Nonlinear dynamics in ecosystem response to climatic change: Case studies and policy implications

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Abstract

Many biological, hydrological, and geological processes are interactively linked in ecosystems. These ecological phenomena normally vary within bounded ranges, but rapid, nonlinear changes to markedly different conditions can be triggered by even small differences if threshold values are exceeded. Intrinsic and extrinsic ecological thresholds can lead to effects that cascade among systems, precluding accurate modeling and prediction of system response to climate change. Ten case studies from North America illustrate how changes in climate can lead to rapid, threshold-type responses within ecological communities; the case studies also highlight the role of human activities that alter the rate or direction of system response to climate change. Understanding and anticipating nonlinear dynamics are important aspects of adaptation planning since responses of biological resources to changes in the physical climate system are not necessarily proportional and sometimes, as in the case of complex ecological systems, inherently nonlinear.
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1. Introduction

Since the first United Nations-sponsored assessment of climate change was published by the Intergovernmental Panel on Climate Change (IPCC, 1990), hundreds of reports and journal articles have described the past and potential impacts of climatic change on species and their habitats (Sagarin et al., 1999; Thomas and Lennon, 1999; Hossell et al., 2000; IPCC, 1996, 2001b; NAST, 2000; Australian Greenhouse Office, 2003; Root et al., 2003). Although these studies documented changes that are clearly related to climate trends, they also revealed many challenges in predicting the outcome on species and ecosystems. These difficulties are commonly attributed to the influence of non-climatic variables, variance among thresholds at which species respond to environmental factors, and complex interactions among responses to environmental change. Challenges in disentangling natural and cultural factors have further limited the scope of ecosystem impact assessments. The fact remains, however, that understanding the complexity of potential impacts of climate change on natural ecosystems is essential if resource managers are to minimize the negative consequences of climate change and maximize the potential benefits that it may offer.

Complex and nonlinear physical, chemical, and biological interactions are becoming an increasingly important focus for climate change impact assessments and basic research (Pielke et al., 2003). The International Geosphere–Biosphere Programme of the International Council for Science hosted a workshop on the topic of ''Nonlinear Responses to Global Environmental Change'' in 2001 and convened a working group in 2003 titled "Development of Earth System Models to Predict Nonlinear Responses/Switches''. Reports from these meetings challenge scientists to identify manifestations of nonlinear behavior in the Earth's physical, biological, and chemical systems so that strategies for adaptation will be expanded beyond the current focus on the proportional, linear responses to climate forcing (IGBP, 2003; Pielke et al., 2003).

2. Complexities in assessing ecosystem response to climatic change

Temperature and moisture regimes have an important influence on the distribution, growth, and reproduction of plants and animals. During the past 100 years, the Earth's climate has warmed approximately 0.6 °C, and continents in the Northern Hemisphere have become significantly wetter (IPCC, 2001a). These changes are generally attributed to an increase in the concentrations of atmospheric carbon dioxide (CO_2) and other greenhouse gases. They are not, however, spatially or temporally monotonic. The warming during the fourth quarter of the 20th century was double that of the entire first half, and the high latitudes have warmed significantly more than the tropic or temperate zones. Warming in Alaska since 1950 was four times greater than the 0.6 °C warming of the contiguous United States during the 1900s (NAST, 2001). Between 1900 and 1998, Canada's annual mean temperature increased between 0.5 and 1.5 °C, while northeastern Canada actually experienced a slight cooling (Zhang et al., 2000). Precipitation increased across most of Canada and the United States during the past century, but winter precipitation and winter temperatures increased more than spring and summer temperatures (NAST, 2001; Zhang et al., 2001). Larger scale discontinuities in the ocean–climate system are also evident in the geologic record. Climatic records suggest that abrupt and widespread climatic changes, interdecadal oscillations, and regime shifts are all characterized by nonlinear dynamics (Trenberth and Hoar, 1997; Alley et al., 2003; Epstein and McCarthy, 2004).

A review of 143 published studies by Root et al. (2003) revealed that animals and plants are already showing discernible changes consistent with temperature trends of the 20th century. Most (80%) of the changes that were observed were linked with temperature change, but it was recognized that temperature can exert its influence in complex ways, for example, by affecting moisture availability. Another review article (Walther et al., 2002) of ecological responses to warming of the Earth concluded that many North American trees are coming into leaf sooner, grasses and forbs are flowering earlier, the abundance of many insects is peaking earlier, and some birds and butterflies are migrating earlier.

Phenological events such as migration, bloom, leafing out, and reproduction are triggered by changes in the environment, by endogenous rhythms, or by pressures from other organisms. Climatic regimes influence the phenology of species in a variety of

ways, but the most completely understood processes are those that link temperature or moisture availability to intrinsic thresholds that govern metabolic and reproductive processes. In addition to phenology, changes in climate can also affect the morphology and behavior of organisms. Since the timing of response in different taxonomic groups is not always synchronous, there may be decoupling of species and their food sources, a disruption of symbiotic or facilitative relationships among species, and a change in competition among species. Changing climate could decouple population cycles of insects and their avian predators, as illustrated in our case study of the spruce budworm (*Choristoneura fumiferana*), thereby affecting both the insect host and the predator that keeps it in check. Hellman (2002) found links between the timing of emergence of bay checkerspot butterfly (*Euphydryas editha bayensis*) larvae and the growth and abundance of two larval host plants (*Plantago erecta* and *Castilleja* spp.). If the phenologies of closely interacting species become out of syncrony, essential ecological processes such as pollination, seed dispersal, and insect control (such as by birds) can be disrupted (Price, 2002). In this manner, effects of climatic change can be transmitted through chains of species interactions that cascade among taxa and systems. These cascading effects can theoretically occur at any point in a food web (Hunter and Price, 2002).

When interactions among components of a system are not directly proportional, the system is considered "nonlinear". These types of relationships are more often the rule rather than the exception in biological systems (Hilbert, 2002), but few studies have provided discrete examples of ecological responses to nonlinear behavior in the geophysical system (Rosser, 2001; Stenseth et al., 2002). Most predictions of the impacts of climate change on species and ecosystems have focused on shifts in geographic range (Sanford, 2002). This focus on range shifts neglects the importance of species interactions and human influences that restrict the migration and sustainability of biological communities. In addition, this approach does not consider other hydrological and geological patterns and processes that are interactively linked with biological systems. These ecological phenomena normally vary within bounded ranges, but rapid, nonlinear changes to markedly different environmental conditions can be

triggered by even small differences if threshold values are exceeded.

Separate from the greenhouse effect of CO_2 on atmospheric temperatures and moisture, it is well established that atmospheric CO_2 enrichment has a fertilizing effect on most herbaceous plants by enhancing photosynthesis and water-use efficiency (Acock et al., 1985; Nijs et al., 1989; Allen et al., 1988; Rabbinge et al., 1993; IPCC, 1996; Anderson et al., 2001). Growth in woody species is also stimulated by increases in CO_2, but there is a wide range of responses among deciduous and coniferous species (Eamus and Jarvis, 1989; NCASI, 1995). Virtually, all plants have a threshold at which further CO_2 enrichment will no longer continue to increase photosynthesis levels because of other limiting factors. For instance, the availability of soil nutrients and water in many natural or semi-natural ecosystems will limit the potential improvement in water-use efficiency caused by suppressed transpiration induced by enhanced CO_2 levels (Lockwood, 1999). Temperature, plant pests, air pollution, and light availability can constrain the potential enhancement of plant growth by elevated CO_2 (NCASI, 1995). These limiting factors and their interactions with other natural and human-induced changes in ecosystems have not typically been accounted for in models that predict the impacts of climate change on biomes.

Plants and animals also respond to secondary and higher order effects of increasing global temperature and changes in precipitation patterns. In the coastal zone, for example, increased salinity will lead to a shift in species that are more salt tolerant. The increased salinity is a third-order effect of atmospheric warming that causes eustacy, which in turn causes increased tidal exchange, increased intensity and frequency of storm surge, and increased mean water levels in coastal systems. Species that have greater tolerance of increased salinity will outcompete those with lower tolerance, leading to changes in the structure and functions of the coastal ecosystem. Changes in community structure can be episodic, and in some cases, ecosystems may be eliminated if thresholds are exceeded, as illustrated in our case study of coastal wetlands and sea-level rise.

Scale is an important consideration in distinguishing nonlinear ecological phenomena from changes in habitats and species that vary stochastically around a

mean. Exponential change, such as that which is introduced through combinations of multiple treatment factors, can be linear along a log scale, however, ecosystem disturbance has been defined as any discrete event that results in the sudden mortality of biomass on a time scale that is shorter (by several orders of magnitude) than that of its accumulation (Huston, 1994). Climate-related disturbance can range from droughts and floods to wildfires and insect outbreaks, all of which can rapidly alter ecosystems. Disturbance is one form of nonlinear ecosystem dynamics that is commonly anticipated, accommodated in planning, and even employed in some cases (e.g., prescribed fire) by natural resource managers to maintain ecosystem structure or services.

Theoretical frameworks for characterizing ecological phase transitions (Loehle et al., 1996; Li, 2002), multiple steady states in ecosystems (Sharma and Dettmann, 1989; Allen-Diaz and Bartolome, 1998), extinction thresholds (Amarasekare, 1998; Ruesink, 1998), and ecological trends in relation to climate variability at the scale of landscapes and centuries (Swetnam and Betancourt, 1998; Shaver et al., 2000) have been developed during the past two decades. While these approaches are not new in the field of ecology, their relevance to habitat and species management is not well established. The expansion of the status of understanding of nonlinear ecosystem response to climate change beyond conceptual theory to empirical observation and prediction is needed.

3. Importance of understanding nonlinear behavior in natural systems

Twentieth century natural resource managers were trained to manage natural resources at seasonal, annual and, to a more limited extent, interannual time frames. Classical concepts of forest succession and climax are the basis for prescribing silvicultural operations; destruction of wetlands is mitigated on a proportional basis in most regulatory programs; total maximum daily loads are additive in regulatory frameworks for permitting the discharge of pollutants into air and water resources. Natural resource managers generally perceive and plan for environmental change assuming linear relationships between ecological processes and outcomes (Canadell, 2000). Ecosystem management

and species conservation can be more effective if predicated on a thorough understanding of both the linear and nonlinear responses to environmental change. The impression that climate change will only lead to incremental and linear changes in ecosystems could delay or flaw actions that may be needed to ensure ecosystem sustainability.

Linear extrapolations of temporal or spatial patterns of environmental change can lead to poor depictions of reality. Management strategies that underestimate the rate of potential change and the sensitivity of natural ecosystems to other pressures may not meet desired objectives or, at a minimum, may be wasteful of resources and societal investment. It is important to understand and anticipate nonlinear responses and ecological thresholds because the outcomes of classical models commonly described in the literature may differ significantly from the states and transitions derived quantitatively from empirical data. For example, Carpenter et al. (1999) analyzed management policies for lacustrine ecosystems subject to alternate states, thresholds, and irreversible changes. They focused on the problem of lake eutrophication by excessive phosphorus input and found that analyses based on deterministic lake dynamics usually lead to higher allowable phosphorus input rates than analyses that assume various nonlinear relationships, uncertainties, and interactions. All of these complications occur in reality, and this particular study indicated that phosphorus input rates should be reduced below levels derived from traditional deterministic models. The authors suggested that this pattern may apply to other situations where diffuse pollution causes nonlinear changes in ecosystem states, such as those associated with greenhouse gas emissions and atmospheric warming.

Eiswerth and Haney (2001) illustrated how the consideration of ecological thresholds could influence the outcomes of biodiversity preservation problems. They evaluated the use of biodiversity indicators and the resource manager's chosen time horizon in conservation priority setting and planning for avian biodiversity in forest ecosystems in the eastern United States. Their findings suggested that the failure to account for nonlinear, threshold effects in an ecosystem's future progression alters preservation decisions and ignores important information that will influence the outcome of management actions intended to

enhance avian diversity. In Pacific Northwest forests, Jansen et al. (1995) compared avian density across natural stands, traditionally managed plantations, and stands managed under ecological forestry approaches. Their results suggested that, although canopy tree retention generally benefited many species, the nonlinear responses of bird abundance revealed thresholds in tree density at which bird abundance changed dramatically. They concluded that knowledge of these thresholds would enable managers to design stands for specific biodiversity objectives.

Several other recent studies revealed the importance of considering nonlinear relationships in natural resources management and planning, but few have dealt with the additional complexities that are associated with a changing climate. Although decision-support tools now exist for managing some types of vegetation (mainly crop species) in the context of temperature and precipitation shifts at interannual and decadal scales, lack of evidence to the contrary suggests that natural resource managers are under the impression that response to increasing atmospheric CO_2 and climatic change will be linear. Rosser (2001) recommends that, in the absence of understanding of nonlinear ecological responses to climatic change, greater emphasis should be placed upon the precautionary principle to avoid catastrophic collapses of ecological systems beyond critical thresholds. The following widely cited use of the precautionary principle appears in the ''Rio Declaration'' of the 1992 United Nations Conference on Environment and Development (Principle 15, United Nations, 1992, p. 3):

In order to protect the environment, the precautionary approach shall be widely applied by States according to their capabilities. Where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation.

4. Case studies

The following case studies were compiled to illustrate a range of nonlinear relationships in habitats, species, and ecological processes that are managed to conserve ecological functions and services that are valued by society. The case studies conclude with discussion of management implications of recognizing (or failing to recognize) that responses may be nonlinear. Authors of the case studies are: D.A. Wilcox (Section 4.1), J. Baron (Section 4.2), C. Allen (Section 4.3), D.B. Fagre and D.L. Peterson (Section 4.4), W. Barrow (Section 4.5), R. Stottlemyer (Sections 4.6 and 4.7), V.R. Burkett and T. Doyle (Section 4.8), J. Nielson and G. Ruggerone (Section 4.9), and J. Price (Section 4.10).

4.1. Ground-water discontinuities influence nonlinear dynamics in wetland succession

Wetland plant communities are very responsive to changes in surface-water levels (Meeks, 1969; Cooke, 1980; van der Valk and Davis, 1980; Keough et al., 1999). Water levels are, in turn, often responsive to changes in climate. In freshwater wetlands, water levels typically increase during cool periods and decrease during warm periods (Winter, 1989; Winter and Rosenberry, 1995; Baedke and Thompson, 2000). The expected linear response of plant communities in the short-term is a reduction in emergent species in years when water levels are high and a resurgence of emergents from the seedbank when water levels are lower and result in exposed sediments (van der Valk and Davis, 1978; Keddy and Reznicek, 1986). Over longer time periods ranging from decades to centuries to millennia, the expected linear response is also deeper open water with few emergent species during cool, wet climate phases, and shallow marsh with shoreline and mudflat species during warm, dry phases (Singer et al., 1996). Prolonged warm, dry phases with greater primary production by emergent species may accelerate basin infilling in protected areas not subject to wave attack (Wilcox et al., 1986; Wilcox and Simonin, 1987). Successional processes may accompany shallowing of the basins, leading to further vegetation changes that include the invasion of shrubs and trees (Walker, 1970; Keddy, 2000), although return of high water can reset the successional stage again (van der Valk, 1981; Jackson et al., 1988; Hannon and Gaillard, 1997).

Recent work in chronosequences of wetlands occurring in ridge and swale terrains of Lakes Michigan and Superior suggests that ground water may mediate effects of climate and successional processes on plant communities in some wetlands.

The observed result in both short- and long-term scenarios is nonlinear behavior, with some wetlands within a relatively small geographic locale responding differently than others to the same climatic trends and successional time periods. The modern vegetation in a series of wetlands between more than 80 beach ridges along the shore of Lake Michigan near Manistique, Michigan, provides a good example of such responses (Fig. 1). Younger wetlands near the lake (Figs. 1 and 2; wetlands 1 and 2) are open shallow marsh dominated by species such as *Scirpus pungens* and *Juncus arcticus*. Next in the age sequence are floating mat wetlands (4, 8) dominated by species such as *Carex lasiocarpa* and *Chamaedaphne calyculata*. Yet older wetlands (9–28) retain these species but also add shrubs such as *Alnus incana* and *Ilex verticillata*, trees such as *Thuja occidentalis*, *Larix laricina*, and *Pinus strobus*, and then increase numbers of *T. occidentalis* (northern white cedar) and royal ferns (*Osmunda regalis*) as the floating mat is lost (29–39). This seemingly successional sequence proceeds to typical cedar swamp by wetland 45, as other tree species drop out, but abruptly reverts back to open floating mat at wetland 71. Shrubs (e.g., *A. incana* and *Cornus sericea*) and trees (e.g., *L. laricina*, *Betula papyrifera*, *Acer rubrum*, and *Abies balsamea*) become dominant again in the oldest wetlands (Figs. 1 and 2; wetlands 81–84) as the floating mat is again lost.
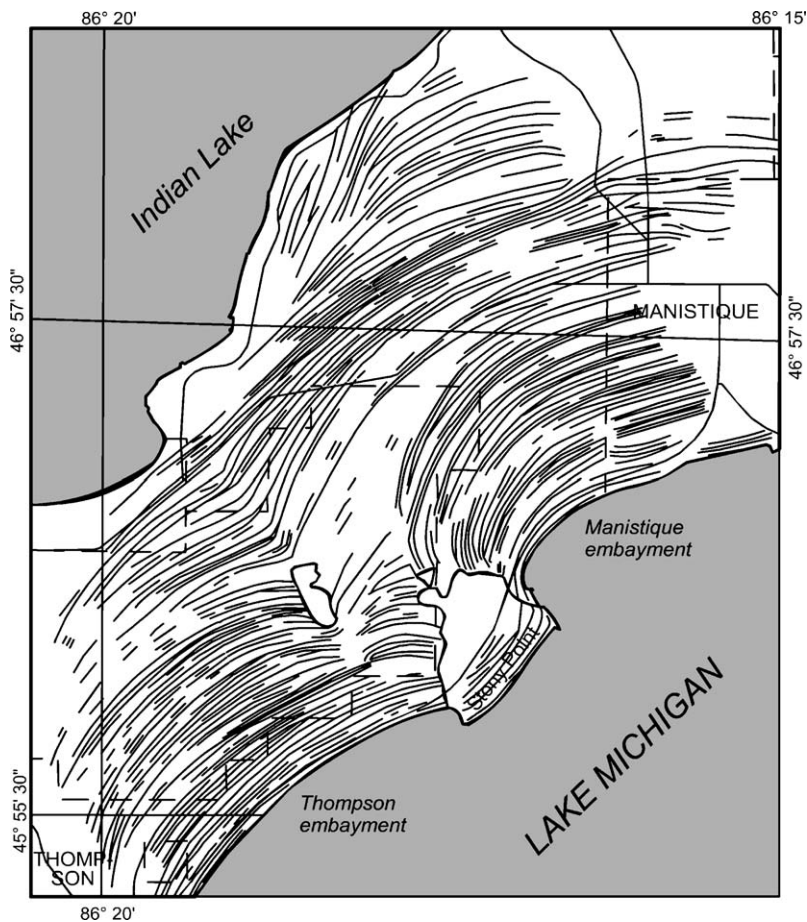

Fig. 1. Map of the chronosequence of beach ridges near Manistique, Michigan. The arcuate lines trace the modern location of beach ridges formed during water-level stages of Lake Michigan over the past 4700 years. The highlighted numbers show the location of selected wetlands described in the text. Modified from Thompson and Baedke (1997) with permission from Geological Society of America.
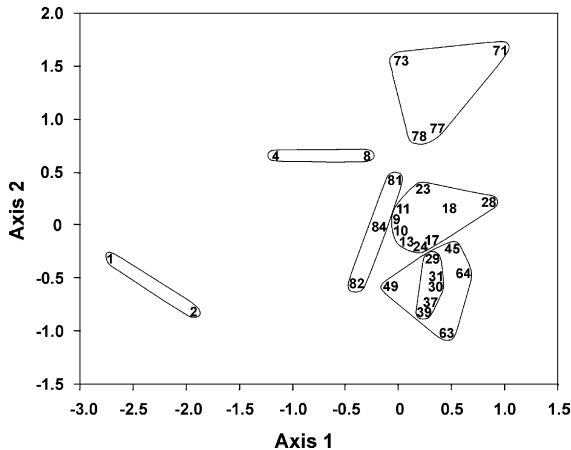
Fig. 2. Non-metric multidimensional scaling (NMS) ordination of understory vegetation sampled along four 1 m wide belt transects placed in a stratified random design across each of 29 wetlands near Manistique, Michigan. Sampling data using the Braun-Blanquet scale were converted to the van der Maarel scale (van der Maarel, 1979; Jager and Looman, 1987), and sums of van der Maarel values from the four transects were used in the ordination. The numbers shown in the ordination represent wetland number from youngest (1) to oldest (84) across the chronosequence. Not all swales between ridges contained wetlands, and others were not sampled because of access restrictions [autopilot on; sorenson distance; no species weighting; final stress = 12.29; final stability = 0.00000; number of iterations = 88].

Paleoecological studies (Singer, 1996) have shown that many changes in vegetation occurred within individual wetlands of this chronosequence during the past (up to) 4000 years in response to climate changes, but not all vegetation changes were parallel in all wetlands. The key to understanding the nonlinear behavior in both the modern vegetation and the paleoecological record is the differential role of ground water across the chronosequence of wetlands.

Ground-water studies identified an upwelling of ground water centered in the vicinity of wetlands 58–60 (Wilcox, unpublished data). This artesian flow likely results from a discontinuity in an underlying clay till sheet that allows flow from a confined aquifer to reach the surface. These hydrologic conditions are conducive to growth of northern white cedars (Voss, 1972; Swink and Wilhelm, 1979; Wilcox et al., 1986) and explain the prominence of cedar swamp in nearby wetlands 45, 49, 63, and 64, as well as a noticeable presence of cedars in lakeward wetlands that receive this flow of water in a pass-through fashion from wetland to wetland. The modern vegetation and the paleoecological record of vegetation changes suggest that this continuous source of cold water provides the predominant control on plant communities. Wetlands 71 and beyond are outside the influence of this upwelling, and control of plant communities can be more directly tied to climate and succession.

During warm climate phases, plant communities with sufficient ground-water supply may be immune to climate-related, water-level reductions that drive vegetation change. Over prolonged periods with no climate-driven flooding to reset the successional stage, plant communities may develop with greater fidelity to ground-water influences than to assumed successional processes. In either case, the expected linear behavior in vegetation patterns does not appear on the landscape. Managers must recognize the potential for this ground-water influence on vegetation in order to understand the nonlinear character of the landscape and to avoid taking management actions that will have a negative effect on the resources under their care. Understanding the mechanisms that influence the heterogeneity of wetland structure and differential response to climate change and lake-level change will aid in establishing successful long-term wetland management objectives and practices in the Great Lakes region.

4.2. Nonlinear responses in Rocky Mountain aquatic ecosystems to nitrogen enrichment and changes in snowpack

The effects of climate change can have direct effects on the trajectories of ecosystems, as illustrated by the wetland example above. Climate change can also affect how other large-scale human-caused disturbances manifest themselves on landscapes; this case study illustrates how climate warming may actually moderate the responses of ecosystems to atmospheric nitrogen deposition. National Park ecosystems are managed to be as natural, or unimpaired, as possible, and yet man-made air pollutants are beginning to cause unnatural ecosystem changes. National parks that are classified as Class I Areas under the Clean Air Act, or are managed as Wilderness under the Wilderness Act are required by law to maintain Air Quality-Related Values, which are ecosystem attributes that represent unimpaired ecological functioning (Porter et al., 2005).

In high elevations of the southern Rocky Mountains, climate change is likely to be signaled by changes in the timing and amount of snowmelt (Smith et al., 2000, Reiners et al., 2003). Snowpack amounts have already declined in much of the western United States since the 1950s, and snowmelt occurs more than 20 days earlier than in the late 1940s due to moderate warming trends (Stewart et al., 2004). Air temperatures have increased 1.1–1.4 °C since the early 1990s in the Loch Vale Watershed of Rocky Mountain National Park, although this is mostly a summer phenomenon, and has not influenced winter snow dynamics (Clow et al., 2003). Climate change scenarios project warmer temperatures throughout the year, and either increasing winter precipitation or similar precipitation patterns to those observed currently (Smith et al., 2000).

The potential hydrologic and ecological responses to earlier snowmelt in Loch Vale Watershed were modeled with climate change and doubling of atmospheric of CO_2 scenarios by using RHESSys, the Regional Hydro-Ecologic Simulation System (Baron et al., 2000a). Model output for an increase of 4 °C showed reductions in snowpack by 50%. Both soil moisture and runoff increased 4–5 weeks earlier than the mean onset of spring conditions from 1984 to 1998 (Baron et al., 2000a,b). There are long-term implications of earlier snow melt and increased warming for permafrost; Clow et al. (2003) project that increased air temperatures are sufficient to raise low elevation permafrost and rock glaciers by 150–190 m, leading to a short-term increase in streamflow. The long-term implications of permafrost melting include highly nonlinear stream flows, including late summer stream drying. Another nonlinear response to climate change will come from the interactions of warming, snowpack, and biogeochemical dynamics, specifically nitrogen cycling.

The global increase in N emissions is commensurate with increases in other human-induced greenhouse gases, and societal sources of reactive nitrogen now exceed natural source contributions by about 200 Tg N year^{-1} (Galloway and Cowling, 2002). The post-1950 increase in emissions of available reactive nitrogen to the atmosphere, specifically ammonia and nitrogen oxides, is a major disruption of the global nitrogen cycle (Smil, 2000, Galloway et al., 1995, Vitousek et al., 1997). Current values in the western

United States are at least an order of magnitude greater than background deposition values (Fenn et al., 2003a).

Mountain environments are generally considered to be oligotrophic, so even the slight introduction of a limiting nutrient can lead to marked change (Baron et al., 2000b). In parts of the U.S. Rocky Mountains, N deposition is 3–6 kg N ha^{-1} year^{-1}, a value that is low compared with other regions of the world, but high mountain ecosystems are particularly vulnerable to change due to harsh climate, large expanses of exposed bedrock and shallow soils, very low vegetation biomass, dilute waters, and a snowmelt-driven hydrograph (Baron et al., 2000b). Forest stands receiving elevated N deposition display high foliar N and low C:N ratio, low lignin:N ratios, and high potential net mineralization rates (Rueth and Baron, 2002). In fertilization experiments, additional N enhanced the loss of inorganic N from soils to streams or lakes (Rueth et al., 2003). The condition of N saturation causes eutrophication in many Rocky Mountain lakes and eventually will lead to acidification (Baron et al., 2000b; Fenn et al., 2003b) (Fig. 3).

The crossover between eutrophication and acidification is a good example of nonlinear dynamics brought about by human-initiated nitrogen deposition
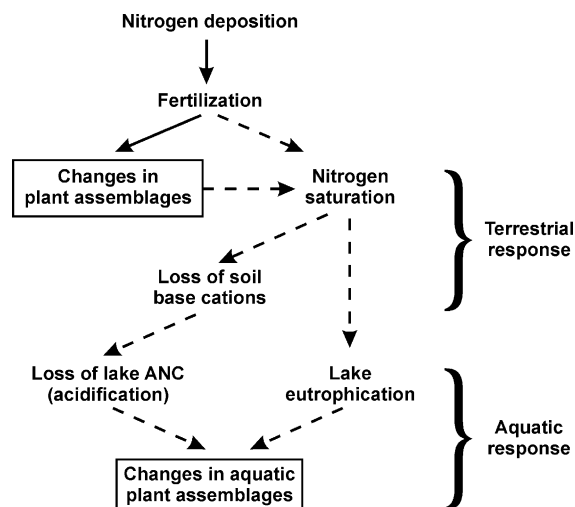

Fig. 3. Cascading effects of nitrogen deposition to terrestrial and aquatic ecosystems. Under current climates this is the natural progression of observed changes. Arrows with dashed lines depict pathways that could be ameliorated with climate changes that lead to earlier snowmelt and longer growing seasons.

(Stoddard, 1994). But climate change may ameliorate both eutrophication and the onset of acidification in aquatic systems by switching the location of ecological effects to terrestrial systems. Because a gradual release of N increases the possibility that nitrate will be actively taken up and retained by soil microbes, organic matter, and plants and that earlier spring conditions will increase plant productivity, stream nitrate concentrations may actually decrease under a warming scenario (Baron et al., 2000a,b). A longer tundra and forest growing season brought about by earlier snowmelt will favor the retention of N in tundra and forests. Atmospheric warming may thus relieve some of the current ecological pressure on aquatic environments brought about by excess N deposition by switching the nonlinear ecological response to nitrogen from aquatic to terrestrial environments.

These processes and interactions are important considerations in setting standards for air and water quality in the Rocky Mountain region. Atmospheric nitrogen deposition is considered a pollutant in areas classified as Class I by the U.S. Clean Air Act Amendments (PL 101-549, November 15, 1990), such as Rocky Mountain National Park and adjacent wilderness areas managed by the USDA Forest Service. Managers of these lands have an affirmative responsibility to act, in concert with regulatory agencies, to ensure that changes to Air Quality-Related Variables do not occur. However, uncertainty as to the magnitude of change increases with climate change.

4.3. Drought-induced dieback of forests and woodlands in New Mexico: nonlinear response to climate variability

Climate is a key determinant of vegetation patterns at landscape and regional spatial scales, such as rapid, climate-induced dieback of forests and woodlands in the southwestern United States. In particular, severe drought has affected ponderosa pine forest (*Pinus ponderosa*) and piñon–juniper woodland (*Pinus edulis* and *Juniperus monosperma*), including persistent shifts in the ecotonal boundary between these vegetation types and increased rates of soil erosion. These examples of nonlinear forest responses to climate variability illustrate the potential for wide-

spread and rapid vegetation dieback and associated ecosystem effects due to global climate change.

Precipitation variability, including recurrent drought conditions, has typified the climate of the American southwest (e.g., New Mexico, Arizona) for thousands of years (Grissino-Mayer, 1996; Sheppard et al., 2002). Dendrochronological studies and historical reports show that past droughts have caused extensive vegetation mortality across this region, best documented for the severe droughts of the 1580s, 1890s to early 1900s, 1950s, and the most recent persistent drought that began in 1996 (Allen and Breshears, 1998, 2002; Swetnam and Betancourt, 1998). Droughts have been documented to cause dieback in many woody plant species in the southwest, including pines, junipers, oaks (*Quercus* spp.), mesquite (*Prosopis* spp.), manzanitas (*Arctostaphylos* spp.), and paloverdes (*Cercidium* spp.) (Turner, 1990; Earl and Bash, 1996; Swetnam and Betancourt, 1998; Allen and Breshears, 2002).

Drought-induced tree mortality shows a variety of nonlinear ecological dynamics. Tree mortality occurs when drought conditions increase plant water stress above intrinsic thresholds, which can result in tree death by loss of within-stem hydraulic conductivity (Allen and Breshears, 2002). Also, herbivorous insect populations can rapidly build up to outbreak levels in response to increased food availability from drought-weakened host trees, such as the various bark beetle species (*Ips* and *Dendroctonus* spp.) that attack ponderosa and piñon pines (Furniss and Carolin, 1977; Allen and Breshears, 2002). As bark beetle populations build up, they become increasingly successful in killing drought-weakened trees through mass attacks, with positive feedbacks for further explosive growth in beetle numbers, which can result in nonlinear ecological interactions and complex spatial dynamics (cf. Bjornstad et al., 2002). Bark beetles also selectively kill larger and low vigor trees, truncating the size and age distributions of host species (Swetnam and Betancourt, 1998).

The temporal and spatial patterns of drought-induced tree mortality also reflect nonlinear dynamics. Through time, mortality is usually at lower back-ground levels, punctuated by large pulses of high tree death when threshold drought conditions are exceeded (Swetnam and Betancourt, 1998; Allen and Breshears, 2002). The spatial pattern of drought-induced dieback

often reveals preferential mortality along the drier, lower fringes of tree species distributions in southwestern mountain ranges. For example, the 1950s drought caused a rapid ecotone shift on the east flank of the Jemez Mountains in northern New Mexico (Allen and Breshears, 1998). A time sequence of aerial photographs shows that the ecotone between semi-arid ponderosa pine forest and piñon–juniper woodland shifted upslope extensively (2 km or more) and rapidly (<5 years) because most ponderosa pines across the lower fringes of that forest type has died (Fig. 4). Historical documents confirm this pattern: ''The effects of beetle attack increased the mortality rate
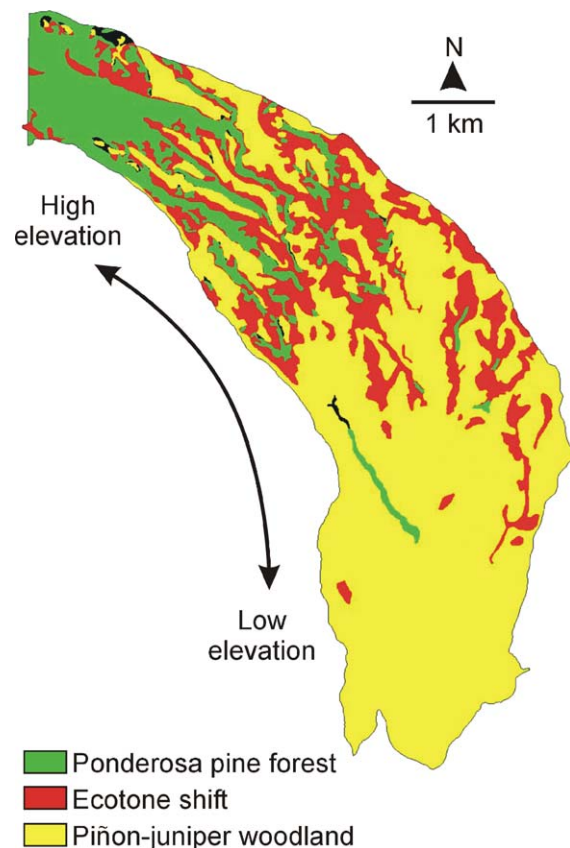

Fig. 4. Changes in vegetation cover between 1954 and 1963 in a portion of Bandelier National Monument in New Mexico, showing persistent ponderosa pine forest (365 ha), persistent piñon–juniper woodland (1527 ha), and the ecotone shift zone (486 ha) where forest changed to woodland (from Allen and Breshears, 1998, reproduced with permission from National Academy of Sciences, USA).

of all age ponderosa and pinyon pine to the point of near extinction on the lower elevations'' (1957, unpublished annual forestry report on file at Bandelier National Monument). Further, this vegetation shift has been persistent since the 1950s, as little ponderosa pine reestablishment has occurred in the ecotone shift zone. There is evidence for similar patterns of low elevation woody mortality elsewhere in the southwest (Allen and Breshears, 2002).

The 1950s drought also markedly reduced the productivity and cover of herbaceous plants like grasses (Young, 1956; Herbel et al., 1972). Such reductions in ground cover can trigger rapid increases in erosion rates once bare soil cover exceeds critical threshold values (Davenport et al., 1998; Wilcox et al., 2003). In concert with historic land-use practices (livestock grazing and fire suppression), the 1950s drought apparently initiated persistent increases in soil erosion in piñon–juniper woodland sites in the eastern Jemez Mountains that require management intervention to reverse (Sydoriak et al., 2000). Thus, a short-duration climatic event may have brought about persistent changes in multiple ecosystem properties.

Most recently (1996–2004), the southwest has been subject to the most significant drought since the 1950s, with associated increases in tree mortality evident. The cumulative effect of this multiyear drought, combined with the extremely dry winter of 2001–2002, was the re-emergence of bark beetle outbreaks. In northern New Mexico, piñon was particularly hard hit in 2002 and 2003, with mortality exceeding 90% of mature individuals across extensive areas (Fig. 5), which is shifting stand compositions strongly toward juniper dominance. By 2003, substantial dieback was observed in Engelmann spruce (*Picea engelmannii*), aspen (*Populus tremuloides*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), ponderosa pine, piñon, junipers, manzanitas, paloverdes, and other woody species in various portions of the southwest (US Forest Service, 2003; C. Allen, personal observation). The substantial and widespread increases in forest and woodland tree densities that have resulted from more than 100 years of fire suppression also contribute to current patterns of mortality, because of competitive increases in tree-water stress and susceptibility to beetle attacks. Live cover of perennial grasses dropped four-fold between 1999 and 2003 over extensive areas of piñon–juniper

Fig. 5. Extensive piñon mortality near Los Alamos, NM, that occurred between June and October 2002.

woodland in the Jemez Mountains (New Mexico) due to drought-induced mortality (C. Allen, unpublished data). Fire activity in the overdense forests of the southwest also increased markedly during this drought period, most notably including the Cerro Grande fire in 2000, in 2002 the Ponil fire (>37,000 ha) in New Mexico and the Rodeo-Chediski fire (~180,000 ha) in Arizona, and in 2003 the Aspen fire (>34,000 ha) in Arizona.

Even relatively brief climatic events (droughts) associated with natural climate variability can have profound and persistent ecosystem effects. The accelerated changes in climate that are expected in coming decades in association with changes in patterns of disturbance (fire, insect outbreaks, soil erosion) could produce rapid and extensive contractions in the geographic distributions of long-lived woody species (Allen and Breshears, 1998; IPCC, 2001c). Because regional droughts of even greater magnitude and longer duration than the 1950s drought are expected as global warming progresses (IPCC, 2001c), the ecological effects of droughts associated with global climate change are likely to be even greater than those effects documented here. Since mortality-induced vegetation

shifts take place more rapidly than do natality-induced shifts associated with plant establishment and migration (Allen and Breshears, 2002), dieback is likely to outpace new forest growth for a period of several years, or possibly decades, in many areas. Further, as woody vegetation contains the bulk of the world's terrestrial carbon, an improved understanding of mortality-induced responses of woody vegetation to climate is essential for addressing some key environmental and policy implications of climate variability and global change. Thus, it is important to incorporate drought-induced vegetation mortality and the complexity of associated ecosystem responses (e.g., insect outbreaks, fires, soil erosion, and changes in carbon pools) into more accurate models that predict vegetation dynamics (Breshears and Allen, 2002).

4.4. Cycles and thresholds in biotic and abiotic components of northwestern mountain ecosystems

The Climate–Landscape Interactions on a Mountain Ecosystem Transect (CLIMET) Research Program has detected prominent signals of environmental change in high elevation mountain ecosystems of

western North America (Fagre and Peterson, 2000). These signals are related to changes in the atmospheric environment over the past 150 years, as well as to long-term patterns of climate variability.

Climate-induced change in mountain ecosystems occurs at multiple spatial and temporal scales, as illustrated in the two previous case studies. One type of change is expressed as a threshold effect in which climate has relatively minor impacts until a critical level is reached, leading to rapid (and continuing) change. Another type of change in which mountain ecosystems react to alternating climatic states is cyclical. Both phenomena have produced measurable changes in mountain ecosystems of the American Northwest and Rocky Mountains.

Changes that are potentially associated with higher temperatures caused by a greenhouse climate must be interpreted in the context of climate variability at interannual, subdecadal (El Niño Southern Oscillation, ENSO; 3–7 years cycles of warm–dry and wet–cool conditions) and multidecadal (Pacific Decadal Oscillation, PDO; 20–30 years cycles of warm–dry and wet–cool conditions) (Mantua et al., 1997) scales. All mountain systems in western North America are affected to some extent by ENSO or PDO impacts on winter snowpack.

The extent and mass of mountain glaciers decreased during the 20th century in response to warmer temperatures. In contrast, glaciers were at their Holocene maxima at the end of the Little Ice Age, a 400-year period of markedly lower temperatures in North America that ended around 1850. The recent glacial recession has been documented by long-term monitoring in Glacier, North Cascades, Olympic, and Mount Rainier National Parks. Since 1958, North Cascades National Park, which contains over half of the glaciers in the continental United States, has experienced a 7% reduction in glacial area and a reduced mass in 80% of the park's glaciers (Granshaw, 2001).

In 1850, Glacier National Park contained 150 glaciers (Carrara, 1989), but in 1966, only 37 were large enough to warrant being named on maps. By 1993, the largest park glaciers had shrunk by 72% of the area they previously covered, and many of the smaller glaciers had vanished or were no longer large enough to be considered glaciers (Key et al., 2002). The area within park boundaries that was covered by ice and permanent snow decreased from 99 to 27 km^2.

Furthermore, glaciers have thinned by hundreds of meters and glaciers such as Grinnell Glacier (Fig. 6), may have less than 10% of the ice volume that existed at the end of the Little Ice Age. The glaciers of Glacier National Park may be gone within our lifetimes (Hall and Fagre, 2003).

The decline of glacial ice may be linked to increases in mean summer temperature and/or a reduction in the winter snowpack that forms and maintains glaciers. Instrumental weather data indicate a trend of increasing temperature but no apparent long-term trend in snowpack. It appears that the temperature threshold for maintaining glaciers was exceeded sometime between 1850 and the 1920s (Selkowitz et al., 2002). This threshold corresponds with the data on glaciers elsewhere on Earth—almost all mountain glaciers are receding as global temperatures increase (IPCC, 2001b). The ecological significance of losing glaciers in mountainous regions includes loss of streamflow in late summer and increased water temperature, which affects the distribution and behavior of aquatic organisms. Plants and animals eventually occupy landscapes vacated by glacial ice, and new alpine lakes often remain after the ice is gone. Although loss of glacial ice affects a small portion of the landscape, it affects large areas of mountain ecosystems and human communities that depend on reliable water resources.

The PDO, caused by fluctuation of sea-surface temperatures in the North Pacific Ocean, affects climate throughout the western United States, with the strongest climate signals from the north Pacific coast to the Rocky Mountains (Mantua et al., 1997). The PDO is negatively correlated with winter precipitation (snow) (Peterson et al., 2002; Selkowitz et al., 2002) (Fig. 7), and snowpack dynamics are critical to glacier mass balance, with more rapid recession during the two warm PDO regimes of the 20th century (Bitz and Battisti, 1999; Key et al., 2002; J. Reidel, unpublished data). The most important economic effect of the PDO is on water production for agriculture, hydroelectric generation, industrial use, and human consumption. This effect is measurable in the Columbia River, in which streamflow during cool PDO phases averages 20% greater than during warm PDO phases (Hamlet and Lettenmaier, 1999).

Analysis of tree-growth chronologies in western North America indicates that growth is increasing in
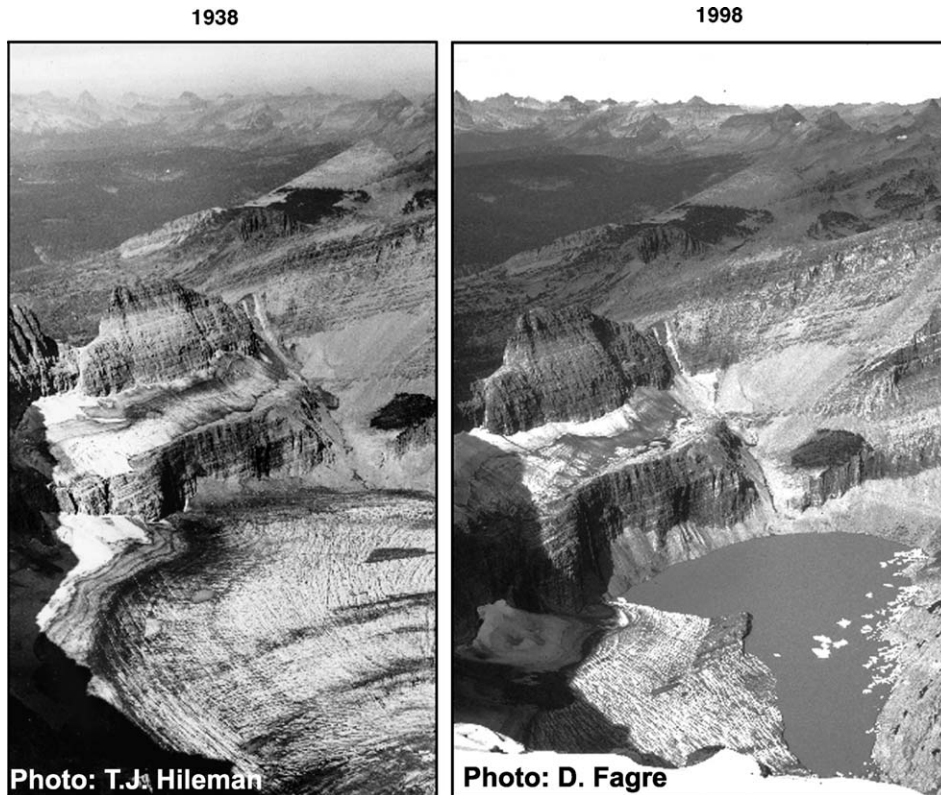
Fig. 6. Photographs taken from the summit of Mt. Gould, Glacier National Park, Montana, clearly demonstrate the changes in area and volume of ice for Grinnell Glacier.
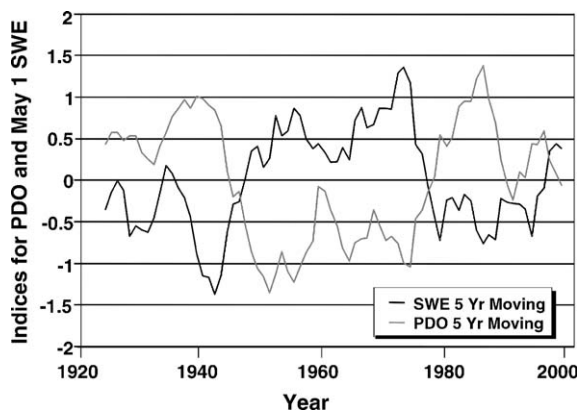

Fig. 7. Relationship between the Pacific Decadal Oscillation (PDO), sea-surface temperature anomaly, and May 1 snowpack (in snow water equivalent, SWE) in Glacier National Park, Montana, east of the continental divide (from Selkowitz et al., 2002 reproduced with permission from John Wiley and Sons Ltd.).

many high elevation forest ecosystems (Fig. 8) (McKenzie et al., 2001). This growth increase started after 1850, concurrent with the start of industrial activity and increased greenhouse gas emissions. There is no statistical evidence that the growth increase has been caused by increased temperature or a change in precipitation. Therefore, we cautiously infer that the growth increase is associated with elevated levels of atmospheric carbon dioxide. If so, this increase is an important signal of the effects of changes in the global atmospheric environment on forest ecosystems and suggests that high elevation forests are functioning as a carbon sink.

Snowpack variability is a dominant force limiting tree growth at high elevations (Peterson, 1998). Growth of mountain hemlock (*Tsuga mertensiana*) (Peterson and Peterson, 2001) and subalpine fir (*Abies lasiocarpa*) (Peterson et al., 2002) is positively
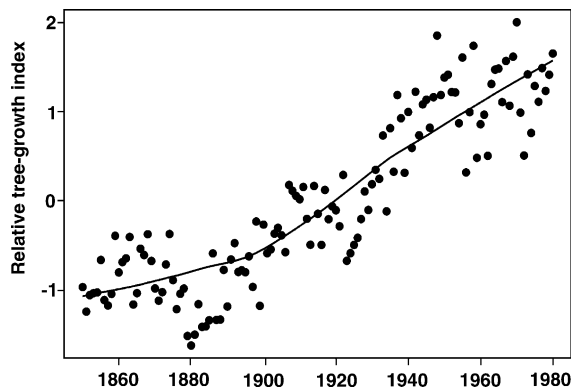
Fig. 8. Factor analysis of tree growth from 185 forest sites in western North America shows that over the past 100 years or so there has been a general growth increase at some locations, primarily in high elevation and Pacific coastal forests. This growth pattern has occurred during a period of increasing atmospheric carbon dioxide and increasing temperature. Data from McKenzie et al. (2001).

correlated with PDO at treeline (where snowpack limits length of growing season) and negatively correlated with PDO at lower elevations (where soil moisture storage limits summer growth) in the Olympic and northern Cascade Mountains (Peterson and Peterson, 2001). Therefore, multidecadal climatic phenomena control growth and productivity of forest ecosystems at local and regional scales, and tree growth is somewhat predictable over a period of several decades.

Regeneration of conifers in high elevation forest ecosystems has increased throughout western North America during the past century, particularly since the 1930s (Rochefort et al., 1994). This increase is manifested primarily by trees establishing along the margins of existing forest edges in the subalpine forest-meadow mosaic, with a loss of meadow habitat. This new establishment of trees is also particularly prominent near treeline during periods of low snowpack, often associated with warm PDO regimes (Woodward et al., 1995). Upright tree establishment into alpine tundra of Glacier National Park began in 1920, when temperatures warmed and snowpack was below average (Bekker et al., 2000). There have been recent upward advances in treeline elevation in some parts of Glacier National Park, but the greatest changes have been in gaps between existing tree patches near the treeline (Butler and DeChano, 2001; Klasner and Fagre, 2002). Therefore, biomass is

increasing, particularly as the morphology of shrubby trees attains a more upright form. Increasing tree growth to the exclusion of herbaceous flora, including a more abrupt alpine ecotone (Butler et al., 1994), represents a change in biological diversity and the potential for subalpine forest ecosystems to act as a sink for carbon.

Productivity, succession and large-scale spatial patterns in the Olympic, Cascade, and Rocky Mountains are controlled by ecological disturbance, especially fire. Area burned by wildfire in any particular year is at least partially related to the PDO regime. For example, years in which fire has damaged more that 80,000 ha in national forests of Washington and Oregon are nearly four times more common during a warm PDO than during a cool PDO (Mote et al., 1999). This regional effect is moderated by synoptic scale meteorology, particularly the effect of high pressure ridges from eastern Washington to western Montana (Gedalof, 2002). We anticipate that a warmer climate will bring extended fire seasons and perhaps more large fires to much of this region.

Mountain environments of the American Northwest and Northern Rocky Mountains have responded in nonlinear patterns to climate variability over the past several centuries. Responses include long-term changes when thresholds are surpassed and short-term responses to cyclical phenomena such as the PDO. These nonlinear responses are increasingly evident in abiotic components of ecosystems (glaciers, snowpack, and streamflow) that drive biological productivity (forest productivity, regeneration, and carbon storage). Understanding the nonlinear nature of climate drivers and their interactions with ecosystems will enhance the predictive capabilities of models and decision making by resource managers of mountain landscapes.

4.5. Synergistic interactions of land-use and climate changes on the invasibility of an exotic tree species

The human-driven movement of organisms over the past 200–500 years, deliberate and accidental, undoubtedly dwarfs in scope, frequency, and impact the movement of organisms by natural forces in any 500-year period in the Earth's history. Such massive alteration in species' ranges rivals the changes

wrought by continental glaciation and deglaciation cycles of past ice ages, despite the fact that these human-driven range shifts have occurred over much less time (e.g., Semken, 1983). Mack et al. (2000)

Numerous studies cited in Section 2 focused on the influence of climatic change on the range of plant and animal species. The rates and novel qualities of these range changes are also of concern. We know that forests have migrated in response to past climatic changes (Delcourt and Delcourt, 1983; Thompson et al., 2000). However, many genera of forest trees were in disequilibrium with climate, as during the Holocene (Gates, 1993). Climate did not always control the rate of spread. The geographic distributions of many trees depended instead on the availability of propagules and the ability of seedlings to survive in competition with plants already growing at a given site (Davis, 1981).

Changes in the distribution and abundance of certain plant species, synergistically driven, may not be gradual in their eventual outcome but rather sudden in occurrence (Myers, 1992). Attributes of biotic invaders make them obvious candidates for these jump events. One such scenario is currently unfolding with one woody species of the North American coastal plain, the Chinese tallow tree (*Triadica sebifera*).

Chinese tallow is widely distributed throughout the coastal plains of southern California and both the United States south Atlantic and the Gulf of Mexico coasts, and it has also been cultivated, mainly as an ornamental tree, in many other parts of the world. In North America, Chinese tallow is believed to have been introduced to Georgia in 1772 (Bell, 1966) and was observed in South Carolina in 1784 (Schoepf, 1911). Between 1900 and 1910, as part of a study to determine the tree's commercial viability, the U.S. Department of Agriculture established four plantations of Chinese tallow in Texas, Louisiana, and Florida (Jamieson and McKinney, 1938). Soon thereafter, plant nurseries along the Gulf of Mexico coast made the species available to the general public (Bruce et al., 1997). In the Royal Botanic Gardens, Surrey, U.K., there are specimens collected from New Orleans in 1832 (in flower) and in 1854 (in fruit), indicating that Chinese tallow was grown in Louisiana prior to 1900 (Howes, 1949). Thus, although the species has been growing on the northern Gulf coast
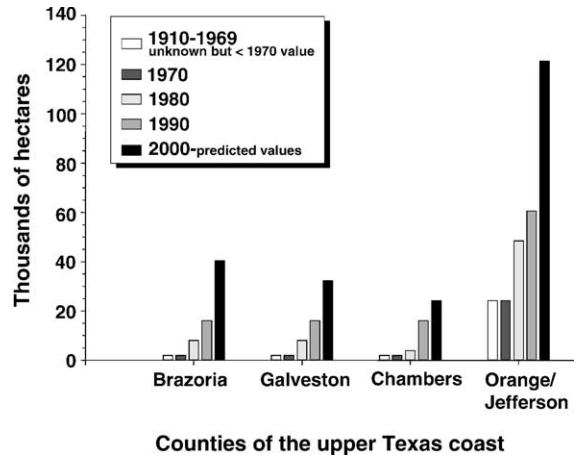

Fig. 9. Area of Chinese tallow in Texas coastal counties, 1910–2000.

for about 170 years, it has only been during the past 30 years that tallow populations along the northern Gulf coast began to increase rapidly in size (Fig. 9).

Tallow grows in poorly or well-drained sites and is tolerant of brackish water in the coastal zone (Bruce et al., 1997). The rate of growth during the early life of the tree is about 1 m year^{-1} (Howes, 1949), which is two to ten times faster than native associates (Hall, 1993; Harper, 1995). In addition to a rapid rate of growth, tallow produces viable seeds by the third year of life (Howes, 1949). In Louisiana, average seed yield is 17,552 seeds for small trees (2.5–10 cm dbh), 33,686 seeds for medium trees (>10–20 cm dbh), and 51,550 seeds for large trees (>20 cm dbh) and some individuals have as many as 84,000 seeds (W. Barrow, unpublished data). Herbivory of tallow stems, roots, and leaves is rare on the Gulf coast. Although numerous insects feed on its leaves in China and Japan, insects defoliated less than 1% of leaf area in Texas. At the same location, insects accounted for 5–25% loss of leaf area from native associates (ash, hackberry, and willow) (Bruce et al., 1997). The potential lifespan of tallow in the southeastern United States is unknown. In China, ''trees are known to be several hundred years old and though prostrated, still send forth branches and bear fruit'' (Hooper, 1904). Increases in soil temperature enhances the tallow's competitive capacity via a more productive and effective enzyme uptake of minerals through its root system (Jones, 1993); consequently tallow may have a

competitive advantage over native trees in warmer conditions. All of these attributes – growth rate, seed production, lack of interested herbivores, longevity, salt tolerance, and nutrient efficiency – have likely played a role in the current success of this invader.

Most seeds produced by Chinese tallow drop near the parent tree. Tallow seeds are dispersed primarily by birds, although water movement contributes to seed dispersion as well. For bird-dispersed seeds, dispersal distance from the parent tree is a function of seed retention and behavior by the bird species. Birds that feed on waxy fruits, like those of Chinese tallow (Howes, 1949), have longer gastrointestinal retention times than do birds feeding on non-waxy fruits (Place and Stiles, 1992). Thus, birds may disperse tallow seeds farther than the non-waxy seeds typical of plants native to a particular region. Among habitats of the Atlantic and gulf coastal plains (spoil areas, mixed pine-hardwood, and bottomland), tallow attracts diverse but variable coteries of dispersal agents that are qualitatively similar in seed usage patterns (Renne et al., 2002). For instance, a recent survey of frugivory by 55 species of birds in Louisiana found that the number of bird species visiting woody plants ranged from one consumer for pigeonberry (*Hirtella triandra*) to as many as 27 species for hackberry (*Celtis laevigata*) fruit (Fontenot, 1998). To date, we have identified 47 species of birds consuming the seeds of tallow (Barrow and Fontenot, unpublished data). There is apparently no other plant in the United States that attracts this many avian consumers to its fruit (Barrow, personal observation). Most dispersers of tallow seeds are wintering birds, but long-distance Nearctic-Neotropical migrants play an important role in dispersal of plant propagules during spring migration on the northern coast of the Gulf of Mexico (Barrow et al., 2001), which can lead to short-term dispersal over longer distances. Plants possessing generalized dispersal syndromes are likely to be more invasive than those relying on specialist dispersal agents. It is likely that such a dispersal syndrome contributes to effective dispersal of tallow seeds by many bird species throughout its range. Of course, humans are also important long-distance dispersal agents of this species because they introduced the species into North America for horticultural purposes.

For many tree species, dispersal will be more difficult this century than it was during past climatic changes because of alterations of the landscape that have created barriers to tree migration. Fragmentation of suitable habitat for native tree species in the south-central United States is well documented (Rudis and Birdsey, 1986). Because habitat remnants attract or concentrate birds, especially en route migrants, they may promote spread of tallow seeds when birds perch and then defecate seeds on the edges or beneath the canopies of forest patches (With, 2002). Human-created landforms, such as levees and spoilbanks, are quickly colonized by Chinese tallow in Louisiana (Bettinger and Hamilton, 1985; Barrow et al., 2001). Since the 1940s, levees and spoil deposits have become increasingly abundant in the coastal zones of Louisiana and Texas. By the 1980s, these new landforms occupied about 66,000 ha in coastal Louisiana alone, about 4% of the state's coastal region (Dell and Chabreck, 1986). In Texas and Louisiana, the introduction of tallow trees has produced large-scale conversion of much of the historical coastal prairie and rice fields to woodland (Bruce et al., 1995; Grace, 1998). Coastal prairie that has been converted to rice field and then abandoned, as well as long-term rotation rice land are almost always colonized by tallow within a year. These new woodlands are essentially monospecific stands of tallow trees with a few native tree and shrub associates.

Due to rapid expansion of human populations in the coastal plain of the Gulf of Mexico (Culliton et al., 1990), landscapes in this region will likely continue to be modified at the expense of native species and to the benefit of resilient invaders like Chinese tallow. The northward spread of tallow is limited only by low winter temperatures (Bruce et al., 1997).

Although it remains unclear why Chinese tallow endured a population lag phase for some 140 years prior to the proliferation and spread of the last 30 years (Mack et al., 2000), it most likely resulted from synergistic interactions of human husbandry, favorable landscape changes, and the ''discovery'' of lipid-rich tallow seeds by many species of birds. These combined factors appear to have provided opportunities for the species' population to persist and eventually reach a breakpoint around 30 years ago.

Humans, through cultivation and husbandry, probably enhanced the likelihood that tallow could reach a threshold of containment and become invasive. The human-created barriers to tree migration that are now commonplace in our landscapes are precisely the

features that facilitate tallow establishment (e.g., isolated remnant forest patches, vast agricultural fields, human settlements, clear-cut patches in forested landscapes, roads, etc.). Synergistic interactions between changing land use and land cover and accelerated warming may facilitate a series of sharp jump events that will enable Chinese tallow to spread northward rapidly relative to both changing climate and to most native tree species.

4.6. Treeline advance into Arctic tundra

Subarctic and Arctic regions of North America have warmed significantly during the last 150 years (Deming, 1995; Overpeck et al., 1997). Climate models predict that the most pronounced warming during the 21st century will occur at high latitudes (IPCC, 2001a). During the last 12 years, the mean annual temperature in northwest Alaska has increased 0.2 °C year^{-1} (Stottlemyer, 2001). The stressed Arctic treeline ecotone is expected to show advances into tundra as the climate continues to warm (Lavoie and Payette, 1996) (Fig. 10).

Paleoecological studies of 3000–1300 BP macrofossil remains at a Canadian taiga–tundra transition zone suggest that the mechanisms regulating treeline geographical shifts may not be easily brought on by climate shifts alone (Lavoie and Payette, 1996). However, treeline shifts in black spruce (*Picea mariana*) during the last 150 years in the subarctic

Fig. 10. Treeline ecotone dominated by white spruce and tussock tundra where spruce have advanced into tundra >100 m during the last 200 years, Agashashok River drainage, Noatak National Preserve, Alaska.

Quebec Province show that the forest limit moved 4 km northward. In addition, pre-established black spruce showed increased height and radial growth, suggesting warmer and wetter conditions (Lavoie and Payette, 1994).

Treeline location has been dynamic for the thousands of years in Alaska (Pielou, 1991). Eighteen thousand years ago, the latitudinal tree line was 35–40°N for white spruce (*Picea glauca*). Nine thousand years ago, white spruce reached the Beaufort Sea (70°N) then receded to its present location on the south slopes of the Brooks Range (Ritchie and MacDonald, 1986; Suarez et al., 1999). As indicated in other studies, during the last 150 years, white spruce has shown sharp increases in recruitment and advances into tundra both in Canada (Szeicz and MacDonald, 1995) and along Alaska's Brooks Range (Rowland, 1996; Suarez et al., 1999).

The rate of change in treeline forest advance and retreat during past millenia is difficult to quantify. However, field surveys of living trees and woody debris, historical photography, and government and private sector notes from the last 150–200 years allow an assessment of the pace of change that is more precise. Treeline advance involves both recruitment and "filling in" of existing stands by increased growth in stem diameter and/or height; both processes appear to be related to climate (Suarez et al., 1999). During the last two centuries, tree-ring growth at treeline has shown a somewhat linear increase, while the recruitment rate is nonlinear (Fig. 11). The forest advance into tundra is generally patchy, suggesting that favorable topography and less saturated soils are related factors that regulate forest establishment and growth. White spruce establishment is promoted by warming temperatures, decreased plant competition, and increased nutrient availability (Hobbie and Chapin, 1998). Processes such as soil mineralization of carbon and nitrogen often have temperature thresholds below which there is little rate response to change in soil temperature (Nadelhoffer et al., 1991). Rate responses become nonlinear at soil temperatures near or above 9 °C. More detailed study of the environmental gradient in soil condition and microclimate across the ecotone is required, however, in order to estimate the extent of these gradients at treeline and the potential for future forest advancement into tundra if the present climate trends continue or accelerate (Suarez et al., 1999).
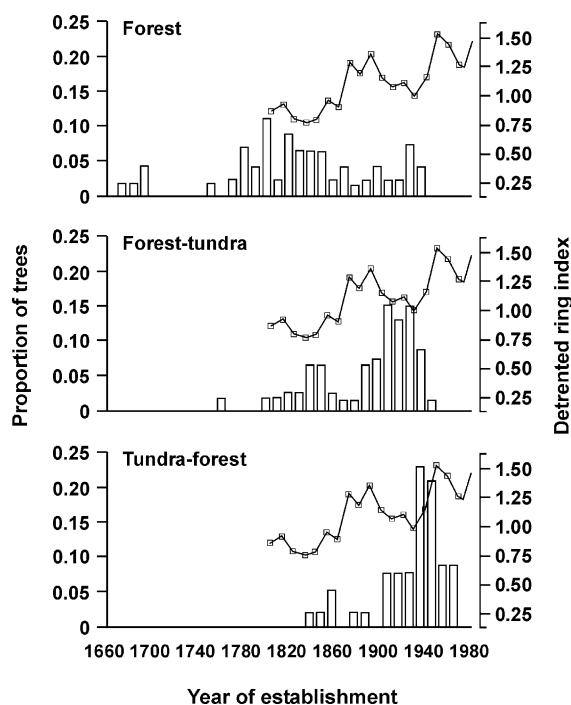
Fig. 11. Relative frequency histograms with 10-year age classes across five expanding white spruce stands, and detrended tree ring growth index, Asik watershed, Agashashok River drainage, Noatak National Preserve, Alaska (from Suarez et al., 1999 reproduced with permission from Ecoscience).

White spruce is the dominant forest species at the taiga–tundra treeline in northwestern Alaska (Rowland, 1996; Suarez et al., 1999). Although the extensive invasion of low density white spruce into tundra can occur rather rapidly, the positive response of white spruce growth and stand infilling to a warmer climate may be of greater significance to natural resource managers. Infilling of spruce and/or shrubs will change ecosystem nutrient status, snowfall retention, and hydrology (Sturm et al., 2001). Such shifts will likely alter both above- and below-ground biodiversity (Kennedy et al., 2002; Porazinska et al., 2003; Heemsbergen et al., 2004). In addition, the expansion of white spruce into tundra will alter fire frequency and distribution so fire suppression may become an important policy issue in natural resource planning (Flannigan and Van Wagner, 1991). Perhaps of equal importance is the fact that a shift in watershed vegetation from tundra to taiga will alter nutrient availability, especially nitrogen. Change in soil

temperature may also affect the spatial extent of *Alnus crispa* (alder), a nitrogen fixer. In the Arctic treeline alder often occur on nutrient-poor sites. Understory shrubs can exploit the added nitrogen increasing their biomass and expansion (Rhoades et al., 2001).

Effects of change in terrestrial nutrient availability could cascade among aquatic nutrient and energy budgets, aquatic productivity, and biodiversity at rates that are difficult to predict (Shaver et al., 1992). Effects of changes in terrestrial nutrient availability will likely be accompanied by change in annual soil thaw depths (soil active layer) which in turn will alter subsurface hydrochemical processes (Woo, 1986). If shallow subsurface flow increases, more nutrients and labile forms of carbon will be transported to the aquatic ecosystem. Surface soil and forest floor organic layers are the primary source of allochthonous aquatic dissolved organic matter (DOM), and the more labile fractions of DOM are major sources of energy and nutrients for the base of the aquatic foodweb (Battin, 1999).

4.7. Coastal wetland response to rising sea level

Accelerated sea-level rise is regarded as one of the most costly and most certain consequences of increasing global temperature. Sea level rose between 10 and 25 cm during the past 150 years, which is the most rapid rate of rise during the past few thousand years (Gornitz, 1995; Varekamp and Thomas, 1998; IPCC, 2001a). The rate of global sea-level rise is projected to accelerate two to four times during the next 100 years as ocean volume increases due to thermal expansion, glacial melt, and ice-cap decline (IPCC, 2001a). Sea-level rise increases tidal flushing in estuaries and storm surge over low-lying coastal landforms. Average and peak salinity levels in estuaries and adjacent habitats increase as sea level rises, thereby altering the zonation of vegetation (Cahoon et al., 1998; Short and Neckles, 1999) and other biota (Burkett, 2002). Increased tidal levels and storm surge also intensify energy regimes in shallow coastal waters, which affects sediment transport and other coastal processes that maintain coastal substrates and intertidal vegetation.

Nonlinear dynamics in coastal systems are evident in the historical patterns of coastal shoreline and

vegetation change in the low-lying southeastern coastal margin of North America (Young, 1995; Cahoon et al., 1998; Thieler et al., 2000). Low-lying coastal marshes that do not accumulate organic and/or mineral sediment at a pace that matches or exceeds the rate of sea-level rise are submerged or are displaced inland. Barrier islands tend to ''roll over'' or move toward the mainland as sea level rises if human activities and changes in storm patterns do not impact this natural landward migration (Scavia et al., 2002). Intrinsic thresholds to sea-level rise may be estimated for coastal ecosystems if their elevation, geomorphology, slope, shoreline erosion/accretion rate, mean tide range, mean wave-height elevation, antecedent geology, salinity tolerance, and other factors that determine elevation and plant community structure are understood.

Sea-level rise observed along the United States coastline varied between and within coastal regions during the 1900s, but in general, the U.S. Gulf of Mexico and South Atlantic coasts (with the exception of Florida) have experienced rates that are significantly greater than those observed on the U.S. Pacific coast (Scavia et al., 2002). Differences in apparent sea-level change at a particular location (referred to as ''relative sea-level rise'') can be caused by land movements such as isostatic rebound and subsidence. Relative sea-level rise along the Louisiana coastline where the land surface of the Mississippi River deltaic plain is subsiding (sinking with respect to sea level) is as much as 10 mm year^{-1} because of a combination of natural and human-induced processes (Burkett et al., 2003). The Mississippi River deltaic plain comprises a series of overlapping delta lobes that formed during the last 6000 years when sea level was relatively stable (less than 0.5 mm year^{-1} annual rate of rise) (Frazier, 1967; IPCC, 2001a).

Between 1932 and 2000, Louisiana lost 1900 square miles of coastal land, eliminating roughly one-third of the deltaic plain wetlands that existed during the early 1900s (Fig. 12). During this period, there were at least two episodes of rapid wetland loss. One ''subsidence event'' occurred during the 1950–1970s, when wetland loss rates roughly doubled the 1930–1990 average rate along large sections of the Louisiana coastline (Penland et al., 1996a,b; Morton et al., 2003). The second event began during the spring of 2000, when approximately 100,000 ha of marsh began to die back long before marshes usually turn brown in the fall. At least 6000 ha of the browned marshes have converted to open water or mud flats (U.S. Geological Survey, 2002). The precise cause of the current large area of marsh dieback is not yet known, but some researchers have postulated that the drought of 2000–2002, interacted with other climatic factors, such as low river discharge, to stress the plants beyond their ability to recover.

Sea-level rise is one of several factors that contributed to the rapid, episodic decline of the Louisiana coast during the 20th century (Gosselink, 1984). Human activities, such as the leveeing of the Mississippi River, the dredging of several thousand kilometers of oil field access and navigation canals (Turner et al., 1994), and the withdrawal of subsurface fluids (Kazmann, 1988; Morton, 2001), have all been linked to wetland loss in South Louisiana. Human interactions with
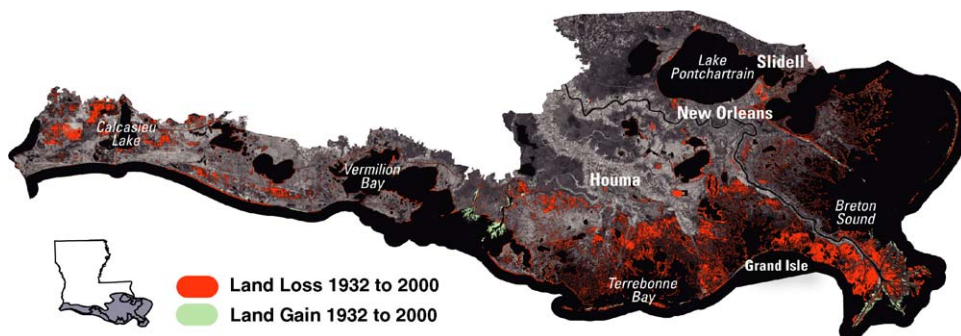

Fig. 12. Map of coastal land loss in the Mississippi River Delta Plain of Louisiana between 1932 and 2000 (*Source*: U.S. Geological Survey, National Wetlands Research Center, Lafayette, LA).

subsidence and sea-level rise have not just caused the rapid conversion of marshes to open water; salinity changes caused by the combination of factors have also led to the restructuring of some emergent and submerged plant communities to more salt-tolerant species (Guntenspergen et al., 1998).

In the Big Bend region of Florida along the Gulf of Mexico shoreline, the rate of sea-level rise is roughly the global average of 1–2 mm year^{-1} because there is relatively no local vertical movement of the land surface. Studies by Williams et al. (1999a,b) and Doyle et al. (2003) suggest that wetlands positioned on this low-lying limestone coastline are highly suscep-tible to sea-level rise and that effects here may also be strongly nonlinear. Wetlands in this microtidal region are perched on a relatively flat limestone surface and may not be affected by sea-level rise until the elevation of the sea reaches the threshold at which large expanses of wetlands are altered by inundation or increased salinity.

The zonation of marsh and forest habitat along an elevation gradient in the Big Bend region is readily apparent, with a narrow band of smooth cordgrass (*Spartina alterniflora*) along tidal creeks and then a broad expanse dominated by black needle rush (*Juncus roemerianus*) that gives way to unvegetated sand flats (Doyle et al., 2003). High marshes are generally encountered inland from the sand flats and typically contain a diverse assemblage of brackish tolerant graminoids in a fairly narrow band at the ecotone of lowland pine–palmetto forest. Interspersed within the salt marsh zones are disjunct pine/palmetto islands. These forest islands are dominated by slash pine (*Pinus elliotti*) and cabbage palm (*Sabal palmetto*) and are perched mounds above mean higher high water (the higher of the two tides each day). Remnant stumps of pine species and standing dead palmetto trunks are evident in high marsh zones and on small islands within the salt marsh zone. Fig. 13 shows a typical elevation profile across the forest-marsh ecotone in relation to tidal flooding developed from a composite of transects to test elevation/vegetation relations at St. Marks National Wildlife Refuge.

Episodes of forest decline in Florida's Big Bend region have been described by Cook (1939) and Williams et al. (1999a,b). Despite low rates of relative sea-level rise, the rapid loss of coastal forests in this
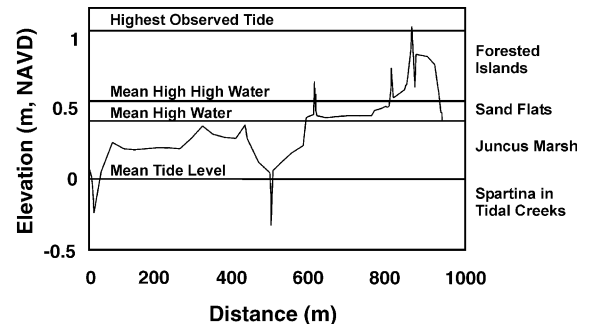

Fig. 13. Typical elevation profile across an elevation gradient in the Big Bend region of the Florida Gulf of Mexico coastline based on surveys conducted by Doyle et al. (2003).

region has been attributed to the effects of sea-level rise. During the course of one field study between 1992 and 1996, Williams et al. (1999a) observed tree mortality in the frequently flooded forest islands. That study indicated that tree regeneration generally ceases before canopy trees are eliminated. The study also suggested that salt water intrusion associated with small changes in sea level, or slight increases in the rate of sea level, could affect large land areas in this coastal region. Aerial surveys of the Big Bend region in 1996 revealed several large tracts of dead or dying coastal forests (Fig. 14). The Big Bend region of the Florida coastline is relatively undeveloped and erosion resistant because of the carbonate basement. The rapid retreat of coastal forests in this region has been attributed primarily to sea-level rise effects, even

Fig. 14. Aerial photograph taken in 1996 showing dead cabbage palm trees in the Big Bend region of Florida near the Gulf of Mexico shoreline.

though the rate of lateral retreat of coastal systems in this region does not correspond linearly with the rate of sea-level rise.

Changes in salinity, shoreline position, and flooding regime experienced over a period of 10 or 20 years may lead managers to believe that coastal systems respond incrementally or proportionally to rising sea level when in fact, some coastal systems will not show any decline or migration until an intrinsic threshold that triggers a response is reached. Understanding the nonlinear dynamics of coastal retreat will enhance the ability of coastal managers and environmental regulatory agencies to plan long-term coastal protection strategies. Understanding thresholds in processes that control coastal geomorphology is also important to community planners, transportation agencies, and emergency preparedness officials who make decisions regarding the placement of coastal buildings and infrastructure.

4.8. Human-induced thresholds in coastal barrier response to storm surge

Coastal barrier island ecosystems that occur along depositional coastal shorelines are dynamic in both time and space (Hayden et al., 1991). Their formation is dependent upon the deposition of sediment, mainly sand, on the nearshore seafloor by waves and currents. At low tide these features are exposed; wind-driven sand builds up the barriers so they remain exposed above water nearly all of the time. These types of coastal barriers are typical along the United States eastern seaboard, where the continental shelf slopes much more gently than it does off the U.S. Pacific coast (Snead, 1982). In a decade, the magnitude of change in geomorphology and ecology of these coastal barriers can exceed centuries-worth of similar change in other ecosystems.

In the absence of human manipulation, the evolution of a coastal barrier island is a function of sediment type and supply, platform slope, direction of prevailing winds, wave fetch and refraction, tidal range, and storm conditions (Dolan, 1974; Snead, 1982). Unmanipulated coastal barrier islands of the U.S. Gulf of Mexico and Atlantic coastlines are characterized by discontinuous sand dunes with intervening marshy flats (Hayden et al., 1991). This arrangement permits high water levels associated with

Fig. 15. General physiography and vegetation zonation of a dynamic coastal barrier island, Cape Hatteras National Seashore, North Carolina.

storm surges and higher sea levels to penetrate the barrier dune and deposit sand lenses varying in area, texture, and depth on the barrier's landward margin. Such multilayered depositional fans provide the necessary new substrate for early successional and stabilizing vegetation adapted to the extreme physical and chemical conditions (Fig. 15) (Godfrey and Godfrey, 1976). The establishment of vegetation on washover fans and dunes is also essential to the inland migration of a coastal barrier as sea level rises. Grassy dunes are often dominated by sea oats (*Uniola paniculata*), which grow vigorously when buried by moving sand. In adjacent flats and salt marshes, the productive salt meadow cordgrass (*Spartina patens*), accompanied by *Euphorbia polygonifolia* and *Cakile edentula*, is common. Such vegetation, which is quite resistant to salt aerosol deposition (Oosting, 1954) and salt water flooding (Seneca, 1969), also serves to trap windborne and marine overwash sands further builds the island interior. Without subsequent overwash and salt aerosols, shrub thickets and savannas develop, and with time, maritime woodlands can form (Au, 1974).

Decades of successional change may be lost in a single storm from high tide surge and overwash which can convert grassy dunes and dry shrub thickets back to bare sand (Fig. 16; Au, 1974). Similarly, several days of high winds may cause dune blowouts and return a once grassy dune to a shallow flat substrate
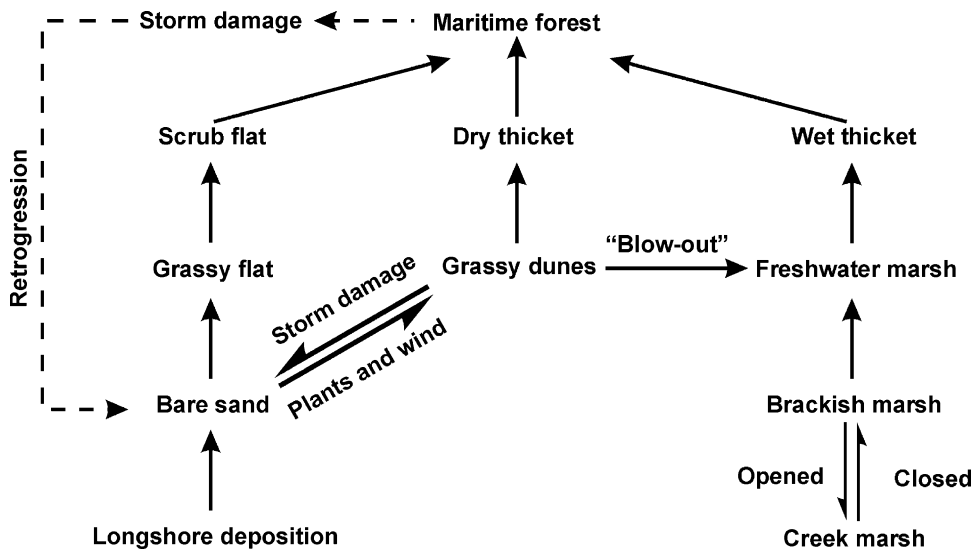
Fig. 16. The relationships between successional stages of coastal vegetation (from Au, 1974).

that will eventually become a freshwater marsh. High winds and surf produce and move salt aerosols inland, burning non-resistant vegetation close to the dunes. Windborne sand can abrade herbaceous plant tissue, further limiting growth in proximity to the surf zone. Later successional vegetation generally takes decades to develop and is normally found some distance inland from the beach.

One of the most pervasive human manipulations of coastal barrier ecosystems is the construction of an artificial, continuous high dune or berm (Godfrey and Godfrey, 1973). Such structures are intended to prevent island overwash and protect capital-intensive developments, such as roads, private homes, industry, and condominiums. The imposition of such a dune alters beach form and erosion rates within weeks or months and alters vegetation quality and quantity across the island within a few years. The artificial dune reduces the natural variation in beach width that is necessary to dissipate the energy in tide surges. The beach slope quickly steepens. A threshold is reached when the higher energy beach begins to lose larger sand grain particle sizes. Instead of the moving sand being deposited on the island interior, the particles are removed from the system by prevailing longshore currents. The net effect is often a rapid increase in substrate erosion rates and sand loss from the barrier ecosystem (Dolan, 1974).

The impacts of an artificial dune on vegetation distribution and biomass amount are generally pronounced and rapid. A continuous high dune substantially reduces overwash and the movement of marine salt aerosols (Godfrey and Godfrey, 1973). Once grassy dunes may quickly be replaced by dry shrub thickets and freshwater grasslands by wet thickets. Shrub vegetation may be enhanced in the region immediately behind the artificial dune, and the biomass per unit area may increase. Change in freshwater wetlands may be particularly pronounced. Freshwater wetlands generally consist of a water lens "floating" on the much more dense saline soil and ground water. With succession to shrubs, evapotranspiration rates increase sharply, and the thin freshwater lens can be lost.

Consequently, although barrier island stabilization via beach nourishment and dune construction may be desirable from a societal perspective, there can be adverse effects. Long-term, ecosystem-level study demonstrated this by the early 1970s for the nine marine coastal barrier national parks. In the 1950s, the National Park Service began stabilizing coastal islands, but by the 1970s, the National Parks had de-emphasized beach stabilization in their management strategies, particularly when applied to coastal barrier national parks (Behn and Clark, 1979). The research led to the National Park Service reversing in

1973 its policy of attempting to stabilize such systems (Stottlemyer, 1981). In 1982, this research was used as a basis for the Coastal Barrier Resources Act (Public Law 97-348), which removed most Federal incentives (such as Federally-subsidized flood insurance) to develop privately owned coastal barrier ecosystems.

The dynamic nature of coastal barriers has allowed quantification of their response to human manipulation in a relatively short time period. The responses are excellent examples of nonlinear change stimulated by interactions among geomorphology, hydrology, and biotic factors. One of the most pervasive effects of the increases in sea level predicted by the IPCC (2001a) and others (Gornitz, 1995; Varekamp and Thomas, 1998.) will likely be accentuation of coastal barrier dynamics associated with storm surges. Consequently, large sections of coastal barriers that may have been stable for decades may again become morphologically dynamic. This may stimulate public pressure on land managers and coastal management agencies to change current policy and provide short-term protection for human developments through dune and beach stabilization. Understanding the processes by which artificial dunes alter coastal barrier ecosystems can aid managers designing coastal barrier restoration programs and can assist managers in making regulatory decisions concerning artificial dune projects.

4.9. Global change, anthropomorphic effects, and nonlinearity in Bering Sea sockeye salmon populations

Cyclical changes in climate and environmental conditions of the North Pacific Ocean (*sensu*; McGowan et al., 1998) have had strong demonstrated effects on biota (Francis and Hare, 1994; Mantua et al., 1997; Anderson and Piatt, 1999; Hare and Mantua, 2000). These changes reflect shifts in community structure and organization, food-web dynamics, predator–prey interactions, and distribution and abundance of commercially important species like Pacific salmon (*Oncorhynchus* spp.) (Brodeur and Ware, 1992; Botsford et al., 1997; Clark et al., 1999). A marine climate shift in the North Pacific Ocean and Bering Sea in the 1970s has been well documented in the literature (Pearcy, 1992; Rogers and Ruggerone, 1993; Mantua et al., 1997). Ocean climate and ocean-linked terrestrial climate affect all phases of Pacific salmon life history in the north Pacific region and play a significant role in salmon production on interannual, as well as interdecadal, time scales (Adkinson et al., 1996; Downton and Miller, 1998). Mortality and maturation of salmon appear to be linked to broadscale fluctuations in ocean climate (Beamish and Bouillon, 1993); however, more localized upwelling circulation patterns can affect local productivity and salmon growth at sea (Fisher and Pearcy, 1988; Kope and Botsford, 1990). The interaction of local and broad-scale environmental conditions can produce complex nonlinear effects.

Significant and coherent linkages between shifts in North Pacific Ocean physical and atmospheric conditions and a marine biological response in Alaskan salmon are well documented (Beamish and Bouillon, 1993; Francis and Hare, 1994; Mantua et al., 1997; Finney et al., 2000). Climate prediction models and our understanding of the mechanisms linking salmon and climate response in the North Pacific Ocean continue to improve as we learn more about the biological response of Pacific salmon to environmental variation and as our long-term data records on ocean condition and salmon production increase (Beamish et al., 1999). The major climate influence on salmon production is thought to operate in a bottom-up fashion through physical influences on primary and secondary production (Brodeur and Ware, 1992; Roemmich and McGowan, 1995). Studies have indicated that salmon are most affected in the early part of the marine life history when these fish first enter the ocean (Pearcy, 1992; Pearcy et al., 1999). Management strategies that are predicated on ocean climate models and salmon production trends, however, frequently fail to address human effects that can influence cycles of productivity at other life stages (Lawson, 1993; Rogers and Ruggerone, 1993; Jackson et al., 2001). It is clear that nonlinear patterns of marine productivity result from multiple modes of variability in physical oceanography and climate, dramatic changes in human effects, and complex North Pacific Ocean ecosystem dynamics, all operating on different timescales (Finney et al., 2002). One nonlinear relationship has been recently documented in the North Pacific Ocean: carrying capacity and competition between wild sockeye salmon from Alaska and hatchery-produced pink salmon (*O. gorbuscha*) from Asia on their summer feeding

grounds in the North Pacific Ocean (Ruggerone et al., 2003).

Sockeye salmon (*O. nerka*) and pink salmon are two of the most abundant salmon species in the Pacific Ocean. Sockeye contribute 14% (by number) to 17% (by weight) of the total salmon harvest in the North Pacific Ocean (Burgner, 1991). Sockeye salmon have a great diversity of life history patterns in both freshwater and marine environments. Anadromous sockeye typically use stream and lake habitats as juveniles for 1 or 2 years and then spend from 1 to 4 years in the ocean before returning to their natal watershed to spawn and die. Pink salmon contribute 40% (by weight) to 60% (by number) of the total salmon harvest in the North Pacific Ocean adjacent waters (Neave et al., 1967). Pink salmon are distinguished from other Pacific salmon by having a fixed 2-year life span, with reproductively isolated odd and even year populations (Heard, 1991). Production of pink salmon along the Eastern Kamchatka Peninsula has increased steadily over the last four decades, with the greatest production occurring in odd-numbered years. Recent peak production of hatchery-produced pink salmon from Asia has contributed to the production of over 200 million adults in the North Pacific Ocean (Rogers, 2001). At the same time, survival of even-numbered year wild Alaskan sockeye salmon from juveniles in the ocean (i.e., smolts) to adults has decreased 26–45% (age-2 and age-1 smolts, respectively).

It has long been known that measurable structures reflected in fish scales (i.e., annual and seasonal growth increments) are highly correlated with fish growth (Clutter and Whitesel, 1956; Stone, 1976). Over the last 40 years, tens of thousands of salmon scales have been routinely collected in Alaska for determining the ages of fish and developing life history tables used in predictive models for regulating harvest and escapement. A recent collaboration among the U.S. Geological Survey, the National Marine Fisheries Service, and the Alaska Department of Fish and Game has developed a protocol for high resolution image capture and optimal image analysis using luminescence profiles for salmon scales. This system allows exact measurements of circuli and annuli spacing in a digital medium to quantify and back-calculate salmon growth patterns (see Davis et al., 1990 for scale methodology). We used these data

to analyze different biological time series in relationship to changes in growth patterns for sockeye populations throughout the Bering Sea, 1955–2000 (Ruggerone et al., 2002). These analyses also tested the relationship between marine growth for Bering Sea sockeye salmon and the large increase in salmon abundance that began with the North Pacific Ocean climate shift of the 1970s. Our data suggested that after the mid-1970s, sockeye salmon scale growth tended to be above average during the first 2 years at sea, and growth during this period was an important factor leading to the large abundance of western and central Alaska sockeye salmon since the mid-1970s. However, scale growth (i.e., salmon growth) of ocean age-3 Bristol Bay sockeye salmon tended to be below average during their third year at sea, especially during odd-numbered years when they competed with Asian pink salmon.

Pacific salmon are highly migratory in the open ocean but tend to aggregate at different life stages in highly productive offshore habitats (French et al., 1976; Myers et al., 1996) (Fig. 17). The importance of interspecific competition as a mechanism regulating population abundance in offshore marine communities is largely unknown. Intraspecific competition for food in marine systems has been shown to lead to density-dependent growth in highly abundant species of Pacific salmon (Rogers and Ruggerone, 1993; Welch and Parsons, 1993; Pearcy et al., 1999). Interspecific competition at sea with Asian pink salmon has been documented in other studies (Bugaev et al., 2001 and literature therein).

Knowledge of these factors and interactions led to speculation on possible effects the increase in hatchery production of pink salmon off the coast of Asia has had on wild sockeye stocks from Alaska when they overlap at sea. The salmon species interaction most likely begins during their first winter at sea in the central North Pacific Ocean (Fig. 19). During spring and early summer as temperatures increase, fish of different age classes of both species migrate northwest and enter the Bering Sea. Tagging studies suggest overlap between pink and sockeye salmon in ocean habitats throughout late winter and spring (French et al., 1976; Myers et al., 1996). Asian pink salmon tend to leave the high seas for coastal areas in June. During odd-numbered years, however, pink salmon are more broadly distributed in the north Pacific region
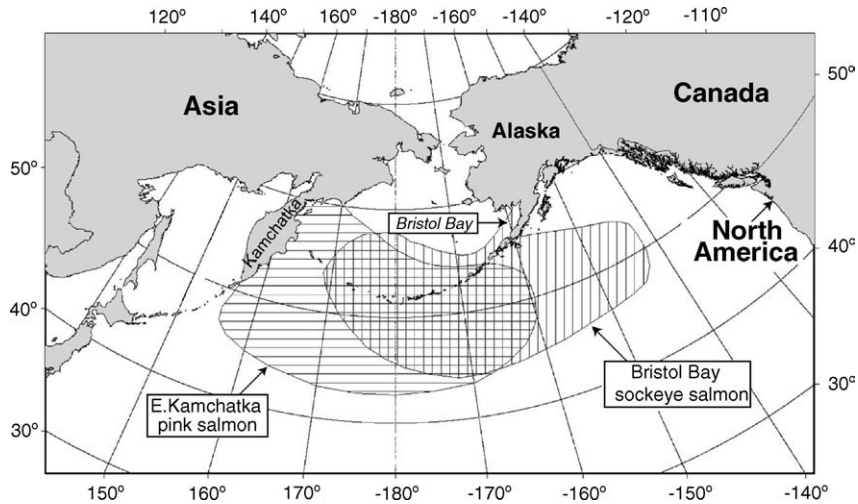
Fig. 17. Known ranges of immature Bristol Bay sockeye salmon and maturing eastern Kamchatka Peninsula pink salmon based on international tag recoveries.

and catch per effort remains high throughout July (Azumaya and Ishida, 2000). Thus, the period of overlap at sea occurs from winter through July, with the greatest area and longest cycle of overlap occurring in odd-numbered years.

A recent study of trophic interactions of salmon at sea suggested that pink and sockeye salmon both feed intensively on micronekton squid after growing to a large size in their second year at sea (Aydin, 2000). Overlap in diet and locations for these species during their open ocean growth suggests possible competitive mechanisms at sea, leading to questions of ocean carrying capacity. These competitive effects would be magnified with increased overlap in time and space and elevated numbers of hatchery pink salmon in the ocean in odd years. High numbers of hatchery produced pink salmon in odd-numbered years may reduce prey abundance prior to their emigration to coastal areas in June and July. Lower growth and survival of Alaskan sockeye in odd-numbered years are most likely related to competition with hatchery produced Asian pink salmon at sea (Ruggerone et al., 2003). Thus, hatchery fish releases in Asia have contributed to nonlinear effects in wild Alaskan sockeye salmon populations that mask the growth of Pacific salmon abundance relative to the mid-1970s ocean regime shift.

Climate change can directly affect physical environmental conditions critical to Pacific salmon in both freshwater (Schindler, 2001) and marine habitats (Beamish et al., 1999). The magnitude and timing of these changes can produce broadscale and local shifts in the distribution and abundance of salmon (Mantua et al., 1997). Changes in ocean temperature may affect fish migrations, shifts in prey abundance, and competitive interactions at sea. Ignoring the synergistic impacts of human-induced effects on the North Pacific Ocean ecosystem, however, leaves out a large proportion of the critical elements leading to nonlinear response in salmonid biology to ongoing climate change. Ecological extinction caused by overfishing, human-induced pollution, changes in water quality and quantity discharged to the sea, human development activities in coastal habitats, navigation dredging, bilge discharge containing non-native species, and anthropogenic climate change have all been linked to changes in marine productivity and habitat quality. Hatchery effects on freshwater systems and wild salmonid populations in Alaska have also been well documented (Hilborn and Eggers, 2000). However, no systematic evaluation of the effects of Asian salmon hatcheries on marine ecosystems in the North Pacific Ocean has been done despite the increasing development and production of those hatcheries. The case study on sockeye and pink salmon presented in Ruggerone et al. (2003) suggested that hatchery production of salmonids is another important factor we need to consider

when evaluating ocean ecosystems, climate change, and nonlinear biological effects.

4.10. Birds, spruce budworms, and the southern boreal forest

Summer bird ranges are often assumed to be tied to particular habitats. For this reason, much of the early work looking at climate change impacts on birds only looked at habitat changes, particularly changes in vegetation; assuming the birds would be present if the habitat was available. However, this assumption is an oversimplification of how species ranges are limited. While certain species may only be found in specific habitats (e.g., Kirtland's warbler, *Dendroica kirtlandii*, breeding in jack pines), others are more flexible in their habitat use. For example, species regularly associated with a particular habitat type are not being found in apparently equivalent habitat north or south of their current distribution, or a species may be found in apparently suitable habitat in some but not all years. Birds are also limited in their distributions by their physiology and food availability. The link between physiology and the winter distributions of many species is well documented (Kendeigh, 1934; Root, 1988a,b). Research shows that physiology likely plays some role in limiting some summer distributions as well (Dawson, 1992). One theory holds that, in some cases, use of a specific habitat by a species may be dependent upon a microclimate suitable for that species' physiology. For this reason, the output of models that incorporate a given species relationship with climate and how that range might change with a changing climate may be more accurate than those that simply assume the species will follow the habitat change.

A number of studies have used logistic regression to develop models that simulate the association between bird distributions (from North American Breeding Bird Survey data) and climate and determine how the ranges of these species are projected to change with a changing climate (Price, 1995, 2000a,b, 2003, 2004, in press; Price and Root, 2001). Only a few of the studies, however, addressed some of the potential ecosystem changes that might be associated with changes in summer ranges of North American birds (Price et al., 2000; Price, 2002; IPCC, 2001b). The following is one of those case studies and is also

an example of one of the types of nonlinear effects that might occur with range changes in species.

The spruce budworm (*C. fumiferana*) is a common, native phytophagous insect of boreal forests in eastern North America (Fleming and Volney, 1995). Its preferred foods include balsam fir (*A. balsamea*) and several spruce species (*Picea* spp.). Spruce budworms are usually present at low densities ($<100,000$ larvae ha^{-1}), but periodic outbreaks occur throughout the species range with densities reaching 22,000,000 larvae ha^{-1} (Crawford and Jennings, 1989). These outbreaks can extend over more than 70 million ha and last for up to 15 years, causing annual loss of more than 80% of foliage on fir and spruce trees. This extreme foliage loss can kill many of the trees in mature stands of balsam fir (Crawford and Jennings, 1989; Fleming and Volney, 1995). Trees not killed by defoliation are often at risk from other phytophagous insects and pathogenic diseases and standing dead trees increase the risk of fire.

While the exact causal mechanisms for the beginning and end of outbreaks are unknown, weather may play a role in at least a portion of the budworm's range. Outbreaks in some areas frequently follow droughts (Mattson and Haack, 1987), and some outbreaks in central Canada have started in stands with many mature firs flowering after hot, dry summers (Fleming and Volney, 1995). Drought can stress host trees, leading to increases in concentrations of sugar and sugar alcohols but also to decreases in complex carbohydrates, both of which can lead to a reduction in plant defense mechanisms. Drought can also change the microhabitat around affected plants with drought-stressed plants averaging 2–4 °C warmer (maximum 15 °C warmer) than abundantly watered plants (Mattson and Haack, 1987). Average temperature also plays a role in regulating the number of eggs laid by spruce budworms: the number of eggs laid at 25 °C is 50% greater than the number laid at 15 °C (Jardine, 1994). Drought and higher temperatures may also shift the timing of reproduction in budworms sufficiently such that they may no longer be affected by some of their natural parasitoid predators (Mattson and Haack, 1987). Weather may also play a role in stopping outbreaks; for example, some outbreaks in central Canada are thought to have been halted by late spring frosts that killed new growth on trees, thereby depriving budworms of their food source (Fleming and Volney, 1995).

The control of some populations of spruce budworm may be aided by avian predators, especially some of the wood warblers (Crawford and Jennings, 1989). Several warbler species, including Cape May (*Dendroica tigrina*), bay-breasted (*D. castanea*), blackburnian (*D. fusca*), Tennessee (*Vermivora peregrina*), and Nashville (*V. ruficapilla*), are important predators of spruce budworms. Some of these species, especially bay-breasted warbler, show functional responses to increases in budworms with individual birds moving into the area and increasing their reproductive output in response to increases in the budworm's population (Crawford and Jennings, 1989). Birds consume up to 84% of budworm larvae and pupae when budworm populations are low (approximately 100,000 ha^{-1}) and up to 22% when populations reach approximately 500,000 ha^{-1}. However, bird predation cannot effectively neutralize budworm populations in concentrations exceeding 1,000,000 larvae ha^{-1} (Crawford and Jennings, 1989).

Climate change may influence almost every component of this system, both individually and in species interactions. For example, budworm distribution is thought to be tied to the completion of larval development before autumn freezes begin (Jardine, 1994). Increasing temperatures and an increase in drought frequency might also lead to more frequent and possibly more severe outbreaks. This change could occur because of the effects of both drought and temperature on host plants and insects (Mattson and Haack, 1987; Fleming and Volney, 1995). Increasing temperatures may also reduce the frequency of late spring frosts in southern boreal forests, possibly increasing the duration of budworm outbreaks in those areas.

A changing climate might also decouple budworm population cycles from the cycles of some of its parasitoid and avian predators (Mattson and Haack, 1987; Price, 2002). Distributions of most of the warblers that feed on spruce budworms could shift significantly farther north. One set of models projects that three of the most significant predators – Tennessee, Cape May, and Bay-breasted warblers – may all occur only in southern Canada and the northeastern fringe of the United States with a doubling of CO_2 (Price, 2001) (Fig. 18). Indeed, the average latitude of occurrence of both Cape May and bay-breasted warblers has already shifted significantly farther north in the last 24 years (Fig. 19).

While there may be decoupling of some budworm populations from their control mechanisms the range and timing of reproduction of budworms would probably stay synchronized with their host species. Given that a large outbreak area could contain as many as 7 thousand trillions of insects, a typical mutation rate would mean that potentially billions of rare genotypes may still be present in the population (Fleming and Volney, 1995). These genotypes could potentially help budworms adapt and remain in synchrony with their host species.

One result of these changes, especially in southern boreal forests, may be an increase in the rate of conversion from boreal forests to other habitat types. Increasing temperatures, drought conditions, and insect damage may increase the likelihood of major fires, particularly in combination. Scientists and land managers are confronted with the key questions of how quickly might southern boreal forests might be converted to a different habitat type and of what habitat that might be? With an increase in fire frequency, the successional pathway changes from fir/spruce to aspen/birch to grasslands (Jardine, 1994). If the climate changes quickly, more southerly plant species may not have the time to migrate as rapidly as boreal species are lost; consequently, there could mean a shift to grassland or grass/shrubland in areas currently dominated by southern boreal forest. That shift in turn may affect regional economies and distributions of animals and insects using southern boreal forests.

Land managers may be able to intervene to help prevent the disruption of some ecosystem services, but the costs of such intervention could be large. The loss of insect predators, for example, may lead to the need to apply more pesticides. Other pollinators and seed dispersers may be artificially introduced to mitigate the loss of desirable insect and bird functions, but these alternatives could be costly. Finding replacements for other services, such as contributions to nutrient cycling and ecosystems stability/biodiversity is more difficult to conceive. In many cases, any attempt at replacement may represent a net loss in other ecosystem functions and values (e.g., losses of the values of wildlife associated with recreation, subsistence hunting, and cultural and religious

Bay-breasted warbler

Cape May warbler

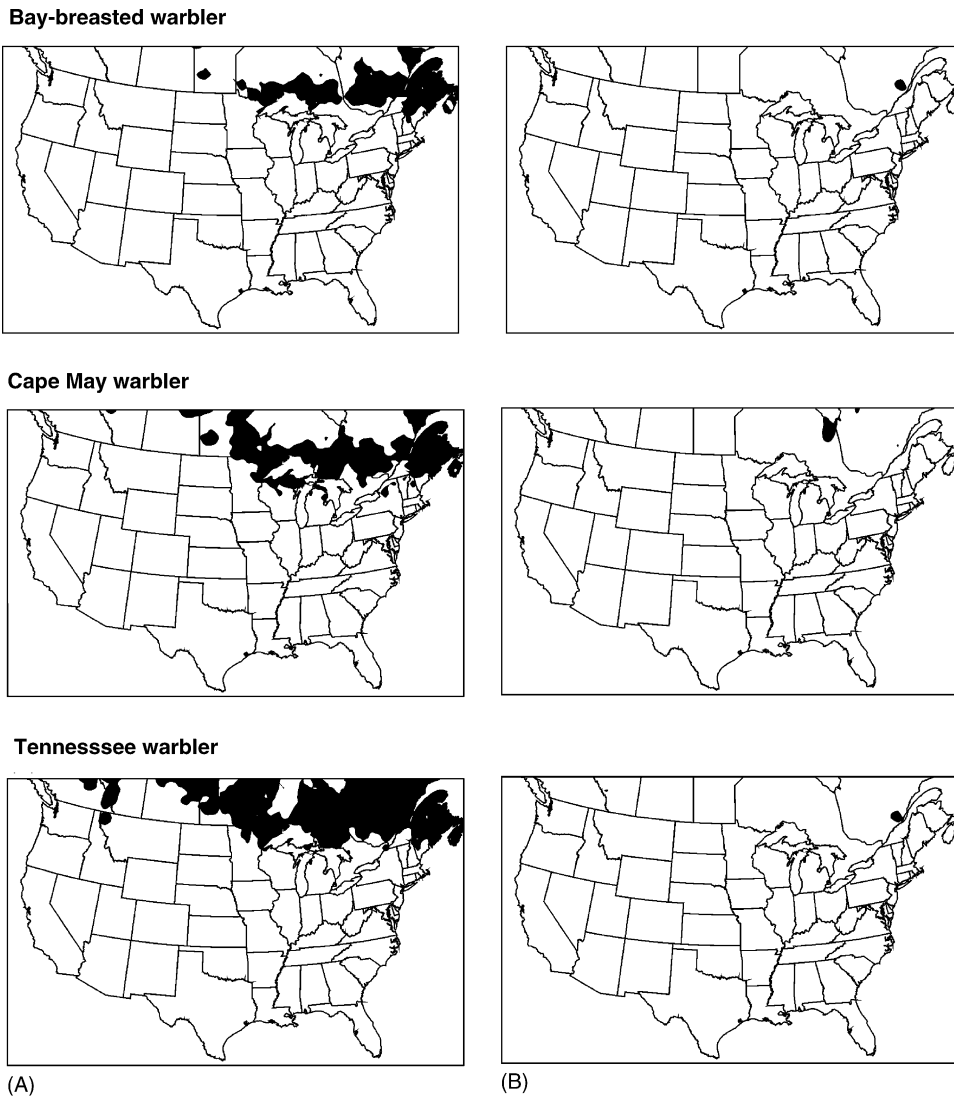**Tennesssee warbler**

(A)   (B)

Fig. 18. Current (left panel, A) and projected (right panel, B) distributions of some warblers specializing in feeding on spruce budworms. Current distribution is based on Breeding Bird Survey data and is modified from maps found in Price (1995). Projected distribution is based on output for a doubling of carbon dioxide from the Canadian Climate Center and was developed following the techniques used in Price, in press and Price (1995).

ceremonies). Overall, problems may not necessarily be caused by the change itself, but rather by the rate of change. Unless all components of the ecosystem change at the same rate, the systems will decouple and the new systems may bear little resemblance to the ecosystems to which managers are accustomed. More research is needed to determine not only how components of the ecosystem work together, but also

how rates of changes affect ecosystem components and their interactions.

Projected rapid climate change is of major concern, especially when viewed with other population stresses (e.g., habitat conversion, pollution, and invasive species). These synergistic stresses are likely to prove to be the greatest challenge to wildlife conservation in the 21st century. Because anticipation of changes
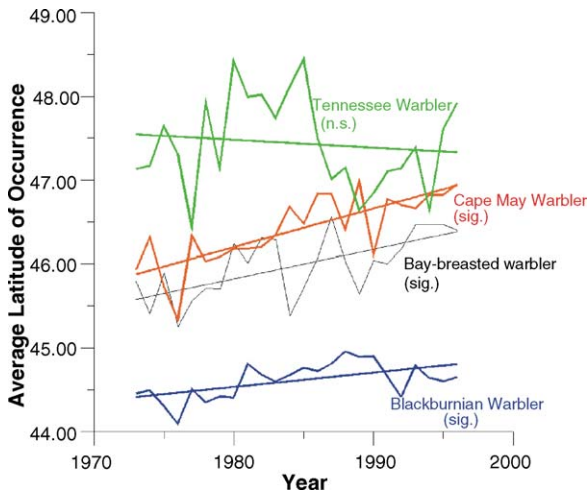
Fig. 19. Change in the average latitude of occurrence (1977–1996) for warblers specializing in feeding on spruce budworms. Average latitude of occurrence is calculated by averaging the latitudes for all North American Breeding Bird Survey routes where the species were detected in a given year. Slope of regression line is either significantly ($p < .05$) or not significantly (n.s.) different from zero.

improves the capacity to manage resources, it is important to understand as much as possible about both the linear and nonlinear responses of animals to a changing climate. For example, in the case study presented here, managers could increase monitoring efforts to determine if changes in bird populations are changing the frequency of budworm outbreaks. Conservation plans could also begin to take into account the knowledge that the ranges of many species ranges will change and the thresholds at which shifts in potential range will occur. Areas currently being managed for one set of species may become unsuitable for that suite of species over time. Therefore, management plans should consider not only where the species currently are but also where they may go as the climate changes. Finally, by considering the ecosystem services currently provided by these species it may be possible to develop alternative management guidelines to replace services lost as species ranges change.

5. Conclusions

Intrinsic thresholds in many physiological and biogeochemical processes that structure ecosystems are directly linked with climatic variables, particularly temperature and precipitation. Thresholds in extrinsic processes, such as those illustrated in our case study of nitrogen deposition in the Rocky Mountains and sea-level change along the northern Gulf of Mexico coastline, can also limit the structure, function, distribution, and resilience of ecosystems. Interactions and feedbacks among extrinsic and intrinsic factors are a third element of nonlinear ecosystem dynamics. These dynamics are generally neither additive nor proportional to the magnitude of environmental change associated with a changing climate. Conversely, the effects of environmental change on linear systems are proportional and additive (for example, ocean volume at constant pressure is proportional to temperature), which means that the various components of natural linear systems may each be described and, in some cases, managed separately. To predict the influence of a climate on linear systems, one process can be superimposed upon another to evaluate the cumulative influence of environmental change. Deterministic models often do not capture nonlinear behavior because thresholds and complex interactions among ecosystem processes are either unaccounted for or they are inadequately parameterized.

Our case studies illustrated nonlinear dynamics in 10 different ecosystems in response to climate change and variability. The case studies of sea-level rise along the Gulf of Mexico Coast and the role of ground water in Great Lakes wetlands revealed how subtle environmental differences can have a major influence over the rate and direction of systems response and how subtle discontinuities can lead to unanticipated consequences ("surprises") for those who manage biological resources. These and other case studies cited in this paper also clearly demonstrated the importance of understanding interactions between and among biotic and abiotic factors in ecosystems and how these interactions alone (even if we could accurately forecast changes in climate) lead to complexities that are very difficult to predict and factor into resource management plans.

Responses of ecosystems to changes in climate can occur at a rate that would make them qualify as ecological disturbances according to the definition cited in Huston (1994). For example, drought-induced mortality in arid southwestern forests and the submergence of wetlands in the Mississippi River

deltaic plain have occurred more rapidly than the time required for biomass accumulation in these systems. In some cases, the disturbance in ecosystem functioning can be triggered by a simple decoupling of predator and prey with secondary and higher order effects that cascade among trophic levels, as described in our case study of spruce budworms in boreal forests. Human-induced disturbance can also have an important, if not predominant, influence on the structure of populations and ecosystems as climate changes, as illustrated in our case studies of wildfire suppression, sockeye salmon, and invasive Chinese tallow. Temporal scale is an important consideration in describing and predicting both nonlinear and linear ecosystem trends. Trends at scales of centuries and millennia may appear linear along a continuum with coarse resolution, but that may not be the operational scale of natural resource management. The rate at which environmental change influences ecosystem services should determine the temporal scale of natural resource impact assessments.

Knowledge of thresholds and rapid shifts in ecosystem state will permit ''decision makers to assess the landscape of intolerable domains that exist beyond certain thresholds'' (Pielke et al., 2003, p. 12). Perhaps more importantly, such knowledge will enable societies to anticipate and respond to changes in the environment in a manner that is needed to sustain ecosystem services.

A better understanding of linear and nonlinear ecosystem processes and patterns will improve science-based management of natural resources. Advancements in our ability to simulate nonlinear ecosystem dynamics are particularly needed to support adaptive management and to provide strategies for mitigation of and adaptation to the interactive effects of climate change and human activities on biological systems. Until this predictive ability is more advanced, applying the precautionary principle in habitat and species management plans, land acquisition for biological conservation, and endangered species recovery plans will provide the most options for maintaining ecosystem structure and function.

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