Reconstructing Disturbances and Their Biogeochemical Consequences over Multiple Timescales

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Abstract:	Ongoing changes in disturbance regimes are predicted to cause acute changes in ecosystem structure and function in coming decades, but many aspects of these predictions are uncertain. A key challenge is to improve the predictability of post-disturbance biogeochemical trajectories at the ecosystem level. Both ecosystem ecologists and paleoecologists have generated complementary datasets about disturbance (type, severity, frequency) and ecosystem response (net primary productivity, nutrient cycling) spanning decadal to multi-millennial timescales. Here, we take the first steps toward a full integration of these datasets by: (1) reviewing how disturbances are reconstructed using dendrochronological and sedimentary archives, and (2) summarizing the conceptual frameworks for carbon, nitrogen, and hydrologic responses to disturbances. Key research priorities include further development of paleoecological techniques that reconstruct both disturbances and terrestrial ecosystem dynamics. Additionally, mechanistic detail from disturbance experiments, long-term observations, and chronosequences can help to increase the temporal understanding of ecosystem resilience.

Reconstructing disturbances and their biogeochemical consequences over multiple timescales

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Abstract

Ongoing changes in disturbance regimes are predicted to cause acute changes in ecosystem structure and function in coming decades, but many aspects of these predictions are uncertain. A key challenge is to improve the predictability of post-disturbance biogeochemical trajectories at the ecosystem level. Both ecosystem ecologists and paleoecologists have generated complementary datasets about disturbance (type, severity, frequency) and ecosystem response (net primary productivity, nutrient cycling) spanning decadal to multi-millennial timescales. Here, we take the first steps toward a full integration of these datasets by: (1) reviewing how disturbances are reconstructed using dendrochronological and sedimentary archives, and (2) summarizing the conceptual frameworks for carbon, nitrogen, and hydrologic responses to disturbances. Key research priorities include further development of paleoecological techniques that reconstruct both disturbances and terrestrial ecosystem dynamics. Additionally, mechanistic detail from disturbance experiments, long-term observations, and chronosequences can help to increase the temporal understanding of ecosystem resilience.

Keywords

ecosystem ecology, disturbance, fire regime, nitrogen cycling, resilience

Introduction

Ecological disturbances in terrestrial systems are discrete events that reduce primary producer biomass and strongly regulate material and energy flows. Several studies document increasing size and/or severity of a variety of disturbance types, including beetle outbreaks, storms, and wildfires during recent decades (Seidl et al. 2011). This amplification is raising questions about which disturbances are unprecedented, and what conditions may lead to threshold behavior in ecosystem responses. It has been particularly difficult to identify incipient shifts in disturbance regimes (Turner 2010). The synergistic effects of interactions among disturbance characteristics, life history parameters, and climate change are of particular concern because disturbances have potentially substantial consequences for carbon and nutrient cycling, and hydrology.

We cannot properly evaluate modern disturbance events without the baseline information provided by decadal- to multimillennial-scale records of disturbances and ecosystem responses. Such long-term records are derived primarily from tree-ring and sedimentary archives, and they allow the reconstruction of past disturbance events and regimes. When combined with both detailed observational data about individual events and with novel proxies of ecosystem processes, the biogeochemical consequences of changing disturbance regimes can begin to be assessed. An important challenge now is to integrate these two approaches with respect to ecological processes and spatiotemporal patterns.

A variety of disturbance agents, such as fire, wind, drought, or insect outbreaks, are familiar to most ecologists as regulating short-term ecosystem processes, such as nutrient cycling and carbon storage (Pickett and White 1985). These same disturbances can also determine long-term ecosystem trajectories. For example, without soil-replenishing disturbance, productivity may decrease and ecosystems may retrograde (Wardle et al. 2004). Chronic disturbance, however, can also lead to long-term reduction of productivity through nutrient depletion (Boerner 1982). Although the importance of disturbance to ecosystem functioning is recognized, the biogeochemical consequences of disturbances have been particularly difficult to quantify over long timescales. An increasing amount of complementary research now provides the basis for understanding decadal- to millennial-scale ecosystem change, including high temporal-resolution post-disturbance chronosequences, innovative techniques applied to sediment and tree-ring records to reconstruct past ecosystem change, and long-term ecological measurements of several decades in duration.

The integration of ecosystem processes across multiple timescales is crucial for identifying the biogeochemical consequences of disturbances. Ecosystem ecologists working on the modern landscape (“neo-ecologists”) have had success in quantifying short-term responses to disturbance through direct measurements (Mack et al. 2011). In contrast, paleoecologists have been successful at quantifying past disturbance regimes to contextualize modern disturbances (Marlon et al. 2012). The long-term perspective that paleorecords provide has proven increasingly useful to conservation management (Willis et al. 2007), ecosystem service analyses

(Dearing et al. 2012), and restoration ecology. There is now potential to use records of disturbance events and regimes to calculate the biogeochemical consequences of disturbance across climate types, vegetation types, and soil development stages.

Integrating the two views— paleo- and neo-ecosystem ecology— is a challenge due to differences between disciplines in methodology, timescale, and spatial extent. Yet this integration is crucial for understanding the dynamic nature of disturbance and potential feedbacks in the Earth system among climate change, disturbance, and biogeochemistry. Without additional information from paleorecords, extrapolating modern ecosystem responses across time and space will likely be ineffective, and direct measurements of ecosystem response are needed to interpret the indirect proxies available in paleorecords. Here, we take the first steps toward this integration by (1) reviewing how disturbances are reconstructed using dendrochronological and sedimentary archives, (2) summarizing the conceptual frameworks for carbon, nitrogen, and hydrologic responses to disturbances, and (3) identifying key research priorities for linking the mechanistic knowledge of disturbance from neo-ecology with the long-term perspective granted by paleoecology.

Reconstructing past disturbance

A variety of disturbance events can be reconstructed from annual to multi-millennial timescales (Table 1). Disturbance agents particularly important in mid-latitude terrestrial ecosystems are fire, drought, and insect outbreaks. From paleorecords, it is possible to reconstruct disturbance agent, severity, spatial location, and spatial extent. We focus here on records available from tree-rings and lacustrine sediment sequences. Long-term instrumental data are helpful for calibration of potential proxy records. The most robust reconstructions use either multiple approaches or a detailed calibration dataset.

Observational, remote-sensing, and historical records of disturbance offer detailed accounts of event timing, location, and ecosystem impacts, but they typically span only decades or centuries at most (Raffa et al. 2008). Tree-ring records can extend this timeframe by providing spatially-precise, sub-annually resolved records of low- and high-severity fires (Falk et al. 2011), insect outbreaks (Veblen et al. 1994), and drought (Cook et al. 2004) across a range of forest types. Proxy variables from sedimentary records can provide disturbance reconstructions on even longer timescales, such as several millennia, but generally have lower spatial and temporal resolution.

Fire. Wildfires are the most commonly reconstructed disturbance events from sediment records that span centuries to millennia (Gavin et al. 2007, Higuera et al. 2010). Two aspects of past fire occurrence are focal points for these reconstructions, spanning two spatial scales. Stand-level or “local” fire occurrence may be interpreted from distinct charcoal peaks in high-resolution sediment records of macroscopic charcoal. For example, fire events in a coniferous montane forest were reconstructed from macroscopic charcoal influx to a small lake basin (figure 1). Several fire regimes can be distinguished over a 6,000 year time period. Regional-level biomass burning or area burned is inferred from standardized summaries of total charcoal accumulation in a record or network of records, and quantified as an index (Marlon et al. 2012), or area burned (Higuera et al. 2011). Biomass burning can then be linked to independent proxies for vegetation to infer the fuel types and fire severity.

Fire history investigations based on tree-ring records employ dating of fire scars, stand establishment, or both depending on the type of wildfire regime being investigated. Fire scar networks in western North America have been particularly effective for identifying past landscape and climate drivers of low-intensity fire events (Falk et al. 2011). Mixed severity fire regimes can be detected with dendrochronological techniques along with reconstructions of fire frequency and area burned (Hessl 2011).

Drought. Paleorecords can also provide accurate reconstructions of drought conditions. Drought is defined in multiple ways based on spatial and temporal changes in precipitation, frequency of precipitation events, and severity of impacts. Relatively short (< 200 years) instrumental time series provide data on streamflow, precipitation, soil moisture, Palmer Drought Severity Index, flood events, and lake levels (Biondi and Strachan 2012). Dendrohydrology uses growth records from long-lived tree species to extend the contemporary instrumental hydrologic records one to two orders of magnitude (Stine 1994).

Lake sediment cores further extend the temporal scale of hydrologic reconstruction to millennial and longer timeframes. From sedimentary records, droughts can be reconstructed from changes in lake level, diatom communities, and geochemical proxies (Laird et al. 2003). These paleolimnological methods have been most commonly applied to closed-basin lakes in arid or semi-arid landscapes where changes in lake-level and salinity are closely related to shifts in hydrologic balance.

Insect outbreaks. During recent decades, irruptive populations of native bark beetles (*Dendroctonus* spp., *Ips* spp.) have exceeded the spatial scale and intensity of past outbreaks by an order of magnitude (Raffa et al. 2008). In western North America, these disturbances have been attributed to the complex interaction of accelerating insect reproductive cycles related to warming air temperatures, decreased tree vigor from moisture deficiencies and concomitant pathogen infestation, and high stand densities of suitably-sized host trees (Mitton and Ferrenberg 2012). Tree-ring reconstructions provide evidence that native bark beetles are an essential component of ecosystem function and promote forest regeneration (Sherriff et al. 2011). However, what is believed to be the unprecedented scale and severity of recent outbreaks suggests that neither the dynamics of beetle disturbances nor their biogeochemical impacts are well understood (Rhoades et al. 2013). Longer-term ecological records would help to contextualize the recent episodes. For example, tree-ring records indicate that the recent mountain pine beetle epidemic in central British Columbia was preceeded by at least two 19th century outbreaks (Hrinkevich and Lewis 2011). The need to extend the temporal record of past bark beetle disturbances is currently being pursued using lake sediments. Proxy and direct evidence, including pollen and plant and insect macrofossils, has been useful to reconstruct past insect disturbances over centennial to millennial timescales (Morris and Brunelle 2012).

Reconstructing biogeochemistry

In addition to reconstructing disturbance regimes, the paleoecological record has the potential to provide key information on ecosystem pools and fluxes. This information is provided through proxy records that range from standard paleoecological techniques to newly-developed methods in lacustrine sediment cores (Smol 2001). The pollen record indicates plant community composition, and pollen influx can provide an index of terrestrial biomass. Organic matter content of lake sediment is an indicator of combined lake productivity and detrital terrestrial sources; separating these sources is possible through the carbon:nitrogen ratio. Stable isotopes of carbon and nitrogen also relate to the cycling and productivity within the aquatic and terrestrial ecosystems. The toolbox of methods is growing rapidly. Newer methods include quantifying the elemental composition of sediments to identify sources of mineral matter, measuring compound-specific isotopes that relate to sources and types of organic matter (e.g., terrestrial vs. aquatic), and using additional proxies such as magnetic properties to interpret geochemical changes.

The biogeochemistry of disturbance

Carbon

The cycling of carbon (C) is a fundamental characteristic of ecosystem functioning, and it is highly sensitive to disturbance. In the absence of change in the disturbance regime, C storage in terrestrial ecosystems is constrained by stable rates of accumulation and degradation. Ecosystems therefore have a characteristic C carrying capacity that may fluctuate around this capacity in time and space, i.e. the shifting mosaic steady state (Bormann and Likens 1979). Thus, over decadal timescales the net ecosystem C balance (NECB) trends toward zero (Chapin et al. 2006), assuming no directional changes in ecosystem composition and/or climate. However, changes in the disturbance regime can lead to dramatic shifts in C cycling and NECB. Often these changes are realized over long time frames (hundreds to thousands of years) that require a broad and integrated temporal perspective available only from paleorecords or chronosequences. Regional-scale vegetation shifts have the potential to influence the global C balance. For example, 96 Tg of C accumulated in boreal peatlands during the Holocene (Dean and Gorham 1998). Thus, one key challenge is to detect and understand how fundamental shifts in disturbance regimes can alter C cycling through ecosystem reorganizations.

Changes in C status may be triggered by unusually severe events, compound disturbances, or major changes in disturbance regimes that exceed the ecological resilience of the system and trigger changes in the vegetation and soil. Therefore understanding long-term C dynamics in ecosystems requires integration of contemporary and paleoecological approaches. Studies of the modern landscape are constrained by their narrow temporal context, without baseline information and past histories to fully interpret measured recent changes in NECB. Thus, it is difficult to determine if recently-observed changes have precedent or if they represent novel conditions.

Paleoecological studies capture the long-term patterns in disturbance regimes, state changes in the vegetation, and coarse measures of C stores. The example sedimentary sequence from an old-growth conifer forest shown in figure 1 simultaneously records organic content, changes in fire regimes, and terrestrial vegetation composition, in some cases in response to rapid climate change. But the nature of proxy records is indirect, and the temporal and spatial resolution is often too low to identify precise mechanisms or consequences of change.

For many modern ecosystems, C lost during a disturbance event is largely recovered before the next disturbance, and NECB can be considered relatively stable. The initial driver of this trajectory is C-fixation in aboveground live biomass such as wood, with relatively linear rates of C accumulation in the first few decades after a disturbance event (figure 2). However, the subsequent redistribution of this C into soil pools with longer turnover times can take centuries, and these slower processes lead to a saturation of C accumulation rate on those timescales. When comparing data from post-disturbance chronosequences with the paleoecological record, it is clear that both compound disturbances and state changes in the disturbance regime alter these trajectories. Additionally, some of these state changes occurred rapidly (i.e. a shift from forest to grassland in less than 300 years) (Williams et al. 2010). There are also contemporary examples of incipient shifts in the disturbance regime, and model results that predict futures with drastically different C balances (Bond et al. 2005). In short, changes in the disturbance regime can drive state changes in ecosystem structure and function with respect to C storage.

We present a conceptual model of how NECB and disturbance interval interact over long timescales, and how this would be seen in a sedimentary paleorecord (figure 3). Our current understanding suggests that a single disturbance event, even one of high severity such as a stand-replacing wildfire, will not necessarily alter long-term C balance. Net Primary Productivity (NPP) can keep pace with periodic disturbance, and NECB is stable. We recognize that recovery patterns will vary, but we expect that these two processes will usually balance, as illustrated by the 1:1 line that compares the time to recover the C lost with the time since disturbance as 1:1 (figure 3b). Observations greater than the 1:1 line imply gains in NECB and slopes less than 1 imply losses in NECB. Conceptually we expect ecosystems with a consistent disturbance regime and ecological community to fluctuate around this 1:1 line.

Severe, progressive, and/or continual deviations away from this 1:1 ratio would indicate a potential biogeochemical state change (figure 3). We set the 1:1 line as the neutral state where C dynamics and disturbance regime are in balance. Perturbations of either the disturbance regime or time to C recovery would drive the system away from the 1:1 line. When there is a state shift, there is a potential for changes in the C balance compared to the previous system. It is important to note that there is no assumption that the baseline is constant. Indeed, the value of this conceptual figure is to explicitly acknowledge that the baseline changes with a shift in the biogeochemical state. Also the interpretation of the ratio of time to disturbance: time to C recovery is not interpreted in isolation (Turner et al. 1993). Other information from the paleoecological record (e.g., charcoal-inferred change in fire frequency, pollen-inferred change in plant community) is necessary to infer the processes involved.

Small changes in the disturbance return interval can lead to cascading biogeochemical effects, as demonstrated by an example from the tallgrass prairie ecosystems of North America. This grassland disturbance regime is defined by a cycle of annual fires with the C losses replaced each year (i.e. 1:1). If these fires are suppressed by human intervention, the time between disturbances lengthens, leading to net C gain as woody plants increase (C balance>1). Evidence from experimental burning suggests that increasing fire return interval from 1 to 4 years can initiate the first steps of vegetation change (Briggs et al. 2005). The initial C gains are intensified by a series of feedbacks that culminates in woody plant encroachment (Knapp et al. 2008). When C ceases to accumulate (apex of curve) under the new disturbance regime, we define it as a biogeochemical state change. There is evidence from many other grassland systems that this state change is currently occurring, leading to increased net aboveground C stocks (Throop and Archer 2008). In these cases, the biogeochemical state change is driven by a shift in plant community composition, which is detectable in the pollen record.

The reverse process has also been seen in the paleorecord. Over time, non-stationary changes in climate (warming and drying) increase the fire frequency leading to a shorter disturbance interval relative to the C recovery time, eventually resulting in a net loss of C and potentially establishment of a different ecological community. When the C losses stabilize around a new average value, another biogeochemical state change is indicated. Again this change is driven by a vegetation shift: this time from woodland to shrubland, such as has been seen in paleorecords from the southwestern U.S. It is an open question at this time if it is possible to get a large change in carbon balance without a major vegetation shift.

Finally, disturbance and atmospheric carbon dioxide concentrations are tightly linked, with C stored in biomass often released to the atmosphere during a single disturbance event. The rate and mechanism of release varies with the type of disturbance, and again NECB may not change in the short-term without significant feedbacks to long-term climate change. Human management of fire regimes has been demonstrated to affect C budgets from local to global scales (Bowman et al. 2011).

Nitrogen

Nitrogen (N) dynamics have many similarities with C dynamics after a single disturbance event, and widespread N limitation of NPP and C accumulation often yields close couplings of N and C dynamics after disturbance (Vitousek and Reiners 1975). However, there are also important differences in the cycling of these two elements that can lead to different long-term trajectories. N_2 is more energetically costly to fix than CO_2, and yet once fixed into an ecosystem, a single atom of N can be recycled to fix many atoms of C. Despite persistent challenges in calculating ecosystem N budgets on decadal timescales, the general paradigm for temperate ecosystems is that after a single disturbance event, ecosystem N stocks recover to pre-disturbance levels within decades. Such dynamics have been seen in the post-fire chronosequences of *Pinus cortorta* forests in the Greater Yellowstone Ecosystem (figure 4, Smithwick et al. 2009). Rapid N accumulation is also demonstrated in the well-studied primary successional chronosequence in Glacier Bay, Alaska, where spruce and hemlock forests accumulated their maximum N contents within 150 years of glacial retreat (Milner et al. 2007). Thus, on decadal to century timescales, disturbance alone often does not alter long-term nutrient stocks or limitation.

However, the biogeochemical impact of a single disturbance event may also serve to initiate an increase or a decrease in long-term ecosystem N stocks (figure 5a). The disturbance initially causes nutrient loss, but recovery trajectories can vary depending on interactions between the disturbance, ecosystem properties, and ecosystem boundary conditions. One scenario is a net long-term loss of N due to disturbance, as in systems where N fixation is so limited that it cannot replace hydrologic and gaseous N losses. Changes in disturbance intensity or frequency as a result of altered boundary conditions, such as changing climate or vegetation shift, may also prevent reaccumulation of N after disturbance (Yelenik et al. 2013). Alternatively, disturbance can in some cases promote long-term increases in N stocks, such as where robust post-fire N fixers like *Alnus* colonize and add more N than is lost in a single disturbance event (Perakis et al. 2011). Similarly, altered boundary conditions such as a wetter climate might permit higher N accumulation after disturbance.

Thus, disturbance-driven increases or losses of nutrients can alter longer-term nutrient limitation when considered over long timescales (figure 5b). Each step of this biogeochemical staircase can therefore serve to either increase (“step up”) or decrease (“step down”) nutrient availability. In turn, these disturbance-driven changes in nutrient status fall within a broader biogeochemical template derived from very long-term chronosequences that reveal how ecosystems change over long-term soil development. Whereas soil fertility often increases through primary succession, ultimately very old ecosystems undergo “retrogression” in the absence of catastrophic disturbance over millennial timescales (Peltzer et al. 2010).

Characteristics of retrogressive ecosystems include reduced availability and amounts of soil nutrients (notably phosphorus), reduced NPP, and low standing biomass. In retrogressive ecosystems, disturbance events that expose unweathered soil parent material can replenish available nutrient pools and increase NPP (figure 5c). This seemingly counterintuitive response to disturbance works much the same way as geological uplift, glacial retreat, or volcanism on longer timescales (Porder et al. 2006).

Our understanding of these millennial- and longer-scale processes has been derived primarily from chronosequences, a series of sites with different histories used to reconstruct both primary (soil-development) and secondary (stand development) successional processes. This approach has been very powerful in ecosystem ecology, even if it often only provides information from discrete points in time (Laliberte et al. 2012). Paleorecords, for example from lake sediment cores, can complement chronosequence studies by providing continuous records that span many millennia (Engstrom et al. 2000). Such records can be used to test theoretical predictions of the conditions when ecosystems should be responsive to disturbance, and the direction of the response. Thus, ecosystems in very young stages of development where NPP is limited by N would be expected to respond differently to disturbance than very old retrogressive ecosystems limited by phosphorus (Peltzer et al. 2010).

There are general patterns in how nutrient limitation shifts from primary succession to very old ecosystems that can aid interpretation of paleorecords through time in different landscapes. Nutrient limitation is strong in early stages of soil development, and is most commonly driven by N as it slowly accumulates from primary atmospheric sources. Nutrient limitation decreases in intermediate stages as N accumulates and rock-derived nutrients (e.g., phosphorus, calcium) are released into available forms by weathering. Nutrient limitation intensifies in late stages of soil development due to depletion of rock-derived nutrients on geologically old substrates (Chadwick et al. 1999), shift of rooting zone from mineral to organic soil horizons (Bormann et al. 1995), or sequestration of accumulated N in unavailable organic forms (Wardle et al. 2012). The sensitivity of ecosystem N cycling and loss to disturbance also changes over geological time. At the young and old ends of the spectrum, N cycling should show weak sensitivity to disturbance, and intermediate-aged ecosystems should exhibit strong sensitivity. In early soil development, intense N limitation prevents strong changes in N cycling with disturbance. In intermediate stages of soil development, high rates of biotic N cycling elicit strong responses of N biogeochemistry to disturbance, with large potential for nutrient losses. Late in soil development, nutrient limitation by rock-derived nutrients (phosphorus, calcium) intensifies, attenuating the response of N cycling as N limitation is relaxed, causing weak response of N cycling and loss to disturbance. Grounding novel geochemical proxies from sediment records in biogeochemical theory is likely to improve interpretation of paleorecords in an ecosystem context.

Hydrology

Many studies have documented hydrologic responses to disturbance, and these provide an opportunity to consider ecosystem resilience to a range of disturbance types. A foundational paradigm is that removal of plant biomass, such as in clearcutting experiments, would increase water available for stream discharge (Bormann and Likens 1979). In addition, a variety of ecosystem responses have been observed following disturbances, including changes in water balance (runoff, recharge, evaporation), chemistry (major ions, nutrients, organic C), and sediment yield. Additionally, responses may vary from regime shifts to no detectable change depending on the combination of disturbance magnitude and the resilience of the ecosystem (figure 6). The total disturbance magnitude could represent the effects of a single event, but may also indicate the combined consequences of repeated disturbances. There are highly-variable observed examples of responses ranging from regime change to no response across the spectrum of total magnitude with the character of the response.

Land cover change in different ecosystems, at different times and rates, reveals the influence of ecosystem resilience and resistance on the scale and style of responses to similar magnitude disturbances (figure 6). For example, at Hubbard Brook, New Hampshire, ecosystem resilience of a mesic forest has led to observed recovery of hydrologic behavior in a clear-cut watershed within decades (Bormann and Likens 1979), but paleoecological studies demonstrate that land clearance can produce persistent change in less resilient ecosystems such as pine barrens (Lytle 2005) or in combination with other long-term influences (like climate change) that weaken ecosystem resistance and reduce the range of resilience. However, disturbance severity can also be important for shaping the type of hydrologic response. For example, forest thinning may produce a smaller change than total removal of trees.

The importance of small disturbances for producing regime changes and severe responses in systems close to thresholds can be demonstrated by permafrost melt events (Smith et al. 2004) and changes in snowpack-drive stream discharge, where small warming can cross the melting threshold and cause a regime change in system state and behavior. Consequently, some ecosystems have the potential to jump permanently from one state to another (e.g., where warming is small, but persistent) even in the face of weak perturbations, while others have the capacity to return to their initial state after some period of recovery (e.g., where only a temporary change in watershed functioning occurred).

The frequency of a type of event in a system may predict the magnitude and nature of the hydrologic response. Volcanism provides an example of an infrequent event, and an ecosystem-independent disturbance agent. With no ecosystem feedbacks on disturbance magnitude or frequency, paleo-ecosystem studies reveal otherwise unknown and infrequent events that cannot be studied on short time frames. For example, the eruption of Mount St. Helens, Washington in 1980 A.D. had immediate and well-documented effects on local hydrology, such as the loss of the mountain glaciers (figure 6). Similarly, an ancient eruption in the same region—the eruption of Mount Mazama in 7600 cal yBP—illustrates how volcanism can have far-reaching impacts. The Mazama ash more than doubled the water-holding capacity of soils which resulted in major vegetation changes especially in dry sites (Gavin et al. 2001). Post-eruption regime shifts in lake level and diatom communities indicate hydrologic changes well to the east in Montana (Stone and Fritz 2006).

Likewise, paleo-ecosystem studies reveal that many other historic observations of apparently large or severe disturbances are not unprecedented when viewed in a long-term context. Recent drought, fire and hurricane events have been placed in the context of many past events, which show that large infrequent disturbances (Foster et al. 1998) are poorly-understood without data representing a long time span (Laird et al. 2003). Disturbances that may initially be considered "catastrophic" such as the 1988 fires in Yellowstone National Park may be viewed as "natural" when compared with the paleorecord (Romme et al. 2011), while others such as the 2007 Anaktuvuk River Fire in Alaskan tundra may be considered unprecedented over the late Holocene (Hu et al. 2010).

Hydrological responses can also have implications for other biogeochemical cycles in a fashion that depends upon the character of the response. For example, severe droughts in the Great Plains have lowered lake levels and limited surface water supply both historically and during the past several millennia (Laird et al. 2003). One consequence of the most severe droughts during the mid-Holocene was to concentrate migrating birds at the few remaining lakes in the Great Plains, and create localized hot spots of nutrient delivery, but because these hydrologic systems are highly resilient, the end of the droughts led to a recovery of earlier broad distribution of bird stop-over locations and nutrient loading (Donovan and Grimm 2007). We suspect that other interactions among systems (e.g., hydrology, fauna, N) and their levels of resilience will produce similarly contingent effects on ecosystem characteristics and function.

On the other hand, hydrologic case studies also reveal important absence of responses. This resilience was also seen in long-term ecosystem response to disturbance for C and N cycling. In particular, multiple studies have sought to document significant changes in water chemistry in lakes following fires in their watersheds and have found little to no change. The absence of such a response has been observed both historically and in response to repeated fires in the same watershed using paleo-ecosystem techniques (Marchand et al. 2009). The absence of expected changes illustrates important gaps in our current understanding of ecosystem response to disturbance.

Research priorities

We identify a number of theoretical and practical approaches to strengthen the insights of ecosystem response to disturbance by linking information across multiple temporal scales. First, the paleorecord is replete with examples of unexpected complacency to relatively large magnitude disturbance events (DiMichele et al. 2004). The disturbances can be reconstructed, but a focus on the drivers that allow ecological resilience or persistence is needed (Swetnam and Betancourt 1998). A general framework for identifying ecosystem characteristics that confer resilience has been difficult to achieve. Disturbance experiments may provide a way forward. For example, a large-scale girdling experiment in a secondary temperate forest identified the role of residual vegetation in retaining N and sustaining ecosystem C accumulation during a period when 20-50% of the existing trees were experimentally killed (Nave et al. 2011). Manipulations of fire severity can provide insights regarding the magnitude of C loss under different fire regimes and the mechanisms influencing post-fire C accumulation in both vegetation and soils. Manipulations of fire frequency can provide insights into resilience and resistance of different vegetation types to disturbance regimes (Briggs et al. 2005). The results of these types of experiments will add short-term mechanistic-oriented detail to long-term pattern-oriented records of past disturbance, providing a powerful joint perspective to understand resilience.

Second, it is clear that disturbances of varying magnitude and type interact at the landscape scale. These interactions have led to the perceived difficulty of predicting multiple successional pathways after disturbance. Directly studying these interactions can increase our predictive power about post-disturbance biogeochemical trajectories. For example, the interactions of sequential disturbances from logging, fire, and wind disturbance in mixed conifer forests in Colorado were non-additive (Buma and Wessman 2011). Surprisingly, disturbance agent, combinations, and resilience mechanisms were more important than number of disturbances. Because multiple disturbance events and agents can be identified in paleorecords, this approach may provide further insights about the interactive nature of disturbance events if explicitly studied. A better understanding of how different disturbances are represented in the paleorecord is required. While fires are well-studied and well-represented in sedimentary charcoal and tree rings, other important disturbance agents (e.g. insect outbreaks, ice storms, windthrow) are often less clear, despite having implications for biogeochemical cycles. Identifying the mechanism of disturbance instead of the disturbance type or agent, such as in the conceptual framework described by Peters et al. (2011) is likely to improve predictability of biogeochemical response.

Several practical avenues can speed the integration of neo and paleo timescales and concepts. A central one is to develop techniques to make the sediment record more informative of terrestrial ecosystem dynamics. We identify three main technical developments in paleoecology as high research priorities : 1) developing improved quantitative proxies of NPP, 2) developing proxies of terrestrial nutrient cycling, and 3) assessing the age and structure of ecosystem C stocks from sedimentary records. There are significant challenges to each of these research areas. But there are also recent advances such as spatially-explicit reconstructions of terrestrial C budgets from pollen records (Boyle et al. 2011), compound-specific N isotopic analysis in sediments (Enders et al. 2008), and rapid high-resolution quantification of sedimentary elemental concentrations (Kylander et al. 2011). Another key is to routinely conduct multiproxy analyses, especially identifying the source of sedimentary organic matter, and the application of whole-lake flux measurements as derived from multiple sediment cores (Engstrom and Rose 2013). Finally, high-resolution temporal sampling across disturbance events, such that disturbance and biogeochemical responses are measured in same record, would be useful.

The primary challenge is to bridge the spatial and temporal scales of neo-and paleo-studies, to produce a more consistent, synthetic understanding of biogeochemical processes than possible from either perspective alone. We identified centennial timescales as an area with the least information on post-disturbance biogeochemical processes, yet critical for understanding ecosystem function during ongoing climate change. Centennial timescales are also where some paleorecords lack sufficient resolution to capture dynamics associated with several disturbance intervals.

The conceptual models developed in this manuscript are largely aspatial, but could be made spatial. There are also particular places and spatial scales that may be most synergistic for linking across timescales. For example, the Arctic tundra is a region already experiencing the effects of global change, including altered fire regimes and permafrost melting (Hu et al. 2010). This region is especially promising as a test area for this new synthetic approach to paleoecosystem ecology, because it contains both detailed long-term ecosystem measurements and many sedimentary records of climate, vegetation, and geochemical change.

Conclusions

1. The unification of long-term ecological monitoring data, chronosequences, and paleorecords provides exciting opportunities for exploring the interactions of multiple disturbance events against a changing background of climate and disturbance frequency.
2. The biogeochemical consequences of a single disturbance are often short-lived, with biogeochemical parameters returning to pre-disturbance conditions on the same timescale as the dominant vegetation type. Thus, biogeochemical cycles in many ecosystems can be considered resilient to disturbance. The true impact of

disturbances may come through changing disturbance regimes, which requires the context of long timescales.

3. Centennial and multi-centennial timescales are critical timeframes for improving our understanding of the biogeochemical consequences of disturbances. This scale is when the understanding of a single disturbance event from a chronosequence begins to break down, while the temporal resolution of paleorecords is usually insufficient to capture biogeochemical processes through multiple disturbance events.
4. Developing proxy records of ecosystem characteristics is a priority for the paleoecological community. Three proxies would be particularly useful: NPP, terrestrial nutrient dynamics, and age of ecosystem C.
5. The existence of unexpected post-disturbance trajectories such as multiple successional pathways continues to challenge ecosystem ecologists and poses a particular problem for the next generation of Earth System Models. The empirical and conceptual perspectives described here help move us closer to the goal of increased predictability of post-disturbance trajectories, including incorporating the role of disturbance agent, severity, and their interactions over centennial to millennial timescales.

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Table 1. Types of disturbances and how they are reconstructed. The key contribution of paleoecology is being able to reconstruct enough disturbance events to characterize disturbance regimes. These are often summarized over a given spatial and temporal extent, and expressed as a distribution or summary statistics [e.g, mean fire return interval (FRI)]. Additional disturbance properties include spatial extent, timing, and interactions (Pickett and White 1985).

disturbance agent	**severity**	**frequency**	**technique**
fire	low	high	fire scars recorded in wood
	high	low	tree establishment dates, sedimentary charcoal
insects	high	low	tree demography, insect fossils in sediment
wind	high	low	downed wood, clastic material in sediments
drought	variable	variable	tree rings, long-term instrumental records, lake level, lake salinity
tree removal (clearance, deforestation)	high	low	pollen preserved in sediment, sedimentation rates, tree demography
mass movement	variable	variable	sedimentation rate

Figure 1. Paleoecological studies capture the long-term disturbance histories, state changes in vegetation, and coarse measures of carbon stores. Multiproxy sedimentary data from Yahoo Lake, Washington, USA show how climate affects biomass and how fire mediates tree species composition during periods of rapid climate change (Gavin et al. in press, 2013). (a) Organic content (loss-on-ignition, LOI) and climate as estimated by sea surface temperature (SST) in the NE Pacific Ocean. (b) Macroscopic charcoal stratigraphy quantified at 1-cm intervals. Red lines indicate interpreted fire events near the lake. (c) Pollen percent (colored areas) and needle macrofossil concentration (top axis, needle equivalents per 5 cubic centimeters of sediment) for three coniferous tree species.

Figure 2. Post-fire aboveground carbon (C) accumulation in forests in Alaska. Post-fire vegetation type determines the rate of C accumulation in living aboveground biomass.

Figure 3. Conceptual diagram of long-term ecosystem carbon state in the context of disturbance regimes. (a) how this would be recorded in the charcoal and pollen paleorecords of a sediment core, (b) the carbon storage in the ecosystem, and (c) the underlying processes of a shift in NECB, including state changes in vegetation and disturbance regime.

Figure 4. A well-replicated post-disturbance chronosequence of lodgepole pine (*Pinus contorta* var. *latifolia*) forests in the western U.S. shows equilibration of ecosystem nitrogen (N) pools but redistribution of ecosystem N among pools after disturbance (Smithwick et al. 2009).

Figure 5. Conceptual diagram showing response of available stocks of growth-limiting nutrients to disturbance. (a) a single disturbance event may serve to increase, decrease, or not affect net stocks of a nutrient depending on post-disturbance accumulation and loss rates. (b) over time, a disturbance regime may gradually increase or decrease nutrient availability, a phenomenon we term the "biogeochemical staircase", (c) over longer timescales, ecosystems often experience the onset of phosphorus limitation and reduced net primary productivity known as retrogression (reproduced from Peltzer 2010). In the oldest stages of ecosystems, disturbances can serve to replenish nutrients.

Figure 6. Conceptual diagram of four types of hydrologic responses to disturbances, encapsulating the range of responses demonstrated in various paleorecords, observations, and modern experiments. Red colors indicate a response of water quality, blue colors indicate a response of water quantity.

Box 1. Background on disturbance ecology.

The theoretical basis for linking biogeochemistry with **disturbance ecology** was developed in the 1970s and largely focused on impacts from, and recovery to, steady-state or equilibrium conditions (Vitousek and Reiners 1975). Newer conceptualizations of complex adaptive systems and resilience in ecological systems now highlight the important role of interactions, system feedbacks, and landscape contingencies when forecasting how disturbances affect ecosystems. Interactions between biogeochemical cycles and vegetation can either reinforce current states or result in shifts to alternate states, depending on the magnitude and timing of the interactions. Importantly, potential shifts in system states can be caused by the disturbance itself, as well as centuries to millennia of vegetation-soil feedbacks that constrain, mediate, or amplify ecological responses (Turner et al. 1993).

The concept of **biogeochemical resilience** incorporates the idea that biogeochemical characteristics are spatially differentiated prior to disturbance, are sensitive to the disturbance event itself, and are coupled to vegetation response patterns and rates (Smithwick 2011). Classically, ecological resilience is focused on organisms, while biogeochemical resilience is focused on pool sizes and input/output rates. Over long spatial and temporal scales, shifts in biogeochemistry influence vegetation response trajectories and *vice versa*. Understanding long-term ecosystem resilience to disturbance requires a full characterization of disturbance regimes—the agent or mechanism of disturbance, as well as the magnitude, severity, and return interval (Table 1, Peters et al. 2011)— alongside an understanding of elemental pools and flows.

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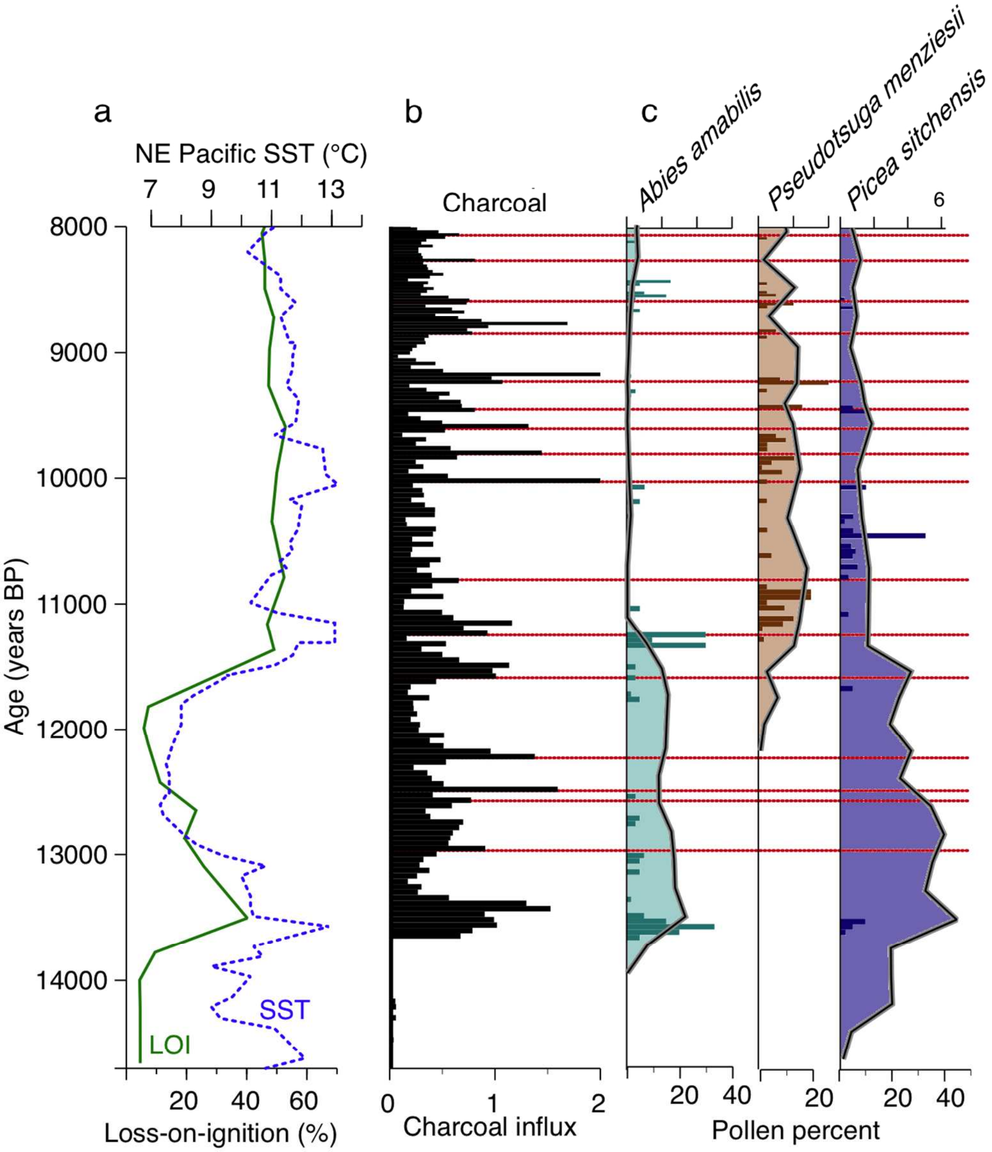

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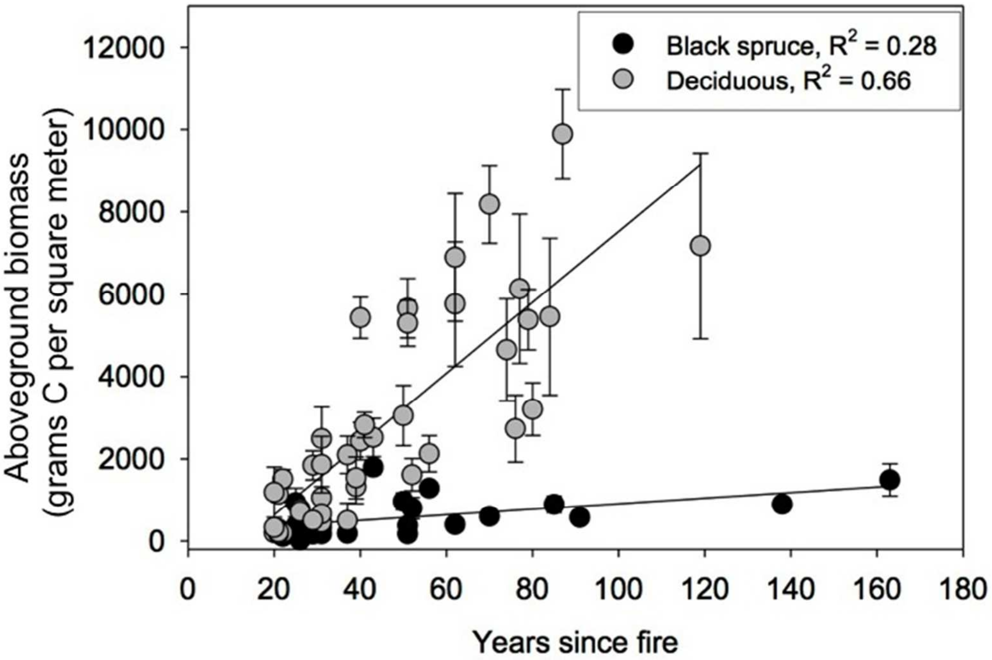
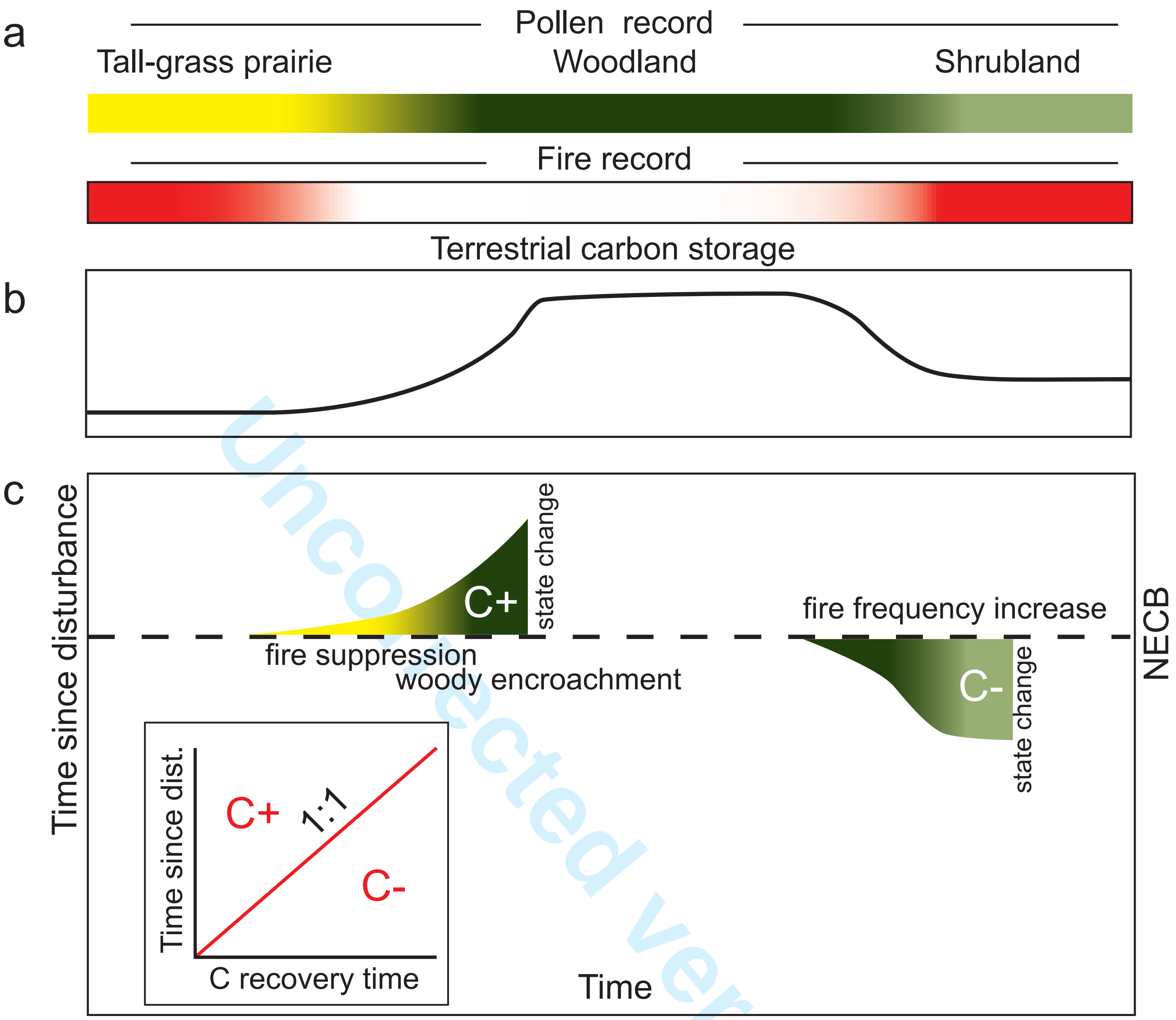


Figure 2. Post-fire aboveground carbon (C) accumulation in forests in Alaska. Post-fire vegetation type determines the rate of C accumulation in living aboveground biomass.
254x190mm (72 x 72 DPI)


a
Pollen record
Tall-grass prairie
Woodland
Shrubland
Fire record
Terrestrial carbon storage
b
c
Time since disturbance
C+
state change
fire frequency increase
NECB
fire suppression
woody encroachment
C-
state change
Time since dist.
C+
1:1
C-
C recovery time
Time

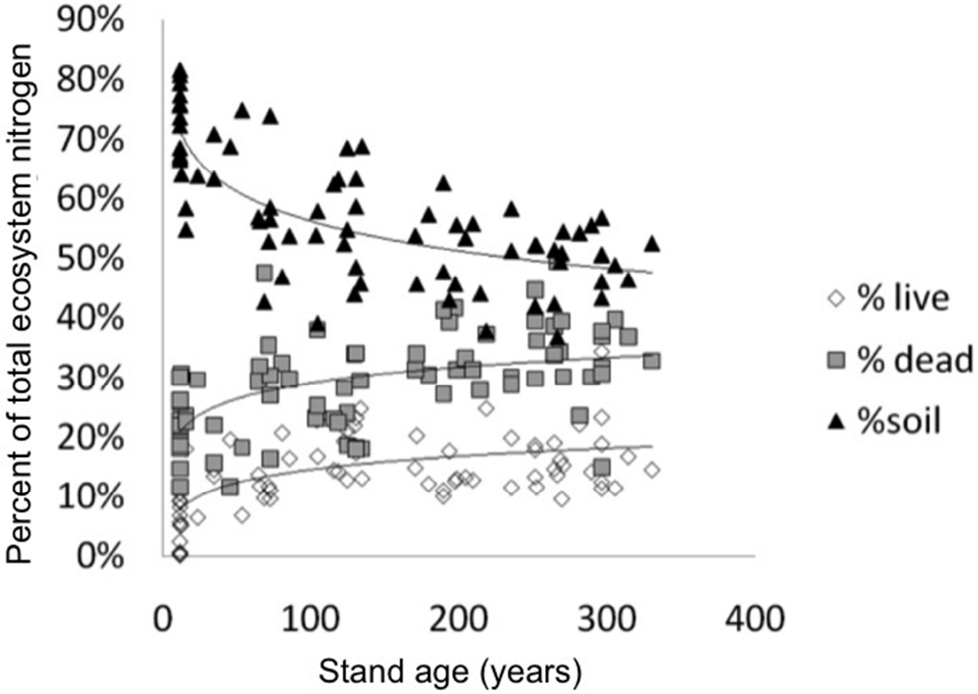


Figure 4. A well-replicated post-disturbance chronosequence of lodgepole pine (Pinus contorta var. latifolia) forests in the western U.S. shows equilibration of ecosystem nitrogen (N) pools but redistribution of ecosystem N among pools after disturbance (Smithwick et al. 2009).
254x190mm (72 x 72 DPI)

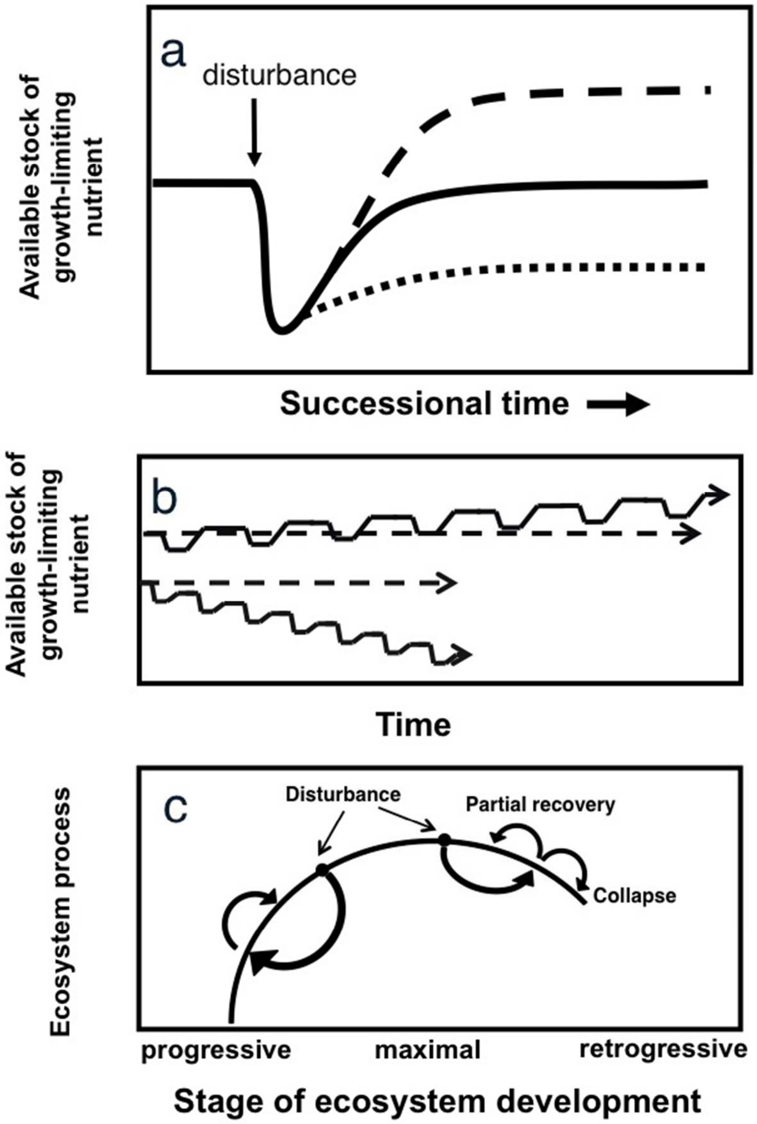
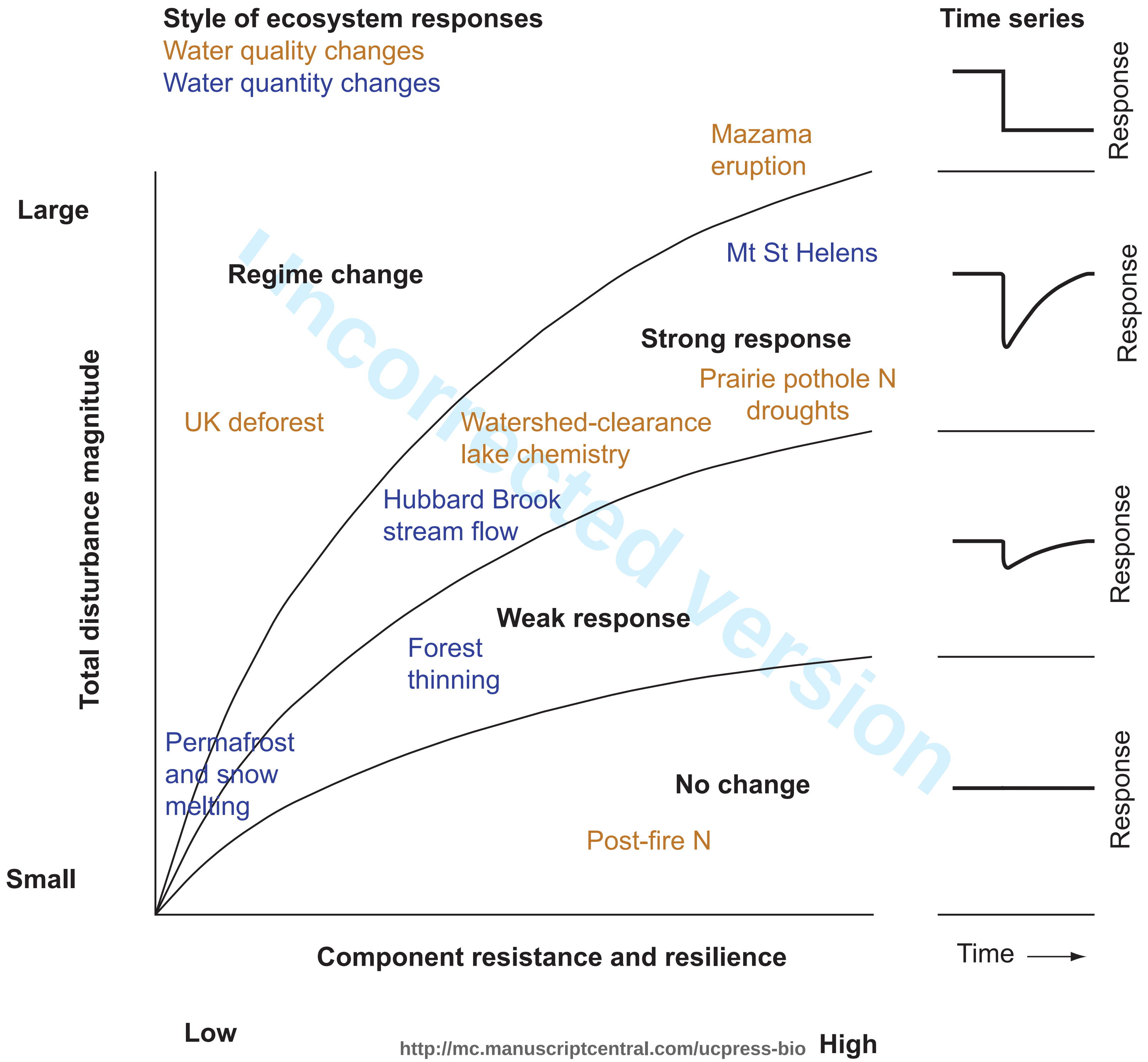


Figure 5. Conceptual diagram showing response of available stocks of growth-limiting nutrients to disturbance. (a) a single disturbance event may serve to increase, decrease, or not affect net stocks of a nutrient depending on post-disturbance accumulation and loss rates. (b) over time, a disturbance regime may gradually increase or decrease nutrient availability, a phenomenon we term the “biogeochemical staircase”, (c) over longer timescales, ecosystems often experience the onset of phosphorus limitation and reduced net primary productivity known as retrogression (reproduced from Peltzer 2010). In the oldest stages of ecosystems, disturbances can serve to replenish nutrients.
254x338mm (72 x 72 DPI)


Style of ecosystem responses
Water quality changes
Water quantity changes
Time series
Mazama eruption
Large
Mt St Helens
Regime change
Strong response
Prairie pothole N droughts
UK deforest
Watershed-clearance lake chemistry
Hubbard Brook stream flow
Total disturbance magnitude
Weak response
Forest thinning
Permafrost and snow melting
No change
Post-fire N
Small
Component resistance and resilience
Low
High
Response
Response
Response
Response
Time