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RESOURCES
FOR THE FUTURE

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## Steven W. Running and L. Scott Mills*

Introduction

In this report, we evaluate adaptation issues for natural ecosystems. We will specifically focus on the interactions with the abiotic environment of plants and animals, along with other organisms with which they interact (e.g., disease-causing bacteria and viruses). We further limit ourselves to natural ecosystems in which the predominant vegetation has developed without having been planted, irrigated, or fertilized. Most of the natural lands in the United States are managed by federal or state governments. Agricultural lands—including range grazing lands —are dealt with in a related adaptation report. This will evaluate the potential magnitudes and challenges facing terrestrial ecosystems in the United States in adapting to changing climate over the next 30–50 years. Our report will *not* address attribution or mitigation of climate change, as these topics have been dealt with in many other forums. We will begin with a brief summary of the current trajectory of the changing climate in the United States, including both temporal and spatial patterns. We will then relate these trends to ecosystem impacts and vulnerabilities.

We consider *adaptation* in the broad sense to include any means by which organisms successfully confront a perturbation such as climate change. This includes both local adaptation in place—either through plastic responses or through evolutionary changes—as well as changes in movements within or outside of the current geographic range. Some species (often invasive and disease species) will adapt spectacularly. By contrast, those unable to adapt will experience decreased average mean fitness, translating into population decline, decreased persistence, and changed community and ecosystem structure (Figure 1).

After considering ecological adaptation mechanisms, it becomes possible to consider potential management options to enhance adaptation. We do not make recommendations of specific adaptation activities at this point; rather, we suggest alternatives to begin the discussion.

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Figure 1. Response of Biotic Communities as Climate Change Affects Individual Species (which adapt in place, move, or decline toward extinction), Changes in Species Interactions, and Ultimately the Structure and Composition of Communities and Ecosystems
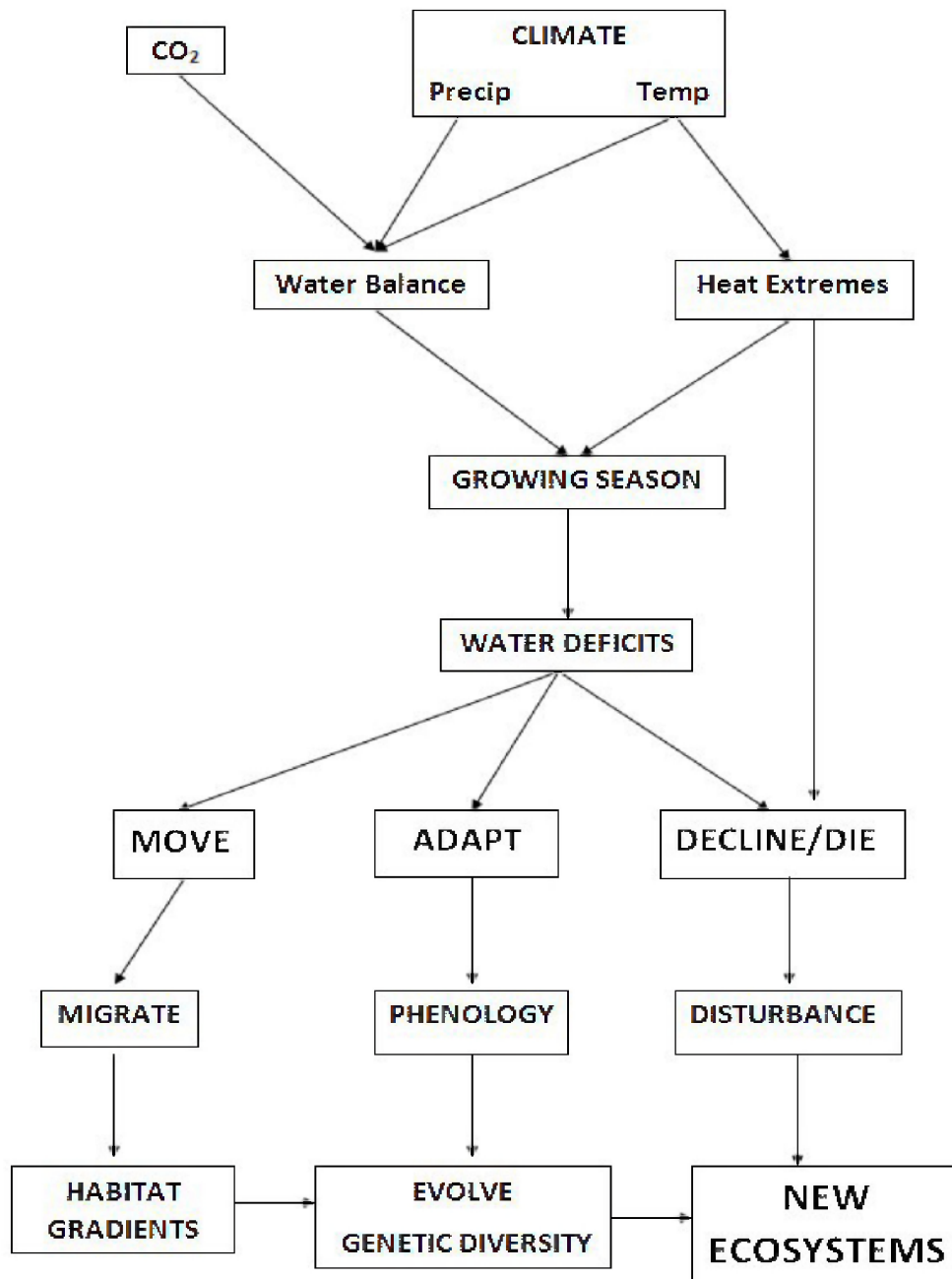
Note: Differential adaptation among species leads inexorably to changes in community and ecosystem structure

Climatic Means versus Extremes

The biophysical and biogeochemical activity of a terrestrial ecosystem is physically constrained by the average meteorological conditions of the site. Processes like photosynthesis, respiration, transpiration, decomposition, and animal physiological responses react to the light, temperature, and water conditions that prevail throughout the growing season and, in some cases, the winter dormant season. In contrast, the mortality of an individual organism can be triggered by an instantaneous extreme event—a freezing or heat threshold or loss of critical hydration. Consequently, the responses of ecosystems to changing climates must pay attention to annual and seasonal averages as well as changing probabilities of extreme events (Figure 2).

Figure 2. Principles of the Importance of Changing Probabilities of Climatic Extremes for Ecosystem Adaptations
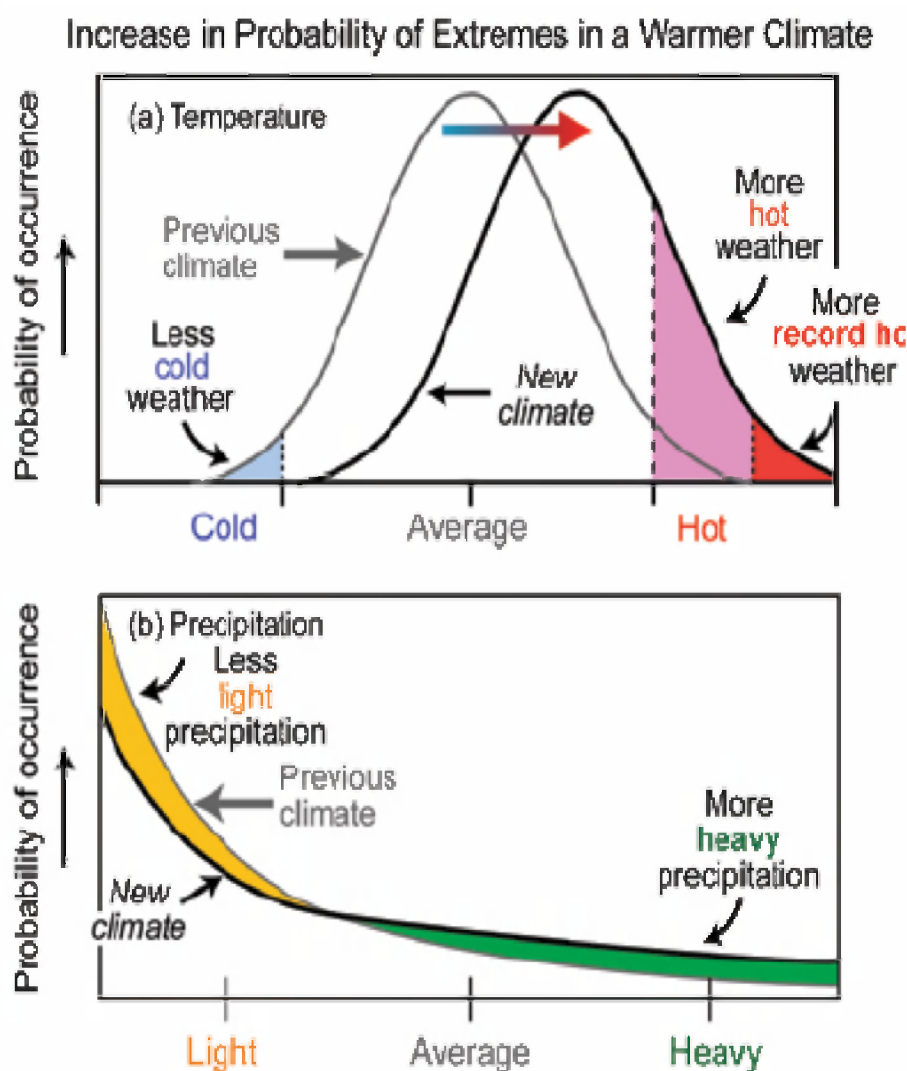
Source: IPCC 2007.

For plants and animals, the climate extremes may be more important than changes in averages. Both high and low temperatures are potential mortality points on which natural selection will act for different organisms. Low-temperature mortality points typically involve late spring or early autumn frosts that are abnormal in their seasonal timing more than their absolute temperature. Midwinter conditions rarely harm native plants because they are in their deepest dormancy at that time of year. High-temperature mortality more directly kills organisms that reach the common 55°C protein denaturation point. Although 55degC would be a nearly impossible weather station temperature in the U.S. it is a common *surface* temperature in midsummer.

An increasing magnitude of environmental variation also has a less appreciated, but potentially powerful, effect on likely population growth rates, or trends, of plants and animals. Because population growth is a multiplicative process, the most likely long-term growth rate in a stochastic (variable) environment is governed by the geometric mean. As variance in the birth and death rates that make up population growth increases, the geometric mean growth rate becomes progressively smaller then the arithmetic mean. In practice, this means that increased variability in climate conditions will tend to decrease expected population growth rates; short-lived species will tend to be affected in more volatile ways by this phenomenon. Importantly, this effect of variability on expected population growth is independent of any changes in the mean rates.

Recent Historical Climate Trends and Variability

For the annual mean air temperature in the contiguous United States, the increase was about 0.56°C per 100 years from 1895 to 2002 (Figure 3 and Zhang *et al.* 2000; Groisman et al. 2004,). Most of the warming has occurred in the spring and winter (Dole *et al.* 2008; Bonsal et al. 2001). Minimum (i.e., nighttime) temperatures have warmed more rapidly than maximum (i.e., daytime) temperatures (Easterling et al. 1997; Zhang et al. 2000; Bonsal et al. 2001).

Annual total precipitation in the United States has increased 7 percent (Groisman et al. 2004 and Figure 4). A recent analysis of long-term daily precipitation records (1895 to 2000) in the United States by Kunkel et al. (2004) found that heavy precipitation frequencies were at a minimum in the 1920s and 1930s and then increased in the 1990s. Groisman et al.(2004) reported increases in heavy and very heavy precipitation in the conterminous United States during the past three decades.

During the past few decades of the 20th century, a greater proportion of the United States was either in severe drought or severe moisture surplus (Zhang et al. 2000a). Dai et al. (2004) found that global land areas in either very wet or very dry conditions increased from 20 to 38 percent of land area since 1972, suggesting more extreme hydrology. Stream flow has *increased* 25 percent in the past 60 years over the eastern United States (Groisman 2004) but has *decreased* in the western United States about 2 percent per decade in the past century (Root et al. 2005). Walter et al. (2004) calculate that evapotranspiration has increased 55 millimeters in the last 50 years in the conterminous United States; however, their data show reduced stream discharge in the Colorado and Columbia River basins since 1950.

Figure 3. Trends in Annual Air Temperatures for the United States
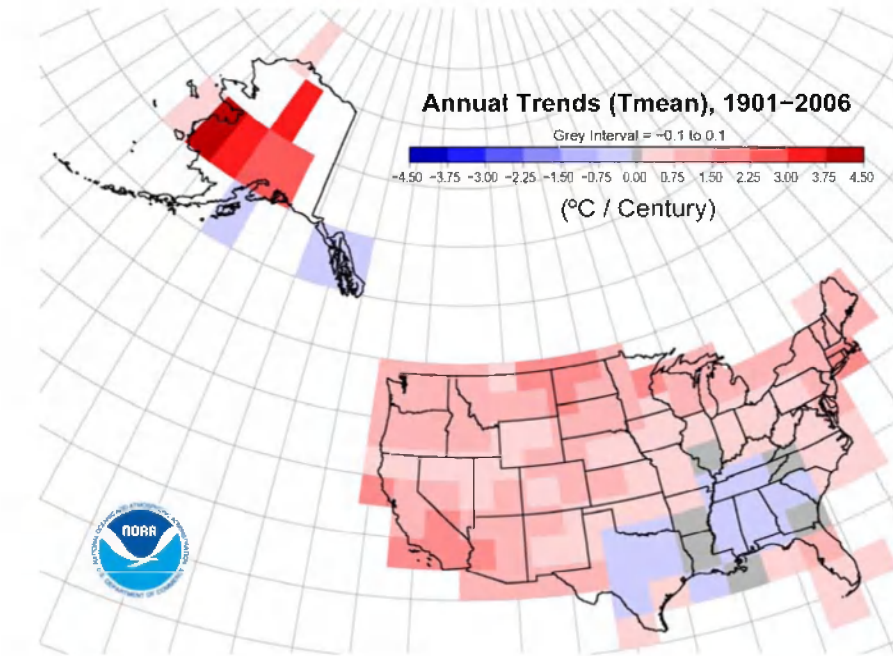
Source: National Oceanic and Atmospheric Administration, National Climate Data Center (NCDC).

Figure 4. Trends in Annual Precipitation for the United States from 1901 to 2006
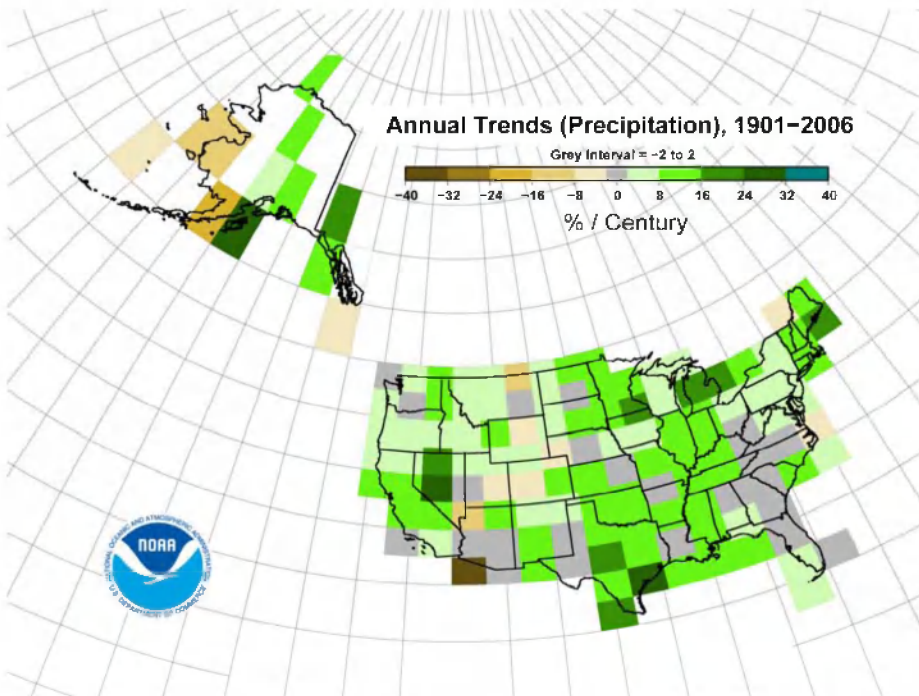
Source: National Oceanic and Atmospheric Administration, National Climate Data Center (NCDC).

In snowmelt regions, the temperature increase has shifted the magnitude and timing of hydrologic events (Figure 5 and Barnett et al. 2008). A greater fraction of annual precipitation is falling as rain rather than snow at 74 percent of the weather stations studied in the western mountains of the United States (Knowles et al. 2006). Snow cover has diminished earlier in the year in the U.S. West (Groisman 2004). The April 1st snow–water equivalent decreased 15–30 percent since 1950 in the Pacific Northwest, particularly at lower elevations (Mote et al. 2003; Mote et al. 2005). Stewart et al. (2005) found that stream flow peaks in the snowmelt-dominated western mountains of the United States occurred one to four weeks earlier than in 1948.

Figure 5. Trends from 1950 to 2000 of Hydrologic Variables in the Mountains of the Western United States
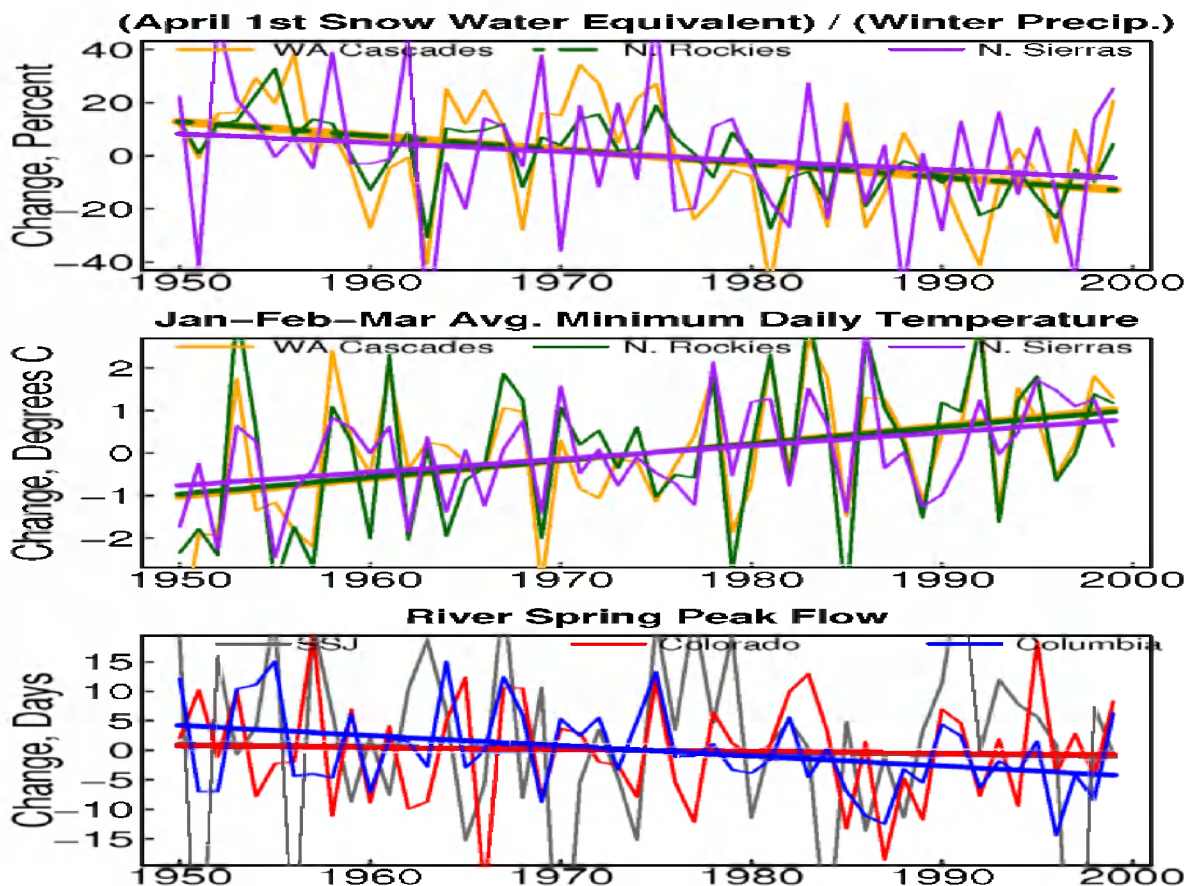
Source: Barnett et al. 2008.

Vegetation Response and Phenology

Climatic constraints on vegetation activity can be generalized as variable limitations of temperature, water availability, and solar radiation, with every point on Earth exhibiting a different mix of these controlling factors every day of the year (Nemani et al. 2003; Jolly et al. 2005). Where a single climatic limiting factor clearly dominates, such as low-temperature constraints on the growing season at high latitudes or water limitations in deserts, plant responses will be fairly predictable. However, in areas where a seasonally changing mix of temperature, daylength, and

water constraints is possible, including most midlatitude regions, a projection of vegetation responses depends both on temperature trends and the land–surface water balance. Although temperature warming trends for North America are well documented, the land–water balance trends over the past half century suggest that roughly the western half of the continent is becoming drier and the eastern half wetter.

The most direct and observable connection between climate and terrestrial ecosystems is in certain life-cycle timing of seasonal phenology and in plant growth responses—annually in primary productivity and decadal over changes in the biogeographical range. These impacts on seasonality and primary productivity in plants may both influence, and be influenced by, interactions with animals (Post and Pederson 2008).

The vegetation growing season, as defined by continuous frost-free air temperatures, has increased by, on average, two days per decade since 1948 in the conterminous United States, with the largest change in the western United States and most of the increase from earlier warming in the spring (Easterling 2002; Feng and Hu 2004; Figure 6). Global daily satellite data, available since 1981, have detected similar changes in earlier onset of spring "greenness" of 10–14 days in 19 years, particularly in temperate latitudes of the Northern Hemisphere (Myneni 2001; Lucht et al. 2002). Field phenological observations of vegetation have confirmed these satellite observations. Schwartz and Reiter (2000) reported an advance of 1.8 days per decade from 1959 to 1993 in lilac bloom dates from 800 sites across North America. Honeysuckle first-bloom dates have advanced 3.8 days per decade at phenology observation sites across the western United States (Cayan et al. 2001), and apple and grape leaf onset has advanced 2 days per decade at 72 sites in the northeastern United States (Wolfe et al. 2004). The first bloom of aspen trees in Edmonton now averages 26 days earlier than in 1901 (Beaubien and Freeland 2000). Autumn leaf senescence timing is jointly controlled by temperature, daylength, and water deficits, so it shows weaker trends (Badeck et al. 2004).

Global terrestrial net primary production (NPP) has increased 6 percent during the 1982–1999 period of satellite record used for these estimates (Nemani et al. 2003; Cao and Prince 2002; see Figure 7). NPP increases of 10 percent from 1982 to 1999 in North America were concentrated in the Central Plains croplands and grasslands as a result of improved water balances (Hicke and Lobell. 2004; Lobell et al. 2002; Nemani et al. 2002). Higher NPP during this period, predominantly in northern Rocky Mountain forests, was attributed to higher spring temperatures and a longer growing season (Hicke et al. 2004). All of these continental-scale estimates of NPP rely on satellite spectral indices of vegetation greenness, the Normalized Difference Vegetation Index (NDVI), and surface weather data to compute a simple production efficiency model.
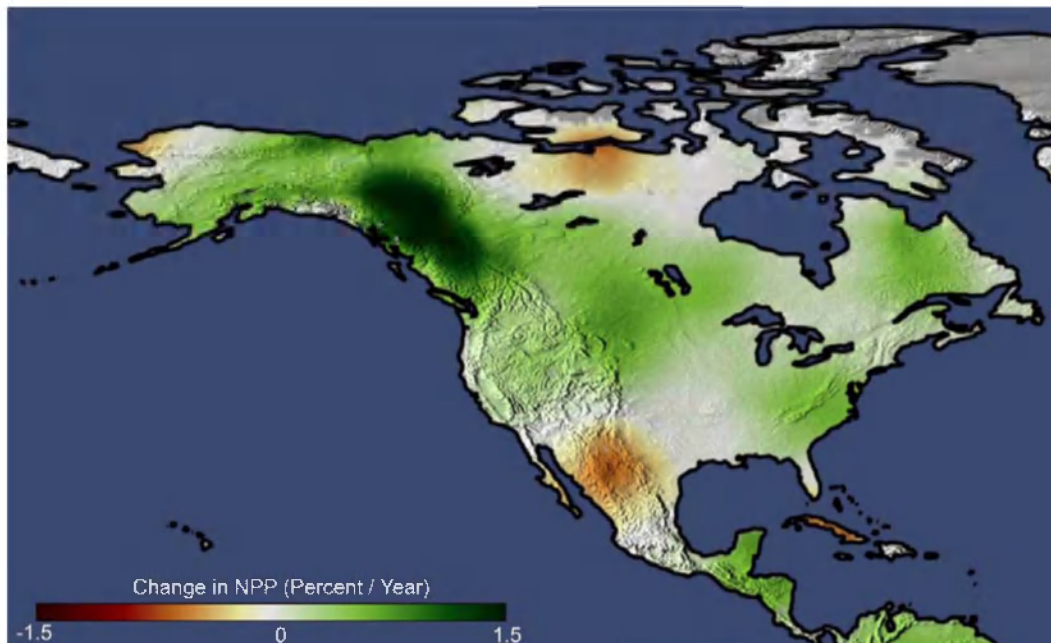
Figure 6. Trends in Frost-Free Growing Season Length and Phenological Observation of Bud Burst

SHADES: TRENDS OF BEGIN DATE OF GROWING SEASON, 1950-99, FROM TEMPERATURES
DOTS: TRENDS IN LILAC FIRST-BLOOM DATES (Sites with 20+yrs of record)
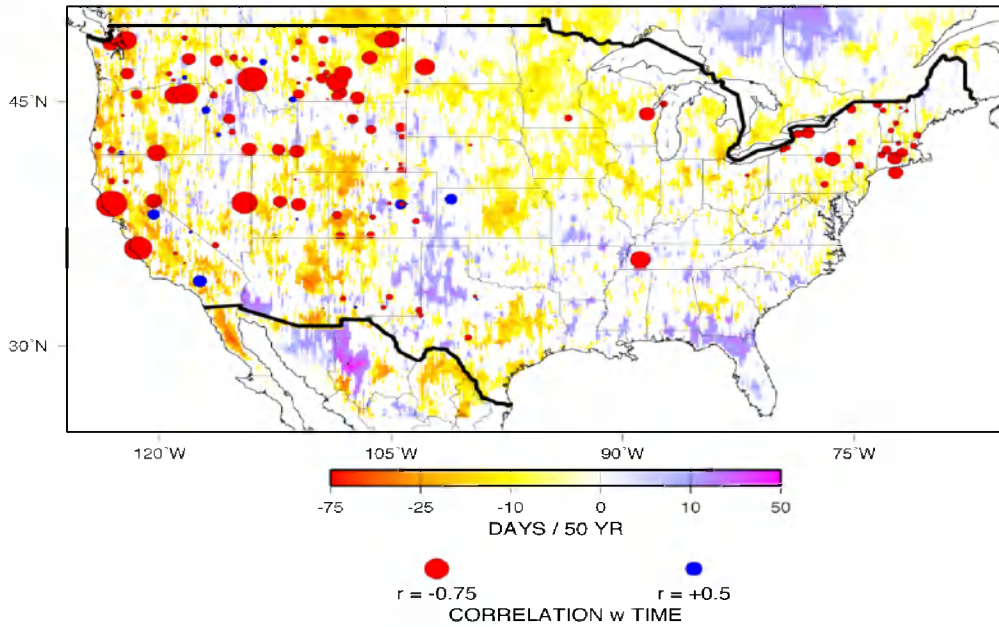
Source: Cayan et al. 2001.

Figure 7. Changes from 1982 to 1999 in Terrestrial NPP

Source: Nemani et al. 2003.

Estimates of the net ecosystem exchange of North America require atmospheric inversion, carbon bookkeeping, and biogeochemical process models combined with satellite, field inventory, and fluxtower data. North America continues to be a carbon sink of 0.5 Petaggrams C per year, although human land management practices control much of the dynamics (Schimel et al. 2001; Pacala et al. 2001). El Niño–Southern Oscillation (ENSO), Arctic Oscillation, and Southern Oscillation climate indices have all shown some correlation with temporal North American carbon fluxes (Potter et al. 2003; Hashimoto et al. 2004).

Comparative analyses of seasonal NDVI and atmospheric carbon dioxide dynamics from 1982 to 2002 suggest that the photosynthetic enhancement from warmer, early spring temperatures is being cancelled out by late-summer drought in much of the Northern Hemisphere (Angert et al. 2005). Lobell and Asner (2003) found a roughly 17 percent decrease in corn and soybean yields in the U.S. Midwest for each degree increase in growing season temperature for the period 1982–1998.

Forest growth appears to be slowly accelerating (less than one percent per decade) in regions where tree growth is limited by low temperatures and short growing seasons that are gradually being alleviated (Boisvenue and Running 2006; McKenzie et al. 2001; Joos et al. 2002; Casperson 2000). Black spruce at the forest–tundra transition in eastern Canada show acceleration of height growth beginning in the 1970s (Gamache and Payette 2004). However, radial growth of white spruce in Alaska has decreased over the past 90 years because of increased drought stress on the dry southern aspects they occupy (Barber et al 2000). Semiarid forests of the southwestern United States also showed a decreasing growth trend since 1895 correlated with drought effects from warming temperatures (McKenzie et al. 2001).

Low–temperature limited geographic ranges show evidence of change resulting from warmer temperatures. Photographs at timberline in Colorado taken 100 years ago that have recently been repeated show the advancement of aspen into the more cold-tolerant spruce–fir forests (Elliott and Baker 2004). The northern range limit of lodgepole pine is advancing competitively against the more cold-tolerant black spruce in the Yukon (Johnstone and Chapin 2003).

Wildfire and Disturbance

Disturbances change the trajectory of ecosystems more substantially than growth processes or population dynamics. Climate change is now changing the probabilities and magnitudes of disturbances in natural ecosystems (Running 2008). In recent decades, the area of forest burned in wildfire has increased substantially. Early in the 20th century, the area burned in North America was as high as 40,000,000 hectares per year, with large areas burned in boreal, western, and southeastern forests. This decreased to about 4,000,000 hectares per year in the middle of the century but is now increasing, with the largest increases in boreal regions (Mouillot and Field 2005).

From 1920 to 1980, the area burned in wildfires in the United States averaged about 13,000 square kilometers per year. Since 1980, the average annual burned area has almost doubled to 22,000 square kilometers per year, and three major fire years have exceeded 30,000 square kilometers (Schoennagel et al 2004). The forested area burned from 1987 to 2003 is 6.7 times the area burned for the period 1970–1986, with a higher fraction burning at higher elevations

(Westerling et al. 2006). Warming climate encourages wildfires by drying of the land surface, which allows more fire ignitions, and through desiccated vegetation and hot, dry meteorology, which allow fires to grow exponentially more quickly, ultimately determining the area burned. Gillett et al. (2004) found a correlation of r = 0.77 between warming summer temperatures of 0.8°C and the acceleration of wildfire-burned area since 1970 in Canada. More active fire years in the southwestern United States have been correlated with ENSO positive phases (Kitzberger et al. 2001; McKenzie et al. 2004) and higher Palmer Drought Severity Indices. Relating climatic trends to fire activity is complicated by regional differences in the seasonality of fire activity. Most fires occur in April–June in the southwestern and southeastern United States, and in July–August in the Pacific Northwest, Alaska, and Canada. Earlier snowmelt, longer growing seasons, and higher summer temperatures observed particularly in western North America are synchronized with the increase of wildfire activity, along with dead fuel buildup from previous decades of fire suppression activity, as shown in Figure 8 (Westerling et al. 2006).

Figure 8. Western Mountain Wildfire Activity Related to Summer Water Deficits from 1970 to 2005
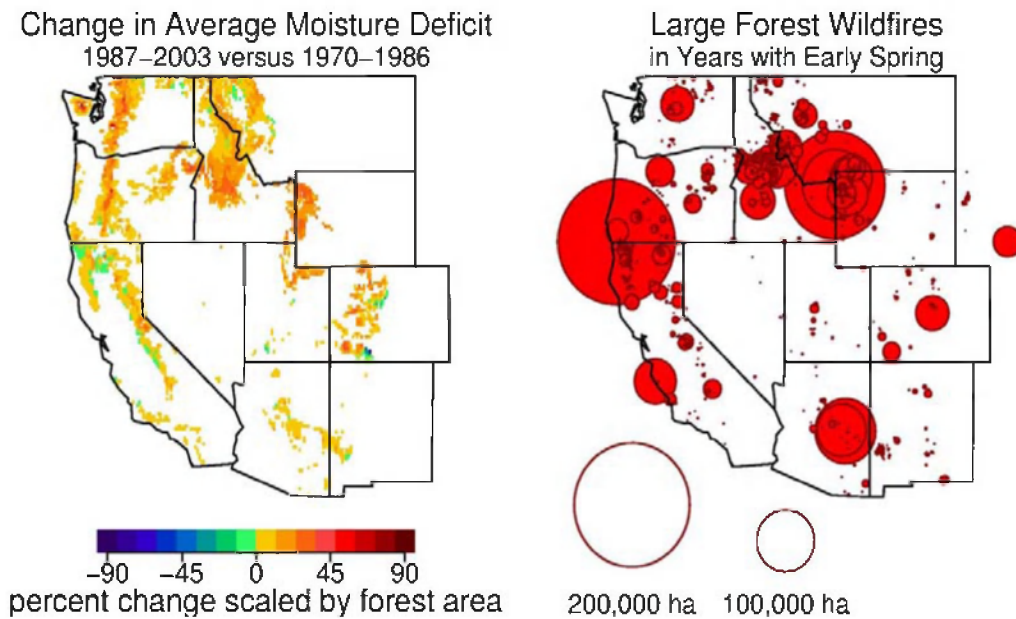
Source: Running 2006.

Insects and diseases are natural components of all ecosystems; however, in forests, periodic insect epidemics can erupt and kill millions of hectares of trees, providing dead, desiccated fuels for large wildfires. The dynamics of these epidemic outbreaks are related to insect life cycles that are tightly tied to climate fluctuations and trends (Williams and Liebhold 2002). Many northern insects have a two-year life cycle, and warmer winter temperatures now allow a larger percentage of overwintering larvae to survive. Recently, Volney and Fleming (2000) found that spruce budworm in Alaska have successfully completed their life cycle in one year, rather than the previous two. Earlier warming spring temperatures allow a longer active growing season, and higher

temperatures directly accelerate the physiology and biochemical kinetics of the insects' life cycles (Logan et al. 2003). Mountain pine beetle has expanded its range in British Columbia into areas previously too cold to support its survival, as shown in Figure 9 (Carroll et al 2003). Multiyear droughts also reduce the available carbohydrate balance of trees as well as their ability to generate defensive chemicals to repel insect attack (Logan et al. 2003).

Figure 9. Timing and Affected Area of Major Forest Insect Epidemics in the Western United States from 1998 to 2002
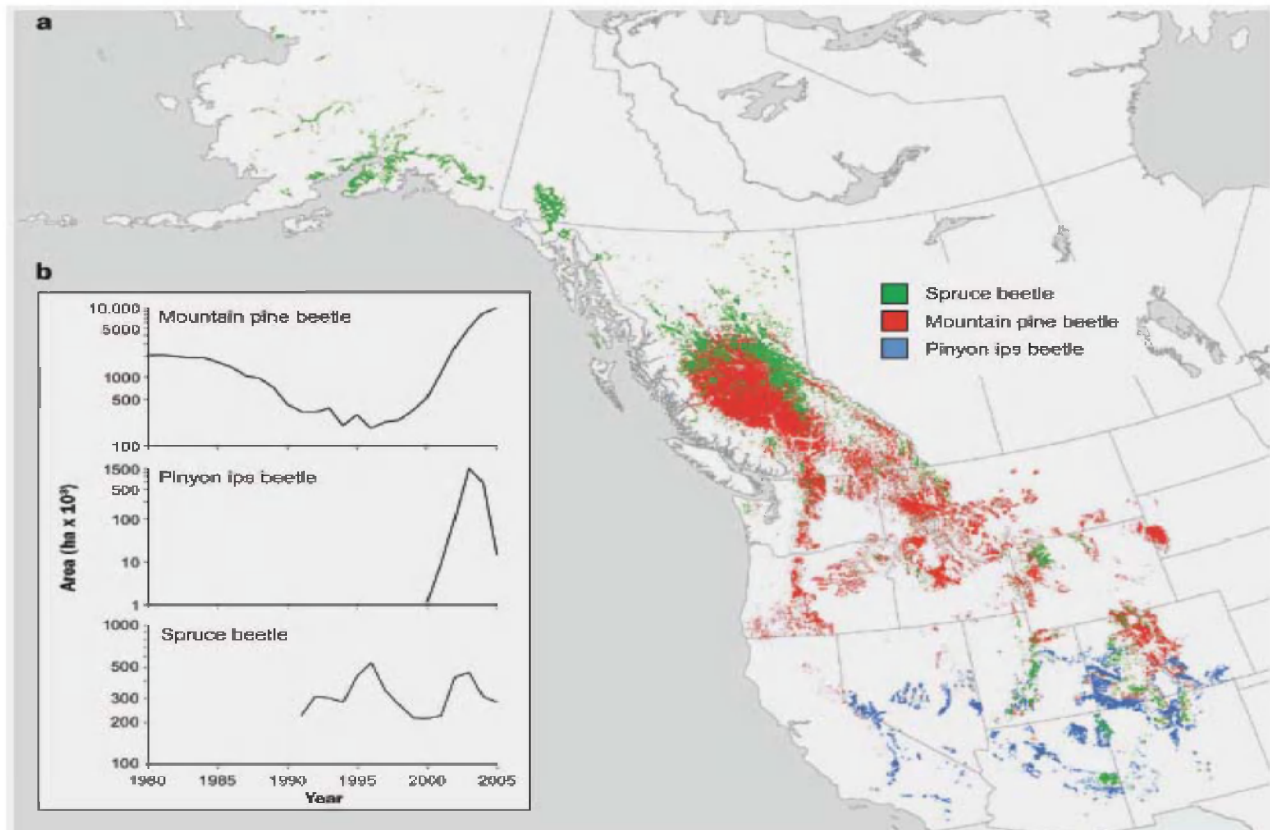
Source: Raffa et al. 2008.

Adaptation to Climate Change in Wild Populations

Plants and animals show a wide variety of responses to changing abiotic (physical) conditions. In turn, animals (and plants) respond to changes in vegetation, and interactions among species. These responses are depicted in Figure 1. Adaptation (in the broad sense) occurs via successfully adapting in place (through phenotypic plasticity and/or evolution), or by shifting geographic range or other movement patterns. Often, more than one of these responses will occur concurrently. Unsuccessful adaptation results in a decline in numbers toward extinction. The emergent effect of successful and unsuccessful adaptation across species is changes in species interactions and

ultimately in community and ecosystem structure and composition. Next, we will critically examine the mechanisms that determine and limit adaptation to climate change.

Adaptation in Place via Plasticity and/or Evolution

Many of the best-documented examples of adaptation in place to climate change include phenological shifts, or changes in the timing of activities such as mating, reproduction, growth, or movement (Root et al. 2005). A majority of 677 species studied show trends toward spring advancement in breeding, flowering, or seasonal migration (Parmesan and Yohe 2003); for species showing substantive change (greater than one day per decade), spring phenology has advanced 5.1 days per decade, with larger shifts at higher latitudes (Root et al. 2003). The following are among the best-documented specific examples of these phenological shifts: (a) red squirrels in Northern Canada breed 18 days earlier than 10 years ago (Réale et al. 2003; Bertreaux et al. 2004); (b) four frog species in New York State initiate breeding calls 10–13 days earlier than a century ago (Gibbs and Breisch 2001); and (c) 70 percent of 23 butterfly species in Southern California advanced the date of their first spring flights by 24 days over the past 31 years (Forester and Shapiro 2003).

Adaptation to climate change will not always be possible and, by definition, failed adaptation will result in decreased fitness and a decline toward extinction (Figure 1). For example, caterpillars, the key food source for migratory pied flycatchers on their spring breeding grounds, now peak in abundance earlier in the year. The flycatchers have responded with adaptation: they have advanced their laying date by decreasing the time between arriving on the breeding grounds and laying their eggs. However, the trigger for migrating to the breeding grounds is daylength, not climate, which constrains the number of days that egg laying can be moved forward. As a result, peak food availability is increasingly mismatched with the flycatcher's arrival on the breeding grounds to lay eggs; the mismatch is leading to a decline of the flycatchers (Both and Visser 2001; Both et al. 2006). Such mismatches in responses across trophic levels—including disconnects between life cycles of predators and prey, parasitoids and their host insects, and insect pollinators with flowering plants—can go beyond the interacting species to the communities and ecosystems of which they are a part (Parmesan 2006).

Two primary mechanisms, phenotypic plasticity and adaptive evolution, facilitate adaptation in place. Phenotypic plasticity occurs when the climate change–related stressor is within the response envelope of the species such that individuals can adjust behavior, morphology, or physiology to accommodate the change (Hendry et al. 2008); plant biologists often refer to phenotypic plasticity as *acclimation*. Such plasticity allows for an individual with a given genotype to modify its phenotype across a *reaction norm* as environmental conditions change (Nussey et al. 2007). For example, the change in egg-laying date of flycatchers described above appears to be largely due to the plasticity of individual female egg-laying behavior. Likewise, plasticity is the primary driver behind the 18-day advancement in mean parturition date of red squirrels in northern Canada (Réale et al. 2003; Berteaux et al. 2004). Many reptiles and some amphibians have sex ratios at birth that are determined by temperature, such that a few degrees' change leads to all-male or all-female offspring (Janzen 1994); in some cases, plasticity in maternal nesting behavior (e.g., choosing shaded vs. open sites) can minimize nest temperature changes, thereby acclimating behaviorally against drastic sex ratio changes (Doody et al. 2006).

Although plasticity may effectively track conditions and prevent fitness degradation, the limits to plasticity must be emphasized. For example, the flycatcher plastic response does not seem to be enough to prevent population decline. Further, the observed individual plasticity in reptile (e.g., turtle) nesting behavior or timing is not likely to be enough, in many cases, to sufficiently track nest temperature changes to prevent changes in sex ratio in a warming climate (Schwanz and Janzen 2008).

While phenotypic plasticity represents an adaptive response to a stressor without a genetic change, adaptive evolution facilitates adaptation in place via changes in gene frequencies caused by natural selection. If the new regime creates a selection gradient, such that fitness is different for individuals carrying different genetic variants of a trait, then gene frequencies for that trait will change and adaptive evolution will have occurred. Evolution by natural selection has traditionally been thought of as a long-term process divorced from the short-term time scale of ecological processes. However, adaptive evolution can be surprisingly rapid, in some cases observable over a period of a few years and occurring on time scales that can affect contemporary ecological dynamics (Hairston et al. 2005). Many of the best examples of contemporary adaptation in natural populations have been in response to anthropogenic changes in the environment, including heavy metal and air pollution tolerance, insecticide and herbicide resistance, and industrial melanism (Reznick and Ghalambor 2001). Thus, in some cases, evolutionary change via natural selection can be a powerful force in "rescuing" populations exposed to new and stressful human-modified environments, leading to the question of the conditions under which contemporary evolution may rescue populations exposed to stressors such as climate change (Reznick and Ghalambor 2001; Stockwell et al. 2003; Kinnison and Hairston 2007; Bell and Collins 2008). Although this is an active area of research, five generalities have emerged to guide expectation of the most likely scope and speed of *evolutionary rescue* (Kinnison and Hairston 2007, Bell and Collins 2008) in response to climate change.

- **Contemporary adaptive evolution is favored by large population size and/or rapid population growth**: Large population size provides an ample supply of raw evolutionary material via mutation and allows natural selection to adaptively shape gene frequencies without being overwhelmed by random genetic drift. On the other hand, adaptive evolution is compromised by small population size or negative population growth rate. Just how small, or how steeply declining, populations need to be to undercut the beneficial rescue effects of evolution is a complicated question depending on the force and constancy of selection, mutation rates, population history, standing levels of genetic variation, and other factors. Rapid population growth from small population size may occur in newly colonized populations, facilitated by reduced competition or perhaps "favored-founder" effects (Kinnison and Hairston 2007), whereby those that colonize a modified environment are predisposed to flourish (with high population growth) under those conditions. For example, Glanville fritillary butterflies that colonize new areas tend to have both higher flight ability and higher fecundity than those in old patches (Hanski et al. 2004), and these traits have a demonstrated genetic basis (Haag et al. 2005).

  The importance of large population size and/or rapid population growth raises the important idea that climate change operates synergistically with other stressors: to the extent that other factors, such as habitat fragmentation, overharvest, or invasive species,

limit population size or growth, the ability of a species to adapt to climate change will be compromised. Similarly, populations that become small and declining remain much more susceptible to the *extinction vortex* (Soulé and Mills 1998), whereby any chance of evolutionary rescue is undercut by an exaggerated risk of extinction.

- **Contemporary adaptive evolution is facilitated by short generation times.** Over a given time interval, say one human lifespan, species with short generation times will be exposed to more bouts of selection and therefore will have a greater potential to manifest evolutionary change. Furthermore, species with short generation times tend to have higher innate capacity for population growth, buffering them against the demographic costs of natural selection.

- **Contemporary adaptive evolution will be more efficient when the stressor is directional and relatively constant**. A textbook example of rapid evolutionary adaptation in place with strong directional selection focuses on guppies exposed to predators (e.g., Reznick et al. 2008). In only about 2 to 30 years (4 to 50 generations), guppies exposed to predators evolved a suite of traits, including cryptic coloration, an earlier and smaller maturation time (a life history adaptation to ensure reproduction in a dangerous environment), higher reproductive effort, and a tendency to swim in larger schools and avoid predators. The context of these experiments, with a novel predation stressor, is appropriate for evaluating responses to climate change as species composition of ecological communities shift. Finally, we note that, by definition, directional selection implies a demographic cost on population growth as some individuals fail to reproduce or survive; thus strong directional selection may lead to extinction before the adaptive changes occur.

- **Contemporary adaptive evolution is facilitated by a medium level of gene flow.** On one hand, a principle of population genetics holds that high gene flow into a population will deter local adaptation, with natural selection undercut when it is exceeded by the migration rate (Wright 1940); furthermore, in some cases, population mixing may induce outbreeding depression, which decreases hybrid fitness (Edmands 2007). On the other hand, gene flow can bring adaptive variation into a population. For example, if immigrants from southern populations bring adaptive genes into northern populations during range shifts, evolutionary adaptation may be enhanced (Kinnison and Hairston 2007). Thus, contemporary evolution will tend to be fostered by a medium level of gene flow among populations separated by a human-modified landscape.

- **Contemporary adaptive evolution to an anthropogenic stressor will be more likely in generalist species.** Evolutionary change requires heritable variation in the traits under selection. For a given trait, highly specialized species will be less likely to possess the variation necessary to adapt to climate change–related stressors. For example, many widespread *Drosophila* (fruit fly) species have high heritability to endure desiccation stress, and so can evolve rapidly in response to increased climatic stress due to desiccation. However, one narrowly distributed rainforest species (*Drosophila birchii*) has low heritability for this trait and is unable to evolve resistance to desiccation stress (Hoffman et al. 2003).

The striking conclusion to emerge from this suite of five characteristics favoring contemporary evolution is that the "winners" will most likely be invasive and pest species. Invasives and native pest species tend to have life histories and genetic makeups characterized by large population size; rapid population growth; short generation times; high connectivity, even across disturbed landscapes; and generalist phenotypes underlain by rich heritable variation. Thus, climate change creates a fertile environment in which any evolutionary rescue that does occur is prone to proliferate exactly the species least desirable in society, ranging from disease organisms to deer mice to coyotes to zebra mussels to knapweed.

Adaptation via Movement and Range Shifts

Although adaptation in place represents one possible response for species exposed to climate change stressors, in other cases, adaptation will occur when populations shift to areas where the stressor is ameliorated. Changes in animal movement patterns—typically poleward and upward—have already been documented as some of the most remarkable signals of climate change (Parmesan 2006). For example, two well-known western butterflies, the Edith's checkerspot and sachem skipper, have shifted their ranges northward and/or upward (Parmesan and Gailbraith 2004; Crozier 2003). For 254 species of North American birds, the northern boundaries of their ranges are shifting an average of 1.5 kilometers per year, and their centers of abundance are shifting 1 kilometer per year, a pattern reflecting a clear climate change signal interacting with regional factors (La Sorte and Thompson 2007; Hitch and Leberg 2007). Similar patterns have been found with dragonflies and damselflies: of 37 species of nonmigratory species examined, all but 3 shifted northward at their range margin by an average of 74 kilometers over a period of two to three decades (Hickling et al. 2005).

Figure 10. Elevational Range Changes for 28 Small-Mammal Species in Yosemite National Park over the Past Century
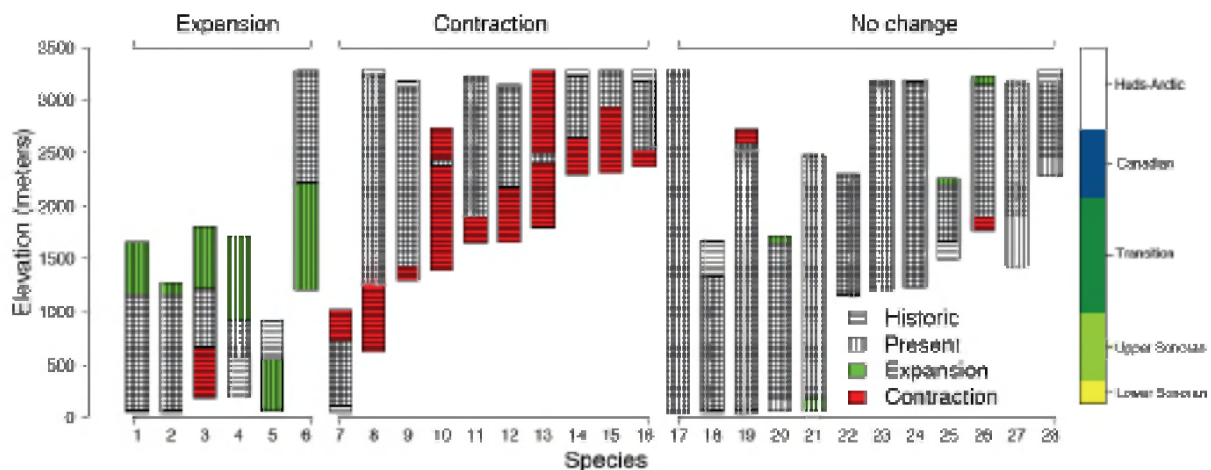
Note: Statistically significant changes are colored green for range expansion and red for contraction. Species were classified as "No change" if range shifts were <100m or <10% of previous elevation range.
Source: Moritz et al. 2008.

A strong case of a range shift within the U.S. has been found for small mammals in Yosemite National Park (an area that would be buffered from many of the alternate stressors that might

facilitate distribution changes). By repeating surveys conducted nearly a century ago across a detailed 3,200-meter elevational transect, Moritz et al. (2008 and Figure 10) found that 10 of 28 species shifted their lower geographic limit upward (2 shifted downward). High-elevation species tended to experience range contractions, whereas low-elevation species expanded their ranges upward. Overall, species richness within Yosemite National Park has changed little, but local associations of species with each other (community structure) have changed as a result of idiosyncratic elevational shifts among species.

When temperatures facilitate the northward expansion of invasive species or diseases, the shifts in community composition can be dramatic. This phenomenon has been widely described for disease, such that the geographic range expansion of pathogens ranging from dengue to eastern oyster disease has been linked to climate change and cascading effects on animal species (e.g., Harvell et al. 2002; Parmesan 2006). A similar threat exists from other invasive species that have reverberating ecosystem effects, such as top predators. For example the red fox, an invasive, highly efficient predator and a prominent rabies vector, appears to have been subsidized by a bottom-up trophic cascade induced by warmer temperatures: higher primary productivity has increased prey biomass, and the red fox has spread northward, expelling the competitively subordinate, native arctic fox (Hersteinsson and Macdonald 1982; Killengreen et al. 2007).

Obviously, adaptive movement is itself a target of plasticity and adaptive evolution as discussed in the previous section. A fantastic, yet unsettling, example of the interaction between range shift and evolutionary change may be found in cane toads, introduced to Australia 70 years ago to control insect pests. They have expanded their range to more than a million square kilometers, and their toxicity and voracity have reverberating ecosystem effects. Phillips et al. (2006) showed that the speed of the invasion front has increased with the evolution of longer legs: during the 1940s–1960s, the toad expanded its range by 10 kilometers per year, but current rates are more than 50 kilometers per year.

The Interaction of Climate Change with Other Human-Caused Stressors

It is rare to find any meaningful ecological phenomenon that is driven entirely by one factor. Therefore, it should not be surprising that few ecosystem changes of interest to humans can be entirely attributed to climate change. Rather, climate change effects on plants, animals, and diseases interact with other human-caused stressors, including habitat fragmentation, agriculture and urbanization, invasive species, pollution, and so on. For example, two of the classic examples of range shifts described above included other anthropogenic factors. In the northern shift for British dragonflies and damselflies, water quality also played a role. Also, in a detailed analysis of poleward shifts in the winter ranges of 254 North American bird species (La Sorte and Thompson 2007), regional anthropogenic factors (e.g., persecution, pesticides, suburban development, and forest management) interacted with climate change to explain the range shift trends for all species; for the five that experienced extreme colonization events, regional anthropogenic events other than climate change were entirely responsible. Finally, the same point emerged from a study of pikas in the Great Basin region, where 28 percent of the populations appear to have undergone recent extirpations (Beever et al. 2003); climate change appears to have played a role, via thermal stress and changes in plant species composition, but other anthropogenic factors and grazing status were

also important. We describe other examples of synergistic interactions between climate change and other additional anthropogenic stressors in the Expected Effects section.

Expected Future Ecosystem Trends

Future Climate Trends

Figure 11 shows climatic patterns expected for the United States by 2030, based on simulations from the Intergovernmental Panel on Climate Change Fourth Assessment Report. Overall average air temperatures are expected to increase 1–2°C, decreasing the number of frost days by 10–20 per year. However, a clear disparity in precipitation is apparent, with some areas of the country expected to show a 5–10 percent increase in precipitation and others expected to show a 5–10 percent decrease.

The most advanced dynamic global vegetation models now project that the carbon sink of North America is contingent on two dynamics: (a) the northward expansion of forests into the tundra and improved boreal NPP from longer growing seasons and (b) sufficient enhancement of precipitation in the midlatitudes to sustain the land–water balance as temperatures rise (Woodward and Lomas 2004; Berthelot et al 2002; Bachelet et al. 2001; Gerberet al. 2004). Berthelot et al. (2002) expect Net Ecosystem Productivity of northern latitude ecosystems to increase 11 percent by 2100, but the tropics to decrease by 80 percent because of increasing water deficits. However, provenance modeling of the strongly temperature-limited white spruce in Quebec predicts that, although tree growth will be enhanced by a 1°C temperature increase, a 4°C increase would be beyond the genetic range of the current population and would cause a growth decrease or species replacement (Andalo et al. 2005). Zolbrod and Peterson (1999) project that a 2°C temperature increase in the Olympic Mountains of Washington State would cause dominant tree species to shift upward in elevation 300–600 meters, causing the subalpine species to be replaced by temperate zone species over a period of 300–500 years. Biomass growth responses in these simulations had a complex relationship with elevation and aspect, such that longer growing seasons enhanced tree growth only if adequate soil moisture was present. Rehfeldt et al. (2001, 367) evaluated potential climate-driven growth responses for the entire biogeographical range of Pinus contorta throughout western North America, concluding that, with present tree populations, a 3°C temperature increase would "increase productivity in the northern latitudes, decrease productivity in the middle latitudes and decimate forests on the southern" limits of the species' current range. The authors concluded that, with evolutionary adjustments or active forest management of the population to account for the changing climate, forest productivity losses could be moderated. However, they noted, the key is that temperature increases must be balanced by equivalent increases in precipitation or widespread mortality and growth losses will occur.

Figure 11. Projections of Future Climate for the United States in 2030, Differences from 1990
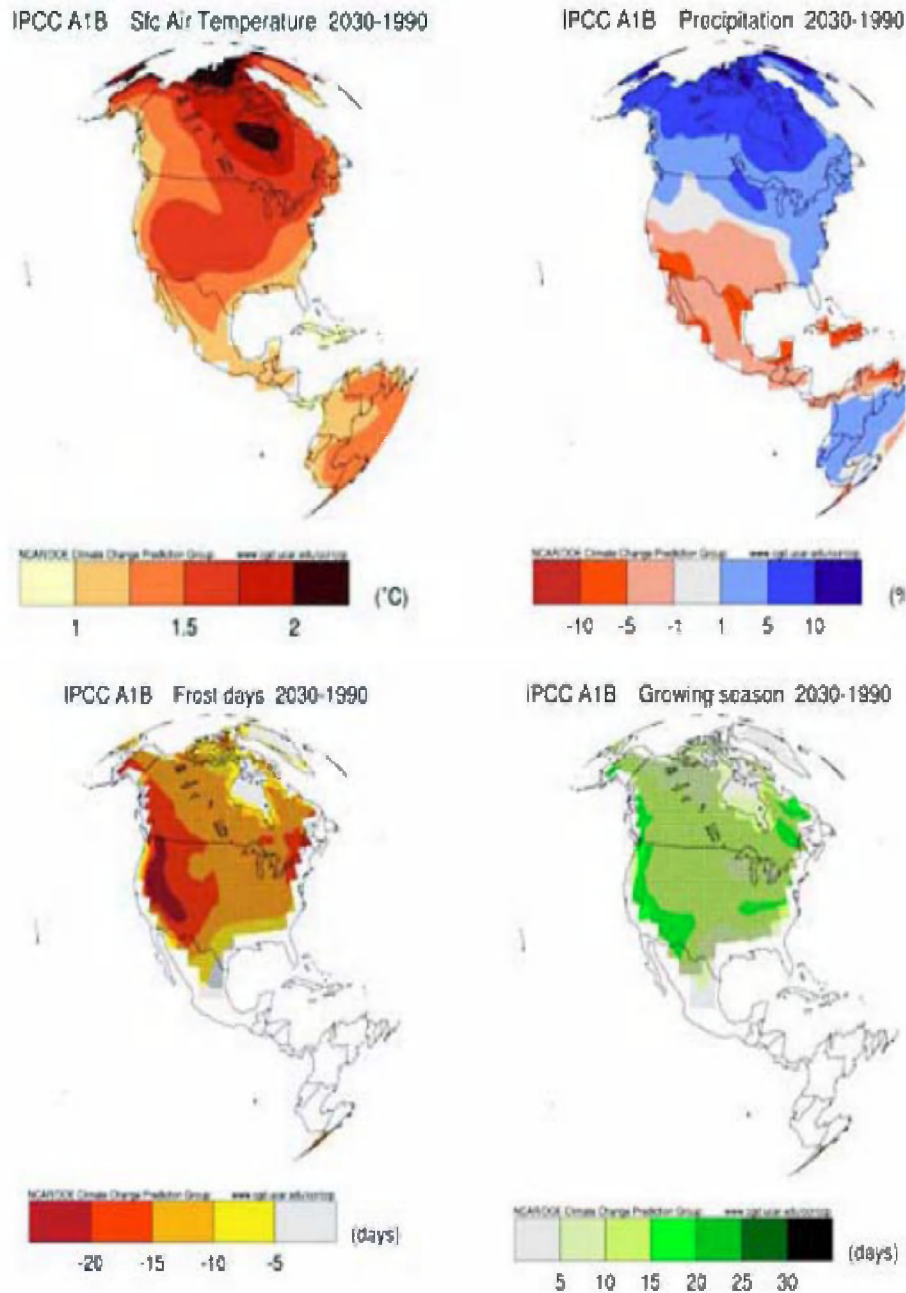
Note: IPCC = Intergovernmental Panel on Climate Change, Sfc = surface.
Source: Dole et al. 2008.

Ecosystem model projections are unanimous in expecting continued temperature-stimulated expansion of boreal and temperate forests into higher latitudes and altitudes (Berthelot et al. 2002). Shrubs have invaded the tundra on the North Slope of Alaska (Sturm et al. 2001). Fung et al.

(2005), in analyzing the trajectory of overall global carbon source–sink dynamics over the next century, concluded that the temperature-driven increases in carbon sinks at high latitudes will be nearly cancelled out by decreasing carbon sinks at low latitudes caused by water limitations and higher biological respiration losses. Tropical and midlatitude ecosystem trajectories are much less clear as the dominant dynamics will be determined by whether the land–surface water balance trend is positive or negative. Bachelet et al. (2001) project that the areal extent of drought-limited ecosystems will increase 11 percent per degree of warming in the continental United States. Impacts on ecosystem structure and function may be amplified by changes in extreme meteorological events and increased disturbance frequencies.

Ecosystem disturbances, caused by either humans or natural events, accelerate both the loss of native species and the invasion of exotics (Sala et al. 2000). Hot or cold temperature extremes and drought or flooding events may provide climatic triggers of disturbance for invasives and extinction dynamics. Alward et al. (1999) found that increased spring minimum temperatures from 1964 to 1992 correlated with decreasing NPP of the native C4 grass, allowing for increased abundance of exotic C3 forbs in a Colorado grassland.

Species Responses Based on Focal Animal Species

Animal responses will follow, on a species-specific basis, the trajectories described above for current trends and captured in Figure 1: some species will move, some will adapt in place (through plasticity and evolutionary change), and some will decline toward extinction, leading to community and ecosystem rearrangement. Next, we give several examples of particular U.S. animal species that may be used to evaluate adaptation responses to climate change.

Snow-Dependent Species: Snowshoe Hares and Wolverines

One of the clearest fingerprints of climate change in North America is the decrease in the number of days with some snow on the ground. This strong signal may have strong effects on snowshoe hares and wolverines. The snowshoe hare is a strongly interacting species within its ecosystems as nearly the sole prey for the Canada lynx (which is listed as threatened under the U.S. Endangered Species Act), and a staple prey for many other forest-dwelling carnivores (Krebs et al. 2001; Ruesink and Hodges 2001; Ruesink et al. 2002). Hares are also of high public profile as a game species in some parts of their range (especially the northeastern United States). Snowshoe hares undergo a seasonal molt to brown or white coat colors, and a white hare on a brown background (or vice versa) is extremely prominent to predators (Stoner et al. 2003); for example, preliminary telemetry data based on >150 hares indicates that hares suffer high mortality in the spring and fall, when mismatch of coat color and background occur (Griffin and Mills In Press). The timing of coat color change appears to be driven by daylength, with temperature apparently playing some role in the rate of molt once it is initiated. Thus, the question becomes, will snowshoe hares be able to evolve changes in the timing of coat color molt to match their increasingly brown background before being driven to decline by the strong selective agent of predation? This question is as yet unanswered, and will require research at a rangewide scale (across northern North America) using field tools (to quantify the fitness effects of mistimed molt), adaptive genetic markers (to evaluate the response to selection), and comprehensive mapping of current and expected snow conditions (Mills et al. In Progress).

Likewise, snow is an important, even critical, component of the wolverine's seasonal habitat requirements and is considered an obligate component of reproductive denning habitat through thermal benefits and protection from predators (Magoun and Copeland 1998). If wolverine productivity is linked to the availability and quality of reproductive den sites, snow cover that persists throughout the denning period may be critical to wolverine reproduction. The distribution of spring snow cover has also been shown to be concordant with year-round wolverine habitat associations as well as specific movement paths (Schwartz et al. in press). As such, the distribution of spring snow cover appears to define a bioclimatic niche for the wolverine, the distribution and productivity of which may be adversely impacted by global warming.
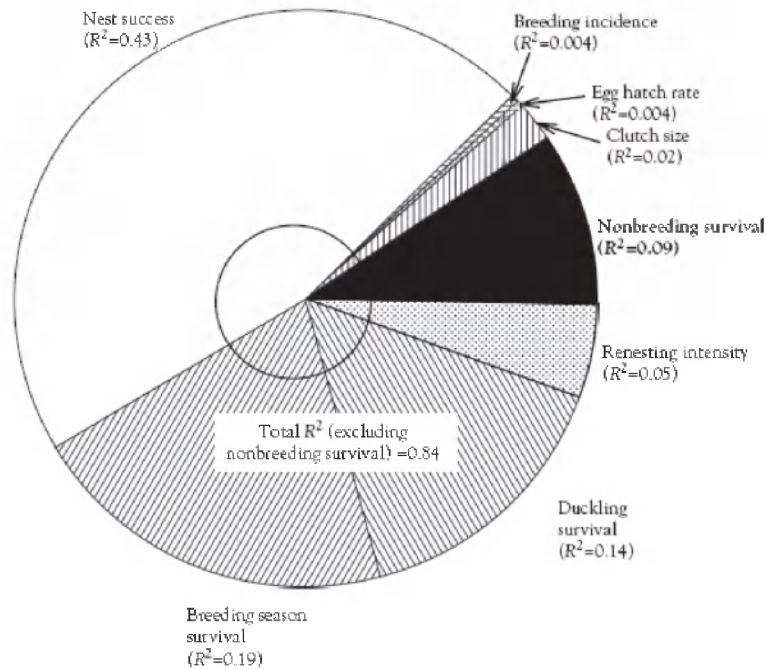
Waterfowl

Waterfowl in the prairie pothole region (PPR) of North America present a well-grounded example of a profoundly important likely projected trend due to climate change (Figure 12). The majority of the continent's ducks are produced in the PPR, and breeding activities in this region determine 90 percent of the variation in population dynamics for midcontinent mallard populations (Hoekman et al. 2002). Thus, waterfowl production in the PPR underlies the $1.6 billion waterfowl sport harvest by 1.5 million U.S. hunters (Williams et al. 2002). Temperature and precipitation—and subsequent wetland abundance and hydroperiod—directly determine waterfowl reproduction and therefore drive population dynamics. Climate change scenarios predict that the future PPR will have fewer wetlands for breeding waterfowl in what historically have been the most productive portions of the PPR (the central and western portions including the Dakotas and southern Saskatchewan). Waterfowl are known to rapidly recolonize drought-stricken landscapes when water returns, but changes in land-use practices further limit the options that birds have to adapt to a changing climate. Simulations by Johnson et al. (2005) suggest that the most favorable climate for waterfowl production will shift to the eastern PPR (in Minnesota and Iowa) where nearly all wetlands have been drained and grassland nesting habitat has been converted to row crop agriculture. The prediction by Sorenson et al. (1998) that waterfowl populations in the PPR could be cut in half by 2050 as a result of climate change would, if correct, strike an economic blow to states that depend on revenues from sport hunting to support local economies.

Another example, drawn from the eastern United States, concerns endangered red-cockaded woodpeckers. Although individuals in North Carolina have demonstrated a shift to earlier laying date, thereby synchronizing hatchlings with temperature-driven changes in food availability, birds that are inbred (due to habitat fragmentation reducing population size) are unable to make the shift (Schiegg et al. 2002). Thus, habitat fragmentation and population declines compromise the resilience of this species to respond to climate change.

Figure 14. Expected Response of Waterfowl to Climate Change
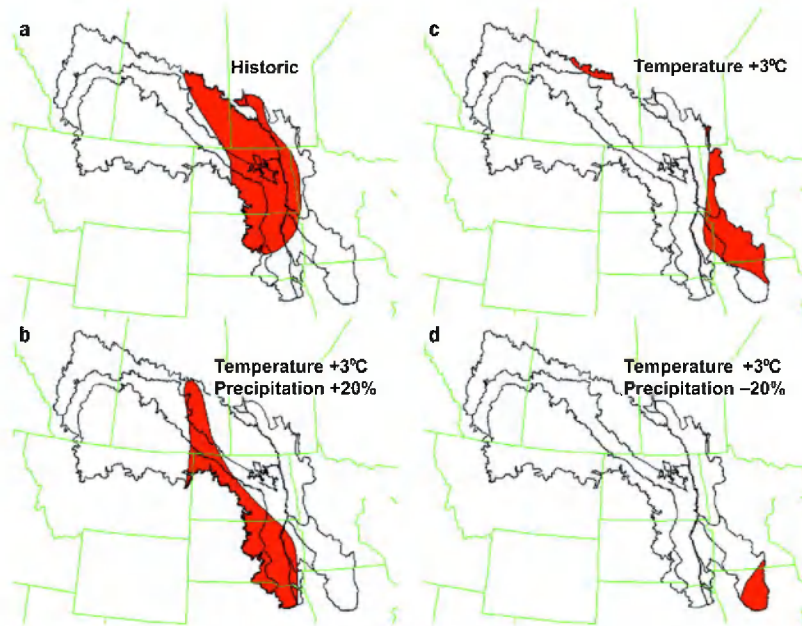
Note: Panels a–d (from Johnson et al. 2005) show the simulated occurrence of highly favorable water and cover conditions for waterfowl breeding across the PPR under historic (a) and alternative future (b–d) climatic conditions. Panel e (from Hoekman et al. 2002 and Mills 2007) shows that activities on the breeding grounds are the primary drivers of population dynamics in waterfowl, explaining approximately 90 percent of the population growth rate (λ). Thus, loss of breeding habitat has a direct connection to population dynamics.

Bighorn Sheep

Bighorn sheep occupy discontinuous habitats at climatic extremes in desert mountains and canyons and in alpine areas of higher mountain ranges (Epps et al. 2004). Consequently, bighorn sheep commonly exist in numerous relatively small subpopulations (many numbering fewer than 100) that are notably vulnerable to extinction. Changes in the distribution of desert bighorn sheep in the 20th century (shifts to areas of higher elevation and greater precipitation) are consistent with climate change. Management will need to address the factors, including disease and infrastructure development, that will make corridors and crucial habitats increasingly impermeable and inevitably limit the species' ability to further shift its range and survive climate change.

Amphibians

Global amphibian declines across multiple taxa are known to be driven by a plethora of interacting human-caused factors, including pathogens, exotic species, pollution, habitat destruction, and ultraviolet radiation (Biek et al. 2002; Lips et al. 2008). Climate change can both exacerbate these stressors (for example by facilitating the spread of pathogens and exotic species) and act directly on amphibians by affecting development and skin moisture (McMenamin et al. 2008). Three main pathways are captured in Figure 15. First, temperature and moisture changes can alter developmental timing and phenology, which leads to a mismatch between life history stages and environmental conditions and can decrease survival and reproductive success (e.g., Reading 2007). Second, desiccation can prevent spawning, kill tadpoles when ponds dry, and cause terrestrial amphibians (many with semipermeable skin) to be more vulnerable to desiccation mortality. Third, temperature and moisture changes can encourage pathogens (native and exotic) that kill amphibians as well as invasive competitors and predators, such as bullfrogs.

Although the potential to move (or shift geographic range) may be more limiting for amphibians than for other species, adaptation via plasticity and evolutionary change can occur within limits. For example, evolutionary changes in thermal tolerance, temperature-specific development rate, and thermal preference have been shown for the frog *Rana sylvatica* (Skelly et al. 2007).

Figure 15. Direct Avenues for Climate Change Effects on Amphibian Populations
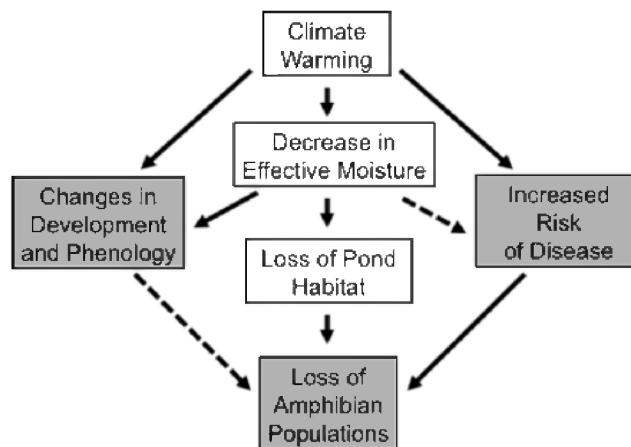
Source: McMenamin et al. 2008.

Infectious Disease Organisms

Infectious disease organisms are a focal group of species that will be greatly affected by climate change and that strongly interact with, and influence the size of, plant and animal populations. For example, increased temperature, humidity, and rainfall generally accelerate parasite life cycles and improve pathogen survival (Harvell et al. 2002). New species interactions, caused by wildlife range shifts in response to warming (Parmesan and Yohe 2003), will lead to new disease exposures (Brooks and Hoberg 2007), and latitudinal and altitudinal shifts in insect vectors will bring a suite of new diseases (Kovats et al. 1999).

Adaptation Options

Only limited opportunities for adaptation choices exist in natural ecosystems compared with agricultural lands as relatively little active management occurs in natural ecosystems, and the complexity of autecological responses and alternative stressors is extremely daunting. For national parks and national wilderness areas, many potential options are not viable because of the semiwild land management status these lands are under. Implementation of any active management actions will probably require fossil fuel inputs, potentially adding to the greenhouse gases that are proximate drivers of climate change.

The following ideas may be controversial, but we offer them to begin a candid discussion of all available options. We are not offering these ideas as recommendations, but rather as talking points.

Water Management

The decline in the duration and extent of western mountain seasonal snowpacks will have progressively detrimental effects on the arid West. One option for adaptation for stream systems may be to develop thousands of small high-mountain water storage reservoirs in the upper cirques of the mountains just below the snowline. This activity was common in the 1800s, where small dams, often only one to two meters high, were built with horses to retain snowmelt for summer stream flow. A modern equivalent of tiny *pico-dams*—impounding areas of only a few hectares—may be worth considering. Slow release of the impounded water from these pico-dams would mimic the snowmelt that in the past has extended into the midsummer, providing stream flow all summer long. The downside of this approach would be the loss of many high-mountain meadows and timberline ecosystems, many of which would not benefit at all from the increased water availability and would be damaged by construction activity. Also, great resistance by the public can be expected if heavy machinery is brought into pristine alpine areas.

The only other option to retaining more water in western ecosystems in an aridifying climate trend would be to substantially reduce municipal water needs and agricultural irrigation demands. This option runs headlong into historical water rights and water law. One thread of logic may be that water rights were granted under the expectation of a stationary climate and resulting hydrologic balance, which now no longer exist. Future execution of water rights must acknowledge the fact that in the western United States streamflows are declining and in all likelihood will continue to decline for the rest of this century.

Although the above ideas are relevant to western water-limited ecosystems that are expected to become more arid, other parts of the country are expected to deal with more intense precipitation periods and flooding. Ecosystems of the Southeast are typically well hydrated and not very stress tolerant. When a drought occurs, as in summer 2008, ecosystem stress and water shortages rapidly develop, yet few water conservation measures are in place. A primary adaptation option to address these events will be to protect and enhance riparian ecosystems and wetlands as hydrologic buffers and system capacitors.

Vegetation Management

Adaptations for natural forest and range vegetation management seem to involve either planting or cutting. The USDA Forest Service is already beginning to plant more southern ecotypes of trees on the lands that are being manually replanted. Although there is some risk of getting "ahead" of the climate, much of the genetic variation in western trees revolves around cold hardiness dormancy timing and frost tolerance. Low daily temperatures are increasing faster than high temperatures. However, autumn temperatures are not increasing as fast as springtime temperatures; therefore, this approach does run some risk for frost damage from early autumn freezes.

Invasive species are reducing the preferred vegetation productivity of many western lands. These invasives are being triggered more by land-use patterns and human disruption than by climate change. However, as climate change stresses natural ecosystems, it is possible that invasive plant species, which often are more mobile than native plants, will increase. In some situations there may be opportunities for biofuel harvest of some of these invasives that could also help restore the native ecosystems.

As discussed above, large-scale insect epidemics and large-scale wildfire is also increasing dramatically in western natural ecosystems. The primary proactive adaptation to these problems is more active forest (and rangeland) thinning and vegetation harvesting. The only real hope of slowing forest epidemics and wildfire is to have significantly less stressed forests of lower density, mimicking pre–fire suppression ecosystems. Most forests naturally grow to a condition of high stem density, as each individual tree tries to survive and grow. (Although a judgment of "overstocking" must be tempered by the realization that certain species, such as snowshoe hares, rely on such stands). The classic natural thinning of developing forest stands illustrates that, at a young age, most forests have too many trees, many of which then naturally must die out as the stand grows. A newly regenerating forest may have more than 10,000 trees per hectare, yet by maturity the stand will have only 500 trees per hectare. An aridifying climate reduces still further the natural *carrying capacity of leaf area* that an ecosystem can support. Currently, much of our western forest land is carrying too much leaf area, so is undergoing the kind of stress that allows insect epidemics and wildfire as natural thinning agents. If humans do not like this mechanism of natural thinning, we will have to replace it with human-driven thinning.

The economic viability of this type of new forest management may be dramatically improved if cellulosic biofuels or biofuel-driven electric power generators become economically viable. Options like replacing oil- and gas-fueled heating systems in public buildings with wood-fueled boilers can be very viable in some places with ample local wood resources. The USDA Forest Service Fuel for

Schools program is an example of an attempt to solve the problem of wildland fire fuel reduction with an opportunity to replace fossil fueled heating with biomass heating for local schools. New estimates are that 5 percent of United States energy production could be sustainably produced by Advanced Wood Combustion facilities that already are operating in Austria (deb Richter Jr. et al 2009). If, in the future, any cellulosic material in a natural ecosystem has biofuel value, more carefully conducted thinning and restoration may be financially viable. Different tree and shrub species of different ages and sizes, dead or alive, which often have variable or no value, could have value as biofuels and could pay for more all-inclusive restoration forestry. The net carbon balance of restoration harvesting from natural forest stands is preferable to agriculturally produced biofuels that might require fertilizing, irrigation and pesticides. (Groom et al 2008).

However, for a new generation of restoration forestry to be acceptable by the public, forest harvest operations will need to leave the landscape much more natural in appearance and connected to the ecological effects on focal wildlife species. Extensive road systems, square-cutting units to property boundaries, visible stumps after harvest, and residual slash all caused the public not to support traditional logging that also had negative direct effects on a range of wildlife species, and encouraged the establishment of invasive plant species. Very careful tree harvesting is possible, but takes more time and specialized more mobile and lighter weight equipment, thus costing more money.

Manage for Resilience

More than a century of ecological research on ecosystem responses to biotic and abiotic conditions has made clear that the effects of climate change can only be understood in synergy with other human-caused stressors, including habitat fragmentation, roads, urbanization, and disease. The waterfowl example, in particular, centers on the fact that ducks have for millennia dealt with drought conditions by moving to other wetlands; however, the plowing under of those alternative sites in the PPR interacts with climate change to leave few avenues for mediation. If, however, the spatial heterogeneity in wetland availability could be restored, then a much wider range of plastic responses are available to waterfowl under climate change, thus facilitating adaptation. In short, synergistic interactions between climate change and other human-caused stressors increase uncertainty and complicate actions to mediate climate change effects. But they also offer a substantial avenue for mediation because amelioration of these other stressors will increase resilience by promoting the ability of species to adapt to climate change.

Because species responses to climate change are and will be largely idiosyncratic, managing for resilience will require a focal-species approach (Mills 2007). Some categories of focal species that might make the most appropriate targets for reducing interacting anthropogenic factors would include: (a) highly vulnerable species ("canaries in the coal mine"), (b) species with a high public profile, (c) data-rich species, and (d) strongly interacting species (keystone and dominant species).

Facilitate Connectivity and Consider Assisted Colonization

Managing land to facilitate the movement of focal species beyond their current occupied range will preserve options for the species to adjust their geographic ranges and movement patterns under climate change. Large, contiguous, intact wildland regions, such as the Crown of the

Continent in Montana (incorporating Glacier National Park, Waterton Lakes National Park in Canada and the Bob Marshall and Scapegoat Wilderness Areas) provide large gradients of elevation and bioclimatic niches for species movement. However, even in human-dominated ecosystems, natural regions of parkland and riparian ecosystems may be critical for facilitating connectivity.

At the extreme, if no options exist for organisms to disperse or migrate on their own, managers may need to consider *assisted colonization* (Hoegh-Guldberg et al. 2008). These translocations would include both movements among currently occupied populations, as well as introductions from extant populations into unoccupied habitat within the species' broad geographic ranges. Intentional translocations via assisted colonization carry high cost and logistical challenges, as well as risks: ecological disasters from introductions are well-known, and translocations among different locally adapted genotypes can have unexpected negative effects on genetic structure. On the other hand, an assisted introduction can facilitate a climate change–induced range shift when the movement pathway is blocked, and assisted colonization from one population to another may increase adaptive genetic variation to respond to climate change in the receiving population.

Directed Evolution of Native Animals

Given the likelihood that the animals that will prosper in a changed climate are likely to be those species that humans consider to be invasive, pests, or overabundant, managers may need to consider a role for directed evolution. In essence, directed evolution would involve human-mediated facilitation or acceleration of evolutionary adaptation to climate change. Individuals displaying favorable traits for adapting to climate change would be identified from the field, or perhaps as last resort from captive breeding, and their differential reproductive success would be assisted. In so doing, successful genes for adaptation to climate change would be propagated faster, and more successfully, than might happen without human assistance. On one hand, directed evolution may be the only bridge to sustain native animal species of concern against the flood of better-adapted, more evolutionarily dynamic invasive and pest species. Furthermore, such a strategy is little more than the familiar process used in agricultural crops and animals for thousands of years; it is analogous to the suggestion above that the USDA Forest Service should plant more southern ecotypes in manual replanting programs. On the other hand, in addition to the severe biological and logistical uncertainties and hurdles, a proposal for a directed evolution program for wild animals would probably ignite a firestorm of debate on ethical and philosophical challenges.

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