiddler crabs (*Uca* spp.). When rearing young, however, ibises switch to feeding in freshwater wetlands, usually on crayfishes (*Procambarus* spp.), which in most years form the bulk of the nestling diet (Bildstein 1993). Parent ibises make this switch, even though doing so requires them to fly long distances (sometimes as far as 50 km, one-way) to reach abundant crayfish prey.

An experiment conducted in 1985 in which nestling White Ibises were hand-reared on crayfish and fiddler-crab diets revealed that parental ibises do so because nestling ibises—despite the presence of a developing salt gland—suffer salt toxicity when fed a diet high in osmoconforming brackish-water fiddler-crab prey (Johnston and Bildstein 1990). (Adult ibises are able to survive on predominantly fiddler-crab prey because they are able to seek out and drink freshwater to dilute the salt content of their diet, something nestlings are unable to accomplish. There is no indication that parent ibises are capable of ferrying freshwater to their pre-fledged young [Bildstein 1993].) White Ibises are not unusual in this regard. Many species of birds, even those nesting in saline wetlands, require freshwater prey and freshwater for their young (cf. Mitcham and Wobeser 1988, Johnston and Bildstein 1990, Bennett et al. 1992).

As a consequence of these physiological constraints, White Ibises breeding in coastal areas are forced to travel long distances inland to find sources of freshwater prey for their young. In coastal South Carolina, when they are unable to do so, both breeding effort and success are reduced markedly (Bildstein et al. 1990, De Santo 1992). In fact, the availability of freshwater crayfish was largely responsible for the fluctuations in White Ibises' breeding efforts at the Pumpkinseed Island colony site throughout the 1980s (Bildstein 1993).

The storm surge that accompanied Hurricane Hugo inundated many of the natural and impounded freshwater wetlands used by ibises breeding at Pumpkinseed Island (De Santo 1992), substantially reducing primary productivity and crayfish availability in the region (Bildstein 1993). Indeed, crayfish population density at a freshwater wetland near the colony site decreased to <25% of their pre-storm levels following the storm (Bildstein 1993). Almost daily observations at the col-

ony site throughout the spring of 1990 revealed that most northbound ibises searching for breeding sites flew around the island for several minutes before departing in the direction of traditional freshwater feeding sites. Few, if any, of these birds were seen again near Pumpkinseed that spring. Coincidental with these events, and for the first and only time, several thousand ibises attempted to nest in herbaceous vegetation near another colony site 100 km northeast of Pumpkinseed Island. These observations suggest that ibises failed to breed at Pumpkinseed Island since the hurricane had disturbed an essential food resource (Bildstein 1993).

By the spring of 1991, as crayfish populations in the region had begun to rebound, ibises once again bred on Pumpkinseed Island, albeit in numbers that were <10% of the pre-storm average. By 1993, crayfish populations appeared to have returned to pre-storm levels, and White Ibis breeding effort at the site had increased to about 50% of what it had been prior to the Hurricane (Fig. 3). Part of the reason for the delay in species return to the pre-storm average may be related to colony site tenacity (cf. Knopf and Sedgwick 1987), with individuals that bred elsewhere in the wake of the storm returning to their new breeding sites, unless or until they failed there, rather than to Pumpkinseed Island. Populations of the other three species of wading birds that breed in large numbers at Pumpkinseed Island were less affected by the storm because their feeding resources differed from those of White Ibises and were not disrupted by the hurricane (Bildstein 1993).

By affecting the breeding ecology of White Ibises at the colony site, Hurricane Hugo also influenced avian-induced nutrient fluxes in the surrounding estuary. Because ibises feed almost exclusively on freshwater crayfishes while raising their young each spring, and because they import this prey from freshwater wetlands outside of the estuary, ibises transport nutrients (nitrogen, phosphorus, potassium, and calcium) into the estuary when breeding at the site (Bildstein 1993). An earlier comparison of the magnitude of this nutrient source compared with that from atmospheric sources (precipitation, steam runoff, etc.) suggested that in some years nutrient flux from ibis feeding can be substantial (Bildstein et al. 1992). (In one of two years of study, for example, White Ibises imported into the estuary 9% as much nitrogen and 33% as much phosphorus as did atmospheric sources [Bildstein et al. 1992].) Nutrient availability is known to affect the primary productivity in saltmarshes (Pomeroy et al. 1981). Because ibises import nutrients during the spring–summer breeding season, when vegetation such as *Spartina* is growing rapidly at the site, their influence as nutrient sources may be significant.

Ibises breeding at Pumpkinseed Island apparently moved elsewhere to breed in response to Hurricane-Hugo-induced losses of feeding opportunities in South Carolina, and the reproductive output of the species as

a whole appeared to have been little affected by this event. Ibises are nomadic specialists (sensu Anderson and Erlinge 1977), species whose local breeding populations appear to fluctuate regionally in response to changing feeding conditions (Bancroft 1989, Bildstein 1993). Indeed, recently compiled historic evidence suggests that the species ''range expansion'' into South and North Carolina earlier this century may, in fact, represent the ''reestablishment'' of the species in the region following intense hurricane activity at the turn of the century (Bildstein 1993). The extent to which changes in the frequency and intensity of tropical storms will fragment existing habitats and affect the ability of ibises to respond to a catastrophe in one portion of their range by moving to other portions, will depend upon the magnitude of the increases, the resiliency of affected areas to return to pre-storm conditions, and the extent to which rising sea level affects the availability of breeding habitats. That human development pressure is simultaneously fragmenting and reducing available breeding habitat exacerbates the potential impact of rising sea level and changes in hurricane and tropical storm activity. It is becoming increasingly obvious that social species with large ecological neighborhoods (e.g., White Ibises, the once-numerous, but now-extinct Passenger Pigeon [*Ectopistes migratorius*], etc.) are especially vulnerable to habitat fragmentation (Temple 1986, Bucher 1992). The ability of White Ibises to respond to current disturbance regimes in no way ensures their ability to do so amidst increased hurricane and tropical storm activity.

The example above reveals the complex nature of the responses of coastal wading birds to hurricanes, as well as the value of long-term studies in separating effects of even catastrophic events from ''background noise.'' Indeed, examination of the 6-yr six-species data set that includes pre- and post-hurricane observations, reveals three increases in species populations, as well as two decreases (Fig. 3), and might lead one to conclude that the changes represented responses to stochastic events in the system, rather than responses to the hurricane. However, long-term studies conducted at the site (Fig. 4), coupled with controlled (Johnston and Bildstein 1990) and natural experiments (De Santo 1992), enabled us to develop an understanding of the White Ibises's dependence on freshwater wetlands in the region (Bildstein 1993) and determine that populations of wading birds breeding at Pumpkinseed Island were both directly affected by storm-induced habitat alteration and indirectly affected by freshwater-wetland disturbances that reduced food resources.

Hurricanes represent significant abiotic disturbances that have naturally shaped population and ecosystem patterns and processes. From this review, it is apparent that hydrology and ecosystem structure, nutrient cycling and biogeochemistry, vegetation, and animal populations all respond to the frequency, intensity, and timing of hurricanes and tropical storms. Comparative studies and long-term research programs have illustrated the high degree of resilience of many populations and unmodified ecosystems to disturbance, the importance of considering indirect as well as direct effects, and the high degree of complexity that characterizes many ecological responses to disturbance.

VULNERABILITY OF COASTAL WETLAND ECOSYSTEMS AND POPULATIONS TO RISING SEA LEVEL AND HURRICANES AND TROPICAL STORMS

Marsh persistence

As sea level rises, barrier-island migration is accompanied by landward retreat of the forest–marsh boundary on the landward side of marsh basins (Oertel et al. 1992). Depending on the relative rates of sea-level rise and barrier-island retreat, the lagoonal area between the barrier island and the mainland may (1) remain constant, if the two rates are in balance; (2) expand, if sea level rises faster than barrier islands retreat; or (3) shrink, if barrier islands retreat faster than sea level rises. Case 2 might occur if global climatic change preferentially influences sea-level rise over barrier-island migration, which primarily responds to the frequency and intensity of hurricanes and tropical storms. Eventually, the expanding lagoonal area may exceed the capacity of sediment sources to maintain the entire marsh, and the ratio of open-water environment to marsh surface will increase. Case 3 might occur if global climate change preferentially increases the frequency and intensity of hurricanes and tropical storms. If so, the demand for sediment by marshes will decrease and open-water environments, if present, may evolve into marshes. However, in this case it should be noted that any increases in hurricane and tropical-storm activity are likely to be accompanied by more frequent storm surges. If so, some areas of low-lying coastal forest will be salinized, resulting in unsuitable conditions for most terrestrial plant species. These salinized areas are likely to be colonized by high marsh plants. If sea level remains more or less constant, this new area of marsh may not require much sediment for its maintenance. Additional hurricane and tropical-storm activity may also increase the area of washover fans in the back-barrier environment as beach ridges are more frequently breached and spread landward. These disturbed areas are also likely to be colonized by high marsh plants.

The ability of coastal wetlands to migrate landward as sea level rises and salt water intrudes the coastal zone will be compromised significantly by human modifications, including the construction of bulkheads and river-flow management to reduce sedimentation (Titus 1988). On the other hand, increased storminess may enhance the survival of impounded marshes on the Mississippi Delta by resuspending lagoonal muds and by breaching the artificial levees.

The effect of global-climate change on the delivery of riverine sediment to the coastal environment is difficult to forecast and will be affected by concurrent land-use changes. Sea-level rise per se should have minimal effect. However, any changes in hurricane and tropical-storm activity should affect river runoff. Because sediment transport increases with discharge, the rate of sediment supply to the coastal environment should vary in response to any alteration in the frequency, intensity, and timing of hurricanes and tropical storms. This relationship may be particularly relevant for the southeastern United States. In Georgia and other Piedmont states, small-scale subsistence farming was replaced by an overwhelming dominance of cotton crops after the invention of the cotton gin in 1793. Serious erosion followed, resulting in removal of nearly all topsoil from 47% of the uplands, gullying on 44% of the land (Brender 1974), and filling Piedmont floodplains with silt and clay from the eroding uplands. Trimble (1970) reports that rapid aggradation filled many of the river valleys up to 5.5 m in depth, not only burying the original floodplain surface, but also causing the wholesale burial of bridges. Stream gradients were reduced, further affecting flooding regimes. Most (90%) of the topsoil eroded from the Piedmont since Colonial settlement has been stored on the floodplains of the region's rivers (Meade and Trimble 1974).

Erosion of topsoil subsequently reduced agricultural productivity, leading to the reversion of row-crop farming to forest land uses (Trimble 1970, Turner 1987, Odum and Turner 1990). Abandonment of farmland and regrowth of forests in uplands resulted in decreased stream discharge (Trimble and Weirich 1987), thereby altering the sediment budget of Piedmont streams. Many of these streams have since incised, and in the process have exported sediment downstream. These areas still are not in equilibrium, although many have incised to the bedrock, which halts downcutting.

If precipitation increases and Piedmont rivers and streams adjust their hydraulic geometry (width, depth) in response to increased flow, even more of this floodplain sediment will be mobilized. However, this effect might be counterbalanced by continued reforestation and increased minimum-tillage farming. Thus, the fate of coastal marshes may depend upon a complex interaction between climatic changes and land-use changes in the watersheds that supply their sediment.

Models developed to predict future states of freshwater and coastal wetlands in response to global climate change must incorporate the interactions of climate and anthropogenic effects. Human-population increases, especially in coastal areas, and further encroachment on coastal wetlands, will continue to affect rates of resource exploitation, pollution, and water use. Perhaps one of the most important determinants of coastal-wetland maintenance will be the human response to sea-level rise. Will we defend our investment in coastal infrastructure with dikes and surge barriers? If so, will these defensive structures be placed only around inhabited areas so that marshes are left to their natural fate? If wetlands are included within the defensive structures, will economic and political pressures emerge to convert these wetlands to productive use (agriculture or aquaculture) so as to help defray the cost of their defense? These questions lie beyond the scope of this paper, but nevertheless overshadow many of the ecological issues addressed here.

Ecosystem patterns and processes

The effects of changes in hurricane frequency, intensity, timing, and distribution on riparian, alluvial, and isolated freshwater wetlands will likely vary directly in response to the degree of vegetative disturbance and the extent, magnitude, and duration of flooding. Moderate vegetation disturbance could enhance growth of understory and subdominant trees by creating canopy gaps and shifting community composition to early successional species. Such changes would create the potential for greater nutrient retention by early successional communities (Vitousek and Reiners 1975) after the initial net nutrient export.

Wetland productivity is directly related to hydroperiods (Odum 1989) and freshwater input (Conner et al. 1989, Morris 1991). Changes in the frequency, intensity, and timing of hurricanes at a site may alter the effective wetland area by decreasing or episodically increasing the area flooded and flooding frequency for portions of the floodplain that are infrequently flooded. Changes in the frequency and extent of inundation could alter nutrient cycling within the wetland by affecting the size of the area that experiences sedimentation and anoxic conditions following hurricanes. For example, an increased anoxic area would potentially provide an increased nitrogen sink by increasing denitrification fluxes, and thus counterbalance (or ameliorate) effects of high inorganic-nitrogen pools from pulsed decomposition of damaged trees. If, however, flooding enhanced only the duration of inundation, anaerobic conditions could shift soil redox and the accumulated phosphorus bound in the sediments could be released to overlying waters and transported from the wetland.

Stress to vegetation caused by waterlogging can be attributed to many factors (Levitt 1980). Anoxic soil conditions reduce the growth rates of many plants (Day et al. 1993), both directly through oxygen deficiencies in the roots (DeLaune et al. 1987), and indirectly as a result of biochemical production of toxins (e.g., Day et al. 1993, Hochachka and Somero 1973). As might be expected, the impact of flooding depends on the magnitude, timing, and duration of inundation. Unfortunately, such impacts have been little studied, except to record the impact of filling reservoirs following dam construction (Day et al. 1993). Salt stress, which in-

jures plants through osmotic stress, ion imbalance, and induced nutrient deficiency (Jones 1981), can work synergistically with waterlogging to reduce the primary productivity of coastal wetlands (Day et al. 1993).

In non-alluvial coastal environments, where storm surges accompany hurricanes, the effects of the storms on ecosystem function may be longer lasting. Alteration of salinity regimes may shift forests and wetlands from sources to sinks for nutrients and organic material, reduce the transport of nutrients and organic material to the coastal ocean that are necessary for supporting oceanic production, and alter the quantity of biogenic gases emitted to the atmosphere. Salts transported in the surge have converted brackish marsh to salt marsh, and fresh to brackish marsh, and have significantly enhanced the storm damage in terrestrial systems (Chabreck and Palmisano 1973, Blood et al. 1991, Gresham et al. 1991, Hook et al. 1991, Duever et al. 1994).

Population patterns and processes

Many evolutionary biologists have argued that biotic interactions such as competition, predation, and parasitism, outweigh abiotic stress as evolutionary forces in all but the perimeter of a species range (e.g., Darwin 1859, Fisher 1930). Such an imbalance in the relative importance of biotic and abiotic effects, if it exists at all (cf. Wiens et al. 1986), is likely to shift during periods of rapid environmental change when populations are more likely to encounter abiotic stress throughout their ranges. Even when biotic factors are, proximally, more important than abiotic factors, factors such as competition, predation, and parasitism are often, in turn, controlled by abiotic factors, including salinity and hydroperiods (Dunson and Travis 1991). Increased salinity, for example, alters the competitive relationships of a number of estuarine organisms, including coastal wetland killifish in the genus *Lucania* (Dunson and Travis 1991).

Long-term effects of changes in the frequency, intensity, timing, and distribution of hurricanes and tropical storms on natural selection, extinction rates, and biodiversity are likely. For example, researchers studying the impacts of hurricanes on Caribbean avifauna have frequently noted that island species in the region tend to have broader niches than their continental counterparts (cf. MacArthur et al. 1966), suggesting that generalists are more resistant to catastrophic hurricanes (Waide 1987, Wunderle et al. 1992). If this is true, then species with broader niches and greater phenotypic plasticity are likely to be selected with increasing frequency in areas in which hurricanes become more common. As extinctions at individual sites occur, eventually beta diversity (sensu Whittaker 1960), along with gamma diversity, may be reduced as diversity indices at individual sites begin to resemble one another more closely (Harrison 1993).

Rising sea level and changes in the frequency, intensity, and timing of hurricanes and tropical storms will likely have significant effects on species that exhibit a high degree of site tenacity throughout some portion of their life cycles. For example, shorebirds often return to feed in specific wetlands along migration pathways. Arrival of shorebirds at a particular wetland depends on seasonal hydrologic cycles and is likely to be affected by changes in seasonal rainfall, as well as rising sea level (Myers and Lester 1992). Since shorebirds represent important consumers of invertebrates at such stopover sites, the addition or removal of these predators from coastal wetlands may have important effects on the structure of communities at lower trophic levels (cf. Paine 1966).

Climate change, rising sea level, and changes in the frequency and intensity of hurricanes and tropical storms will indirectly affect population patterns and processes in numerous ways. For example, wildfires that swept through Quintana Roo in the Yucatan, Mexico, less than one year following the passage of Hurricane Gilbert, had a greater effect on the avifauna than the hurricane itself (Lynch 1991). Such fires are typical after hurricanes (Perez Villegas 1980). Similarly, changes in the distributions of plants will affect animal distributions (Root and Schneider 1993). A case in point is the endangered Red-cockaded Woodpecker (*Picoides borealis*), a southeastern U.S. endemic that could spiral to extinction before newly matured coastal-pine flatwoods develop north of its present range (Root and Schneider 1993).

Because different species are likely to respond differently to global climate change (Graham 1988), existing ecological communities may eventually be replaced by entirely new assemblages of species (Root and Schneider 1993). Although the extent to which disturbance in general can affect rates of invasion in ecosystems is controversial (Lodge 1993), it has been suggested that exotic species may also increase in importance with climate change (Sweeney et al. 1992). Further, there is a growing consensus that one of humankind's greatest effects on natural systems has been to hasten the spread of exotic species (Lodge 1993). The challenges may be both to estimate which communities will be affected or what percentage of colonists will become established invaders, and to predict the likely impact of such invasions on ecosystem processes.

Global biodiversity

The world's six hurricane zones fall largely within the tropics, where over half of all terrestrial species reside (Wilson 1988). The regions also encompass numerous oceanic and continental archipelagos, home to many extremely vulnerable endemic species of plants and animals (cf. Vitousek 1988). Thus, any change in hurricane frequency, intensity, and timing is likely to have a disproportionate impact on global biodiversity.
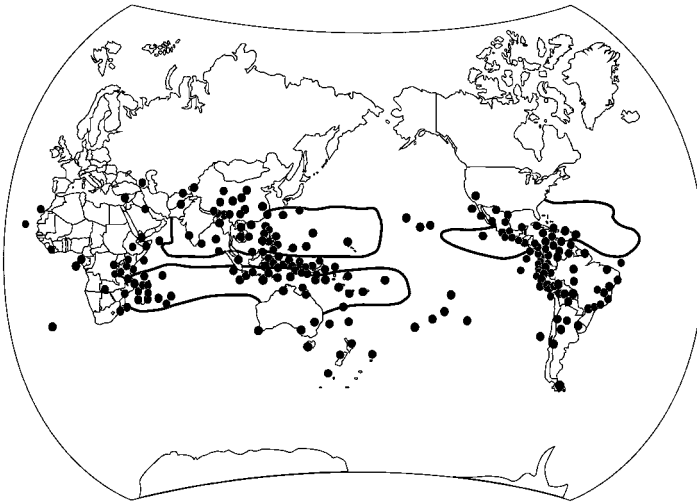
FIG. 5. Global distribution of endemic bird areas (● areas with two or more species with breeding ranges of 50 000 km^2 or less [Bibby et al. 1992]) superimposed on a map of NOAA (1988) tropical-cyclone regions (outlined with heavy black lines). Thirty-five percent of the world's 211 endemic bird areas currently lie in hurricane and tropical-storm zones. (Note that even a slight increase in the geographic distribution of hurricanes would result in substantially increased overlap.)

Consider, for example, the potential impact on avian diversity. Recent analyses suggest that 20% of all bird species—representing 70% of the world's 1000 threatened species of birds—are restricted to 221 ''endemic bird areas'' that together cover just 2% of the earth's land area (Bibby et al. 1992). Literature reviews suggest that most of these areas are also important centers for other endemic animal and plant groups. In short, much of the world's biodiversity is concentrated in these areas. A map overlaying these areas on the world's major tropical cyclone regions reveals that 35% of them are currently vulnerable to hurricanes and tropical storms (Fig. 5). The map also indicates that even a slight broadening in the geographic distribution of tropical cyclones would significantly increase the extent of that overlap.

CONCEPTUAL MODELS FOR TARGETING RESEARCH

Scientific assessments performed by the Intergovernmental Panel on Climate Change (IPCC) have emphasized the need for improving our understanding of greenhouse gas and aerosol sources and sinks, elements of the atmospheric water budget, oceans, polar ice sheets and their effect on sea-level rise, and ''land surface processes and feedbacks, including hydrological and ecological processes which couple regional and global climates'' (Houghton et al. 1990, 1992:19–20). In the 1990 IPCC report, McBean and McCarthy (1990) further highlighted the need for higher resolution climate models that adequately simulate extreme events, and suggested that we need to develop a better understanding of how ecosystems may respond to climate change by scaling up in situ studies. More recently, the U.S. Global Change Research Program (1995) emphasized the need to better understand potential aquatic and terrestrial ecosystem responses to global climate change, including their capacity for adjusting to climate change, and identifying mechanisms for enhancing ecosystem resilience to change.

Reliable predictions of how global change will affect coastal landscapes and development of prescriptive strategies for mitigating adverse impacts will require understanding the linkages among terrestrial, aquatic, wetland, atmospheric, oceanic, and anthropogenic components. The dynamics of coastal ecosystems can only be understood when the functional connections among these components are addressed. Several different scientific approaches, including modeling and theoretical studies, observational studies (including long-term ecological research), comparative studies, paleoecological studies, and focused experimentation have individually advanced our current understanding of how population and ecosystem patterns and processes respond to environmental change.

Despite our increased mechanistic understanding of ecological responses to environmental change, the predictive knowledge necessary for forecasting the ecological consequences of global change such as climate warming, rising sea level, and habitat fragmentation is lacking (Pace 1993). Projected rates of global climate change, population growth, and land-use change are unprecedented. Furthermore, the extent to which any single scientific approach can facilitate comprehensive understanding of how global change will alter coastal landscapes may be limited. For example, spatial and temporal scales of climate change are too large and the interactions among species and their physical environment are too complex to allow manipulative or experimental approaches to entirely resolve such issues. This is particularly true in the case of ''global change'' where the ''experiment'' is not under the control of ecologists and cannot be replicated. Similarly, the power of long-term research for documenting environmental change and uncovering mechanisms underlying ecological responses to such environmental change is well documented. However, such long-term studies are rare and expensive, statistical resolution of status and trends

may require an exceedingly long period of record, and critical information may be supplied only after corrective actions become cost-inefficient.

Developing a comprehensive understanding of the ecological ramifications of global change will necessitate close coordination among scientists from multiple disciplines and a balanced mixture of appropriate scientific approaches. For example, new insights and understanding could be gained through the careful design and implementation of broad-scale, comparative studies that incorporate salient patterns and processes, including treatment of anthropogenic influences. Well-designed, broad-scale, comparative studies could further serve as the scientific framework for developing relevant and focused long-term ecological research, monitoring programs, experiments, and modeling studies. For example, it may be essential to incorporate a long-term monitoring program into broad-scale, comparative studies in order to document ecological responses to global change and provide relevant data for modeling and validation (National Research Council 1986, 1988, Franklin 1989, Bruns et al. 1992). Utilizing broad-scale, comparative studies as a conceptual base could, therefore, facilitate greater scientific rigor and interaction among observational, experimental, and modeling and theoretical studies (Pace 1993).

Our assessment of the potential responses of coastal-wetland ecosystems and populations to rising sea level and changes in hurricanes and tropical storms was based on the assumption that post-hurricane studies offer predictive power because they represent a phase (recovery from disturbance) that would occur more or less frequently with altered disturbance frequencies. In the remainder of this section, we present two examples of the types of broad-scale, comparative studies that will be essential for increasing our knowledge base. Each example is drawn from hypotheses based on conceptual models for assessing ecological responses to climate change. First, a strategy employing space-for-time substitution and long-term monitoring is utilized to address the hypothesis that the spatial continuum between terrestrial coastland and estuarine aquatic ecosystems is recapitulated over time as sea level rises and ultimately subsumes the terrestrial environment. Further, the process is unidirectional and irreversible, with few localized exceptions. Second, the moisture-continuum hypothesis suggests that a warming and drying climate in a particular area will produce conditions that already exist for wetlands in the present climate, but at different geographic locations. The moisture-continuum model could, therefore, be used as a predictive tool for assessing the effects of global change on watersheds and their associated wetlands.

Example 1: Utilizing space-for-time substitution and long-term monitoring to assess impacts of sea-level rise and disturbance on coastal wetlands

Few ecosystems remain unchanged for long intervals of time, especially in response to intense human activity. In most cases, the time scale for ecosystem change is decadal to millennial. The study of ecosystem change at such time scales is often only feasible in situations where it can be shown that space acts as a surrogate for time. For example, secondary succession studies are frequently based on the premise that sequences of spatial zones are homologous with temporal sequences. Assuming that spatial and temporal variation are equivalent, temporal trends can be extrapolated from a chronosequence that is obtained by sampling populations and communities of different ages (Pickett 1989). Similarly, a space-for-time strategy has been widely used in paleolimnological studies to infer ecological and biogeochemical changes through time (Oldfield et al. 1980, Charles and Smol 1988).

Substitution of space for time represents one of the more commonly used techniques in ecology. Pickett (1989) provides a comprehensive analysis of the benefits and shortcomings of space-for-time substitution as it has been applied to studies of natural disturbance, acid deposition, stripmine recovery, marine-upwelling community succession, and structural and functional patterns of primary and secondary succession and organic-debris dam dynamics. Generally, the strengths of space-for-time substitution include its power in identifying general and qualitative trends and generating hypotheses, and its ability to document variability among replicate sites, whereas the weaknesses of the approach include the difficulty in exposing mechanisms and the difficulty in extrapolating general trends to specific sites since large areas are averaged and within-site heterogeneity is often neglected (Pickett 1989). Furthermore, important factors that control ecological dynamics, such as changes in disturbance regimes and the invasion of functionally important exotic species, may distort interpretations of space-for-time substitution (Pickett 1989). Pickett (1989) asserts that space-for-time substitution has been most successful in systems that exhibit strong successional dynamics and in cases where sites can be exactly or geomorphically dated, but cautions that the past history of sites must be evaluated in order to determine the adequacy of space-for-time assumptions.

Space-for-time substitution, coupled with long-term monitoring, may also be applied to the study of how coastal wetlands respond to episodic (hurricanes and tropical storms) and gradual (rising sea level) disturbances. For example, if geological or historical data exist that allow elements of the landscape to be dated or ordered in time, then it may be possible to reconstruct sequences of ecosystem change by studying spatial patterns in ecosystem structure and function across the landscape. Such chronological sequences of landforms commonly can be recognized in coastal wetlands where the geological evolution of these systems has been controlled mainly by the slow rise in relative sea level. Gardner et al. (1992), for example, have used

Tall <u>Spartina</u>   <u>Salicornia</u>   <u>Iva</u>   <u>Pinus / Quercus</u>
    medium <u>Spartina</u>   <u>Borrichia</u>
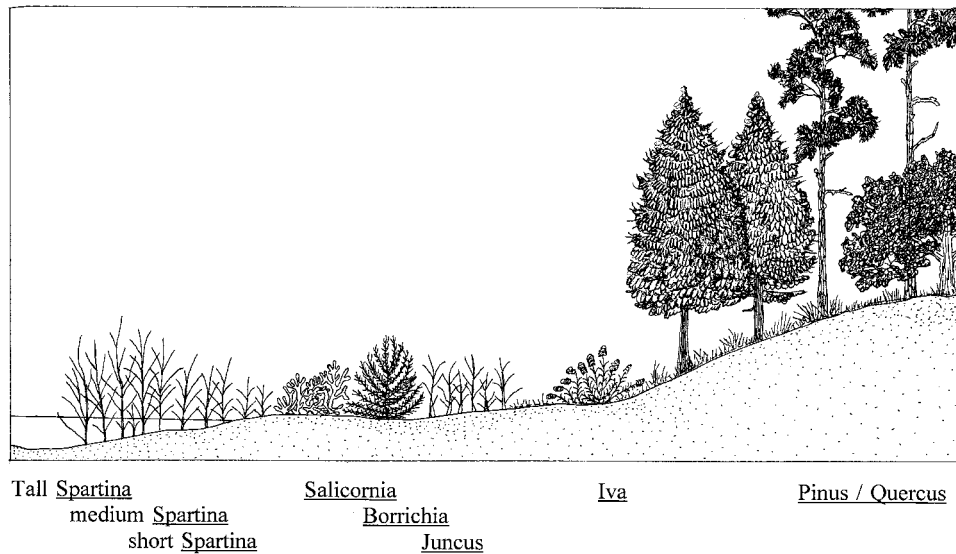   short <u>Spartina</u>   <u>Juncus</u>

FIG. 6.   Vegetation sequence observed in coastal marsh transects extending from forest to creek.

this paradigm to examine the succession of soils and botanical zones along a forest–marsh transect.

In the remainder of this section, we first present examples of how space-for-time substitution could be applied to the study of successional patterns and processes in areas undergoing conversion of forest into marsh due to rising sea level, in wetland communities that exist along elevation and salinity gradients, and in washover-fan communities and deltaic marshes. We then discuss how space-for-time substitution and long-term studies could be most effectively incorporated into broad-scale, comparative studies that are designed to increase our understanding of potential ecological responses to global change.

In unmodified coastal wetlands, slowly rising sea level causes the boundary between forest and marsh to slowly migrate upslope. In South Carolina, for example, the typical vegetation sequence (pine/oak) > cedar > *Iva* > *Juncus* > *Borrichia* > *Salicornia* > short *Spartina* > medium *Spartina*) that is observed along transects from the forest across the high marsh can be interpreted as the succession of plant communities that accompanies the conversion of forest into marsh under a regime of rising sea level (Fig. 6). This conversion of forest into marsh is indicated by the presence of forest soil horizons (spodic horizons) and tree roots at depths of a meter or so below the surface of the mid-marsh (Gardner et al. 1992). Thus, if one wishes to understand how primary production and decomposition evolve during the conversion of forest into marsh, one could make measurements of these processes along a transect from forest to mid-marsh. One also could examine how physicochemical parameters, such as soil texture and salinity, evolve by measuring these parameters along the transect. Better understanding of successional dynamics, coupled with projections of rela-

tive rates of rising sea level and accurate maps of elevation, community zonation, and boundary constraints (coastal development), could lead to improved forecasts of the potential effects of rising sea level on coastal-wetland patterns and processes. Furthermore, by observing such systems over a long period one also might discern the relative role of disturbances, such as hurricanes and accompanying wrack deposition, in triggering sudden changes in state from forest to intertidal marsh (Brinson et al. 1995).

Spatial studies of terrestrial and wetland ecosystems occurring along salinity gradients such as those conducted by DeLaune et al. (1989) in a subsiding-marsh ecosystem in coastal Louisiana provide valuable insights into the effects of storm surges and sea-level rise on nutrient processing. However, because the Louisiana marsh is not representative of all marsh ecosystems, additional studies in other coastal landscapes are needed to generalize from such analyses. In addition to nutrient processes, sea water is known to regulate biotic structure, physicochemical properties such as pH and ion speciation, related ecosystem processes such as carbon metabolism (production, decomposition), and soil processes such as sulfur and iron transformations (Patrick and DeLaune 1972, DeLaune et al. 1984, Feijtel et al. 1985, Morris and Haskin 1990, Morris 1991).

Significant insights could be gained by conducting ecosystem process studies along existing elevation and salinity gradients along the East coast. On a broader scale, for example, the space-for-time strategy can be used to study the succession of wetlands along an estuarine salinity gradient. Under a regime of rising sea level, wetlands at the low-salinity head of the estuary are newly formed while those near the mouth formed earlier and have progressed through the sequence of fresh water > brackish > saline types. The marshes

along the Pee Dee–Black River system in South Carolina offer an excellent example of this sequence. They begin at the lower end with saline *Spartina alterniflora* marshes and transform upstream gradually into *Spartina cynosuroides* followed by wild rice, then arrowweed, and finally terminate in freshwater tidal hardwood swamp at the limit of tidal influence. The peaty soil and tree stumps of the swamp can be traced downstream along the Black River where they become buried by younger marsh mud. Again, one could study the long-term succession at such sites under a regime of rising sea level by measuring structural (e.g., plant species composition) and functional (e.g., primary production, decomposition) attributes along the salinity gradient. Once data from a number of such transects along the Atlantic Coast have been obtained, it might be possible to arrange wetlands of similar type (i.e., similar tide range and salinity regime) along a north–south gradient to examine the effects of climatic conditions on wetland structure and function. Such studies, coupled with regional and watershed-specific hydrological models, would provide information that is critical for forecasting the ecological consequences of rising sea level, alterations in riverine discharge, and other global and regional changes.

The back-barrier environments along the seaward side of marsh basins likewise can be exploited for space-for-time studies. Here washover fans formed during severe storms create landscape elements of varying age. Some of these are young enough that they can be dated by air-photo time series and tied to specific storms. Older fans can be dated by carbon-14 if they overlie organic-soil horizons of even older fans or oyster reefs. Once a spectrum of fan surfaces of varying ages have been identified, one can measure the structural and functional attributes of each fan and thereby infer the ecological succession. By extending studies into the subsurface stratigraphy one is likely to encounter a sequence of buried fans that, if dated, may provide information on the frequency of severe storms (Fisher 1962, Heron et al. 1984). Information obtained in these studies could be used to forecast successional dynamics under altered regimes of hurricane and tropical-storm activity.

The space-for-time strategy also could be applied to the deltaic marshes of the Gulf coast where ecological succession on delta lobes of various ages could be studied. In some areas, such as the newly emerging Atchafalaya River Delta, marshlands are prograding into open water, rather than retreating, so that a spectrum of marsh ages exists on a single delta lobe. Transects across such a delta cross former positions of the delta front. If the ages of these former delta fronts can be determined from time series of remote-sensing imagery or stratigraphic studies, and if structural and functional attributes of landscape elements within the delta have been measured, such data could be used to develop a spatially explicit simulation model for the geological and ecological history of the delta (Costanza et al. 1990), as well as to forecast ecological responses to global and regional change.

The brief examples presented above demonstrate how space-for-time substitution could be employed in studies of deltaic and washover-fan communities, as well as freshwater, brackish, and salt marshes. By sampling important abiotic and biotic parameters in discrete communities that exist along topographic and salinity gradients, general trends, increased qualitative understanding, and new hypotheses related to ecological patterns and processes are likely to emerge in a timely fashion. By replicating such studies throughout a region, intersite variability can be documented and greater confidence can be placed on inferences that are made pertaining to how ecological patterns and processes may respond to global change (e.g., rising sea level). Furthermore, increased replication and incorporation of space-for-time substitution into coordinated, broad-scale, comparative studies could lead to increased understanding of the role of disturbances (e.g., hurricanes and tropical storms) and the invasion of exotic species in regulating ecological patterns and processes.

Increased mechanistic understanding of ecological responses to global change will require that broad-scale, comparative studies include a long-term research component. For example, long-term monitoring programs are necessary if we are to understand the factors that govern marsh persistence. A network of permanent benchmarks, and possibly radioisotope profiles and marker layers, installed at representative marsh sites along the Atlantic and Gulf coasts of the United States, would be required to directly monitor rates of sediment accumulation and erosion. If such a network was surveyed to standard Coast and Geodetic Survey benchmarks and incorporated into periodic releveling surveys, the effects, if any, of subsidence or tectonic movements on marsh persistence could be detected. Ideally, tide gauges would also be installed to permit comparisons of local sediment accumulation and releveling data with sea-level change. The resulting data could then be compared to aerial photographs and satellite images to ascertain the impacts of local changes in sea level and sediment accumulation on marsh geography and vegetation.

Existing long-term databases and new long-term monitoring programs can be very effective for determining the adequacy of space-for-time substitution assumptions, exposing mechanisms, and validating model forecasts. For example, space-for-time studies will be directly affected by site history (Pickett 1989). Dredging, diking, damming, groundwater extraction, bulkheading, and other human activities will affect relative rates of sea-level rise and the extent to which saltwater fronts migrate upstream and wetland com-

munities migrate inland or upslope. Such anthropogenic effects, as well as other important factors (exotic species, loss of key predators, etc.) can frequently be ascertained from long-term monitoring data. In many cases, current and past site conditions could be advantageously utilized in study design. In salt marshes that are experiencing high relative rates of sea-level rise, for example, dense temporal and spatial sampling along an elevation gradient would support direct observation of community successional dynamics. Similarly, large water-diversion projects, such as a 1985 project in South Carolina where much of the water from the Cooper River was diverted into the Santee River, provide an opportunity to directly study ecological changes associated with broad-scale alteration of salinity regimes that may represent archetypes of global change (Kjerfve et al. 1994).

In this example, several scenarios of how space-for-time substitution could be employed to increase our general understanding of ecological responses to rising sea level and disturbance were presented. Replication of this approach within an ecosystem and throughout a region would form the basis for broad-scale, comparative studies that lead to increased understanding of ecological patterns and processes and intra- and inter-site variability, are more likely to document large-scale human and natural disturbance impacts, and support development of probabilistic models that can be used to forecast change (Pace 1993). It is likely that more timely, general knowledge of potential ecological responses to global change will emerge from broad-scale, comparative studies than from studies focused within one or a few sites. However, neither space-for-time substitution nor broad-scale, comparative studies are mechanistically based. Thus, experimentation and long-term monitoring within at least a subset of sites will be necessary for documenting environmental change (e.g., rates of rising sea level), unraveling mechanisms of ecological responses, recording transient effects, and examining impacts and long-term recovery processes associated with the invasion of exotic species, hurricanes and tropical storms, anthropogenic influences, and other potentially important disturbances.

Example 2: Utilizing the moisture-continuum model for assessing the effects of global change and associated shifts in moisture regimes on wetland ecosystems

Predicting the effects of global climate change, population growth, and land-use change on wetland ecosystems is virtually impossible unless associated effects on adjacent watersheds are also taken into account. Although these watershed-scale effects are particularly relevant to fluvial wetlands, they also apply to depressional wetlands, peatlands, coastal-fringe wetlands, and many other wetland classes. Wetlands will be affected as their watersheds undergo climate-induced changes in temperature, water balance, vegetation cover, sediment yield, and seasonality of physical and biotic processes. One method for assessing the impact of such events is to use the moisture continuum as a predictive tool.

Before dealing with the moisture-gradient concept for wetlands, it is useful to point out differences between uplands and wetlands that may relate to global change. First, many wetlands do not rely on precipitation alone as their water source. Thus, in wetlands, plant and animal species are often influenced more by local edaphic and hydrologic conditions than their upland counterparts, which are more strongly coupled to climate. These local conditions include persistent soil moisture during droughts, anoxic soil conditions and associated stressors, and flood-related disturbances. As a result, wetlands may be more resistant than uplands to changes attributable to climate alone.

Second, there is a greater tendency for wetlands to undergo abrupt, stepwise changes rather than gradual, continuous changes in environmental factors. For example, the presence or absence of anaerobiosis and the intermittent nature of sediment movement conform more to stepwise environmental changes than a continuum of such changes. These abrupt changes are exemplified by the dynamism of arid riparian ecosystems and their dependence on channel meandering for the destruction and renewal of plant communities (Stromberg et al. 1991, Stromberg 1993).

Although modeling the response of uplands to global change is not adequate for predicting the fate of adjacent wetlands, comparing wetlands that currently exist along a moisture continuum offers considerable predictive power (Grimm 1993). This approach assumes that most, if not all abiotic variables (i.e., geomorphologic changes, seasonality of temperature and precipitation, etc.) are characteristic features of intrinsic system states along the moisture continuum. By associating salient abiotic patterns and processes with discrete states that exist along the moisture continuum, one can begin to isolate factors that control dispersal and successful colonization of plant and animal species.

The moisture-gradient model is based on the assumption that a warming and drying climate in a particular region will produce conditions that already exist for wetlands in the present climate, but at different geographic locations. Thus, as in Example 1 above, we assume that space may act as a surrogate for time. If all species had instantaneous dispersal powers, there would be no lag between climate change and the capacity of plants and animals elsewhere to disperse to the now-drier and warmer sites and colonize them. If that were so, community composition would change at the same rate as that of the environmental factors, and whole communities would shift intact (Paine 1993)
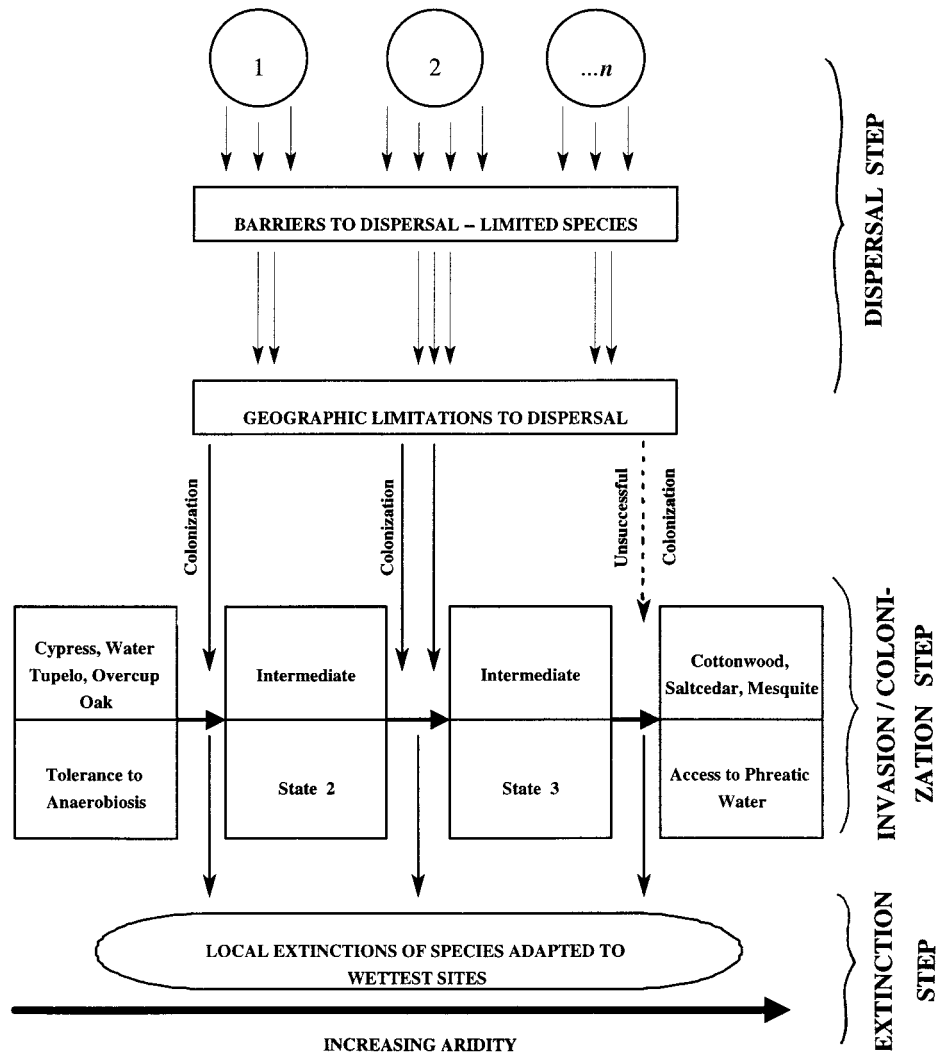
FIG. 7. Schematic representation of coastal riverine wetlands undergoing state changes over time from continually saturated swamp to intermittently flooded riparian zone in the warm-temperate region. At the top, centers of dispersal (1, 2, . . . *n*) represent potential sources of plant and animal species that may shift geographically during the course of climate change. Geographic barriers and life-history characteristics of individual species limit dispersal. The paired rectangular boxes represent four of many possible states, ranging from continually saturated wetland ecosystem (left side) to arid riparian ecosystem (right side). Changes in species composition of the four states depends upon both colonization and species extirpations.

rather than individually as independent species. However, most if not all species fall short of this condition. For reasons discussed above, wetland-dependent species may be particularly prone to slow dispersal because of the geographic isolation by upland barriers.

The major variables influencing dispersal and successful colonization under changing climate at a site are illustrated in Fig. 7. Centers of dispersal give rise to potential colonizers. Dispersal-limited species will not become colonizers while those that have strong dispersal powers and are successful in overcoming geographic barriers reach the colonization step. The combination of colonization and local extinction changes species composition of the ecosystem states (rectangular boxes). In the transition to more arid ecosystem states, species at the wettest end of the wetland continuum become locally extinct because of intolerable periods of water stress or other changes that render them less competitive.

Wetlands that are connected by water and have either unidirectional (riverine) or bi-directional (tidal fringe) flow are more easily invaded for at least two reasons: (1) a corridor of continuous ecosystem type is available for dispersal of propagules relative to isolated (depressional) wetlands, and (2) a medium (water) is available to facilitate dispersal relative to its absence in terrestrial ecosystems. Barriers to free dispersal exist where agriculture and urbanization interrupt the corridors for dispersal that riverine and some tidal wetlands otherwise provide.

The net result of the three steps depicted in Fig. 7—dispersal, invasion/colonization, and extinction—is the conversion of a continually saturated wetland to an arid riparian ecosystem. Although the diagram depicts four distinct states, this separation is highly artificial. There have been so few comparative treatments of riverine wetlands along moisture gradients that one is not able to resolve a finite number of states (but see Rice 1965).

CONCLUSION

Coastal wetlands have naturally evolved in response to sea-level changes and specific patterns of hurricane frequency, intensity, and timing. Based upon the numerous studies of ecological impacts of hurricanes and tropical storms (especially those associated with Hurricane Hugo, which affected sites in Puerto Rico and South Carolina that had ongoing long-term research programs in place and, more recently, Hurricane Andrew) it is possible to infer how climate-change-induced alteration of the frequency, intensity, timing, and distribution of hurricanes and tropical storms may affect ecosystem and population patterns and processes. Generally, research findings indicate that hurricanes and tropical storms may promote recruitment of propagules (including exotic species) into unvegetated areas, gap dynamics that reduce standing-crop biomass but stimulate net primary productivity, nutrient input and regeneration, and the development of ecotones in storm-affected areas. Hurricanes may act as major selective forces governing coastal ecosystem structure and have been observed to result in the broad-scale conversion of one ecosystem state into another state (e.g., forest into marsh, mangrove into open water).

Studies conducted in forests in Puerto Rico and South Carolina following Hurricane Hugo illustrate the diversity of responses that are observed at scales ranging from the population to ecosystem. Resilience of population and ecosystem patterns and processes was related to disturbance intensity, types of disturbance, and their interaction (e.g., wind, storm surge, salt stress, insect infestation). Timing of hurricanes and tropical storms may be an especially important disturbance characteristic that is relatively understudied. For example, plant phenological and physiological patterns interact with the timing of the disturbance to affect nutrient-cycling patterns.

Examples from avian population studies highlight the importance of both direct (e.g., long-distance transport, death) and indirect (e.g., destruction or reduction of nesting habitat, protective cover, forest habitat, prey populations) effects. Indirect effects frequently exceeded the direct effects of the storm, and ecological responses varied significantly. For example, secondary productivity within and outside the hurricane impact zone and biodiversity have been observed to either increase or decrease. Long-term studies of colonial waterbirds in South Carolina illustrate the extent to which

individual physiological constraints could influence the responses to hurricanes that were observed at population and regional scales.

Numerous studies document the resilience of populations and unmodified ecosystems to natural disturbances. Changes in the frequency, intensity, timing, and distribution of hurricanes and tropical storms, coupled with anthropogenic influences, are likely to have a disproportionate impact on biodiversity and certain species, populations, and communities (e.g., species exhibiting a high degree of site tenacity such as migratory colonial waterbirds, and those populations associated with remaining old-growth forested wetlands).

Inferences about climate-change impacts are generally based on short-term studies that were implemented post hoc in order to examine impacts associated with a single event; studies designed a priori to assess climate-change impacts remain an exception. Examples provided in this review highlight the important need for the careful design and implementation of broad-scale, comparative studies that incorporate salient patterns and processes, including treatment of indirect effects, complex interactions, and anthropogenic influences. We presented two examples of the types of studies that are necessary for increasing our understanding of climate-change impacts: utilizing space-for-time substitution coupled with long-term studies to assess impacts of sea-level rise and disturbance on coastal wetlands, and utilizing the moisture-continuum model for assessing the effects of global change and associated shifts in moisture regimes on wetland ecosystems.

Projected rates of climate change are unprecedented. Schneider (1993) suggests that the only predictable outcome of global change is that surprises will occur and that their number will increase with the rapidity with which climates change. For example, we can expect surprises in species responses because we often do not know the extent of the fundamental niches of most species, only their realized niches (Kareiva et al. 1993). Nevertheless, the careful design and implementation of broad-scale, comparative studies such as the two suggested in this paper should significantly reduce the number of surprises that we encounter. It will be especially important to replicate studies across broad geographic areas so that both extreme abiotic stresses and biotic responses can be characterized. Smith and Buddemeier (1992:91) have suggested that ''changes in the frequency and intensity of extreme events are probably more ecologically significant than moderate changes in the mean values of environmental factors.'' Similarly, ''mean annual changes in regional precipitation and temperature patterns have little relevance to plant productivity and decomposition rates,'' if the changes occur unevenly spatially and temporally (Ojima et al. 1991:320). There are relatively few studies in the scientific literature that examine the impacts of climatic extremes on biotic systems, and important

thresholds are yet to be assessed (Ausubel 1991). It may be particularly important to pay attention to populations at the limits of a species' range (Kareiva et al. 1993).

We currently possess only a rudimentary understanding of species' tolerances and the relationships between species diversity and ecosystem function (Ray et al. 1992). Predicting the effects of climate change on such intricate ecosystem functions as nutrient cycling presents a considerable challenge given our current state of knowledge (Mooney 1991). Ecosystem processes are often characterized by complex nonlinear interactions involving numerous biological, chemical, and physical components. Little is known about the character or location of thresholds of nonlinearity in the responses of systems to future stresses (Mintzer 1992). Predicting climate-change impacts in coastal wetlands is further complicated by the inherent spatial and temporal scales of key processes and episodic events that characterize the variety of such ecosystems.

Studies of environmental stresses should record their effects on both structural and functional components of the systems in question, and should also try to develop a standard index to assess stresses across systems (Barrett et al. 1976). We also need to express climate patterns in daily, weekly, and monthly time frames to identify abiotic events that affect biological processes (Ojima et al. 1991). Studies of butterfly populations in California (Ehrlich et al. 1980) demonstrate that understanding annual variations can produce knowledge about how climate controls growth and development of larvae, which can then lead to predictive models (Mooney 1991).

Developing the scientific basis for management, protection, and sustainable use of coastal and freshwater wetlands amidst a changing climate will require that we change the ways we think about and perform science (Gosz 1994). Populations and ecosystems responding to climate change do not recognize academic, intra-, and intergovernmental boundaries. Many of the issues outlined in this paper will require true interdisciplinary (including systematists, ecologists, physical scientists, and social scientists), long-term, and broad-scale, comparative studies. Such studies are frequently counter to the traditional university and Federal agency settings where interdepartmental, intercollegiate, and interagency boundaries prevent many of the necessary interactions from occurring. Specific attention must be focused on removing organizational impediments to data sharing (Gosz 1994, Porter and Callahan 1994).

Long-term and broad-scale comparative studies require that particular attention be paid to data continuity, quality assurance, data and information management, and training a new breed of scientist who is comfortable with both the relevant sciences and the essential technologies (Brown 1994, Stafford et al. 1994). The proposed National Center for Ecological Analysis and Synthesis will address many of the challenges associated with analyzing large data sets and synthesizing information from disparate sources (J. Brown and S. Carpenter, *unpublished report* [1993] from a joint committee of the Ecological Society of America and the Association of Ecosystem Research Centers). However, many problems remain to be addressed. For example, many of the long-term data sets that have been critical to the development of ecology have either been lost or are in danger of being lost through lack of a national environmental-data archival facility. The Carbon Dioxide Information and Analysis Center offers an example of how such a facility may serve the ecological community (Boden et al. 1991).

Increased understanding of global change will require development of the long-term funding base, as well as new funding strategies. However, long-term and broad-scale compartative studies cannot encompass everything. What are the salient features of populations, ecosystems, and landscapes? Creative thought and attention must be devoted to identification of these features and the formulation of relevant scientific hypotheses. Insights into climate-change impacts may be gained by taking fuller advantage of the opportunities afforded by natural disturbances. For example, droughts, volcanic eruptions, and hurricanes and tropical storms represent broad-scale, natural experiments that cannot be replicated, nor mimicked in the laboratory despite our best efforts at experimental sophistication. However, with the exception of the U.S. National Science Foundation's Small Grants for Exploratory Research Program, few mechanisms exist for funding studies that can take advantage of these natural experiments.

Finally, there is a need for additional assessments of how climate change may impact wetlands. For example, (1) permafrost wetlands, such as those in the Arctic tundra, maintain organic carbon in peat as long as temperatures minimize decomposition and the ice below the active layer impedes drainage. The implication of losing this peat to the atmosphere as carbon dioxide is potentially one of the most substantial positive feedbacks to global warming (Gorham 1991). (2) The majority of our commercially and recreationally important fish species are dependent upon coastal wetlands for some portion of their life cycle. Analyses of catch statistics provide only an a posteriori indication of changes in distribution and abundance patterns. Future assessments of fisheries responses to climate change should emphasize how climate change will affect the roles that coastal wetlands play in supporting adult populations. (3) Human alteration of wetlands and the surrounding landscape may increase rates of response to climate change or totally overwhelm such responses. For example, activities such as groundwater pumping and development practices can bring about a very much accelerated rate of local relative sea-level change (Tan-

gley 1988). A recent estimate suggests that $> 75\%$ of the human population will live within 60 km of the coast by the year 2000 (Bernal and Holligan 1992). Thus, it is important that we document the extent to which humans have affected and continue to affect wetland ecosystem and population patterns and process.

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