Chapter 21
Forest Health in the Anthropocene

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21.1 Introduction

Forests cover approximately one third of Earth's terrestrial surface (FAO and UNEP 2020). They provide a wide range of vital environmental and socioeconomic benefits to all people in the form of ecosystem services. These services include fibre, fuel, non-timber forest products, biodiversity, carbon sequestration, soil and water protection and socio-cultural values (Shvidenko et al. 2005; Brandt et al. 2013; Sing et al. 2017). As the global population rises, the demand for ecosystem services has increased while the capacity of forests to deliver them has declined due to high rates of deforestation (Carpenter et al. 2009; Seidl et al.2016; FAO and UNEP 2020), and increased rates of disturbance (Johnstone et al. 2016; Seidl et al. 2017). The capacity to quantify the health of forests and assess their ability to sustain ecosystem services into the future has become a fundamental challenge to resource managers in a rapidly changing world.

All forests are adapted in some way to disturbance events that alter ecosystem processes [(White and Pickett 1985; Turner 2010;) see Box 21.1 for definitions]. Following disturbance, forest ecosystems will either regenerate or reorganize. If an ecosystem is resistant to disturbance and returns to a similar pre-disturbance state, it is considered resilient (Holling 1973; Gunderson 2000; Folke et al. 2004; Scheffer 2009). If instead the disturbed ecosystem is sufficiently changed that it regenerates to a different state (e.g. a forest becomes a grassland; Fig. 21.1), then it has undergone a regime shift (Folke et al. 2004; Scheffer 2009; Allen et al. 2016; Johnstone et al. 2016). Relationships between forms of disturbance and the probability of a regime shift are highly non-linear and characterized by thresholds where a relatively small

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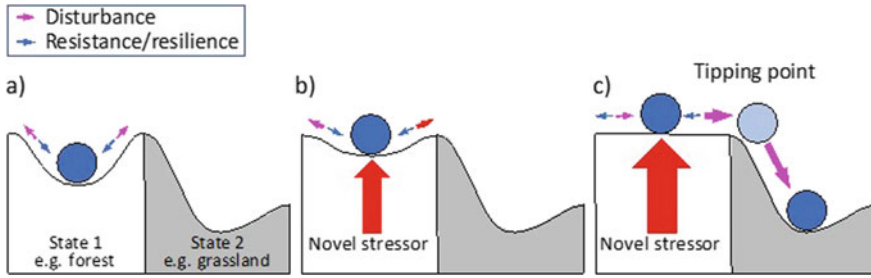
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Fig. 21.1 Conventional cup-and-ball model of ecosystem resilience (Lamothe et al. 2019). The ball represents the current ecosystem, the valleys indicate the possible ecosystem states [e.g. forests (white region) and grasslands (grey region)] and the weight of the arrows indicates the relative strength of interactions. **a)** Forests are resistant and resilient to disturbance where ecosystem processes (blue arrows) maintain them in or return them to their original state following perturbation (pink arrows). **b)** Forests are less resistant and resilient to disturbance due to alteration of ecosystem processes by a novel stressor (red arrow) such as climate change and are therefore less likely to return to their original state following perturbation. **c)** Forests have lost resistance and resilience due to a novel stressor and disturbance has perturbed them beyond their original state to a tipping point where they undergo a regime shift and rapidly reorganize into a new ecosystem

change may lead to a large shift in the state of an ecosystem (Scheffer et al. 2001)—a process known as a tipping point (Brook et al. 2013; Reyer et al. 2015). Over large spatial scales and long time spans, and without significant human intervention, disturbances tend to recur within a natural range of variability (Landres et al.1999). At these scales the characteristics of disturbances together with their return intervals make up a disturbance regime (Turner 2010). Whereas disturbance instigates processes of ecosystem renewal (White and Pickett 1985; Thom et al. 2016), disturbance regimes generate diverse landscapes (Turner 2010; Turner and Gardner 2015; Thom and Seidl 2016).

Box 21.1 Terms and definitions associated with forest ecosystem health

Term	Definition
Disturbance	Any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment (White and Pickett 1985)
Natural range of variability	The ecological conditions, and the spatial and temporal variation in these conditions, that are relatively unaffected by people, within a period of time and geographical area appropriate to an expressed goal (Landres et al. 1999)

Term	Definition
Disturbance regime	The spatial and temporal dynamics of disturbances that include spatial distribution, frequency, return interval, rotation period, size, intensity, and severity (Turner 2010)
Resistance	The influence of structure and composition on the severity of disturbance (DeRose and Long 2014)
Resilience	The ability of an ecosystem to absorb disturbances and re-organize under change to maintain similar functioning and structure (Scheffer 2009)
Tipping point	A threshold at which a small change in conditions leads to a strong change in the state of a system (Brook et al. 2013)
Regime shift	A rapid modification of ecosystem organization and dynamics with prolonged consequences (Scheffer and Carpenter 2003)

(continued)

Sustainable extraction of services from forests is contingent upon ecosystems that are resistant and resilient to disturbance (Seidl et al. 2016; Grimm et al. 2016). However, forests around the world are increasingly forced to contend with anthropogenic stressors that influence disturbances both directly via fragmentation, pollution and introduced alien invasive species (Vilà et al. 2010; Paoletti et al. 2010; FAO and UNEP 2020) and indirectly through climate change-mediated alterations to ecosystem processes (Raffa et al. 2009; Seidl et al. 2017; Williams et al. 2019). These novel stressors may reduce the resiliency of forest ecosystems (Fig. 21.1b), increase the probability of abrupt tipping points and regime shifts (Fig. 21.1c), and ultimately threaten the sustainability of ecosystem services. Quantification of the resilience of forest ecosystems and detection of critical changes in condition that may compromise ecosystem service sustainability grows more essential with ongoing global change. In this chapter I will review the concept of forest health, its utility as an indicator of forest ecosystem resistance and resilience to disturbance, and its relevance in an era of extensive global change known as the Anthropocene.

21.2 A Working Definition of Forest Health

The concept of "forest health" as an indicator of ecosystem sustainability is widely accepted; however, its broad adoption has been associated with applications that do not correspond with the term's intent to describe the health of forest ecosystems (Raffa et al. 2009). Thus, a clear and concise definition of forest health is required before it is possible to fully consider its utility and relevance in a changing world. Edmonds et al. (2011) provide a list of eight definitions of forest health. Several

refer to management objectives and human needs, and are considered "utilitarian" (Kolb et al. 1994; Edmonds et al. 2011; Trumbore et al. 2015), while the remainder are based on aspects of ecosystem function and processes. Utilitarian concepts of health are appropriate in agriculture or agroforestry systems that have well-defined management objectives such as the plantation shown in Fig. 21.2a established for the production of fibre. These systems provide valuable services, but they are limited in most aspects of ecological function and are unlikely to be very resistant or resilient to disturbance. Moreover, allowing such systems to behave naturally, for example permitting the growth of competing vegetation, would likely lead to their failure because their goals are to provide socioeconomic benefits often at the expense of ecological processes (Raffa et al. 2009). Based on a utilitarian definition of forest health, the success or failure of a plantation to meet the objective of fibre production would cause it to be deemed a healthy or unhealthy forest, respectively, regardless of ecological condition.

The pitfalls of utilitarian definitions of forest health become more obvious when applied to natural forests. If a disturbance like the native bark beetle outbreak in Fig. 21.2b were to occur in a working forest, the beetle would be considered a pest and the forest unhealthy; however, if the forest was part of a park or protected area,
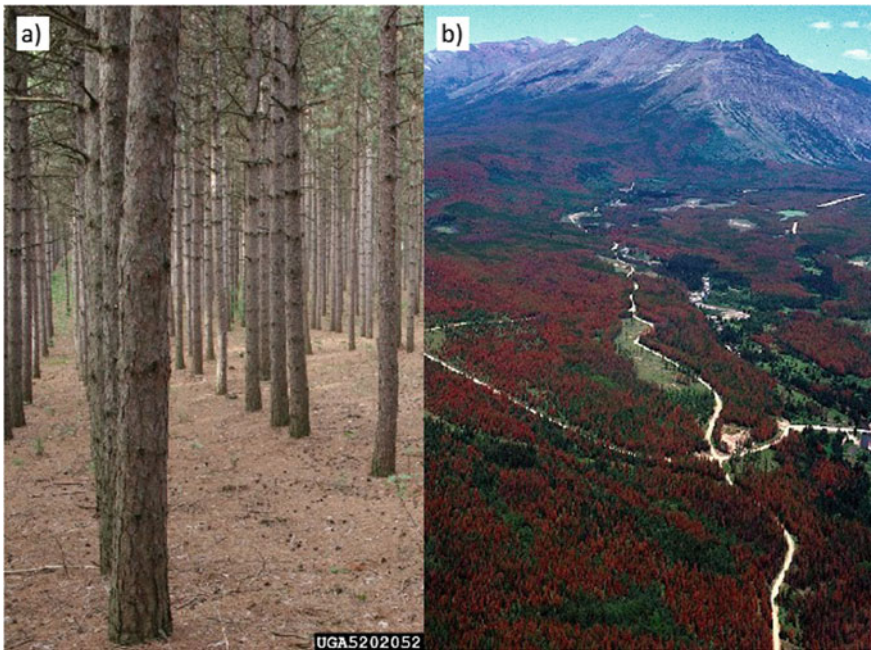

Fig. 21.2 a) A red pine (Pinus resinosa) plantation in central Wisconsin established to produce fibre (*Source* Steven Katovich, Bugwood.org). **b)** A lodgepole pine (*P. contorta* var. *latifolia*) forest in southern British Columbia affected by an outbreak of the mountain pine beetle (*Dendroctonus ponderosae*)

then the beetle would be considered a natural disturbance agent and part of the normal healthy functioning of such an ecosystem (Raffa et al. 2009). Layering of human expectations onto natural forest ecosystems leads to conflicts that preclude the general use of the term "forest health" as an indicator of forest vitality. Processes that make up a functioning forest ecosystem do so independent of human expectations. They include not only the inherent biological, geochemical and physical elements that form the basis of the ecosystem, but also natural disturbances such as windstorms, insect and disease outbreaks and wildfire that arise from interactions among them. All of these processes are essential to resilient ecosystems (Folke et al. 2004; Turner 2010; Johnstone et al. 2016) and should therefore be the basis of a healthy forest. Indeed, several recent studies have emphasized that processes associated with ecosystem resilience must be emphasized when considering forest health, and that health should be measured against ecosystem responses to external drivers and perturbations arising from global change (Raffa et al. 2009; Millar and Stephenson 2015; Trumbore et al. 2015).

Based on the preceding argument, I propose the following definition of forest health that is free from human values and expectations:

> Forests are healthy when their underlying ecological processes operate within a natural range of variability so that on any temporal or spatial scale they are resistant and resilient to disturbance.

It is important to note that this definition is not intended to imply that management of forests toward objectives associated with human values should be abandoned in favour of natural ecological processes. Indeed, careful management of both natural and planted forests can deliver products and services while maintaining ecosystem function (Brandt et al. 2013; Gauthier et al. 2015; Trumbore et al. 2015; Wingfield et al. 2015; Pohjanmies et al. 2017). Instead, restricting the definition of forest health to ecosystem processes allows assessments of the potential of forests (natural, planted or combinations) to remain resilient and provide services in an era of global change.

21.3   Forest Health: From Stands to Landscapes

Since forest health has been defined in terms of resistance and resilience to disturbance, the processes of disturbance and how they interact with ecosystems must be considered in detail. Forest disturbances comprise discrete events that can be manmade (e.g. harvesting or land clearing) or natural. Natural disturbances are either biotic, such as insect or pathogen outbreaks, or abiotic such as wildfires, windstorms, floods, avalanches and volcanic eruptions. By definition, disturbances can operate at spatial scales ranging from individual trees to entire landscapes. However, from the perspective of forest health, a stand[1] is the finest scale at which disturbance will

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[1] Defined as an area of forest or woodland whose structure or composition is different from adjacent areas (Lindenmayer and Franklin 2002).

be considered because the stand (i) is the fundamental unit of forest management programs, and (ii) it captures key processes associated with ecosystem resilience (McElhinny et al. 2005). The broadest scale of consideration will be the forest landscape which is simply defined as multiple sets of stands that cover an area ranging from hundreds to tens of thousands of hectares (Lindenmayer and Franklin 2002).

21.3.1   Health of Forest Stands

At the scale of a forest stand, the outcome of a disturbance event, and the potential for an ecosystem to either regenerate or reorganize, is a result of complex interactions among disturbance type, severity, structure and composition, and topography of the stand in question (White and Jentsch 2001). Abiotic disturbances such as fire can cause the direct mortality of the majority of plants and animals in an individual stand depending on its severity (Turner et al. 1998). If a fire results in destruction of propagules from the original stand (e.g. a seed bank), then the reduced likelihood of regeneration to an equivalent pre-disturbance state means that the stand was neither resistant to disturbance nor resilient, and therefore unhealthy prior to being disturbed. In contrast, biotic disturbance by an insect defoliator may not directly cause the mortality of any component of a stand, but simply alter the competitive advantage of dominant trees within the overstory leading to a change in canopy composition (Cooke et al. 2007). In this case the stand was largely resistant and resilient to the disturbance, and therefore healthy. Between these extremes, disturbance by both abiotic and biotic agents can be less or more severe, respectively. The severity continuum is further influenced by stand structure and composition. A young stand, or one with a low density of trees, may comprise insufficient fuels to support a high-severity fire (Turner et al. 1994) allowing the stand to regenerate and remain resilient. Similarly, stands without suitable and susceptible host-tree species would be completely resistant to an outbreak of a specialist pathogen or insect disturbance agent (Jactel et al. 2017). Lastly, topographical features of a stand, such as slope and aspect, may influence the severity of both abiotic and biotic disturbances (White and Jentsch 2001) thereby affecting the health of a given stand.

The resilience and health of stands is also potentially influenced by biological legacies that persist through the disturbance event such as surviving trees, seedbanks and/or other below ground organs (Seidl et al. 2014; Johnstone et al. 2016). Given that forest ecosystems have evolved with disturbance, species within them may also display long-term biological legacies in the form of adaptive traits that improve their resistance and/or resilience (Keeley et al. 2011). For example, cone serotiny (the release of seeds in response to an environmental trigger) in some *Pinus* species facilitates the dissemination of seeds immediately following a stand-replacing fire, thus ensuring regeneration of a similar pre-disturbance ecosystem (Turner et al. 1998). Alternatively, many tree species resist disturbance by insect herbivores through adaptations that allow them tolerate tissue loss such as increased photosynthetic and

growth rates, and reallocation of stored resources (Strauss and Agrawal 1999). Similarly, following high-severity fires *Eucalyptus* species resprout epicormically from suppressed, dormant buds along their boles and replace stand canopies within a year of disturbance (Keeley et al. 2011).

21.3.2   Health of Forest Landscapes

While the same disturbances that affect stands will affect landscapes, their relevance to resiliency and forest health may change as spatial and temporal scales increase. For example, disturbance that results in the local destruction of propagules, as with our example of fire above, may lead to the conclusion that a stand was unhealthy prior to fire. But if the stand is situated among other stands (i.e. in a landscape) capable of dispersing seeds into the disturbed area, then regeneration is possible and resiliency is likely. In contrast, local eruption of an aggressive bark beetle population may cause the mortality of a relatively small proportion of mature trees in a mixed species stand, leaving it largely intact. But if surrounding stands contain susceptible host trees the eruption may propagate over the landscape causing extensive tree mortality and threatening ecological processes such as biodiversity and carbon sequestration (Kurz et al. 2008; Raffa et al. 2008).

Disturbance creates gaps in vegetation and alters available light and nutrients, initiating secondary succession within the openings (White and Pickett 1985; White and Jentsch 2001; Turner and Gardner 2015). Variation in these processes will, over time, produce a mosaic of stands across a landscape in different states of regeneration or reorganization (Fig. 21.3). Although the impacts of disturbance may be scale dependent, some forms of disturbance to stands such as that caused by fire or insects can have long-term, persistent impacts on species, communities and ecosystems (White and Jentsch 2001) as a consequence of the biological legacies described above. These forms of disturbance have been referred to as key structuring processes that dominate the formation of patterns over spatial scales of hundreds of metres to hundreds of kilometers (Holling 1992), leading to heterogeneous landscapes. The resultant heterogeneity will influence interactions and exchanges among stands, and ultimately the biotic and abiotic processes associated with forest health at the landscape scale (Turner 1989; Krawchuk et al. 2020).

Heterogeneity influences the resistance of forest landscapes to disturbance through impacts on the susceptibility of stands and the capacity for disturbances to spread within landscapes (Turner and Gardner 2015; Krawchuk et al. 2020). Tree species composition, physiological condition, age and climatic conditions are well known factors that influence the susceptibility of forest stands within a landscape to biotic disturbances by insects and pathogens (Cooke et al. 2007; Raffa et al. 2008; Jactel et al. 2017). The susceptibility of stands to abiotic disturbances will also vary across forested landscapes. For example, areas that are more exposed (edges, gaps, ridgelines) will suffer more windthrow, and drier regions (south-facing slopes, valley
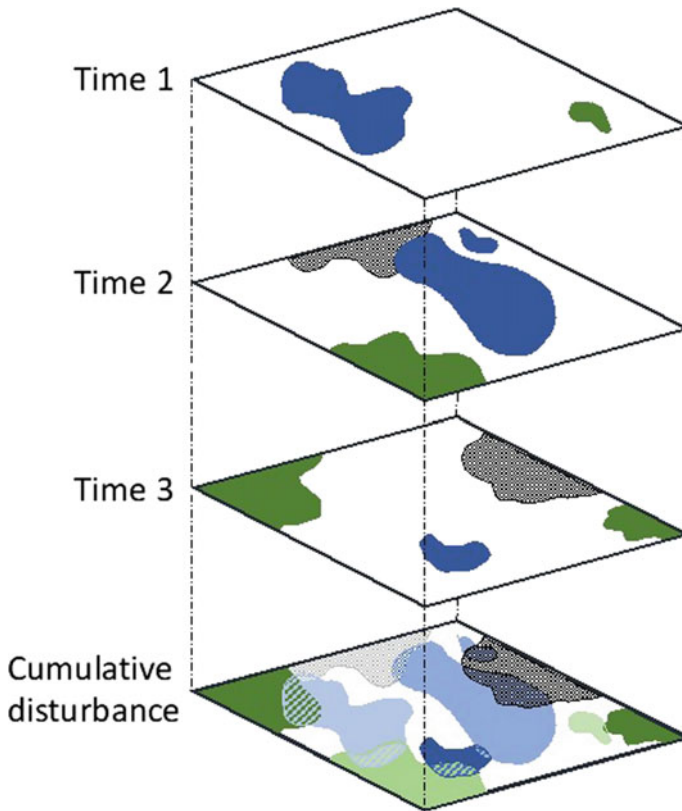
Fig. 21.3 Representation of multiple disturbances acting on the same landscape through time and cumulatively. Colour and pattern indicate different processes, darker shading in the cumulative landscape indicates more recent events. Modified from Parker and Pickett (1998)

bottoms) are more conducive to fire (Turner and Gardner 2015). The spread of disturbances through landscapes may also be impeded by heterogeneity. For example, the distribution of susceptible stands in a landscape will affect the ability of bark beetles to traverse it (Barclay et al. 2005; Raffa et al. 2008). Similarly, low- and moderate-severity wildfires in coniferous forests may be constrained by natural fire breaks and young stands (Turner et al. 1994; Turner and Gardner 2015). Due to the influence of landscape heterogeneity on disturbance susceptibility and spread, even extensive, potentially homogenizing disturbances such as large wildfires will perpetuate further heterogeneity (Turner et al. 1994; Turner 2010; Turner and Gardner 2015). Consider the landscape in Fig. 21.4. The disturbed area within the fire boundary contains areas of varying size with fire severities ranging from none to severe. Such a landscape may be considered resilient and healthy due to the increased probability that areas of severe disturbance can recruit key species to maintain ecological processes from nearby intact areas (Loreau et al. 2001; Krawchuk et al. 2020). By contrast, the
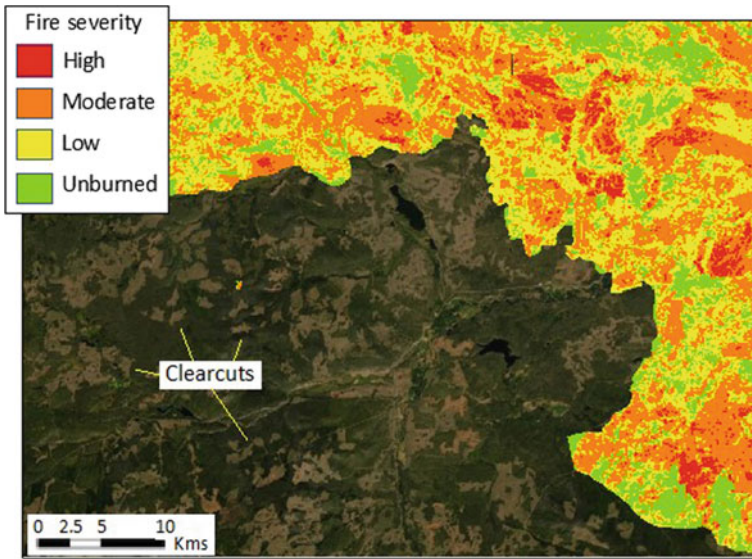
Fig. 21.4 Satellite image of a working forest in central British Columbia, Canada, and adjacent area that burned in a wildfire in 2017. Note the size, distribution and varying severity of the patches disturbed by fire as compared to the clearcuts in the unaffected forest. *Source* ESRI, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGrid, IGN, and the GIS User Community

unburned portion of the landscape in Fig. 21.4 has been disturbed by more regular clear-cut harvesting and is relatively less heterogeneous. Maintenance of heterogeneity over landscapes provides "spatial insurance" for healthy ecosystem function by facilitating spatial exchanges among local systems (Loreau et al. 2003).

Over long time-spans patterns of forest disturbance (i.e. disturbance regimes) become apparent with distinct distributions of type, severity, frequency and size (White and Jentsch 2001; Turner 2010; Turner and Gardner 2015). In the absence of anthropogenic alterations, disturbance regimes function within an historic or natural range of variability that can be used to represent the envelope of possible ecosystem conditions over a landscape (Landres et al. 1999). Implicit within the concept of a natural range of variability are the assumptions that ecosystems are dynamic and their responses to change are represented by past variability, and that they have a range of conditions within which they are self-sustaining, beyond which they are not (Keane et al. 2009). Thus, historical conditions can serve as a proxy for forest health (Swetnam et al. 1999) where the resilience of ecosystems is considered in the context of the type, severity, frequency, size, spatial distribution, and return intervals of disturbance. Deviation of disturbance processes within a forest landscape beyond the natural range of variability would threaten its resilience and health.

21.4   Forest Health and Global Change

Global change refers to the independent and interacting effects of anthropogenic stressors on ecosystems at a planetary scale. The primary drivers of global change affecting forests are climate change, land-use change and biotic invasions (Tylianakis et al. 2008). Impacts by these broad stressors on forests can be very complex and sometimes difficult to distinguish from natural variability. Given that the definition of a healthy forest defined above is derived from the processes of disturbance, resistance and resilience, I will examine the interactions of global change drivers with each process in turn using a range of recent examples. My emphasis will be on impacts by novel stressors that perturb forests beyond their natural range of variability (see Fig. 21.1). It is important to note that interactions seldom operate in isolation, and so I will also consider interdependencies for which there is documented evidence and acknowledge that many more interactions are likely at work. Finally, while most examples originate from the northern hemisphere, this is simply a byproduct of available data. The concepts they illustrate are relevant around the world.

21.4.1   Climate Change

Climate change refers to both global warming caused by human emissions of greenhouse gases and the resultant large-scale shifts in weather patterns and extremes. Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millennia (IPCC 2014). Increasingly, impacts to natural and human systems have been documented on all continents and across the oceans.

21.4.1.1   Disturbance Versus Climate Change

Changing the tempo, intensity, or spatial attributes of disturbance can alter disturbance regimes (Turner 2010; Johnstone et al. 2016; Seidl et al. 2017). As discussed above, when a regime has been modified beyond its natural range of variability then forest landscapes may no longer be resistant and/or resilient, and their health will have been compromised. Perhaps the greatest impact that climate change will have on forest ecosystems in the coming decades will arise from altered disturbance regimes (Lindner et al. 2010). Indeed, many forms of disturbance have already been influenced by climate change (Seidl et al. 2011, 2017). Among the most significant forms of disturbance affected to date are insect outbreaks and wildfire.

Biotic disturbances, primarily caused by insects, affect almost 44 million ha of forests in the northern hemisphere each year (Kautz et al. 2017). Insects are ectothermic, and therefore highly sensitive to changing climate. Not surprisingly, climate change has been implicated in alterations to many aspects of the spatial and

temporal dynamics of forest insects and their potential to cause disturbance. These alterations include shortened life cycle durations (Berg et al. 2006; Choi et al. 2011), increased thermally benign habitats (Carroll et al. 2004; Battisti et al. 2005; Jepsen et al. 2008), enhanced seasonal synchrony among trophic levels and/or the environment (Logan and Powell 2001; Jepsen et al. 2011) and reduced mortality from natural enemies (Stireman et al. 2005; Menéndez et al. 2008). The predominant outcome of these altered dynamics has been a general increase in the rate of biotic disturbance (Kautz et al. 2017; Seidl et al. 2017) potentially leading to modified disturbance regimes.

Despite the general perception that wildfires are increasing in severity around the world, evidence suggests that there is actually less fire in the global landscape today than centuries ago (Doerr and Santín 2016). That said, there are regions where disturbance by wildfire has increased, particularly in western North America. These increases have been attributed to warming-induced changes in atmospheric aridity leading to elevated evaporative demand and reduced fuel moisture, snowpack, and summer precipitation frequency (Abatzoglou and Williams 2016; Williams et al. 2019). Between 1972 and 2018, the area burned in California increased by over 400% (Williams et al. 2019), and virtually all projections based on climate scenarios suggest wildfire potential will continue to rise across western North America (Liu et al. 2010; Jolly et al. 2015). Increased rates of disturbance by fire beyond historic levels raise uncertainties regarding the capacity for forest ecosystem to remain healthy (Turner 2010; Kelly et al. 2013; Millar and Stephenson 2015; Coop et al. 2020).

Interactions among disturbance agents are a major component of disturbance regimes that create heterogeneous, resistant and resilient landscapes (see Fig. 21.3). However, increasing disturbance activity under climate change also means an increasing propensity for disturbance interactions, potentially exacerbating their severity (Buma 2015). In a review and synthesis of climate change effects on important abiotic and biotic disturbances, Seidl et al. (2017) found that links between an initial abiotic agent and subsequent biotic disturbances, especially by bark beetles in conifer forests, were particularly strong and led to amplification of disturbance in the majority of interactions. Bark beetle outbreaks generally arise following an acute pulse of defensively impaired trees that facilitate rapid population increases (Raffa et al. 2008, 2015). This resource pulse is often a result of an initial abiotic disturbance such as a wind storm (Kausrud et al. 2012), wildfire (Hood and Bentz 2007), or drought (Seidl et al. 2016a, b). These interactions can lead to the mortality of trees over many millions of hectares (Raffa et al. 2008). Disturbances at these scales are of particular concern since they are very likely to exceed natural ranges of variation.

21.4.1.2 Resistance Versus Climate Change

Rising temperatures have amplified drought-induced stress in forests around the world (Young et al. 2017; Stephens et al. 2018) and have affected the capacity of ecosystems to resist disturbance. This aspect of climate change is most evident in

interactions of forest ecosystems with phloem-feeding insects such as the bark beetles whose attack and colonization success are constrained by tree defenses that are sensitive to water availability (Raffa et al. 2015; Marini et al. 2017). Many conifers close stomata to protect xylem cells from cavitation during drought, reducing photosynthesis to near zero (Koepke and Kolb 2013). However, production and deployment of defensive resin is reduced under conditions of limited photosynthesis, thus lowering tree resistance to bark beetle attacks during droughts (Raffa et al. 2015).

Climate change-exacerbated droughts have also affected forest resistance to abiotic disturbances such as wildfire. Drought not only causes increased amounts of fuels in forests in the form of dead wood, it also reduces the moisture content within those fuels and alters the ratio of dead to live fuels within the canopy of living trees, thus reducing the resistance of some forests to fire and facilitating larger, more severe fires (Stephens et al. 2018; Nolan et al. 2020).

21.4.1.3 Resilience Versus Climate Change

The structural and functional changes in forests in response to disturbance may compromise their capacity to recover in a warming environment. Evidence is accumulating that forest ecosystem resilience may be affected by climate change-exacerbated wildfires. In the western region of the North American boreal forest, drier and warmer weather associated with climate change has decreased the resilience of ecosystems by reducing the interval between wildfires leading to altered patterns of regeneration (Whitman et al. 2019; Coop et al. 2020).

Similarly, in the western US, increasingly unfavorable post-fire growing conditions due to a changing climate have compromised ecosystem resilience by reducing seedling establishment and increasing regeneration failures (Harvey et al. 2016; Stevens-Rumann et al. 2018; Davis et al. 2019; Coop et al. 2020). These impacts comprise an abrupt tipping point given that fire has killed the adult trees that could have persisted in the warmer conditions, but since those conditions are no longer suitable for seedling establishment and survival, ecosystems cannot return to similar pre-disturbance conditions (Davis et al. 2019).

21.4.2 Land-Use Change

Land-use change typically refers to the permanent conversion of forests as opposed to temporary losses from wildfires or harvesting. Where land-use change leads to loss of forest, it results in disturbance well beyond the natural range of variability and complete negation of forest health. This form of global change is a significant impact to forested landscapes. Deforestation through land-use change is responsible for over one-quarter of forest loss around the world (Curtis et al. 2018). By contrast, partial land-use changes, also known as forest degradation, may be less severe and involve retention of some ecological processes (Ghazoul et al. 2015; Ghazoul and Chazdon

2017), allowing consideration of forest health. Since partial land-use changes are associated with diminished or constrained ecological function within forests, examples are broad and include extraction of non-timber forest products, collection of fuel wood, free-range livestock grazing, shifting cultivation, selective logging, urban encroachment and wildfire suppression (Thompson et al. 2013). These activities have the potential to alter all aspects of forest health.

21.4.2.1 Disturbance Versus Land-Use Change

Partial land-use changes can significantly alter the behaviour and characteristics of disturbances, especially abiotic disturbance. Wildfires depend on the coincidence of dry weather, available fuel and ignition sources (Jolly et al. 2015). As outlined above, weather conditions conducive to fire have increased due to climate change-related drought in many regions. In western North America, land-use changes have also affected the remaining two requirements for severe wildfires. The legacy of human settlement and fire suppression has contributed to increased fuel loads in forests (Higuera et al. 2015; Parks et al. 2015). Moreover, growing populations and urban encroachment have resulted in increased frequency and type of human-caused ignitions (Balch et al. 2017; Radeloff et al. 2018). Thus, land-use changes have further exacerbated the impacts of climate change in terms of fire severity, particularly in the western US as evidenced by recent record-breaking fire seasons.

21.4.2.2 Resistance Versus Land-Use Change

In many cases, partial land-use changes have reduced the resistance of forests to disturbances by constraining or removing critical ecosystem functions. For example, widespread fire suppression in biomes adapted to frequent wildfires can severely compromise resistance to both abiotic and biotic disturbances. In western Canada, aggressive fire suppression over the past century allowed large areas of pine-dominated forests to age to the point of becoming highly susceptible (i.e. less resistant) to the mountain pine beetle (Taylor and Carroll 2004), leading to a "hyperepidemic" that reached an order of magnitude greater extent and severity than any previously recorded (Sambaraju et al. 2019).

Wind is one of the most important abiotic forest disturbances in many parts of the world (Seidl et al. 2017). In tropical forests prone to cyclones and hurricanes, altered forest structure (increased gaps, edges) and shifts in plant species composition as a result of forest fragmentation reduce the resistance of forests to storm damage (Laurance and Curran 2008). Similarly, in the Norway spruce forests of Europe, resistance to wind disturbances is compromised by fragmentation (Zeng et al. 2009). In these forests wind disturbance is further amplified by outbreaks of the European spruce beetle that erupt from freshly broken or uprooted trees and spread into intact forests (Stadelmann et al. 2014).

21.4.2.3   Resilience Versus Land-Use Change

Reduced resilience of forest ecosystems associated with partial land-use change is common when the change interrupts biological legacies and impairs regeneration. For example, repeated burning of forested areas to promote livestock grazing in the Amazon has led to reduced seed availability and seedling recruitment and subsequent reorganization to shrub-dominated landscapes (Mesquita et al. 2015). Similarly, the resilience of some old-growth eucalypt forests in Australia have been diminished by clear cut logging that increases both fine fuels and the prevalence of young densely stocked stands that together support elevated fire severity compromising the capacity for systems to regenerate to equivalent pre-logging conditions (Lindenmayer et al. 2011).

21.4.3   Biotic Invasions

Biological invasions have become a defining feature of the Anthropocene (Lewis and Maslin 2015). Dramatic increases in human transport and commerce have increased the rate of introductions of non-native species into virtually all habitats around the world. Although most species introduced into new habitats will not survive, some will establish and persist. A small percentage of those that persist can become invasive where they proliferate and spread to the detriment of the environment (Mack et al. 2000; Aukema et al. 2010). Invasive species can affect all ecological processes within forests causing altered diversity, nutrient cycling, succession, and frequency and intensity of wildfires (Kenis et al, 2009; Liebhold et al. 2017). Non-native organisms from nearly every taxon have been introduced into forests; however, insects represent the most diverse group of invaders (Brockerhoff and Liebhold 2017; Liebhold et al. 2017). Thus, the examples discussed below will be mostly derived from invasive forest insects.

21.4.3.1   Disturbance Versus Biotic Invasions

The most apparent impact of biotic invasions within forest ecosystems involves altered disturbance rates as a result of direct tree mortality caused by the invasive organisms. There are many examples of these types of disturbances (Gandhi and Herms 2009; Kenis et al. 2009; Brockerhoff and Liebhold 2017). Among the most severe are the hemlock woolly adelgid and the emerald ash borer. The hemlock woolly adelgid, a sap feeder, was accidentally introduced from Japan to the eastern US during the early decades of the last century (Brockerhoff and Liebhold 2017). It has caused extensive mortality of eastern hemlock, causing its decline as a dominant forest species throughout eastern North America (Morin and Liebhold 2015). More recently, the emerald ash borer was introduced from north-eastern Asia to both North America and western Russia (Herms and McCullough 2014). Since its arrival it has

caused extensive mortality and eliminated the majority of ash trees (*Fraxinus* spp.) within the areas it has invaded (Straw et al. 2013; Herms and McCullough 2014; Morin et al. 2017).

Disturbances associated with biotic invasions will potentially worsen under climate change. Hellman et al. (2008) discuss the potential impacts of a warming environment on invasive species. Three impacts in particular are relevant to forest disturbance; (i) altered climatic constraints on invasive species, (ii) altered distribution of existing invasive species, and (iii) altered impact of existing invasive species. The sum of these impacts implies a general increase in thermally benign habitats available to invasive species that may lead to higher rates of disturbances in forests as the climate continues to warm. Indeed, the number of established alien species is projected to continue increasing through the current century (Seebens et al. 2021).

21.4.3.2   Resistance Versus Biotic Invasions

The term biotic resistance is used to describe the ability of communities to resist invasive species. In general, forests tend to be more resistant to invasions than other terrestrial systems due to their inherently high diversity and the resultant interactions of introduced organisms with native competitors, predators, etc. (Iannone et al. 2016; Nunez-Mir et al. 2017). However, when invasive species cause extensive forest disturbances, it is most often a consequence of an insufficient or inadequate response on the part of trees to defend themselves from herbivores (Brockerhoff and Liebhold 2017). This is referred to as the defense-free space hypothesis in which population growth and spread of an invader is facilitated by low resistance of evolutionarily naïve host plants (Gandhi and Herms 2009). Defense-free space has been implicated in the exacerbated impacts of many invasive forest insects and pathogens including hemlock woolly adelgid and emerald ash borer mentioned above (Showalter et al. 2018).

The concept of defense-free space is not confined to interactions of non-native organisms with forest ecosystems. Native herbivorous insects are often constrained by climate to a portion of the range of their host trees. As discussed above, a warming environment has been associated with increases in the availability of thermally benign habitats for several insect species, facilitating an expansion of ranges into evolutionarily naïve populations and species of host trees (Burke et al. 2017). Due to an insufficiently evolved defensive response, the resistance of naïve host tree populations and species to native climate migrants is inadequate to prevent severe disturbance (Cudmore et al. 2010; Raffa et al. 2013; Clark et al. 2014). This phenomenon is best exemplified by the recent expansion of the mountain pine beetle across the Rocky Mountains of North American and invasion of the transcontinental boreal forest (Cooke and Carroll 2017).

21.4.3.3   Resilience Versus Biotic Invasions

Biotic invasions that result in extensive disturbances to evolutionarily naïve forests are by definition beyond the range of historic variability. Hence, impacts to the processes associated with ecosystem resilience are often extreme and forests are forced to reorganize. Many examples exist of drastically altered ecosystems as a consequence of biotic invasion, but perhaps the best known is that associated with a fungal pathogen, the chestnut blight, accidentally introduced from Asia into North America in the early 1900s (Griffin 1986). The resultant devastation of the American chestnut by the fungus represents one of the greatest recorded changes to a forest biome caused by an introduced organism (Liebhold et al. 1995). Within a relatively short period of its introduction, the pathogen spread and functionally eliminated the American chestnut through most of its range. The loss of chestnut trees throughout eastern North America has had spectacular and long-term effects on forest ecosystems including reorganization to oak-dominated overstories, altered disturbance regimes and loss of wildlife habitat.

21.5   Forest Health in Practice

This chapter has defined forest health, outlined its constituent components across spatial and temporal scales, and reviewed the impacts of global change on each. How then are changes in forest health detected and how can forests be managed to allow sustainable extraction of ecosystem services? The foundation of the definition of a healthy forest is that its ecological processes operate within an envelope of possible ecosystem conditions. This concept of a natural range of variability (Landres et al. 1999) provides a framework for understanding the ecological context of a forest and in evaluating changes in its health.

Quantifying natural variability in forests requires information on the ecological processes and conditions of interest and their variation through time and space. This information is obtained from studies in the fields of dendroecology, dendroclimatology, palynology, landscape ecology and remote sensing that provide measurements over a sufficiently long time period and spatial extent so that meaningful information can be gained about changes in populations, ecosystem structures, disturbance frequencies, process rates, trends, periodicities, and other dynamical behaviors (Swetnam et al. 1999). Application of the concept of natural range of variability to ecosystem management is based on the following premises as reviewed by Landres et al. (1999):

- contemporary anthropogenic change may diminish the viability of many species that are adapted to past or historical conditions and processes;
- approximating historical conditions will sustain the viability of diverse species, even for those for which we have limited information;

- natural variability is a reference for evaluating the influence of anthropogenic change in ecological systems at local and shorter time scales;
- natural variability encompasses the dynamic ecological processes that drive both spatial and temporal variation in ecological systems, as well as the influence of this variation on evolution and biological diversity;
- disturbances have a strong and lasting influence on species, communities, and ecosystems;
- spatial heterogeneity is an integral component of ecological systems that is positively related to biodiversity, and resistance and resilience to disturbance.

Although difficult to generate, considerable information regarding the natural range of variability of ecological processes within many forest types has been amassed in recent decades (Keane et al. 2009). Indeed, it is now widely recognized that forest management should seek to emulate the natural range of variability of forests to maintain biodiversity and ecological function (Drever et al. 2006; Keane et al. 2009; Čada et al. 2020; Donato et al. 2020). This recognition has stimulated efforts to minimize differences between managed and natural forests by, for example, modifying harvesting practices to generate spatial and temporal patterns consistent with historical disturbance regimes (Bergeron et al. 2002; Harvey et al. 2002; Kuuluvainen and Grenfell 2012; Leclerc et al. 2021).

Consideration of disturbance, resistance and resilience within the context of natural range of variability may at first seem overly simplistic since it assumes that the record of historical conditions must reflect the range of possible conditions for future landscapes, thus ignoring the potential impacts of global change. However, determination of the natural range of variability of forest ecosystems necessarily captures large variations in the conditions of past centuries (Swetnam et al. 1999), and therefore it remains relevant even when faced with anthropogenic change. Moreover, the potential impacts of global change may be buffered by aspects of forest health. Landscape heterogeneity is directly related to species diversity (Tews et al. 2004; Fahrig et al. 2011) and diversity improves resistance and resilience to disturbance by virtue of spatial exchanges among local systems in heterogeneous landscapes (Loreau et al. 2003; Brockerhoff et al. 2017; Krawchuk et al. 2020). Thus, a forest type with higher species diversity will be healthier than an otherwise equivalent, but depauperate one, and better able to withstand novel stressors. Species diversity can be quantified at each spatial scale relevant to forest health using the concept of α-, β- and γ-diversity (Whittaker 1972; Veech et al. 2002), where α-diversity refers to species diversity within stands, β-diversity refers to species diversity among stands in a landscape, and γ-diversity is the total species diversity of the biome (i.e. sets of landscapes comprising distinct biological communities that have formed in response to a shared physical climate).

Indicators of forest health vary from stands to biomes and can be expressed in terms of each of our components of forest health—disturbance, resistance and resilience (Fig. 21.5). At the finest scale, a healthy stand is one where the type, severity and frequency of any disturbance falls within the range of natural variability. The capacity for a stand to respond to disturbance and remain within the historic range

of ecosystem conditions (i.e. avoid tipping points and regime shifts) is contingent upon its inherent resistance and resilience. Since resistance and resilience increase with increasing diversity, then at any point in time, a stand will be healthier with greater α-diversity relative to equivalent stands at similar successional stages. And as discussed above, stands are further considered healthy if following disturbance, they successfully regenerate (naturally or by planting) along a successional trajectory that will return them to a functionally equivalent pre-disturbance state. Similarly, indicators of forest health at the scale of landscapes comprise disturbance regimes (type, severity, frequency, size and return interval) that remain within the natural range of variability, high relative β-diversity and heterogeneous structures derived from diverse seral stages with high connectivity. And finally, forest biomes will be healthy when disturbance regimes within constituent landscapes remain within the natural range of variability, there is high absolute γ -diversity and all constituent landscapes persist through time (Trumbore et al. 2015).

21.5.1 Forest Health Monitoring

Given that the processes of forest health vary across scales (Fig. 21.5), forest health monitoring programs must collect and synthesize data within and among scales to support managers, decision makers, and politicians in their decisions regarding forest management. Within stands, health conditions are often measured directly from individual forest inventory plots where species diversity, and the status of trees, vegetation, soils and other ecosystem properties are quantified. These data may be augmented with high-resolution remote-sensing techniques such RADAR or LiDAR which have the potential to reconstruct forest structures within and below the canopy (Lausch et al. 2017). Data at broader scales can be derived from networks of forest inventory plots (Woodall et al. 2011) and from a wide variety of broad-scale remote sensing techniques (Lausch et al. 2016).

Despite considerable efforts by many countries to develop comprehensive forest health monitoring programs, there still remains some discrepancy between the information required by forest managers and the data that are available for understanding and assessing the complexity of forest health processes (Lausch et al. 2018). Long-term monitoring based on forest inventory plot networks provides valuable information regarding trends in forest health processes (Tkacz et al. 2008; Woodall et al. 2011); however, short-term perturbations that may trigger abrupt nonlinear declines in health are not sufficiently assessed since measurement intervals are often multiple years (Lausch et al. 2017). More recently, integration of forest inventory plot networks with remote sensing tools has facilitated generalization of intensive and expensive ground-based measurements to temporal and spatial scales required by forest managers (McDowell et al. 2015).

Forest health indicators

- *Disturbance*:
  Type, severity, frequency
- *Resistance*:
  Relative **α** diversity
- *Resilience*:
  Regeneration success,
  Successional trajectory

- *Disturbance*:
  Type, severity, frequency,
  size, return interval
- *Resistance*:
  Relative **β** diversity
- *Resilience*:
  Seral diversity, connectivity
  heterogeneity

- *Disturbance*:
  Type, severity, frequency,
  size, return interval
- *Resistance*:
  γ diversity
- *Resilience*:
  Landscape persistence

Stand

Landscape

Biome

Forest health monitoring tools

- Forest inventory plot
- High-resolution remote
  sensing

- Forest inventory plot
  network
- Remote sensing

- Remote sensing

Fig. 21.5 Indicators and monitoring tools for forest health at the stand-, landscape- and biome-scale. Indicators are scale dependent, and refer to (i) disturbance (type, severity, frequency, size, return interval) within a natural range of variability, (ii) resistance defined by stand- (**α**) and landscape- (**β**) diversity relative to equivalent stands and landscapes in the biome, or total species diversity (**γ**) in the biome, and (iii) resilience to disturbance defined as the capacity for forests to return to equivalent pre-disturbance states at each scale. Forest health monitoring tools are also scale dependent and range from individual plots in stands to broad-scale remote sensing

21.6 Forest Health Versus Nonconventional Forests

Although planted forests comprise approximately 7% of forests around the world, they account for roughly 70% of industrial wood products (Carle and Homgren 2008). The demand for wood products from plantations has been growing, and so has the area devoted to plantations such that the area of planted forest is likely to double by the end of the century (Brockerhoff et al. 2013). The majority of plantation forests comprise non-native *Pinus*, *Eucalyptus* and *Acacia* species in the southern hemisphere and mostly native species in several northern hemisphere countries (Payn et al. 2015). As the emphasis on plantation forestry has grown, so has the need for assessments of ecosystem health.

As discussed above, the definition of forest health derived from processes of disturbance, resistance and resilience does not necessarily exclude intensively managed

plantations, so how is it applied? Since plantations are largely artificial constructs the concepts of natural range of variability and disturbance regimes are not applicable. Indeed, disturbances are mainly restricted to biotic agents such as insects and pathogens (Wingfield et al. 2015). Further, issues of resilience to disturbance (and associated tipping points and regime shifts) are rendered largely irrelevant since intensive management will lead to immediate investments toward regeneration of any disturbed areas. In contrast, resistance processes that influence the severity of disturbance are vital to forest plantations (Brockerhoff et al. 2013; Wingfield et al. 2015) and provide the basis for the assessment of their health.

Planted forests are typically of a single, non-native species grown primarily for efficient wood production. They tend to be characterised by lower levels of biodiversity than natural and semi-natural forests (Brockerhoff et al. 2008) and they achieve high productivity mainly through intensive pest control efforts or the outright exclusion of pests (Liebhold et al. 2017; Wingfield et al. 2015). When pest impacts do occur, large amounts of damage can result.

Mixed-species forests are more resistant than monocultures to biotic disturbance due to the greater abundance of trophic interactions that regulate biotic disturbance agents (Jactel et al. 2017). Although plantations are normally established as monocultures, they afford an ideal opportunity to create diversity and increase resistance to disturbance given that replanting after harvesting is a frequent and recurrent process (Brockerhoff et al. 2017; Paquette and Messier 2010). Based on the expectation of increasing disturbance in a warmer world (see discussion above), greater resistance to disturbance through creation of mixed-species plantations should offset any short-term costs associated with their establishment.

In light of the capacity for innovative management of intensive plantations to promote diversity and resistance, Brockerhoff et al. (2013) recommend that clearing natural vegetation should be avoided prior to planting, native tree species should be preferred, and where possible mixed-species plantations should be established. Furthermore, in keeping with the expectations of a healthy forest landscape, they recommend the protection and enhancement of remnants of natural vegetation, the creation of mosaics of stand ages and tree species and the establishment of corridors linking habitat patches.

21.7 Conclusions

Increasingly forests are threatened by anthropogenic stressors arising from global change that compromise provisioning of vital ecosystem services. Therefore, the need to promote forest ecosystems that are resistant and resilient to stressors has never been greater. Forests are highly complex and their response to natural and anthropogenic stressors is difficult to quantify. Given an increasing global population, forests cannot and should not be viewed as independent of human influences; however, the capacity to identify the source and impact of natural and anthropogenic stressors is essential for effective forest management intended to foster forest health. A definition of

forest health derived from ecological processes, and independent of human values, facilitates baseline assessments of forest function at all temporal and spatial scales and allows partitioning of the relative impacts of natural and anthropogenic stressors and their interactions. Defining forest health in terms of the processes of disturbance, resistance and resilience within natural ranges of variability allows quantification of the vitality of any forest type in any conceivable state and determine its probability of persistence.

The ability of forests to be resistant and resilient to disturbance is dependent upon species diversity and landscape heterogeneity. Resistant and resilient forests will retain ecological processes and the capacity to deliver ecosystem services. Therefore, management toward healthy forests should seek to maximize relative biodiversity at all scales as much as is practicable. In so doing, we can provide spatial insurance for ecosystem functioning (Loreau et al. 2003) by increasing the probability of robust resistance and resilience in the face of global change.

References

Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. Proc Natl Acad Sci 113:11770–11775

Allen CR, Angeler DG, Cumming GS, Folke C, Twidwell D, Uden DR (2016) Quantifying spatial resilience. J Appl Ecol 53:625–635

Aukema JE, McCullough DG, Holle BV, Liebhold AM, Britton K, Frankel SJ (2010) Historical accumulation of nonindigenous forest pests in the Continental United States. Bioscience 60:886–897

Balch JK, Bradley BA, Abatzoglou JT, Nagy RC, Fusco EJ, Mahood AL (2017) Human-started wildfires expand the fire niche across the United States. Proc Natl Acad Sci 114:2946–2951

Barclay HJ, Li C, Benson L, Taylor S, Shore T (2005) Effects of fire return rates on traversability of lodgepole pine forests for mountain pine beetle (Coleoptera: Scolytidae) and the use of patch metrics to estimate traversability. Can Entomol 137:566–583

Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A, Larsson S (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecol Appl 15:2084–2096

Berg EE, Henry JD, Fastie CL, Volder ADD, Matsuoka SM (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. For Ecol Manage 227:219–232

Bergeron Y, Leduc A, Harvey B, Gauthier S (2002). Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fenn 36. https://doi.org/10.14214/sf.553

Brandt JP, Flannigan MD, Maynard DG, Thompson ID, Volney WJA (2013) An introduction to Canada's boreal zone: ecosystem processes, health, sustainability, and environmental issues1. Environ Rev 21:207–226

Brockerhoff EG, Barbaro L, Castagneyrol B, Forrester DI, Gardiner B, González-Olabarria JR et al (2017) Forest biodiversity, ecosystem functioning and the provision of ecosystem services. Biodivers Conserv 26:3005–3035

Brockerhoff EG, Jactel H, Parrotta JA, Ferraz SFB (2013) Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. For Ecol Manage 301:43–50

Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J (2008) Plantation forests and biodiversity: oxymoron or opportunity? Biodivers Conserv 17:925–951

Brockerhoff EG, Liebhold AM (2017) Ecology of forest insect invasions. Biol Invasions 19:3141–3159

Brook BW, Ellis EC, Perring MP, Mackay AW, Blomqvist L (2013) Does the terrestrial biosphere have planetary tipping points? Trends Ecol Evol 28:396–401

Buma B (2015) Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere 6:1–15

Burke JL, Bohlmann J, Carroll AL (2017) Consequences of distributional asymmetry in a warming environment: invasion of novel forests by the mountain pine beetle. Ecosphere 8:e01778

Čada V, Trotsiuk V, Janda P, Mikoláš M, Bače R, Nagel TA et al (2020) Quantifying natural disturbances using a large-scale dendrochronological reconstruction to guide forest management. Ecol Appl 30. https://doi.org/10.1002/eap.2189

Carle J, Homgren P (2008) Wood from planted forests: a global outlook 2005–2030. For Prod J 58:6–18

Carpenter SR, Mooney HA, Agard J, Capistrano D, DeFries RS, Díaz S et al (2009) Science for managing ecosystem services: beyond the Millennium Ecosystem Assessment. Proc Natl Acad Sci 106:1305–1312

Carroll AL, Taylor SW, Régnière J, Safranyik L (2004). Effects of climate change on range expansion by the mountain Pine Beetle in British Columbia. In: Shore TL, Stone JE Stone (eds) Mountain Pine Beetle symposium: challenges and solutions. Natural Resources Canada, Canadian Forest Service, Victoria, BC, Canada, pp 223–232

Choi WI, Park Y-K, Park Y-S, Ryoo MI, Lee H-P (2011) Changes in voltinism in a pine moth Dendrolimus spectabilis (Lepidoptera: Lasiocampidae) population: implications of climate change. Appl Entomol Zool 46:319–325

Clark EL, Pitt C, Carroll AL, Lindgren BS, Huber DPW (2014) Comparison of lodgepole and jack pine resin chemistry: implications for range expansion by the mountain pine beetle, Dendroctonus ponderosae (Coleoptera: Curculionidae). PeerJ 2:e240

Cooke BJ, Carroll AL (2017) Predicting the risk of mountain pine beetle spread to eastern pine forests: Considering uncertainty in uncertain times. For Ecol Manage 396:11–25

Cooke BJ, Nealis VG, Régnière J (2007) Insect defoliators as periodic disturbances in northern forest ecosystems. In: Johnson EA, Miyanishi K (eds) Plant disturbance ecology: the process and the response. Elsevier Academic Press, Burlington, Mass, USA, pp 487–525

Coop JD, Parks SA, Stevens-Rumann CS, Crausbay SD, Higuera PE, Hurteau MD et al (2020) Wildfire-Driven forest conversion in Western North American landscapes. Bioscience 70:659–673

Cudmore TJ, Björklund N, Carroll AL, Lindgren BS (2010) Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naïve host tree populations. J Appl Ecol 47:1036–1043

Curtis PG, Slay CM, Harris NL, Tyukavina A, Hansen MC (2018) Classifying drivers of global forest loss. Science 361:1108–1111

Davis KT, Dobrowski SZ, Higuera PE, Holden ZA, Veblen TT, Rother MT et al (2019) Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc Natl Acad Sci 116:201815107

DeRose RJ, Long JN (2014) Resistance and resilience: a conceptual framework for silviculture. For Sci 60:1205–1212

de Mesquita R, C. G., Massoca, P. E. dos S., Jakovac, C. C., Bentos, T. V., & Williamson, G. B. (2015) Amazon rain forest succession: stochasticity or land-use legacy? Bioscience 65:849–861

Doerr SH, Santín C (2016) Global trends in wildfire and its impacts: perceptions versus realities in a changing world. Philosophical transactions of the royal society : Biol Sci 371:20150345

Donato DC, Halofsky JS, Reilly MJ (2020) Corralling a black swan: natural range of variation in a forest landscape driven by rare, extreme events. Ecol Appl 30. https://doi.org/10.1002/eap.2013

Drever CR, Peterson G, Messier C, Bergeron Y, Flannigan M (2006) Can forest management based on natural disturbances maintain ecological resilience? Can J for Res 36:2285–2299

Edmonds RL, Agee JK, Gara RI (2011) Forest health and protection. Waveland Press, Long Grove, IL, USA

Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ et al (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol Lett 14:101–112

FAO, and UNEP (2020) The state of the world's forests 2020. forests, biodiversity and people. Rome: food and agriculture organization of the United Nations and UN Environment Program.

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. Annu Rev Ecol Evol Syst 35:557–581

Gandhi KJK, Herms DA (2009) Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biol Invasions. https://doi.org/10.1007/s10530-009-9627-9

Gauthier S, Bernier P, Kuuluvainen T, Shvidenko AZ, Schepaschenko DG (2015) Boreal forest health and global change. Science 349:819–822

Ghazoul J, Burivalova Z, Garcia-Ulloa J, King LA (2015) Conceptualizing forest degradation. Trends Ecol Evol 30:622–632

Ghazoul J, Chazdon R (2017) Degradation and recovery in changing forest landscapes: a multiscale conceptual framework. Annu Rev Environ Resour 42:161–188

Griffin GJ (1986) Chestnut blight and its control. Horticultural Review 8:291–335

Grimm NB, Groffman P, Staudinger M, Tallis H (2016) Climate change impacts on ecosystems and ecosystem services in the United States: process and prospects for sustained assessment. Clim Change 135:97–109

Gunderson LH (2000) Ecological resilience—in theory and application. Annu Rev Ecol Syst 31:425–439

Harvey BJ, Donato DC, Turner MG (2016) High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Glob Ecol Biogeogr 25:655–669

Harvey BJ, Leduc A, Gauthier S, Bergeron Y (2002) Stand-landscape integration in natural disturbance-based management of the southern boreal forest. For Ecol Manage 155:369–385

Hellman JJ, Byers JE, Biergarden BG, Dukes JS (2008) Five potential consequences of climate change for invasive species. Conserv Biol 22:534–543

Herms DA, McCullough DG (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annu Rev Entomol 59:13–30

Higuera PE, Abatzoglou JT, Littell JS, Morgan P (2015) The changing strength and nature of fire-climate relationships in the Northern rocky mountains, U.S.A., 1902–2008. PLOS One, 10:e0127563.

Holling CS (1973) Resilience and stability of ecological systems. Annu Rev Ecol Syst 4:1–23

Holling CS (1992) Cross-scale morphology, geometry, and dynamics of ecosystems. Ecol Monogr 62:447–502

Hood S, Bentz B (2007) Predicting postfire Douglas-fir beetle attacks and tree mortality in the northern Rocky Mountains. Can J for Res 37:1058–1069

Iannone BV, Potter KM, Hamil K-AD, Huang W, Zhang H, Guo Q et al (2016) Evidence of biotic resistance to invasions in forests of the Eastern USA. Landscape Ecol 31:85–99

IPCC. (2014). Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change, Geneva, Switzerland: IPCC, p 151

Jactel H, Bauhus J, Boberg J, Bonal D, Castagneyrol B, Gardiner B et al (2017) Tree diversity drives forest stand resistance to natural disturbances. Curr For Rep 3:223–243

Jepsen JU, Hagen SB, Ims RA, Yoccoz NG (2008) Climate change and outbreaks of the geometrids Operophtera brumata and Epirrita autumnata in subarctic birch forest: evidence of a recent outbreak range expansion. J Anim Ecol 77:257–264

Jepsen JU, Kapari L, Hagen SB, Schott T, Vindstad OPL, Nilssen AC, Ims RA (2011) Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch. Glob Change Biol 17:2071–2083

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE et al (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14:369–378

Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DMJS (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. Nat Commun 6:7537

Kausrud K, Okland B, Skarpaas O, Grégoire J-C, Erbilgin N, Stenseth NC (2012) Population dynamics in changing environments: the case of an eruptive forest pest species. Biol Rev Camb Philos Soc 87:34–51

Kautz M, Meddens AJH, Hall RJ, Arneth A (2017) Biotic disturbances in Northern Hemisphere forests—a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. Glob Ecol Biogeogr 26:533–552

Keane RE, Hessburg PF, Landres PB, Swanson FJ (2009) The use of historical range and variability (HRV) in landscape management. For Ecol Manage 258:1025–1037

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA (2011) Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci 16:406–411

Kelly R, Chipman ML, Higuera PE, Stefanova I, Brubaker LB, Hu FS (2013) Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. Proc Natl Acad Sci 110:13055–13060

Kenis M, Auger-Rozenberg M-A, Roques A, Timms L, Péré C, Cock MJW et al (2009) Ecological effects of invasive alien insects. Biol Invasions 11:21–45

Koepke DF, Kolb TE (2013) Species variation in water relations and xylem vulnerability to cavitation at a forest-woodland ecotone. For Sci 59:524–535

Kolb TE, Wagner MR, Covington WW (1994) Utilitarian and ecosystem perspectives: concepts of forest health. J Forest 92:10–15

Krawchuk MA, Meigs GW, Cartwright JM, Coop JD, Davis R, Holz A et al (2020) Disturbance refugia within mosaics of forest fire, drought, and insect outbreaks. Front Ecol Environ 18:235–244

Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL et al (2008) Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–990

Kuuluvainen T, Grenfell R (2012) Natural disturbance emulation in boreal forest ecosystem management—theories, strategies, and a comparison with conventional even-aged management. Can J for Res 42:1185–1203

Lamothe KA, Somers KM, Jackson DA (2019) Linking the ball-and-cup analogy and ordination trajectories to describe ecosystem stability, resistance, and resilience. Ecosphere 10:e02629

Landres PB, Morgan P, Swanson FJ (1999) Overview of the use of natural variability concepts in managing ecological systems. Ecol Appl 9:1179–1188

Laurance WF, Curran TJ (2008) Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. Austral Ecol 33:399–408

Lausch A, Borg E, Bumberger J, Dietrich P, Heurich M, Huth A et al (2018) Understanding forest health with remote sensing, part III: requirements for a scalable multi-source forest health monitoring network based on data science approaches. Remote Sens 10:1120

Lausch A, Erasmi S, King DJ, Magdon P, Heurich M (2017) Understanding forest health with Rrmote sensing-part II—A review of approaches and data models. Remote Sens 9:129

Lausch A, Erasmi S, King D, Magdon P, Heurich M (2016) Understanding forest health with remote sensing–part I—A review of spectral traits. processes and remote-sensing characteristics. Remote Sens 8:1029

Leclerc M-AF, Daniels LD, Carroll AL (2021) Managing wildlife habitat: complex interactions with biotic and abiotic disturbances. Front Ecol Evol 9:613371

Lewis SL, Maslin MA (2015) Defining the anthropocene. Nature 519:171–180

Liebhold AM, Brockerhoff EG, Kalisz S, Nuñez MA, Wardle DA, Wingfield MJ (2017) Biological invasions in forest ecosystems. Biol Invasions 19:3437–3458

Liebhold AM, MacDonald WL, Bergdahl D, Mastro VC (1995) Invasion by exotic forest pests: a threat to forest ecosystems. Forest Science Monographs 30:1–49

Lindenmayer DB, Hobbs RJ, Likens GE, Krebs CJ, Banks SC (2011) Newly discovered landscape traps produce regime shifts in wet forests. Proc Natl Acad Sci 108:15887–15891

Lindenmayer DB, Franklin JF (2002) Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J et al (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For Ecol Manage 259:698–709

Liu Y, Stanturf J, Goodrick S (2010) Trends in global wildfire potential in a changing climate. For Ecol Manage 259:685–697

Logan JA, Powell JA (2001) Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). Am Entomol 47:160–172

Loreau M, Mouquet N, Gonzalez A (2003) Biodiversity as spatial insurance in heterogeneous landscapes. Proc Natl Acad Sci 100:12765–12770

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A et al (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Marini L, Okland B, Jönsson AM, Bentz B, Carroll AL, Forster B et al (2017) Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. Ecography. https://doi.org/10.1111/ecog.02769

McDowell NG, Coops NC, Beck PSA, Chambers JQ, Gangodagamage C, Hicke JA et al (2015) Global satellite monitoring of climate-induced vegetation disturbances. Trends Plant Sci 20:114–123

McElhinny C, Gibbons P, Brack C, Bauhus J (2005) Forest and woodland stand structural complexity: Its definition and measurement. For Ecol Manage 218:1–24

Menéndez R, González-Megías A, Lewis OT, Shaw MR, Thomas CD (2008) Escape from natural enemies during climate-driven range expansion: a case study. Ecological Entomology 33:413–421

Millar CI, Stephenson NL (2015) Temperate forest health in an era of emerging megadisturbance. Science 349:823–826

Morin RS, Liebhold AM (2015) Invasions by two non-native insects alter regional forest species composition and successional trajectories. For Ecol Manage 341:67–74

Morin RS, Liebhold AM, Pugh SA, Crocker SJ (2017) Regional assessment of emerald ash borer, Agrilus planipennis, impacts in forests of the Eastern United States. Biol Invasions 19:703–711

Nolan RH, Blackman CJ, de Dios VR, Choat B, Medlyn BE, Li X et al (2020) Linking forest flammability and plant vulnerability to drought. For 11:779

Nunez-Mir GC, Liebhold AM, Guo Q, Brockerhoff EG, Jo I, Ordonez K, Fei S (2017) Biotic resistance to exotic invasions: its role in forest ecosystems, confounding artifacts, and future directions. Biol Invasions 19:3287–3299

Paoletti E, Schaub M, Matyssek R, Wieser G, Augustaitis A, Bastrup-Birk AM et al (2010) Advances of air pollution science: From forest decline to multiple-stress effects on forest ecosystem services. Environ Pollut 158:1986–1989

Paquette A, Messier C (2010) The role of plantations in managing the world's forests in the Anthropocene. Front Ecol Environ 8:27–34

Parker, V. T., & Pickett, S. T. A. (1998). Historical contingency and multiple scales of dynamics within plant communities. In Ecological scale: theory and applications, Columbia University Press, pp. 171–192

Parks SA, Miller C, Parisien M-A, Holsinger LM, Dobrowski SZ, Abatzoglou J (2015) Wildland fire deficit and surplus in the western United States, 1984–2012. Ecosphere 6:1–13

Payn T, Carnus J-M, Freer-Smith P, Kimberley M, Kollert W, Liu S et al (2015) Changes in planted forests and future global implications. For Ecol Manage 352:57–67

Pohjanmies T, Triviño M, Tortorec EL, Mazziotta A, Snäll T, Mönkkönen M (2017) Impacts of forestry on boreal forests: An ecosystem services perspective. Ambio 46:743–755

Radeloff VC, Helmers DP, Kramer HA, Mockrin MH, Alexandre PM, Bar-Massada A et al (2018) Rapid growth of the US wildland-urban interface raises wildfire risk. Proc Natl Acad Sci 115:201718850

Raffa KF, Aukema B, Bentz BJ, Carroll A, Erbilgin N, Herms DA et al (2009) A Literal Use of'Forest Health' Safeguards against Misuse and Misapplication. J Forest 107:276–277

Raffa KF, Aukema B, Bentz BJ, Carroll AL, Hicke JA., Kolb TE (2015) Responses of tree-killing bark beetles to a changing climate. In Climate change and insect pests. CABI, pp 173–201

Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58:501–517

Raffa KF, Powell EN, Townsend PA (2013) Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. Proc Natl Acad Sci USA 110:2193–2198

Reyer CPO, Brouwers N, Rammig A, Brook BW, Epila J, Grant RF et al (2015) Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. J Ecol 103:5–15

Sambaraju KR, Carroll AL, Aukema BH (2019) Multiyear weather anomalies associated with range shifts by the mountain pine beetle preceding large epidemics. For Ecol Manage 438:86–95

Scheffer M (2009) Critical transitions in nature and society. Princeton University Press, Princeton, USA

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Evol 18:648–656

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Seebens H, Bacher S, Blackburn TM, Capinha C, Dawson W, Dullinger S et al (2021) Projecting the continental accumulation of alien species through to 2050. Glob Change Biol 27:970–982

Seidl R, Müller J, Hothorn T, Bässler C, Heurich M, Kautz M (2016) Small beetle, large-scale drivers: how regional and landscape factors affect outbreaks of the European spruce bark beetle. J Appl Ecol 53:530–540

Seidl R, Rammer W, Spies TA (2014) Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. Ecol Appl 24:2063–2077

Seidl R, Schelhaas M-J, Lexer MJ (2011) Unraveling the drivers of intensifying forest disturbance regimes in Europe. Glob Change Biol 17:2842–2852

Seidl R, Spies TA, Peterson DL, Stephens SL, Hicke JA (2016b) Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J Appl Ecol 53:120–129

Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G et al (2017) Forest disturbances under climate change. Nat Clim Chang 7:395–402

Showalter DN, Raffa KF, Sniezko RA, Herms DA, Liebhold AM, Smith JA, Bonello P (2018) Strategic development of tree resistance against forest pathogen and insect invasions in defense-free space. Front Ecol Evol 6:124

Shvidenko A, Barber CV, Persson R, Gonzales P, Hassan R, Lakyda P et al (2005). Forest and woodland systems. In M. de los Angeles & C. Sastry (eds) Millennium ecosystem assessment: current state & trends Aasessment. Island Press, Washington, pp 587–614

Sing L, Metzger MJ, Paterson JS, Ray D (2017) A review of the effects of forest management intensity on ecosystem services for northern European temperate forests with a focus on the UK. For: Int J For Res, 91:151–164.

Stadelmann G, Bugmann H, Wermelinger B, Bigler C (2014) Spatial interactions between storm damage and subsequent infestations by the European spruce bark beetle. For Ecol Manage 318:167–174

Stephens SL, Collins BM, Fettig CJ, Finney MA, Hoffman CM, Knapp EE et al (2018) Drought, tree mortality, and wildfire in forests adapted to frequent fire. Bioscience 68:77–88

Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC et al (2018) Evidence for declining forest resilience to wildfires under climate change. Ecol Lett 21:243–252

Stireman JO, Dyer LA, Janzen DH, Singer MS, Lill JT, Marquis RJ et al (2005) Climatic unpredictability and parasitism of caterpillars: implications of global warming. Proc Natl Acad Sci USA 102:17384–17387

Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. Trends Ecol Evol 14:179–185

Straw NA, Williams DT, Kulinich O, Gninenko YI (2013) Distribution, impact and rate of spread of emerald ash borer Agrilus planipennis (Coleoptera: Buprestidae) in the Moscow region of Russia. For: Int J For Res, 86, 515–522.

Swetnam TW, Allen CD, Betancourt JL (1999) Applied historical ecology: using the past to manage for the future. Ecol Appl 9:1189–1206

Taylor, S. W., & Carroll, A. L. (2004). Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: a historical perspective. In: Shore TL , Brooks JE, Stone JE (eds) Mountain Pine Beetle Symposium: Challenges and Solutions . Natural Resources Canada, Canadian Forest Service, Victoria, BC, Canada, pp 41–51

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92

Thom D, Rammer W, Seidl R (2016) Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. Glob Change Biol 23:269–282

Thom D, Seidl R (2016) Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biol Rev 91:760–781

Thompson ID, Guariguata MR, Okabe K, Bahamondez C, Nasi R, Heymell V, Sabogal C (2013) An operational framework for defining and monitoring forest degradation. Ecol Soc 18:1–23

Tkacz B, Moody B, Castillo JV, Fenn ME (2008) Forest health conditions in North America. Environ Pollut 155:409–425

Trumbore S, Brando P, Hartmann H (2015) Forest health and global change. Science 349:814–818

Turner MG (1989) Landscape Ecology: the effect of pattern on process. Annu Rev Ecol Syst 20:171–197

Turner MG (2010) Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849

Turner MG, Baker WL, Peterson CJ, Peet RK (1998) Factors Influencing Succession: lessons from large, infrequent natural disturbances. Ecosystems 1:511–523

Turner MG, Gardner RH (2015) Landscape ecology in theory and practice, pattern and process. 175–228.

Turner MG, Hargrove WW, Gardner RH, Romme WH (1994) Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. J Veg Sci 5:731–742

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363

Veech JA, Summerville KS, Crist TO, Gering JC (2002) The additive partitioning of species diversity: recent revival of an old idea. Oikos 99:3–9

Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S et al (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Front Ecol Environ 8:135–144

White PS, Jentsch A (2001) The search for generality in studies of disturbance and ecosystem dynamics. Progress in Botany 62:399–450

White PS, Pickett STA (1985) Natural disturbance and patch dynamics: an introduction. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, New York, NY, USA, pp 3–13

Whitman E, Parisien M-A, Thompson DK, Flannigan MD (2019) Short-interval wildfire and drought overwhelm boreal forest resilience. Sci Rep 9:18796

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251

Williams AP, Abatzoglou JT, Gershunov A, Guzman-Morales J, Bishop DA, Balch JK, Lettenmaier DP (2019) Observed impacts of anthropogenic climate change on wildfire in California. Earth's Futur 7:892–910

Wingfield MJ, Brockerhoff EG, Wingfield BD, Slippers B (2015) Planted forest health: the need for a global strategy. Science 349:832–836

Woodall CW, Amacher MC, Bechtold WA, Coulston JW, Jovan S, Perry CH et al (2011) Status and future of the forest health indicators program of the USA. Environ Monit Assess 177:419–436

Young DJN, Stevens JT, Earles JM, Moore J, Ellis A, Jirka AL, Latimer AM (2017) Long-term climate and competition explain forest mortality patterns under extreme drought. Ecol Lett 20:78–86

Zeng H, Peltola H, Väisänen H, Kellomäki S (2009) The effects of fragmentation on the susceptibility of a boreal forest ecosystem to wind damage. For Ecol Manage 257:1165–1173