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Global warming and stress complexes in forests of western North America

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Book chapter in press: in Forest Fires and Air Pollution Issues

Editors: Andrzej Bytnerowicz, Michael Arbaugh, Chris Andersen and Al Riebau
Elsevier Ltd.

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.

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 to 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 and 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 (Johnson and Wowchuk 1993, Skinner et al. 1999, Gedalof et al. 2005). Outbreaks of insect defoliators are associated with years of high vegetation productivity (Swetnam and Lynch 1993, Weber and Schweingruber 1995), whereas cambium feeders such as bark beetles are associated with drought years, in which tree defenses are compromised (Ferrell 1996, Swetnam and Betancourt 1998).

Steadily increasing global temperatures are expected to change the frequency, severity, and extent of natural disturbances (McKenzie et al. 2004, Littell 2006, 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 (Veblen et al. 1991, Swetnam and Betancourt 1998, Logan and Powell 2001). 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.

Models of stress complexes

The environmental niche space

Climate provides an overarching control on the distribution of tree species (Woodward 1987, 1991), in that species do not establish or persist outside a characteristic bioclimatic “envelope”, sometimes referred to as the *fundamental niche* (Pearson and Dawson 2003). Within the fundamental niche, areas of bioclimatic suitability are often identified probabilistically by either gradient modeling or machine-learning methods (Franklin 1995, Guisan and Zimmerman 2000, McKenzie et al. 2003, Cushman et al. 2007). 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 and 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 (Figure 1 – McKenzie et al. 2004).

Energy- and water-limited systems

Climatic limiting factors operate mechanistically through the interface between organisms and their environment. Plant performance is 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 vs. water-limited domains (Milne et al. 2002, McKenzie et al. 2003, Littell and Peterson 2005, Littell 2006). 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 CO₂ 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 and 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.

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 (Stephenson 1998, Milne et al. 2002, Littell 2006) and indirectly through increased frequency, severity, and extent of disturbances, chiefly fire and insect outbreaks (Logan and Powell 2001, 2006; McKenzie et al. 2004; Skinner et al. 2006). 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.

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 and 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 and Breshears 1998, Breshears et al. 2005), but the current dieback is massive (Figure 2) and its combination of low precipitation and high temperatures, indicative of global warming, is unprecedented (Breshears et al. 2005). Figure 3 shows the stress complex associated with pinyon-juniper ecosystems. Ecosystem 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.

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 (Swetnam 1993, Stine 1996). Stine (1996) attributes this to decreased fuel loads from sheep grazing and decreased ignition from the demise of Native Ameri-

can 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).

Elevated levels of ambient ozone (Figure 4) have affected plant vigor in the Sierra Nevada and the mountains of southern California (Peterson and Arbaugh 1988; Peterson et al. 1991; Bytnerowicz and Grulke 1992; Miller 1992, 1996). Ozone reduces net photosynthesis and growth (Reich and Amundson 1985, Peterson et al. 1991) and ozone from vehicular and industrial sources in urban environments often concentrates at middle and upper elevations (Brace and 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 5 shows the stress complex associated with Sierra Nevada forest ecosystems, and is likely applicable also to the mountain ranges east and north of the Los Angeles basin. High stand densities and ozone generate more stress pathways than in the southwestern pinyon-juniper complex, wherein drought, insects, and fire are the principal stressors.

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 (Figure 6 – Logan and Powell 2001, 2006), 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 cycles – Werner and Holsten 1985, Logan and Bentz 1999, Logan and Powell 2001). Warming temperatures would be expected to exacerbate these already devastating outbreaks northward and even eastward across the continental divide (Logan and Powell 2006, but see Hicke et al. 2006), but even at current levels of recent mortality lodgepole pine ecosystems may be poised for significant changes.

Figure 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, for example interior Douglas-fir or even ponderosa pine.

Alaskan forests

The state of Alaska has experienced massive fires in the last decade (Figure 8), including the five largest fires in the USA (NIFC 2006). 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 (Figures 8 and 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 – Ross et al. 2001, Berg et al. 2006).

Both these phenomena are likely associated with warmer temperatures in recent decades (Duffy et al. 2005, Berg et al. 2006, Werner et al. 2006). Summer temperatures in the Arctic have risen 0.3 – 0.4 deg. 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 two-fold effect on beetle outbreaks in spruce forests (see above).

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 *pers. comm.*). 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 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 (Johnstone et al. 2004, Bachelet et al. 2005, Boucher and Mead 2006).

Discussion

Rapid climatic change and qualitative changes in disturbance regimes may send ecosystems across thresholds into dominance by different life 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 and 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 and 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 (Milne et al. 2002, Littell 2006), 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 changes will be preventable by management intervention (McKenzie et al. 2004). The following adaptive strategies may help maintain 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. Bets based on the previous statement can be hedged, not only because we may guess wrong about local climatic trends but also to 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 and Alexander 2003).

Finally, 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.

References

- Allen, C.D., and D.D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *PNAS* 95:14839-14842.
- Allen, C.D., M. Savage, D.A. Falk, K.F. Suckling, T.W. Swetnam, T. Schulke, P.B. Stacey, P. Morgan, M. Hoffman, and J.T. Klingeli. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications* 12:1418-1433.
- Bachelet, D., J. Lenihan, R. Neilson, R. Drapek, and T. Kittel. 2005. Simulating the response of natural ecosystems and their fire regimes to climatic variability in Alaska. *Canadian Journal of Forest Research* 35:2244-2257.
- Berg, E.E., J.D. Henry, C.L. Fastie, A.D. de Volder, and S.M. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management* 227:219-232.
- Bigler, C., D. Kulakowski, and T.T. Veblen. 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. *Ecology* 86:3018-3029.
- Boucher, T.V., and B.R. Mead. 2006. Vegetation change and forest regeneration on the Kenai Peninsula, Alaska, following a spruce beetle outbreak, 1987-2000. *Forest Ecology and Management* 227:233-246.
- Brace, S., and D.L. Peterson. 1998. Tropospheric ozone distribution in the Mount Rainier region of the Cascade Mountains, U.S.A. *Atmospheric Environment* 32:3629-3637.
- Breshears, D.D., N.S. Cobb, P.M. Rich, K.P. Price, C.D. Allen, R.G. Balice, W.H. Romme, J.H. Kastens, M.L. Floyd, J. Belnap, J.J. Anderson, O.B. Myers, and C.W. Meyer. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences* 102:15144-15148.
- Briffa, K.R., P.D. Jones, and F.H. Schweingruber. 1992. Tree-ring density reconstructions of summer temperature patterns across western North America since 1600. *Journal of Climate* 5:735-754.
- Bytnerowicz, A., and N.E. Grulke. 1992. Physiological effects of air pollutants on western trees. Pages 183-233 in R.K. Olson, D. Binkley, and M. Böhm, eds., *Response of Western Forests to Air Pollution*, Springer-verlag, New York.
- Carey, C., and M.A. Alexander. 2003. Climate change and amphibian declines: is there a link? *Diversity and Distributions* 9:111-121.
- Carroll, A. 2006. Changing the climate, changing the rules: global warming and insect disturbance in western North American forests. Paper presented at the 2006 MTNCLIM conference, Timberline, OR.
- Chapin III, F.S., M. Sturm, M.C. Serreze, J.P. McFadden, J.R. Key, A.H. Lloyd, A.D. McGuire, T.S. Rupp, A.H. Lynch, J.P. Schimel, J. Beringer, W.L. Chapman, H.E. Epstein, E.S. Euskirchen, L.D. Hinzman, G. Jia, C.-L. Ping, K.D. Tape, C.D.C. Thompson, D.A. Walker, J.M. Welker. 2005. Role of land-surface changes in Arctic summer warming. *Science* 28:657-660.

- Cushman, S.C., D. McKenzie, J.S. Littell, and D.L. Peterson. 2007. Climatic change, fire, and ecosystems: a research agenda for landscape modeling. USDA Forest Service Research Paper RMRS-XXX. In press.
- Duffy, P.A., J.E. Walsh, J.M. Graham, D.H. Mann, and T.S. Rupp. 2005. Impacts of large-scale atmospheric-ocean variability on Alaskan fire season severity. *Ecological Applications* 15:1317-1330.
- Ferrell, G.T. 1996. The influence of insect pests and pathogens on Sierra forests. Pages 1177-1192 in *Sierra Nevada Ecosystem Project: final report to Congress, v. II, Assessments and scientific basis for management options*. Davis: University of California, Centers for Water and Wildland Resources.
- Franklin, J. 1995. Predictive vegetation mapping: geographical modeling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography*. 19:474-499.
- Gedalof, Z., D.L. Peterson, and N. Mantua. 2005. Atmospheric, climatic, and ecological controls on extreme wildfire years in the northwestern United States. *Ecological Applications* 15:154-174.
- Graumlich, L.J. 1993. A 1000-year record of temperature and precipitation in the Sierra Nevada. *Quaternary Research* 39:249-255.
- Guisan, A., and N.E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling*. 135:147-186.
- Hessl, A.E., D. McKenzie, and R. Schellhaas. 2004. Drought and Pacific Decadal Oscillation linked to fire occurrence in the inland Pacific Northwest. *Ecological Applications* 14:425-442.
- Hicke, J.A., G.P. Asner, J.T. Randerson, C. Tucker, S. Los, R. Birdsey, J.C. Jenkins, and C. Field. 2002. Trends in North American net primary productivity derived from satellite observations. *Global Biogeochemical Cycles* 16,2,1018, 10.1029/2001GB001550.
- Hicke, J.A., J.A. Logan, J.A. Powell, and D.S. Ojima. 2006. Changes in temperature influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *JGR Biogeosciences. Journal of Geophysical Research Volume III* G02019, doi:10.1029/2005JG000101.
- IPCC (Intergovernmental Panel on Climate Change). 2007. *Climate Change 2007: the Physical Science Basis. Summary for policymakers*. <http://www.ipcc.ch> accessed 23 February, 2007.
- Johnson, E.A., and D.R. Wowchuk. 1993. Wildfires in the southern Canadian Rocky Mountains and their relationships to mid-tropospheric anomalies. *Canadian Journal of Forest Research* 23:1213-1222.
- Johnstone, J.F., F.S. Chapin III, J. Foote, S. Kemmett, K. Price, and L. Viereck. 2004. Decadal observations of tree regeneration following fire in boreal forests. *Canadian Journal of Forest Research* 34:267-273.
- Jorgensen, M.T., C.H. Racine, J.C. Walters, and T.E. Osterkamp. 2001. Permafrost degradation and ecological changes associated with a warming climate in central Alaska. *Climatic Change* 48: 551-579.
- Klein, E., E.E. Berg, and R. Dial. 2005. Wetland Drying and succession across the Kenai Peninsula Lowlands, south-central Alaska. *Canadian Journal of Forest Research* 35:1931-1941.

- Littell, J.S. 2006. Climate impacts to forest ecosystem processes: Douglas-fir growth in north-western U.S. mountain landscapes and area burned by wildfire in western U.S. eco-provinces. Ph.D. dissertation, University of Washington, Seattle. 171 p.
- Littell, J.S. and D.L. Peterson. 2005. A method for estimating vulnerability of Douglas-fir growth to climate change in the northwestern US. *Forestry Chronicle* 81:369-374.
- Littell, J.S., D. McKenzie, and D.L. Peterson. 2006. Climate and area burned by fire in eco-provinces of the western U.S., 1916-2003. *Ecological Applications*, *in review*.
- Little, E.L., Jr., 1971, Atlas of United States trees, volume 1, conifers and important hardwoods: U.S. Department of Agriculture Miscellaneous Publication 1146, 9 p., 200 maps.
- Logan, J.A., and B.J. Bentz. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. *Environmental Entomology* 28:924-934.
- Logan, J.A., and J.A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47:160-172.
- Logan, J.A., J. Regniere, and J.A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers of Ecology and the Environment* 1:130-137.
- Logan, J.A., and J.A. Powell. 2006. Ecological consequences of climate change altered forest insect disturbance regimes. In F. H. Wagner (ed.), *Climate change in western North America: evidence and environmental effects*. Allen Press (in review).
- McKelvey, K.S., C.N. Skinner, C. Chang, D.C. Etman, S.J. Husan, D.J. Parsons, J.W. van Wag-tendonk, and C.P. Weatherspoon. 1996. An overview of Fire in the Sierra Nevada. Pages 1033-1040 in *Sierra Nevada Ecosystem Project: final report to Congress, v. II, Assessments and scientific basis for management options*. Davis: University of California, Centers for Water and Wildland Resources.
- McKenzie, D., A.E. Hessler, and D.L. Peterson. 2001. Recent growth in conifer species of western North America: assessing the spatial patterns of radial growth trends. *Canadian Journal of Forest Research* 31:526-538.
- McKenzie, D., Z.M. Gedalof, D.L. Peterson, and P. Mote. 2004. Climatic change, wildfire, and conservation. *Conservation Biology* 18:890-902.
- McKenzie, D., D.W. Peterson, D.L. Peterson, and P.E. Thornton. 2003. Climatic and biophysical controls on conifer species distributions in mountain forests of Washington State, USA. *Journal of Biogeography* 30:1093-1108.
- Miller, P.R. 1992. Mixed conifer forests of the San Bernardino Mountains, California. Pages 461-497 in R.K. Olson, D. Binkley, and M. Böhm, eds., *Response of Western Forests to Air Pollution*, Springer-verlag, New York.
- Miller, P.R. 1996. Biological effects of air pollution in the Sierra Nevada. Pages 885-900 in *Sierra Nevada Ecosystem Project: final report to Congress, v. II, Assessments and scientific basis for management options*. Davis: University of California, Centers for Water and Wild-land Resources.
- Milne, B. T., V. K. Gupta, and C. Restrepo. 2002. A scale-invariant coupling of plants, water, energy, and terrain. *EcoScience* 9:191-199.
- Milne, B.T., A.R. Johnson, T.H. Keitt, C.A. Hatfield, J. David, and P.T. Hrabert. 1996. Detection of critical densities associated with pinyon-juniper woodland ecotones. *Ecology* 77:805-821.

- Neilson, R.P., L.F. Pitelka, A.M. Solomon, R. Nathan, G.F. Midgley, J.M.V. Fragoso, H. Lischke, and K. Thompson. 2005. Forecasting regional to global plant migration in response to climate change. *BioScience* 55:749-759.
- NIFC (National Interagency Fire Center). 2006. <http://www.nifc.gov>
- Pearson, R.G., and T.P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12:361-371.
- Peterson, D.L., and M.J. Arbaugh. 1988. Growth patterns of ozone-injured ponderosa pine (*Pinus ponderosa*) in the southern Sierra Nevada. *Journal of the Air Pollution Control Association* 38: 921-927.
- Peterson, D.L., M.J. Arbaugh, and L.J. Robinson. 1991. Growth trends of ozone-stressed ponderosa pine (*Pinus ponderosa*) in the Sierra Nevada of California, USA. *The Holocene* 1:50-61.
- Peterson, D.W., and D.L. Peterson. 2001. Mountain hemlock growth responds to climatic variability at annual and decadal scales. *Ecology* 82:3330-3345.
- Reich, P.B., and R.G. Amundson. 1985. Ambient levels of ozone reduce net photosynthesis in tree and crop species. *Science* 230:566-570.
- Ross, D.W., G.E. Daterman, J.L. Boughton, and T.M. Quigley. 2001. Forest health restoration in south-central Alaska: a problem analysis. USDA Forest Service General Technical Report PNW-GTR-523, Pacific Northwest Research Station, Portland, OR.
- Samuels, M.L., and J.L. Betancourt. 1982. Modeling the long-term effects of fuelwood harvest on piñon-juniper woodlands. *Environmental Management* 6:505-515.
- Skinner, W.R., B.J. Stocks, D.L. Martell, B. Bonsal and A. Shabbar. 1999. The association between circulation anomalies in the mid-troposphere and area burned by wildfire in Canada. *Theoretical and Applied Climatology* 63:89-105.
- Stephenson, N.L. 1990. Climatic control of vegetation distribution: the role of the water balance. *American Naturalist* 135:649-670.
- Stephenson, N.L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography* 25: 855-870.
- Stephenson, N.L., D.L. Peterson, D. Fagre, C.D. Allen, D. McKenzie, J.S. Baron, and K. O'Brian. 2006. Response of western mountain ecosystems to climatic variability and change: the Western Mountain Initiative. *Park Science* 24:24-29.
- Stine, S. 1996. Climate, 1650-1850. Pages 25-30 in *Sierra Nevada Ecosystem Project: final report to Congress, v. II, Assessments and scientific basis for management options*. Davis: University of California, Centers for Water and Wildland Resources.
- Swetnam, T.W. 1993. Fire history and climate change in giant sequoia groves. *Science* 262:885-889.
- Swetnam, T.W., and J.L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate* 11:3128-3147.
- Swetnam, T.W., and A.M. Lynch. 1993. Multicentury regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs* 63:399-424.

- USDA (United States Department of Agriculture) Forest Service. 1990. Silvics of North America: Volume 1. Conifers. USDA Forest Service, Agriculture Handbook 54, Russell M. Burns and Barbara H. Honkala: Coordinators.
- van Mantgem, P.J., N.L. Stephenson, M. Keifer, and J. Kelley. 2004. Effects of an introduced pathogen and fire exclusion on the demography of sugar pine. *Ecological Applications* 14:1590-1602.
- Veblen, T.T., K.S. Hadley, E.M. Nel, T. Kitzberger, M. Reid, and R. Villalba. 1994. Disturbance regimes and disturbance interactions in a Rocky Mountain subalpine forest. *Journal of Ecology* 82:125-135.
- Veblen, T.T., K.S. Hadley, M.S. Reid, and A.J. Rebertus. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology* 72:213-231.
- Veblen, T.T., T. Kitzberger, and J. Donnegan. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications* 10:1178-1195.
- Werner, R.A., and E.H. Holsten. 1985. Factors influencing generation times of spruce beetles in Alaska. *Canadian Journal of Forest Research* 15:438-443.
- Werner, R.A., E.H. Holsten, S.M. Matsuoka, and R.E. Burnside. 2006. Spruce beetles and forest ecosystems in south-central Alaska: a review of 30 years of research. *Forest Ecology and Management* 227:195-206.
- Weber, U., and F.H. Schweingruber. 1995. A dendroecological reconstruction of western spruce budworm outbreaks (*Choristoneura occidentalis*) in the Front Range, Colorado, from 1720 to 1986. *Tree* 9:204-213.
- Westerling, A.L., H.G. Hidalgo, D.R. Cayan, and T.W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940-943.
- Woodward, F.I. 1987. *Climate and Plant Distribution*. Cambridge University Press, London.
- Woodward, F.I., and I.F. McKee. 1991. Vegetation and climate. *Environmental International* 17:535-546.

Figure captions

Figure 1: Conceptual model of the relative time scales for disturbance vs. climatic change alone to alter ecosystems. Times are approximate. Adapted from McKenzie et al. 2004.

Figure 2: Massive dieback of pinyon pine in the Jemez Mountains, New Mexico, USA. Photo courtesy of Craig Allen, USGS.

Figure 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.

Figure 4: Photochemical haze over Sequoia National Park in October, 2003. Photo by D. McKenzie.

Figure 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.

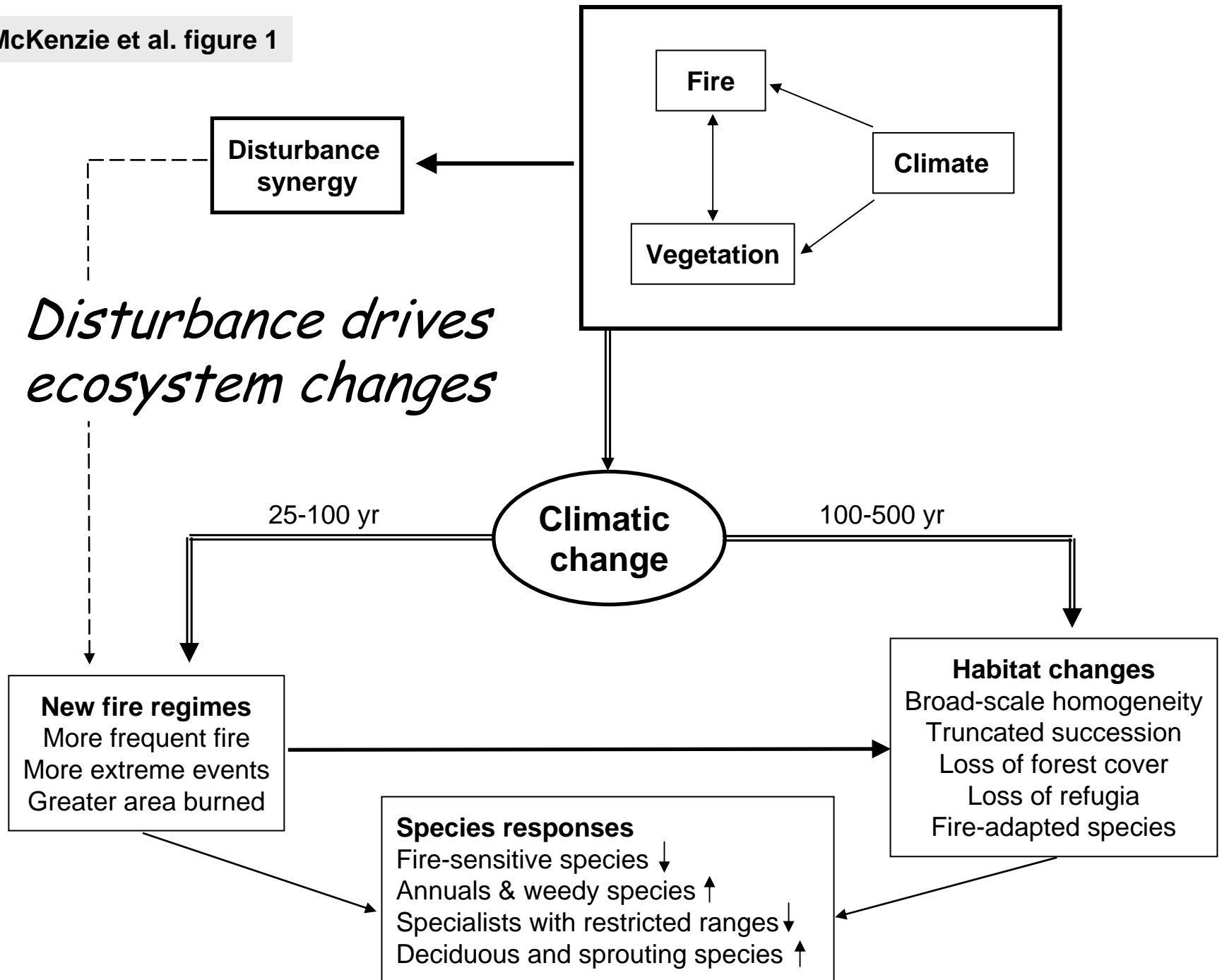
Figure 6: Massive lodgepole pine mortality from mountain pine beetles in south-central British Columbia, Canada. Photo courtesy of Alan Carroll, Canadian Forest Service.

Figure 7: Stress complex in interior (BC and USA) lodgepole pine forests. The effects of disturbance regimes (insects and fire) are exacerbated by global warming. Stand-replacing fires, beetle mortality, and changes in environmental niche space (see text) contribute to species changes.

Figure 8: Recent wildfire and insect activity in Alaska. Data from the Alaska Fire Service.

Figure 9: Nearly complete stand mortality of white spruce (*Picea glauca*) from spruce bark beetle on the Kenai Peninsula, Alaska. Photo courtesy of Robert Vihnanek, USDA Forest Service.

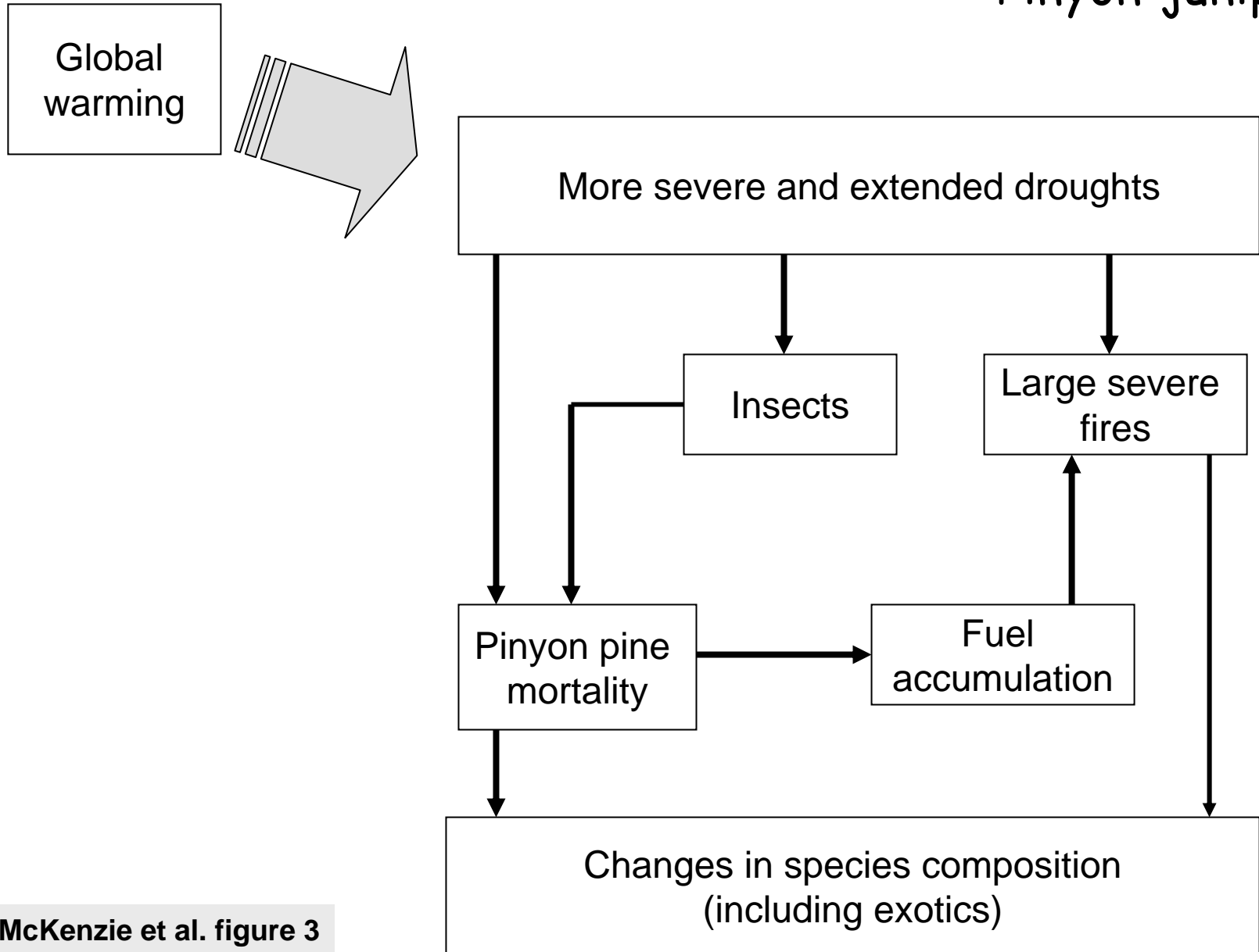
Figure 10: Stress complex in the interior and coastal forests of Alaska. Rapid increases in the severity of disturbance regimes (insects and fire) are triggered by global warming. Stand-replacing fires, massive mortality from insects, and permafrost degradation contribute to species changes and conversion to deciduous life forms.





McKenzie et al. figure 2

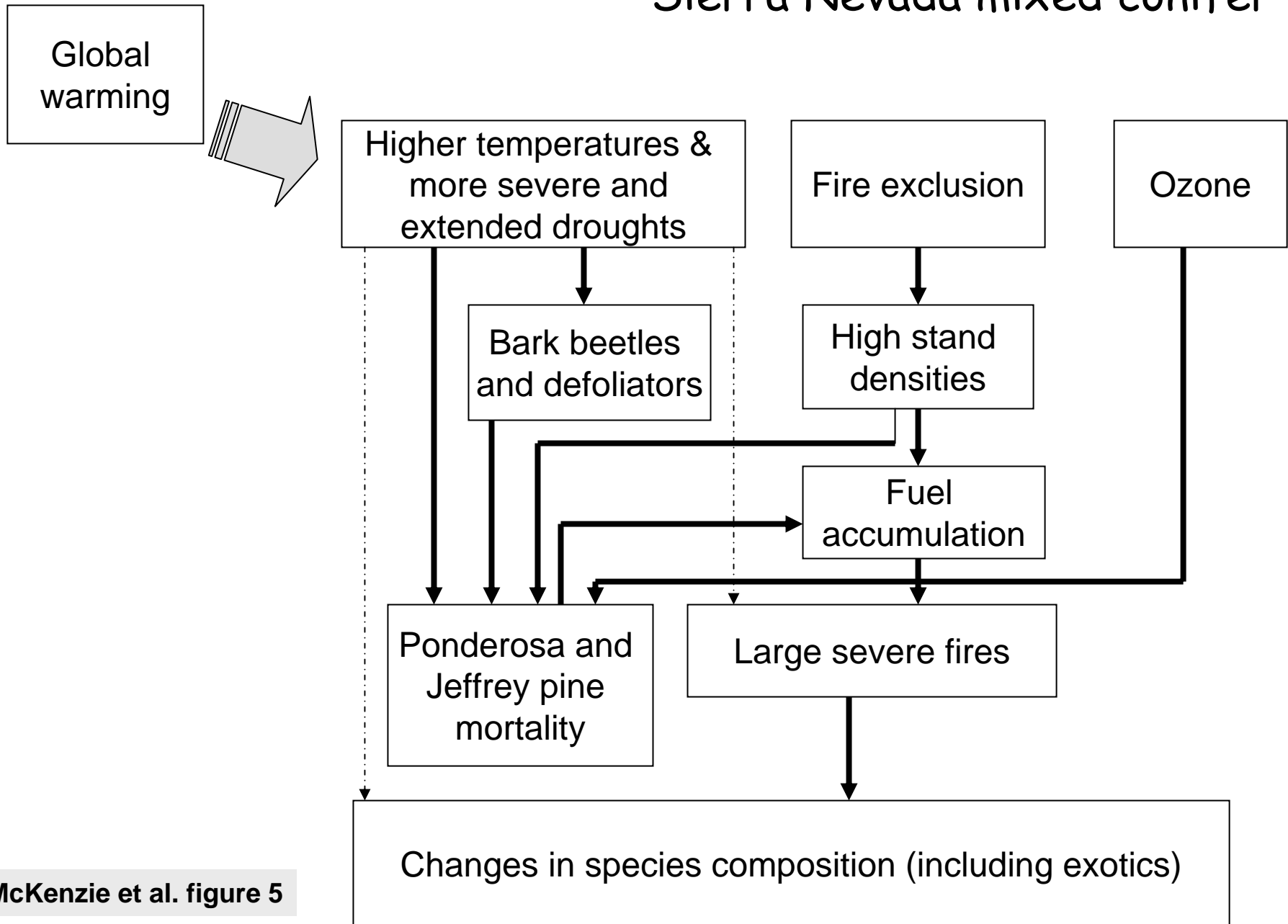
Pinyon-juniper





McKenzie et al. figure 4

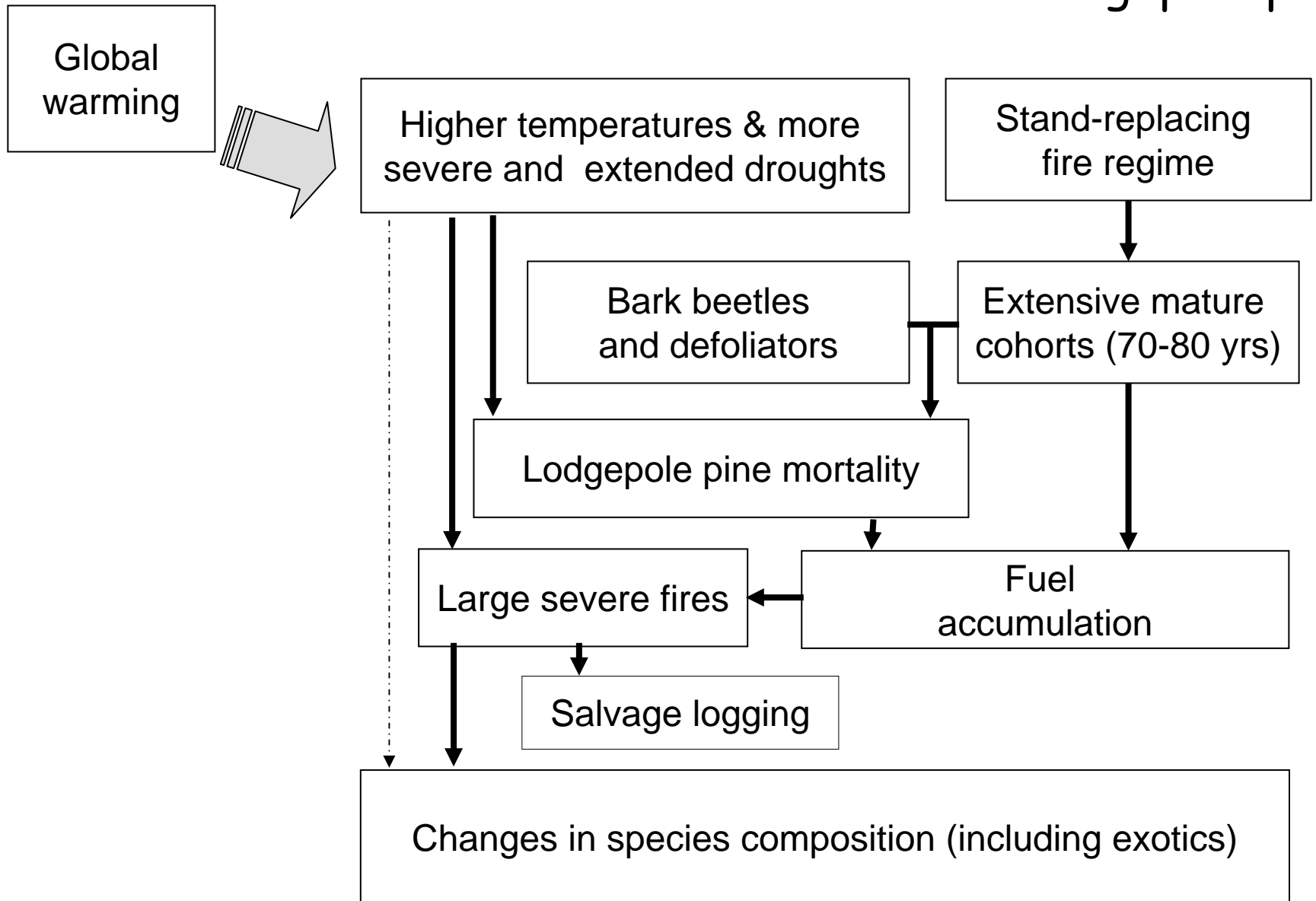
Sierra Nevada mixed conifer



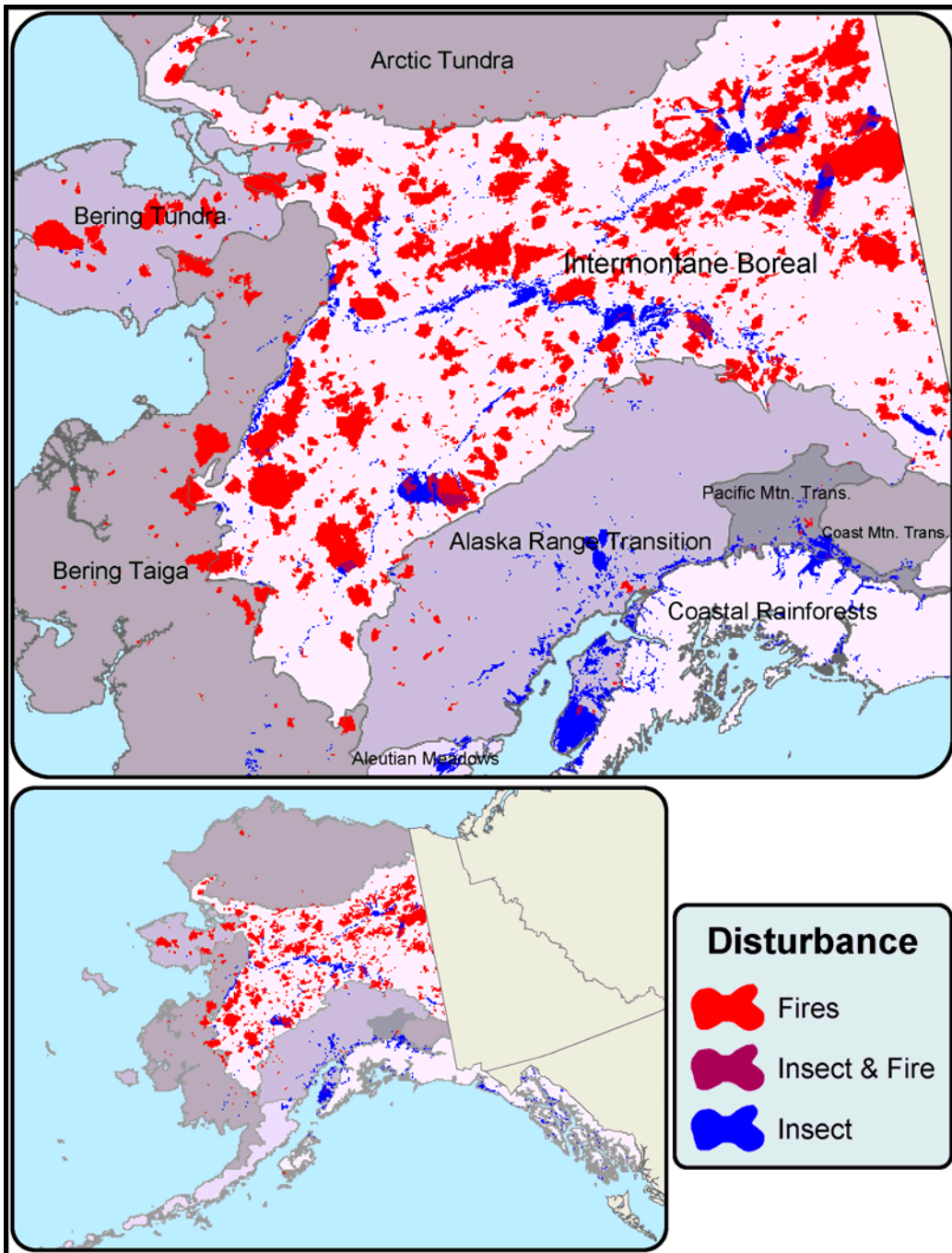
McKenzie et al. figure 6



Interior lodgepole pine



McKenzie et al. figure 8





McKenzie et al. figure 9

Global warming

