


The value of linking paleoecological and neocological perspectives to understand spatially-explicit ecosystem resilience

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Abstract

Context Predicting ecosystem resilience is a challenge, especially as climate change alters disturbance regimes and conditions for recovery. Recent research has highlighted the importance of spatially-explicit disturbance and resilience processes to long-term ecosystem dynamics. “Neocological” approaches characterize resilience mechanisms at relatively fine spatio-temporal resolutions, but results are difficult to extrapolate across broad temporal scales or climatic

ranges. Paleoecological methodologies can consider the effects of climates that differ from today. However, they are often limited to coarse-grained spatio-temporal resolutions.

Methods In this synthesis, we describe implicit and explicit examples of studies that incorporate both neo- and paleoecological approaches. We propose ways to build on the strengths of both approaches in an explicit and proactive fashion.

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Results Linking the two approaches is a powerful way to surpass their respective limitations. Aligning spatial scales is critical: Paleocological sampling design should incorporate knowledge of the spatial characteristics of the disturbance process, and neocological studies benefit from a longer-term context to their conclusions. In some cases, modeling can incorporate non-spatial data from paleocological records or emerging spatial paleo-data networks with mechanistic disturbance/recovery processes that operate at fine spatiotemporal scales.

Conclusions Linking these two complementary approaches is a powerful way to build a complete understanding of ecosystem disturbance and resilience.

Keywords Disturbance · Resilience · Paleocology · Climate change · Synthesis · Scale

Introduction

Disturbances occur at various spatio-temporal scales and are integral components of all ecological systems (Pickett and White 1985). These processes initiate succession, selectively alter genotypes, populations, or communities, and cause biogeochemical changes with long-term implications for productivity (McLauchlan et al. 2014). Disturbance/recovery processes are sensitive to climate (Dale et al. 2001) and exhibit complex feedbacks with previous disturbances (Buma and Barrett 2015). Resilience, here defined as post-disturbance recovery to a similar functional and compositional state (Holling 1973; Gunderson 2000) is a complex process, depending on a variety of factors. Some of these factors are biotic mechanisms like serotinous cones, seed dispersal, resprouting ability, and abiotic tolerances, while others result from the disturbance process itself, like the intensity or duration of the event. Understanding the interaction between characteristic or dominant organisms, disturbance, and subsequent resilience is a major task in ecology (for example, tropical forests and hurricanes: Chazdon 2003; coral reefs and hurricanes: Gardner

et al. 2005, subtropical forests and landslides: Walker et al. 1996; temperate forests and ice storms: Duguay et al. 2001). A reliable understanding of the process of disturbance and resilience is a prerequisite to anticipating future ecosystem changes in a shifting climate.

The spatial arrangement of vegetation structure and disturbance events strongly influence resilience (Cumming 2011; Kemp et al. 2016). Disturbances are rarely truly independent of the landscape they affect; their behavior is shaped by interactions with vegetation, topography, and prior disturbance legacies (Buma and Wessman 2011, Johnstone et al. 2016). Processes that are spatially contagious, interactive, or that have directionality are likely to be influenced by the spatial arrangement of landscape elements (e.g. Turner and Romme 1994; Seidl et al. 2016). In susceptible parts of a landscape, contagious processes are likely to propagate through large, homogeneous patches, such as fires spreading through contiguous forests. Conversely, homogeneity may reduce risk if large patches are not susceptible. Heterogeneous landscapes can also affect disturbance processes, such as the limited ability of crown fires to spread through discontinuous boreal forests (Johnstone et al. 2016). In terms of resilience, heterogeneous systems may exhibit a loss in connectivity (Fahrig 2003) but may also foster disturbance refugia (e.g., Camp et al. 1997) and be important sources of resilience and adaptive capacity (Serra-Diaz et al. 2015; Krawchuk et al. 2016). Spatially-constrained resilience mechanisms like seed dispersal (e.g. Buma and Wessman 2011; Harvey et al. 2016) are also sensitive to changes in landscape pattern. As the recovering vegetation sets the biotic template for the next disturbance, a series of disturbance-recovery sequences can shape the spatial pattern of a landscape over multiple events. However, the spatial biotic pattern may also change post-disturbance as a result of climate altering the probability of regeneration for various taxa (Calder and Shuman 2017). Disentangling these two non-mutually exclusive drivers (climate and vegetation) is a necessary step towards understanding and predicting ecosystem resilience, but a significant challenge in the current era of rapid climate change.

As a result, a truly robust understanding of the role of space in ecosystem resilience requires not only knowledge of the mechanisms involved but also how those mechanisms vary with time and under different abiotic (climatic and biogeochemical) states.

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Paleoecological data, which explores changes in vegetation communities over long periods of time through a variety of methods, might be a solution. Several reviews have addressed the benefit of paleoecological data to other contemporary ecological questions (Delcourt and Delcourt 1988; Schoonmaker and Foster 1991), conservation implications of paleoecological findings (Willis et al. 2010), and restoration targets (Jackson and Hobbs 2009). In the context of resilience, the development of spatial indicators that summarize landscape structure has been a promising advance (Allen et al. 2016; Sundstrom et al. 2017). However, the utility of these indicators is still limited by a lack of temporal perspective encompassing a variety of climate conditions in a given system (e.g., Kranabetter et al. 2016). Our understanding of how space shapes post-disturbance resilience is especially limited in the longer-term context of changing environmental conditions (e.g. precipitation changes, snow loss, atmospheric CO₂, herbivory). Without long-term context, it is difficult to predict the influence of disturbance patch size, distribution, and homogeneity on resilience under altered environmental conditions. Yet changes are likely; for example, drought interacts with spatial disturbance patterns to reduce the effectiveness of seed dispersal in post-fire recovery (Harvey et al. 2016). This leaves significant uncertainties when predicting resilience to future events based on research under current climatic conditions.

Ecology as a field, and resilience and disturbance ecology especially, would benefit from a more intentional linkage between short and long-timescale perspectives. Our goal is to outline the relative strengths and weaknesses of two broad types of ecological studies—“neoecological,” or relatively short-term research, and paleoecological research, encompassing longer timespans. The focus is specifically on ecosystem resilience to disturbance in the context of spatial patterning and its role in post-disturbance recovery. We intend to present a useful perspective and recommendations for explicit incorporation of paleo and neoecological perspectives in landscape ecology study design.

First, we outline how those two perspectives are complimentary and how the limitations of one are often matched by strengths of the other. Next, we provide multiple examples of how the two perspectives have been utilized successfully to inform each other implicitly in various study systems. We then

build on this review by describing explicit ways to “merge” the methods with intentionality, bringing the two approaches into study design at the beginning of a given project rather than simple coincidental comparisons. Finally, we conclude by suggesting productive lines of research, both methodological and ecological, that will further this integration.

Two complementary perspectives

Studies of ecosystem resilience to disturbances can be grouped into two broad categories by their temporal scope: “neoecological” and paleoecological. Neoecological methods are those focused on recent disturbance events, usually within the observational record and typically spanning at most a few decades (Table 1). This category includes observations of post-fire vegetation and ecosystem functioning, experiments that vary fire frequency, and pattern analyses using remote sensing platforms. The strength and emphasis of these methods is the focus on a mechanistic understanding of the drivers of recovery and their interactions. The ability to sample extensively, measure a substantial number of covariates, and perform controlled experiments has led to powerful understandings of disturbance influences on ecosystem functioning (e.g. the Yellowstone system, Turner et al. 2003; Romme et al. 2016), nitrogen cycling in lakes, (Lodge et al. 2016), competition and net primary productivity (Fahey et al. 2016), and environmental filters which influence near-term recovery (Hansen et al. 2016).

But even when resilience processes are well-described there are significant difficulties in predicting resilience to future disturbance events using neoecological methods. First, the observation period is limited and climate conditions in the future are likely to range beyond current climates or historical averages. Both the future disturbance regime and the future recovery processes may be unlike any in the instrumental record (Millar et al. 2007). Furthermore, most inquiries into the spatial component of disturbances (e.g., recovery as a function of unburned patch distributions, Kemp et al. 2016) are limited to the availability of moderate- to fine-resolution satellite data. This timeframe limits not only the climatic conditions that can be observed to the very recent past but also the number of events that can be investigated

Table 1 Characteristics of neoecological and paleoecological approaches in the context of spatial and temporal aspects of study design

	Temporal		Spatial	
	Resolution	Duration	Resolution	Extent
Neoecological	Sub-daily sampling possible	Limited to < 100 years in most cases	Sub-meter sampling possible	Extensive sampling using plots and/or remote sensing; Controlled manipulations
Paleoecological	Limited by resolution of methods, potentially annual to sub-annual	Multi-millennial records possible	Point data possible but metrics are limited (tree rings)	Integrative records (pollen), extensive sampling possible in some methods (e.g., tree rings)

in a given place/context. Despite the known importance of the spatial processes (e.g., disturbance legacies) to ecosystem recovery and future disturbance events, many disturbance processes are so infrequent (Foster et al. 1998) that researchers have not had adequate opportunity to directly characterize resilience.

Paleoecological techniques, in contrast, employ records that might span millennia and encompass multiple disturbances under a variety of climatic conditions. This research generally focuses on variation in time. Paleoecological studies use a variety of vegetation (e.g., pollen in sediment cores) and abiotic (e.g., charcoal, eroded material) proxies to reconstruct the presence, distribution, and dynamics of plant communities. Lake sediment analyses, for example, are a powerful way to quantify the dynamics of vegetation, climate, and disturbance regimes over long temporal scales (Clark 1988; Willis et al. 2010; Williams et al. 2011). Dendrochronological records (here considered a paleo technique, as it is based on inferences about past conditions based on a proxy rather than direct observation) are especially powerful, providing high temporal resolutions of, among many things, tree growth and composition at precise locations. This ability to track ecosystem recovery, or lack thereof, over a variety of climates both warmer and colder than current conditions has led to important understandings into the climatic tolerances of ecosystems and broad-scale changes in species distributions in the context of disturbance (Nelson et al. 2006; Minckley et al. 2012). These paleoecological records can span several hundreds to many thousands of years and have identified repeated ecosystem turnover likely driven by changes in climate (e.g., Deevey and Flint 1957; Shuman et al. 2004, 2009), but also long-term

ecosystem stability potentially linked to disturbance (e.g., Wright 1974; Winkler 1985). As such they provide a unique perspective on ecosystem stability and resilience in a variety of climatic contexts (e.g., Webb 1986, Aranbarri et al. 2014), many of which may be useful for predicting vegetation change (or lack thereof) to future climates. This long-term perspective is invaluable. A global synthesis of biomass burning from paleofire records, for example, highlighted the decline in fire activity during the twentieth century that accompanied increasing landscape fragmentation and later fire suppression in many parts of the world (Marlon et al. 2008), a “deficit” that has not yet been alleviated in some regions (western US, Marlon et al. 2012). This demonstrates the importance of “shifting baselines.” Short-term studies are conducted within short-term climatic conditions, and as those conditions shift directionally the short-term studies may lose some relevance or require reinterpretation. Thus the long term perspective is critical to understand the significance of current changes which might go undetected by neoecological studies.

However, while the paleoecological perspective provides rich insight into community dynamics under multiple climates and can be linked to ecosystem functioning (e.g., C-cycling: McLauchlan et al. 2014), there is a general emphasis on correlative, contemporaneous change in ecosystems and climate rather than the mechanisms of those changes (but see Berland et al. 2011; Blois et al. 2014). Sampling is often limited to a few locations and thus disentangling multiple influences that co-occur simultaneously is difficult (i.e. episodic drought and shifting fire regimes). Spatial resolution of the data is often limited because proxies often integrate over landscapes (e.g.,

Table 2 Examples of current and/or future productive lines of inquiry for the further integration of neocological and paleoecological data

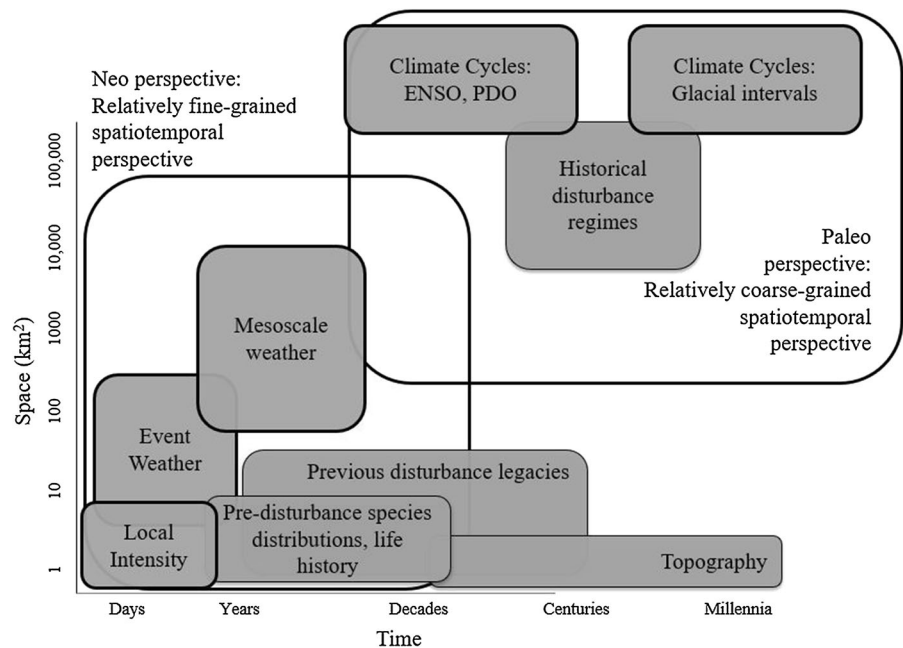
Paleoecological methods	Experimental treatments	Determine spatial correlations between fires and fire proxies (charcoal); e.g. Lynch et al. (2004)
	New proxies	Determine proxies for other disturbance agents via experiments (wind: Cannon et al. 2014; icestorms: Rustad and Campbell 2012)
Paleoecological design	Sampling density	Design spatially explicit paleoecological sampling schemes with lags set to known disturbance behavior
	Pattern detection	Test sensitivity of spatial patterns in same location to differing climates (synchrony)
Neocological methods	Model testing	Test persistence of patterns in various contexts (e.g., disturbance refugia) for matching to paleo records
	Model implementation	Incorporate paleoecological patterns into neocologically generated models
Neocological design	Sampling density	Determine appropriate grain and extents for determining stability to inform paleoecological sampling (e.g., spatial autocorrelation in disturbance/resilience processes)
	Direct comparison	Pair landcover change data from satellites directly to transitions in recent pollen data

pollen influx onto a lake surface) and because analysis requires intense effort at suitable locations (e.g., a lake with appropriate depositional conditions). For example, few clear proxies for plant diseases exist, and it is uncertain whether presence of insects in lake sediments truly reflects reproducing local populations or merely substantial depositions that might fall from atmospheric currents far from their point of reproduction (Furniss and Furniss 1972; Edwards 1987). With the exception of dendrochronological studies (discussed later), networks of dense paleo-sampling sites are relatively uncommon, though some are beginning to be assembled for larger-scale questions. However, they are still generally not fine-grained enough to study patch dynamics at stand or plot scales (Calder et al. 2015; Kelly et al. 2013). Some have attempted to overcome this constrain by using accumulating soils and the occurrence of “small bedrock hollows” which can reconstruct patch-scale (< 100 m) vegetation and fire and thus reveal development of vegetation patches (Davis et al. 1998; Sugimura et al. 2008). However, the temporal resolution of sediment records (especially in soils and small hollows) is limited by a slow sedimentation rate, radiometric dating uncertainty, bioturbation, or inability to contiguously sample for all proxies. As a result, while a variety of climatic or anthropogenic contexts can be observed it can be difficult to constrain the data to a specific, individual event or reconstruct the other ancillary data known to

be significant to resilience, like weather conditions, pre-disturbance fuel loading, or secondary pathogens.

In summary, the strengths of neocological studies—extensive sampling in many spatial contexts using many metrics and manipulative experiments—are tempered by a lack of long-term temporal context. Paleoecological approaches excel at providing long-term context but are often hampered by a limitation in what can be reconstructed and a need to operate at spatial scales not well matched to known resilience mechanisms or spatial pattern of disturbances. (Note that spatially explicit dendroecological methods can span centennial timescales, discussed below). Combining the strengths of these two approaches provides a way to address the limitations of both (Foster et al. 1990; McLauchlan et al. 2014), yet there is little theoretical work integrating the spatially-explicit perspective of neocological disturbance/resilience studies with the long-time span perspective offered by paleoecological approaches (Fig. 1). Some classic work has drawn on historic documentation of landscape patterns and their changes (e.g., Grimm 1984; Buma et al. 2017) and linked it with paleoecological studies (e.g., Grimm 1983), but recent improvement in mechanistic modeling, statistical methods, and climate and disturbance reconstruction can enhance such pairing now (e.g., Dawson et al., 2016; Umbanhowar 2004) and provide important insights to fields like conservation (Lindbladh et al. 2013) or climate adaptation/management (Henne et al. 2015).

Fig. 1 Drivers of ecosystem resilience (both mechanistic and contextual) well addressed by one of the two perspectives



Integrating these paleoecological approaches with spatially-oriented neocological perspectives is timely and important, especially given a growing recognition that tipping points in large, spatially-extended systems (e.g., the boreal forests of north America) may be reached abruptly and synchronously across very broad regions (van de Leemput et al. 2015) under future climates.

Matching limitations to strengths

Several study systems have opportunistically matched the strengths of neo- and paleoecological perspectives. The following examples show how (1) a primarily neo-oriented investigation of post-fire resilience is supported by a paleo perspective, (2) a primarily paleo research project could be interpreted through mechanistic understandings derived from a neocological perspective, and (3) a system where neocological studies of novel disturbance agents pose new questions that will require adopting long-term paleoecological perspectives.

Example 1. Multiple disturbances in Rocky Mountain forests: paleo supporting neo interpretations

Subalpine fires in the central and southern Rockies have been extensively studied (Baker 2009) and are generally characterized by high spatial heterogeneity in fire severity (0–100% mortality), consistent with large, infrequent disturbance in general, which are characterized by high spatial heterogeneity in both impact and surviving biological legacies (Turner and Dale 1998). The resilience mechanisms of species in the biome interact with the spatial pattern of both burned area and burn intensity (Turner et al. 1998). Recovery is influenced by (1) the size of the burned patch versus seed dispersal, (2) recovery via serotiny (influenced by the predisturbance spatial distribution of serotinous individuals and burn intensity/duration), and (3) resprouting ability (which can be limited in high severity burns that consume the upper layers of soil).

Neocological studies suggests that multiple events can override the resilience mechanisms of multiple species, impacting recovery (Buma and Wessman 2011). By studying how a large, extensive blowdown in 1997 (Lindemann and Baker 2001) contributed to the spread and intensity of a subsequent fire in 2002 (Kulakowski and Veblen 2007; Buma and Wessman

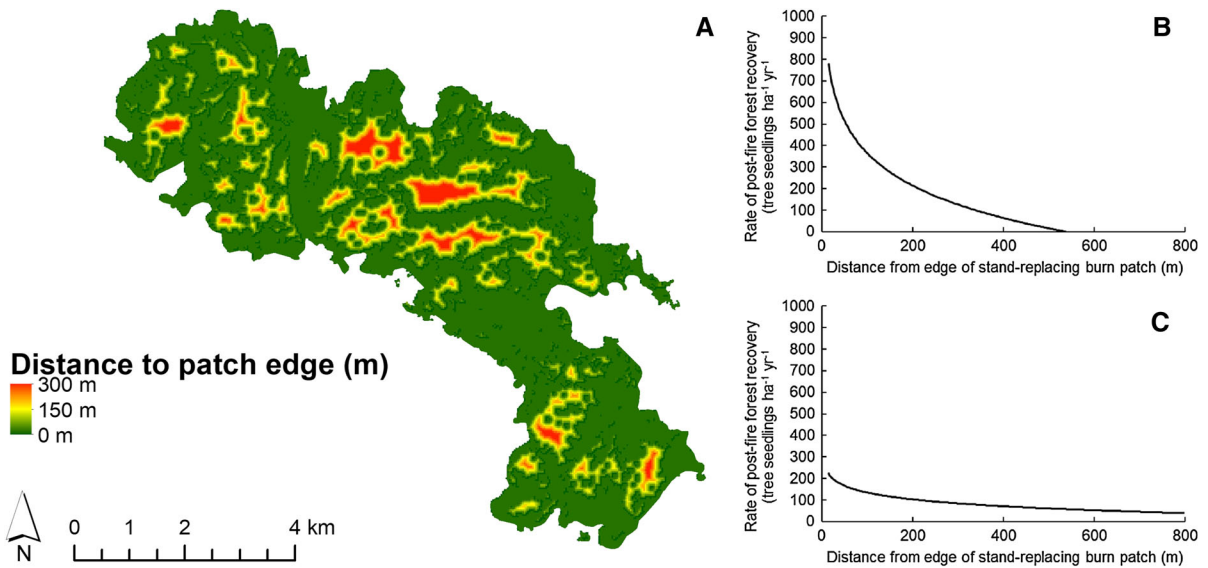


Fig. 2 Variation climate over time can alter the resilience mechanism-spatial pattern relationship, a complicating factor that may be missed in short-term studies. **a** Pattern of distance to un-burned forest in the 2011 Red Rocks fire, Wyoming USA.

2011) several papers have documented how overlapping disturbances correlate with lower resilience of both serotinous and seed dispersing species. Thus, those studies have concluded that the lack of regeneration was related to the interaction of disturbances in space, a hypothesis that assumes that climate during the time period of observation (which was similar to historical averages) was not a factor. However, severe droughts can change the way resilience mechanisms like seed dispersal interact with spatial patterning of specific burn events (Harvey et al. 2016; Gill et al., 2017; Fig. 2). A longer perspective was needed to understand the climatic range in which the ecosystem is expected to be resilient.

Paleoecological work has filled this gap, with lake sediment studies in the region demonstrating that the regional ecosystem has been relatively resilient over a broad range of temperature and precipitation, for at least 7000 years (Minckley et al. 2012), though legacies of past climate events persist on the landscape. Near the area of the 1997 blowdown and 2002 fire, modern forest patterns developed following a lack of recovery after large, severe fires 1000 years ago (Calder and Shuman 2017). Frequent or large fires burned $\sim 80\%$ of the study sites on the landscape at that time but the climate subsequently cooled at the

b In cool/wet climate conditions, seed dispersal is a more effective resilience mechanism at long distances. **c** In warm/dry conditions, seed dispersal is a less effective resilience mechanism

onset of the Little Ice Age and that cooling appears to have prevented forests from recovering over large portions of the burned area, as evidenced by regional patterns of pollen—coarse grained but relevant at broad scales. These historical climatic events are temporally correlated with the formation of the modern forest and meadow mosaic (Calder and Shuman 2017). The vegetation shift both created new spatial patterns across the landscape, which have persisted for a millennium, and was dependent on the factors that shaped the spatial extent of past fires (e.g., fuel continuity). The linking of paleo and neo perspective here validates and supports conclusions from the mechanistic, neocological field studies; conversely, the neocological studies provide a general mechanism (multiple disturbances overwhelming resilience) to explain the historical patterns observed in the paleo record.

Example 2. Changing vegetation composition in New Zealand: neo explaining paleo correlations

During the initial populating of New Zealand around 750 years ago, the landscape was transformed from relatively inflammable forests (covering 85–90% of the land area with fire return intervals of centuries to

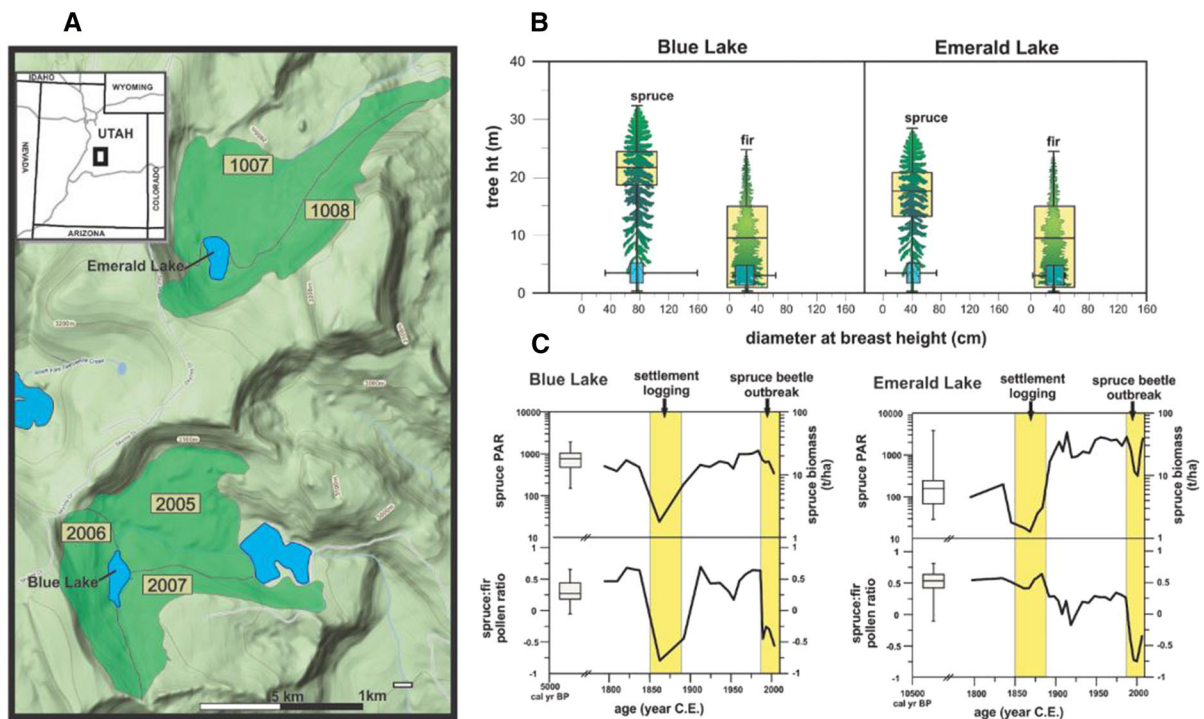


Fig. 3 Integrating neocological data with paleoecological data to reconstruct spruce carbon spatial distribution (between two watersheds) and changes through time. **a** Map depicting the Wasatch Plateau study area located in central Utah, USA and area of USFS forest inventory plots within the catchments of Emerald Lake (1007 and 1008) and Blue Lake (2005, 2006, and 2007). **b** Inventory summaries for Engelmann spruce and subalpine fir. **c** 5 Line and box plots for reconstructed Engelmann spruce pollen accumulation rates (PAR) calibrated to carbon biomass (C t/ha) at Emerald Lake (**a**) and Blue Lake

(**b**). Lower plots shows the ratio of spruce to fir, which is indicative of disturbances that preferentially cause spruce mortality (e.g. spruce beetle). The shaded boxes highlight periods of documented disturbances that favored spruce mortality, such as settlement-era logging and a spruce beetle outbreak. Box plots indicate the range of variability recorded over the length of the sediment records, 10,500 cal year BP for Emerald Lake and 5000 cal year BP for Blue Lake, to compare with the historical range of variability (post-1800 CE). From Morris et al. 2015

millennia; Ogden et al. 1998) to flammable grasslands. During this expansion of human population, total forest cover was reduced to $\sim 25\%$ (Perry et al. 2014). This remarkable shift has been documented from pollen preserved in high temporal resolution sediment cores (though limited in spatial extent; McWethy et al. 2009).

Fire modeling experiments, conducted using a neocologically derived understanding of fire spread and species resilience, have generated a more complete hypothesis of the actual mechanisms involved in this transition. Specifically, it appears that the change from forested to open vegetation occurred through several to many individual disturbance events that rapidly shifted the spatial configuration of the landscape from relatively homogeneous low-flammability fuels, with only isolated pockets of higher

flammability early-seral vegetation, to a spatial configuration where higher flammability vegetation was highly connected (Perry et al. 2012). After passing this spatially-mediated tipping point the landscape was rapidly transformed by subsequent fire events which burned much larger areas than what had occurred for millennia. Recent ecological work has not only highlighted the spatial patterning required but the specific species characteristics and fine-scale (meters) structural characteristics of post-fire stands which lead to the positive feedback cycle between fire and post-fire vegetation flammability. This cycle can maintain high fire frequencies and prevent re-establishment of continuous forest coverage (Tepley et al. 2016). The linking of paleo records and neocological data via modeling thus supports the hypothesis that positive feedbacks in post-fire vegetation recovery and

spatially targeted burning transformed the islands into a highly-connected flammable vegetation type (McWethy et al. 2014; Tepley et al. 2016). This illustrates the power of modern, spatially explicit modeling techniques to fully explore the mechanistic underpinnings of a detailed, yet correlative, paleo record.

Example 3. Gypsy moths in eastern North American forests: asking new questions

Finally, we draw from a case study of gypsy moths in eastern North American forests to illustrate how neoecological studies of novel disturbance agents pose new questions that require adopting long-term perspectives. Insect defoliators such as the invasive gypsy moth (*Lymantria dispar*) can have dramatic effects on ecosystem functioning and vegetation dynamics (Lovett et al. 2002; Morin and Liebhold 2015). In many forests, these periodic disturbances cause N mobilization and subsequent loss from the system (Townsend et al. 2004; Cowles et al. 2014). Moreover, satellite monitoring has revealed that these outbreak effects accumulate over time and can increase forest N limitation (Deel et al. 2012). This increasing N limitation could interact with the disturbance process itself over short (Wilson and Tilman 2002) or long (Peltzer et al. 2010) time scales, and the resilience of individual species (MacGillivray and Grime 1995), potentially leading to a changed ecosystem type with altered vegetation and ecosystem services.

The current heterogeneous spatial arrangement of forest types on the landscape appears to enhance resiliency against such a polyphagous herbivore by moderating the frequency and intensity of gypsy moth defoliation effects on N cycling. While the more N-poor oak-hickory (*Quercus* spp., *Carya* spp.) forest types tend to experience gypsy moth outbreaks approximately every 5 years, forests occurring in more N-rich riparian or mesic portions of the landscape have tree species with less palatable leaves (Schultz and Baldwin 1982) and a longer, 10-year outbreak periodicity (Johnson et al. 2006). But the durability of this heterogeneous and resilient landscape configuration is uncertain with climate change. Unless asynchrony among leaf-out and gypsy moth egg hatch dates (Foster et al. 2013) and natural enemies such as entomopathogens (Hajek and Tobin

2011) curtail future gypsy moth outbreaks, N losses from the disturbance may exacerbate anticipated increased N demand from earlier springs (Elmore et al. 2016). These mutually reinforcing N limitation processes could interact with other stressors, such as drought (which inhibits entomopathogens, Reilly et al. 2014) to tip the system toward a forest type (e.g. a pine forest) that has dramatically altered ecosystem functioning. This prediction, well supported from the neoecological viewpoint, is difficult to validate without historical data under differing climates. Such data could be used to understand the spatial tipping points suggested by modern entomological and biogeochemical work described above. This illustrates a case where neoecological methods have provided a strong understanding of the mechanisms and fine-scale processes that impact landscape resilience. But, given the relative novelty of gypsy moths on the landscape (i.e., 150 years.), integrating the long-term perspective will require fieldwork and a modeling approach capable of forecasting resilience to future, no-analog climatic conditions. Inclusion of the complimentary paleo perspective could provide the necessary context to place current observations of pest behavior in a variable climatic context.

From characterization to prediction: approaches that merge the methods

Clearly, bridging temporal scales better informs our understanding of how systems function and ad hoc incorporation of both perspectives has been useful in the past. Looking forward in time, predicting landscape resilience in the future will benefit from *explicitly* linking our understanding of mechanisms of resilience (especially spatially dependent processes) to our understanding of how resilience changes under non-contemporary climates.

The explicit incorporation of paleoecological data with neoecological mechanistic understanding is perhaps best exemplified by dendrochronology. Dendrochronological techniques are well suited to spatially-explicit disturbance questions due to the dense amount of “records,” i.e., individual trees, in a given area (McBride 1983; Hessl 2011). The spatial structure of fire events can be well-described for fire regimes with reliably low-intensity, often high-frequency fires and tree species that form fire scars (i.e.

ponderosa pine). In the Front Range of Colorado, spatial reconstructions of historical (~ 3 century) fire regimes coupled to a fire intensity model has contradicted the idea that recent fires were larger than those experienced historically while also identifying specific areas where landscape configuration was outside the range of historical norms, potentially altering resilience to future events (Sherriff et al. 2014). In another effort, Krapek et al. (2017) combined spatially explicit range mapping, plant community analysis, disturbance exposure maps, regeneration surveys, and dendrochronology to chart recent migration in a climate-threatened conifer. The authors concluded that the neocological understanding of slow migration driven by short seed dispersal distances and disturbance was insufficient, and long-term fluctuations in climate were important in determining broad-scale migration rates. This linking of neocological mechanisms with the paleoecological understandings of non-contemporary climates creates a powerful understanding of the interaction between species, climate, and disturbance.

Example 4: explicit linking of paleo and neo methods to estimate long-term landscape carbon density via mathematical transfer functions

Directly linking neocological mechanisms with longer-term paleoecological records is also possible via mathematical linkages. A general increase in the spatial density of paleoecological sediment records is resulting in more detailed reconstructions that leverage neocological understandings of disturbance, dispersal, and recovery. Several decades of research are beginning to yield reliable quantitative maps of vegetation structure from pollen records for the past 10,000 years (Seppä et al. 2009; Fyfe et al. 2013; Mehl and Hjelle 2015) and even the Late Glacial (Allen et al. 2010). This can be tied to ecosystem functioning metrics from neocological studies to great benefit. For example, Morris et al. (2015) used district-specific stand inventories that were collected by the USFS in 1994 during a severe outbreak of spruce beetle (*Dendroctonus rufipennis*) (Dymerski et al. 2001). Outbreaks by this native insect are largely triggered by several well-described mechanisms: drought, elevated temperatures, positive density-dependent interactions among the beetles, and relatively spatially homogeneous host distributions (Wallin and Raffa 2004; Raffa

et al. 2008; Sherriff et al. 2011; Hart et al. 2015, 2017). Tree-level carbon biomass estimates generated from the inventory were summed for total and species-specific estimates at the plot-level. The plots were then averaged for a catchment-level estimate of host (spruce) and non-host (fir) tree species biomass. To pair the observational data to paleoecological datasets, lake sediment cores were collected and analyzed for pollen, geochemical indicators, and charcoal (Morris et al. 2013). The plot-level biomass values were used to calibrate pollen accumulation rates (PAR) using a transfer function (Seppä et al. 2009). This method provided a long-term reconstruction of spruce biomass (C t/ha) as a proxy for stand conditions (Fig. 3).

This approach linking forest stand inventories (Hall 2001) with lake sediment cores and charcoal stratigraphy enabled Morris et al. (2015) to conclude that historical logging in the nineteenth century simplified the stand and spatial structure (in terms of spruce biomass/carbon) of the region, leading to accelerated beetle population growth and subsequent major spruce beetle outbreaks. Clearly, paleoecological data are useful to contextualize recent disturbances, and their effect on carbon, into a longer-term understanding.

For other systems where such spatially dense paleoecological data is not available (such as in the gypsy moth example above) or disturbance processes are not as well represented in the paleo record, explicit and deliberate incorporation of the two perspectives into a cohesive study design can be more difficult. Here, spatial modeling provides a useful tool to bridge time scales. It can be used to extend knowledge of fine-scaled disturbance behavior and system recovery garnered from observations of actual events by taking known disturbance behavior from modern, physical understandings of disturbance characteristics and parameterizing that behavior to recreate patterns that match the paleoecological record (or the hypothesized patterns). The result is an explicit integration of neocological mechanisms with paleoecological records to create an integrated view of disturbance and resilience over space and time. These models can then be validated against known disturbance events and/or paleo-reconstructed regimes for a particular climate condition. For example, in New England, hurricane disturbance frequency has been well characterized with proxy records in sediment cores (e.g., Donnelly et al. 2015) and exposure is spatially constrained due to characteristics of potential storm

tracks (e.g., Foster and Boose 1992). These two perspectives enabled Boose et al. (2001) to create a spatiotemporal estimate of wind exposure over several centuries in New England, and Buma and Barrett (2015) to explore the relationship between long-term disturbance exposure and carbon balance in Alaska. Similarly, using process-driven fire modeling techniques, Ager et al. (2014) estimated fire exposure over western U.S. forests. This was done by simulating thousands of fire events using spatially explicit fire spread models and current vegetation maps and validated against observed events. Conversely, Berland et al. (2011) used relevant neoecological data to calibrate a spatially-explicit forest landscape model and test hypotheses about the roles of disturbance and dispersal for driving the patterns of landscape change observed in paleoecological records. These methods are a way to transfer the sparse point-data of paleoecological records to a fine-grained coverage, useful to land managers in modeling hazard and for other uses. It is also a way to calibrate spatial disturbance models for climates that have not occurred during the instrumental record, potentially lessening the need to extrapolate into future climates.

Research opportunities

Given the strengths of explicitly incorporating both perspectives, we propose that the intentional pairing of neo- and paleoecological methods, as part of a unified study design, will benefit a wide range of disturbance and resilience ecology research. Therefore, we suggest several research opportunities that can unify the temporal strengths of the paleoecological methodology with the mechanistic understandings of neoecological work. Some opportunities have examples of successful integration but should be applied in other geographic areas. Others are less developed and should be explored (Table 2).

Paleoecological methods: increase understanding of the spatial aspect of paleoecological datasets

Knowing the spatial neighborhood represented by paleo records is imperative to linking those records to spatially explicit processes. Techniques to reconstruct fire frequency have been well-developed in paleoecology. For example, charcoal particle size in the

sedimentary record does reflect local versus regional fires in high severity fire regimes such as pine forests of the western U.S. (Whitlock and Larsen 2002), potentially enabling spatially explicit fire regime reconstructions. Dense networks of sedimentary charcoal records have also begun to allow researchers to estimate overall landscape fire frequency by measuring synchronicity among fire events (Calder et al. 2015; Higuera et al. 2014). Radiocarbon dated soil charcoal combined with spatially integrating lake-sediment charcoal can provide even greater insights into the long-term spatial pattern of fire (Gavin et al. 2003; Kasin et al. 2016). The majority of this work has been done in forested systems. In grassland and savanna systems, where frequent fires maintain ecotone boundaries, the ability to tie sedimentary charcoal to local fire distribution is more constrained and potentially limited to ~ 5 km scales (Leys et al. 2015). Very small sediment basins, “small hollows”, depends on the occurrence of such basins and has not been widely applied (Davis et al. 1998).

There is potential for sediment-based reconstructions of other types of disturbances other than fire. These include wind (e.g., Donnelly and Woodruff 2007), insect and pathogen outbreaks (e.g., Morris et al. 2013; Montoro Girona et al. 2018), and flooding and erosion (e.g., Chipman et al. 2016; Colombaroli et al. 2018) other emerging phenomena (e.g., freezing mortality, Buma 2018) need proxies developed to build a longer-term climatic context to the research. Development of these techniques would increase understanding of those events, disturbances interactions, overall disturbance regimes, and how climate may drive new regime behavior (Buma and Barrett 2015). The specific spatial resolution needed should be informed by current neoecological work on the scales relevant to the disturbance and system resilience.

Paleoecological design: using neoecological understandings to inform paleoecological sampling schemes

Ideally, paleoecological sampling designs will be developed in accordance with our understanding of the spatial scales relevant to disturbance and ecosystem resilience mechanisms (developed from neoecological work). Neoecological research can determine how relative likelihood of a disturbance varies at multiple spatial scales via observation or modeling: For

example, Bigio et al. (2016) demonstrated that rugged terrain had a strong influence on fire return interval within the same vegetation type. Similarly, Ager et al. (2014) produced a gradient of disturbance exposure for broad areas in the Pacific Northwest. These gradients, built from neoecological models, can be utilized to design optimal spatial sampling schemes for paleoecological records.

Neoecological methods: validate neoecological conclusions with paleoecological data

The analog to the idea of spatially explicit paleo reconstructions is creating long-term estimates of disturbance frequency (or exposure) by utilizing mechanistic knowledge of disturbance likelihood and spread patterns. Krawchuk et al. (2016) explored how spatial patterns of disturbance interacted with topography to determine the location of disturbance refugia (small areas of low historic disturbance frequency). The empirical verification of disturbance exposure maps like Krawchuk et al. (2016) is useful for current climatic conditions but could be made more robust by pairing with paleoclimate reconstructions of non-contemporary climates. This pairing would address important questions about the stability of the refugia patches on a given landscape (Camp et al. 1997). Targeted paleo sampling of refugia and exposed locations in close proximity would be valuable. Mustaphi and Pisaric (2013, 2014) sampled lake cores across a range of aspects in central British Columbia, Canada, to test the significance of aspect on fire frequency (well established as a strong bottom-up control on fires via neoecological research). This work not only validated the significance of aspect over time but supported the hypothesis that the relative strength of aspect control varied as a function of climate and species composition.

Neoecological design: linking current spatial observations of disturbances to historical records

Spatial observations of historical disturbance extents and severities can be utilized to determine if current landscapes are outside the range of historical spatial variability. For the pre-satellite era, sketch maps of fire severity have been used to reconstruct boreal forest disturbance regimes, as have historical stand example data (Collins et al. 2015). Remote sensing

technologies, and especially multitemporal satellite data analyses, can map fire events (Giglio et al. 2010), biotic disturbances such as insect outbreaks (Meddens et al. 2013; Cowles et al. 2014), and wind disturbance (Sinton 1996; Ulanova 2000). These data are particularly useful as they can be calculated rapidly for a range of sizes around any given paleoecological record (e.g., tree ring records, Hoffman et al. 2018). As the remote sensing time-period now extends nearly 50 years, direct comparisons between paleoecological and satellite-derived disturbance metrics are becoming possible—direct methodological comparisons between observed fire extent/intensity and paleo proxies would inform proxy-based interpretations of historical events. Systems with rapid disturbance-recovery cycles like fire-influenced grasslands may be particularly useful. As time continues the global satellite data archive will increase and promote insight into the typical longer-term processes of ecosystem resiliency as well.

Conclusions

Despite the substantial progress made toward understanding the mechanisms of ecosystem resilience to disturbance, fundamental difficulties remain in projecting that knowledge into the future. The limited perspective offered by the historical and instrumental records about disturbance hampers the ability of neoecological studies to make predictions about responses to disturbance in future climate conditions. Paleoecological techniques, which describe community and disturbance frequency changes over long-time spans and multiple climate conditions, offer a complementary perspective. However, constraints on spatial and temporal resolution, and their correlative nature, make tying resilience to landscape configuration during any particular disturbance event challenging.

Linking the two perspectives provides a powerful way to alleviate the limitations of each. Several studies have done this in an implicit way, and some explicitly. These demonstrate the utility of incorporating the two perspectives into initial study design rather in an ad hoc fashion. By uniting paleorecords of disturbance and community structure (especially when conducted in a spatially explicit fashion) with the neoecology perspective about mechanisms of resilience, we can

gain a new, long-term perspective on resilience. Moving forward, both disciplines would benefit from intentional collaboration, especially designing sampling schemes to fit the strengths of the other.

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