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The disturbance regime concept

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Introduction to disturbance in landscape ecology

A focal area of exploration using the lens of landscape ecology is the concept of *disturbance* as 'any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment' (White and Pickett 1985, 7). As natural and human-caused disturbances are key drivers of ecosystem dynamics, they have provided a ripe arena for ecological analyses of landscape change. Further, understanding and characterizing repeated patterns of disturbance along multiple dimensions (i.e., disturbance 'regimes'; Sousa 1984, Agee 1993, Turner 2010) is an area where landscape ecological theory has provided, and continues to provide, key insight.

Just as landscape ecology examines reciprocal interactions between spatial pattern and ecological process, the field of landscape ecology has an enduring series of reciprocal interactions with the field of disturbance ecology. The importance of the interconnectedness of landscape ecology with disturbance comes down to a fundamental characteristic of disturbances: disturbances and their repeated occurrence in ecosystems are inherently spatial processes that respond to and create spatial heterogeneity (Turner 2010). Insights about the causes and consequences of natural and anthropogenic disturbances have arisen from the application of landscape ecological theory and concepts, which have, in turn, been tested and refined on many large disturbances. A prime example of these interactions between fields can be found in a special issue published during the first year (1998) of the journal *Ecosystems* focused on '*Large Infrequent Disturbances'*. Using examples and lessons learned from disturbances that ranged from the 1980 eruption of Mt. St. Helens to the 1988 Yellowstone Fires to the 1993 floods in the Mississippi River, this key set of papers synthesized insights to date and laid out an ambitious research agenda and set of hypotheses about general landscape patterns of disturbance, ecosystem recovery, and management (Dale et al. 1998, Foster et al. 1998, Paine et al. 1998, Turner and Dale 1998, Turner et al. 1998, Romme et al. 1998).

Ecological inquiry into disturbance and subsequent ecological change across space and time has roots dating back to before the 20th century. Foundational work by (Cowles 1899) demonstrated the utility of 'space for time' substitution (i.e., chronosequence) studies to look at dynamic vegetation patterns through time in sand dunes near the Great Lakes—though disturbance was not explicitly mentioned (for a contemporary critical review of chronosequence methods, see Johnson and Miyanishi 2008). Early conceptualizations often posited disturbances as exogenous forces: ecosystems were in relative *equilibrium*, and disturbance events disrupted that equilibrium (Clements 1916, 1936). Studies considering disturbance were generally focused not on disturbance per se but on succession—the dynamics of ecosystem response to disturbance, which many ecologists viewed as a predictable sequence of changes that would eventually return the ecosystem to the pre-disturbance equilibrium (Clements 1936). With time came an increasing recognition of the vital role that disturbance has in maintaining ecosystems and their spatial mosaics of patches comprising different areas at different successional stages since the last disturbance (Wieslander 1935, Watt 1947)—that is, disturbances are fundamental to most natural ecosystems (Sousa 1984, Pickett and White 1985, Attiwill 1994). Along with the shift to a broader acceptance of disturbances as inherent in ecosystems came an intense focus on the processes governing ecological succession following disturbance, such as competition, facilitation, and chance events (or contingencies) (Gleason 1926, Egler 1954, Drury and Nisbet 1973, Connell and Slatyer 1977, Grime 1977). With progressively more study came the recognition that equilibrium is rare, and disturbance and *non-equilibrium* dynamics are the norm in most ecosystems (Drury and Nisbet 1973, Perry 2002). Moreover, equilibrium is dependent on the scale at which one examines ecological dynamics (Sprugel 1991, Turner et al. 1993, Jentsch and White 2019), and ecosystem dynamics often follow varied successional pathways rather than a single deterministic pathway (Cattelino et al. 1979, Fastie 1995, Kipfmueller and Kupfer 2005, Johnstone and Chapin 2006, Harvey and Holzman 2014).

Disturbance regime as a core concept

With the growing recognition of the ecological role of disturbance came focused attention on understanding the *disturbance regime*—the repeated pattern of disturbance over space and time, typically characterized by spatial, temporal, and mechanistic (e.g., intensity or magnitude) attributes (Sousa 1984, Agee 1993, Turner 2010). A disturbance event usually occurs over a discrete time period—minutes to months (though in some cases, droughts or insect outbreaks can last years). However, the disturbance regime is more appropriately characterized over broad time and space dimensions, allowing a fuller picture of the disturbance rotation (the time required to disturb an area equal to the landscape of interest) to unfold. Disturbance regime attributes can be, and often have been, characterized based on measures of central tendency (e.g., mean or median rotations). However, since rare and large disturbance events are often of disproportional importance for structuring ecosystems, the distributions (e.g., range, variance, or extreme values) of regime attributes across time and space are often of greater utility than measures of central tendency (Katz et al. 2005).

In a useful synthesis, Peters et al. (2011) separate disturbance events into three components that can help facilitate comparisons among mechanisms across systems. First, the *environmental drivers* of a disturbance event (climate, physical, biotic, and anthropogenic processes) each have their own characteristics (e.g., magnitude, duration, timing) and can be compared across systems. Second, the state of a system when disturbed (e.g., susceptibility, connectivity) is important to how the disturbance will unfold. Third, the mechanism of disturbance (e.g., combustion in fire, abrasion from wind, defoliation from organisms) may vary across disturbance types and systems. The interactions of drivers, system properties, and mechanisms produce a disturbance event, which then results in *legacies* (Figure 8.1)—the organic materials and organically derived patterns that persist through a disturbance (Franklin et al. 2000). Legacies can be of material (e.g., physical structures) or informational (e.g., genetic information) nature (Johnstone et al. 2016) and form the '*ecological memory*' that are the ingredients for post-disturbance ecosystem trajectories (Peters et al. 2011). Acceptance of repeated disturbances (i.e., regimes) as a part of system dynamics also coincided with concepts of *resilience*, or the capacity of a system to experience disturbance and maintain its essential structure and function (Holling 1973). If

Figure 8.1 Mature trees that survive disturbances are important biological legacies, providing seed sources for new tree establishment, increasing structural diversity of the forest over the course of post-disturbance succession, and providing wildlife habitat. (Photo from the Frank Church – River of No Return Wilderness, Idaho, United States, 2018, by C.A. Cansler.)

the adaptive traits present in an ecosystem are aligned with the disturbance regime, a system is more likely to be in a 'safe operating space' whereby disturbance and recovery cycles are part of the inherent system dynamics that promote resilience (Johnstone et al. 2016). Alternatively, if the disturbance-recovery cycle, changing environmental context, or exogenous factors (e.g., invasive species) move an ecosystem out of a state (e.g., forest), shifting among *alternative stable states* (e.g., repeated long-term cycles between forest and non-forest conditions) may be possible (Beisner et al. 2003).

The desire to merge knowledge regarding natural disturbance regimes with landscape ecology became a more important goal of research as ecosystem management rose to the forefront of natural resource management. Ecosystem management aims to maintain viable native species populations, representative amounts of native ecosystem types, and ecological processes—including disturbances—while also allowing long-term sustainable human use of ecosystem goods and services (Grumbine 1994). The implementation of ecosystem management benefits from a recognition of the dynamic nature of ecosystems, which emerges as a result of natural and anthropogenic disturbances as well as variation in climate (Morgan et al. 1994). The most common approach to this was to use reference conditions prior to major land-use changes due to European colonization and industrialization as a benchmark. These efforts are not without serious challenges, however, as ecosystems are in constant flux, and defining the temporal and spatial scale of reference conditions is non-trivial (Sprugel 1991). Often described as 'natural variability' (Landres et al. 1999), the '*natural range of variability*', or the 'historical range of variability' (Keane et al. 2009), these reference conditions strive to include more than a single static target, typically incorporate the full variation and range of conditions (e.g., communities, successional stages, disturbances) into a landscape, and often include spatial attributes of ecosystem components (Keane et al. 2002). There are two important ties to natural disturbance regimes. First, descriptions of the natural range of variability often incorporated the frequency or rotation of different disturbances and various severities of a single disturbance (e.g., 'surface fire' and 'stand-replacing fire') on a landscape. Second, because direct evidence—such as early aerial photography or stand age maps—of historical landscape composition is often lacking, simulation models are often used to identify the natural range of variability of different community types or successional stages on a landscape (see Chapter 14 for links between paleo ecology and landscape ecology). For simulation models to be parameterized, quantitative descriptions of the frequency and severity (etc.) of different disturbance types are needed. This, in turn, requires the collection of observational data on disturbance regime attributes.

Some of the important work on landscape patterns of disturbance proposed the concept of a '*shifting-mosaic steady state*' (Bormann and Likens 1979), which suggests that even though components of the landscape may change successional state and species composition due to disturbance, the landscape itself (at a sufficient spatial extent) is at equilibrium, as new patches created by disturbance are balanced by successional development in old patches. Fine-scale (small spatial grain at small spatial extents) spatial and temporal variation could produce broad-scale (small spatial grain over broad spatial extents) consistency in landscape composition. This conceptualization was revised to recognize that non-equilibrium landscapes can be created by large disturbances that impact most of the landscape (Sprugel 1991, Turner et al. 1993). Thus, not only was equilibrium scale-dependent (i.e., typically evident at larger scales but not at smaller—a concept sometimes referred to as meta-stability), but empirical studies (Romme and Despain 1989) and modeling studies (Turner et al. 1993) showed that landscape composition can fluctuate widely over time. Non-stationary climate, which causes non-stationarity in both species composition and disturbance regime attributes, further undermines the theoretical conceptualization of equilibrium (Jackson 2006, Blonder et al. 2018). Climate change also presents practical problems for managers trying to use the 'natural range of variability', since climate change will cause continual changes in decadal-scale characteristics of many disturbance regimes (Bebi et al. 2001, Allen et al. 2010, Bentz et al. 2010) and century-scale shifts in dominant species and locations of biomes, which will feed back on disturbance dynamics. Plans for adapting ecosystems and management practices to expected conditions under climate changes have begun to identify the 'future range of variability' (Thompson et al. 2009, Duncan et al. 2010) or 'future climate-analogue reference conditions' (Churchill et al. 2013). These methods can range from identifying regional-scale references that help managers anticipate future conditions in a different region (Keane et al. 2018) to stand-scale reference sites that provide pattern and compositional targets for restoration silviculture practices (Churchill et al. 2013).

A plethora of geospatial data and accompanying field measurements prior to, during, and after disturbances has catalyzed a renaissance of research examining the disturbances themselves and their various components. These data have allowed much greater investigation of what are often termed *'top-down' and 'bottom-up' controls* on disturbance regimes. It is important to note that these terms have a different meaning in landscape ecology and disturbance ecology than in ecological studies of predator–prey relationships (Power 1992, Estes and Duggins 1995). In relation to disturbance, 'top-down' refers to broad-scale climatic controls on disturbance regimes, such as century-to-decadal-scale climate controlling the biogeography of plant species, and inter-annual variation in climate, which drives inter-annual variability in the extent and severity of disturbances (McKenzie and Kennedy 2011). In contrast, 'bottom-up' controls include biophysical drivers such as topography and soil moisture holding capacity as well as biotic factors such as plant species composition, or plant trait composition, and vegetation structure.

The top-down control of climate is an important driver of the distribution of many abiotic disturbance processes. Snow avalanche disturbances only occur where there is sufficient snowpack, wind-throw from tropical cyclones is much more likely in coastal areas in the Intertropical Convergence Zone, and fires are not an important disturbance process in barren alpine and desert environments where there is insufficient fuel to support fire spread. Inter-annual variability in weather also provides a strong control on many disturbance processes. Multi-year drought is a strong driver of widespread tree die-off events, during which the proximate cause of mortality is usually bark beetles (Allen et al. 2010)—the populations of which are also strongly influenced by climatic variation (Bentz et al. 2010) (Figure 8.2). Climatic variation also strongly influences fire frequency and extent, primarily by influencing fuel aridity and fire season length (Jolly et al. 2015) but also via fuel accumulation and the number of ignitions. In arid, fuel-limited systems, wet years lead to increased growth of grass and forbs, and the increase in fine fuels supports increased fire occurrences and extent (Littell et al. 2018). In contrast, flammability-limited systems experience strong increases in area burned in response to increased aridity (Littell et al. 2018).

The perceived importance of 'bottom-up' controls on disturbance regimes has increased with the increased availability of geospatial data that can be used to quantify the local biophysical

Figure 8.2 The 2006 Tatoosh Buttes fire (background slopes with little live tree cover) was a high-severity wind-driven fire that created extremely large homogeneous patches of almost complete tree mortality. A subsequent bark beetle outbreak (trees with red needles in the foreground) caused tree mortality outside the fire perimeter where host trees were available post-fire. These are two examples of top-down disturbances modified by bottom-up controls. Pasayten Wilderness, Washington, United States. (Photo from 2008 by C.A. Cansler.)

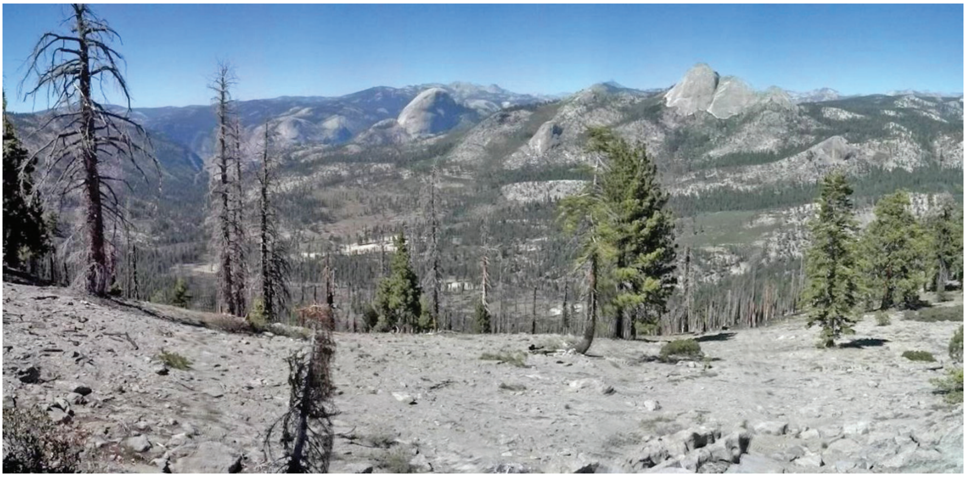

Figure 8.3 A complex mosaic of patches of rock, herbaceous vegetation, shrublands, and forest stands with differing structures can be seen in this photo of the Illilouette Creek Basin in Yosemite National Park, California, United States. A recently burned area in the foreground has biological legacies in the form of dead standing trees (snags) and mature trees. In the background, denser forests are found in ravines, and non-forest and open forest stands are predominantly on convex topography. These topographic controls are expressed after 40 years in which wildfires have been allowed to burn for resource benefit by the National Park Service. (Photo from 2012 by C.A. Cansler.)

setting and disturbance impacts. Early work on wind and fire disturbances (Heinselman 1973, Bormann and Likens 1979, Sprugel and Bormann 1981) examined the mosaic of disturbances across a landscape with little consideration of the local frequency or severity of disturbance. The 'shifting-mosaic-steady state' framework implied an axiomatic assumption that disturbances were stochastic. Since then, research has revealed strong topographical controls on wind-throw (Harcombe et al. 2004), avalanche impacts (Bebi et al. 2001), fire frequency (Kellogg et al. 2008), high-severity fire (Dillon et al. 2011), and fire refugia (Meddens et al. 2018). There is an increasing acknowledgment that disturbance impacts can be both predictable and stochastic (Meddens et al. 2016), depending on the scale being analyzed, the disturbance type, and the relative local strengths of top-down and bottom-up controls, and the relative strength of different controls may be non-stationary in time (Newman et al. 2019). For contagious disturbances (e.g., fire, pathogen spread) in particular, high variation in local topography and vegetation weakens the strength of the relationship between top-down controls and disturbance extent and severity (Turner and Romme 1994, McKenzie and Kennedy 2011, Cansler and McKenzie 2014, Harvey et al. 2016) (Figure 8.3).

Current themes and issues for research on disturbance regimes

While much has been learned about how disturbances are fundamental to ecosystems across the world, current themes in the field center around two key questions: How do multiple disturbances interact? and how are disturbance regimes changing? Collectively, these two questions feed into inquiries of how disturbances and disturbance-recovery cycles in ecosystems promote resilience in single states or shifts between alternative stable states.

Increasing disturbance activity in many regions of the world over the last few decades (Dale et al. 2001) has led to a drastic increase in the recognition that disturbances do not occur in isolation but instead, are always overlapping in space with varying time intervals between individual events. Further, such interactions produce lasting effects on patterns of ecosystem composition and structure (Peterson 2002). While accepting the paradigm of the disturbance regime concept (see earlier) means that individual disturbance events are constantly overlapping prior such events, until recently, there was less mechanistic understanding of how these interactions unfolded and how they affected ecosystems. Since the late 1990s and early 2000s, there has been a proliferation of research examining disturbance interactions and the development of multiple frameworks for conceptualizing how these interactions operate.

Several terms introduced since the late 1990s collectively provide a helpful framework for testing different ways that disturbances can interact. First, two disturbances may be *linked*, in that the occurrence of one disturbance influences the likelihood, size, or severity of a subsequent disturbance (Simard et al. 2011). In such settings, the focal response variable is the occurrence and/or characteristics of any subsequent disturbance. For example, recent increases in insect outbreak and fire disturbance across North America since the late 1990s led to researchers asking whether insect outbreaks influence the likelihood of subsequent fire occurrence (Meigs et al. 2015), area burned (Hart et al. 2015a), fire behavior (Simard et al. 2011, Schoennagel et al. 2012), or fire severity (e.g., ecological effects) (Harvey et al. 2014, Meigs et al. 2016). Linked disturbances either facilitate or impede the incidence of subsequent disturbances or either amplify or reduce the intensity of a subsequent disturbance (Kane et al. 2017).

Whether or not two disturbances are linked, sequential overlap of two disturbances (of the same or different disturbance type) may produce effects that are *synergistic*, or greater than the sum of the two disturbances individually; such an interaction has been termed *compound disturbances* (Paine et al. 1998). In such settings, the focal response variable is the ecosystem state, or response to the combinations of disturbances, rather than the second disturbance per se. Examples in North America have focused on how forest ecosystems can be impacted by compound effects of fire disturbance that follows wind blow-downs (Buma and Wessman 2011), previous fires (Turner et al. 2019), and insect outbreaks (Harvey et al. 2013). Finally, interacting disturbances can produce *cascading effects* wherein interactions among disturbances can increase the climate sensitivity of an ecosystem (Buma 2015, Seidl and Rammer 2017). Key factors that govern disturbance interactions and their outcomes are the time since the first disturbance (and therefore, the interval between the two disturbances when a second occurs), the severity/magnitude of the first disturbance, the order of the disturbance sequence (i.e., which disturbance comes first), and whether the first disturbance amplifies or attenuates the subsequent disturbance (Burton et al. 2020).

In addition to a focus on interactions among disturbances, much research in the first decades of the 21st century has focused on how disturbance regimes are changing (Turner 2010, Johnstone et al. 2016). A warming climate, changing land-use patterns, and human-aided transport of plants and animals into novel regions (i.e., invasive species), as well as interactions among these factors, have been identified as key drivers of disturbance regime change. Changing disturbance regimes will have profound implications for ecosystem services (Seidl et al. 2016), yet many impacts are currently poorly understood.

Many disturbances are sensitive to climate, and warming temperatures—as a key driver in releasing previous constraints on disturbance activity—are profoundly affecting many aspects of disturbance regimes. A warming climate is lengthening the ‘season’ for many disturbance regimes worldwide. For example, global climate warming increased the length of the fire season (i.e., the period of time during each year when weather is conducive to fire spread) by nearly

20% over the period from 1979 to 2013 (Jolly et al. 2015), which has been accompanied by a corresponding increase in the frequency of large fires in many regions (Westerling 2016). Biotic disturbances that are also driven by climate (e.g., bark beetle outbreaks) have increased in severity and extent since the late 1990s (Raffa et al. 2008). Continued warming is expected to drive continued changes in both abiotic and biotic disturbance regimes (Bentz et al. 2010, Westerling et al. 2011, Seidl et al. 2017), yet for many systems, feedbacks among climate, vegetation, and disturbance may modify the direct effects of warming on disturbance regimes (Hart et al. 2015b). Characterizing the spatial, or landscape, patterns of disturbances and how they are changing as the climate warms has also become a focus—yet this remains an area of current exploration. For example, satellite-derived burn severity atlases have been used to track changes in spatial heterogeneity in fire patterns over time and space (Cansler and McKenzie 2014, Harvey et al. 2016, Reilly et al. 2017, Collins et al. 2017). Finally, synergies among changing components of regimes have been documented in some systems. For example, increasing fire frequency in some conifer forests is leading to anomalously short intervals between severe fires (severe fires are inherent in system dynamics when occurring over long fire-free intervals), which is, in turn, driving increases in fire severity (e.g., fire-caused vegetation mortality and woody biomass combustion) (Turner et al. 2019).

The growing human population on the planet and the accompanying increasing mobility of people around the globe has driven land-use changes and introductions of novel species assemblages—ultimately affecting the ways that disturbances operate and how they impact ecosystems (Gaertner et al. 2014). For example, in many areas where widespread and frequent disturbances such as prairie fires historically occurred, broad-scale agricultural development and fragmentation of native vegetation has led to a cessation of disturbance and corresponding losses in native biodiversity (Leach and Givnish 1996). In such cases, land-use and land-cover change have dampened the occurrence and severity of disturbance. Alternatively, many historically fire-prone forested regions have been affected by nearly a century of fire suppression or exclusion, which has increased the likelihood of uncharacteristically large and severe fires through fuel accumulation (Hessburg et al. 2015). In these cases, land-use and land-cover change have amplified the potential for disturbance while also increasing human exposure to disturbance where settlements have expanded into previously fire-frequent landscapes (Moritz et al. 2014, Schoennagel et al. 2017). In many areas, the introduction of non-native vegetation that is more flammable than native vegetation has led to novel fire regimes and ecosystem dynamics. For example, the arrival of humans (providing an ignition source) and more recent exotic plantation forests and invasive species (providing highly flammable vegetation) in the southern hemisphere promotes the spread of large fires in systems that historically had infrequent or no fire, with native species lacking adaptations to frequent and severe fire (Perry et al. 2012, Kitzberger et al. 2016, McWethy et al. 2018). Finally, introduced pathogens (which are a novel disturbance) can alter subsequent fire disturbances, with implications for changing disturbance regimes (Metz et al. 2013, Simler et al. 2018). Continued land-use change and spread of non-native species are likely to play a major role in further alteration of disturbance regimes and landscape patterns worldwide.

Disturbance, resilience, and scale

With recognition of the inherent role of disturbance as a controlling ecological process came the conceptualization of ecological resilience, the capacity of an ecosystem to retain essentially the same structures and functions following disturbance (Holling 1973). Resilience is conferred by an ecosystem's *information legacies*, the *disturbance-adaptive traits* of the system, and *material legacies*, the individuals, propagules, and other remnants that persist through disturbance (Johnstone et al. 2016). Information legacies emerge as a result of long-term selective pressures and thus, broad spatial scales, rather than a single disturbance event. In contrast, material legacies are determined by characteristics of the disturbance event and the state of the system when disturbed and so may vary across finer spatial and temporal scales (Johnstone et al. 2016). Thus, resilience often emerges from processes at one scale interacting with processes at a different scale, often with complex nonlinear dynamics (i.e., cross-scale interactions; Peters et al. 2004, Reyer et al. 2015).

Changes in disturbance regimes that alter legacies may compromise resilience (Johnstone et al. 2016). A well-studied example is found in conifer forests of boreal North America, where stand-replacing wildfire is a key disturbance (Payette 1992). A central mechanism promoting resilience of conifer forest to wildfire is the production of serotinous cones in pine (*Pinus* spp.) and black spruce (*Picea mariana*), which allows rapid post-fire establishment of conifer trees (Greene et al. 1999). Resilience may be compromised when wildfires burn too intensely, leading to combustion of seed or soil organic layers. Exposure of mineral soils and local absence of conifer seed confer a competitive advantage on deciduous broadleaf species (Johnstone and Chapin 2006, Greene et al. 2007). When deciduous trees become established, they initiate changes in plant–soil feedbacks that alter fuels and lead to the establishment of a low-severity fire regime (Johnstone et al. 2010). Thus, predicting when and where disturbance may initiate shifts to alternative states requires a multi-scale understanding of the mechanisms that promote resilience.

In light of the potential for erosion of resilience to drive dramatic shifts in ecosystem state that are often hard to reverse, resilience has also become a central theme in environmental sustainability. In this context, resilience is often viewed as a desirable attribute of an ecosystem because it implies a predictable, although varying, supply of expected ecosystem services (Angeler and Allen 2016). This interpretation contrasts with Holling's (1973) original definition, which describes resilience as an emergent property of a system. In a recent effort to differentiate and link these two views, Higuera et al. (2019) suggest that socioecological systems would be best described in terms of the probability of a state change (i.e., *value-free resilience*) and the social acceptability of a state change (i.e., *value-laden resilience*). This separation is helpful, because ecological resilience and social values are not always in alignment (Higuera et al. 2019). For instance, cheatgrass (*Bromus tecotrum*) invasion of rangelands of the Great Basin led to the establishment of an ecosystem that exhibits high value-free resilience to wildfire, which is conferred by the life-history traits of cheatgrass (i.e., early-season growth and abundant seed production; D'Antonio and Vitousek 1992). However, because cheatgrass-dominated grasslands are characterized by high-frequency wildfire (Balch et al. 2013) and lower forage quality, these attributes are not highly valued by society (Brunson and Tanaka 2011). Further, ecosystems may be unlikely to change states, but the rate of return to the pre-disturbance state may be socially unacceptable. For example, subalpine forests of the Southern Rocky Mountains in the United States generally show high value-free resilience to infrequent high-severity wildfire (Minckley et al. 2012), but the recovery is often slow (Kipfmueller and Kupfer 2005, Rodman et al. 2019). Thus, when societal values emphasize forested conditions, silvicultural treatment may be used to expediate forest regeneration and stand development despite high ecological resilience (DeRose and Long 2014). Linking value-free resilience with the social acceptability of disturbance-driven change is critical to operationalizing the resilience framework in socioecological systems.

Looking ahead to the future: challenges and opportunities

Over recent decades, we have learned a lot about how environmental drivers, initial ecosystem conditions, and mechanisms underlying disturbance effects influence disturbance regimes. This research has revealed that many disturbances regimes are characterized by complex cross-scale interactions (Peters et al. 2004). For example, in their review of the drivers of bark beetle outbreaks, Raffa et al. (2008) describe how outbreaks occur in response to interactions among fine-scale processes, such as tree entry by an individual beetle, and broad-scale processes, like regional patterns in host abundance and susceptibility. Spatially extensive outbreaks occur when thresholds are surpassed and new positive feedbacks are established. Such nonlinear and cross-scale interactions represent a key challenge for disturbance ecology because they often result in emergent behavior that cannot be predicted from the individual processes or observations from single events (Peters et al. 2004). For instance, empirical models of bark beetle–induced tree mortality are often of little predictive capacity because they were developed under a limited set of conditions (Bentz et al. 1993, Hart et al. 2014). Combining long-term field data and spatially extensive remote sensing datasets can facilitate the prediction of ecological thresholds. However, the integration of such data remains a major challenge in understanding the current and future effects of disturbances (Lindenmayer et al. 2010, Weed et al. 2013, Peters et al. 2018).

Contemporary changes in climate, land-use practices, human population size, and biotic communities, and the resulting changes in disturbance regimes, have altered landscape spatial patterns in ecosystems around the world, with important consequences for the provisioning of ecosystem services (Turner 2010, Turner et al. 2013, Seidl et al. 2016). For example, the Great Barrier Reef, which is home to more than 1,700 aquatic animal species, contributes $6.4 billion to Australia's economy annually and is culturally important to many of Australia's aboriginal people (O'Mahoney et al. 2017). Across the Great Barrier Reef, coral cover has declined by more than half since 1985 due to cyclonic disturbance, population outbreaks of predatory crown-of-thorns starfish (*Acanthaster planci*), and temperature-driven coral bleaching events (De'ath et al. 2012). Concurrently, coral recovery rates have declined by more than 80% due to decreased water quality, warming, and the compound effects of frequent cyclones (Ortiz et al. 2018). Yet, both die-off and recovery rates vary in space and time across the Great Barrier Reef due to complex interactions among biological processes, environmental conditions, and geographic setting (De'ath et al. 2012, Ortiz et al. 2018). A central challenge for ecology is to predict how future global change and the ensuing changes in disturbance regimes will affect ecosystems around the world. There are many challenges to forecasting future disturbance regimes, including (1) uncertainty in future climate projections, (2) the potential for new drivers to be introduced (e.g., invasive species), (3) feedbacks between disturbances and climate, and (4) non-stationarity in environmental drivers.

As we head into the third decade of the 21st century, landscape ecology will continue to be an important lens through which to examine and understand disturbances. While much is still to be learned about the fundamental nature of many ecological disturbances, regimes themselves are rapidly changing as the climate warms and the human imprint on the biosphere expands. Questions and answers about how disturbances operate, how they are changing, and how we can manage social ecological systems are topics that are inherently spatial and that occur across a wide range of spatial and temporal scales. Landscape ecology is primed to play a critical role in bringing together ecological insights from the field with massive streams of remotely-sensed big data to aid in understanding, tracking, and predicting disturbance regimes of the Earth's future.

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