Chapter 4
Disturbance Regimes and Stressors

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4.1 Introduction

Disturbances such as wildfire, insect outbreaks, pathogens, invasive species, drought, and storms are part of the ecological history of most forest ecosystems, influencing vegetation age and structure, plant species composition, productivity,

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carbon (C) storage, water yield, nutrient retention, and wildlife habitat. Climate influences the timing, frequency, and magnitude of disturbances (Dale et al. 2001). As the climate continues to change, we expect increased disturbance through more frequent extreme weather events, including severe drought, wind storms, and ice storms. Indirect effects may amplify these changes, with conditions that favor wildfire, insects, pathogens, and invasive species.

If frequency and severity of disturbances increase in the future, they will almost certainly have a bigger impact on forest ecosystems than gradual changes in other forest processes in response to higher temperature (see Chap. 3). This will lead to rapid changes in forest structure and function. It will also create landscapes in which regeneration of vegetation will occur in a warmer environment, possibly with new competitive relationships among species. In this way, the indirect effects of climate change in forest ecosystems may be more important than direct effects.

4.2 Wildfire

Climate and fuels are the two most important factors controlling patterns of wildfire within forest ecosystems. Climate controls the frequency of weather conditions that promote fire, whereas the amount and arrangement of fuels influence fire intensity and spread. Climate influences fuels on longer time scales by shaping species composition and productivity (Marlon et al. 2008; Power et al. 2008), and large-scale climatic patterns such as the El Niño Southern Oscillation, Pacific Decadal Oscillation, Atlantic Multidecadal Oscillation, and Arctic Oscillation are important drivers of forest productivity and susceptibility to disturbance (Duffy et al. 2005; Collins et al. 2006; Fauria and Johnson 2006; Kitzberger et al. 2007).

Current and past land use, including timber harvest, forest clearing, fire suppression, and fire exclusion through grazing (Swetnam and Betancourt 1998; Allen et al. 2002) have affected the amount and structure of fuels in the United States. For example, in montane forests in the Southwest (Allen et al. 2002) and other dry forests in the interior West, removal of fine fuels by grazing and fire suppression have increased the number of trees and amount of fuels; these forest conditions have increased fire size and intensified fire behavior. In colder and wetter forests in the western United States, such as subalpine forests in Yellowstone National Park and forests in the maritime Northwest, grazing and fire suppression have not altered fire regimes as extensively. Forests in the northeastern United States (Foster et al. 2002) and the upper Midwest developed after widespread timber harvest, land clearing, and forest re-growth after land abandonment. Compared to other regions of the United States, forests in the Northeast and upper Midwest burn less often and with smaller fires. Forests in the southeastern United States are often managed for timber, and prescribed fire is generally more prevalent than uncontrolled ignitions (National Interagency Coordination Center 2011). Prescribed fire is applied every

2–4 years in some fire-dependent ecosystems in the Southeast (Mitchell et al. 2006). Fire suppression and deer herbivory in the central hardwoods section of the eastern United States have pushed the composition toward more mesic and fire intolerant species (e.g., from oak dominated to maple dominated) (Nowacki and Abrams 2008).

Weather remains the best predictor of how much area will burn, despite changes in land use and the resulting effects on fuels. Correlations between weather and either area burned by fire or number of large fires are similar for both pre-settlement fires and fires of the last few decades. These syntheses of fire-weather relationships for both pre-settlement and modern records exist in several subregions of the West (Northwest: Heyerdahl et al. 2002, 2008a; Hessl et al. 2004. Southwest: Swetnam and Betancourt 1998; Grissino-Mayer and Swetnam 2000. Northern Rocky Mountains: Heyerdahl et al. 2008b. Westwide: Westerling et al. 2003, 2006; Littell et al. 2009) and the East (Hutchinson et al. 2008). Pre-settlement fire-weather relationships are derived from trees scarred by fires or age classes of trees established after fire and independently reconstructed climate; modern fire-weather comparisons are derived from observed fire events and observed weather in seasons leading up to the fire. Drought and increased temperature promote large fires, but effects differ by forest and region (Westerling et al. 2003; Littell et al. 2009). Weather can also influence fire through higher precipitation, increasing understory vegetation growth, which later becomes fuel (Swetnam and Betancourt 1998; Littell et al. 2009). Increased temperature and altered precipitation also affect fuel moisture and the length of time during which wildfires can burn during a given year.

The potential effects of climate change on forest fire area have been assessed using statistical models that project area burned from climatic variables, and by using global climate models to project future climatic variables (Westwide: McKenzie et al. 2004; Spracklen et al. 2009; Littell et al. 2010. Pacific Northwest: Littell et al. 2010; Yellowstone region: Westerling et al. 2011). Estimated future changes in annual area burned in the West ranges from declines of 80 % to increases greater than 500 %, depending on the region, timeframe, methods, and climate model/emission scenario (Bachelet et al. 2001). Future fire potential is expected to increase in summer and autumn from low to moderate in eastern regions of the South, and from moderate to high levels in western regions of the South (Liu et al. 2010).

The risk posed by future fire activity in a changing climate can be assessed by its likely effects on human and ecological systems. At the wildland-urban interface (WUI), higher population and forest density have created forest conditions that are likely to experience more area burned and possibly greater fire severity than in the historical record. Fire risk is likely to increase in a warmer climate because of the longer duration of the fire season, and the greater availability of fuels if temperature increases and precipitation does not sufficiently increase to offset summer water balance deficit. Where fuels management is common, forest fuel reduction and restoration to pre-settlement tree density and surface fire regimes help mitigate fire

hazard under current and future climatic conditions. Finally, future fire risk may depend on whether extreme fire weather conditions will change in step with monthly to seasonal climate changes. Even if fire weather and ignitions do not change, it is likely that risk driven only by seasonal climate changes will increase; particularly in the WUI and managed forests, where fire has been historically rare or fully suppressed. The current increase in annual area burned may be partially related to increased fuels in frequent-fire forest types, in addition to more frequent weather conditions conducive to fire.

The effects of climate change intersecting with increased fuel loads in frequent-fire forests will be an exceptional challenge for resource managers on both public and private lands. As noted above, active management is highly effective in reducing fuel quantity and continuity, thus reducing fire intensity and mortality in the forest overstory (see Chap. 9). Prescribed fire is applied routinely and extensively in pine forests in the Southeast, but funding for fuel treatment in Western forests is sufficient to treat only a small portion of the landscape that currently has elevated fuels. Fire suppression is currently a large proportion of federal agency budgets (approximately 50 % for the U.S. Forest Service). If area burned does in fact increase by 100 % or more in future decades, this will pose a major budgetary and policy issue, and create challenges in managing landscapes increasingly occupied by younger forests.

4.3   Insects and Pathogens

4.3.1   *General Concepts*

Biotic disturbances are natural features of forests that play key roles in ecosystem processes (Adams et al. 2010; Boon 2012; Hicke et al. 2012a). Epidemics by forest insects and pathogens affect more area and result in greater economic costs than other forest disturbances in the United States (Dale et al. 2001). By causing local to widespread tree mortality or reductions in forest productivity, insect and pathogen outbreaks have broad ecological and socioeconomic effects (Tkacz et al. 2010; Pfeifer et al. 2011). The first National Climate Assessment (Melillo et al. 2001) projected increased disturbance in forests, especially from insects, and especially from bark beetles, because of their high physiological sensitivity to climate, short generation times, high mobility, and explosive reproductive potential. These projections have been upheld, and current observations suggest that disturbances are occurring more rapidly than imagined a decade ago. Understanding how these disturbances are influenced by climate change is therefore critical for quantifying and projecting effects (Fig. 4.1).

The powerful general effect of temperature on insects and pathogens is well known (Gillooly et al. 2002). Clear examples exist of climatic effects on insects, yet the most important insects and pathogens in American forests remain poorly
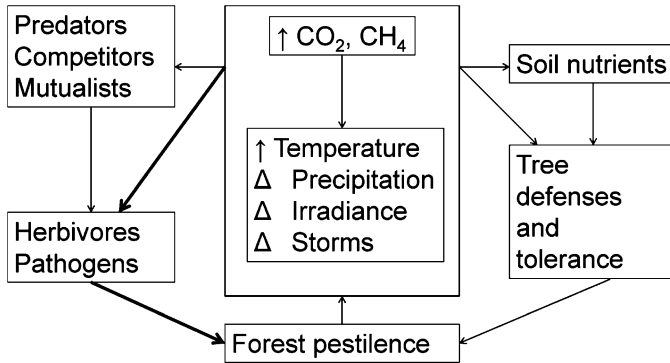
Fig. 4.1 General pathways by which atmospheric changes associated with increasing greenhouse gases can influence forest disturbance from insects and pathogens. *CO₂* carbon dioxide, *CH₄* methane

studied with respect to how interactions with climate will affect forests. Climatic warming can influence biotic disturbances of forests through effects on (1) the physiology of insects and pathogens that cause changes in their abundance and distribution, (2) tree defenses and tolerance, and (3) interactions of insects and pathogens with enemies, competitors, and mutualists (Fig. 4.1). Higher temperature has reduced winter mortality of insects, increased their range northward (Trân et al. 2007; Paradis et al. 2008; Safranyik et al. 2010), and increased their development rate during the growing season (Gillooly et al. 2002; Bentz et al. 2010). Temperature increases can also alter phenology, such as bringing leaf maturation into synchrony with insect feeding (Jepsen et al. 2011) or changing the life cycle synchrony of bark beetles, which depend on mass attack to overwhelm tree defenses (Powell et al. 2000; Friedenberg et al. 2007; Bentz et al. 2010).

A broader set of atmospheric drivers affects tree defenses against, and tolerance to, herbivores and pathogens (Lindroth 2010; Sturrock et al. 2011). Deficiencies of water or mineral nutrients can both increase and decrease tree defenses, depending on the severity of the deficiency, biochemical pathways, and the type of defense (Lombardero et al. 2000; Breshears et al. 2005; Worrall et al. 2008). In addition, tree mortality from severe drought may facilitate an increase in bark beetles, which then become sufficiently abundant to successfully attack healthy trees (Greenwood and Weisberg 2008; Raffa et al. 2008). Information on the effects of climate on tree-pathogen interactions is sparse, despite a theoretical expectation for temperature and moisture to have significant effects (Grulke 2011; Rohrs-Richey et al. 2011; Sturrock et al. 2011).

Outbreak dynamics of forest insects respond to interactions between herbivores and their enemies (Dwyer et al. 2004), and these interactions should be sensitive to temperature (Berggren et al. 2009; Klapwijk et al. 2012), but empirical studies are rare (Siegert et al. 2009). Similarly, for the many forest insects that involve

mutualisms with fungi, it is logical that outbreak dynamics will be sensitive to climatic effects on the mutualism (Lombardero et al. 2000; Hofstetter et al. 2007; Six and Bentz 2007; Evans et al. 2011).

4.3.2 Climate and Biotic Disturbances

4.3.2.1 Bark Beetles

Multiple species of indigenous bark beetles affect millions of hectares of coniferous forests in North America. Major species include mountain pine beetle (*Dendroctonus ponderosae* Hopkins), the most important disturbance agent of pines in the western United States (Box 4.1; see Chap. 1); southern pine beetle (*D. frontalis* Zimmermann) in pine forests of the southeastern United States (Box 4.2), and spruce beetle (*D. rufipennis* Kirby). In the early 2000s, severe drought, coupled with several species of bark beetles, killed trees of several conifer species in the Southwest (Ganey and Vojta 2011), most notably pinyon pine (*Pinus edulis* Engelm.) attacked by pinyon ips (*Ips confusus* LeConte) across 1.2 million ha (Breshears et al. 2005).

Box 4.1: Mountain Pine Beetle and Five-Needle Pines

Five-needle pines, including whitebark (*Pinus albicaulis* Engelm.), limber (*P. flexilis* James), and bristlecone (*P. aristata* Engelm.) pines, play key roles in forest ecosystems of the western United States. They provide food resources for wildlife, affect snow distribution and melt, stabilize the soil, and provide cover for other vegetation, and are valued by the public for these services. However, these conifers are currently subjected to a climatically induced increase in biotic disturbance that is expected to continue in the coming decades. Mountain pine beetles (*Dendrotonus ponderosae* Hopkins) are attacking five-needle pines across the West; aerial surveys indicate that one million ha were affected by five-needle pine mortality during 1997 through 2010. Higher temperatures and drier conditions affect winter survival and development rate and population synchronization of beetles, as well as susceptibility of host trees.

Similar epidemics occurred in the 1930s, also associated with a period of warmer years, but several differences exist between the mortality then and today. Most importantly, a cooler period followed the 1930s that was less suitable for the beetle. In contrast, the current warming trend has persisted for several decades, with resultant increases in climatic suitability for mountain pine beetle, and is expected to continue for decades to come. The recent beetle epidemics in five-needle pine stands are already more extensive than in the 1930s and are killing very old trees that survived previous outbreaks. Finally, white pine blister rust is predisposing whitebark pines to lethal attacks by

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Box 4.1 (continued)

mountain pine beetle (*Cronartium ribicola* J.C. Fisch). Given the trajectory of future warming, strong ties between temperature and beetle epidemics, and extensive mortality that has already occurred in some areas, significant consequences are expected for these forests and the ecosystem services they provide.

Box 4.2: The Southern Pine Beetle Reaches the New Jersey Pinelands

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) is the most destructive herbivore in the most productive forests of the United States. Like the closely related mountain pine beetle (*Dendroctounus ponderosae* Hopkins), it uses aggregation pheromones to coordinate mass attacks that overwhelm the resin defenses of otherwise healthy trees; virtually every attacked tree dies within weeks. It has multiple generations per year (at least four to five in the warm Gulf Coast region), so the aggregations that typically form in spring can expand throughout the year as growing "spots" of tree mortality within forest landscapes. Effective suppression of these epidemics involves locating the spots and cutting the infested trees. Effective prevention involves silvicultural thinning to reduce the occurrence of stands with high basal area (overstocked) that are especially suitable for beetle population growth. Monitoring, suppression, and prevention of southern pine beetle are integral to the management of pine ecosystems in the southeastern United States.

The northern distribution of southern pine beetle is constrained by the occurrence of lethal winter temperatures. As part of the first National Climate Assessment, it was estimated that an increase of 3 °C in minimum annual temperature would permit a northern expansion of about 180 km for this beetle. In fact, there was a regional increase of just over 3 °C from 1960 through 2005, and beetle populations are now epidemic in the New Jersey Pinelands, about 200 km north of forests with a long history of such epidemics. Warming winters did not cause the current epidemic but may have permitted it. Given the natural population dynamics of southern pine beetle and the projected absence of lethal winter temperatures, the New Jersey Pinelands has entered a new phase in which southern pine beetle will be influencing many aspects of forest ecology and management, as they have throughout the southeastern United States.

(*Photo shows an infestation of southern pine beetle in the New Jersey Pinelands in 2011. Aerial photo by Bob Williams, Land Dimensions. Close-up of beetle by Erich Vallery, U.S. Forest Service*)

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The population dynamics of these native beetles are sensitive to climatic variation, and the extent of recent outbreaks have been facilitated by increasing temperatures during the last decade (Breshears et al. 2005; Raffa et al. 2008; Sherriff et al. 2011). Greater effects on forest ecosystems are anticipated from recent range expansions by beetles into areas with hosts that are new and may have low resistance (Cudmore et al. 2010). Mexican pine beetle (*D. mexicanus* Hopkins), previously known only in Mexico, has been recorded in the southwestern United States (Moser et al. 2005) and represents one of several species of Mexican bark beetles that may expand into U.S. forests in a warmer climate (Bentz et al. 2010; Salinas-Moreno et al. 2010). Climate change will continue to reshape the patterns of bark beetle outbreaks in U.S. forests, with outbreak tendencies increasing for some species in some regions and decreasing in others (Bentz et al. 2010; Littell et al. 2010; Evangelista et al. 2011).

4.3.2.2 Defoliating Insects

Defoliating insects are a continentally important biotic disturbance in American forests. For example, western spruce budworm (*Choristoneura occidentalis*

Freeman) is currently important in the West (USDA FS 2010), and Eastern boreal forests have been affected by many cycles of spruce budworm (*Archips fumiferana* Clemens) outbreaks (Candau and Fleming 2005). Other important defoliators include tussock moths, tent caterpillars, gypsy moths, and jack pine budworm (*A. pinus* Freeman). Most defoliating insects are indigenous to American forests, and many have cyclical outbreak dynamics involving predators, parasitoids, and pathogens (Dwyer et al. 2004).

Climatic effects on these predator–prey interactions remain largely unstudied (Klapwijk et al. 2012). In general, it is less clear (compared to what is known about bark beetles) how climatic patterns influence the frequency, extent, and geographic distribution of defoliators in American forests. There is limited evidence in some forest systems of climatic effects on winter populations (Thomson et al. 1984; Kemp et al. 1985; Williams and Liebhold 1995a; but see Reynolds et al. 2007; Thomson and Benton 2007), drought stress of host trees (Williams and Liebhold 1995b; Campbell et al. 2006), and phenological synchronization of larval emergence and bud break (Thomson et al. 1984). Considerable uncertainty remains about future responses of defoliators to climate change (Dukes et al. 2009; Rodenhouse et al. 2009). Hemlock woolly adelgid (*Adelges tsugae* Annand), a non-native, stem-feeding insect, has been spreading in the eastern United States (Box 4.3).

Box 4.3: Hemlock Woolly Adelgid

Invasive insects can cause extensive tree mortality owing to lack of genetic resistance in host trees and the absence of natural enemies. Thus, non-native insects and pathogens are likely to cause the loss of native tree species and produce other substantial effects on forests, wildlife, and biodiversity. Climate change can exacerbate the effects of established invasives by permitting their expansion into previously unsuitable climatic regions, as with the expansion of the hemlock woolly adelgid (*Adelges tsugae* Annand) into the northeastern United States.

Hemlock woolly adelgid, an aphid-like insect, was accidentally introduced from Japan some time before 1951 and has been a major biotic disturbance in American forests, killing eastern hemlock (*Tsuga canadensis* [L.] Carrière) and Carolina hemlock (*T. caroliniana* Engelm.) in advancing waves from its point of establishment in Virginia. Since establishment, this insect has largely eliminated hemlocks from a large swath of Eastern forests, including national icons such as the Shenandoah and Great Smoky Mountains National Parks. Consequences include lost value to property owners and persistent alterations to hydrological regimes, soil biogeochemistry, C stores, biodiversity, and forest composition, including permitting the establishment of undesirable invasive plants.

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Hemlocks north of the infested regions have thus far been protected by winter temperatures that are lethal to hemlock woolly adelgid. However, these conditions are changing with the amelioration of extreme winter temperatures in the eastern United States, and projections under even conservative climatic scenarios predict the loss of hemlock through most of its current range.

4.3.2.3 Plant Pathogens

We identified 21 plant pathogens that are notable agents of disturbance in U.S. forests and may respond to climate change. Climatic effects on these pathogens are generally not well studied, but we expect that some of these pathogens will be affected directly by climatic influences on sporulation and infection, indirectly by predisposing trees to infection, or both (Sturrock et al. 2011). For pathogens that involve associations with insects, climatic effects on the animal associates may also be important.

A few cases of climate-pathogen interactions have been documented. For example, Swiss needle cast (*Phaeocryptopus gaeumannii* T. Rohde), a native foliar pathogen in the Northwest, is influenced by winter warming and spring precipitation. Climatic projections suggest an increase in Swiss needle cast distribution and severity (Stone et al. 2008). The susceptibility of alder to a cankering pathogen is related to the phenology of the plant, the pathogen, and water availability (Grulke 2011; Rohrs-Richey et al. 2011). Outbreaks of some virulent invasive pathogens can also be enhanced by climate (e.g., sudden oak death; Sturrock et al. 2011), whereas others are not very sensitive to climate (Garnas et al. 2011b).

The potential effects of climate change on root pathogens are difficult to project (Ayres and Lombardero 2000), but it will be important to understand this relationship because endemic root diseases are widespread and often have a major influence on forest dynamics and management. One would expect root diseases to be affected by both the distribution of host species and the effects of a changing climate on susceptibility of host species and prevalence of fungal pathogens. If a warmer climate increases physiological stress in a particular tree species, then it may be less resistant to some root diseases, potentially causing lower tree vigor, higher mortality in mature trees and seedlings, and lower C storage. Although some initial modeling of future changes in root pathogens has been attempted (*Armillaria* spp.; Klopfenstein et al. 2009), geographic specificity for host-pathogen relationships is highly uncertain based on current knowledge.

4.3.2.4 Non-native and Emerging Insects and Pathogens

Invasive, non-native insects and pathogens are becoming an increasingly important component of forest disturbance (Lovett et al. 2006; Seppälä et al. 2009), and warming and precipitation shifts associated with climate change can affect forest vulnerability (Paradis et al. 2008; Sturrock et al. 2011). For example, the geographic range and incidence of dothistroma needle blight (*Dothistroma septosporum* [Dorog.] M. Morelet and *D. pini* Hulbary), which reduces growth of many conifers by causing premature needle defoliation, may shift with changing precipitation patterns (Woods et al. 2010).

At present, the primary cause of biological invasions is global commerce. However, increasing temperatures are generally expanding the geographic zones where potential invasive species could survive and reproduce if they arrive, for example, at ports of entry on the Eastern seaboard and in the Great Lakes waterway. The potential for global, climate-driven increases in invasion risks has prompted international organizations to discuss changes in trade restrictions to manage associated phytosanitation risks (Standards and Trade Development Facility 2009).

Outbreaks of lesser known forest insects have recently occurred in U.S. forests. Aspen leaf miner (*Phyllocnistis populiella* Chambers), which reduces longevity of aspen leaves, has damaged 2.5 million ha of quaking aspen (*Populus tremuloides* Michx.) in Alaska since 1996 (Wagner et al. 2008). Large areas of willows were damaged during two eruptive outbreaks of the willow leafblotch miner (*Micurapteryx salicifoliella* Chambers) in the 1990s in two major river drainages in Alaska (Furniss et al. 2001); outbreaks of this leaf miner had not been previously reported. Substantial defoliation by Janet's looper (*Nepytia janetae* Rindge) of stressed trees in Southwestern spruce-fir forests was preceded by uncharacteristically warm winters; defoliation by Janet's looper encouraged attack by opportunistic bark beetles. These examples demonstrate that previously rare native insects that displayed new eruptive behavior and caused notable forest disturbances.

4.3.3 Effects and Interactions with Other Disturbances

Through their effects on tree growth and mortality, insects and pathogens have broad effects on ecosystem processes (see Chap. 3). Insects and pathogens, by virtue of their host preferences, can alter tree species composition within stands, remove most host trees from some landscapes (Lovett et al. 2006), and modify forest types (e.g., from conifers to hardwoods) (Veblen et al. 1991; Orwig et al. 2002; Collins 2011). Forests typically shift toward younger, smaller trees after biotic disturbances (Ylioja et al. 2005; Garnas et al. 2011a; Tchakerian and Couslon 2011), which can affect wildlife habitat and biodiversity by quickly modifying multiple trophic levels (Chan-McLeod 2006; Drever et al. 2009). Both positive and negative effects occur depending on species, time since disturbance, surviving vegetation, ecosystem type, and spatial extent of outbreak.

Fire and biotic disturbances interact in several ways. Fires lead to younger stands that may be less susceptible to attack, and dead trees provide a food resource for some insects and pathogens (Parker et al. 2006). Insect-killed trees influence fuels and therefore fire behavior, although the effect depends on a number of factors, including the number of attacked trees within a stand and time since outbreak (e.g., Ayres and Lombardero 2000; Hicke et al. 2012b; Jenkins et al. 2008; Simard et al. 2011), and fire-induced increases in tree defenses can mitigate bark beetle risks (Lombardero and Ayres 2011).

Extreme soil water deficits (drought) that reduce tree growth might also reduce tree defenses to insects and pathogens (Bentz et al. 2009; Sturrock et al. 2011), although previous studies suggest there may be either no effect (Gaylord et al. 2007; McNulty et al. 1997) or the opposite effect (Lombardero et al. 2000). Drought also facilitates population increases of western bark beetles. Some aggressive species such as mountain pine beetle are able to maintain epidemics after return to normal conditions, whereas others such as pinyon ips decline with alleviation of drought stress (Raffa et al. 2008).

Insects and pathogens clearly affect the economic value of forests that are intended for harvest for wood products, and direct economic effects occur for tree removal and replacement, such as the $10 billion spent after emerald ash borer (*Agrilus planipennis* Fairmaire) infestations (Kovacs et al. 2010, 2011). A more complete valuation of socioeconomic effects is challenging because it is difficult to quantify all ecosystem services, especially those with non-market values (Holmes et al. 2010). Regions with dead and dying trees have reduced aesthetic value (Sheppard and Picard 2006) and may have reduced housing prices (Holmes et al. 2010; Price et al. 2010).

4.4 Invasive Plants

4.4.1 Introduction

Invasive plants are recent introductions of non-native, exotic, or nonindigenous species that are (or have the potential to become) successfully established or naturalized, and that spread into new localized natural habitats or ecoregions with the potential to cause economic or environmental harm (Lodge et al. 2006). This definition of "invasive" (1) does not consider native species that have recently expanded their range, such as juniper (*Juniperus* spp.) in the western United States (Miller and Wigand 1994; Miller et al. 2005), (2) involves defined temporal and spatial scales, and (3) considers social values related to economic and environmental effects.

An estimated 5,000 nonnative plant species exist in U.S. natural ecosystems (Pimentel et al. 2005) (Table 4.1). The effects of invasive plants include reduced native biodiversity, altered species composition, loss of habitat for dependent

Table 4.1 Common invasive plant species and environmental impacts for forests and woodlands in the United States

Species	Common name	Growth form	Environmental impacts
Acer platanoides L.	Norway maple	Tree	Reduces abundance and diversity of native species; alters community structure (shading of understory)
Ailanthus altissima Desf.	Tree of heaven	Tree	Alters ecosystem processes (increases soil N, alters successional trajectories); displaces native vegetation; allelopathic; roots can damage buildings and sewer lines; risk to human health (pollen allergies, sap-caused dermatitis)
Alliaria petiolata (M. Bieb.) Cavara and Grande	Garlic mustard	Biennial forb	Reduces abundance and diversity of native species; potentially allelopathic
Berberis thunbergii DC.	Japanese barberry	Shrub	Displaces native shrubs; changes soil properties (soil microbial composition, nitrate concentration); alters successional patterns; potentially increases fire risk (increased biomass)
Bromus tectorum L.	Cheatgrass	Annual grass	Decreases community diversity; increases fire frequency and severity; alters successional patterns and nutrient cycling
Celastrus orbiculatus Thunb.	Oriental bittersweet	Vine	Alters soil chemistry (e.g., increased pH, increased calcium), plant succession, and stand structure (e.g., shades out understory, increases continuity of overstory vegetation); decreases native plant diversity; reduces productivity
Centaurea solstitialis L.	Yellow star-thistle	Annual forb	Displaces native plants, reduces native wildlife and forage; decreases native diversity; depletes soil moisture, altering water cycle; reduces productivity in agricultural systems (lowers yield and forage quality)
Centaurea stoebe L.	Spotted knapweed	Biennial/perennial	Reduces plant richness, diversity, cryptogam cover, soil fertility; reduces forage production; increases bare ground and surface water runoff, and can lead to stream sedimentation; allelopathic
Cirsium arvense (L.) Scop.	Canada thistle	Perennial forb	Possible allelopathy; displaces native vegetation; alters community structure and composition; reduces diversity; reduces forage and livestock production
Cytisus scoparius (L.) Link	Scotch broom	Shrub	Interferes with conifer establishment; reduces growth and biomass of trees; alters community composition and structure (increases stand density, often creating monospecific stands); alters soil chemistry (increases N); toxic to livestock

Table 4.1 (continued)

Species	Common name	Growth form	Environmental impacts
Hedera helix L.	English ivy	Vine	Alters community structure; displaces native ground flora; weakens or kills host trees; potentially reduces water quality and increases soil erosion
Imperata cylindrica (L.) P. Beauv.	Cogongrass	Grass	Alters ecosystem structure (e.g., decreases growth and increases mortality of young trees) and function and decreases diversity; shortens fire return intervals and increases fire intensity; interferes with pine and oak regeneration
Ligustrum sinense Lour.	Chinese privet	Shrub	Interferes with native hardwood regeneration; alters species composition and community structure (forms dense monospecific stands)
Lonicera japonica Thunb.	Japanese honeysuckle	Vine	Alters forest structure and species composition; inhibits pine regeneration and weakens or kills host trees; suppresses native vegetation; provides food for wildlife; early- and late-season host for agricultural pests
Lygodium japonicum (Thunb.) Sw.	Japanese climbing fern	Climbing fern	Reduces native understory vegetation; potentially weakens or kills host trees; interferes with overstory tree regeneration
Microstegium vimineum (Trin.) A. Camus	Japanese stiltgrass, Nepalese browntop	Annual grass	Reduces ecosystem function (alters soil characteristics and microfaunal composition, decreases diversity, alters stand structure); reduces timber production; possibly allelopathic
Pueraria montana (Lour.) Merr.	Kudzu	Vine	Potentially eliminates forest cover; overtops, weakens, and kills host trees; reduces timber production; increases winter fire hazard
Triadica sebifera (Willd.) Maesen and S.M. Alemeida ex Sanjappa and Predeep	Chinese tallow, tallowtree	Tree	Displaces native species and reduces diversity; increases soil nutrient availability; reduces fire frequency and intensity

species (e.g., wildlife), changes in biogeochemical cycling, changes in ecosystem water use, and altered disturbance regimes. Billions of dollars are spent every year to mitigate invasive plants or control their effects (Pimentel et al. 2005). Negative environmental effects are scale-dependent (Powell et al. 2011), with some subtle beneficial properties (Sage et al. 2009) on ecosystem function (Myers et al. 2000; Zavaleta et al. 2001). For example, some consider species in the genus *Tamarix* to be among the most aggressively invasive and detrimental plants in the United States (Stein and Flack 1996), but others point out benefits, including sediment stabilization and the creation of vertebrate habitat in riparian areas that can no longer support native vegetation (Cohn 2005).

The spatial extent of many invasive plants at any point in time has been difficult to determine, limiting assessment of overall consequences. One assessment (Duncan et al. 2004) for the western United States indicates that 16 invasive plants account for most current invasive plant problems. *Centaurea* species are particularly widespread and persistent in the West. Cogongrass (*Imperata cylindrica* [L.] Raeusch.), which has invaded extensive forested areas of the Southeast, is considered to be one of the most problematic invasive plants in the world (Box 4.4). Mountain ecosystems tend to have fewer invasive plant species than other regions because of a short growing season, limited settlement history, relatively low frequency of seed sources, and prevalence of closed-canopy conifer forests that limit light in the understory and acidify the soil (Parks et al. 2005).

Box 4.4: Invasive Grasses, Fire, and Forests

Cogongrass (*Imperata cylindrica* [L.] P. Beauv.) in the Southeast and cheatgrass (*Bromus tectorum* [L.]) in the West are invaders that alter fire regimes and are some of the most important ecosystem-altering species on the planet. Cogongrass threatens native ecosystems and forest plantations, generally invading areas after a disturbance (e.g., mining, timber harvest, highway construction, natural fire). It is a major problem for forest industry, invading and persisting in newly established pine plantations. In sandhill plant communities, cogongrass provides horizontal and vertical fuel continuity, shifting surface fire regimes to crown fire regimes and increasing fire-caused mortality in longleaf pine (*Pinus palustris* Mill.), potentially shifting a species-diverse pine savanna to a grassland dominated by cogongrass. Cogongrass does not tolerate low temperatures, but increased warming could increase the threat of cogongrass invasion into new areas. In a warmer climate, cogongrass

(continued)

is expected to greatly increase in the Gulf Coast region. (*Photo shows an infestation of cogongrass in a longleaf pine upland in central Florida.* [*Photo by James R. Meeker, U.S. Forest Service, available from Forestry Images,* http://www.forestryimages.org/browse/detail.cfm?imgnum=3970058])

Cheatgrass is widely distributed in western North America and dominates many steppe communities. After disturbance, this species can invade low-elevation forests, creating surface fuel continuity from arid lowlands into forested uplands. After establishment, cheatgrass contributes to fine, highly combustible fuel components that dry out early in the year, thus increasing the length of the fire season. Future changes in the climatic habitat of cheatgrass will depend on precipitation as well as temperature. If precipitation decreases, especially in summer, cheatgrass will likely expand, whereas increased precipitation may reduce suitable habitat. Elevated CO_2 increases cheatgrass productivity, a phenomenon that may already be contributing to the vigor and spread of this species. Increased productivity causes higher fuel loads, potentially resulting in more frequent, higher intensity fires and altered fire regimes.

4.4.2   Interactions Between Climate Change and Plant Invasion

Plant invasions can be influenced by warmer temperatures, earlier springs and earlier snowmelt, reduced snowpack, changes in fire regimes, elevated nitrogen (N)

deposition, and elevated CO_2 concentrations. The responses of invasive plants to climate change should be considered separately from those of native species, because invasive plants (1) have characteristics that may differ from native species, (2) can be highly adaptive (Sexton et al. 2002), (3) have life history characteristics that facilitate rapid population expansion, and (4) often require different management approaches than for native species (Hellmann et al. 2008). Successful invasion of areas dominated by native plants depends on environment, disturbance, resource availability, biotic resistance, and propagule pressure (Davis et al. 2000; D'Antonio et al. 2001; Levine et al. 2004; Eschtruth and Battles 2009; Pauchard et al. 2009). Climate change may influence all of these drivers of invasion, with high variability across space and time.

4.4.2.1   Temperature, Precipitation, and CO_2

Climate change will alter the abiotic conditions under which plant species can establish, survive, reproduce, and spread. These effects are expected to increase plant stress and decrease survival in the drier, warmer, and lower elevation portions of species ranges (Allen and Breshears 1998). Abiotic factors probably constrain the range of many invasive plants and limit their successful establishment (Alpert et al. 2000; Pauchard et al. 2009). With climate change, however, new habitat, once too cold or wet, may become available, enabling plants to survive outside their historical ranges and expand beyond their current ranges.

Many native plants are projected to move northward or upward in elevation with climate change. Examples of invasive plants projected to follow this pattern are rare, but information on species tolerances provides insight on potential responses. For example, the northern limit of Japanese barberry (*Berberis thunbergii* DC.), an invasive shrub in the eastern United States, is determined by low temperature tolerance, the southern limit by cold stratification requirements for germination, and the western limit by drought tolerance (Silander and Klepeis 1999). The widespread invasive tree of heaven (*Ailanthus altissima* [P. Mill.] Swingle) is limited by cold and prolonged snow cover to lower mountain slopes, but it may be able to colonize during several successive years of mild climate, conditions that may become more common under climate change (Miller 1990). Soil water availability and regional changes in climatic water balance may be important for plant invasions, particularly at lower elevations (Chambers et al. 2007; Crimmins et al. 2011). Species growth, productivity, and reproduction may also change as climatic conditions change. For example, invasive plants may be better able to adjust to rapid changes in abiotic conditions by tracking seasonal temperature trends and shifting their phenologies (e.g., earlier spring warming) (Willis et al. 2010).

Increased productivity in response to elevated CO_2 has been documented under controlled conditions for several invasive plant species, including cheatgrass (*Bromus tectorum* L.) (Box 4.4), Canada thistle (*Cirsium arvense* [L.] Scop.), spotted knapweed (*Centaurea melitensis* L.), yellow star-thistle (*C. solstitialis* L.), and kudzu (*Pueraria montana* [Lour.] Merr.) (Dukes et al. 2011; Ziska and Dukes 2011;

Ziska and George 2004). Response to CO_2 enrichment is less predictable when plants are grown in the field (Dukes and Mooney 1999; Ziska and Dukes 2011), where response may be limited by nutrients and water availability. Carbon dioxide enrichment can also increase water use efficiency, which can partially ameliorate conditions associated with decreased water availability, particularly for C_3 plants (Eamus 1991). This phenomenon may be partially responsible for global patterns of encroachment of C_3 plants in grasslands dominated by C_4 plants or mixed species (Bond and Midgley 2000).

4.4.2.2 Disturbance and Resource Availability

Disturbances such as fire, landslides, volcanic activity, logging, and road building open forest canopies, reduce competition, and expose mineral soil, increasing light and nutrient availability. Invasive plants are generally well adapted to use increased resources. Fluctuating resource availability, coinciding with available propagules, facilitates regeneration and establishment of invasive species associated with forest development after disturbance (Halpern 1989; Davis et al. 2000; Parks et al. 2005). Opportunities for invasions may also be created by forest thinning, fuel treatments, and biofuel harvesting (Bailey et al. 1998; Silveri et al. 2001; Nelson et al. 2008). However, the spatial extent of invasions may be limited (Nelson et al. 2008), especially for shade intolerant species in closed-canopy Western forests.

The reintroduction of fire is a high priority for restoration and management of fire-adapted forests such as ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson), longleaf pine (*P. palustris* Mill.), and loblolly pine (*P. taeda* L.). Invasive plants, especially annual grasses (Box 4.4), can spread rapidly after fire, particularly in high-severity burns (D'Antonio 2000; Kerns et al. 2006; Keeley and McGinnis 2007). Forest sites treated with prescribed fire, which are often near the wildland-urban interface and roads, are also well positioned for invasive plant introduction and spread (Keeley et al. 2003).

The success of plant invasions is regulated by competition from resident plants (Levine 2000; Seabloom et al. 2003), and land managers can alter post-disturbance (logging, fire) invasive establishment by seeding to increase native plant competition. Although native plant competition can be overwhelmed by invasive plant seed abundance (D'Antonio et al. 2001; Lonsdale 1999), resistance related to soil properties is more likely to withstand seed abundance. Native plant competition with invasive plants can also be affected by the effects of predation, herbivory, and pathogens associated with native species. Native plant competition may change as temperature and ambient CO_2 increase; numerous studies have documented that weedy plants are more productive in an elevated CO_2 environment (Ziska and George 2004).

Propagule pressure, which includes seed size, numbers, and temporal and spatial patterns, is perhaps the most important driver of successful invasions in

forest ecosystems (Tilman 1997; Colautti et al. 2006; Eschtruth and Battles 2009; Simberloff 2009). For invasive plants, propagule pressure is largely controlled by factors other than climate. For example, the most critical factors projecting plant invasion in eastern hemlock (*Tsuga canadensis* [L.] Carrière) forests in the eastern United States are overstory canopy disturbance and propagule pressure (Eschtruth and Battles 2009). However, little is known about how biotic and abiotic resistance factors interact with propagule supply to influence exotic plant invasion (D'Antonio et al. 2001; Lonsdale 1999).

Atmospheric CO_2 may influence seed production through enhanced flowering under elevated CO_2, increasing the probability that a smaller seed can establish a viable population (Simberloff 2009). Of greater concern is how climate change may alter human activities that transfer seeds. For example, climate change could alter tourism and commerce, enhance survival of seeds during transport (Hellmann et al. 2008), and shift recreation to higher elevations. Changes in atmospheric circulation patterns could also alter wind-dispersed species, allowing new species to arrive in areas that previously had few seeds.

Climate change will affect invasive plants in forests because of the potential for increased ecological disturbance, effects of warming on species distributions, enhanced competitiveness of invasive plants owing to elevated CO_2, and increased stress to native species and ecosystems (Dukes and Mooney 1999; Breshears et al. 2005; Pauchard et al. 2009; Ziska and Dukes 2011). Warming will increase the risk of invasion in temperate mountainous regions because cold temperature has tended to limit the establishment of invasive plants.

Empirical models suggest that a warmer climate could result in both range expansion and contraction for common invasive plants (Sasek and Strain 1990; Pattison and Mack 2008; Bradley et al. 2009; Kerns et al. 2009), although these types of species distribution models do not account for species ecophysiology and biotic interactions. Process-based models may ultimately prove more robust for prediction, although model parameters are quantified from experimental data or the research literature, which themselves have uncertainties.

For management responses to plant invasions to be cost effective and successful, assertive action is needed in the early phase of invasion. A potentially useful approach is a climate change-based modification of the Early Detection and Rapid Response System (National Invasive Species Council 2001). For example, risk assessment could be done over broader geographic areas than has been performed in the past (Hellman et al. 2008). Unfortunately, some biocontrol methods may no longer be effective in a warmer climate (Hellmann et al. 2008), and some herbicides are less effective on plants grown in elevated CO_2 (Ziska and Teasdale 2000). The successful control of invasive plants over large forest landscapes will depend on knowledge about resistance of native species to invasion and our ability to limit propagule pressure.

4.5 Erosion, Landslides, and Precipitation Variability

Based on analysis of recent climate records and the projections of climate change simulations, hydroclimatic extremes will become more prominent with a warming climate (O'Gorman and Schneider 2009; Trenberth et al. 2009), with potential increases in flood frequency, droughts and low flow conditions, saturation events, landslide occurrence, and erosion. Ecosystems are expected to differ in their response to changes in precipitation intensity and inter-storm length because of differences in geomorphic conditions, climate, species assemblages, and susceptibility to drought. For erosion, these differences may be predictable with a general mass balance framework, but other processes are poorly understood, such as the effect of drought on tree mortality, vegetation resistance to insects and pathogens, and subsequent feedbacks to erosion processes. The indirect effects of disturbances (e.g., fire, insect infestations, pathogens) to shifts in water balance will complicate the response of erosion. Changing species composition will also potentially affect forest ecosystem water balance (see Chap. 3).

4.5.1 Erosion and Landslides

Changes in precipitation intensity, and in the magnitude and frequency of precipitation events that saturate soil and cause runoff, will interact with mass wasting and erosion. Potential annual increases and decreases in precipitation will directly contribute to the amount of water available to drive mass wasting at seasonal and event scales. Increases in extremes of precipitation intensity (Easterling et al. 2000; Karl and Knight 1998), rain-on-snow during mid-winter melt (Hamlet and Lettenmaier 2007; Wenger et al. 2011), and transport of moisture in atmospheric rivers (Ralph et al. 2006; Dettinger 2011) can increase pore water pressure on hillslopes, thus increasing the risk of landslides, erosion, and gully formation for individual storms. Seasonal to annual changes in precipitation will contribute to soil moisture and groundwater levels, which can amplify or mitigate individual events.

Direct effects of some climatic changes on sediment yield and mass wasting may be overshadowed by longer term, indirect effects through vegetation response (Istanbulluoglu and Bras 2006; Collins and Bras 2008; Goode et al. 2011). Although decreasing precipitation in some places might suggest reduced risks of erosion or landslides, this change may have indirect effects on mortality and thinning of vegetation and fire risk, which could in turn increase erosion and landslides through lower root reinforcement of soil and higher exposure of soil to precipitation. For example, paleoclimatic and paleoecological evidence links periods of drought and severe fire to severe erosion events (Briffa 2000; Meyer and Pierce 2003; Whitlock et al. 2003; Pierce et al. 2004; Marlon et al. 2006). At shorter time scales, years of widespread fire are linked to severely dry and warm years (e.g., McKenzie et al. 2004; Morgan et al. 2008; Littell et al. 2009). As we shift toward a drier and warmer climate in the western United States, more areas are likely to burn

annually (e.g., Littell et al. 2009; Spracklen et al. 2009), with resulting postfire debris flows (Meyer and Pierce 2003; Luce 2005; Shakesby and Doerr 2006; Moody and Martin 2009; Cannon et al. 2010). Breshears et al. (2005) documented drought-induced canopy mortality of ponderosa pine, followed by erosional loss of topsoil and nutrients, with subsequent species replacement by pinyon pine and juniper. These types of state transitions may indicate the type of complex feedbacks that will lead to permanent shifts in dominant vegetation, rather than to recovery following disturbance.

Adjustment of canopy density and root distributions to longer inter-storm periods may increase the efficiency of use of rain or snowmelt (Hwang et al. 2009; Brooks et al. 2011). The response of both annual runoff and runoff from extreme events may be amplified or mitigated by forest canopy adjustment to temperature, moisture, N, and atmospheric CO_2. Increased precipitation intensity and amount, combined with lower root biomass from a drier climate, can yield more unstable slopes. Shifts in species dominance can also cause changes in root depth and cohesion (Hales et al. 2009). The spatial pattern of unstable slope conditions that can lead to landslides is influenced by interactions among the lateral redistribution of soil water in large events, the resulting pattern of high pore pressures with topographic slope, and root cohesive strength (Band et al. 2011).

4.5.2 Drought and Water Supply

Projections of drought extent over the next 75 years show that the proportion of global land mass experiencing drought will double from 15 to 30 % (Burke et al. 2006), and on most land masses, dry season precipitation is expected to decline by 15 % (Solomon et al. 2009). Projections for the largest declines in the United States are in the Southwest, strongly affecting water supply (Barnett and Pierce 2008; Rajagopalan et al. 2009). As noted above, lower precipitation will probably increase both forest mortality (Allen et al. 2010; Holden et al. 2011a) and fire risk (Westerling et al. 2011); however, forest mortality may not substantially mitigate runoff reductions associated with decreased precipitation (Adams et al. 2012). Historical observations of interannual variability in precipitation in the western United States have shown substantial increases in variability in the last 50 years (Luce and Holden 2009; Pagano and Garen 2005), even in areas not projected to show precipitation declines. Short-term severe droughts have consequences for vegetation (Holden et al. 2011b; van Mantgem et al. 2009) and water supply.

Although there has been interest in using forest harvest to augment water supplies, most increases in water yield after harvest occur in wet years (Brown et al. 2005; Ford et al. 2011), which may be less frequent in the future. In addition, water yield increases in snow environments occur earlier in the year, exacerbating flow timing issues caused by climate change (Troendle et al. 2010). Finally, in warmer and moister locations, increases in water yields can be replaced by decreases as young vegetation reestablishes within a few years (Brown et al. 2005; Ford et al. 2011).

4.6 Disturbance Interactions

4.6.1 Disturbances and Thresholds

Understanding interactions among disturbance regimes is a significant challenge for projecting the effects of climate change on forest ecosystems (Bigler et al. 2005; Busby et al. 2008) (Box 4.5). For example, how will massive outbreaks of bark beetles, which kill trees by feeding on cambial tissues, increase the potential for large severe wildfires in a warming climate (Box 4.1)? Interactions between processes can amplify or mute the overall effects of changes in complex forest ecosystems. The predominance of negative and positive feedbacks within and between processes will determine the stability or instability of the system.

Box 4.5: Response of Western Mountain Ecosystems to Climatic Variability and Change: The Western Mountain Initiative

The Western Mountain Initiative (WMI) uses paleoecological studies, contemporary studies, and modeling to understand responses to climatic variability and change in mountainous landscapes in the 11 large conterminous Western states (http://westernmountains.org). Initiated in 1991, the WMI consists of ten scientific laboratories in two federal agencies and four universities.
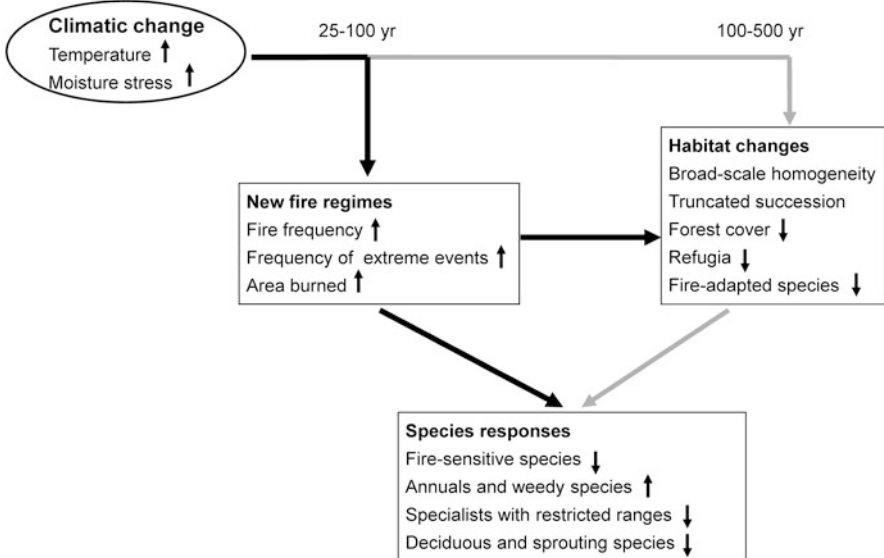
Research has documented how climatic variability and change affect long-term patterns of snow, glaciers, and water geochemistry; forest productivity, vigor, and demography; and changing patterns of treeline dynamics and forest disturbances. Empirical and simulation modeling indicates that major changes in hydrologic function and ecological disturbance will occur in a warming climate. WMI data show that extreme disturbances have rapidly altered the structure and function of forest ecosystems over the past decade (Peterson et al. 2012).

WMI research on disturbance interactions and their effects on ecosystem processes indicates that *synergistic interactions between disturbances produce larger effects than would occur from an individual disturbance*, especially when combined with chronic stressors such as air pollution, periodic drought, and reduced snowpack. For example, bark beetle outbreaks have been linked to increased likelihood of stand-replacing fire and changes in fire behavior, with the nature of the effect depending on the time since outbreak. Combined with increasing climatic stress on tree populations and growth, disturbance interactions can alter forest structure and function faster than could be expected from species redistribution or disturbance alone. Simultaneous climatically driven shifts in the locations of species optima, ecosystem productivity, disturbance regimes, and interactions between them

(continued)

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can reset forest succession over large areas and short timeframes. (Figure is a conceptual model of relative time scales for disturbance versus climate change alone to alter ecosystems. The focus is on fire, but the same logic applies to insect outbreaks. Adapted from McKenzie et al. (2004))

Climatic change
Temperature ↑
Moisture stress ↑

25-100 yr   100-500 yr

Habitat changes
Broad-scale homogeneity
Truncated succession
Forest cover ↓
Refugia ↓
Fire-adapted species ↓

New fire regimes
Fire frequency ↑
Frequency of extreme events ↑
Area burned ↑

Species responses
Fire-sensitive species ↓
Annuals and weedy species ↑
Specialists with restricted ranges ↓
Deciduous and sprouting species ↓

Disturbance interactions may rapidly bring ecosystems to thresholds (Groffman et al. 2006). For example, Allen and Breshears (1998) and Breshears et al. (2005) documented rapid dieback of pinyon pine across the arid Southwest. Mature trees were pushed over a threshold by a combination of "global-change type drought" (Breshears et al. 2005) and an opportunistic bark beetle invasion. Regeneration of pinyon pine will determine whether this mortality represents a threshold for the ecosystem. Characteristic patterns of patchiness or continuity may indicate thresholds that have been approached or crossed (Scheffer et al. 2009). For example, the invasion of sagebrush (*Artemisia tridentata* Nutt.) steppe by cheatgrass (Fischer et al. 1996) and of the Sonoran Desert by buffelgrass (*Cenchrus ciliaris* L.) (Esque et al. 2007) provide fuel continuity and the potential for much more extensive wildfires than non-invaded areas with patchy fuels.

A notable threshold response to multiple stressors is the reproductive cycle of mountain pine beetle (Logan and Powell 2001) (see Sect. 4.3), whose outbreaks have killed mature trees across millions of hectares of pine in western North America. Within particular ranges of winter temperatures and growing-season degree days, the reproductive cycle is synchronized to the seasonal cycle, permitting

maximum survival and epidemic population size. This "adaptive seasonality," combined with drought-caused and age-related vulnerability of the host species, may promote an abrupt increase in mortality of lodgepole pine (Hicke et al. 2006).

Conceptually, thresholds are fairly well understood. Modeling of thresholds has by necessity taken place in simplified (often virtual) ecosystems, and a major challenge remains to apply such sophistication to real-world systems outside the specific examples chosen by modelers to test their hypotheses. A larger challenge will always be the unpredictability of the occurrence of contingent, interacting events that push systems across thresholds.

4.6.2 Stress Complexes: From Conceptual to Quantitative Models

In the context of the effects of climate change on ecosystems, sensitivity to disturbance interactions is extended to environmental drivers not usually identified as disturbances. For example, extreme temperatures, drought, and air pollution put forest ecosystems under stress, which may increase their vulnerability to "true" disturbances such as fire, insect outbreaks, and pathogens. Following McKenzie et al. (2009), we refer to interacting stresses as stress complexes and present three examples from the Sierra Nevada, Alaska, and the Southeast.

A striking feature of mixed conifer forests in the southern Sierra Nevada and southern California is ambient air pollution, particularly elevated ozone, which affects plant vigor by reducing net photosynthesis and therefore growth (Peterson et al. 1991) and is often concentrated at middle and upper elevations (Brace and Peterson 1998). Air pollution exacerbates drought stress from warmer temperatures, which amplifies biotic stresses such as insects and pathogens (Ferrell 1996). The stress complex for California forests is represented in Fig. 4.2; interacting disturbances form the core of drivers of ecosystem change, modified by climate, management, and air pollution.

Alaska has experienced massive fires in the last decade, including the five largest fires in the United States. Over 2.5 million ha burned in the interior in 2004. Concurrently (1990s), massive outbreaks of the spruce bark beetle occurred on and near the Kenai Peninsula in south-central Alaska (Berg et al. 2006) (Fig. 4.3). 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 both extent and percentage mortality (over 90 % in many places) (Berg et al. 2006). Both wildfire and bark beetle outbreaks are associated with warmer temperatures in recent decades (Duffy et al. 2005; Werner et al. 2006). At the same time, major hydrological changes are underway from the cumulative effects of warming. Permafrost degradation is widespread in central Alaska, shifting ecosystems from birch forests to wetland types such as bogs and fens (Jorgenson et al. 2001). If broad-scale water balances become increasingly negative, peatlands may begin to support upland forest species (Klein et al. 2005).
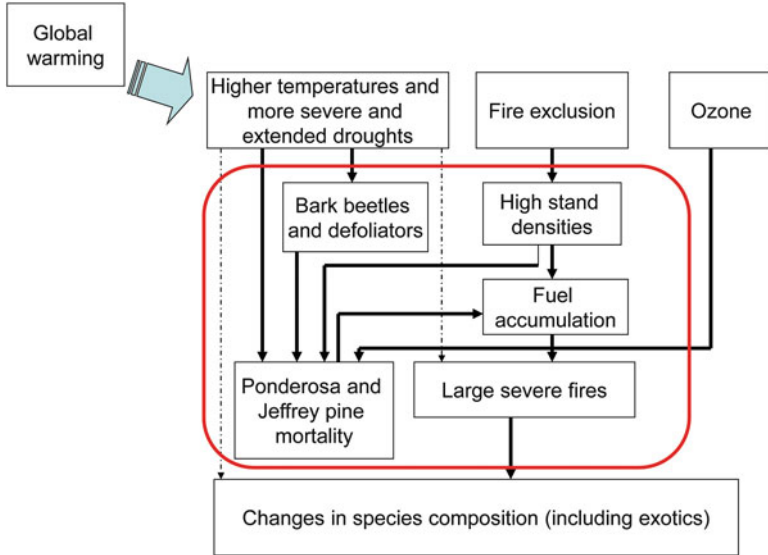
Fig. 4.2 Conceptual model of stress complexes in mixed conifer forests of the southern Sierra Nevada and southern California. The effects of insects and fire disturbance regimes (*red box*) and of fire exclusion are exacerbated by higher temperature. Stand-replacing fires and drought-induced mortality both contribute to species changes and invasive species (Modified from McKenzie et al. 2009)

Fig. 4.3 Mortality of white spruce from bark beetle attack on the Kenai Peninsula, Alaska (Photo by W.M. Ciesla, Forest Health Management International, Bugwood.org)
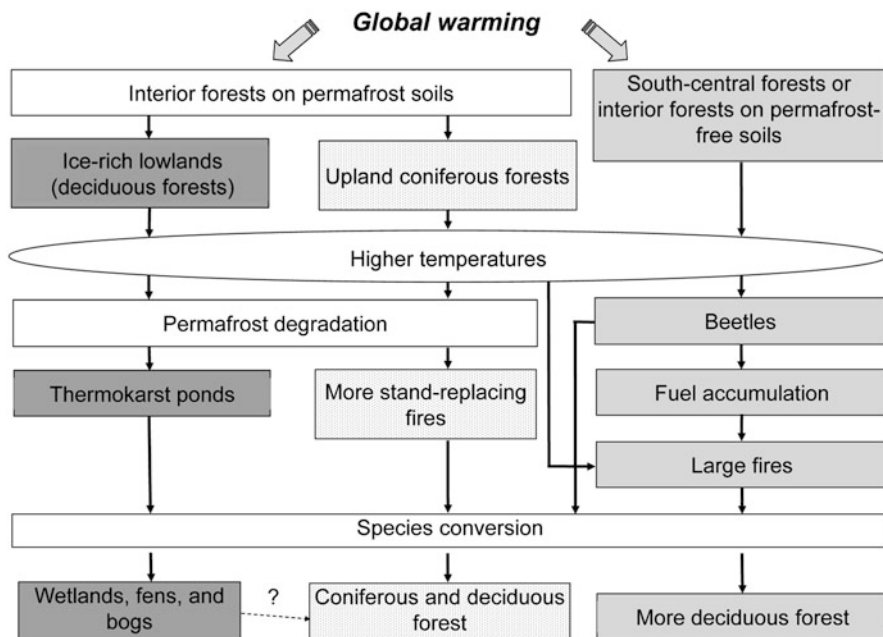
Fig. 4.4 Conceptual model of stress complexes in the interior and coastal forests of Alaska. Rapid increases in the severity of disturbance regimes (insects and fire) are triggered by a warmer climate. Stand-replacing fires, massive mortality from insects, and permafrost degradation contribute to species changes and conversion to deciduous life forms (Modified from McKenzie et al. 2009)

The stress complex for Alaska is represented conceptually in Fig. 4.4; upland and lowland ecosystems may follow parallel but contrasting paths toward new structure and species composition.

Much of the forested landscape in the southeastern United States is adapted to frequent fire, and prescribed fire is a mainstay of ecosystem management. Fire-adapted inland forests overlap geographically with coastal areas affected by hurricanes and potentially by sea-level rise (Ross et al. 2009), such that interactions between wildfires and hurricanes are synergistic (Fig. 4.5). For example, dry-season (prescribed) fires may have actually been more severe than wet-season (lightning) fires in some areas, causing structural damage via cambium kill and subsequent increased vulnerability to hurricane damage (Platt et al. 2002). The stress complex for the Southeast is represented conceptually in Fig. 4.6.

4.6.3   Uncertainties

Current knowledge about multiple stressors is mainly qualitative, despite case studies in various ecosystems that have measured the effects of interactions and

Fig. 4.5 Interactions between wildfire and hurricanes are synergistic in the southern United States. Figure depicts a longleaf pine/saw palmetto flatwoods stand on the Atlantic coastal plain, 2.5 years after a hurricane and with a previous history of prescribed fire (Courtesy of the Fire and Environmental Research Applications team, U.S. Forest Service, Digital Photo Series)

even followed them over time (Hicke et al. 2012b). In the three examples above, the directional effects of warming-induced stressors may be clear (e.g., in California, species composition shifts to those associated with frequent fire). However, the magnitudes of these effects are not, nor are the potentially irreversible crossings of ecological thresholds. Given the complexity and diversity of potential interacting stressors in U.S. forests, a fruitful way to advance quantitative knowledge may be with explicit simulations with models of "intermediate complexity" to ascertain the sensitivity of ecosystems to uncertainties associated with key parameters (e.g., the thickness of the arrows in Figs. 4.2, 4.4 and 4.6). As the climate continues to warm, new empirical data will incrementally help to quantify disturbance and stressor interactions, providing greater certainty about the nature of stress complexes in forest ecosystems.
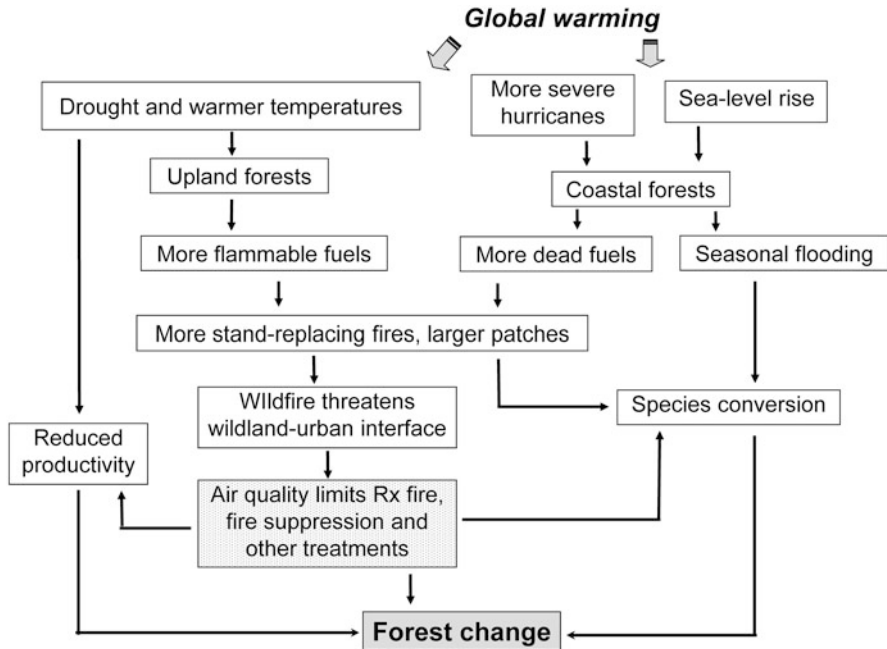
Fig. 4.6 Conceptual model of stress complexes in the interior and coastal forests of the Southeast. Increases in the severity of hurricanes are triggered by global warming as sea level rises. Warmer and drier climate in uplands leads to longer periods with flammable fuels. Changes in fire and hydrologic regimes, and responses to them, lead to species change and altered C dynamics

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