Developments in Environmental Science, Volume 8
A. Bytnerowicz, M. Arbaugh, A. Riebau and C. Andersen (Editors)

ISSN: 1474-8177/DOI:10.1016/S1474-8177(08)00015-6

Chapter 15

Global Warming and Stress Complexes in Forests of Western North America

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Abstract

A warmer climate in western North America will likely affect forests directly through soil moisture stress and indirectly through increased extent and severity of disturbances. We propose that *stress complexes*, combinations of biotic and abiotic stresses, compromise the vigor and ultimate sustainability of forest ecosystems. Across western North America, increased water deficit will accelerate the normal stress complex experienced in forests, which typically involves some combination of multi-year drought, insects, and fire. Four examples suggest how stress complexes are region-specific. Symptoms of prolonged drought and insects are currently manifested in extensive dieback of pine species in the pinyon-juniper forest of the American Southwest, an area where only a few tree species can survive. Air pollution and high stand densities from fire exclusion have compromised mixed-conifer forests of the Sierra Nevada. Bark beetles are proliferating and killing millions of hectares of dry forest in the northern interior of western North America, setting up the prospect of large and intense fires. Fire and insect mortality have also exceeded previously recorded levels in both interior and south-central Alaska, possibly precipitating extensive ecosystem changes, while extensive permafrost degradation is causing other changes. Increases in fire disturbance superimposed on forests with increased stress from drought and insects may have significant effects on growth, regeneration, long-term distribution and abundance of forest species, and short- and long-term carbon sequestration. The effects of stress complexes will be magnified given a warming climate.

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15.1. Introduction

Forests are rarely at dynamic equilibrium. Succession occurs even in relatively constant climate, punctuated by disturbance episodes that may or may not be associated with climatic variability. The principal disturbance regimes of western North America, wildfire and insect outbreaks, respond to short-term weather and annual decadal cycles in climate. For example, synchronous fire years are associated with the El Niño Southern Oscillation (ENSO) cycle in the Southwest and southern Rocky Mountains (Swetnam & Betancourt, 1998; Veblen et al., 2000), though less so in Oregon and Washington (Hessl et al., 2004). In higher-severity fire regimes, short-term weather anomalies associated with atmospheric blocking ridges of high pressure are responsible for extreme wildfire years (Gedalof et al., 2005; Johnson & Wowchuk, 1993; Skinner et al., 1999). Outbreaks of insect defoliators are associated with years of high vegetation productivity (Swetnam & Lynch, 1993; Weber & Schweingruber, 1995), whereas cambium feeders such as bark beetles are associated with drought years, in which tree defenses are compromised (Ferrell, 1996; Swetnam & Betancourt, 1998).

Steadily increasing global temperatures are expected to change the frequency, severity, and extent of natural disturbances (Littell, 2006; McKenzie et al., 2004; Westerling et al., 2006). Recently, hot dry conditions have led to large wildfires such as the Biscuit Fire (2002) in southwestern Oregon, the Hayman Fire (2002) on the Colorado Front Range, the Cerro Grande Fire (2000) in northern New Mexico, the Cedar Fire (2003) in southern California, and the complex of fires in interior Alaska (2004). Similarly, bark beetles, whose life cycles are accelerated by increased temperatures, particularly winter minima, are causing extensive mortality across the West (Logan et al., 2003; Swetnam & Betancourt, 1998; Veblen et al., 1991). Fire and insect disturbance clearly interact, often synergistically, compounding rates of change in forest ecosystems (Veblen et al., 1994). For example, fire severity in subalpine forests, though usually associated with weather anomalies, can be altered by a combination of bark beetles and annual-scale drought (Bigler et al., 2005). A third factor, air pollution, is not so much a function of increasing temperatures as of anthropogenic emissions, principally from vehicle use and industrial sources. However, in a warming climate, pollution acts as an additional stressor interacting synergistically with insects and fire.

In a warming climate, what will be the effects of increasing disturbance on forest ecosystems? Will disturbances act synergistically, and in conjunction with direct climatic stress (e.g., drought), air pollution, and perhaps pathogens and invasive species, to cause rapid or irreversible changes, or both, in species composition and ecosystem function? In this chapter we refer to these interacting stresses as *stress complexes* and suggest how they may bring about rapid ecosystem changes in a warming climate, using four examples that span a latitudinal gradient from the American Southwest to interior Alaska. We conclude by identifying challenges for land management and suggest potential adaptive strategies that may be of value when changes in stress complexes are not too abrupt or severe.

15.2. Models of stress complexes

15.2.1. The environmental niche space

Climate provides an overarching control on the distribution of tree species (Woodward, 1987; Woodward & McKee, 1991), in that species do not establish or persist outside a characteristic bioclimatic ‘‘envelope’’, sometimes referred to as the *fundamental niche* (Pearson & Dawson, 2003). Within the fundamental niche, areas of bioclimatic suitability are often identified probabilistically by either gradient modeling or machine-learning methods (Franklin, 1995; Cushman et al., 2007; Guisan & Zimmermann, 2000; McKenzie et al., 2003). Gradient modeling with carefully chosen predictor variables can identify specific limiting factors, where in a species’ range they are most operative, and how they change among species (Cushman et al., 2007). For example, in the Pacific Northwest, USA, mountain hemlock (*Tsuga mertensiana*) growth is limited by winter snowpack at high elevations in the northern part of its range but limited by summer moisture in the southern part (Peterson & Peterson, 2001).

Climate-induced stress occurs in low-suitability areas within a species’ fundamental niche, and as a consequence, shifts in climatic regime lead to compositional changes. In forests with long-lived dominant species, compositional changes could be slow even in a rapidly warming climate, because mature individuals can survive at the edges of their ranges. Disturbance is therefore expected to be the principal agent of change, operating at shorter time scales than the direct influences of climate (Fig. 15.1; McKenzie et al., 2004).

15.2.2. Energy- and water-limited systems

Climatic limiting factors operate mechanistically through the interface between organisms and their environment. Plant performance is

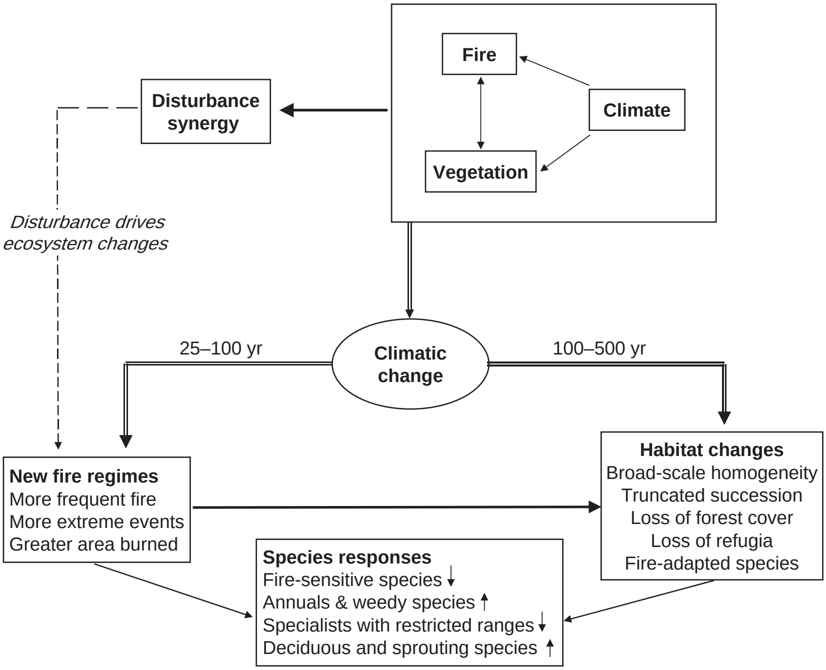

Figure 15.1. Conceptual model of the relative time scales for disturbance versus climatic change alone to alter ecosystems. Times are approximate. (Adapted from McKenzie et al., 2004.)

compromised when one or more resources (e.g., light/energy, water, nutrients) is limited. At broad scales, forests of western North America can be partitioned into energy-limited versus water-limited domains (Littell, 2006; Littell & Peterson, 2005; McKenzie et al., 2003; Milne et al., 2002). Energy-limiting factors are chiefly light (e.g., productive forests where competition reduces light to most individuals) and temperature (e.g., high-latitude or high-elevation forests). Tree growth in energy-limited ecosystems appears to be responding positively to warming temperatures over the past 100 years (McKenzie et al., 2001).

In contrast, productivity in water-limited systems is expected to decline with warming temperatures, as negative water balances constrain photosynthesis across more of the West (Hicke et al., 2002), although this may be partially offset if CO_2 fertilization significantly increases water-use efficiency in plants (Neilson et al., 2005). For example, Littell (2006) found that most montane Douglas-fir (*Pseudotsuga menziesii*) forests across the northwestern United States appear to be water-limited; under current climate projections these limits will increase in both area affected and magnitude, because temperatures are expected to increase while there is much uncertainty about precipitation and no indication of a trend (IPCC, 2007).

Limiting factors can of course shift within a species range (Peterson & Peterson, 2001), or between seasons, as water demands abate and energy needs increase (Stephenson, 1990, 1998). For example, in high-elevation or high-latitude arid forests (e.g., eastern slopes of the Sierra Nevada, Rocky Mountain Front Range, interior boreal spruce), short growing seasons limit energy inputs, but drought stress still occurs in summer.

15.3. Stress complexes and warmer climate

Temperature increases predispose forest ecosystems of western North America to often lethal stresses, acting both directly through increasingly negative water balances (Littell, 2006; Milne et al., 2002; Stephenson, 1998) and indirectly through increased frequency, severity, and extent of disturbances, chiefly fire and insect outbreaks (Logan et al., 2003; McKenzie et al., 2004). Here, we briefly present four examples of forest ecosystems whose species composition and stability are currently compromised by stress complexes precipitated by the recent period of warm dry weather. Two cases involve the loss of a single dominant species; the other two involve two or more dominant species.

15.3.1. Pinyon-juniper woodlands of the American Southwest

Pinyon pine (*Pinus edulis*) and various juniper species (*Juniperus* spp.) are among the most drought-tolerant trees in western North America. As such, pinyon-juniper ecosystems characterize lower treelines across much of the West. Although pinyon-juniper woodlands appear to be expanding in some areas, possibly due to fire suppression or cessation of Native American fuelwood harvesting (Samuels & Betancourt, 1982), they are clearly water-limited systems. At fine scales, pinyon-juniper ecotones are sensitive to feedbacks both from environmental fluctuations and existing canopy structure that may buffer trees against drought to some degree (Milne et al., 1996). Periodically, however, severe multi-year droughts cause massive dieback of pinyon pines, overwhelming any local buffering.

Dieback of pine species—both ponderosa and pinyon pine—occurred during and before the 20th century (Allen & Breshears, 1998; Breshears et al., 2005), but the current dieback is massive (Fig. 15.2), and its combination of low precipitation and high temperatures, indicative of global warming, is unprecedented (Breshears et al., 2005). Ecosystem

Figure 15.2. Massive dieback of pinyon pine in the Jemez Mountains, New Mexico. (Photo courtesy of Craig Allen, U.S. Geological Survey.)

change, possibly irreversible, comes from large-scale severe fires that lead to colonization of invasive species that further compromises the ability of pinyon pines to re-establish. This stress complex is illustrated in Fig. 15.3.

15.3.2. Mixed-conifer forests of the Sierra Nevada and southern California

These forests experience a Mediterranean climate. Summers are dry and long, with significant precipitation beginning around mid-October through most of the Sierra Nevada and later in the San Bernardino and San Gabriel Mountains of southern California. Increasing temperatures since 1850 contrast with a relatively cool (and dry) period from 1650 to 1850 (Briffa et al., 1992; Graumlich, 1993; Stine, 1996). Fire frequency and extent have not increased concomitantly with warmer temperatures (McKelvey et al., 1996), rather they have decreased to their lowest levels in the last 2000 years (Stine, 1996; Swetnam, 1993). Stine (1996) attributes this to decreased fuel loads from sheep grazing and decreased ignition from the demise of Native American cultures, leading to fire exclusion. Fire exclusion subsequently led to increased fuel loadings (McKelvey et al., 1996) and competitive stresses on individual trees as stand densities have increased (Ferrell, 1996; van Mantgem et al., 2004).

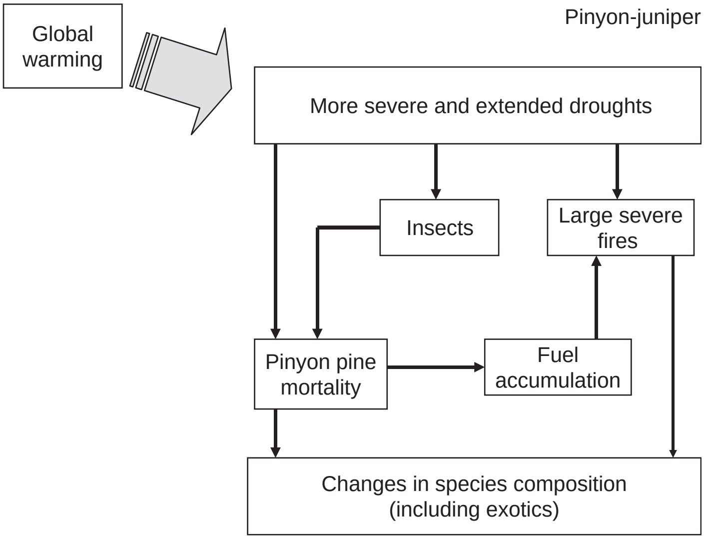

Figure 15.3. Stress complex in pinyon-juniper woodlands of the American Southwest. The effects of disturbance regimes (insects and fire) are exacerbated by global warming. Stand-replacing fires and drought-induced mortality both contribute to species changes and exotic invasions.

Elevated levels of ambient ozone (Fig. 15.4) have affected plant vigor in the Sierra Nevada and the mountains of southern California (Byternowicz & Grulke, 1992; Miller, 1992, 1996; Peterson & Arbaugh, 1988; Peterson et al., 1991). Ozone reduces net photosynthesis and growth (Peterson et al., 1991; Reich & Amundson, 1985), and ozone from vehicular and industrial sources in urban environments often concentrates at middle and upper elevations (Brace & Peterson, 1998) where mixed-conifer forests occur.

Sierra Nevada forests support endemic levels of a diverse group of insect defoliators and bark beetles, but bark beetles in particular have reached outbreak levels in recent years facilitated by protracted droughts (Ferrell, 1996). Ferrell (1996) refers to *biotic complexes* where bark beetles interact with root diseases and mistletoes. Dense stands, fire suppression, and new pathogens such as white pine blister rust (*Cronartium ribicola*) exacerbate both biotic interactions (van Mantgem et al., 2004) and drought stress. Figure 15.5 shows the stress complex associated with Sierra Nevada forest ecosystems, which is also likely applicable to the mountain ranges east and north of the Los Angeles basin. High stand densities and ozone generate more stress pathways than in the

Figure 15.4. Photochemical haze over Sequoia National Park, California, in October 2003. (Photo by Don McKenzie.)

southwestern pinyon-juniper complex, wherein drought, insects, and fire are the principal stressors.

15.3.3. Interior lodgepole pine forests

Lodgepole pine (*Pinus contorta* var. latifolia) is widely distributed across western North America. It is the dominant species over much of its range, forming nearly monospecific stands that are maintained either because poor soils preclude other species or through adapting to stand-replacing fires via cone serotiny (USDA, 1990). Lodgepole pine is the principal host of the mountain pine beetle (*Dendroctonus ponderosae*), and monospecific stands are vulnerable to massive mortality during beetle outbreaks.

Recent beetle outbreaks have caused extensive mortality across millions of hectares in western North America (Fig. 15.6; Logan & Powell, 2001), with large mature cohorts (age 70–80 yr) contributing to widespread vulnerability (Carroll, 2006). Warmer temperatures facilitate insect outbreaks in two ways: (1) drought stress makes trees more vulnerable to attack and (2) insect populations respond to increased temperatures by speeding up their reproductive cycles (e.g., to 1-year life

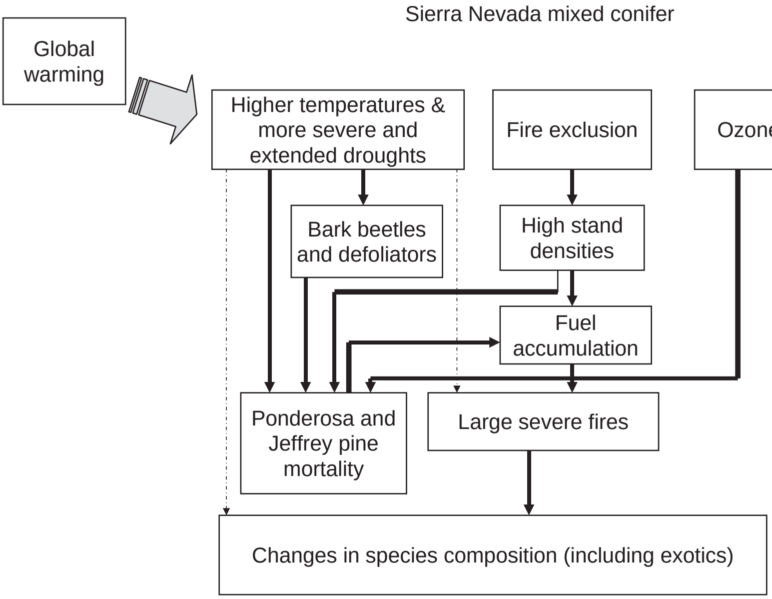

Figure 15.5. Stress complex in Sierra Nevada and southern Californian mixed-conifer forests. The effects of disturbance regimes (insects and fire) and fire exclusion are exacerbated by global warming. Stand-replacing fires and drought-induced mortality both contribute to species changes and exotic invasions.

cycles; Logan & Bentz, 1999; Logan & Powell, 2001; Werner & Holsten, 1985). Warming temperatures would be expected to exacerbate these already devastating outbreaks northward and even eastward across the continental divide (Logan et al., 2003, but see Hicke et al., 2006), but even at current levels of recent mortality lodgepole pine ecosystems may be poised for significant changes.

Figure 15.7 shows the stress complex for interior lodgepole pine forests. Warmer temperatures in combination with the greater flammability of dead biomass associated with beetle mortality sets up these ecosystems for extensive species conversion following stand-replacing fires plus a favorable environment for the establishment of species adapted to warmer temperatures, such as interior Douglas-fir or even ponderosa pine.

15.3.4. Alaskan forests

The state of Alaska has experienced massive fires in the last decade (Fig. 15.8), including the five largest fires in the United States (NIFC, 2006).

Figure 15.6. Massive lodgepole pine mortality from mountain pine beetles in south-central British Columbia, Canada. (Photo courtesy of Alan Carroll, Canadian Forest Service.)

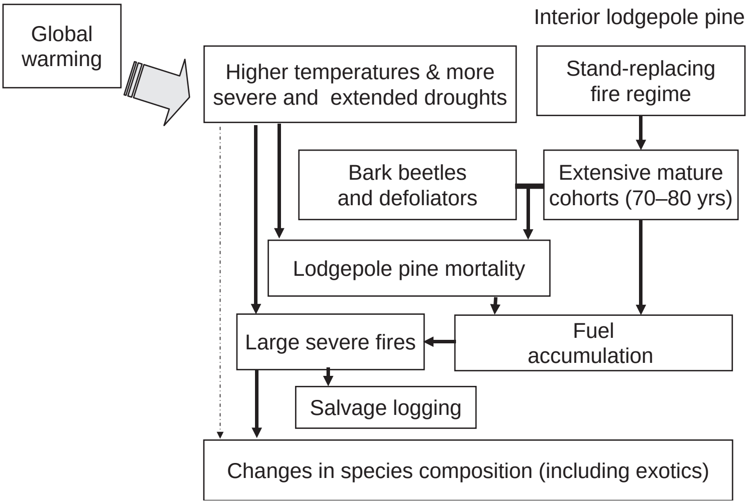

Figure 15.7. Stress complex in interior lodgepole pine forests (British Columbia and USA). The effects of disturbance regimes (insects and fire) are exacerbated by global warming. Stand-replacing fires, beetle mortality, and changes in environmental niche space contribute to species changes.

Over 2.5 million ha burned in the interior in 2004. Concurrently (1990s), massive outbreaks of the spruce bark beetle (*Dendroctonus rufipennis*) occurred on and near the Kenai Peninsula in south-central Alaska (Figs. 15.8, 15.9; Berg et al., 2006). Although periodic outbreaks have occurred throughout the historical record, both in south-central Alaska and the southwestern Yukon, these most recent outbreaks may be unprecedented in extent and percentage mortality (over 90% in many places; Berg et al., 2006; Ross et al., 2001).

Both these phenomena are likely associated with warmer temperatures in recent decades (Berg et al., 2006; Duffy et al., 2005; Werner et al., 2006). Summer temperatures in the Arctic have risen 0.3–0.4 °C per decade since 1961 (Chapin et al., 2005). Although fire-season length in interior Alaska is associated with the timing of onset of the late-summer monsoon, the principal driver of annual area burned is early summer temperature (Duffy et al., 2005). As with lodgepole pine, warmer temperatures have the same twofold effect on beetle outbreaks in spruce forests.

Disturbance regimes place unequal competitive stress on species most vulnerable to the particular disturbance. In the interior, conifer species—white spruce and black spruce (*Picea mariana*)—are more flammable than their sympatric deciduous species (chiefly paper birch (*Betula papyrifera*)). Similarly, conifers are the target of bark beetles, so in south-central Alaska they will be disadvantaged compared to deciduous species.

Permafrost degradation is widespread in central Alaska, shifting ecosystems from birch forests to wetland types such as bogs and fens (Jorgensen et al., 2001; T. Boucher, personal communication). The expected gain in area of deciduous forests from fire and insect mortality may be offset by the loss from permafrost degradation. If broad-scale water balances become increasingly negative, peatlands may begin to support upland forest species (Klein et al., 2005). Fire could play a major role in accelerating this ecosystem change by preparing seedbed for both conifer and deciduous tree species.

Figure 15.10 shows the stress complex for Alaska forest ecosystems, predicting a significant transition to deciduous life forms via more frequent and extensive disturbance associated with global warming, offset by the expected loss of some deciduous forests from permafrost degradation (Jorgensen et al., 2001), and subsequent or simultaneous potential conversion of peatlands to forests. These transitions would be unlikely without changes in disturbance regimes even under global warming, because both empirical and modeling studies suggest that warmer temperatures alone will not favor a life-form transition except in the case of permafrost loss (Bachelet et al., 2005; Boucher & Mead, 2006; Johnstone et al., 2004).

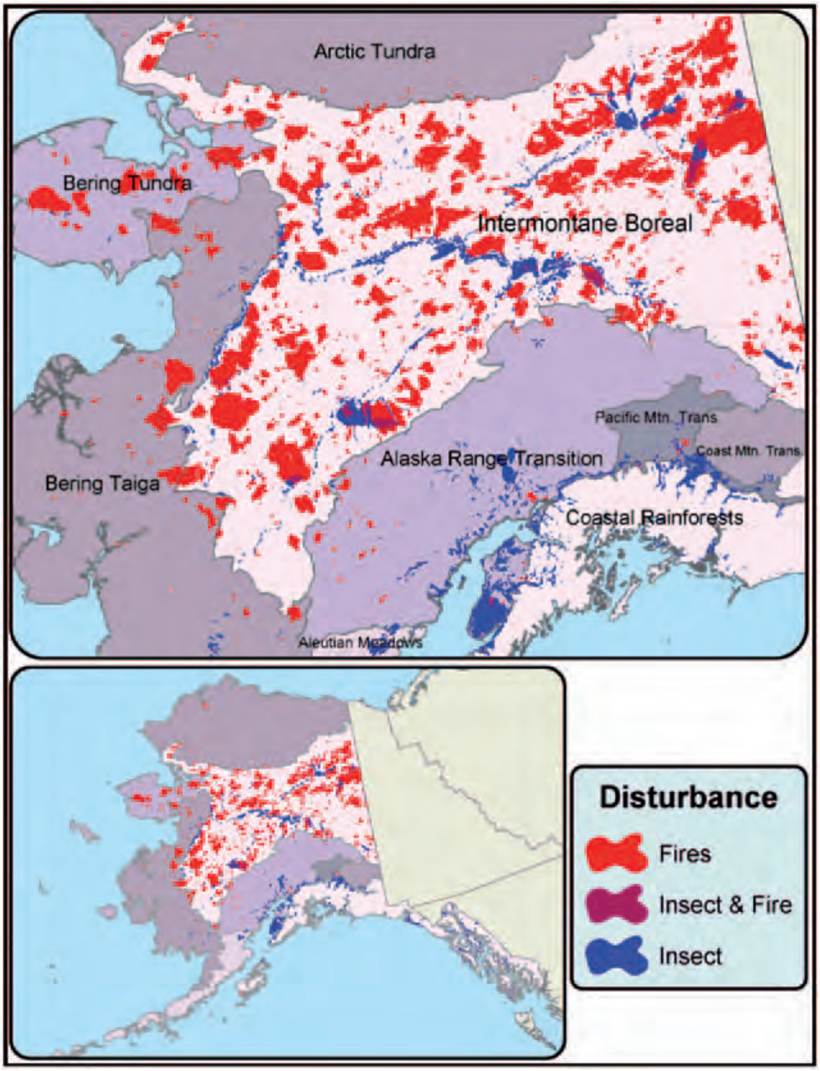

Figure 15.8. Recent wildfire and insect activity in Alaska. (Data from the Alaska Fire Service.)

15.4. Discussion

Rapid climatic change and qualitative changes in disturbance regimes may send ecosystems across thresholds into dominance by different life

Figure 15.9. Nearly complete stand mortality of white spruce (*Picea glauca*) from spruce bark beetle on the Kenai Peninsula, Alaska. (Photo courtesy of Diana Olson, USDA Forest Service.)

forms and significant changes in productivity and capacity for carbon storage. For example, in the Southwest, stand-replacing fires are becoming common in what were historically low-severity fire regimes (Allen et al., 2002), and protracted drought is killing species (ponderosa pine) that are adapted to low-severity fire (Allen & Breshears, 1998). If these trends continue, ponderosa pine may be lost from some of its current range in the Southwest, and productivity of these systems will decline. In contrast, if warming temperatures permit doubling of mountain pine beetle reproductive cycles (Logan & Powell, 2001) such that outbreaks are more frequent and more prolonged, lodgepole pine might be replaced by a more productive species such as Douglas-fir, at least on more mesic sites where conditions for establishment are favorable.

We expect that more ecosystems will become water-limited (Littell, 2006; Milne et al., 2002), more sensitive to variability in temperature, and prone to more frequent disturbance. Consequently, productivity may decline across much of the West (Hicke et al., 2002), and long-term carbon sequestration may be interrupted by an increasing area being subject to high-severity fire and insect-caused mortality. Species and ecosystems will be affected in various ways, and not all undesirable

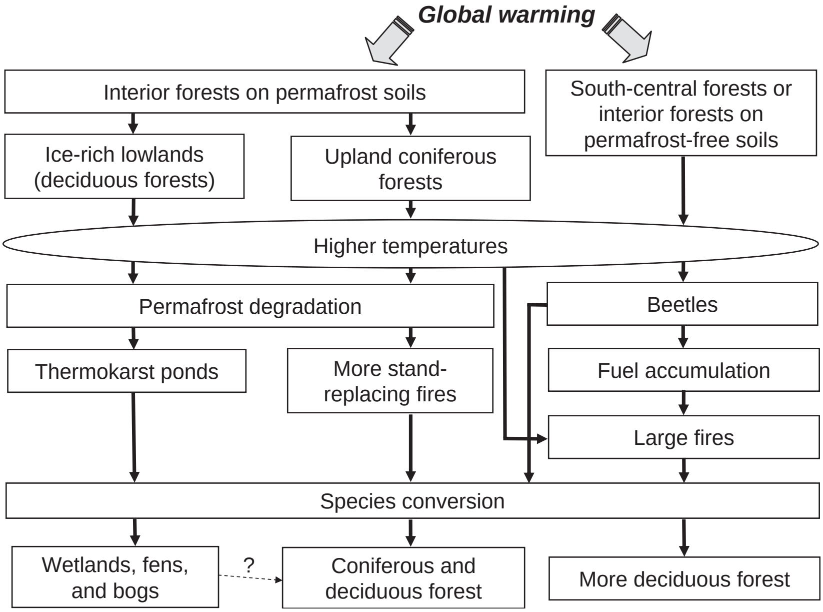

Figure 15.10. Stress complex in the interior and coastal forests of Alaska. Rapid increases in the severity of disturbance regimes (insects and fire) are triggered by global warming. Stand-replacing fires, massive mortality from insects, and permafrost degradation contribute to species changes and conversion to deciduous life forms.

changes will be preventable by management intervention (McKenzie et al., 2004).

The following adaptive strategies, however, may help in maintaining ecosystem resilience in some systems in which changes are not too abrupt or severe, although we caution that they are only suggestions whose value will have to be considered carefully for specific applications.

- *Use nursery stock tolerant to low soil moisture and high temperature*. With most systems moving toward being more water-limited, resistant individuals will be those from the drier and warmer provenances.
- *Use a variety of genotypes in nursery stock*. If we are unable to accurately predict local climatic trends, then the variety of genotypes will help maintain diversity when headed into an uncertain future that may include rapid climatic change.
- *Consider planting mixed-species stands*. This gives forests more ecological amplitude (i.e., the combined bioclimatic envelope is broader) to respond to climatic change.

- *Retain large downed logs on sites to moderate temperature and provide micro-refugia*. As landscape conditions become drier and warmer, interior habitat for mesic species will be lost and sensitive taxa will be more compromised (Carey & Alexander, 2003).

There is no historical or current analogue to the combination of climate conditions, disturbance regimes, and land-use changes expected for the next century. For example, tempering the idea of "desired future conditions" with "achievable future conditions" will facilitate more adaptive management and more efficient allocation of resources to maintain forest resilience. We have taken a small step here toward understanding potential disturbance interactions in forest ecosystems affected by global warming. Robust models are needed that can be tested with either simulation studies or ongoing natural "experiments" (Stephenson et al., 2006) to understand alternative future states in a rapidly changing world.

ACKNOWLEDGMENTS

We thank Constance Millar and Andrzej Byternowicz for providing the initial fora for the presentation of these ideas, and Tina Boucher and Kevin McKelvey for comments that substantially improved the manuscript. Alynne Bayard, Ellen Eberhardt, and Robert Norheim assisted with graphics. This research was funded by the USDA Forest Service, Pacific Northwest Research Station, the USGS Global Change Research Program, and the Joint Institute for the Study of the Atmosphere and Ocean under cooperative agreement NA178RG11232 of the National Oceanic and Atmospheric Administration. This is a contribution of the Western Mountain Initiative.

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