Chapter 3—Case Studies

Thresholds of ecological change can occur at many spatiotemporal scales and in a diversity of ecosystems. The following examples were chosen to illustrate that thresholds probably have already been crossed in ecosystems in response to climate change and that the crossing of these thresholds will likely have implications at continental and global scales. Because these changes will likely impact American society significantly, these examples make clear the usefulness of considering thresholds in the monitoring and management of natural resources.

Four case studies are presented below in detail; they cover distinctly different types of ecosystems, all of which are potentially undergoing threshold-type changes. These studies are arranged in order of latitude, beginning with the highest. The first study is of a latitude in the far north where climate change has resulted in large temperature changes. The next study is of the midlatitude PPR where continental drying is expected because the subtropical high-pressure zone is broadening. The third case study is of forests of the West and Southwest, which are at a slightly lower latitude, are generally already water-limited, and will be sensitive to the decreased water availability that would profoundly impact the western half of the United States. Finally, in the lowest latitude example, the effects of climate change in forcing threshold changes in coral reef ecosystems are examined.

Case Study 1. Ecological Thresholds in Alaska

In recent decades, Alaska has warmed at more than twice the rate of the rest of the United States. The Statewide annual average temperature has increased by 3.4°F since the mid-20th century, and the increase is much greater in winter (6.3°F). A substantial portion of the increase occurred during the shift of the Pacific decadal oscillation in the 1970s. The higher temperatures of recent decades have been associated with changes in the physical environment, such as earlier snowmelt in the spring (Dye, 2002; Stoneet al.et al. 2002; Dye and Tucker, 2003; Euskirchenet al.et al. 2006, 2007), a reduction of sea ice coverage (Stroeveet al.et al. 2005), a retreat of many glaciers (Hinzmanet al.et al. 2005), and a warming of permafrost (Osterkamp, 2007). In parallel with these changes in the physical environment, substantial changes in ecological systems have been observed, including dramatic increases in the frequency and spatial extent of (stet) (Balshi *et al.*, 2008) wildfire (Westerling et al. 2006), wildfire, dramatic changes in the wetlands of interior Alaska (Yoshikawa and Hinzman, 2003), vegetation changes in the tundra of northern Alaska (Goetz *et al.*, 2005), and ecological changes that are affecting fisheries in the Bering Sea. The temporal pattern of these responses to climatic change in Alaska, the understanding of the drivers of the responses, the degree to which these responses represent gradual versus threshold responses, and implications for the services provided to society by ecological systems in Alaska are described bellow.

Ecological Thresholds and Changes in Insect and Wildfire Regimes of Interior Alaska.—Analyses of historical insect and fire disturbance in Alaska indicate that the extent and severity of these disturbances are intimately associated with longer and drier summers (Judayet al.et al. 2005; Balshiet al.et al. 2008). Between 1970 and 2000, the snow-free season increased by approximately 10 days across Alaska primarily because of earlier snowmelt in the spring (Euskirchenet al.et al. 2006, 2007). Longer summers have the potential to be beneficial to the growth of plants. However, the satellite record suggests that the response of plant growth to warming differs in different regions of the

State with growth increasing in the tundra of northern Alaska and decreasing in the boreal forest of interior Alaska (Jiaet al.et al. 2003; Goetzet al.et al. 2005). Analysis of forest growth data indicates that the growth of white spruce forests in interior Alaska is declining because of drought stress (Barberet al.et al. 2002), and there is the potential that continued warming could lead to forest dieback in interior Alaska (Judayet al.et al. 2005). The drought stress that has been experienced by trees in Alaska during recent decades makes them particularly vulnerable to attack by insects.

During the 1990s, south-central Alaska experienced the largest outbreak of spruce bark beetles in the world (Judayet al.et al. 2005). This outbreak was associated with a threshold response to milder winters and warmer temperatures that increased the over-winter survival of the spruce bark beetle and allowed the bark beetle to complete its life cycle in 1 year instead of the normal 2 years. This was superimposed on 9 years of drought stress between 1989 and 1997, which resulted in spruce trees that were too distressed to fight off the infestation. The forests of interior Alaska are now threatened by an outbreak of spruce budworms, which generally erupt after hot, dry summers (Fleming and Volney, 1995). The spruce budworm has been a major insect pest in Canadian forests, where it has erupted approximately every 30 years (Kurz and Apps, 1999), but was not able to reproduce in interior Alaska before 1990 (Judayet al.et al. 2005). Areas that experience the death of trees over large areas of forest are vulnerable to wildfire as the dead trees are highly flammable. This is of particular concern in Alaska where wildfire incidence has been increasing in recent decades.

The area burned in the North American boreal region has tripled from the 1960s to the 1990s owing to the increased frequency of large-fire years (Kasischke and

Turetsky, 2006). For example, two of the three most extensive wildfire seasons in Alaska’s 56-year record occurred in 2004 and 2005, and half of the years with the largest fires during this 50-year time period have been since 1990 (Kasischkeet al.et al. 2002, 2006; Kasischke and Turetsky, 2006). The increase in fire frequency in Alaska appears to be primarily associated with the shift in the Pacific decadal oscillation that occurred in the late 1970s as large-fire years occurred once every 6 years before the shift and increased to once every 3 years after the shift (Kasischkeet al.et al. 2002). Analyses of fire probability in interior Alaska indicate that fire probability increases as a step function when the mean temperature in June increases above 14°C or when the August mean precipitation decreases below 40 millimeters (mm) (Paul Duffy, oral commun., 05/02/2008). Because the mean June temperature has been increasing in interior Alaska during the last several decades, the crossing of these thresholds will likely lead to substantial increases in area burned in interior Alaska, and there is the potential that the large-fire years of 2004 and 2005 in Alaska may occur several times a decade instead of once or twice every 50 years.

Analyses of the response of fire to scenarios of future climate change indicate that the average area burned per year in Alaska will double by the middle of the 21st century for scenarios of both moderate and high rates of fossil fuel burning (Balshiet al.et al. 2008). By the end of the 21st century, fire is projected to triple in Alaska for a scenario of moderate rates of increase in fossil fuel burning and to quadruple for scenarios of high rates of increase in fossil fuel burning. Such increases have the potential to release large stocks of carbon stored in Alaska soils to the atmosphere, which would be a positive feedback to climate warming (Balshiet al.et al. 2008). The projected increase in the burned area also increases the fire risk to rural indigenous communities, reduces subsistence opportunities, and has implications for fire policy (Chapinet al.et al. 2008).

Ecological Thresholds and Changes in Wetlands of Interior Alaska.—There has been a documented decrease in the area of closed-basin lakes (*that is*, lakes without stream inputs and outputs) during the latter half of the 20th century in the southern two-thirds of Alaska (Kleinet al.et al. 2005; Riordanet al.et al. 2006). The decrease in lake area appears to be caused by greater evaporation associated with longer and drier summers and by catastrophic drainage associated with thawing of permafrost in areas where the temperature of permafrost is close to melting. A decrease in the area of closed-basin lakes has also been documented in Siberia in areas of “warm” permafrost (Smithet al.et al. 2005).

Discontinuous permafrost in Alaska is warming and thawing, and extensive areas of thermokarst terrain (marked subsidence of the surface resulting from thawing of ice-rich permafrost) are now developing as a result of climatic change. Estimates of the magnitude of the warming at the discontinuous permafrost surface are 0.5° to 1.5°C (Osterkamp and Romanovsky, 1999). Thermokarst is developing in the boreal forests of Alaska where ice-rich discontinuous permafrost is thawing. Thaw subsidence at the thermokarst sites is typically 1 to 2 meters (m) with some sites experiencing subsidence of up to 6 m (Osterkampet al.et al. 1997). Much of the discontinuous permafrost in Alaska is warm and is highly susceptible to thermal degradation if regional warming continues. Warming of permafrost may be causing a significant loss of open water across Alaska as thawing of permafrost connects closed watersheds with groundwater (Yoshikawa and Hinzman, 2003).

Examination of satellite imagery indicates that the loss of water can occur suddenly, which suggests catastrophic drainage associated with thawing of permafrost (Riordanet al.et al. 2006). However, the reduction of open water bodies may also reflect increased evaporation under a warmer and effectively drier climate as the loss of open water has also been observed in permafrost-free areas (Kleinet al.et al. 2005).

In wetland complexes underlain by ice-rich permafrost in areas of hydrologic upwelling (for example, wetland complexes abutting up against the foothills of large mountain ranges), the thawing of that permafrost may result in wetland expansion as trees die when their roots are regularly flooded, causing wet sedge meadows, bogs, and thermokarst ponds and lakes to replace forests (Osterkampet al.et al. 2000). The Tanana flats, which extends nearly 70 miles from the northern foothills of the Alaska Range to Fairbanks, Alaska, is underlain by ice-rich permafrost that is thawing rapidly and causing birch forests to be converted to minerotrophic floating mat fens (Jorgensonet al.et al. 2001). It is estimated that 84% of a 260,000-hectare (ha) (642,000-acre) area of the Tanana flats was underlain by permafrost a century or more ago. About one-half of this permafrost has partially or totally degraded. These new ecosystems favor aquatic birds and mammals, whereas the previous forest ecosystems favored land-based birds and mammals.

During the past 50 years, it appears that warming has generally resulted in the loss of open water in closed-basin lakes in wetland complexes located in areas of discontinuous permafrost in the southern two-thirds of Alaska (Riordanet al.et al. 2006). The Tanana flats near Fairbanks is the only area where an increase in water area has been documented (Jorgensonet al.et al. 2001), and closed-basin lakes in the tundra region of northern Alaska have shown no changes in area during the past 50 years (Riordanet al.et al. 2006). The loss of area of closed-basin lakes in interior Alaska may be indicative of a lowering of the water table that has the potential to convert wetland ecosystems in interior Alaska into upland vegetation. A substantial loss of wetlands in Alaska has profound consequences for management of natural resources on national wildlife refuges in Alaska, which cover about 3.1 million hectares (more than 77 million acres) and comprise 81% of the National Wildlife Refuge System. These refuges provide breeding habitat for millions of waterfowl and shorebirds that winter in more southerly regions of North America; reduction of habitat area would present a substantial challenge for waterfowl management across the National Wildlife Refuge System (Juliuset al.et al. 2008). Wetland areas have also been traditionally important in the subsistence lifestyles of native peoples in interior Alaska as many villages are located adjacent to wetland complexes that support an abundance of wildlife subsistence resources. Thus, the loss of wetland area has the potential to affect the sustainability of subsistence lifestyles of indigenous peoples in interior Alaska.

Ecological Thresholds and Vegetation Changes in Northern Alaska.—Shrub cover in northern Alaska has increased by about 16% since 1950 (Sturmet al.et al. 2001; Tapeet al.et al. 2006), and the treeline is expanding in most places (Lloyd and Fastie, 2003; Lloyd, in press). This is consistent with satellite observations of an approximately 16% increase per decade in the normalized difference vegetation index (NDVI) (Jiaet al.et al. 2003; Goetzet al.et al. 2005). The increased growth of vegetation at or above the treeline appears to be a response to longer and warmer growing seasons. Tundra vegetation in northern Alaska may not be experiencing drought stress to the extent experienced by forests in interior Alaska because the surface water in tundra regions is not able to drain away through the ice-rich continuous permafrost. Experimental studies demonstrate that arctic summer warming of 1°C increases shrub growth within a decade (Arftet al.et al. 1999). Satellite analyses of relationships between NDVI and summer warming (Jiaet al.et al. 2003) suggest that the response of tundra vegetation is linearly related to summer warmth. Thus, it appears that the response of tundra vegetation to warming is not a threshold response.

While growth of shrubs and trees may not be threshold responses to warming, the changing snow cover and vegetation in northern Alaska have the potential to result in sudden changes in the absorption of heat from incoming solar radiation and the transfer of that heat to warm the atmosphere. For example, the advance in snowmelt reduces spring albedo, causing the ecosystem to absorb more heat and transfer it to the atmosphere. The snowmelt-induced increase in heating in northern Alaska has been about 3.3 watts per square meter (W m^{-2}) averaged over the summer, similar in magnitude to the 4.4 W m^{-2} caused by a doubling of atmospheric CO_2 over several decades (Chapinet al.et al. 2005). Thus, gradual warming has caused a rapid advance in the snowmelt date and a very large increase in local heating. Although vegetation changes to date have had minimal effects on atmospheric heating, conversion to shrubland would increase summer heating by 8.9 W m^{-2}, with even larger changes triggered by conversion to forest. Warming experiments that increase shrubs also reduce the abundance of lichens, an important winter food of caribou (Cornelissenet al.et al. 2001). Most arctic caribou herds are currently declining in population, although the reasons are uncertain. In summary, positive feedback associated with earlier snowmelt and shrub expansion is amplifying arctic warming and may be altering food-web dynamics in ways that have important cultural and nutritional implications for northern indigenous people.

Ecological Thresholds and Fisheries of the Bering Sea.—Alaska leads the United States in the value of its commercial fishing catch, and most of the Nation's salmon, crab, and herring come from Alaska, and specifically from the Bering Sea. The Bering Sea is one of the most productive marine ecosystems in the world, supporting some of the largest oceanic populations of fish, seabirds, and marine mammals anywhere (Loughlinet al.et al. 1999). The Bering Sea provides 47% of total U.S. fishery production by mass, including the largest single species fishery in the United States, walleye pollock (*Theragra chalcogramma)* (Criddleet al.et al. 1998). It is also an important source of subsistence resources (fish, marine mammals, and seabirds) for more than 30 Alaska Native communities and supports 95% of the worldwide population of northern fur seals, 80% of the total number of seabirds that breed in the United States, and major populations of tens of thousands of Pacific walrus, steller sea lion, and several species of great whales. This production is fueled by nutrients annually replenished from slope and oceanic waters across the very broad [more-than-500-kilometer (km)-wide] continental shelf (Stabenoet al.et al. 2001, 2006).

Changes in fisheries of the Bering Sea occurred in the transition of cool to warm conditions in 1977, in association with a shift of the North Pacific oscillation, and were followed by historically high commercial catches of salmon and pollock, as well as a shift away from crab dominance on the ocean floor. In the past decade, geographic displacement of marine mammal populations has been documented in the Bering Sea region. The displacements of walrus and seal populations are already apparent to coastal communities. The displacements of fauna in the Bering Sea has coincided with a reduction of benthic prey populations, an increase in pelagic fish, an increase in air and ocean temperatures, and a reduction in sea ice (Grebmeier et al. 2006). Ultimately, populations of fish, seabirds, seals, walruses, and other species depend on plankton blooms that are regulated by the extent and location of the ice edge in spring. As the sea ice continues to decline, the location, timing, and species makeup of the blooms is changing, vastly decreasing the amount of food reaching the living things on the ocean floor. This radically changes the species makeup and populations of the fish and other marine life forms, with significant repercussions for fisheries (Grebmeieret al.et al. 2006; Hatfieldet al.et al. 2008; Juliuset al.et al. 2008). Thus, changes in sea ice are the major driver of concern with respect to threshold changes in fisheries of the Bering Sea.

Seasonal sea ice extent currently divides the Bering Sea eastern shelf into two biogeographic provinces, which differ in production pathways. In the subarctic biogeographic province (south of the average-annual maximum sea ice extent), most primary production remains within the pelagic ecosystem, and pollock is the dominant tertiary consumer (Macklin and Hunt, 2004). In contrast, in the arctic biogeographic province, tight coupling between pelagic primary production and the benthos benefits benthic foragers, such as gray whales, walrus, and diving ducks (Grebmeieret al.et al. 2006). The boundary between the two biogeographic provinces varies in location on longer time scales (decadal or longer) and is expected to move northward as the region becomes warmer. The average southern edge of the maximum ice extent currently lies north of the Pribilof Islands (Byrdet al.et al. 2008).

The Bering Sea ecosystem, however, is in a state of rapid flux owing to climate change. Present data and climate projections from atmosphere-ocean models predict major loss of sea ice during the next few decades (Overland and Stabeno, 2004); the Bering Sea is particularly sensitive to global warming (Grebmeieret al.et al. 2006). Recent relative temperature extremes in Alaska and adjacent waters (more than 2°C) represent the largest recent change on the planet (Hansenet al.et al. 2006). However, these models and data also demonstrate large natural variability. Ecosystems will *likely* be affected by how the path of such warming occurs, that is, whether there will be a continued slow warming trend with little interannual variability versus a warming trend that incorporates wide swings in temperature and extent of sea ice.

Warming of the Bering Sea is expected to alter the current geographic distributions and behaviors of humans, marine mammals, seabirds, and fish by restructuring their habitats and food webs (Grebmeier et al. 2006). As a result of warming, changes in the time and place of food production lead to dominance of top-down control processes in the pelagic marine environment and the decline of benthic production. Under a long-term warming scenario with early ice retreat, bottom-up control mechanisms (temperature, sea ice extent and duration, ocean currents, and nutrient fluxes) set the stage for the emergence and dominance of top-down control processes in the pelagic marine environment and the decline of benthic production. Increased heat content would increase the combined populations of the subarctic piscivores—arrowtooth flounder, pollock, and cod—in proportion to expanded breeding grounds and increased availability of food during critical developmental stages (Hunt and Stabeno, 2002). Because arrowtooth flounder is not targeted by fishing, it is likely to become the dominant component of the biomass of the three subarctic piscivores in this study and is predicted to be one of the principal agents of top-down control in the Bering Sea, as predator and competitor of the now-dominant, but commercially exploited, pollock and cod.

Arrowtooth flounder is also an agent of change as a direct and indirect competitor of fur seals, murres, and kittiwakes for their respective forage species (euphausiids, copepods, juvenile pollock, capelin, and myctophids). Populations of fur seals, murres, and kittiwakes could fluctuate in the near term depending on the locality of rookeries and nesting colonies, but long-term overall trends would be downward under warming. Fur seals, murres, and kittiwakes would further decline owing to competition from humpback and fin whales, with fur seal declines being further accelerated by increasing killer whale predation. Dislocation of feeding hot spots would likely disadvantage breeding fur seals, murres, and kittiwakes as central place foragers, but would work to the advantage of humpback and fin whales, further exacerbating direct and indirect competition between these two groups of species. Dislocations and declines in fur seals, kittiwakes, murres, pollock, and cod would stress human communities by increasing the costs of maintaining a livelihood and obtaining food and by necessitating changes in the types of food taken and the means of harvest.

The northern Bering Sea, in particular, is experiencing a rapid shift in the structure and function of the formerly arctic climate regime to conditions typical of marine ecosystems of the subarctic (Grebmeier et al. 2006; Hunt et al. 2002). The earlier sea ice retreat results in a later, warm-water spring phytoplankton bloom, increased grazing by zooplankton, and greater pelagic secondary productivity (Huntet al.et al.

2002). Concurrently, benthic productivity is decreasing (Grebmeieret al.et al. 2006). The formerly ice-dominated, shallow marine ecosystem that favored highly productive benthic communities also supported high densities of upper trophic level bottom-feeders, such as Pacific walruses, gray whales, and seaducks, including the Ecological Society of America (ESA)-listed spectacled eider.

The northward flowing Anadyr Current, which originates in the southern Bering Sea, transports nutrient-rich water far onto the Bering Shelf and the northern Bering Sea. This transport creates unusually productive shelf waters in the area north of St. Lawrence Island and south of the Bering Strait, known as the Chirikov Basin (Springeret al.et al. 1989; Piatt and Springer, 2003). Oceanic copepods, such as *Neocalanus cristatus* and *N. flemingeri,* transported by the Anadyr Current, along with the large euphausiid *Thysanoessa raschii* provide abundant prey for planktivores foraging near St. Lawrence Island (Piattet al.et al. 1988). The Anadyr Current is highly variable on a seasonal and annual basis, reaching its greatest velocity during July [about 1.3 Sv (13 million cubic meters per second)] (Roachet al.et al. 1995). Consequently, the primary productivity on the Bering Shelf during summer months varies with the strength of northward flow associated with the Anadyr Current (Springeret al.et al. 1989; Russellet al.et al. 1999).

When the Anadyr Current is weaker, planktivores presumably rely more on zooplankton associated with northern Bering Shelf waters, such as the small copepod *Calanus marshallae* and the large amphipod *Themisto libellula* (Coyle, Chavtur, and Pinchuk, 1996; Russellet al.et al. 1999). *Neocalanus* copepods are larger and have higher energy content per prey item than the small, neritic copepod *C. marshallae* which is characteristic of Bering Shelf water. The lipid content of *Neocalanus* copepods is also probably higher (Obstet al.et al. 1995), making these oceanic species more energy-dense than their shelf domain counterparts. When preferred *Neocalanus* copepods are not available, planktivores must switch to other prey types. The progressively earlier transition from winter to spring in the Bering Sea and the resulting changes in primary and secondary productivity are expected to have large impacts on upper trophic-level consumers (Stabeno and Overland, 2001; Grebmeieret al.et al. 2006).

Projected warming of the Bering Sea is also expected to profoundly alter the structure of the southeastern Bering Sea ecosystem by changing pathways and fluxes of energy flow, as well as the abundance, spatial distribution, and species composition of fish, seabirds, and marine mammals, thereby affecting commercial and subsistence fisheries that support local, regional, and national economies Grebmeier et al. 2006; Hunt and Stabeno 2002). Climate-induced changes in physical forcing of the Bering Sea modifies the partitioning of food resources at all trophic levels on the continental shelf through bottom-up processes.

Case Study 2. The Mid-Continent Prairie Pothole Region: Threshold Responses to Climate Change

The Prairie Pothole Region (PPR) of north-central North America is one of the most ecologically valuable freshwater resources of the Nation (van der Valk, 1989). It contains 5 million to 8 million wetlands, which supply critical habitat for continental waterfowl populations and provide numerous valuable ecosystem services for the region and nation. The weather extremes associated with this region are particularly important for the long-term productivity of waterfowl dependent on these wetlands.

The PPR (fig. 3.1) exhibits a variable climate, ranging from severe droughts exemplified by the 1930s when agriculture was devastated, grassland communities shifted eastward, and trees died by the millions (Albertson and Weaver, 1942, 1945; Woodhouse and Overpeck, 1998; Rosenzweig and Hillel, 1993) to periods of deluge, such as occurred in the late 1900s when closed-basin lakes flooded, causing high mortality of shoreline trees and considerable economic damage to farmland, roads, and towns (Winter and Rosenberry, 1998; Johnsonet al.et al. 2005; Shapleyet al.et al. 2005). The 20th-century climate of the PPR was punctuated by significant droughts. These conditions have occurred over small and large areas and lasted as short as several growing seasons to as long as a decade (Skaggs, 1975; Laird and Cumming, 1998; Nkemdirim and Weber, 1999).

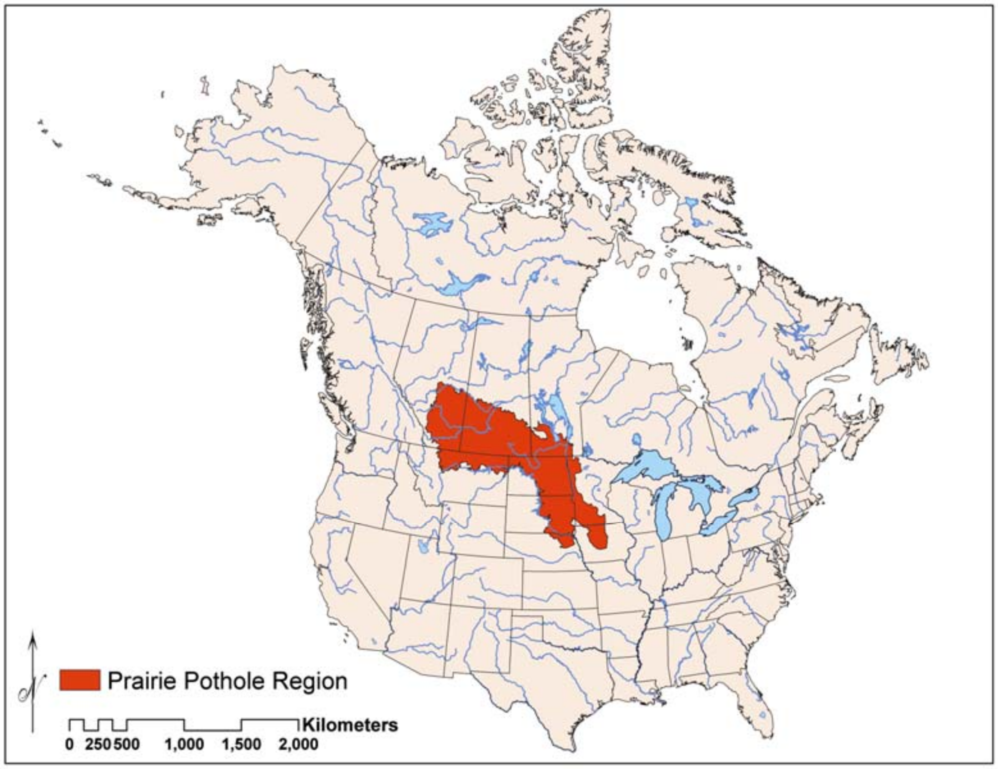


Figure 3.1. Location of the Prairie Pothole Region (PPR) of North America (red highlighted area). (Boldsethet al.et al. 2007)

Wetlands in the PPR are likely to be strongly affected by gradual changes in climate (Poiani and Johnson, 1991; Covichet al.et al. 1997). Climate drives surface processes, such as the hydrologic cycle, and hydrology is the most important factor that controls key wetland processes and services (Winter and Woo, 1990). A warmer and drier climate, as indicated by general circulation models (GCM) for the northern Great Plains (Ojima and Lackett, 2002), could affect the wetland hydroperiod, the ratio of emergent plant cover to open water, the species composition, wetland permanence, and primary and secondary productivity, among others (van der Valk, 1989). Winter (2000) predicted that the surface area of seasonal and semipermanent wetlands in the PPR would be reduced by increases in evapotranspiration and reduced summer soil moisture. With increased temperatures, summer evapotranspiration would put increasing demands on groundwater, resulting in earlier drying of wetlands. Thus, additional climate variability of the magnitude suggested by global climate change models would profoundly affect wetland water budgets and the many processes and attributes linked to these wetlands..

Changing climate can have direct effects on the trajectories of these wetland ecosystems and their sustainability. Shifts in climate in this region over decadal time scales could result in longer or more frequent drought periods and may lead to threshold responses by the wetland systems. The interaction of extrinsic and intrinsic processes reflected in such hydrologically, geologically and biologically linked systems as wetlands and their surrounding watersheds could result in rapid nonlinear changes at broad spatial scales that are triggered by small differences in temperature and precipitation if threshold values are exceeded that may also result in these systems exhibiting hysteresis.

The first quantitative assessments of the possible effects of climate change on PPR wetlands used the WETSIM (WETland SIMulator), which is a rule-based, spatially explicit simulation model that is composed of hydrology and vegetation submodels (Poiani and Johnson, 1991, 1993a, b; Poianiet al.et al.1995, 1996). Simulations using this model and GCM climate forcings indicate that semipermanent wetlands would lose their historic highly dynamic character by drying up more frequently and becoming chronically choked with emergent cover. Shortened hydroperiods and monotonous stands of emergent cover for semipermanent wetlands across the PPR would have strong negative effects on the continental population of waterbirds (particularly ducks).

Johnsonet al.et al. (2005) used a simulation model (WETSIM) to contrast historical and future wetland conditions across the PPR of North America (fig. 1). They assembled 95-year climate data sets for 18 weather stations across the PPR as input to a revised version of WETSIM (version 3.1), which enabled a much broader geographic assessment to be conducted of the effects of past and future climate variability on wetland conditions across the PPR. Their model runs reflected the high level of spatial and temporal heterogeneity in wetland water levels historically across the PPR. They were able to use model output to simulate the number of completions of the wetland cover cycle across the PPR (fig. 3.2; Weller, 1965).

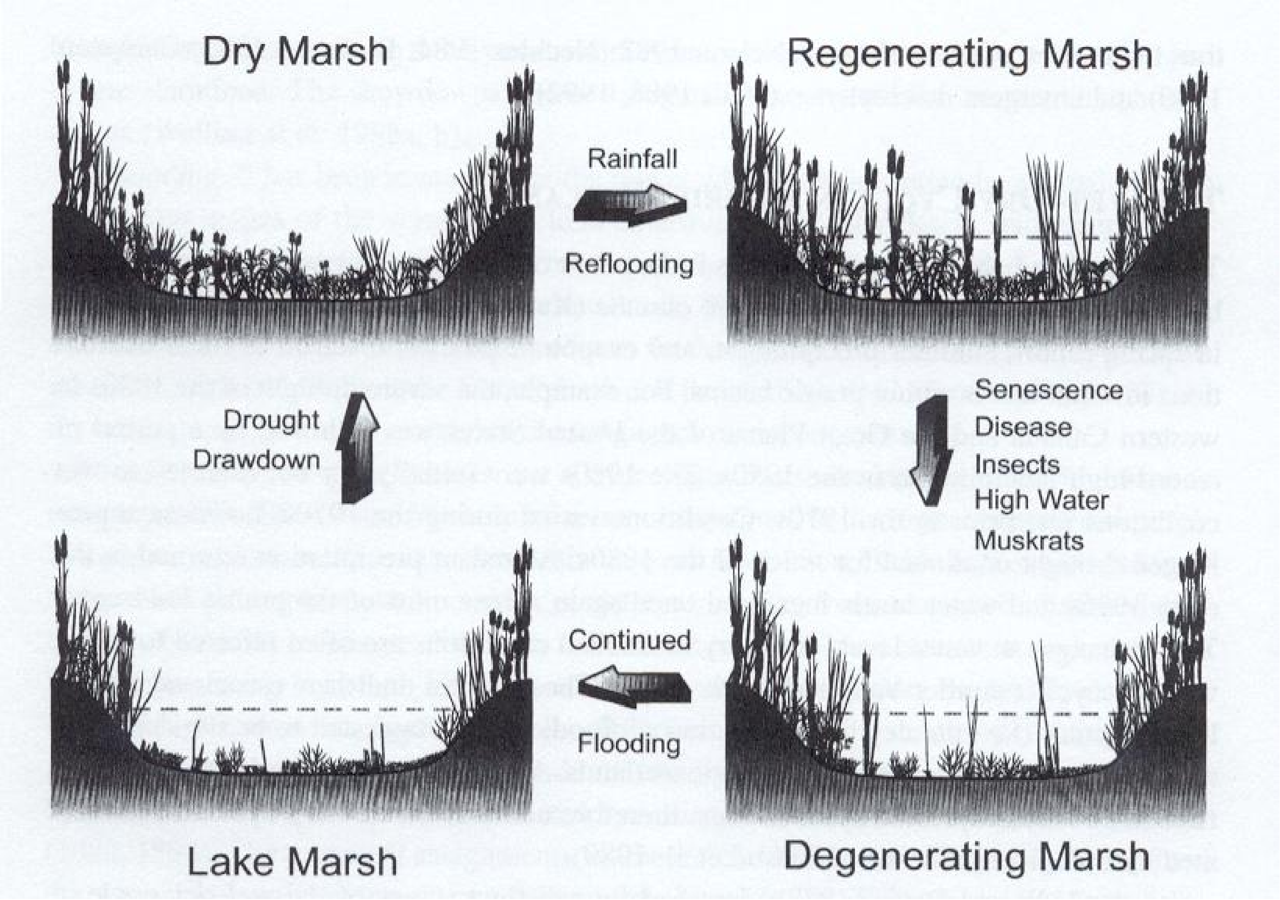


Figure 3.2. Wetland cover cycle (modified from Weller, 1965).

The wetland cover cycle was highly sensitive to alternative future climates. The geographic pattern of return times shifted markedly with changes in temperature and precipitation. A 3°C increase in temperature and no change in precipitation resulted in a greatly diminished area and geographic shift eastward for the region of fastest return times. However, reduced precipitation and warmer air temperatures resulted in no complete cover cycle return times across the PPR except in a small area of north-central Iowa (fig. 3.3), thus representing a threshold response to climate change. Such dramatic shifts in wetland conditions emphasize the sensitivity of PPR wetlands to climate variability.

Using this information, Johnsonet al.et al. (2005) simulated the occurrence of highly favorable water and cover conditions for breeding waterfowl (fig. 3.4). The most productive habitat for breeding water birds would shift under an effectively drier climate from the center of the PPR (the Dakotas and southeastern Saskatchewan) to the wetter eastern and northern fringes (in sync with the changes in the cover cycle return results).

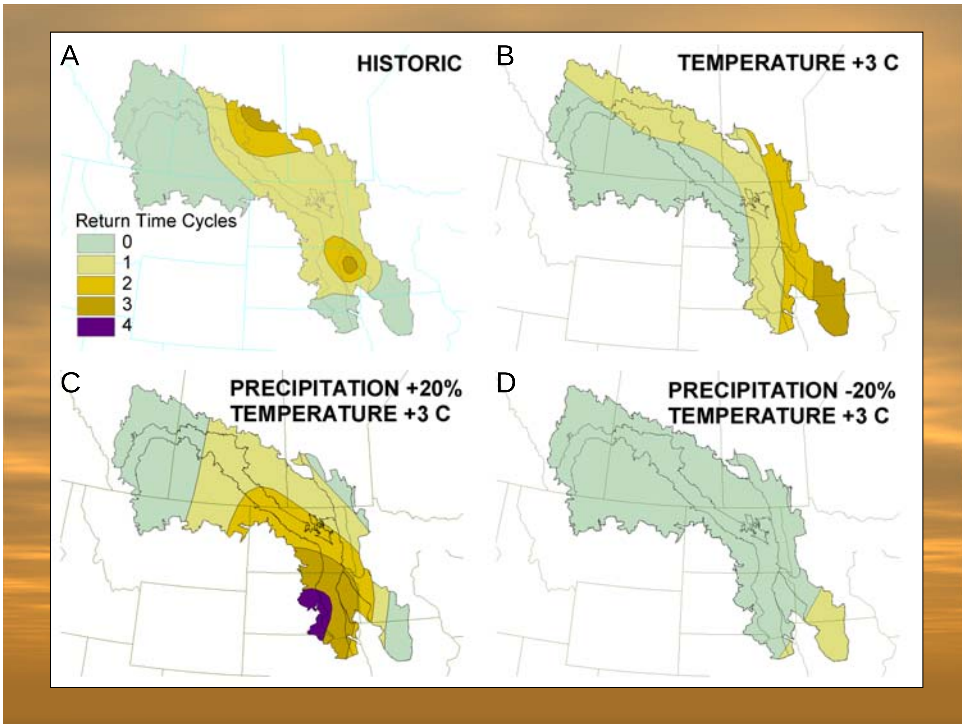


Figure 3.3. Geographic patterns of the speed of the wetland cover cycle, simulated for the Prairie Pothole Region (PPR) under historic (a) and alternative future (b, c, and d) climatic conditions. (Johnsonet al.et al. 2005)

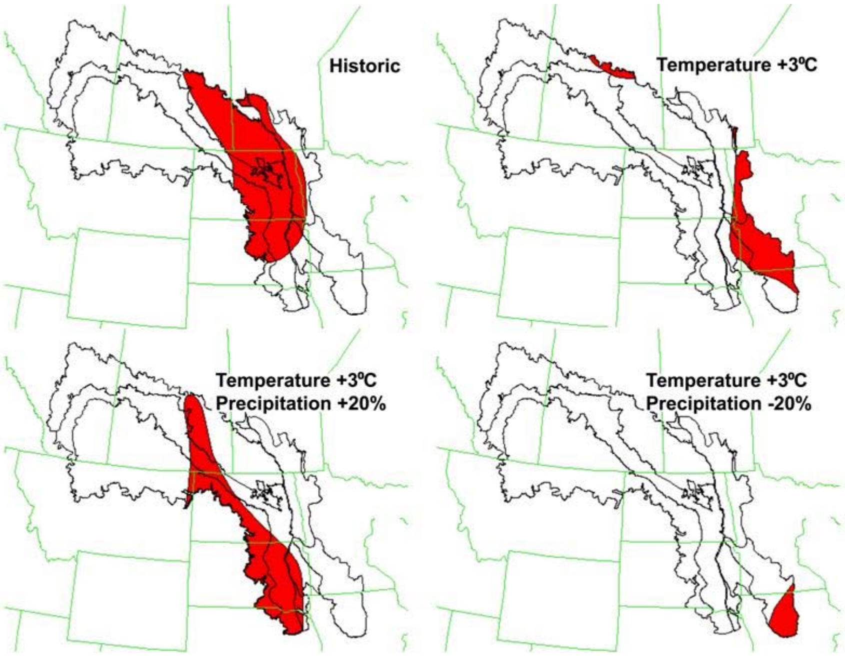


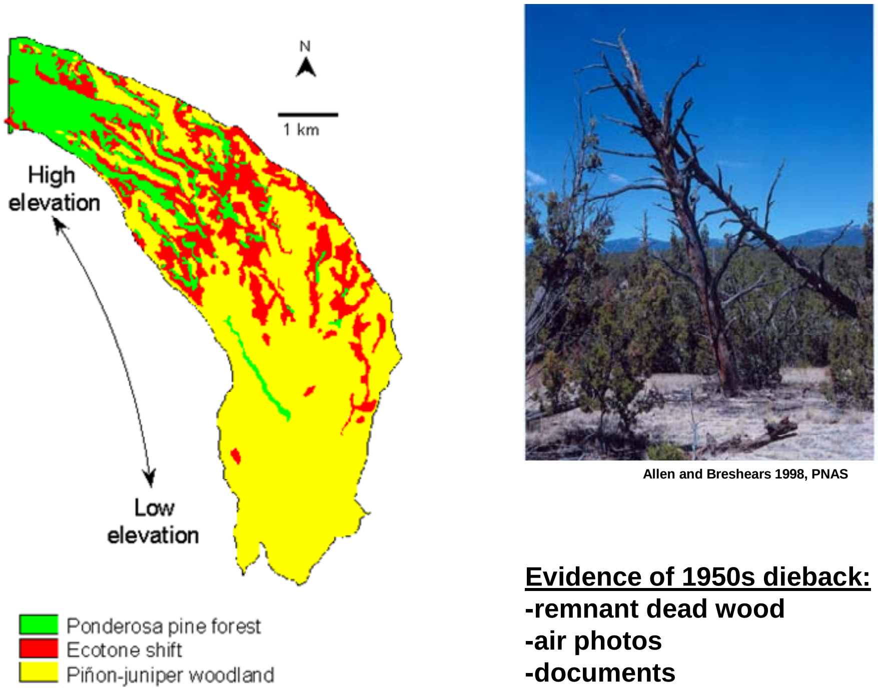
Figure 3.4. Simulated occurrence of highly favorable water and cover conditions for waterfowl breeding (occurrence of at least one return time and hemimarsh conditions at more than 30% frequency) across the Prairie Pothole Region (PPR) under historic (a) and alternative (b, c, and d) future climatic conditions. (Johnsonet al.et al. 2005)

Case Study 3. Broad-Scale Forest Die-Back as a Threshold Response to Climate Change in the Southwestern United States

The ecological dynamics of semiarid forests and woodlands in the southwestern United States are observed to respond strongly to climate-driven variation in water-availability, with major pulses of woody plant establishment and mortality commonly corresponding to wet and dry periods (Swetnam and Betancourt, 1998). In particular, climate-induced water stress can trigger rapid, extensive, and dramatic forest dieback (Breshearset al.et al. 2005), exemplifying significant ecosystem threshold responses to climate. Broad-scale tree mortality can shift ecotones between vegetation types (Allen and Breshears 1998) and alter regional distributions of overstory and understory vegetation (Gitlinet al.et al. 2006; Richet al.et al. 2008). Rapid forest dieback also has nonlinear feedbacks at multiple spatial scales with other ecological disturbance processes, such as fire and erosion (Allen, 2007), which, in some cases, leads to additional nonlinear threshold behaviors. Massive forest mortality is an example of a threshold phenomenon with substantial implications for future ecosystem dynamics and management of lands undergoing such changes (Millaret al.et al. 2007).

Assessments of potential global change impacts initially focused on how vegetation types matched given climatic envelopes (IPCC, 1996). Subsequent research has considered how vegetation patterns might migrate in response to changing climate with a focus on rates of plant establishment, has documented that forest turnover rates follow global and regional patterns of productivity (significantly driven by climate) (Stephenson and van Mantgem, 2005), and has increasingly moved toward dynamic global vegetation models that try to incorporate more realistic disturbance dynamics (Scholzeet al.et al. 2006; Purves and Pacala, 2008). Currently, climate-induced dieback of woody plants is being recognized as an important vegetation response to climate variation and change, with examples of forest dieback emerging from around the world (Allen and Breshears, 2007). Recent research shows that water stress appears to be driving increases in background tree mortality rates in western North American forests (van Mantgem and Stephenson, 2007; van Mantgemet al.et al. in review). In addition, observations of extensive tree die-off—especially from semiarid ecosystems where woody plants are near their physiological limits of water stress tolerance—are being documented globally, for example, in Australia (Fensham and Holman, 1999), Africa (Gonzalez, 2001), west Asia (Fisher, 1997), Europe (Dobertinet al.et al. 2007), South America (Suarezet al.et al. 2004), and North America (Breshearset al.et al. 2005). Climate-induced water stress during extended time periods can exceed the physiological tolerance thresholds of individual plants and directly cause mortality through either: 1) cavitation of water columns in the xylem conduits (“hydraulic failure”); or 2) forcing plants to shut down photosynthesis to conserve water, leading to “carbon starvation” (McDowellet al.et al. 2008; Breshearset al.et al. in press). These individual-scale threshold responses to climate stress can trigger tree mortality that propagates to landscape and even regional spatial scales (Allen, 2007), sometimes amplified by biotic agents (like bark beetles) that can successfully attack and reproduce in weakened tree populations and generate massive insect population outbreaks with positive feedbacks that greatly increase broad-scale forest mortality (Kurzet al.et al. 2008).

Ecotones are areas where vegetation changes in response to climate are expected to be most rapid and prominent (Beckageet al.et al. 2008), as highlighted by a southwestern case study of drought effects on vegetation during the 1950s (fig. 3.5; Allen and Breshears, 1998). Severe drought across the southwestern United States during the 1950s caused ponderosa pine (*Pinus ponderosa*) trees at lower, drier sites to die, resulting in an upslope shift of the ponderosa pine forest and piñon-juniper woodland ecotone of as much as 2 km in less than 5 years, producing a rapid and persistent change in dominant vegetation cover. Similarly, within the distributional range for the piñon pine (*Pinus edulis*), many trees at lower or drier sites also died (Swetnam and Betancourt, 1998).



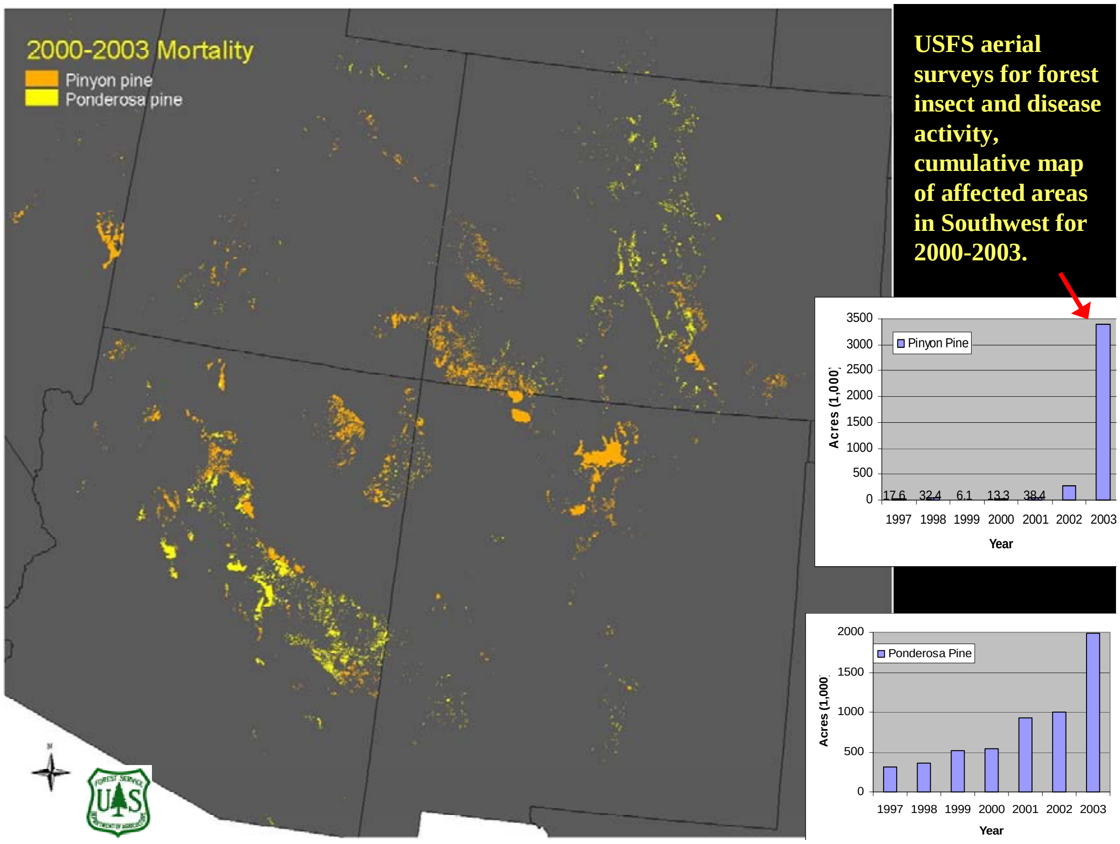
Allen and Breshears 1998, PNAS

Evidence of 1950s dieback:
-remnant dead wood
-air photos
-documents

Figure 3.5. Changes in vegetation cover between 1954 and 1963 at Frijolito Mesa, Jemez Mountains, New Mexico, showing the persistent ponderosa pine forest (365 ha), the persistent piñon-juniper woodland (1527 ha), and the ecotone shift zone (486 ha) where forest changed to woodland (from Allen and Breshears, 1998).

Although tree mortality almost certainly occurred across much of the southwestern United States in response to the 1950s drought (and probably for previous regional-scale droughts as well), few studies exist that allow scientists to test projections about the rapidity and extent of potential vegetation die-off response to drought. A recent drought beginning in the late 1990s and peaking in the early 2000s affected most of the western United States; this was the most severe drought in the Southwest since the 1950s. Substantial mortality of multiple tree species has been observed throughout the Southwest during this 2000s drought (fig. 3.6; Gitlinet al.et al. 1996; U.S. Forest Service, 2006; Allen, 2007). For example, mortality of the piñon pine spanned major portions of the species' range, with substantial die-off occurring across at least 1,000,000 ha from

2002 to 2004 (Breshearset al.et al. 2005; U.S. Forest Service, 2006). For both droughts, much of the forest mortality was associated with bark beetle infestations, but the underlying cause of dieback appears to be water stress associated with the drought conditions.



USFS aerial surveys for forest insect and disease activity, cumulative map of affected areas in Southwest for 2000-2003.

Figure 3.6. Graph of the acreage of piñon pine (*Pinus edulis)* and ponderosa pine (*Pinus ponderosa)* dieback from 1997-2004 in the Four Corners states of Arizona, New Mexico, Colorado, and Utah; map showing cumulative area from 2000 to 2004. Based upon annual aerial forest insect and disease activity inventories by the U.S. Forest Service.

The precipitation deficit that triggered the recent regional-scale die-off of the piñon pine across the Southwest was not as severe (dry) as the previous regional drought of the 1950s, but the recent 2000s drought was hotter than the 1950s drought by several metrics, including mean, maximum, minimum, and summer (June-July) mean temperature (Breshearset al.et al. 2005). Although historic data from the 1950s is limited, available data suggest that piñon pine mortality in response to the recent drought has been more extensive, affected greater proportions of more age classes, and occurred at higher elevation and wetter sites than in the previous 1950s drought. Hence, the warmer temperatures associated with the 2000s drought may have driven greater plant water stress through increased evapotranspirational demand, and resulted in more-extensive tree die-off. Because global change is projected to result in droughts under warmer conditions—referred to as *global-change type drought*, the severe piñon pine dieback from the recent drought may be a harbinger of vegetation response to future global-change type droughts (Breshearset al.et al. 2005).

In addition to the die-off of dominant overstory tree species, high levels of dieback also were observed in other southwestern U.S. species and lifeforms in response to the warm regional drought in the 2000s (Gitlinet al.et al. 2006; Allen, 2007). These include species where bark beetles are unimportant or nonexistent, including one-seed juniper (*Juniperus monosperma*)—a co-dominant with piñon pine for much of its range; shrubs such as wavy-leaf oak (Quercus undulate) and mountain mahogany (Cercocarpus montanus); and blue grama (*Bouteloua gracilis*), the dominant herbaceous species in many of these woodland systems.

In addition to direct climate-induced mortality, severe protracted drought also can cause substantial reductions in the productivity and soil surface cover of herbaceous plants, which in turn affects numerous other ecological processes. In particular, reductions in herbaceous ground cover can trigger a nonlinear increase in soil erosion once a threshold of decreased herbaceous cover has been crossed, through increased connectivity of bare soil patches (fig. 3.7; Davenportet al.et al. 1998; Wilcoxet al.et al.

2003; Ludwiget al.et al. 2005; Mayoret al.et al. in press). On the other hand, dieback of woody canopies tends to cause an immediate successional shift toward greater cover of understory vegetation if moisture conditions are adequate (for example, Richet al.et al. 2008), which propagates a different set of effects.

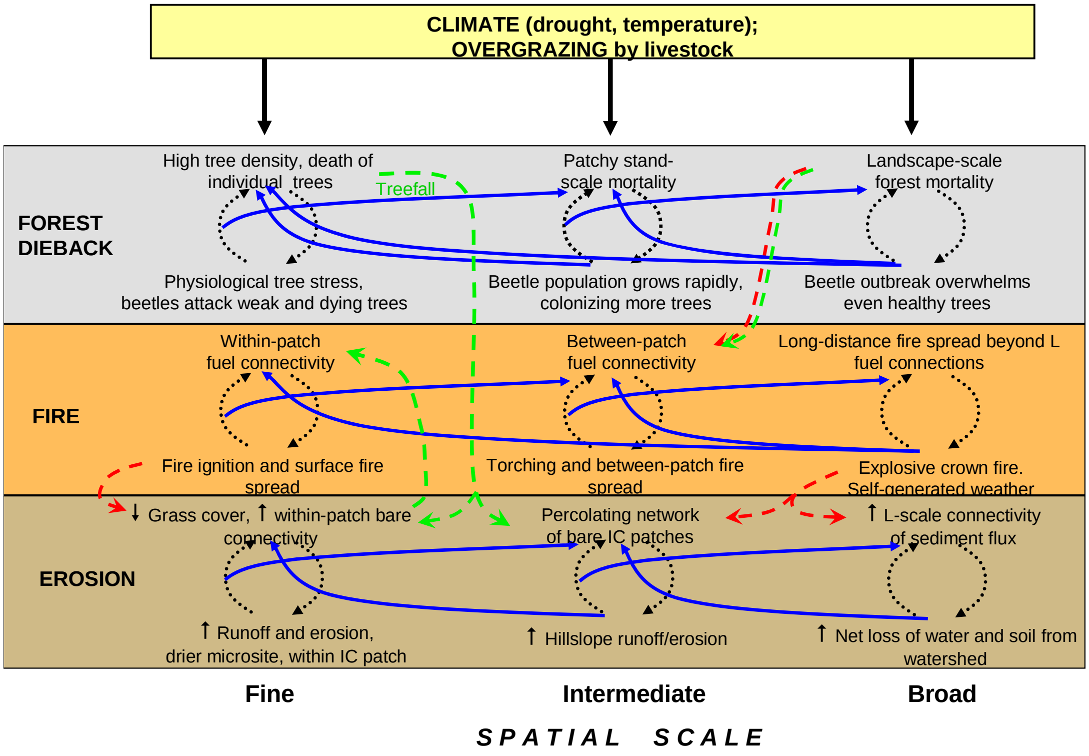


Figure 3.7. Diagram representing interactions across spatial scales for three different disturbance processes (forest dieback, fire, and erosion) in northern New Mexico landscapes (from Allen 2007). Dashed black arrows represent pattern-process feedbacks within three different spatial-scale domains, with one example of pattern and process shown for each domain for each disturbance. Solid black arrows indicate the overarching direct effects of widespread environmental drivers or disturbances (such as climate and overgrazing) on patterns and processes at all scales. Blue arrows indicate the point at which altered feedbacks at finer spatial scales induce changes in feedbacks at broader scales (for example, fine-scale changes cascade to broader scales), and also where changes at broader scales overwhelm pattern-process relationships at finer scales. Red dashed arrows illustrate some examples of amplifying (positive feedback) interactions between disturbance processes within and between spatial scales; green dashed arrows illustrate dampening (negative feedback) interactions between disturbance processes. Abbreviations: L = landscape; IC = intercanopy (interspaces between tree canopies).

Overall, the dieback of overstory vegetation affects numerous key ecosystem processes, which are tied to site-specific distributions of incoming energy and water (Zouet al.et al. 2007), and has multiple cascading ecological effects. Widespread tree mortality may propagate additional pervasive changes in various ecosystem patterns and processes. Breshears (2007) summarizes the important ecological role of woody plant mosaics in semiarid ecosystems:

> *A large portion of the terrestrial biosphere can be viewed as lying within a continuum of increasing coverage by woody plants (shrubs and trees), ranging from grasslands with no woody plants to forests with nearly complete closure and coverage by woody plants (Breshears & Barnes, 1999; Breshears, 2006). The characteristics of woody plants determine fundamental descriptors of vegetation types including grassland, shrubland, savanna, woodland, and forest. Because woody plants fundamentally affect many key aspects of energy, water and biogeochemical patterns and processes, changes in woody plant cover are of particular concern (Breshears, 2006).*

Climate-driven, rapid forest dieback has feedbacks with other ecological disturbance processes, such as fire and erosion, in some cases leading to further nonlinear ecosystem threshold behaviors (fig. 3.7). Warming and drying climate conditions are driving higher-severity fire activity at broader scales in the southwestern United States directly (Swetnam & Betancourt, 1998; Westerlinget al.et al. 2006), and probably also indirectly where forest dieback changes fuel conditions (fig. 3.7: Bigleret al.et al. 2005). High-severity stand-replacing fires within woodlands and forests can almost instantly cause large reductions in tree canopies and soil surface covers, thereby also triggering dramatically increased rates of runoff and soil erosion for several years post-fire until vegetation regrowth restores adequate land surface cover (Veenhuis, 2002; Moody and Martin, in press). Forest dieback, fire, and erosion also have significant effects on ecosystem carbon pools (Breshears and Allen, 2002; Kurzet al.et al. 2008). The combined interactive effects of climate-driven ecological disturbance processes (vegetation dieback, fire, and erosion) are highlighted by the major changes in woodland and forest ecosystems that have occurred in northern New Mexico during the past 60 years (fig. 3.8; Allen, 2007). Climate-induced forest dieback, fire, and accelerated erosion already may be causing permanent “type conversion” changes to some southwestern ecosystems. Even without factoring in ongoing/predicted climate changes, it will be at least several decades to centuries before reestablishment of pre-disturbance tree canopy covers will occur on many semiarid woodland and forest sites in this region (Allen and Breshears, 1998; Savage and Mast, 2005).

Figure 3.8 Increased herbaceous cover has developed since recent piñon pine forest dieback in the Jemez Mountains of New Mexico and may promote surface fire regimes and changes in runoff and erosion patterns. July 2004.

Examples of drought-induced tree die-off in semiarid forests and woodlands highlight the rapidity and extensiveness with which climate stress can trigger pervasive and persistent ecosystem changes. Climate change has the potential to drive multiple nonlinear or threshold-like processes that can interact in complex ways, including tree mortality, altered fire regimes, energy and water budget changes, and soil erosion thresholds (Allen, 2007), making ecological predictions difficult (McKenzie and Allen, 2007). For example, the projections of state-of-the-art dynamic global vegetation models "are currently highly uncertain, making vegetation dynamics one of the largest sources of uncertainty in Earth system models" (Purves and Pacala, 2008). Additional research, including research on threshold responses, is needed to improve projections of the nonlinear ecological effects of expected climate changes, such as broad-scale forest dieback, associated ecosystem dynamics, and effects on carbon budgets and other ecosystem goods and services (Breshears and Allen, 2002; Millennium Ecosystem Assessment, 2005; Millaret al.et al. 2007).

Case Study 4. Thresholds in Climate Change for Coral-Reef Ecosystem Functioning

Corals are perpetually subjected to environmental changes in time and space. As adult colonies, corals are sessile and so are subjected to changes in the environmental factors through time in one location. As larvae, corals are motile, and each must select a location from a complex and variable array of available sites. Corals are resilient to changes in both space and time through acclimatization, adaptation, local environmental ameliorations, initial community composition, and the morphological characteristics of the reef. It is reasonable to assume that most corals will not go extinct with global climate change because of their abilities to acclimatize, to adapt, and to broadcast their larvae geographically. The threshold or tipping point for coral-reef ecosystems is the point along the environmental gradient at which the ecological or biological processes change from negative feedback for net accretion to positive feedback or reef erosion. Systems consist of mixtures of positive and negative feedbacks, with positive feedbacks tending to alter the nature of the system, and negative feedbacks tending to minimize these changes (Chapinet al.et al. 1996). Once the feedback process starts and net accretion decreases to a point of erosion of the reef, there is no return to the functioning coral-reef ecosystem.

The following natural and anthropogenic stressors and coral reef responses to them may include (Birkeland 2004):

- Inverse density dependence (or Allee effectAlgal abundance at levels beyond the capacity of herbivores to keep in balance;
- Predators of corals at a rate higher than the rate of recovery and coral population replenishment;
- Bioerosion of corals;
- The prevalence of crustose coralline algae, which weakens binding of the substratum, is decreased and thereby decreases successful coral recruitment; and
- Invasives—establishment of introduced species, which modify the habitat in ways that favor the survival and dominance of the introduced species is displacing natural species.

Such local processes as these stressors and the feedback mechanisms of corals to these stressors have determined the substantial degradation of coral reefs over the past 3 decades in the tropical western Atlantic Ocean (Gardneret al.et al. 2003) and in the Indo-Pacific Ocean (Bruno and Selig, 2007). It is *likely* that the crossing of thresholds in coral ecosystems began nearly 3 decades ago with no evidence the rate of degradation is decreasing.

Although anthropogenic modification of local ecological processes has been the dominant force in coral-reef degradation (Birkeland, 2004) and tipping points have been crossed decades ago in many areas (Gardneret al.et al. 2003; Bruno and Selig, 2007), global changes in climate and oceanic characteristics are now becoming more apparent.

Global processes that are affecting coral reefs, which are related to the increased concentration of atmospheric CO_2,, are sea level rise, the decline in pH of seawater, and the increase in seawater temperature.

Rise and Fall of Sea Level.—Coral reef ecosystems have experienced rise and fall of sea levels several times in geological history with associated effects on reef functioning (defined as constructing reefs upwardly). Reef accretion has stopped for periods of time in excess of 10 million years, the threshold for the cessation of reef upward growth being the time of decreasing sea level. It is hard to determine the effect of climate change alone on whether corals will keep pace with sea level rise, increasing water temperatures, and change in ocean pH. Whether coral reefs keep up with sea level rise depends on a multitude of local environmental factors and the degree to which these factors stress the corals themselves. The rate of sea level rise alone does not provide a predictable tipping point for reef deposition that can be generalized over a region (Hallock et al. 1993, Garrison et al. 2003).

Decrease in Seawater pH.—The concentration of CO_2 in the atmosphere is generally expected to reach two times the preindustrial (late 18th century) levels by 2065 (Houghtonet al.et al. 1996). As CO_2 concentration increases in the atmosphere, the surface seawaters take up more CO_2. The increased uptake of atmospheric CO_2 by the surface waters of the ocean leads to a decrease in pH of surface waters, an increase in the proportion of bicarbonate ions (HCO_3^-), and a decrease in the proportion of carbonate ions (CO_3^{2-})(Feely et al. 2008). . The overall effect is on the rate of precipitation of coral skeleton.

$$CO_2 + H_2O \Leftrightarrow HCO_3^- + H^+ \Leftrightarrow CO_3^{2-} + 2H^+$$

The oceans have already taken up an additional one-third to one-half of industrial-age emissions of CO_2, and the concentrations of carbonate ions in the oceans have decreased from 11% (preindustrial), to 9% (now) and are projected to decrease to 7% when carbonate concentrations are double the preindustrial concentrations, perhaps in 3 to 5 decades (ISRS, 2007).

Kleypas and others (1999) determined that doubled atmospheric CO_2 will lead to a 14% to 30% decrease in reef calcification rates. This was estimated to be a general tipping point from net carbonate accretion to net carbonate loss by Kleypas and others (2001). Net reef accretion is potentially reduced to zero when increased CO_2 in the atmosphere reaches about 500 to 600 ppm. On the other hand, CO_2 is less soluble in seawater at higher temperatures. While increased concentrations of atmospheric CO_2 may be accelerating the uptake of CO_2 by surface seawater, global warming may be slightly damping the uptake. But of more substantial influence in accelerating the tipping point of net reef accretion are the synergistic biological effects on corals of reduced growth in the face of natural and anthropogenic stressors.

Sabine and others (2004) showed that uptake of anthropogenic CO_2 by subtropical Atlantic waters has been greater than by Pacific waters. The north Atlantic stores 23% of the total anthropogenic (fossil-fuel and cement-manufacturing emissions) CO_2 taken up by the world oceans, even though the north Atlantic occupies only 15% of the world's total ocean area. Pacific waters are less receptive to the uptake of CO_2 and therefore are buffered from a decrease in pH because of higher concentrations of dissolved inorganic carbon. As seawater becomes warmer coral reef net accretion will probably become slightly more restricted in latitude (Kleypaset al.et al. 1999, 2001) because of the changes in chemistry from CO_2 uptake in the world's oceans.

Seawater Warming.—The thresholds in tolerance of corals to an increase in water temperature and its duration before "bleaching" (expelling the symbiotic zooxanthellae) is predicted by the degree heating week (DHW) record, 12-week accumulations measured as °C weeks. The DHW product is an accumulation of hotspot values over the bleaching threshold [1°C over the maximum monthly mean (MMM)]. The threshold values of DHW vary from site to site because the MMM varies from site to site; thus, corals are likely adapted to their own threshold temperatures at each site. Furthermore, the past history of events in the physical environment and local characteristics of the physical environment can modify the actual location of the threshold or tipping point (Smith and Birkeland 2007). Based on our knowledge of tolerances and the gaps in the literature on thresholds identified in developing this SAP, corals are *likely* to reach a threshold with an increase in sea water temperatures.

Mechanisms of Reef Resilience That Alter Thresholds.— The resilience of corals to environmental changes is largely determined by their capacity to acclimatize (adjust physiologically and behaviorally). The thresholds of resilience of corals to environmental factors, such as water temperature and ultraviolet (UV) radiation, are altered by changes in symbiotic interactions. Reef-building corals are dependent on symbiotic dinoflagellate algae (zooxanthellae) in their endodermal cells for their nutrition and proficiency in deposition of skeleton. There are a number of clades or types of zooxanthellae, and the physiological and ecological attributes of zooxanthellae vary among clades. The symbiotic relationship breaks down under stressful conditions of extra warm seawater or strong UV radiation. Under these conditions, corals sometimes expel much of the zooxanthellae of clade C and allow the buildup of clade D, with which the coral growth rate is slower but survival under stressful conditions may be greater. As with morphological adjustments, the symbiotic adjustments of corals may be determined by a balance between the stresses imposed by the physical environment and by ecological interactions with other species (Bruno and Selig 2007). In addition to adjustments in morphology and symbiotic relationships, acclimatization can occur through biochemical conditioning. Increased water temperature triggers a substantial increase in biochemical activity in corals, Intense biochemical activities resulting from changes in water temperature may indicate a processes of acclimatization that might increase the distance to the threshold for mortality of the coral from seawater temperature (Smith and Birkeland 2007).

Whether changes in morphology, symbiotic relationships, physiological conditioning, or production of biochemicals are the mechanisms to shift the threshold for survival from climate change, acclimatization costs the coral in terms of energy and materials that would otherwise be available for growth and successful competition. Acclimatization can be approached by robustness or plasticity. The mound-shaped species of *Porites* (such as *P. lobata*) are robust and live in a wide range of habitats. They are the last to drop out of the coral community near a river mouth or in bays with increasing turbidity. Species of *Acropora* dominated the reef front at the municipal sewer outfall for Koror, Palau, until predation on corals by the crown-of-thorns starfish and bleaching by the large-scale seawater warming of 1997–98 killed the *Acropora* spp. but not the *Porites* spp. (Richmond et al. 2002). *Porites* can maintain itself rather constantly despite fluctuations in the external physical environment, but at a metabolic cost (fig. 3.9).

The relatively rapidly growing *Pocillopora eydouxi* display plasticity and can differ substantially among habitats in rates of growth, colony morphology, and types of zooxanthellae hosted. *Pocillopora* are generally more vulnerable to the physical environment and so their growth rates vary among habitats and they are more likely to bleach [expel zooxanthellae and/or photosynthetic pigments] with higher than usual water temperatures and with more intense UV radiation.

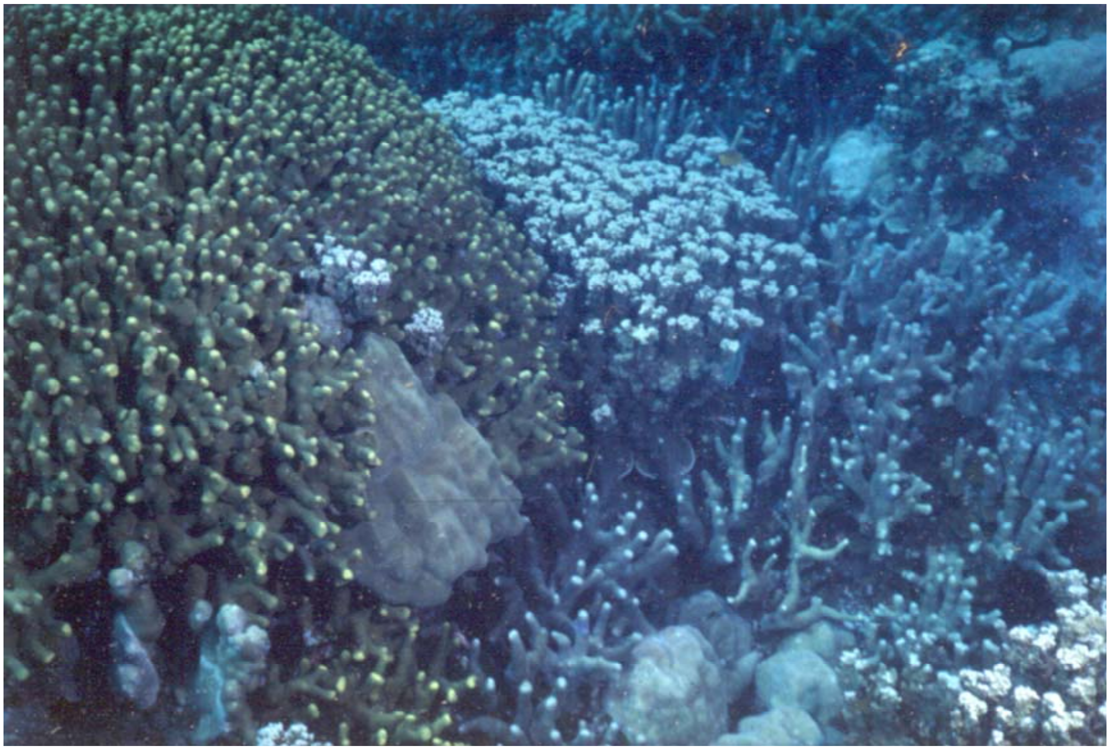


Figure 3.9. Branching corals overgrowing mound-shaped corals.

Factors that Shift the Thresholds.—Corals are most vulnerable to infrequent or very frequent environmental changes. As explained in the previous section, corals can acclimatize (physiological or behavioral response) or adapt (genetic response) to environmental changes of intermediate frequency. If the phenomena, such as extraordinarily warm seawater, are infrequent enough to be unpredictable, then the corals will not be able to acclimatize or adapt. However, if the events are too frequent, the corals will not have time to recover between events.

The factor of duration relates to the different effects of acute and chronic disturbances on the resilience of coral communities. The threshold seawater temperature associated with global climate change is determined in part by the duration of the warm water event. In 1997–98, an increased average surface seawater temperature of 1.0° to 1.5°C (to about 30° or 31°C) over a period of several weeks caused extensive mortality of corals in the Indian Ocean, the southwestern Pacific Ocean, and the western Atlantic Ocean (Bruno and Selig 2007). In contrast, daily fluctuations of 6°C to 6.5°C (to about 34° or 35.5°C) in reef flat pools in American Samoa are endured in good health by about 80 species of corals.

The threshold seawater temperature that severely affects a coral will be higher in areas of constant or even intermittent high water motion and the threshold of temperature tolerance will be lower in areas of low water motion (Smith and Birkeland, 2007). Thresholds in levels of tolerable input of nutrients or sediment will be low in backwaters and relatively much higher in areas of strong current. In contrast, it will take substantially longer for the ecosystem to solidify rubble into a stable substratum for reef recovery in areas of strong water motion than in areas of low water motion. The threshold of tolerance of corals to infection by disease is sometimes lowered by stress from other environmental factors and by abrasion of surface tissue by predators or other objects (Garrison et al. 2003). The physical and biological environments are a complex system of factors that potentially act synergistically to shift the threshold of the specific factor associated with climate change.

Levels of Thresholds.—Thresholds should be considered at two levels: the first at which the population is killed or the ecosystem becomes dysfunctional, and the second at which the population or the ecosystem is prevented from becoming reestablished. An acute disturbance to a coral reef is a distinct event. A chronic disturbance is an ongoing process. The coral-reef communities of American Samoa have been severely affected by large-scale acute disturbances, such as outbreaks of the coral-eating crown-of-thorns starfish *Acanthaster planci* (1938, 1978), hurricanes (1981, 1987, 1990, 1991, 2004, 2005), and bleaching in response to seawater warming (1994, 2002, 2003). When allowed a 15-year interval between disturbances, the coral communities have recovered (Birkelandet al.et al. 2008). This is in contrast to the western Atlantic where there has been a continual degradation of coral reef systems for a half a century (Gardneret al.et al. 2003). The relatively small area of the tropical western Atlantic allows widescale events on continents to affect the whole region (Hallocket al.et al. 1993; Garrisonet al.et al. 2003). The nutrients (Hallocket al.et al. 1993), pollutants (Garrisonet al.et al. 2003), and diseases (Lessioset al.et al. 1984) can disperse across the entire region. A recent paper by Bruno and Selig (2007) reported that 3,168 square kilometers of reef has been dying each year rather uniformly throughout the Indo-Pacific Ocean. Reefs are appearing to be losing their resilience globally.

American Samoan reefs have managed to maintain resilience by receiving disturbances only as acute events and being largely isolated from nearby large landmasses. Overfishing, however, has been chronic, and the fish communities have not been as resilient as the corals (Zelleret al.et al. 2006 a, b). Some localized and well-defined areas experience chronic stresses, such as sedimentation at the mouths of rivers or in the backs of bays, and have not been recovering for decades.