Changing disturbance regimes, ecological memory, and forest resilience

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Ecological memory is central to how ecosystems respond to disturbance and is maintained by two types of legacies – information and material. Species life-history traits represent an adaptive response to disturbance and are an information legacy; in contrast, the abiotic and biotic structures (such as seeds or nutrients) produced by single disturbance events are material legacies. Disturbance characteristics that support or maintain these legacies enhance ecological resilience and maintain a "safe operating space" for ecosystem recovery. However, legacies can be lost or diminished as disturbance regimes and environmental conditions change, generating a "resilience debt" that manifests only after the system is disturbed. Strong effects of ecological memory on post-disturbance dynamics imply that contingencies (effects that cannot be predicted with certainty) of individual disturbances, interactions among disturbances, and climate variability combine to affect ecosystem resilience. We illustrate these concepts and introduce a novel ecosystem resilience framework with examples of forest disturbances, primarily from North America. Identifying legacies that support resilience in a particular ecosystem can help scientists and resource managers anticipate when disturbances may trigger abrupt shifts in forest ecosystems, and when forests are likely to be resilient.

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Patterns and processes of disturbance and recovery shape the dynamics of many ecosystems (White and Jentsch 2001). As the climate changes, however, the nature of disturbances is also changing, increasing uncertainty in how ecosystem dynamics will play out in the future (Turner 2010). Alterations in disturbance regimes (eg patterns of severity, frequency, and timing) are being observed more often, along with historically novel disturbance events and disturbance interactions (Turner 2010; Trumbore *et al*. 2015). Contemporary and paleoecological observations indicate substantial ecosystem *resilience* to historical disturbances, meaning that ecosystems recover their essential structure and function after perturbation (Holling 1973). However, disturbances can also trigger persistent changes in ecosystem state (Scheffer *et al*. 2001) and increase vulnerability to degradation (Ghazoul *et al*. 2015; Seidl *et al*. 2016). Understanding the mechanisms that determine when, where, and how shifting climate and changing disturbance regimes fundamentally alter ecosystem dynamics is a critical question in the 21st century (Turner 2010; Trumbore *et al*. 2015).

In a nutshell:

- Disturbances shape forest landscape patterns and processes over years, decades, and centuries; changes in disturbance characteristics drive forest responses to environmental change
- Forest resilience to disturbance is shaped by ecological memory of past ecosystem states, transmitted as legacies of species adaptations and materials that support recovery
- Changes in disturbance regimes (eg disturbance frequency, severity, size, or timing) that modify key legacies can trigger rapid reorganization into new ecosystem states
- Directional changes in climate can cause misalignment of legacies that erode resilience but are not apparent until after the system is disturbed
- We can anticipate when and where forests will be most vulnerable to changes in climate and disturbance by focusing on mechanisms that alter key disturbance legacies

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Ecosystem processes and patterns depend on the contemporary environment and the persistent effects, or *legacies*, of past events (Franklin *et al*. 2000; Seidl *et al*. 2014; Monger *et al*. 2015). Disturbances generate biological legacies that interact with environmental conditions to shape ecosystem recovery (Franklin *et al*. 2000). Today, global changes in climate, land use, and species invasions are rapidly altering disturbance characteristics and legacies, triggering abrupt shifts among multiple ecosystem states (Frelich 2002; Hughes *et al*. 2013) and creating novel environments and ecosystems (Williams and Jackson 2007). Following a transition, alternate states may be maintained by new sets of legacies and reinforcing feedbacks (Scheffer *et al*. 2001; Bowman *et al*. 2015).

Environmental change also alters the context in which ecosystems recover from disturbance (Trumbore *et al*. 2015). As a result, ecosystems may be shifting from dynamic equilibria in variable but broadly stationary environments to non-equilibrium dynamics under conditions of ongoing, directional change. Anticipating these dynamics in forests is challenging because disturbance and resilience unfold over decades to centuries and across vast areas (Hughes *et al.* 2013; Ghazoul *et al.* 2015). Nevertheless, forecasting future forest responses to disturbance is increasingly important, especially where human livelihoods and well-being depend on maintaining forest structure and function (Seidl *et al.* 2016).

We anticipate that changes to climate, disturbance regimes, and biological legacies will substantively influence forest landscapes, potentially disrupting feedbacks that confer resilience and amplifying processes that may trigger state changes in forest ecosystems. Thus, key questions emerge: under what conditions are forests likely to be resilient to altered disturbance regimes, and how do different components of "ecological memory" enhance or erode resilience? We synthesize examples from forests that have been strongly affected by fire or other disturbances to provide insights into mechanisms that support ecosystem resilience to changing climate and disturbance regimes. In doing so, we identify a new framework for ecosystem resilience that highlights how changes in ecological memory may contribute to abrupt transitions in forests and other ecosystems in the coming decades to centuries.

Ecological memory and forest resilience

Forests typically are well adapted to a particular historical disturbance regime – the characteristic patterns of disturbance along axes of frequency, severity, size, or other attributes (Turner 2010). Recurring disturbance patterns exert strong selective pressure on life-history strategies that affect population survival and spread (Keeley *et al.* 2011). Consequently, forest species evolve survival and regeneration strategies that are tuned to disturbance regimes rather than individual disturbance events (Keeley *et al.* 2011). In the biotic community, the suite of disturbance-response traits provides one component of ecological memory in the form of *information legacies* of evolutionary adaptations to historical disturbances (Panel 1). Species with regeneration traits that are well aligned with a given disturbance regime have an immediate and powerful recruitment advantage after a typical disturbance event. For example, persistent understory seedling banks of shade-tolerant species have a regeneration advantage following windstorms that injure canopy trees (Frelich 2002). Similarly, severe stand-replacing fires that remove competing vegetation favor species that can resprout or regenerate rapidly from seed banks (Pausas and Keeley 2014). Stand-replacing fire regimes thus frequently select for serotiny (aerial seed banks held on the plant, as in many *Pinus* and *Banksia* species), thereby ensuring abundant, rapid postfire re-establishment (Lamont and Enright 2000). Thus, the information legacy of species traits that are present in a community or population allows an ecosystem to recover to a similar state when the system is perturbed. Disturbances with characteristics that fall within the range of past variation (which may be wide or narrow, depending on the system)

Panel 1. Glossary of terms

Disturbance legacies: biologically derived legacies that persist in an ecosystem or landscape following disturbance (akin to the *biological legacies* of Franklin *et al.* [2000]). Our definition includes species traits and adaptations that contain information about successful strategies to past disturbances, as well as residual organisms, propagules, and physical structures arising from past biological activity. We distinguish two types of disturbance legacy, *information* and *material legacies*, which maintain the *ecological memory* of a system.

- ***Information legacies:*** responses (adaptations) to historical disturbance cycles, described by the presence, frequency, and distribution of species traits in a community or population. Information legacies emerge over long temporal scales and across broad spatial scales and are adaptations to a disturbance regime, rather than a disturbance event. Information legacies will constrain the ecosystem's response to an individual disturbance event.
- ***Material legacies:*** individuals or matter (eg survivors, seeds, dead trees, nitrogen pools) present in an ecosystem after a disturbance event. Material legacies emerge on short temporal scales and local spatial scales. They are determined by the state of the ecosystem at the time it was disturbed and by characteristics (eg severity and size) of the disturbance event.

Ecological memory: information and material legacies – that is, the adaptations, individuals, and materials that persist after a disturbance and shape responses to future disturbance. Ecological memory may be encoded across a range of spatial and temporal scales, from small, patch-scale legacies to those expressed across broad landscapes and evolutionary timescales. Here we emphasize aspects of ecological memory that operate at stand or ecosystem scales and time spans of successional cycles.

Resilience debt: a loss of resilience in a system due to misalignment of information legacies and disturbance but which is only apparent *after* the system is disturbed. Resilience debt may arise due to a change in disturbance regime or conditions required for recovery, or changes in ecological communities that affect information legacies.

Safe operating space: at the global scale, refers to biophysical planetary boundaries within which human societies can continue to develop and thrive (Steffen *et al.* 2015). The goal is to stay within acceptable levels, or boundaries, of global stressors, though a safe level of one stressor may depend locally on the level of other stressors (Scheffer *et al.* 2015). Here, we use the "safe operating space" framework to consider interactions of disturbance characteristics and environmental conditions with the components of ecological memory that support forest resilience to disturbance.

will tend to perpetuate the same set of species traits that performed well in the past, creating a reinforcing eco-evolutionary feedback that supports ecological resilience.

Individuals, propagules, and other biotic and abiotic residuals (ie materials that persist through a specific disturbance event) represent a second component of ecological memory, *material legacies*, which have passed through a disturbance filter and transfer memory of past ecosystem condition into the future (Panel 1; Franklin *et al.* 2000; Monger *et al.* 2015). Survivors and seed supply determine patterns of colonization, and physical legacies (such as standing dead trees, logs, and other organic matter) affect establishment success. Material legacies are therefore critical for ecosystem resilience and are a conduit for the perpetuation of information legacies: for example, material legacies that facilitate recovery of a particular species or community maintain the information legacies of those species into the future. For instance, the prevalence of serotiny (an information legacy) leads to large quantities of postfire seed (a material legacy) that perpetuate the dominance of serotinous species after fire (Lamont and Enright 2000). Other adaptations, such as surface or belowground organs that can resprout, produce legacies that enable individuals to survive multiple disturbance events. The fitness consequences of material legacies depend on the relative abundance and spatial arrangement of surviving individuals, intact seed banks, or patches of undisturbed vegetation that serve as a source for colonization, as well as the physical structure and environmental conditions that affect regeneration success. In sum, ecological memory includes information legacies shaped by disturbance history over large temporal and spatial scales, and material legacies shaped by local effects of specific disturbance events.

Disturbance processes that could trigger abrupt forest transitions

The alignment of historical disturbance regimes with information legacies in the form of dominant regeneration traits defines a *safe operating space* (Scheffer *et al.* 2015; Steffen *et al.* 2015), where forests are likely to be resilient to disturbance (Figure 1a; Panel 1). When disturbance regimes shift so that key information or material legacies are lost or become mismatched (Figure 1b), erosion of ecological memory can facilitate shifts to new ecological states. Understanding conditions that cause disturbance regimes and information legacies to become misaligned is central to anticipating when and where forests will be most vulnerable to state changes. We highlight four example conditions that could reduce resilience to disturbance in forest ecosystems and trigger transitions to alternate ecosystem states (Figure 2).

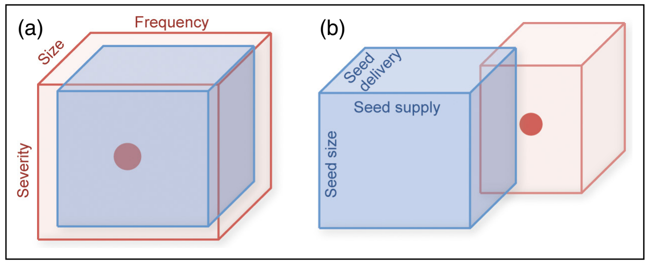


Figure 1. *A conceptual representation of the safe operating space supporting ecosystem resilience formed when characteristics of disturbance regimes (illustrated by a red box representing patterns of severity, size, frequency, and other attributes) are aligned, as in (a), with information legacies of species traits (blue box representing traits affecting response to disturbance, such as seed size, supply, and delivery). In contrast, the safe operating space shrinks and resilience is degraded when a shift in the disturbance regime erodes the suitability of existing information legacies, as in (b), where a shift in fire frequency causes misalignment with traits that ensure adequate seed supply. This situation increases the likelihood that material legacies generated by individual disturbance events (red dot) will lie outside the safe operating space and be insufficient to support ecosystem resilience.*

Novel disturbances

An extreme disruption to information legacies can arise from introducing new disturbances in ecosystems that lack pre-existing adaptive capacity to that disturbance; such a disturbance lies completely outside the safe operating space. The late-Holocene transformations that occurred in New Zealand after humans introduced fire are an example. Within a century after Polynesian settlement, anthropogenic ignitions in forests capable of burning but without a history of fire were responsible for abrupt, widespread, and persistent loss of forest cover (McWethy *et al.* 2014). The motivation for widespread Polynesian burning likely included clearing land for horticulture, improved travel, and possibly warfare, with localized burning amplified by strong vegetation–fire feedbacks (Perry *et al.* 2012, 2014).

Similarly, European settlers burned intentionally to clear land for extensive pastoralism, and fire was often associated with logging activities (Perry *et al.* 2014). This pattern appears to be repeating itself in modern tropical forests in South America and Southeast Asia (Cochrane 2003). The relative vulnerability of New Zealand forests to the introduction of fire has been attributed to an absence of regeneration adaptations as well as the removal of accumulated topsoil by frequent fire (loss of a material legacy) and invasion by non-native, fire-adapted plant species (shift to new information legacies) (Whitlock *et al.* 2015). Even under current reduced levels of fire activity, the loss of material legacies and shifts to novel information

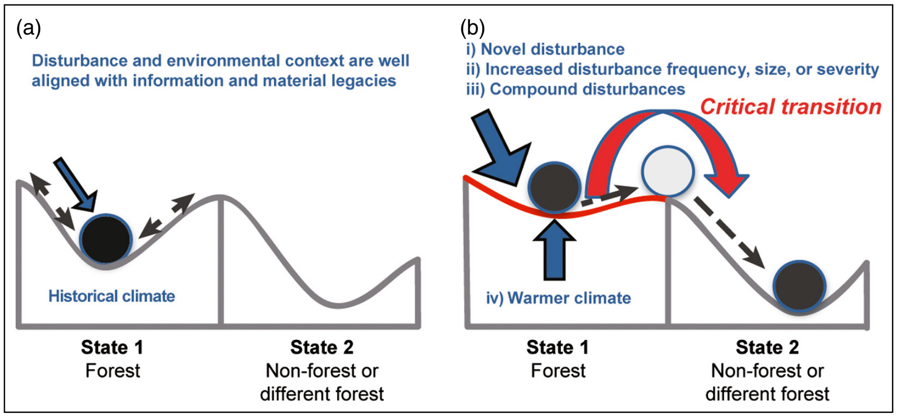


Figure 2. *Conceptual representation of forest ecosystems (black ball) within a theoretical landscape of alternative ecosystem states (valleys separated by peaks). (a) Forests are resilient to disturbances lying within the safe operating space, indicated by disturbances that may move the system but not cause it to shift to another state. (b) Forests are likely to shift to a different state in response to four hypothesized mechanisms (i–iv) that move a system outside its safe operating space and trigger a shift to a different forest or non-forest state.*

legacies suggest ecosystem recovery will be extremely slow (Perry *et al.* 2015).

Changing disturbance characteristics

Changing the tempo, intensity, or spatial attributes of disturbance can filter out certain trait sets or taxa (Keeley *et al.* 2011), shifting a system away from its safe operating space. Extreme events that lie outside the historical disturbance regime may be particularly important in disrupting the alignment between species traits and disturbance characteristics that confer ecosystem resilience. The increasing occurrence of unusual disturbance events in response to climate change and other factors offers insights into how changing disturbance characteristics may alter forest resilience (Fraterrigo and Rusak 2008). For instance, changes in fire frequency, severity, and size alter the effectiveness of adaptations related to survival, resprouting, and seed recruitment after fire, thus favoring different species (Frelich 2002; Enright *et al.* 2015). Increased fire frequency can alter recovery when the interval between fires is less than the time required for woody species to mature (Buma *et al.* 2013; Enright *et al.* 2015). Greater fire intensity can kill thick-barked, seed-retaining trees that would otherwise survive lower intensity fires (Lydersen *et al.* 2014), consume viable seeds in serotinous cones that would otherwise contribute to postfire forest recovery (Turner *et al.* 1999), or alter species-specific survival of seedlings through changes to postfire substrates (Johnstone *et al.* 2010). Increased patch size of high-severity burns can reduce seed delivery when distances to unburned forest exceed the dispersal distance of the dominant trees (Lindenmayer *et al.* 2011). Thus, when changing disturbance characteristics alter material legacies that determine regeneration success, forest ecosystems become vulnerable to rapid changes in ecosystem state, including transitions to non-forested systems (Table 1).

Changes in disturbance characteristics that alter material legacies of biomass and nutrients affect forest resilience by changing the environmental conditions that shape succession (McLauchlan *et al.* 2014). For example, moist soils in black spruce (*Picea mariana*) ecosystems of boreal North America accumulate thick organic layers that typically are only partly consumed in stand-replacing fires (Johnstone *et al.* 2010). The residual layer of organic matter creates conditions well suited for black spruce regeneration. Black spruce and the attendant moss flora have functional traits that support plant–soil–microbial feedbacks, cycling nutrients slowly and reinforcing the accumulation of deep organic soils (Figure 3). Climate-driven increases in fire frequency and intensity promote combustion of the soil organic layer in black spruce ecosystems, exposing mineral soil seedbeds and warmer soil conditions well suited for recruitment of deciduous tree species. Functional traits of these deciduous trees (rapid growth, high-quality litter) initiate new plant–soil–microbial feedbacks that support shallow soil organic layers,

Table 1. Regeneration mechanisms of resilience to fire disturbance, and their vulnerabilities to changing disturbance characteristics

Mechanism	*Vulnerability to altered disturbance*	*Consequences*
Seed supply	Increased fire frequency or severity	Reduced tree recruitment if fire intervals are less than those required for an adequate seed crop, or severe fires consume stored seed
Seed delivery	Increased fire size	Reduced or retarded tree regeneration if high-severity burned patch size exceeds seed dispersal distances
Seedbed	Increased fire severity	Altered canopy composition due to environmental filters on tree seedling establishment and growth

rapid nutrient cycling, and low-intensity fire that perpetuate recovery of the alternate, deciduous forest state (Johnstone *et al.* 2010; Alexander *et al.* 2012). In this way, changes in material legacies caused by increased consumption of surface organic material can trigger a state change that is maintained by new internal feedbacks (Figure 3).

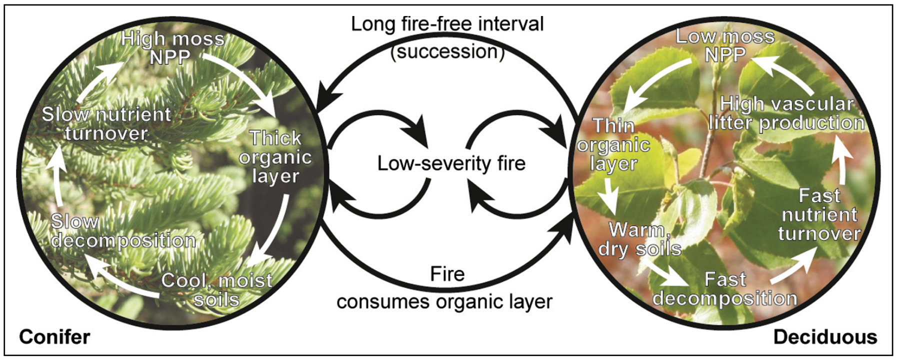


Figure 3. *Feedbacks associated with material legacies shaped by changing fire characteristics in the northern boreal forests of Alaska. Resilience of a conifer forest state is conferred by maintenance of a thick organic layer after stand-replacing fire. Loss of that material legacy when consumed by severe fires can trigger a switch to a deciduous broadleaf forest, which persists through a new set of plant–soil–microbial feedbacks. Both states are maintained by a typical regime of low-severity fire, and return from a deciduous- to conifer-dominated forest is likely to be possible only with succession occurring over an unusually long fire-free interval. Figure modified from Johnstone* et al. *(2010). NPP = net primary production.*

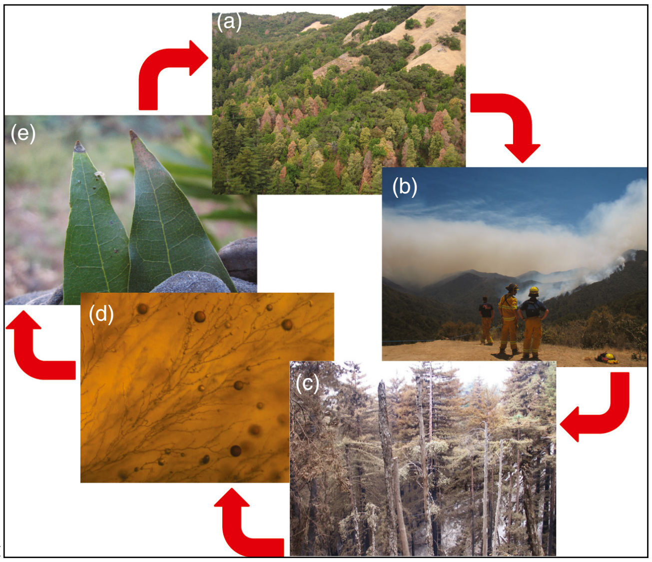
Multiple disturbance interactions

Interactions among disturbances may alter forest resilience via multiple pathways. Disturbances can be "linked" (Simard *et al.* 2011), so that the material legacies of one disturbance alter the likelihood, extent, or severity of another. Two disturbances can also produce "compound effects" (Paine *et al.* 1998) if one disturbance affects material legacies required for recovery following a second event. Changes in ecosystem resilience to disturbance depend on types, order, timing, and characteristics of successive disturbances and the suite of species traits present (information legacies). Below, we highlight examples of interactions between wildfires and biotic or abiotic disturbances common to many forests worldwide.

The material legacies of an insect outbreak can constrain an ecosystem's response to a subsequent disturbance. Insects can defoliate (eg spruce budworm, *Choristoneura* spp) or kill (eg bark beetle, *Dendroctonus* spp) trees, leaving a legacy of altered forest composition, propagules, and fuel structure. Although legacies of insect outbreaks are likely to influence fire behavior to some degree, there is little evidence of past outbreaks acting as primary drivers of wildfire activity; for instance, insect outbreaks in western North America have little to no effect on fire occurrence (Meigs *et al.* 2015), extent (Hart *et al.* 2015), and severity (Harvey *et al.* 2014; Andrus *et al.* 2016). However, legacies of insect outbreaks can affect key mechanisms of recovery from fire and lead to compound effects of successive insect and fire disturbance. For example, among non-serotinous conifers (eg Douglas-fir, *Pseudotsuga menziesii*, and Engelmann spruce, *Picea engelmannii*), early postfire recovery of beetle-killed forest depends on mature trees that survive the bark beetle attack and the fire, as well as distance to live seed sources outside the burned area (Harvey *et al.* 2013). In contrast, persistence of serotinous cones on beetle-killed lodgepole pine (*Pinus contorta* var *latifolia*) reduces the compound effects of disturbance on postfire regeneration if fires occur when viable seed is still available on dead trees (Harvey *et al.* 2014). Similarly, defoliators such as spruce budworm reduce seed production for several decades in boreal black spruce, affecting seed availability and delaying regeneration of black spruce after subsequent fires (Simard and Payette 2005). Forest resilience to insect outbreaks followed by wildfire depends on how the severity, frequency, and size of successive disturbances affect material legacies related to regeneration (Table 1).

Pathogens that cause widespread mortality of their host species can affect subsequent disturbances through linked interactions and produce compound effects on forest recovery (Figure 4). For example, spread of *Phytophthora ramorum*, a non-native fungus that causes sudden oak death, has led to widespread mortality in host tree species in fire-prone coastal forests of California and Oregon (Rizzo and Garbelotto 2003). Pathogen-killed trees are material legacies of the outbreak that shape fuel structures for subsequent fires and influence patterns of fire severity through linked interactions (Metz *et al.* 2011). Effects of these material legacies may cascade to non-primary hosts that have a negligible role in epidemiology, as when redwood trees (*Sequoia sempervirens*) experience unusually high fire-related mortality in a stand affected by sudden oak death (Metz *et al.* 2013). Conversely, previous fires may leave material legacies of stand composition that affect subsequent disease transmission, as when hosts that are more responsible for transmission (eg tanoak, *Notholithocarpus densiflorus*) also experience high fire-related mortality (Metz *et al.* 2013).

Land-use changes caused by human management may also interact with natural disturbances to cause linked and compound disturbance interactions. Extensive harvesting of forests often shortens disturbance intervals, changing stand-age distribution, forest structure, and species composition (Bergeron *et al.* 2006), thus altering both material and information legacies across the land-



(a,b,e) K Frangioso

(d) K Aram

(c) H Kuljian

Figure 4. *Interactions between disease transmission, host mortality, and subsequent fire behavior and mortality that may feed back to influence changes in forest states. Moving clockwise, photos represent: (a) The pathogen* Phytophthora ramorum *alters forest structure by selectively killing host species, as in this landscape near Big Sur, CA. (b) Structural changes may then alter fire behavior across the forest landscape, such as in (c) when injured host species, such as tanoaks (*Notholithocarpus densiflorus*), carried flames into the forest crowns, increasing the mortality of redwood (*Sequoia sempervirens*) trees after the 2008 Basin Fire. (d) Hosts vary in susceptibility to the pathogen: for example, through cellular processes that influence the spread of* P ramorum *hyphae and* chlamydospores. *(e) Spread of the pathogen is shaped by the distribution and connectivity of potential hosts, such as these infested leaves of California bay laurel (*Umbellularia californica*), and the pathogen returns to influence forest structure and future disturbance.*

scape. These changes may in turn cascade to alter subsequent fire behavior and susceptibility to wind, drought, and insect disturbance (Frelich 2002; Frelich and Reich 2010). Similarly, land-use change that alters forest composition, landscape connectivity, and/or local microclimate creates legacies affecting disease transmission and fire dynamics (Meentemeyer *et al.* 2012).

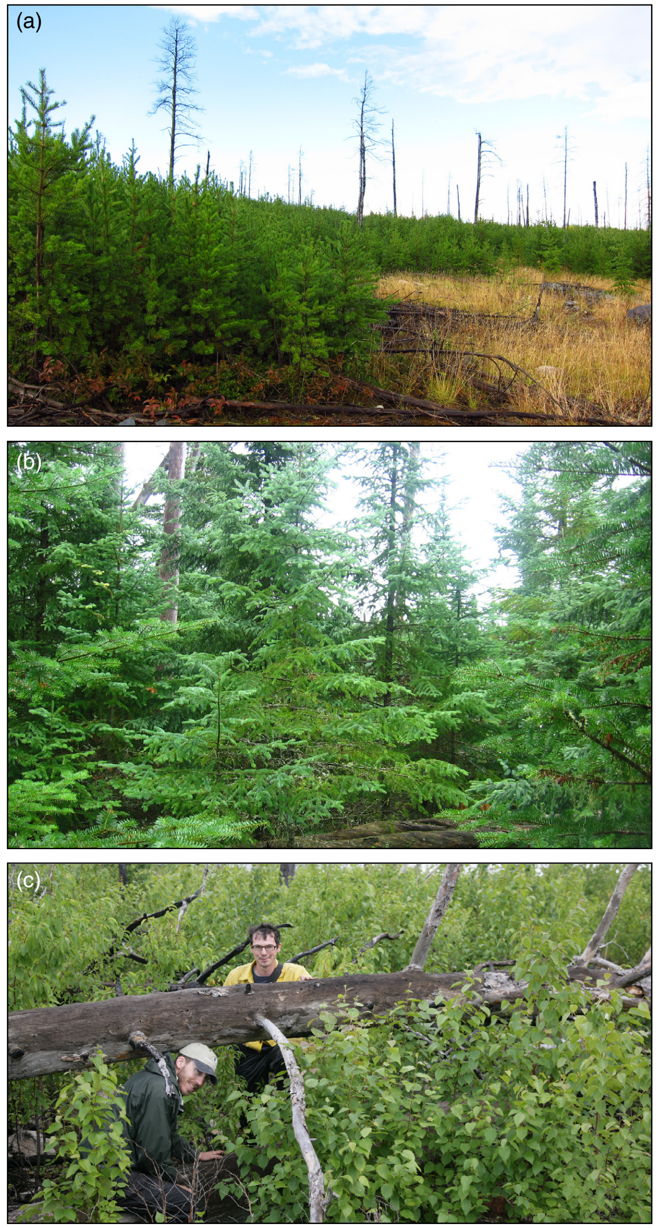
Successive disturbances that cause a mismatch between material and information legacies can produce contrasting outcomes in the same landscape. In forests of northern Minnesota, information legacies arising from adaptations to the historical disturbance regime support the perpetuation of serotinous jack pine (*Pinus banksiana*) by crown fires. Shade-tolerant fir (*Abies balsamifera*) and spruce (*P mariana*) are perpetuated by windthrow (breakage and felling by extreme winds), which favors advance regeneration of surviving understory saplings (Frelich 2002). If windthrow is followed by fire, however, advance regeneration is killed, and cones near the ground on fallen conifer trees are burned. This combination fails to produce the material legacies that support recovery of conifer forests, instead favoring establishment of wind-dispersed aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) (Frelich 2002). Thus, alternative outcomes may emerge in the same conifer forest landscape, depending on the types and sequence of disturbances (Figure 5). When material legacies of a disturbance event fail to confer information arising from past events, resilience is degraded and new recovery trajectories may emerge.

Climate-disturbance interactions and resilience debt

Pre-disturbance climate affects the vulnerability of trees to later events, sets the context for ecosystem recovery, and can indirectly affect the success of colonists through interactions with invasive species. Antecedent climate conditions that are physiologically stressful can increase disturbance-induced tree mortality and reduce ecosystem resilience (Figure 6, a and b). For instance, in low-elevation forests of the western US, populations of fire-resistant trees persist under a regime of frequent, low-intensity fires. However, prolonged pre-fire drought can increase fire-related tree mortality in these forests independent of variations in fire intensity (van Mantgem *et al.* 2013). Drought stress also weakens conifer defenses to bark beetle attack, increasing tree mortality (Raffa *et al.* 2008). Warmer temperatures may therefore amplify forest drought stress and associated tree mortality from both fires and bark beetles (Williams *et al.* 2013), and increased fuel loads during drought years can lead to unusually severe fires (Brando *et al.* 2014).

Interactions of disturbances with ongoing climate and environmental change are likely to drive punctuated and potentially unexpected responses in ecosystems (Millar and Stephenson 2015). Strong stabilizing interactions in intact forests and resistance of mature trees to environmental stress may mask a decline in recovery potential (resilience) until a disturbance occurs (Ghazoul *et al.* 2015). Contemporary regeneration of long-lived trees may occur under climate conditions that are substantially different from those of the preceding regeneration cycle. For instance, in subalpine and montane forests in western North America, trees regenerating from recent fires followed by unusually dry years have substantially lower postfire seedling densities than in similar fires followed by wetter years (Rother *et al.* 2015; Harvey *et al.* 2016) (Figure 6, c and d). Because postfire seedling recruitment typically occurs during a short postfire window in these conifer-dominated forests (eg Turner *et al.* 1999), climate effects on recruitment success can persist for many decades. Under climate warming, greater variability in weather and disturbance may increasingly lead to recruitment failures, even when material legacies remain relatively unchanged.

Such interactions between changing disturbance regimes and environmental conditions create a *resilience* *debt* in which the reduced capacity of a system to recover from disturbance is apparent only after the disturbance has occurred (Panel 1). Akin to extinction debt (Tilman *et al.* 1994), time lags in system response lead to a system that becomes compositionally and functionally misaligned to the disturbance regime(s) it experiences. Such lagged responses to changing drivers are extremely difficult to detect using contemporary snapshot data (Camill and Clark 2000), but climate impacts on regeneration clearly illustrate this characteristic (Harvey *et al.* 2016). Processes such as climate- or human-mediated extinction or invasion may also create a resilience debt by eroding the value of information legacies, as when the arrival of new species alters the biotic interactions that affect resilience (Gaertner *et al.* 2014; Perry *et al.* 2015). For example, new biotic interactions arising from species immigration in Minnesota may alter the outcomes of forest regeneration from disturbance, as expanding native white-tailed deer (*Odocoileus virginianus*) populations consume tree seedlings, non-native invasive plants compete with native plants, and non-native (European) earthworms exacerbate drought and nutrient stress on regenerating trees (Frelich and Reich 2010). Human activities that alter disturbance patterns may indirectly cause a loss of information legacies that confer resilience to disturbances favored under climate change. For example, fire suppression in the northwest US is associated with declining populations of fire-adapted conifers, eroding potential resilience to climate-induced increases in fire activity (Buma *et al.* 2013). Such resilience debts are highly likely to cause critical system transitions in response to future disturbances because misalignments between information legacies and disturbance conditions have reduced the safe operating space (Figure 2).



(a) and (b) E Anoszko

(c) D Hansen

Figure 5. *Examples of alternative vegetation types arising from different combinations of disturbances in the forests of the Boundary Waters Canoe Area Wilderness, Minnesota. Disturbances in similar jack pine (*Pinus banksiana*) forests may give rise to at least three different patterns of regeneration: (a) reestablishment of jack pine dominance following a single high-severity fire, (b) black spruce (*Picea mariana*) and fir (*Abies balsamifera*) regenerating after a severe windthrow event, and (c) birch (*Betula papyrifera*) regeneration following successive disturbances of windthrow and then fire.*

Feedbacks affecting landscape patterns of forest resilience

Once a system transition is initiated, ecosystem feedbacks may stabilize the new system or dampen the effects of change, thereby determining whether the changes in climate and disturbance characteristics produce persistent state changes that fundamentally alter ecosystems and landscapes (Bowman *et al.* 2015). Introduction of new functional traits that affect disturbance characteristics can change information and material legacies that establish feedbacks and entrain the system in a new state (eg Gaertner *et al.* 2014). The grass–fire cycle is a classic example of this type of feedback-driven dynamic, where introduction of fine grass fuels increases tree mortality and drives grass–fire feedbacks that favor grassland (D'Antonio and Vitousek 1992). Similarly, introduction of fire-adapted weedy shrubs (eg *Hakea* spp and *Ulex* spp) that bring novel traits such as serotiny to New Zealand may alter successional trajectories and increase future fire risk (Perry *et al.* 2014).

Vegetation change can either amplify or dampen the effects of climate on disturbance regimes, making it especially important to understand and anticipate shifts in the distributions of dominant species. For instance, development of the modern boreal forest in Alaska circa 3000–5000 years ago was broadly associated with millennial-scale climatic cooling and moistening,

Figure 6. *Illustrations of direct climate interactions with disturbance that alter patterns of forest recovery. (a) Severe drought prior to the June 2011 Las Conchas Fire in New Mexico contributed to extreme fire behavior that consumed material legacies (nearly all aboveground biomass) and killed fire-resistant trees such as this alligator juniper (*Juniperus deppeana*) (August 2011). (b) Five growing seasons postfire, limited regeneration at the same site remains dominated by weedy herbaceous vegetation, with few resprouting shrubs and no tree seedlings (October 2015). (c) Abundant regeneration of serotinous lodgepole pine (*Pinus contorta*) 15 years after the 1988 Yellowstone Fires in Wyoming can be contrasted with (d) sparse regeneration 13 years after the 2000 Beaver Creek Fire, which was also in Yellowstone but was followed by 3 years of drought (2001–2003).*

which should have favored reduced fire activity. However, invasion of flammable black spruce into areas occupied by white spruce (*Picea glauca*) and deciduous woodlands altered fuel structure, resulting in increased fire frequency (Brubaker *et al.* 2009; Kelly *et al.* 2013). In contrast, during relatively warm periods, such as the Medieval Climate Anomaly (circa 950–1450 CE) and recent decades, increased fire severity promoted expansion of deciduous forests in the interior of Alaska (Kelly *et al.* 2013). Reduced flammability of a landscape dominated by deciduous trees may mitigate the direct impacts of climate warming on fire frequency (Kelly *et al.* 2013). These cases illustrate that the indirect effects of climate on fire regimes, through changes in fuels and landscape flammability, can lead to unexpected feedbacks and outcomes for disturbance regimes and forest resilience.

Conclusions

Reciprocal interactions between pattern and process are embedded in ecological memory and central to ecosystem response to disturbance. Strong effects of legacies on ecosystem recovery mean that contingencies – such as the size, frequency, severity, and spatial pattern of previous disturbances; the order, timing, and severity of interacting disturbances; and species responses to variation in climate, especially during regeneration windows – will interact to affect ecosystem resilience. Widespread change in forest ecosystems will develop over decades to centuries, and apparently slow responses to environmental change may be mistaken for resilience because of the potential resilience debt. The contingent dynamics that typify legacy effects make it difficult to predict forest resilience to future environmental change. Species-specific disturbances, such as host-specific pathogens or insects, drive distinct effects in communities, in contrast to generalist disturbances like fire or drought. Understanding ecosystem resilience in the face of shifting disturbance regimes, climate, and land-use change requires knowledge of life-history traits, disturbance characteristics, climate sensitivity, and successional dynamics. Each of the mechanisms identified here can be evaluated in different ecosystem types and geographic settings. We challenge ecologists to test these ideas, using empirical studies and process-based models across a range of spatial and temporal scales, to determine whether post-disturbance forest dynamics are consistent with changes already playing out slowly in response to climate and land-use change. Forests and other ecosystems will be more resilient to such changes when species traits remain aligned with disturbance characteristics and climate conditions. As species respond to changing environmental conditions, interactions among biota, climate, and disturbance regimes will determine whether ecosystems remain within a safe operating space in the face of future disturbance.

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