



Sensitivity and complacency of sedimentary biogeochemical records to climate-mediated forest disturbances



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ABSTRACT

We provide a synthesis and framework for using lacustrine sedimentary records to study the biogeochemical outcomes of landscape disturbances. Although disturbance regimes can now be effectively reconstructed in sedimentary records, biogeochemical responses to disturbance events are less frequently assessed. Further, there is a lack of consensus on the characteristics of disturbances or ecosystems that would lead to biogeochemical resilience. Both sensitivity (a change in a biogeochemical proxy following a disturbance event relative to a pre-disturbance condition) and complacency (absence of change in a biogeochemical proxy after a disturbance event) have been observed in paleorecords. Here, we discuss the factors that contribute to sensitivity/complacency as well as the short- and long-term biogeochemical effects of terrestrial disturbance agents such as fire and insect outbreaks. We discuss the appropriate strategies for sampling lacustrine sediment cores to assess the biogeochemical outcomes of disturbances and provide a review of the appropriate data scaling techniques for analyzing multiple records in space and time.

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1. Introduction

Increasing temperatures in the lower atmosphere mediate the frequency and severity of forest disturbances, such as wildfire, insect and pathogen outbreaks, drought, and windthrow (Raffa et al., 2008; Pechony and Shindell, 2010; van Mantgem et al., 2013). Disturbances are discrete events in time that reduce biomass and regulate material and energy flow through ecosystems (Pickett and White, 1985). High severity disturbances shift ecosystem structure and function across spatial scales. Potentially, these shifts can provide positive feedbacks to a warming climate system by converting biomass to greenhouse gases, including carbon dioxide (CO₂) and methane (CH₄). For instance, during the 1997 fire season, over 8 million ha of tropical rainforest burned across Indonesia releasing 40% equivalent in CO₂ emissions from all fossil fuel sources during the same year (Page et al., 2002). Recent model projections forecast that temperature-mediated disturbances will increase in severity and frequency during the coming century, which will exacerbate pervasive moisture deficiencies and the legacies of historical land use (Bentz et al., 2010; Williams et al., 2012).

Paleoenvironmental reconstructions provide detailed understanding of past environmental conditions across a range of temporal and spatial scales (Marlon et al., 2012; Salonen et al., 2012). A key research area focuses on understanding how biogeochemical and nutrient stocks at the landscape-scale respond to climate-mediated shifts in disturbance regimes. Information about the biogeochemical outcomes of disturbances can be assessed from geologic archives, namely environmental reconstructions from lacustrine sedimentary records. Sediment-based studies focus on the analysis of proxy data, such as pollen and charcoal, and reveal past vegetation composition and wildfire dynamics within small catchments with minimal inflow. Stable isotopes and elemental concentrations can be used to determine the biogeochemical response of ecosystem disturbances detected by pollen, charcoal, and other macrofossil indicators. Forest disturbances reconstructed at the catchment-scale using lake sediment records is permitted because severe disturbances alter surficial processes, including erosion rates, the spatial pattern of erosion, fluxes in sediment delivery, activating new sediment sources, and augmenting connectivity of transport pathways to the catchment. These processes are influenced by the biotic and abiotic characteristics of the catchment, such as detrital sources, slope, and aspect. Therefore sedimentary records integrate materials and processes that occur during the recovery following a disturbance, which are measured in proxy records as short-term shifts in depositional materials relative to a baseline condition.

Wildfire disturbance events can now be detected reasonably well in paleorecords. The increasing number of high temporal resolution, multiproxy lacustrine records with well-constrained chronologies has made reconstruction of past fire events almost routine and during the last few years, during which paleofire studies have been published from six continents (e.g., Aleman et al., 2013; Fletcher et al., 2014; Higuera et al., 2014; Iglesias et al., 2014; Kuosmanen et al., 2014; Long et al., 2014). These reconstructions are most fruitful in forested landscapes prone to high severity fire events and/or episodic burning, because fires burn significant biomass and decades to centuries elapse between burning episodes (e.g., Clear et al., 2014). In high severity fire regimes, time between fire events permits the study of ecological responses (including biogeochemical outcomes) to the disturbance. For example, a recent study from Colorado USA investigated the impacts of high-severity fires on ecosystem-level biogeochemical processes, including N dynamics (Dunnette et al., 2014). Additionally, advances in charcoal morphometric techniques (Enache and Cumming, 2007) enable the examination of the biogeochemical outcomes of forest vs. grassland fire regimes at ecotonal sites in Wisconsin USA (Morris et al., 2014a).

Reconstructions of fire events and their biogeochemical impacts are important because, frequent and/or high severity disturbances can lead to nutrient limitations that ultimately govern the capability of a landscape to return to its pre-disturbed condition. Yet ecosystem

consequences are rarely examined alongside fire histories, which make it difficult to assess the carbon or nutrient consequences of biomass burning. Despite infrequent evaluation of biogeochemical records in paleoecological studies, longer time scales are essential to understanding ecosystem trajectories during periods of rapid environmental change due to shifting climate and disturbance regimes (McLauchlan et al., 2014). Further, one would not expect all ecosystems to exhibit a biogeochemical response to a disturbance. Specifically, some ecosystems are biogeochemically sensitive to disturbance events while others are unexpectedly complacent. We define *sensitivity* as the measure of change in a biogeochemical property following a disturbance relative to its pre-disturbance level. By contrast, we define *complacency* as an absence of change in a biogeochemical property after a disturbance event (i.e., sensitivity of 0). Quantifying the sensitivity of a biogeochemical property depends upon if and how the signal of biogeochemical change is transmitted from the ecosystem to a given proxy. Thus a biogeochemical response may not be detected after a disturbance event for at least three reasons: (1) the biogeochemical property may truly be complacent; (2) the biogeochemical property may be sensitive, but the signal may not be transmitted to the proxy being measured; or (3) the variable may be sensitive, and the signal transmitted, but the sampling protocol may not be sufficient to detect the signal.

Here, we provide a synthesis and propose a conceptual framework to reconstructing biogeochemical responses to disturbances from lacustrine sedimentary records. This template can be tested with further data acquisition, as it predicts under what conditions a lacustrine sedimentary sequence would (or would not) record a biogeochemical response to a terrestrial disturbance. To sufficiently address disturbance-mediated controls on biogeochemical cycles, paleoecology now requires formalization of the appropriate protocols for site selection, minimum sample resolution, spatial and temporal data scaling methods, and statistical approaches. Specifically, understanding the longer-term drivers and controls on key nutrient stocks, including nitrogen (N), phosphorus (P), sulfur (S), and potassium (K), is a priority question identified by the paleoecological research community (Seddon et al., 2014). To better identify the controls on sensitivity and complacency of sediment-derived biogeochemical records, we address the following questions:

- (1) Under what circumstances do ecosystems exhibit biogeochemical responses to disturbance events?
- (2) How are disturbance signals transmitted to depositional environments?
- (3) What are the appropriate approaches to aggregating biogeochemical data across multiple spatial and temporal scales?

2. When is ecosystem biogeochemistry sensitive to disturbance events?

The sensitivity of a biogeochemical property to disturbance events varies by disturbance agent, disturbance severity (i.e., proportion of vegetation killed), and pre- and post-disturbance vegetation composition and structure (Fig. 1). The biogeochemical consequences of landscape disturbances can either diminish or increase bioavailability of nutrients from an ecosystem. Fire is a well-studied, common depleting disturbance agent, and a keystone ecological process in many landscapes (Bowman et al., 2009). The rate and severity of fires varies greatly over time and across space, which is controlled largely by fuel quantity and moisture, ignition rates, and wind speed, in addition to other local-scale and site-specific factors such as slope and aspect. Non-fire depleting disturbances include outbreaks of phytophagous and/or defoliating insects, plant pathogens, windthrow, and snow avalanches.

2.1. Fire

As high severity burns are required to enhance the ferromagnetic properties of soils or enhanced flux of eroded soils, observational

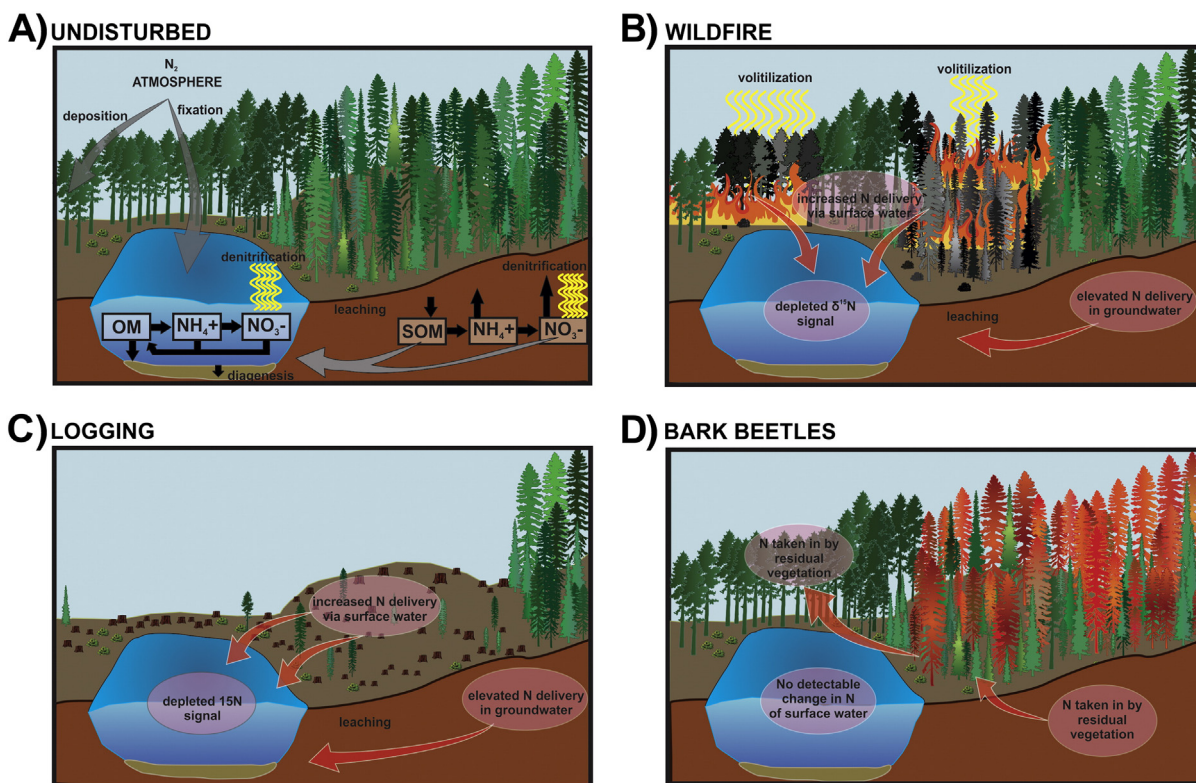


Fig. 1. The assimilation and loss pathways for nitrogen (N) in a coniferous forest during undisturbed and how the signal is transmitted to the sedimentary profile in lake sediments. (A) An undisturbed coniferous forest, (B) high-intensity wildfire, (C) clear-cut timber harvest, and (D) a severe bark beetle outbreak specific to one tree species.

evidence suggests that peaks in magnetic susceptibility records reflect high-severity events within a lake catchment (Whitlock and Millspaugh, 1996; Dunnette et al., 2014). Low severity burns in pine forests, where temperatures range between 200 and 300 °C, promote soil cohesion through the thermal conversion of leaf litter residues to organic cements, a phenomena not observed at sites that burn at high temperatures (>400 °C) (Mataix-Solera and Doerr, 2004). Following high severity burns, erosional delivery of iron-rich minerals to depositional environments should predictably enhance the magnetic susceptibility signal in sediments concomitant with peaks in sedimentary charcoal. By identifying peaks in both the charcoal and magnetic susceptibility profile, it is reasonable to assume that local, high severity fires occurred within a catchment (Whitlock and Millspaugh, 1996; Gedye et al., 2000; Dunnette et al., 2014). Now that more detailed elemental analysis of sedimentary composition is available through a variety of geochemical techniques (e.g., microscanning X-ray Fluorescence, or XRF), it is possible to quantify the elemental constituents in a post-fire, erosional pulse.

From a biogeochemical perspective, the temperature achieved in a given fire will strongly dictate biogeochemical impacts. In general, this should be proportional to fire line intensity, the rate of energy release along a flaming front (i.e., kW/m). At temperatures below ~500 °C, terrestrial nutrient pools are not greatly altered (Binkley et al., 1992). However, lab experiments indicate that N and S are can be volatilized between 200 and 300 °C while S volatilizes at 300 °C, P and K at 750 °C, Mg at 1100 °C, and Ca at 1500 °C (Gillon et al., 1995). In general, temperatures above 500 °C will modify the abundance and bioavailable form of nutrients through volatilization and conversion of N from organic to inorganic forms, namely ammonium (NH_4^+) and nitrate (NO_3^-). While combustion converts organic N in plant tissues to NH_4^+ , which returns to the landscape as ash, NO_3^- production lags fire events because post-fire NO_3^- is derived from nitrification of NH_4^+ (Covington and Sackett, 1992). As plants recolonize burned areas, both NH_4^+ and NO_3^- are equally bioavailable; however, their fates, if unassimilated by plants or microbes, differ in that NH_4^+ is more commonly retained in the soil

matrix while NO_3^- is leached, either downward into the soil profile or exported via surface water (Raison, 1979). Therefore, in the analysis of lake sediment records, transmission of a biogeochemical signal depends upon erosion and surface and ground water delivery of inorganic N to (and from) the catchment. Ash-fall onto lake surfaces is also an important delivery pathway. Because low intensity fires affect terrestrial N pools less than high intensity fires, the sensitivity of lake sediments records to disturbance-caused nutrient fluxes is biased towards local, high intensity burns. This is important to note because several studies observed long-distance transport of charcoal and ash (e.g., Pisaric, 2002) and fire history records should be screened against the detection of extra-local fire disturbances (see Section 4). Here we define a local fire as one occurring within a watershed boundary and within c. 500–1000 m of a lake (Fig. 2).

The bioavailability of elements may increase following fires, due to ash and charcoal deposition. While particulate deposition is locally abundant at most burned sites, a fraction of potential nutrient availability is lost when ash and charcoal become entrained into the smoke plume, are deposited elsewhere, and become locally unavailable. Observations from a combination of laboratory and field burns suggests that nutrient losses increase linearly in proportion to the amount of biomass combusted at progressively higher temperature intervals (Raison et al., 1985). Potential losses of these elements from ecosystems through surficial transport into lakes suggest that elemental scanning techniques, such as XRF (see below), may be used to help understand how post-fire erosional events may deplete key nutrients from ecosystems. For example, leaching and volatilization of P can occur at ~750 °C (Gillon et al., 1995). Therefore, even high intensity fires may not impact the availability, abundance, and form of P to re-colonizing plants. This interpretation could be refined by accounting for connectivity between the catchment and the lake, and for the relationship between ecosystem recovery and landscape erosion. Durán et al. (2008) reports short-term, post-fire increases in the bioavailability of P, which was followed by steep declines in P abundance as a result of erosional processes. The

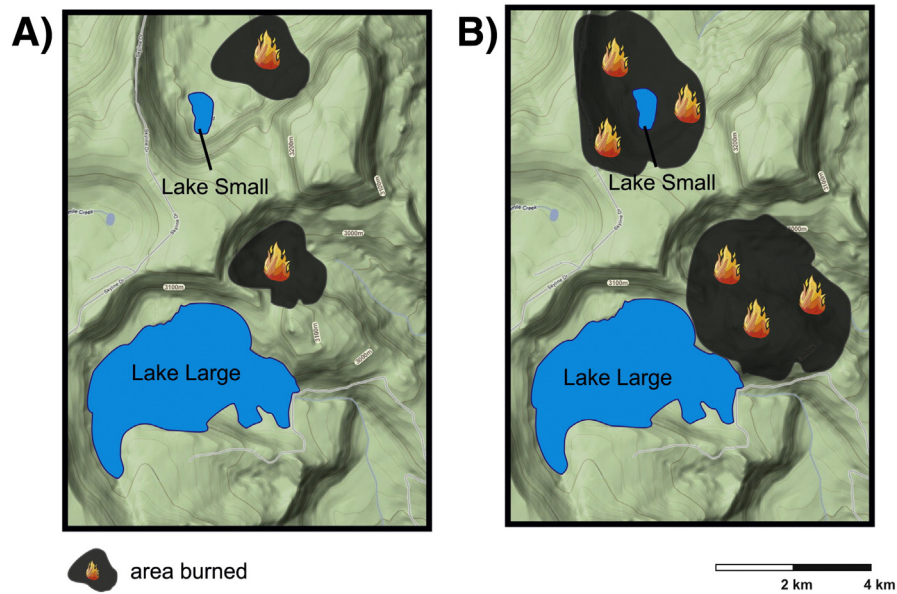


Fig. 2. Conceptual diagram depicting the importance of catchment size and proximity to disturbance when investigating a biogeochemical response: (A) two scenarios with low probability for detection because the disturbed area is outside of the catchment; and (B) an ideal scenario for detection where spatially extensive disturbances occur within the catchment and in close proximity to the lake.

findings of Durán et al. (2008) suggest that episodic increases in P abundance found in lake sediments may be indicative of post-fire erosional pulses.

For lake sediment-based reconstructions, the nutrients lost through volatilization pathways (i.e., non-particulate) are difficult to measure directly, whereas nutrient and elements brought to a catchment via surface erosion or delivered aerially via ash would transmit as disturbance signals. Ash from fire can be deposited either through dry fallout or during rainfall (Raison et al., 1985). Nutrient losses through volatilization may be inferred indirectly if decreasing values in a sedimentary record can be interpreted as a proxy for increasing biotic demand relative to terrestrial availability. Only during high-intensity fires are soil mineral components converted, where clays and organic particles are either volatilized or altered through dehydroxylation and produce elevated concentrations of ferromagnetic minerals. For example, using X-ray Diffraction (XRD) to study the soil impacts of slash-and-burn treatments, Ketterings et al. (2000) determined that when burn temperatures exceed 600 °C, the weakly magnetic Fe-oxide goethite was converted to the highly magnetic, Fe-rich mineral maghemite. Maghemite-rich soil layers and paleosols are generally interpreted to result from high intensity fires and are detected by their strong magnetic enhancement (Crockford and Willett, 2001). Though surface heating in both human-caused and natural fires may be intense, only the upper-most unit of the A-horizon (1–10 cm) of the soil profile is commonly affected.

2.2. Non-fire and biotic disturbances

Non-fire and biotic disturbances are generally less represented in sediment-based environmental reconstructions compared to wildfires (Waller, 2013), mainly because wildfire produces charcoal and erosive pulses that can be directly linked with the disturbance event. In contrast, non-fire disturbances (e.g., insect outbreaks) are less likely to leave direct evidence in lake sediments, and are not known to increase sediment transport. Therefore, they must be reconstructed through secondary or derivative proxies, such as pollen, insect macrofossils, or biogeochemical and particulate measures (Anderson et al., 2010; Morris et al., 2013, 2014b; Morris and Brunelle, 2012). Nevertheless, non-fire disturbances are of considerable economic and ecological importance, particularly in North America and Europe. For example, in

western North America, the spatial extent and economic losses resulting from non-fire disturbances equals, and sometimes exceeds, the annual impacts of wildfire (Baker and Veblen, 1990; Logan and Powell, 2001). Despite challenges in reconstructing non-fire disturbances, the impacts of these disturbances have considerable implications for biogeochemical cycling.

A key difference between non-fire and fire disturbance types is that during non-fire disturbances, vegetation mortality is often species or size-class specific. For instance, only conifers of sufficient maturity to achieve canopy dominance are toppled in windthrow events (Kulakowski and Veblen, 2002), and those of cambial thickness adequate to support brood production are infested by bark beetles (Raffa et al., 2008). Pathogens and insects are often host-specific and affect only one demographic of an ecosystem. For example, during spruce beetle (*Dendroctonus rufipennis*) outbreaks in Rocky Mountain ecosystems, only Engelmann spruce (*Picea engelmannii*) of suitable diameter (>10 cm) are colonized and killed (Schmid and Frye, 1977). The loss of canopy-dominant spruce invigorates sub-canopy subalpine fir (*Abies lasiocarpa*) and other understory taxa, which experience a growth release from increased availability of nutrients, sunlight, and moisture (Veblen et al., 1994).

Recent research suggests that the biogeochemical signals from non-fire disturbances are weaker than expected from theory. Observations from high severity bark beetle outbreaks (>90% host mortality) in western North America indicate that %N and NO_3^- levels in lake sediments and surface water do not increase following outbreaks (Morris et al., 2013; Rhoades et al., 2013), despite detection of elevated levels of total N and P in surficial and detrital soil layers (Clow et al., 2011). Elevated nutrient concentrations in soils probably results from increased deposition and decomposition of organic material as canopy plant matter drops to the forest floor (i.e., needlefall). Using chronosequences, Huber (2005) investigated the biogeochemical outcomes of a spruce bark beetle (*Ips typographus*) infestation of Norway spruce (*Picea abies*) and found evidence for persistent, elevated nitrate export until five years post-outbreak. A study examining soils in mountain pine beetle (*Dendroctonus ponderosae*) infested ponderosa pine (*Pinus ponderosa*) stands indicates lower C:N mass ratios attributable to needlefall (Morehouse et al., 2008). Post-outbreak conditions in beetle-affected forests differ from forests affected by fire, primarily

because of the persistence of live understory vegetation. Live vegetation mutes any signals from landscape erosion, or other alterations in the connectivity between the catchment and the lake.

The findings of Clow et al. (2011) are similar to those of Morehouse et al. (2008), which together suggest that increased mineralized N in the decomposing detrital layer is subsequently lost through nitrification. These authors also observed higher nitrification rates and increased NH_4^+ levels in infested stands versus un-attacked stands. Yet Morehouse et al. (2008) found no evidence of changes to soil respiration rates between attacked and un-attacked stands, although this study was conducted (only) over a single growing season. A potential explanation is that due to the multi-decadal to centennial-scale recurrence interval of beetle outbreaks in coniferous forests (e.g., Sherriff et al., 2011), biotic demand of residual vegetation for N is sufficient to readily assimilate available N as it is released from dead vegetation. Though this hypothesis has not been explicitly tested, it could potentially be examined by analyzing stable N isotopes ($\delta^{15}\text{N}$) in the growth rings of residual subcanopy trees (e.g., subalpine fir during spruce beetle outbreaks) for evidence of increased nutrient assimilation. This hypothesis could also help evaluate the relative importance of ground- and surface-water in transporting N from the catchment to the lake environment.

2.3. The biogeochemical signal of disturbances

High severity disturbances are expected to transmit a biogeochemical signal to a catchment as a result of increased export of nutrients and base cations in surface water and increased delivery of terrestrial organic material via erosion to depositional environments. The post-disturbance fluxes of N and P in solute forms are relatively well-studied when compared to other elements. For example, elevated stream nitrate is observed in response to several ecosystem conditions which include: (1) conditions of N saturation (Aber et al., 2003); (2) deposition of high levels of N from the atmosphere and/or point-source pollution; and (3) following severe disturbances (Aber et al., 2002).

2.4. Biogeochemical processes after fire disturbances

Even within landscapes that experience widespread, high severity wildfires vegetation mortality is often spatially heterogeneous, due to variability in vegetation composition and structure and fire behavior. For example, during the fire season of 1988, at the landscape-scale Yellowstone National Park experienced surprisingly variable levels of mortality despite the historically unprecedented nature of the fire season (Christensen et al., 1989; Turner et al., 1994). Therefore, when scaling disturbances across space, fine-scale variations in fire intensity are likely to yield contrasting levels of vegetation mortality across what may otherwise appear to be uniform impacts when viewed at the landscape scale. Similarly, low intensity fires primarily consume herbaceous fuels, shrubs, and saplings, leaving mature thick-barked trees relatively unaffected (e.g., ponderosa pine). Both high intensity crown fires and low intensity surface fires cause reductions in living biomass and decrease the delivery of terrestrial carbon to lake sediments. A suppressed C signal (by mass) may persist for several decades following a disturbance event in lake sediments (Dunnette et al., 2014).

2.5. Biogeochemical processes after non-fire disturbances

Non-fire disturbances increase mortality rates of primary producers and therefore contribute organic matter to the surface duff and detrital layers of the forest floor, which affects microbial decomposition rates and belowground processes. To what degree subsurface microbial processes are altered subsequent to cessation of evapotranspiration and gas exchange has yet to be systematically evaluated for most non-fire disturbances. Further, many forest insects have symbiotic associations with fungal pathogens that interact with biogeochemical processes

during and after host tree mortality. For example, some bark beetles (*Dendroctonus* spp.) introduce fungal spores into the cambial tissue of host trees, which aide in developing pupae in larval chambers by 'pre-treating' sap wood to enhance nutrition (Six and Bentz, 2003). Blue stain fungi (*Ophiostoma* spp.; *Grosmannia clavigera*) concentrate N from the host tree's cambium as the fungus develops mycelium upon which beetle larva feed. These fungi are widespread throughout the boles of infested trees. To what extent blue stain fungi alter nutrient cycling of infested timber and subsequent decomposition is unknown, but are potentially important drivers of biogeochemical cycling in bark beetle-affected forests over decadal timescales.

In the deciduous forests of eastern North America, elevated nitrogen loads (TDN, nitrate) have been recorded in surface water following clear cuts and outbreaks of defoliating insects such as gypsy moth (*Lymantria dispar*) and fall canker worm (*Alsophila pomataria*) (Swank et al., 1981; Cowles et al., 2014). Yet some studies record no significant N losses following disturbances in either deciduous or coniferous forest types. In general, this complacency is attributed to a 'tight' nitrogen cycle, where free N is assimilated readily by residual vegetation (e.g., Rhoades et al., 2013). A tight N cycle may interact with biological control via several pathways including compensatory uptake by undisturbed vegetation, slowing of the N cycle, low rates of atmospheric N deposition, and low bioavailability of soil N (Aber et al., 1983). Therefore in disturbances where bioavailability of N limits plant growth, it is unlikely that N will be released from the terrestrial system and 'captured' by surface water. In contrast, in settings where N stocks are relative high and/or the disturbance eliminates vegetation (e.g., clear-cutting and herbicide), substantial quantities of N are leached from the landscape via surface water and therefore have a greater chance of transmitting a disturbance signal through a catchment (Rhoades et al., 2013).

A pulse of mobile terrestrial organic material following non-fire disturbances could provide a detectable biogeochemical signal relative to pre-disturbed conditions. Changes in N cycling are expected if microbial decomposition rates accelerate in response to increases in detrital material and/or increases of nitrate concentrations in surface water and/or mobilization of organic particulates into depositional environments. A number of published studies suggest that following mortality of the canopy trees and cessation of evapotranspiration, increases in available moisture are experienced in watersheds through rising water tables and localized paludification (Huber, 2005; Clow et al., 2011), although recent work suggests that increases in evaporation rates due to loss of canopy shading may counterbalance moisture surpluses (Biederman et al., 2014). Huber (2005) proposes that in regions of high average annual precipitation, nitrate concentrations in surface water would remain generally low following outbreaks as a result of dilution. Other authors propose that nitrate levels in surface water remain low because increases in residual vegetation would increase uptake of available N would diminish nitrate leaching following outbreaks (Parsons et al., 1994).

3. How are disturbance signals transmitted to depositional environments?

3.1. Taphonomy

The taphonomy and depositional pathway of elemental compounds used for assessing biogeochemical change differ from terrestrial proxies common to paleoecological analysis (e.g., pollen, charcoal). Terrestrial proxies are transmitted to depositional environments by airborne deposition and surficial processes, including surface water and aeolian transport. In contrast, geochemical indicators (including stable isotopes of C and N) integrate terrestrial and aquatic processes and are delivered to catchments through ground and surface water pathways. Isotopes reflect in-lake conditions and groundwater fluxes, as well as the composition of terrestrial organic material. Because of their integrative and explanatory power, stable isotopes are becoming increasingly common in

paleoecological investigations ranging from site studies (e.g., Jeffers et al., 2011, 2012) to multi-site syntheses (Wolfe et al., 2003). Frequently, isotopic and elemental data are presented alongside other terrestrial proxies as supporting information to help interpret past changes in vegetation composition, climate, hydrologic conditions, and net primary productivity, often without acknowledging the fundamental differences in depositional pathways and processes when interpreting these different data sources. Further, disturbances often produce brief increases in erosion and signal detection focuses on this short-term increase, or recovery period, relative to baseline conditions.

3.2. Proxy selection and supporting information

Several proxies preserved in lacustrine sediments can provide information on nutrient availability in the aquatic and terrestrial environment, facilitating the reconstruction of biogeochemical response to a disturbance. It is becoming relatively common to measure carbon concentrations (%C), nitrogen concentrations (%N), and stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) from dried bulk sediment samples by combustion and mass spectrometry (e.g., McLauchlan et al., 2013). Standards are calibrated to Vienna Pee Dee Belemnite ($\delta^{13}\text{C}$) and atmospheric N_2 gas ($\delta^{15}\text{N}$). The presence of inorganic carbon must be evaluated throughout the core, potentially leading to the need for carbonate (CaCO_3) removal or treatment prior to isotopic analysis so that the organic C signal can be isolated. Sediment $\delta^{13}\text{C}_{\text{org}}$ is often correlated with lake productivity. The ratio of organic C to total N in bulk sediment, expressed as an atomic mass ratio, can be used to infer the relative contributions of terrestrial vs. aquatic organic matter to lake sediments (Kaushal and Binford, 1999). Disturbances can cause changes to source and delivery of C and N to lacustrine sediments, such as remobilization of stored C in catchment soils or peat.

Sediment $\delta^{15}\text{N}$ integrates a variety of nutrient cycling processes in terrestrial and aquatic ecosystems, especially reflecting the strongly fractionating process of gaseous loss of inorganic N to the atmosphere through denitrification. The recurrence, severity, and/or prolonged cessation of forest disturbances can affect the $\delta^{15}\text{N}$ values of bulk sedimentary organic matter (McLauchlan et al., 2007; Dunnette et al., 2014). In the absence of disturbance, such as a wildfire or bark beetle outbreaks, the isotopic composition of sediments is controlled by N availability in the integrated terrestrial–aquatic system, including plants on the landscape and primary producers in the lake. When N supply is high relative to biotic demand, the remaining N is enriched in ^{15}N . This is due, ultimately, to the fractionating losses of N in gaseous forms in soils, litter layers, and vegetation, such as denitrification, where ^{14}N is preferentially lost (Högberg, 1997). Conversely, when N supply is low relative to biotic demand, ecosystem pools are depleted in ^{15}N . This is because under low N availability scenarios, plant and microbial uptake minimizes N losses, thereby reducing the $\delta^{15}\text{N}$ values of detrital and other terrestrially-derived organic materials (Martinelli et al., 1999). Fire also affects $\delta^{15}\text{N}$ levels through volatilization of N during combustion of organic material. Because of the kinetic fractionation when plant tissues are exposed to temperatures $>180^\circ\text{C}$, fires can leave charred residuals that are enriched in ^{15}N (Turekian et al., 1998).

Sampling procedures for this suite of proxies (%C, %N, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) have not been standardized, but in general, continuous subsampling is desirable to investigate the outcomes of disturbance events. For example, the detection of a N response to high severity fires in the catchment of Chickaree Lake, Colorado, was only possible because of the high temporal resolution sampling of sedimentary $\delta^{15}\text{N}$ along with high temporal resolution charcoal data (Dunnette et al., 2014). The high sedimentation rate of this lake coupled with a well-developed age–depth model permitted a relatively high, continuous sampling interval with an average of 4 years per sample, targeted around high-severity fires that likely burned within the watershed. However, in other sampling scenarios for this dataset, when the temporal resolution is reduced to 25 or 50 years, the link between the fire events and the $\delta^{15}\text{N}$ response

is either undetectable or greatly simplified (Fig. 3). At this site, high severity fires were followed by immediate increased sedimentary $\delta^{15}\text{N}$ values for ~two decades, and then decreased $\delta^{15}\text{N}$ values for ~50 years after fire events. In general, lower resolution sampling of biogeochemical proxies, whether discrete or continuous, minimizes the likelihood of detecting the presence or nature of distinct biogeochemical responses (Fig. 3), and may even limit the ability to describe general patterns of N availability through changes in disturbance regimes (e.g., Morris et al., 2014a).

Compound-specific organic geochemistry may enable identification of molecules that contain specialized information about a certain type of nutrient condition. For example, phytate and inositol-phosphates have been used to identify bioavailable forms of phosphorus in sedimentary records (Turner et al., 2002; Turner and Weckström, 2008). Another example of a promising new biogeochemical proxy is the purification of chlorin—chlorophyll *a* and its degradative products pheophytin *a* and pheophorbide *a*—from bulk sediment to compare the temporal trends in algal- $\delta^{15}\text{N}$ to bulk sedimentary $\delta^{15}\text{N}$ at Sky Pond, Colorado (Enders et al., 2008). These proxies are useful for assessing post-disturbance changes to catchment hydrology and nutrient delivery, but because they are quite specialized and expensive, they have received limited use to date.

Detection of biogeochemical responses to disturbance events is also enabled by the increasingly frequent use of microscanning XRF technology on sediment cores. This technology provides high-resolution data of elemental counts for a variety of elements ranging from Mg to U on the periodic table, potentially providing sub-millimeter scans of core sections (Croudace et al., 2006). XRF provides value in measuring lithological elements, including Ti, K, Zr, Rb, Sr, Y, Si, and Al, and it can be used to identify volcanic disturbance events through the geochemical analysis of tephra. However, XRF has not yet been used to quantify biogeochemical responses to disturbance; this method could be used to assess disturbance-mediated changes in the bioavailability of nutrients such as P, K, S, and Ca. For elements that exhibit responses to disturbances such as increased hydrologic loss, association with clastic inputs, or altered terrestrial cycling due to changes in plant demand, XRF methods could provide the high-resolution data necessary to quantify both disturbance and biogeochemical response. The application of XRF to assessing disturbance would benefit from formalized standardization procedures to enable flux calculations, including standard guidelines for scanning, standardization for variations in organic concentration and water content in sediment cores, and data treatment methods that allow comparisons among and within cores.

In addition to these biogeochemical proxies, it is helpful to acquire two types of additional information for robust interpretation of the sedimentary record. First, information about aquatic community composition can be helpful for understanding terrestrial–aquatic linkages over the duration of the sequence. Although the techniques are specialized, there are several options, including algal pigments (Leavitt et al., 1994) and diatom assemblages (Fritz, 2007). Second, information about the source of the sediment can help partition terrestrial and lacustrine productivity, and provide information about climate conditions relevant to understanding ecosystem response. Options here include the relatively accessible lithological core description (Schnurrenberger et al., 2002), as well as mineral identification through XRD (Grimm et al., 2011), sophisticated magnetic measurements (Lascu et al., 2010), and calculations using mixing models (Kaushal and Binford, 1999). Ultimately, utilizing a multiproxy approach is essential to compare all datastreams in an integrated framework.

4. Inferring sensitivity and complacency in the paleoecological record

Even if all of the previous conditions have been met—that is, a site has been chosen carefully, disturbance events alter biogeochemical processes, the signals are transmitted to a sedimentary archive, and an

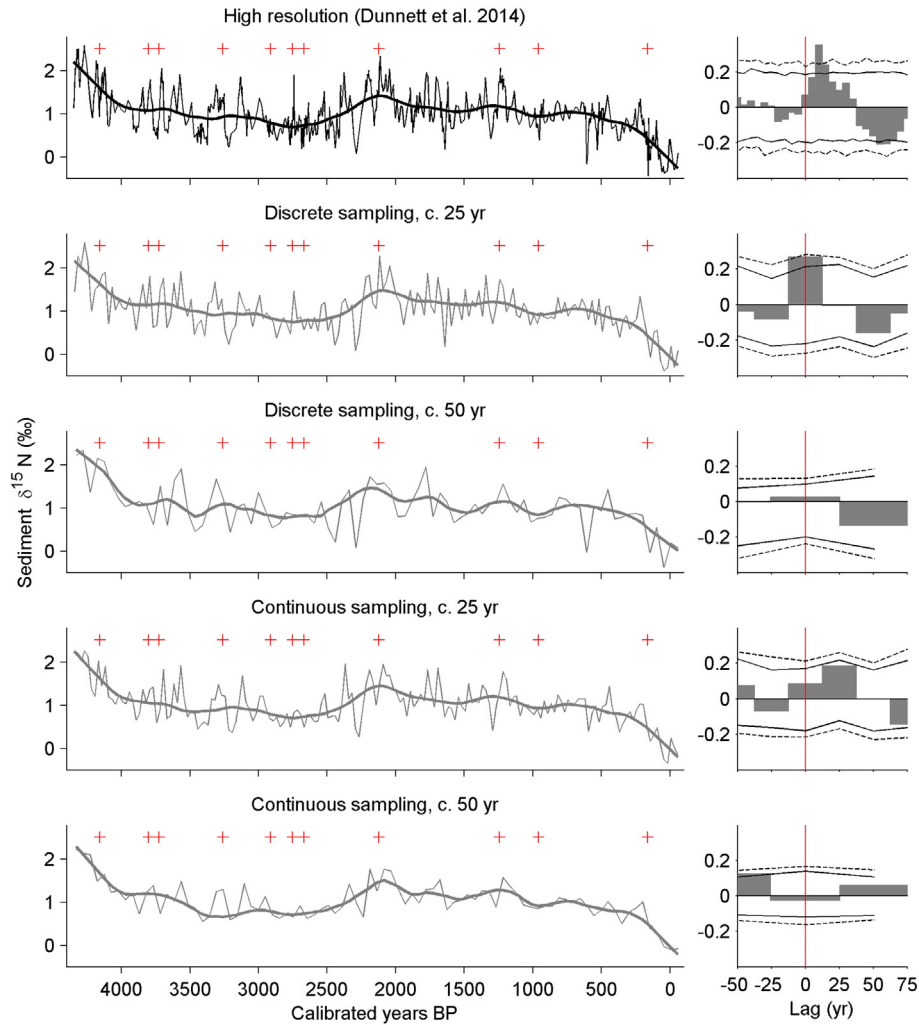


Fig. 3. Impacts of changing sampling resolution for detecting disturbance signatures via superposed epoch analysis (SEA). Top row: $\delta^{15}\text{N}$ record and SEA published by Dunnett et al. (2014, Figs. 4, 5), in its native resolution (median = 4 yr per sample). Red “+” indicate high-severity catchment fires, the events used in the SEA. Rows 2–4: the same record resample at c. 25- and c. 50-yr resolutions, by selecting individual samples (i.e., “discrete sampling”) or averaging within time windows (i.e., “continuous sampling”). These bottom four rows represent potential results if the biogeochemical proxies were not sampled at high resolution: in all cases the presence of a significant response and/or the nature of the response is significantly altered from the original record. Horizontal lines in the SEA (second column) represent the 95% and 99% confidence intervals, following methods from Dunnett et al. (2014). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

appropriate proxy is measured—there are still situations where this sensitivity might not be detected by a researcher. Thus, we conducted a more thorough examination of the conditions under which a complacent dataset might arise and when a dataset is truly sensitive. Complacency is inferred by failing to reject the null hypothesis that biogeochemical variability in a record is no different after disturbance events, relative to intervals without disturbance events. If an ecosystem or lake is truly insensitive to the disturbance event, then this inference is correct. Alternatively, if the disturbance events impact the ecosystem and those impacts are truly reflected in the sediment record, then this inference is an example of Type II error, β : failing to reject the null hypothesis when it is actually false.

A key challenge in inferring the sensitivity or complacency of an ecosystem property to disturbance events is understanding the probability of detecting a disturbance signature, should one truly exist. This is the definition of statistical power: the probability of correctly rejecting the null hypothesis ($1-\beta$, Zar, 1999). In a paleoecological record, there are three key properties that will determine the statistical power in scenarios where a disturbance truly leaves a signature in a sediment record: (1) the sensitivity of the sediment record to the disturbance event (“sensitivity”), (2) the duration of the impact of the event in the sediment record (“event duration”) relative to the resolution of the record,

and (3) the number of disturbance events used to characterize the disturbance signature. Inferences into sensitivity or complacency may be implicit, if the analysis is qualitative, or explicit, if the analysis uses a formal statistical test (e.g., superposed epoch analysis, as in Dunnett et al., 2014).

To illustrate the consequences of these three variables on the ability to detect change after disturbance events, we developed simulated records representing 60 different scenarios and applied superposed epoch analysis (SEA) to formally evaluate the null hypothesis that variability after disturbance events does not differ from chance alone (Fig. 4). Our simulated records represent the type of random variability we would expect to find in a number of proxies in a lake sediment record. Specifically, each record was created by generating a red noise time series, with samples originating from a normal distribution with mean 0 and standard deviation 1, and with first-order autocorrelation of 0.4. We then added in n disturbance events to this time series, based on a uniform random distribution. After each simulated disturbance event, we modified the time series by adding in a positive value, representing the simulated disturbance signature. The magnitude and duration of this disturbance signature varied based on “sensitivity” and “duration” parameters. A sensitivity of 0 indicates a lack of response to the disturbance event (i.e., complacency), whereas increasing

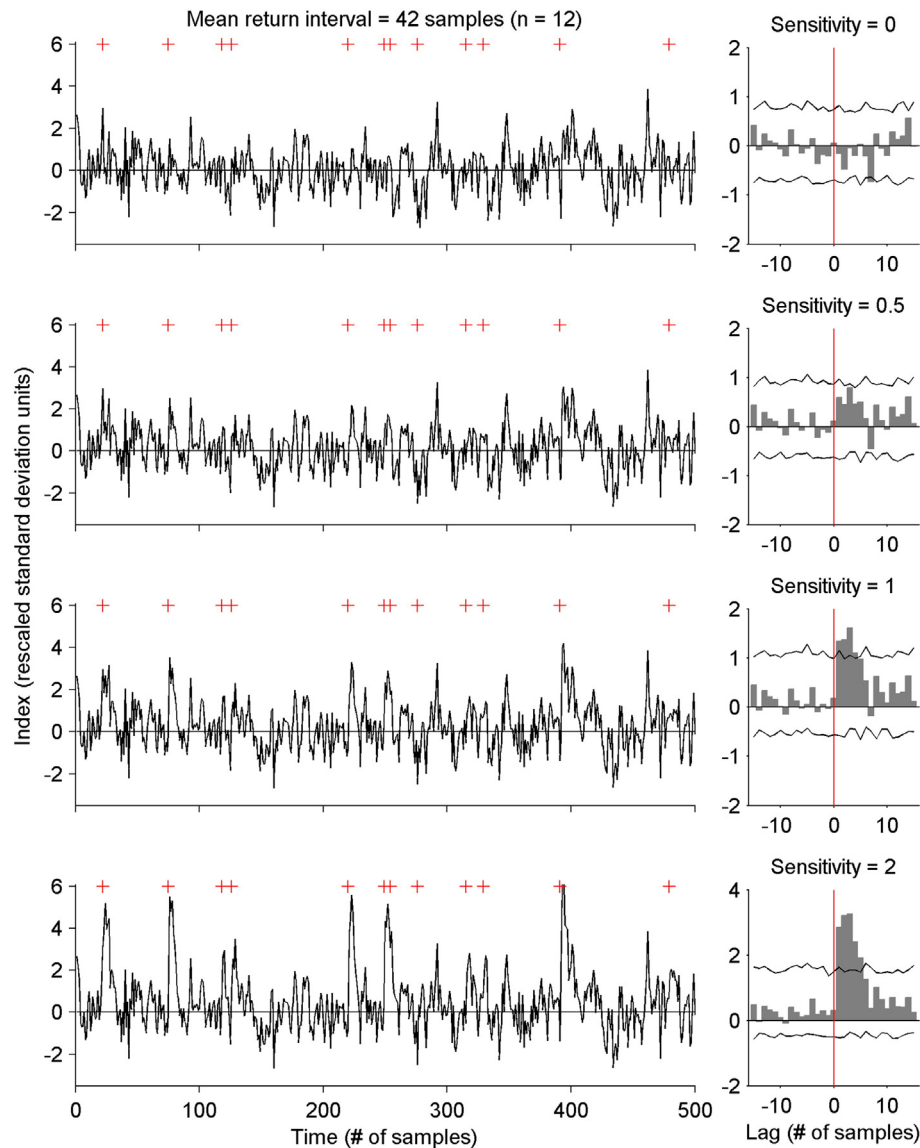


Fig. 4. Simulated records and disturbance events, and superposed epoch analysis (SEA) with varying levels of sensitivity. The simulated represents on realization of a red noise time series with 12 disturbance events, sensitivity values varying from 0 to 2, and event duration of 8 samples. When sensitivity equals 0, the SEA correctly indicates that the response to the disturbance events is not different from random. As sensitivity increases, values after disturbance events increase accordingly (left column), as do the composite response series in the SEA (right column). In this simulation the scenario with sensitivity = 0.5 (row 2) represents Type II error: the SEA failed to detect what was a real signature added to the time series. The other three scenarios were correctly identified by the SEA.

sensitivity represents increasingly large responses to a disturbance event. For example, a sensitivity of 1 indicates a one standard deviation increase in the simulated response variable after the disturbance event. The duration of this response was quantified by the number of samples accounting for 95% of the disturbance impact (i.e., 8, 14, or 32 samples). We present time in units of samples, not years, to make our inferences generalizable. To compare or apply these results to an empirical record, multiply the number of samples by the average sample resolution in the record. For example, if the average sample resolution in an empirical record is 10 years, then the time series in Fig. 4 represents 5000 years, and the disturbance signatures underlying these records last for 80 years.

The simulated records illustrate the intuitive result that the ability to detect disturbance signatures increases with the sensitivity of a sediment record (Fig. 4). Because a disturbance signature occurs in the context of “background” variability, the more sensitive a record is to the disturbance event, the greater the impact relative to background variability and the greater the chance of detecting the impact. In essence, the sensitivity of a record dictates the “effect size” in the disturbance signature, one determinant of statistical power (Zar, 1999). In

addition to effect size, the total number of events sampled and the event duration also directly impact statistical power. To explore the nature of these parameters, we tested the ability of the SEA to detect a biogeochemical change while changing the number of events considered and event duration (Fig. 5). For any given sensitivity, statistical power increases with the number of events sampled and with event duration. Event duration effectively increases sample size, because the signature of the event is spread across increasingly more samples. Because event duration is represented as number of samples, it is thus sensitive to the absolute duration of the event *and* the sample resolution of the record.

These results highlight the importance of sample size (i.e., number of events sampled) and sample resolution (i.e., years per sample) to infer complacency confidently in the paleorecord. Disturbance signatures in records with low sensitivity or short event durations can easily go undetected. For example, in our simulations when only six disturbance events were sampled, the chance of detecting a disturbance signature in a record with low sensitivity (<0.5) was less than 60%, and the chances were less than 40% if the event duration was shorter

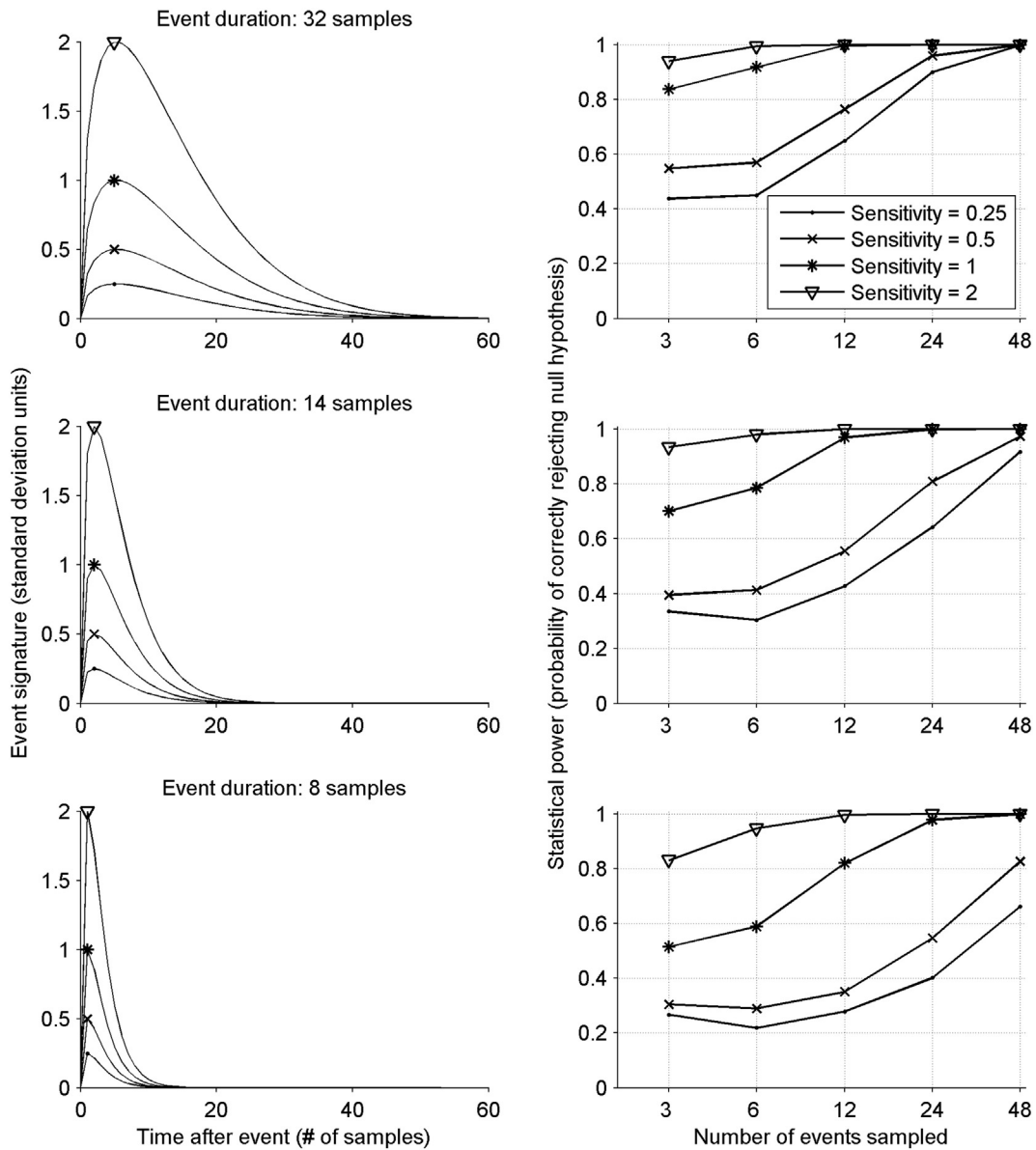


Fig. 5. Power analysis for superposed epoch analysis (SEA) for 60 simulated scenarios, each with 1000 realizations. The underlying event signature is represented in column 1, with the magnitude of the response reflecting “sensitivity,” expressed in standard deviation units relative to the original red noise time series (i.e., row 1 in Fig. 4). The duration of the event decreases from rows 1–3. Column 2 illustrates statistical power as a function of the number of events included in the SEA, and four different levels of sensitivity. Statistical power increases with the number of events sampled, the sensitivity of the underlying record, and the duration of the event.

(i.e., eight samples; Fig. 5). Therefore, if the true sensitivity of the system to a disturbance event is low, then one must sample numerous events (e.g., >30) to be able to detect this low level of sensitivity. Conversely, if no signal is detected in an analysis, it is critical to consider the statistical power of the test. When sensitivity or sample size is low, a lack of response does not necessarily equate to complacency in ecosystem or sediment-generating processes.

5. What are the appropriate approaches to spatial and temporal compositing of biogeochemical data?

5.1. Site scale

Site selection has long been a focus of paleoecology, with choice of lake basins aligned with characteristics that are compatible with the aims of the study. To address disturbance-related topics, lakes with small surface areas (<15 ha) and minimal in- and outflow surface water are generally desirable. It is also ideal that the disturbance process

of interest has occurred in close proximity to the lake, or at least within the catchment during the historical period (Fig. 2). This offers an opportunity to calibrate a disturbance event of known size and severity to interpret events that occurred prior to the historical period. Other important site characteristics that would potentially affect the biogeochemical record of sediments—and therefore may preclude a site from analysis—are impoundments and diversions, as well as agricultural byproducts including fish stocking, livestock grazing, and application of fertilizers.

A second issue is establishment of an accurate chronology (see below). Even with an extremely well-dated sediment core, it is common that different proxies are sampled at different temporal resolutions. When using the same core to reconstruct disturbance events and biogeochemical responses, especially if there are temporal lags between events, it is essential to develop a sampling strategy for multiple proxies. The main decision is whether all proxies are required to be sampled for the same (i.e., highest) resolution. For example, a lake sediment core is often subsampled at varying intervals for different proxy analyses.

The sampling resolution of pollen tends to be low and discontinuous while charcoal sampling intervals tend to be high resolution and continuous by comparison. During the analysis phase, one way to overcome disparate temporal resolution is to use an interpolation strategy. This approach also helps to overcome changes in sedimentation rates, common in many cores that cause equally spaced samples along a core to represent different units of time. Almost all time series analyses require evenly-spaced data in time, and analyzing these data requires some type of interpolation or resampling.

The final type of consideration for a single-site analysis is the statistical method used to assess biogeochemical response to disturbance. In addition to the SEA method described previously (e.g., Colombaroli and Gavin, 2010; Dunnette et al., 2014), there are other correlation approaches that formally test the relationship of proxies in sediment records. Fletcher et al. (2014) utilized a cross-correlation approach to analyze their multi-proxy dataset and fire events (see also Tinner et al., 1999, 2005). Following Green (1981), Fletcher et al.'s approach centers on 'binning' samples into equally spaced time intervals, which is useful for assessing lags in response variables to disturbances. This approach helps to overcome changes in sedimentation rates, compaction and poorly consolidated upper sedimentary layers which all result in unequal temporal resolution among samples analyzed at regular intervals. An additional advantage to this approach is that it overcomes uncertainty in age–depth chronologies. Binning of proxy data facilitates detection of long-term ecological response to wildfire disturbances and facilitates the comparison of biogeochemical data to other sedimentary proxies, such as pollen, that were analyzed at dissimilar sampling intervals (Fletcher et al., 2014).

5.2. Regional scale

Major advances in the field of geochronology have greatly improved the chronological control of most lacustrine sedimentary records, including AMS methods that provide high-precision dates, affordability and thus the use of more dates in a chronology, and quantitative methods to account for age uncertainty. However, two persistent limitations are: (1) sediment sampling and analysis often occur prior to the establishment of a chronology, so sampling must therefore be based on depth, and (2) lake sediment records typically have non-constant sedimentation rates. Further, disturbance events can actually affect sedimentation rates through changes in erosion rates and delivery of sediment to the basin (Colombaroli and Gavin, 2010). Well-constrained chronologies become essential when compiling records across sites or when comparing disturbance events across a region for potential synchronicity (Blaauw et al., 2010). For many types of syntheses, chronologies must be recalculated to enable these comparisons.

One example of assessing a regional biogeochemical response to disturbance is from western North America. Morris et al. (2013) examined the biogeochemical consequences of bark beetle disturbances from a network of six sites across northern Colorado Plateau. Engelmann spruce forests above 3000 m in elevation were severely impacted (>90% mortality) by spruce beetle during the 1990s (Dymerski et al., 2001; DeRose and Long, 2007). The lakes selected in this study had documented recent spruce beetle outbreaks, minimal surface water inflow/outflow, absence of man-made impoundments, no known wildfire activity during the 20th century, and no history logging activities to remove beetle-killed trees (Morris et al., 2013). The ratio of host to non-host pollen abundance (i.e., spruce–fir ratio) was used to identify the stratigraphic signature of the outbreaks, and then these sediments were analyzed for elemental N and isotopic $\delta^{15}\text{N}$ data to assess the biogeochemical impacts of the beetle disturbances. The dataset was tested for change from pre-outbreak to outbreak conditions using a generalized linear mixed model (GLMM) to determine whether a significant biogeochemical change had occurred. The GLMM mixed model approach assessed cumulative change in the isotopic, magnetic susceptibility, and loss-on-ignition data across the six sites, in all cases these

proxies were complacent to beetle outbreaks. This approach may be suitable for determining how robust a response variable is to a disturbance across sites at regional scales (Fig. 6).

5.3. Continental-scale

To our knowledge, there have not been any continental-scale syntheses of event-response data; rather syntheses at these scales have focused on identifying coherent patterns across multiple records. Studies that examine continental-scale processes typically employ a single approach to assess if several sites are exhibiting a temporally synchronous biogeochemical response to a driver acting over a large spatial extent. The driver is often not reconstructed in detail, or it is assumed to be climate. Testing for temporal synchrony in events between single sites is relatively straightforward (Gavin et al., 2006). Testing for temporal synchrony among several sites can be accomplished via an iterative approach using Ripley's K function (Gavin et al., 2006) over several proximal sites (e.g., Courtney Mustaphi and Pisarcic, 2013) or a hierarchical Bayesian modeling framework (Holtgrieve et al., 2011). The latter paper identified a synchronous change beginning in 1895 C.E. of sedimentary $\delta^{15}\text{N}$ in 25 lakes in high elevations and latitudes in North America. But even if temporal synchrony is occurring among 25 sites spanning a continental extent, assessing the signal as a biogeochemical response to disturbance is not possible with this approach. The signal of both the disturbance events and the biogeochemical response would be contained in the single-site records.

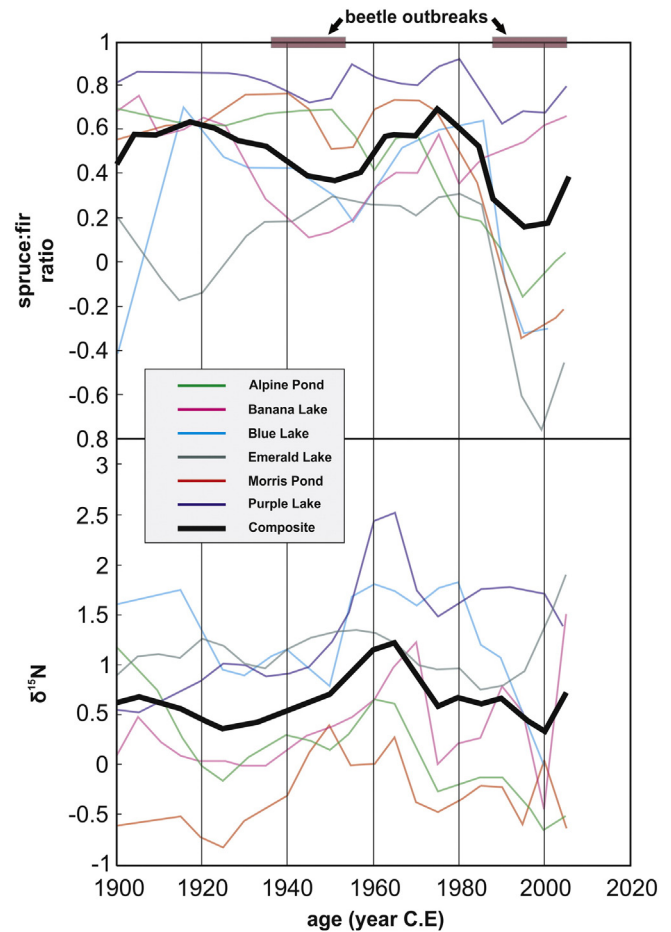


Fig. 6. Composed and interpolated sedimentary $\delta^{15}\text{N}$ records for six subalpine sites located in central Utah that experienced high severity spruce beetle outbreaks during the 20th century. The black line is the composed sedimentary $\delta^{15}\text{N}$ value over this region. Outbreaks did not cause significant changes in the $\delta^{15}\text{N}$ profiles at any site (Morris et al., 2013).

5.4. Global-scale

To our knowledge, no studies have quantitatively compared a global reconstruction of disturbance (e.g., Marlon et al., 2013) with a biogeochemical signal at the global scale (McLauchlan et al., 2013). One possible exception at the regional scale would be the work of Holtgrieve et al. (2011), who studied anthropogenic N deposition as a disturbance. Using criteria proposed by Lake (2000), an important distinction is that anthropogenic N deposition is a ‘press’, or slow-building disturbance, while the disturbance types reviewed in our manuscript, e.g., wildfire and bark beetle outbreaks, would be classified as ‘pulse’ (or episodic) disturbances. Therefore, interpreting press disturbances in sedimentary records may require a modified, or alternative, framework to the work reviewed here.

For comparing disturbance reconstructions with biogeochemical reconstructions at the global scale, there are potentially two approaches. The first is identification of appropriate globally-integrated signals to compare with site-specific records, such as an ice core record, that is accepted to be a globally representative signal of past temperature (e.g., GISP2, Stuiver et al., 1995), with a charcoal record from a single site or multiple sites. The patterns observed in a site (or region) record could be evaluated against long-term trends in the global composite to assess whether the site (or region) appeared to be sensitive to broad scale controls. A second approach would be to assemble a composite global disturbance proxy, such as fire, which is now feasible as significant progress has been made in the assessment of changes in global biomass burning using sedimentary charcoal (Marlon et al., 2013). Differences among continents and regions in climate-mediated

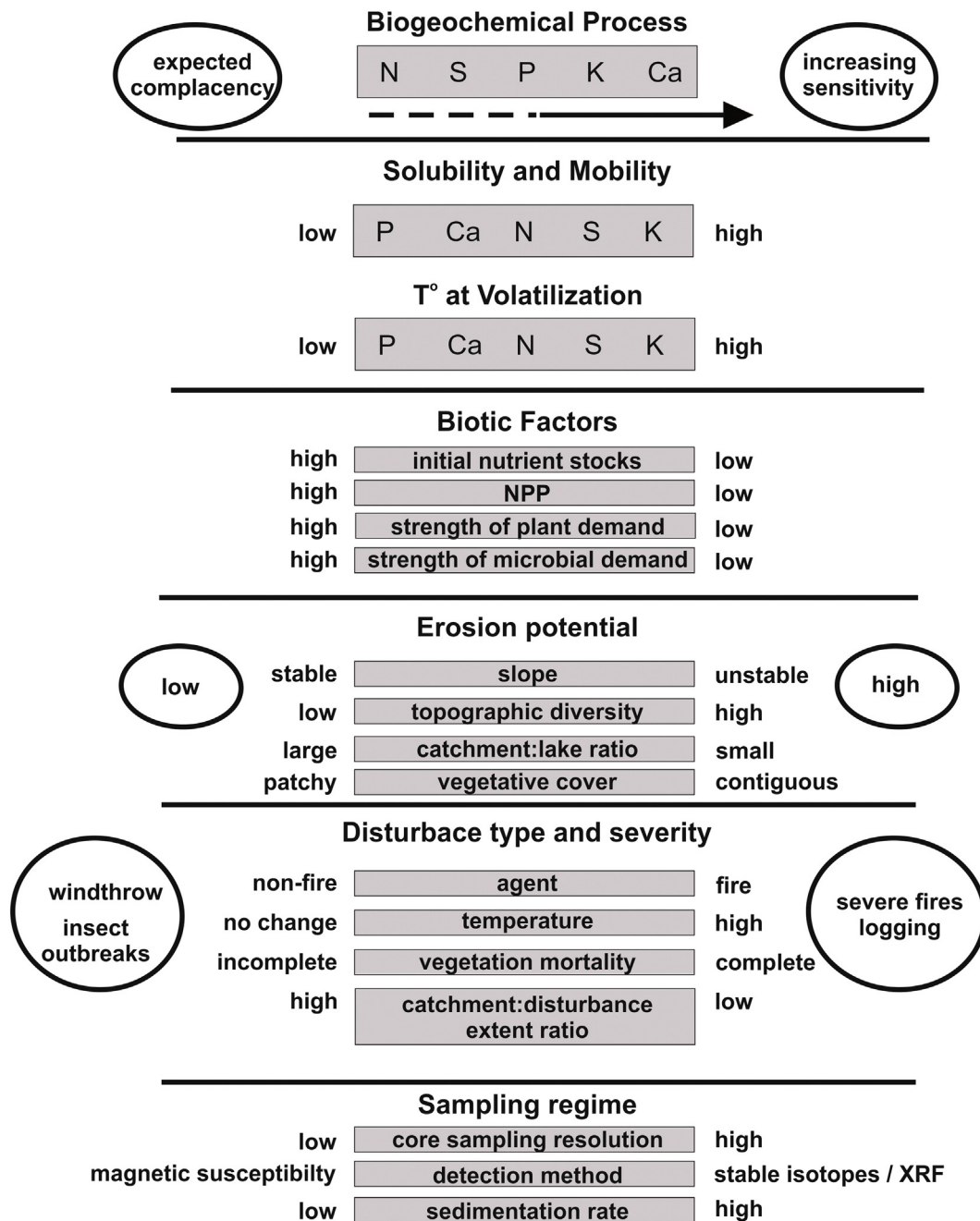


Fig. 7. This framework depicts the process-based, site, and physical factors that are important to consider in the development of a study that investigates the biogeochemical outcomes of disturbances. Factors on the right side of the framework are advantageous for sensitivity while factors on the left side favor complacency.

disturbance regimes are currently being explored (e.g., Whitlock et al., 2015). Approximately 736 sedimentary charcoal records with good chronological control have been contributed to the Global Charcoal Database (Power et al., 2010; Marlon et al., 2012), and standardization methods (e.g., z-scores) and tools (e.g., paleofire R package) make these potentially useful for establishing global and regional disturbance histories (Blarquez et al., 2014). Unfortunately, it would be difficult to match the site-specific disturbance proxies with composited biogeochemical response at the global scale (i.e., sedimentary $\delta^{15}\text{N}$ in McLauchlan et al., 2013). However, one avenue worthy of exploration would be to compare composited disturbance proxies with composited biogeochemical responses.

6. Conclusions

We provided a review of methodological procedures to guide the generation and interpretation of data for studying biogeochemical impacts of terrestrial disturbances using lake sediment records. Although these impacts may be short-lived, paleoecological records are essential for capturing their full range of variability, and for assessing their sensitivity in varying biophysical contexts. The template we provide will help researchers in predicting which sites are biogeochemically complacent and which ones are biogeochemically sensitive to disturbance. By explicitly considering site characteristics, biogeochemical response variables, sampling choices, and data analysis, researchers can increase the likelihood of detecting a biogeochemical response to disturbance, should one exist, and better interpret complacency in the paleorecord (Fig. 7). This is a critical research priority as the Earth becomes dominated by anthropogenic global change, including altered disturbance regimes.

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