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Novel Disturbance Regimes and Ecological Responses

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Abstract

Many natural disturbances have a strong climate forcing, and concern is rising about how ecosystems will respond to disturbance regimes to which they are not adapted. Novelty can arise either as attributes of the disturbance regime (e.g., frequency, severity, duration) shift beyond their historical ranges of variation or as new disturbance agents not present historically emerge. How much novelty ecological systems can absorb and whether changing disturbance regimes will lead to novel outcomes is determined by the ecological responses of communities, which are also subject to change. Powerful conceptual frameworks exist for anticipating consequences of novel disturbance regimes, but these remain challenging to apply in real-world settings. Nonlinear relationships (e.g., tipping points, feedbacks) are of particular concern because of their disproportionate effects. Future research should quantify the rise of novelty in disturbance regimes and assess the capacity of ecosystems to respond to these changes. Novel disturbance regimes will be potent catalysts for ecological change.

INTRODUCTION

Concern is rising about how ecosystems will respond to novel disturbance regimes—that is, disturbance regimes to which ecosystems are not adapted—as climate continues to change. Many natural disturbances such as fires, floods, hurricanes, and pest or pathogen outbreaks are driven in part by climate (Seidl et al. 2020), so change in climate will alter disturbances. Disturbances shape ecosystems and landscapes by generating heterogeneity in space and time, and biota are well adapted to the disturbance regimes with which they have evolved (Johnstone et al. 2016, Keeley & Pausas 2022). Disturbances and recovery processes are tightly linked, and changes that disrupt this linkage can lead to novel outcomes (Turner 2010, Seidl & Turner 2022). However, there is tremendous uncertainty about where and when novelty will unfold.

Anticipating novel disturbance regimes and ecological responses is challenging. In part, this is because nonlinear relationships between climate drivers and disturbances can have surprising consequences. For example, burned area increases nonlinearly with aridity (Abatzoglou & Williams 2016, Grünig et al. 2023), so small increases in aridity can lead to astonishingly large fires. Similarly, warming events that exceed a threshold of accumulated heat exposure lead to widespread mortality of corals (Hughes et al. 2018). Identifying such tipping points is difficult when they have not been exceeded in the historical record (Turner et al. 2020). Interactions among disturbances or between disturbances and other drivers also can lead to unexpected consequences, as when massive flooding results from intense rainfall events where impervious surfaces have replaced natural vegetation (e.g., Sebastian et al. 2019). Understanding such dynamics is crucial because disturbances may be proximal drivers of profound ecological change.

DIMENSIONS OF NOVELTY IN CHANGING DISTURBANCE REGIMES

What constitutes novelty in disturbances, and how can novelty be assessed? Addressing these questions is particularly challenging, as disturbances frequently have long return intervals and an inherent element of stochasticity. It is necessary first to distinguish between a disturbance event and the disturbance regime that characterizes a landscape (e.g., White & Pickett 1985). A disturbance event happens over a relatively short interval of time. For example, a hurricane or windstorm occurs over hours to days, and fires and floods occur over hours to months. A disturbance regime refers to the spatial and temporal dynamics of disturbance across a landscape over a long time. Disturbance regimes are described by parameters that include disturbance intensity and severity; temporal characteristics, including disturbance frequency, return interval, seasonality, duration, and rotation period; and spatial attributes, such as overall disturbance extent and distributions of patch sizes and shapes (White & Pickett 1985, Johnstone et al. 2016). We here define novelty as the degree of dissimilarity, measured in one or more dimensions of the disturbance regime relative to a reference baseline (Radeloff et al. 2015). This definition explicitly recognizes that novelty exists along a continuum.

Novel Disturbance Parameters: Beyond the Historical Range of Variability

The historical range of variability (HRV) concept captures the notion of a system that is constantly changing in response to disturbance and recovery but in which the dynamics remain bounded (Landres et al. 1999). These bounds emerge because recurring disturbances select for populations with life-history traits that align with a given disturbance regime and support postdisturbance recovery (Johnstone et al. 2016, Keeley & Pausas 2022). To define the HRV, attributes of historical disturbances (e.g., size, severity, frequency, duration, seasonality) and ecosystem structure and function (e.g., age class distributions, net primary production) are quantified over

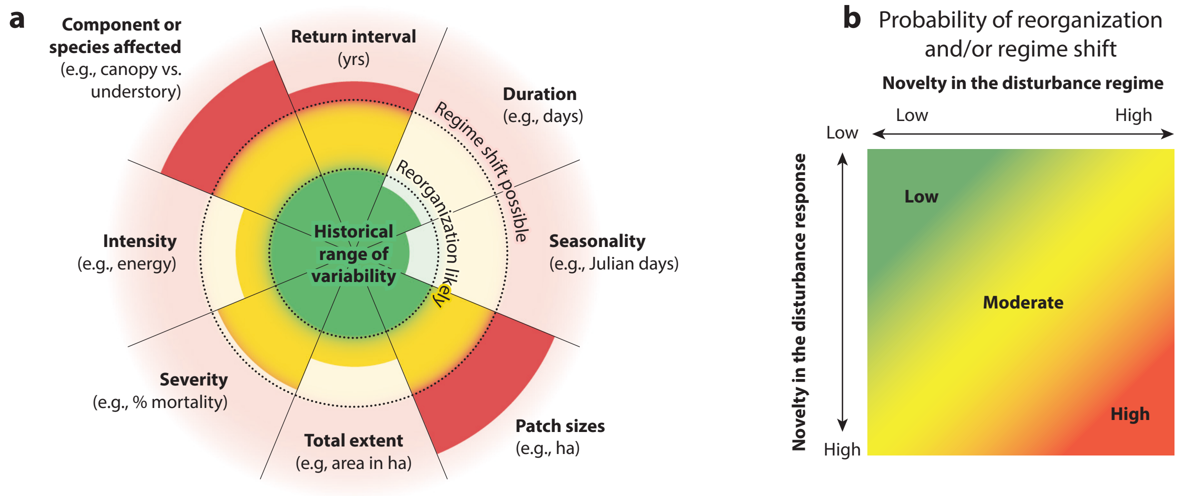

Figure 1

(*a*) Radar diagram to illustrate novelty in disturbance attributes. Ecosystems can maintain resilience when disturbances remain within their historical range of variability (HRV) (*green*). As disturbance characteristics change, greater anomalies are more likely to lead to reorganization (sensu Seidl & Turner 2022) (*yellow*), in which the structure and/or composition of the ecosystem change or to regime shift (*red*), in which the system is converted to a new state. (*b*) Novelty can occur in either the disturbance, the response, or both. Novelty in the disturbance regime can sometimes be buffered by robust response mechanisms, and novelty in responses will be less influential if disturbances remain within the HRV. Greater novelty in both dimensions increases the likelihood of ecosystem reorganization or regime shift.

appropriately large and long scales of space and time (Keane et al. 2009); a static snapshot is insufficient to characterize the HRV. Disturbances that fall outside their HRV in one or more attributes are novel, although the degree of departure from the HRV can vary (**Figure 1*a***). For example, successive stand-replacing fires that occur within <30 years in subalpine forests adapted to historical 100-to-300-year fire return intervals (FRIs) (Turner et al. 2019) are novel within that ecosystem. Disturbance intensity and severity can also shift away from the HRV. For example, the intensity of tropical cyclones increased between 1979 and 2017, and the fraction of all hurricanes considered major rose from ~0.32 to nearly 0.40, consistent with expectations due to warming climate (Kossin et al. 2020).

Novel Disturbance Agents

Disturbance agents that were not present historically and to which the ecosystem is not adapted are a second dimension of novelty. Examples include abiotic disturbances that lack precedent, such as climate-driven wildfires in Arctic tundra (Witze 2020), Tasmanian (Holz et al. 2015) and mainland Australian rainforests (Bergstrom et al. 2021), and temperate forests in Europe (Grünig et al. 2023). Biotic disturbances induced by nonnative pests or pathogens are also novel. For example, the nonnative emerald ash borer (*Agrilus planipennis*) has been decimating *Fraxinus* spp. trees throughout eastern North America since its discovery in 2002 (Herms & McCullough 2014). Warming temperatures are also relaxing constraints that prevented some native species from affecting high-elevation or high-latitude ecosystems. For example, some *Pinus* forests in western North America were protected historically from *Dendroctonus ponderosae*, a native bark beetle, because temperatures were too cold for the beetles to overwinter. Warming winters have fostered bark beetle outbreaks and widespread tree mortality (Buotte et al. 2016). Novel disturbance agents can have severe impacts because prevailing communities did not coevolve with these agents and consequently lack specific traits of resistance and recovery.

DIMENSIONS OF NOVELTY IN ECOLOGICAL RESPONSES TO DISTURBANCE

Whether novel disturbance regimes lead to novel ecosystems hinges on the response to disturbance. Robust responses buffer ecosystems from changing disturbance regimes if response capacity is not exceeded. For instance, although disturbance rates have doubled in recent decades in central Europe (Senf et al. 2018), tree recovery remains robust in most of the region (Senf & Seidl 2022). Novel ecosystems can emerge if changing disturbance overwhelms the response capacity of the system. For example, more frequent disturbances can alter biotic community composition in grasslands (Yuan et al. 2016) and forests (Falster et al. 2017), selecting against long-lived, late-seral species that outcompete others in the absence of disturbance. However, even if disturbances remain within their HRV, novel ecological responses can reorganize ecosystems in ways that change composition (reassembly), structure (restructuring), or both (replacement) following a disturbance (Seidl & Turner 2022). For example, if climate change alters reproduction [e.g., masting frequency in trees (Hacket-Pain & Bogdziewicz 2021)] or establishment (Hansen & Turner 2019), a disturbance event whose size, frequency, and severity were within the HRV will be followed by novel pathways of recovery. The likelihood of fundamental ecological change is greatest when there is novelty in both the disturbance regime and the ecological responses to disturbance (**Figure 1*b***).

What factors can lead to novel disturbance responses? A change in the state of the system at the time of disturbance is one driver that can alter responses (**Figure 2**). For example, the postfire response of a forest of obligate seeders is influenced by stand age at the time of fire because an

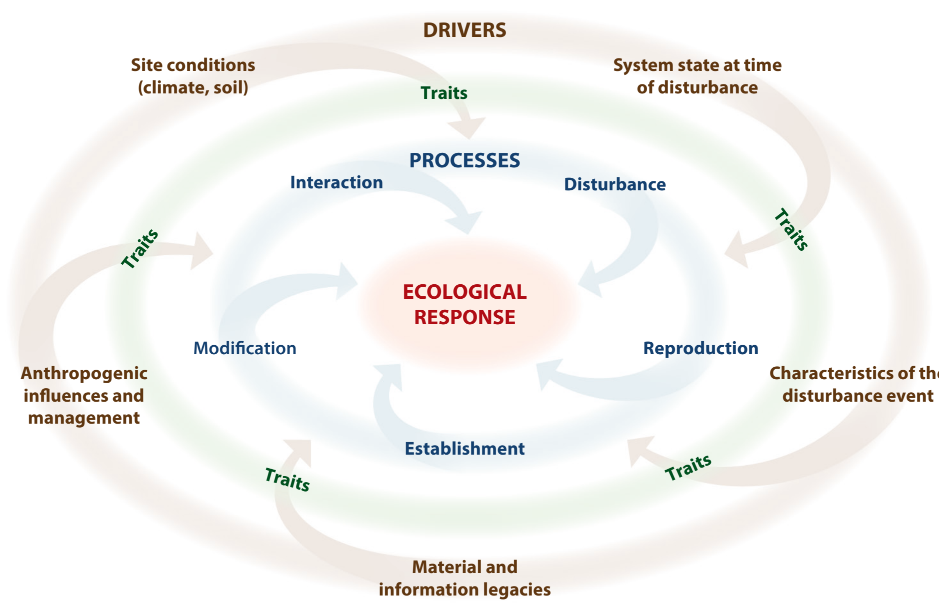

Figure 2

Drivers (*brown*) and fundamental processes (*blue*) control ecological responses to disturbances. Effects of drivers on processes are mediated by functional traits (*green*) of the biotic community.

immature stand lacks a canopy seedbank (Keeley et al. 1999, Bowman et al. 2016). Characteristics of a disturbance event establish the biological and physical template for postdisturbance recovery; changes therein can result in novel disturbance responses. For instance, propagules may not reach the interiors of very large patches of high-severity disturbance (Gill et al. 2022), illustrating that patch sizes matter for disturbance recovery. This example also underlines the importance of material and information legacies (i.e., elements of the predisturbance state that persist postdisturbance), as the presence of mature survivors and viable seed banks can accelerate recovery (Hoecker & Turner 2022). Postdisturbance management often modulates such legacies (e.g., via salvage logging) or overrides response processes (e.g., reproduction, in the case of tree planting), potentially leading to novel disturbance responses (Senf et al. 2019). Site conditions fundamentally govern disturbance response processes, and changes therein, such as increased drought frequency (Hansen & Turner 2019), can result in novel disturbance responses.

The effects of drivers on disturbance response processes are critically modulated by functional traits of the prevailing community (**Figure 2**). Functional traits are measurable properties of an organism that influence its performance (McGill et al. 2006). Response traits determine the strategies by which organisms resist and recover from disturbance (Enright et al. 2014). They thus affect how a community responds to disturbances and crucially influence the ability to absorb novelty in disturbance regimes. For example, species that can resprout after disturbance gain advantage over obligate seeders with increasing disturbance frequency because of their well-established root system (Keeley & Pausas 2022). In turn, response traits affect a range of processes (**Figure 2**) that determine postdisturbance pathways. These include demographic processes associated with reproduction and establishment, interactions within or among populations, and ways by which species modify local edaphic and abiotic conditions (Seidl & Turner 2022). Major alterations in any of these processes may lead to novel responses.

CONCEPTUAL FRAMEWORKS FOR UNDERSTANDING NOVEL DISTURBANCE REGIMES

What conceptual frameworks are useful for grappling with novel disturbance regimes? We touch briefly on foundations of disturbance ecology, then review current conceptual frameworks and assess their level of support from empirical evidence, whether current methods are adequate to evaluate them, and how widely they have been applied to real-world ecosystems and problems.

The rise of disturbance ecology saw development of frameworks that provided a strong foundation for conceptualizing disturbance events and regimes (**Supplemental Table 1**). Seminal work by Bormann & Likens (1979) at Hubbard Brook (New Hampshire, USA) found that small, frequent disturbances produced a constantly changing mosaic of forest stands that nonetheless maintained steady-state proportions of the landscape in different successional stages and standing-stock biomass. A landmark book consolidated understanding of patch dynamics (Pickett & White 1985) and catalyzed new research to characterize disturbance regimes and test the generality of the steady-state mosaic. Field ecologists found evidence for nonequilibrium landscapes in which proportions of the landscape in different successional stages fluctuated substantially through time, especially in response to large, infrequent disturbances (**Supplemental Table 1**). Scaling characteristics of a disturbance regime to expected recovery times and landscape size led to a more general understanding of when steady-state versus nonequilibrium dynamics were expected (**Supplemental Table 1**). These conceptual frameworks were important because they explicitly accounted for disturbance-recovery processes, and they demonstrated that disturbance-driven systems are naturally dynamic. However, these foundational frameworks also assumed stationarity of the disturbance regime, i.e., that it would remain within the HRV, and thus did not incorporate the potential for novel disturbance regimes.

DISTURBANCE REGIMES		Evidence	Methodology	Applications
Resilience theory	Thresholds and tipping points	Several specific examples exist, mainly using space-for-time substitution or experiments to infer thresholds	Many indicators have been proposed, but they are difficult to apply in ecosystems with long-lived organisms, such as forests	Theory has outpaced empirical study; most experiments have been done in grasslands and lakes
	Ecological memory	There is strong support for the role of informational and material legacies in multiple systems	Field measurements and remote sensing both have the capability to detect postdisturbance legacies	Examples abound, and the importance of disturbance legacies is well integrated into resource management
	Resilience debt	Paleo evidence is strong, but data for current systems being beyond their HRV and unable to regenerate following a new disturbance are few	Most work to date is experimental; extending studies to quantify resilience debt and time lags at the landscape scale is in its infancy	Few studies have assessed how environmental changes will preclude self-replacement after disturbance
Interacting disturbances	Compound disturbances	Studies have demonstrated a wide range of nonadditive consequences of sequential disturbances	Limited, because detecting compound effects requires assessing each disturbance individually along with the combined effects	These effects are projected to increase in the future and expected to lead to surprising ecological consequences
	Linked disturbances	Strong evidence exists but for few disturbance types; magnitude and direction of effects are uncertain	Varied measures of severity make generalization to occurrence or severity of subsequent disturbance difficult	Studies have often emphasized fire or biotic disturbances
Disturbance–driver interactions	Amplifying interactions	Most studies to date consider effect of postdisturbance climate during the regeneration window	Field measurements and remote sensing both offer potential, but the range of historical conditions may be inadequate for anticipating the future	Postdisturbance climate is recognized, but many more drivers need attention
	Dampening interactions	Few studies have focused on how one driver may mitigate effects of another	Field measurements and remote sensing again offer potential	Relatively few applications, but land use has been used to reduce disturbance spread or severity

Good evidence/many studies
Moderate evidence/some studies
Poor evidence/few studies

Figure 3

Conceptual frameworks that are useful for understanding novelty in changing disturbance regimes include resilience theory, interacting disturbances, and interactions between disturbance and other environmental drivers.

What conceptual frameworks do allow for dimensions of novelty? We consider three frameworks that have catalyzed recent advances (**Figure 3**).

Resilience Theory

Much contemporary research on changing disturbance regimes has used the framework of resilience theory (**Figure 3**). Resilience concepts were introduced by Holling (1973), and a key advance was recognizing the need for ecosystems to "absorb and accommodate future events in whatever unexpected form they may take" (Holling 1973, p. 21). Resilience theory offers a

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powerful framework for considering novel disturbance parameters and agents (Yi & Jackson 2021, Seidl & Turner 2022). A motivating question is whether and how changes in a disturbance regime can push an ecosystem beyond a tipping point that leads to a fundamental change in system state (i.e., regime shift). Note that a tipping point refers to threshold relationships between driver and response variables and not change over time (Hughes et al. 2013, Ratajczak et al. 2018). For example, a tipping point could exist between postdisturbance tree regeneration and disturbance severity, such that the success or failure of tree regeneration depends on change in disturbance severity and whether the threshold was exceeded. Importantly, ecosystems can appear resilient to changing disturbance regimes, even when a tipping point exists, if that threshold has not yet been passed. Consider declining return intervals for a high-severity disturbance, such as a stand-replacing fire, for example. When the return interval is less than the time required for dominant species to reach reproductive maturity (i.e., immaturity risk) (Keeley et al. 1999), the system cannot recover. However, the system appears resilient as return interval declines until that threshold is crossed. In subalpine conifer forests where historical FRIs exceeded 100 years, short-interval fires (<30 years FRI) have caused severe reductions in postfire tree regeneration (Turner et al. 2019). Loss of resilience following climate-driven disturbances has occurred in many systems, including coral reefs (Hughes et al. 2018) and temperate coastal kelp forests (Wernberg et al. 2016), with more anticipated as climate change continues (e.g., Burrell et al. 2022).

Resilience theory inspired explorations of whether novel disturbance regimes would lead to hysteresis, whereby the threshold that causes the system to change differs from the threshold needed to reverse the transformation. The potential for novel disturbance to convert forests to nonforests has garnered particular attention because the consequences of irreversible forest declines are profound (e.g., Johnstone et al. 2016, Coop et al. 2020, Burrell et al. 2022). Forest transitions can be irreversible for thousands of years (Albrich et al. 2020a), especially if seed sources are depleted (Bowman et al. 2016). Persistent transformations require the establishment of new feedbacks that maintain the system in its new state, and restoring resilience requires overcoming these new resistance thresholds. For example, introduction of nonnative grasses (e.g., *Bromus tectorum*) in dry conifer forests of North America can increase fire activity. Abundant herbaceous fuels establish a new positive feedback that promotes frequent fire, precludes tree regeneration, and maintains the nonforest state (Kerns et al. 2020).

Resilience theory offers context for understanding how ecological memory shapes recovery (Johnstone et al. 2016). Ecological memory is embodied in legacies that include physical structures and biotic remnants that persist after disturbance (**Figure 3**). Biotic legacies include both material (individuals or matter present after a disturbance event) and information (presence and frequency of species traits) legacies that reflect adaptations to the prevailing disturbance regime (Johnstone et al. 2016). Losses of ecological memory erode resilience (e.g., Turner et al. 2019). Furthermore, misalignment of information legacies and disturbance can lead to a resilience debt wherein the system has lost its ability to recover, but this loss is apparent only after a disturbance (Johnstone et al. 2016). Recovery to the predisturbance state is no longer possible because species traits are mismatched with environmental conditions or novel disturbances. Resilience debt is most likely where long-lived species (e.g., trees, corals) mask the erosion of resilience as the environment is changing (Hughes et al. 2013).

Despite its conceptual appeal, translating resilience theory into practice in real-world landscapes has not been easy, and empirical studies have lagged behind the theory (Thrush et al. 2009, Yi & Jackson 2021). The usefulness of threshold-related concepts hinges upon the ability to detect or predict thresholds, yet this is not at all certain. Discerning tipping points in driver-response relationships and anticipating thresholds yet to be crossed are difficult (Hughes et al. 2013, Ratajczak et al. 2018). It is also challenging to diagnose alternative stable states in ecosystems with inherently slow dynamics (Hughes et al. 2013). Theoretical early warning indicators of hysteresis are difficult to adapt for ecosystems in which responses to disturbance manifest over decades to centuries.

Given the tension between conceptualizing and operationalizing resilience theory, where has research advanced? Among the most fruitful lines of inquiry are studies of mechanisms that could erode resilience to changing disturbance regimes and initiate novel outcomes (Falk et al. 2022). Promising work has focused on conditions during the crucial regeneration window. For example, there are thresholds in the relationship between postfire tree recruitment and annual climate (annual vapor pressure deficit, soil moisture, and maximum surface temperature) for two conifers (*Pinus ponderosa*, *Pseudotsuga menziesii*) common in lower montane forests of western North America (Davis et al. 2019). Seasonal and annual climate conditions have crossed these thresholds during recent decades and increased the potential for postfire regime shifts (Davis et al. 2019). Experiments have also identified thresholds in environmental conditions that allow tree seedling regeneration following disturbance. A 4-year field experiment found nearly complete failure of *Pinus contorta* var. *latifolia* seedling establishment in postfire soils when mean soil surface temperatures during the growing season exceeded 16°C (Hansen & Turner 2019).

Propagule supply appears critical for maintaining resilience (Gill et al. 2022). As climate warms, loss of seed sources increases the likelihood of forest collapse following high-severity disturbance (Van de Leemput et al. 2018). Communities dominated by obligate seeders are most vulnerable, as demonstrated for declines in alpine ash (*Eucalyptus delegatensis*) forests in the face of fire and climate change (Bowman et al. 2016). Simulations of forest dynamics in Greater Yellowstone (USA) also found the greatest loss of resilience where increased burning in fire-sensitive conifer forests eliminated local seed sources (Rammer et al. 2021, Turner et al. 2022).

Interacting Disturbances

Many ecosystems experience multiple disturbances, and variation in the timing, sequence, and type of disturbance events can produce novel outcomes. Two general kinds of interaction have emerged (**Figure 3**).

Compound disturbances occur when two disturbances occur in a short period of time and have a synergistic effect that cannot be predicted from the sum of the individual disturbances (Paine et al. 1998). The unpredictable effects of compound disturbances can result in novel outcomes, including regime shifts (Jasinski & Payette 2005). For example, compound effects were observed when a hailstorm was followed by fire in a Mediterranean-type ecosystem in southwestern Australia (Gower et al. 2015). The ecosystem was resilient to either disturbance alone, but compound effects altered species composition and structure. Compounding effects also explained the lack of tree recruitment following a high-severity fire that occurred 4–13 years after a Douglas-fir bark beetle (*Dendroctonus pseudotsugae*) outbreak (Harvey et al. 2013). The beetle-killed trees lacked propagules, and postfire tree recruitment was observed only adjacent to live forest. Most reports of compound disturbances in forests come from North America and involve 5 or fewer years between disturbances (Kleinman et al. 2019), but compound disturbances are increasingly reported in diverse ecosystems worldwide.

Linked disturbances (Simard et al. 2011) occur when the severity of one disturbance influences the likelihood or severity of a subsequent disturbance, and effects can either be amplified or dampened. For example, Stevens-Rumann et al. (2016) found a dampening effect whereby areas burned at any severity by wildfires during the previous three decades had lower burn severity in the subsequent fire. However, Harvey et al. (2016) found that amplifying effects were possible in subalpine forests, depending on the interval between fires. A review of disturbance interactions in forests around the globe showed that amplifying interactions strongly dominate (Seidl et al. 2017).

With either compound or linked disturbances, different sequences of the same types of disturbance can generate qualitatively different outcomes. In Mediterranean forests, extreme drought followed by a large fire promoted a change in dominant vegetation from resprouters to seeders; forest persisted, but the composition changed (Batllori et al. 2018). In contrast, large fire followed by extreme drought promoted a change from seeders to resprouters; seeds could not establish under dry conditions, and forest did not persist. Experiments with riparian tree seedlings also revealed different outcomes of flooding followed by drought versus drought followed by flooding (Miao et al. 2009); sequences that started with flooding consistently showed greater impacts compared to those that started with drought.

Disturbance × Driver Interactions

Ecosystems do not respond to drivers in isolation, and recovery does not take place in a vacuum. Understanding how disturbances interact with other (changing) drivers is important because climate change can alter relationships among drivers, disturbances, and responses (Zscheischler et al. 2018) and amplify or dampen the effects of a disturbance event (**Figure 3**).

Interactions of disturbances with subsequent climate conditions have received considerable attention; environmental filtering disrupts disturbance-recovery processes when climate conditions exceed the limits of tolerance for self-replacement of the community. Climate–fire interactions explain the recent conversion of dry conifer forests in the western US to nonforest (Stevens-Rumann et al. 2017, Davis et al. 2019). Consequences of a disease outbreak that caused mass mortality of sea stars (*Pycnopodia helianthoides*) were amplified when followed by 3 years of warm ocean temperatures, transforming a bull kelp (*Nereocystis luetkeana*) forest into a sea urchin (*Strongylocentrotus purpuratus*) barren (Rogers-Bennett & Catton 2019). In boreal peatlands, a moderate drop in the water table promoted burning and converted a low productivity, moss-dominated peatland to a shrub–grass ecosystem that does not accumulate carbon (Kettridge et al. 2015). Sea-level rise disrupted the response of mangrove forests to tropical cyclones, reinforcing the transition to mudflats because sediment accretion could not keep up with the rising seas (Osland et al. 2020).

While many studies report amplifying effects, interacting drivers can also dampen the effects of disturbance. For example, dampening interactions can occur when climate teleconnections synchronize seed crops. Across North American boreal forests, the year before a synchronized masting event in white spruce (*Picea glauca*) was drier and more fire prone, indicating a climate–fire interaction that could dampen the risk of regeneration failure (Ascoli et al. 2019) and enhance climate adaptation capacity for this species. Habitat connectivity can also play a role; increased connectivity of Norway spruce (*Picea abies*) amplifies European spruce bark beetle (*Ips typographus*) outbreaks, and reduced connectivity dampens the outbreaks (Honkaniemi et al. 2020).

CONCEPTUAL FRAMEWORKS FOR UNDERSTANDING NOVEL ECOLOGICAL RESPONSES

Frameworks for understanding ecological responses are less developed because disturbances have received more attention (Seidl & Turner 2022). Nonetheless, conceptual frameworks exist for novel ecological responses to disturbance, and we cluster these into two broad groups (**Figure 4**).

Postdisturbance Dynamics

Succession is a key foundational concept (**Supplemental Table 1**) that emerged from many studies of ecosystem development following disturbance (Pulsford et al. 2016). However, novel

			Evidence	Methodology	Applications
ECOLOGICAL RESPONSES	Post-disturbance dynamics	Multiple successional pathways	Ample evidence documents the existence of multiple development pathways in ecosystems from around the globe	Multiple methods exist to quantify the probability and occurrence of different pathways, but they remain hard to predict	Different development pathways are increasingly recognized in management, yet planning approaches often are deterministic rather than probabilistic
ECOLOGICAL RESPONSES	Post-disturbance dynamics	Post-disturbance reorganization	Different modes of reorg-anization are increasingly observed, yet underlying pro-cesses are often incompletely understood	A variety of methods exist, but their joint application towards questions of reorga-nization remains lacking	The framework of postdis-turbance reorganization has not yet been widely adapted to the context of ecological applications
ECOLOGICAL RESPONSES	Trait-based concepts	Response diversity	Evidence for the effects of response traits and response diversity on postdisturbance recovery are ample	Different methods have been used to study the effects of response diversity; most studies, however, focus only on short-term responses after disturbance	Diversity is increasingly recognized as a key element in ecosystem management, yet species diversity remains a more widely used heuristic
ECOLOGICAL RESPONSES	Trait-based concepts	Insurance hypothesis	A large and growing body of evidence exists on the spatio-temporal insurance effects of biodiversity	Temporal effects remain better studied than spatial effects, intraspecific variation remains poorly quantified	Management frequently acknowledges functional redundancy; yet intraspecific and landscape dimensions of insurance remain underutilized
MANAGEMENT		Adaptive management	Many practical examples for adaptive management exist from different ecosystems and regions across the globe	Adaptive management has been studied intensively with different methods, from ex-periments and observations to simulation	Widely adopted by applied ecologists; nonetheless the latter parts of the cycle (mon-itoring, evaluation) remain a challenge for application
MANAGEMENT		Resilience management	Ambiguity remains high, and concrete evidence of the effects of resilience-based management approaches remains scarce	The implementation, effects, and outcomes of resil-ience-based management remain difficult to measure	Wording is increasingly used in management documents, yet implementation remains challenging
MANAGEMENT		Vulnerability assessment	The framework is mature, and a wide range of applications provide evidence for how vulnerability to novel distur-bances can be assessed	Exposure and susceptibility remain easier to quantify than (social) adaptive capac-ity; consideration of extreme events is often challenging	A number of applications exist; however, they often focus on policy-relevant scales rather than on those of management decision making
MANAGEMENT		Resist, adapt, direct	While the formal framework is still young, the ideas have been around for some time and are in line with evidence from different systems and regions	Whether resistance is a viable option remains difficult to assess; also, how to decide between the three options under uncertainty is often unclear	While the concept is increas-ingly used in planning documents, its implementa-tion on the ground remains largely elusive

Good evidence/many studies
Moderate evidence/some studies
Poor evidence//few studies

Figure 4

Conceptual frameworks for understanding novel ecological responses to disturbance include postdisturbance dynamics and trait-based approaches. Similarly, frameworks to guide natural resource management in the face of changing disturbance regimes include adaptive management, resilience, vulnerability assessment, and the resist–adapt–direct framing.

disturbance regimes and ecological responses are absent from classical concepts of succession. An expansion of the concept of succession that considers the potential for novelty is the idea of multiple successional pathways (**Figure 4**). This idea recognizes that a system can follow a range of trajectories after disturbance (Donato et al. 2012). While not new (Cattelino et al. 1979), the concept is highly relevant because divergence in postdisturbance development trajectories from historical reference conditions can lead to novel outcomes. Characterizing postdisturbance pathways and their probability of occurrence offers a powerful means for detecting novel ecological responses.

While characterizing postdisturbance pathways often remains descriptive, process-based frameworks of postdisturbance dynamics target mechanisms that underpin recovery (see also processes in **Figure 2**). These frameworks frequently focus on key demographic processes such as mortality, survival, and regeneration (Pickett et al. 2009, McDowell et al. 2020) that have been recognized for over 100 years (**Supplemental Table 1**). In the context of novel disturbance responses, process-based frameworks are, for instance, used to anticipate effects of climate-mediated changes in fire regimes on forest development (Davis et al. 2018). Advances in mechanistic understanding of ecological responses also fostered new conceptual frameworks for ecosystem reorganization after disturbance (Falk et al. 2022, Seidl & Turner 2022). These frameworks emphasize the reorganization window [i.e., the phase of the adaptive cycle that immediately follows a disturbance (Holling & Gunderson 2002)] and consider resilience and regime shift as endmembers of the outcomes of change. Reorganization can take a variety of forms (Falk et al. 2022) and be arrayed along axes of change in ecosystem structure and community composition (Seidl & Turner 2022). Emphasizing the processes and outcomes of postdisturbance reorganization allows for predictive inference on how future ecosystems will be shaped by novelty in disturbance and responses.

Trait-Based Concepts

A second group of frameworks is based on traits (**Figure 4**). The prevalence of response traits in a population, such as the ability to regenerate from a seed bank or resprout after disturbance, can inform ecosystem responses to compound disturbance events (Andrus et al. 2021) and novel disturbance regimes (Rammer et al. 2021). An important group of concepts focuses on diversity in traits. It is not species diversity per se that confers ecosystem resilience to disturbance but rather the diversity in functional traits. Most relevant is response diversity, which describes variation in responses within a community to environmental changes (Mori et al. 2013). Diverse regeneration modes, for instance, enable ecosystems to persist across a wide range of disturbance sizes and frequencies (Carpenter et al. 2012), e.g., resisting, resprouting, and reseeding offer complementary benefits in fire-prone landscapes (Keeley & Pausas 2022). High response diversity also can reduce disturbance severity and increase resilience in coral reefs (Baskett et al. 2014) and forests (Silva Pedro et al. 2015).

The insurance hypothesis emphasizes the relationship between biodiversity and ecological stability. It posits that diverse ecosystems are less likely to lose functionality in the face of environmental fluctuation (Yachi & Loreau 1999). Initially formulated for temporal stability, the insurance hypothesis was extended to spatially heterogeneous landscapes, suggesting that diversity within and between systems (i.e., α and β diversity) can confer stability (Loreau et al. 2003, Gladstone-Gallagher et al. 2019). Central to the insurance hypothesis is functional redundancy, i.e., the number of species contributing in similar ways to ecosystem function (Biggs et al. 2020). While functional redundancy was less important than response diversity for boreal forest development after severe disturbance (Correia et al. 2018), it was found to increase the disturbance resilience of communities along shorelines (Elsberry & Bracken 2021).

Importantly, disturbances and traits have reciprocal influences; traits and trait diversity modify disturbance responses, but disturbance regimes influence the prevalence of traits on the landscape (e.g., Herben et al. 2018). Trait-based responses to novel disturbances are not static; novelty in one will—in the long run—trigger novelty in the other. Whether traits can respond via selection at the same rate at which disturbance regimes are changing remains unresolved. If so, it is a mechanism by which biotic communities can adapt to environmental change; if not, it is a mechanism likely to generate novelty.

FRAMEWORKS FOR MANAGING NOVEL DISTURBANCES AND RESPONSES

Disturbances play an important role in ecosystem management. Indigenous peoples often intentionally used disturbance—especially fire—to manage landscapes for resources on which they depended and lower the risk of large catastrophic events (e.g., Trauernicht et al. 2015). After colonization, resource management often tried to tame natural processes and considered disturbances as catastrophes that interrupted normal development (Puettmann et al. 2009). Nineteenth and early twentieth century resource management tried to suppress disturbances and largely ignored them in management planning (Woods & Coates 2013). Management also aimed to accelerate recovery, often homogenizing postdisturbance ecosystem states and recovery pathways (Senf et al. 2019). This command-and-control approach to disturbance had (unintended) negative effects on ecological resilience (Holling & Meffe 1996). Natural resource management frameworks began to incorporate disturbance only in the latter half of the twentieth century (**Supplemental Table 1**). The concept of ecosystem management acknowledged the dynamic nature of ecosystems and the role of disturbance and has been successfully applied in terrestrial, aquatic, and marine systems around the globe. Other frameworks sought to emulate natural disturbance regimes (**Supplemental Table 1**). These concepts recognized that native species assemblages have coevolved with disturbances, so human activities that mimic the natural disturbance regime should minimize deleterious ecological effects. While these frameworks incorporate disturbance, they do not consider novel disturbance regimes and responses.

Adaptive management (**Figure 4**) was developed to address change and novelty, recognizing that management must constantly adapt to change. Adaptive management allows action despite uncertainty and requires assimilating new knowledge into the decision-making process by iterating through phases of planning, acting, monitoring, and evaluating (Walters 1986, Allen et al. 2011). Experimentation is important because it accelerates learning and allows for proactive (i.e., anticipatory) management rather than only reactive responses. Adaptive management has been successfully applied, for example, to managing forests for ecosystem services under changing climate and disturbance regimes (e.g., Yousefpour et al. 2013). However, several decades elapse in many ecosystems between management actions and their realized outcomes (e.g., between planting trees after a disturbance and harvesting them for timber), making adaptive feedbacks difficult. Furthermore, reactive adaptive management might be impractical in systems with tipping points, as it is difficult to anticipate regime shifts and respond adaptively to incremental changes in drivers.

Resilience is frequently invoked in resource management, and the resilience framework offers powerful heuristics in systems with thresholds and multiple stable states (Seidl et al. 2016) (**Figure 4**). Novel disturbance regimes highlight the need for adaptive resilience (sensu Schoennagel et al. 2017). Dudney et al. (2018) presented a framework for addressing novelty in resilience-based management, suggesting the enhancement of adaptive capacity as a central element, along with managing drivers of change and enabling transformation. While resilience concepts remain hard to operationalize for managers, the spatial ecosystem patterns influencing resilience are tangible. For example, Mina et al. (2022) applied a functional network approach to identify resilient management strategies in the face of native and novel insect disturbances.

Vulnerability assessment frameworks can also address novel disturbances in management. While bearing some similarity to resilience frameworks, vulnerability assessments emphasize exposure and susceptibility to a hazard (e.g., novel disturbance regimes) and the adaptive capacity of the system to this hazard (e.g., disturbance response mechanisms). Ecosystem service indicators are frequent foci of vulnerability assessments, making them useful for management. Lecina-Diaz et al. (2021), for instance, assessed the vulnerability of ecosystem service supply to wildfire, showing that extreme fire weather can substantially increase the risks for regulating services such as the forest-based carbon sink and erosion control.

Managers can resist, accept, or direct change (the RAD framework) (Schuurman et al. 2022). Challenges in applying this framework include deciding where and how to apply each option and assessing their relative costs and benefits. Landscape heterogeneity is important in this context, as some parts of the landscape contribute disproportionally to overall risk, while managerial control over change might be limited on others (Seidl et al. 2018). Analyses of current policy suggest strategies focused on resistance (and restoration) dominate current management (Rissman et al. 2018).

Despite the best of efforts, novel disturbance regimes might render established management goals impossible to achieve. For individual decision makers, the feeling of being overwhelmed by environmental changes can lead to paralysis or defaulting to business-as-usual decisions, precluding adaptive change (Jackson 2021). For society, the possibility of novel disturbances resulting in a loss of ecosystem services must be recognized by stakeholders and policy makers. If such losses are unacceptable to society, components of the social-ecological system must be adjusted to deliver desired values (Walker 2020). Holding on to management systems and objectives that are no longer tenable under novel disturbance regimes amounts to digging the hole even deeper.

MOVING TOWARD A NOVEL FUTURE

Research Priorities

How much novelty in the disturbance regime can systems absorb before they collapse? Several knowledge gaps must be bridged to make progress toward answering this question (light shading in **Figures 3** and **4**). Nonlinear consequences of novel disturbance regimes and ecological responses will have disproportionate effects on ecosystems and landscapes. Building the body of empirical evidence that identifies thresholds and tipping points is a priority, because of the increased likelihood of unexpected ecological changes. Identifying dampening interactions among disturbances and other drivers is also a priority, because negative feedbacks may slow rates of change or even avoid undesired regime shifts.

Discerning the myriad ways ecosystems can (and will) reorganize after disturbance is another research priority. Resilience sensu stricto is increasingly unlikely; novel disturbances will trigger change, but how will those changes unfold, in what time frame, and how variable will they be? Ecological responses to disturbance should be monitored closely, especially during the early reorganization window, to gain insights into future trajectories (Seidl & Turner 2022). Detecting and diagnosing response anomalies relative to historical patterns is critical for anticipating change.

Additional knowledge gaps constrain the ability to predict effects of novel disturbance regimes. Some limitations result from insufficient knowledge of disturbance effects on biotic communities. For example, cascading effects of disturbance-driven changes in foundation species on other taxa are poorly understood. How will disturbance-driven changes in habitat extent, structure, or quality interact with climate change to affect biodiversity? In forests, for instance, herbaceous understories (which harbor much of the vascular plant diversity in temperate forests) are subject to profound changes as a consequence of novel disturbance regimes, yet their disturbance response remains understudied. Intraspecific variation in response traits has also received little attention, yet novel disturbances will select for new trait assemblages.

Ecosystem processes will be fundamentally changed by novel disturbance regimes and responses, and greater attention to biogeochemical and hydrological processes is needed. Carbon has (appropriately) received much attention because of its direct linkage to climate (e.g., Pugh et al. 2019). However, novel disturbances are likely to induce profound changes in ecohydrology (timing, magnitude, and variability of water storage and fluxes) (e.g., Moeser et al. 2020), biogeochemistry (stocks, fluxes, and cycling of essential elements such as nitrogen) (e.g., Gustine et al. 2022), and the microbial communities that govern nutrient transformations (e.g., Bowd et al. 2022). Teleconnections may even produce distant consequences of novel disturbance events. For example, deposition of wildfire aerosols from the severe 2019–2020 Australian wildfires resulted in phytoplankton blooms in downwind portions of the Southern Ocean (Tang et al. 2021).

Establishing criteria for assessing whether and how resource management should respond to novel disturbances is of growing import. Managing for historical states and fluxes may be impossible, yet how to respond is far from clear. Managing ecosystems requires anticipating the future rather than clinging to the HRV (Duncan et al. 2010). Seeking outcomes amenable to management under novel conditions and communicating the resultant effects on ecosystem service supply to society will be an important task of ecosystem stewardship. The central task of management in a rapidly changing world is transformation (Schoennagel et al. 2017), and the lingering focus of many managers on preserving the past should be abandoned.

Tools for Detecting, Diagnosing, and Projecting Disturbance Change

Assessing novelty requires baselines against which to assess change. To date, however, quantitative understanding of past disturbance regimes is often lacking, and the HRV of many systems remains unknown. Remote sensing offers powerful tools to quantify historical baselines and assess disturbance change. For instance, multi-decadal Landsat satellite data were used to quantify the forest disturbance regimes of Europe (Senf & Seidl 2021a). This baseline could subsequently be used to assess a recent wave of tree mortality—triggered by severe drought—in relation to the long-term variation of the system, giving a first indication that disturbance regimes have moved outside of their recent range of variability (Senf & Seidl 2021b). While the remote sensing of disturbances has made great advances in recent years, analyzing ecological responses to disturbance from space remains challenging, because it can take years or decades before satellite data can differentiate pathways of recovery (Kiel & Turner 2022). Novel analysis approaches, such as spectral unmixing (Viana-Soto et al. 2022), can help to make inferences in this regard. Also, lidar offers great potential for characterizing ecological responses to disturbance (Senf et al. 2019, Lepczyk et al. 2021), and novel tools such as Global Ecosystem Dynamics Investigation (Dubayah et al. 2020) can help overcome limitations in terms of spatial coverage.

Getting a better sense of the potential future range of variability is equally important as quantifying the HRV, given the expected changes in climate and considering the long lead times in ecosystem management. Consequently, developing robust future projections is critical. Simulation modeling can, for instance, help in determining the climate sensitivity of disturbance regimes (e.g., Turner et al. 2022), highlight potential tipping points (e.g., Albrich et al. 2020a), and investigate alternative management responses to novel disturbance regimes (e.g., Seidl et al. 2018). Many current models ignore key processes that underpin disturbance and responses (Albrich et al. 2020b) and hence are unable to assess when and where novel disturbance regimes will lead to novel outcomes. One way to harness growing data availability (e.g., from remote sensing) to make models more robust is by using machine learning. Novel approaches such as deep learning offer potential not only to detect cryptic patterns of change and generate testable hypotheses about underlying mechanisms but also to overcome previous limitations of simulation modeling regarding process representation and scale (Perry et al. 2022).

Along with new technologies, we strongly endorse additional field studies and experiments, as there is no substitute for boots on the ground. Robust inferences are needed from diverse approaches including observations, experiments, and models across a range of spatial and temporal scales; no single approach will suffice. Coordinated observational and experimental studies have great potential to provide a better understanding of both disturbance impacts and responses, as seen in other joint collaborative efforts of the scientific community. Moreover, advanced methods in genetics and genomics make quantifying intraspecific variation and the strength of disturbance as a selective force more feasible. These methods may also open the door to understanding effects of novel disturbances on microbial diversity. Understanding the causes and consequences of novel disturbance regimes requires purposeful combination of different methodologies in an interdisciplinary approach.

CONCLUSIONS

Novel disturbance regimes will increasingly impact landscapes in surprising ways, and scientists and managers must expect the unexpected and think outside the box. As colorfully stated by Moore & Schindler (2022, p. 1421), "shift happens," and the pace of change is accelerating at an alarming rate. Regarding novel disturbance regimes, we draw the following conclusions:

1. Novel outcomes are determined by the interlinked nature of disturbance and response. Analyzing changes in disturbance and recovery separately is insufficient to anticipate outcomes of change. A joint perspective on changes in disturbance regimes and ecological responses to disturbance is needed for anticipating future trajectories.
2. Novel outcomes are more likely as more dimensions of the disturbance regime change simultaneously. Novelty in disturbance regimes has many guises. Changes in any one dimension can lead to novelty, yet the propensity for novel outcomes increases with the number of dimensions that shift beyond the HRV.
3. Novelty is likely to arise from interactions and feedbacks. Ecological systems have contended with environmental variation and disturbance for millennia. However, when successive disturbances compound or drivers interact to amplify ecological effects, novel outcomes are increasingly likely. The timing, sequence, and number of disturbance events matter.
4. Novel disturbance agents will profoundly change many or all dimensions of the disturbance regime. Novel disturbance agents are likely to arise more frequently in the future, yet their consequences are difficult to foresee because they lack historical analogs.
5. A focus on reorganization after disturbance will help to anticipate novel outcomes. The reorganization phase is a key window for anticipating the emergence of novelty. Response traits and propagule supply will play keystone roles in establishing pathways of recovery. Closely monitoring dynamics during the reorganization phase can shed light on which of the many possible pathways a system is likely to follow.
6. The landscape scale offers important opportunities to detect and diagnose novel disturbance regimes and ecological responses. Changing disturbance regimes and processes that underpin recovery dynamics must be studied at the spatial scales at which they operate. Studies that are either too fine or too broad in extent will likely miss key dynamics.

7. Conceptual frameworks offer valuable guidance for addressing novel disturbances and responses in research and management. Current frameworks are powerful, and it is time to exercise these frameworks in more real-world settings. However, each has its strengths and limitations, and they should be applied wisely in the context of the specific questions and systems under study.
8. Management must plan for a novel future rather than a familiar past. Management planning must incorporate disturbance and anticipate changes in the disturbance regime. Despite remaining uncertainties, management actions must be taken now to buffer undesired effects of novelty in the future, and—where possible—align emerging novel systems with management goals.

The need to understand the complex causal chains that lead to novel outcomes is pressing (Zscheischler et al. 2018). We advocate for a new wave of studies to quantify the rise in novelty in disturbance regimes, to assess deviations of recent and future ecological responses relative to historical norms, and to elucidate the role of novel disturbance regimes as potent catalysts for ecological change. Such studies are urgent, as the future is upon us: Change in disturbance regimes is already outpacing response capacities in many ecosystems. Science and management must join forces to anticipate and prepare society for the profound changes yet to come.

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