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Abstract

The concept of resilience has become increasingly important in ecological and socio-ecological literature. With its focus on the temporal behaviour of ecosystems, palaeoecology has an important role to play in developing a scientific understanding of ecological resilience. We provide a critical review of the ways in which resilience is being addressed by palaeoecologists. We review ~180 papers, identifying the definitions or conceptualisations of ‘resilience’ that they use, and analysing the ways in which palaeoecology is contributing to our understanding of ecological resilience. We identify three key areas for further development. Firstly, the term ‘resilience’ is frequently defined too broadly to be meaningful without further qualification. In particular, palaeoecologists need to distinguish between ‘press’ vs. ‘pulse’ disturbances, and ‘ecological’ vs. ‘engineering’ resilience. Palaeoecologists are well placed to critically assess the extent to which these dichotomies apply in real (rather than theoretical) ecosystems, where climate and other environmental parameters are constantly changing. Secondly, defining a formal ‘response model’ - a statement of the anticipated relationships between proxies, disturbances and resilience properties - can help to clarify arguments, especially inferred causal links, since the difficulty of proving causation is a fundamental limitation of palaeoecology for understanding ecosystem drivers and responses. Thirdly, there is a need for critical analysis of the role of scale in ecosystem resilience. Different palaeoenvironmental proxies are differently able to address the various temporal and spatial scales of ecological change, and these limitations, as well as methodological constraints on inherently noisy proxy data, need to be explored and addressed.

Keywords

palaeoenvironmental; disturbance regime; environmental change; socio-ecological systems; ecosystem modelling; ecosystem dynamics

Introduction

Resilience has emerged as a focal theme in ecology and socio-ecological systems research, and as a key goal for management and policy (Holling 1973, Chapin et al. 2000, Folke et al. 2002, Sutherland et al. 2013). Ecological discussion of resilience now includes a growing critical literature that highlights terminological ambiguities and emphasises the challenges of defining and measuring resilience in practice (Brand & Jax 2007, Morecroft et al. 2012, Spears et al. 2015, Hodgson et al. 2015, Newton 2016, Allen et al. 2016). Alongside this debate and arising from the conceptual literature, a range of quantitative tools has been developed for assessing resilience, with an emphasis on detecting thresholds and changes in system characteristics that may provide early warning signals of impending regime shift (e.g. Carpenter & Brock 2006, Andersen et al. 2009, Dakos et al. 2012, Kefi et al. 2014).

While there is substantial debate over how to measure resilience in ecology, ecologists generally recognise two main definitions of resilience (e.g. Hodgson et al. 2015, Mori 2016). The first focuses on the recovery of a system back to its equilibrium state following disturbance, often measured by the rate of recovery (Pimm 1984); this is frequently called

‘engineering resilience’. The second focuses on the ability of a system to retain its current state, defined as the magnitude of disturbance that a system can tolerate or resist without or before rearranging into an alternative, functionally and structurally different state (Holling 1973, Gunderson & Holling 2002, Walker et al. 2004); this is also referred to as ‘ecological resilience’. Hodgson et al. (2015) have argued that both types of resilience are important in most ecological research settings, and that they should ideally be considered simultaneously.

There is a growing interest in resilience amongst palaeoecologists (Froyd & Willis 2008). Several relevant priority research questions have been identified by the community (Dearing 2008, Seddon et al. 2014b), including: How do past legacies affect the structure, dynamics and resilience of contemporary ecological and socio-ecological systems? What factors make some systems more resilient to environmental change than others? How do ‘slow’ (multi-decadal and longer) processes influence transitions from one quasi-stable state to another? Quantitative resilience metrics are also being translated from ecology to palaeoecology (Thomas 2016). However, applying ideas developed in one field (ecology) to another (palaeoecology) carries risks: subtly different or ambiguous definitions of resilience are likely to limit cross-study comparisons and undermine practical application (Côté & Darling 2010, Myers-Smith et al. 2012), including in ecological modelling (Allen et al. 2016).

Here we review the palaeoecological literature to understand the ways in which resilience concepts are being exploited and addressed by the palaeo-community. We identify three key issues that affect the study of resilience using palaeoenvironmental proxies: (1) the different meanings and types of ‘resilience’; (2) how we define and analyse a response model that connects the disturbance, response and causal mechanisms that underpin resilience; and (3) the influence of scale on the sensitivity of palaeoecological metrics for resilience. These form the basis for recommendations for future research that can strengthen palaeoenvironmental contributions to long-term aspects of ecosystem resilience.

Literature review

To assess the frequency and usage of resilience concepts amongst the palaeo-community, a literature search was conducted in Thomson-ISI Web of Science using the topic search terms (resilien* AND palaeo*) OR (resilien* AND paleo*). This returned 450 references (14/7/2016), which were reduced to 193 after a first stage review of title, keywords and abstracts to remove non-journal sources (books, datasets), duplicates, papers dealing with the pre-Quaternary period, references that did not include the search terms, used an alternative definition of resilience (e.g. chemical, taphonomic, rather than system behaviour), or did not contain palaeo-data, and papers that used the ‘pal(a)eo’ prefix in a non-ecological context (e.g. palaeodiet, palaeoanthropology) or as a biogeographic term (e.g. Paleoendemic). A second stage full content review excluded papers that did not include primary or secondary palaeo-data (e.g. papers that mentioned palaeo-data in passing as part of the broader context, discussion or implications). Finally, four papers were excluded as the articles were not available (two representing early use of the term in a palaeoecological context: Dodson 1986, Barnosky 1992). While this search strategy may exclude papers that use terms which are relevant to the concept of resilience (e.g. thresholds: Carrión et al. 2001, regime shift: Seddon et al. 2014a), the review considers many of these concepts and we draw on the broader literature in the discussion. To express the number of papers as a proportion of all palaeoecological papers published, an additional search was conducted using palaeoecol* OR paleoecol* as the search terms. This will not capture the full literature, but it provides a consistent basis for how the relative proportion of palaeoecological work on resilience has changed over time.

Our analysis shows that there has been a sustained increase in both the absolute number and proportion of papers addressing resilience in a palaeoecological context over the last 20 years (Fig. 1). In terms of their palaeoenvironmental context (Fig. 2), terrestrial ecosystems (including peatlands) are the most frequent study context, followed by aquatic or socio-ecological systems; resilience-based studies of geomorphic systems and faunal communities are rare. In a non-exhaustive assessment, 72% of the references (excluding review papers) used multiple proxies, with palynology as the most common technique (85 out of 162 non-review papers), followed by sedimentary, geochemical and geomorphological proxies (59 papers), then charcoal (43 papers), with approximately equal numbers of papers using palaeolimnological organisms (e.g. diatoms, chironomids, cladocera; 32 papers), plant macrofossils or phytoliths (32 papers), and cultural archives (archaeology, documents; 30 papers).

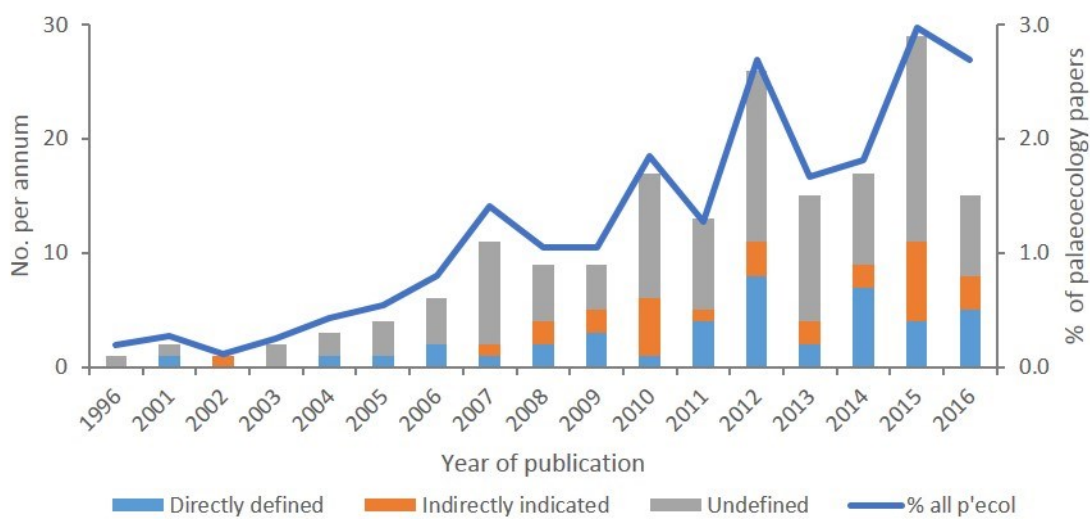


Figure 1. Number of published papers in Web of Science using resilience in a palaeoecological context, classified according to whether or not the term resilience was defined. Also showing palaeo-resilience papers as a percentage of all palaeoecological articles published in each year (up to July 2016)

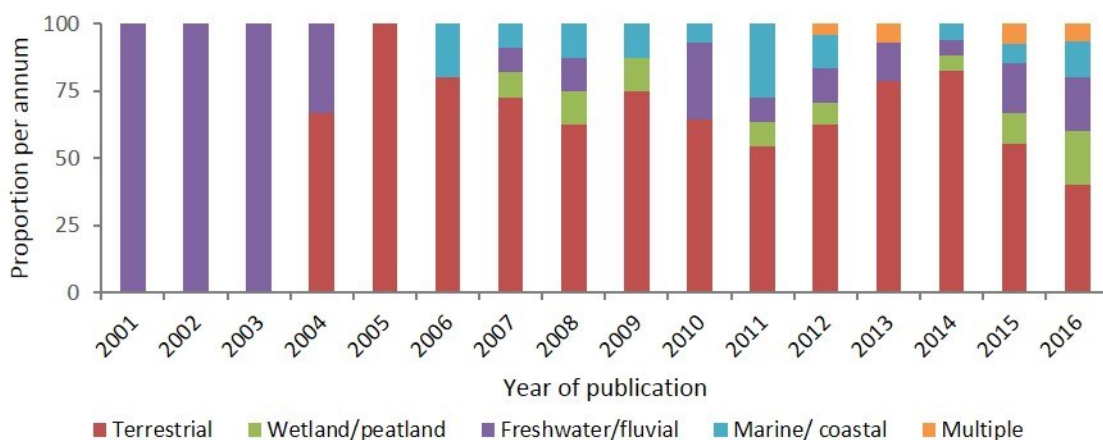


Figure 2. Ecosystem contexts in which resilience has been applied in palaeoecology, expressed as a percentage of palaeo-resilience papers published in each year

The terms used to discuss resilience have also become more explicit in the last 12 years, as indicated by the increase in papers where resilience is directly defined or indirectly inferred from the use of terminology from resilience theory (Fig. 1) (e.g. Holling 1973, Gunderson 2000). However, 61% of the papers reviewed offer no definition. Even where an explicit definition is given, there is considerable variation. Table 1 presents a selection of illustrative examples and indicates how these relate to the two definitions that are accepted in the ecological literature. Amongst the reviewed papers that provided a direct definition of resilience, 69% focused on 'ecological resilience' (e.g. Gillson & Eklom 2009, Seddon et al. 2011), but overall these studies provide examples of ecosystems that have exhibited both types of resilience. These include instances of recovery (e.g. Cole et al. 2014, Fregeau et al. 2015) and of tolerance (the ability to persist through or absorb disturbance, e.g. Brncic et al. 2007, Lynch et al. 2014, Eklom et al. 2012), as well as examples of reorganisation when disturbance levels exceeded the limits of tolerance and a critical threshold was crossed (e.g. Lopez-Merino et al. 2012, Spanbauer et al. 2014). Numerous studies (24% of direct definitions) mention both forms of resilience, represented by differences between sites or by a change in the type of resilience through time (e.g. Bhagwat et al. 2012, Lopez-Merino et al. 2012, Macken and Reed 2014, Kowlalewski et al. 2015, Cvetkoska et al. 2016, Ryan et al. 2016, Swindles et al. 2016).

Table 1. Examples of directly and indirectly defined resilience, and the context in which they were applied

Definition and key concepts	Context	Quote & source
Direct: ecological resilience (reorganisation)	Coastal geomorphology	“This research leads us to reflect on the concept of “coastal resilience” which, we conclude, means little without a clearly defined spatial and temporal framework... We therefore envisage multiple scales of “resilience” operating simultaneously across the complex, responding to different forcing agents with particular magnitudes and frequencies... “Coastal resilience” describes the self-organising ability of a coast to respond in a sustainable manner to morphological, biological and/or socio-economic pressures” (Long et al. 2006: 309-310)
Direct: ecological resilience (tolerance or reorganisation)	Mangrove	“The ability of an ecosystem to ‘tolerate or adapt to disturbance without collapsing into a different or qualitative state’... is an emergent property known as ecosystem resilience” (Seddon et al. 2011: 2) “According to resilience theory, the accumulation of slow processes can result in an erosion of resilience over time, making a system more susceptible to smaller perturbations and environmental changes. We propose that the historical period of disturbances occurring after 2000 cal yr BP, which had the effect of the opening up the mangrove canopy, caused an erosion of resilience at our study site” (Seddon et al. 2011: 9)
Direct: ecological resilience (resistance and reorganisation)	Biogeochemical systems	“Newer conceptualizations of complex adaptive systems and resilience in ecological systems highlight the important role of interactions, system feedbacks, and landscape contingencies when forecasting how disturbances affect ecosystems. Interactions between biogeochemical cycles and vegetation can reinforce current states or can result in shifts to alternate states, depending on the magnitude and timing of the interactions” (McLauchlan et al. 2014: 106)
Indirect: engineering resilience (recovery)	Peatland	“We hypothesize that these ombrotrophic peatlands are resilient to fire, and that local vegetation communities should return to pre-disturbance conditions within a short period of time” (Magnan et al. 2012: 110)

Indirect: ecological resilience (reorganisation)	Wetland	“The shifts between phases [identified using PCA] were probably due to reorganisations of the system when the limits of the mire to absorb disturbances were exceeded, although it was able to change its structure without substantial alteration of its function... Even [though] we have detected four phases and multiple states during the transitional phase between the minerotrophic mire and the tendency towards ombrotrophic conditions, La Molina mire seems to be an example of a system that successfully buffered the changes with a resilient nature. It was a mire and is still a mire” (Lopez-Merino et al. 2011: 2753)
Indirect: ecological resilience (reorganisation)	Forest	“[T]he decline of oak relative to the increase of birch, which became significant in the 1960s despite earlier disturbances, may imply that the oak-dominated forests in Takkobu have been pushed beyond their threshold of resilience by continuous anthropogenic disturbances” (Kumagai et al. 2008: 230)
Indirect: ecological resilience (resistance)	Coral reef	“Such community persistence may also be linked to an increased resilience of the coral communities to extrinsic disturbance events... because high suspended sediment concentrations... may alleviate light stress and provide alternative food sources for temperature-stressed corals... Thus high turbidity may, somewhat counterintuitively, aid the long-term stability of inner-shelf coral assemblages by buffering coral communities against extrinsic disturbance events” (Perry et al. 2008: 693)

Since 2008 a small proportion of the papers published annually have applied quantitative methods to assess aspects of ecosystem resilience (Fig. 3). These range from phase plots or scatterplots to represent changing interactions between system variables and drivers, to methods of detecting abrupt change, and comparison of metrics to differentiate between inherent variability (e.g. turnover) and significant functional shifts (see Table 2 for representative examples). Our classification of quantitative resilience papers excludes studies that use statistical tools to detect patterns in proxies or multivariate datasets (e.g. ordination, CharAnalysis, cross-correlograms) without explicitly relating the findings to resilience attributes. Papers applying quantitative methods are more likely to define resilience, either directly (48%) or indirectly (24%), than non-quantitative papers (undefined in 70% of cases).

[Insert Figure 3]

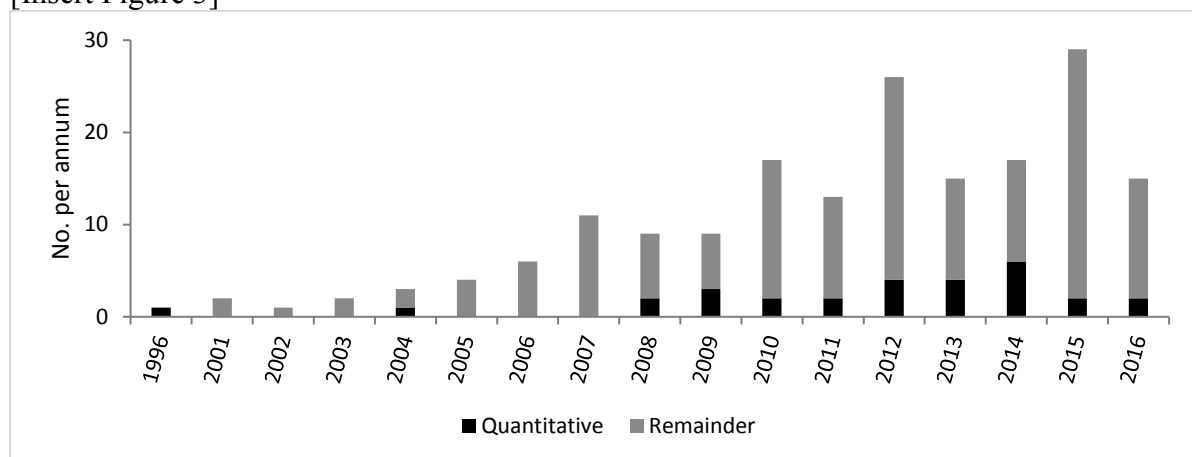


Figure 3. Total number of palaeo-resilience papers published each year, showing the number that applied quantitative tools to assess aspects of resilience. See Table 2 for examples

Table 2. Examples of quantitative tools and metrics used to assess palaeoecological resilience (i.e. statistical relationships between system and disturbance variables, or changes in system properties used in resilience theory)

Method	Example & insight into resilience
Ordination to test disturbance response	<p>Lopez-Merino et al. (2011) apply principal components (PCA)-based factor analysis to understand covariation between of hydro-hygrophyes (aquatic and wet-loving taxa) and non-pollen palynomorphs. This was used to identify structural changes in mire assemblage associated with wetland development and detect assemblage shifts which do not result in function change, indicating system ability to absorb disturbance (i.e. below threshold)</p> <p>Lopez-Merino et al. (2012) apply transposed PCA to examine co-variation amongst samples to classify response type following disturbance as threshold (complete assemblage change), elastic (recovery) or gradual (partial or complete assemblage replacement). They identified all three response types with centennial delays in regional scale woodland response compared with local disturbance mosaics</p> <p>Collins et al. (2013) apply analysis of similarity (ANOSIM) to five temporal groups identified from detrended correspondence analysis (DCA) of pollen data to test for significant changes in community composition before, after and during mid-Holocene dry event (MHDE) in Galapagos highlands. They identify significantly different assemblages during and after MHDE, but resilience of mesic taxa throughout suggests that the site is a microrefugium</p>
Recovery time	<p>Cole et al. (2014) calculate the time taken for 95.5% recovery in forest pollen abundance (compared with pre-disturbance levels) relative to rate of disturbance (average number of events at a site per 1000 years) in tropical forest, noting longer recovery intervals in forests with lower disturbance history</p>
Threshold testing via pollen-vegetation modelling	<p>Gillson (2009) tests the long-term applicability of an intervention threshold (threshold of potential concern, TPC) set by managers (using tree cover as an indicator of changes in woody vegetation resilience to elephant disturbance) by applying pollen-vegetation modelling to calibrate pollen abundance to tree cover over recent millennia. Results were used to suggest improvements in the choice of TPC as an early warning signal</p>
Phase plot, scatterplot to examine regime	<p>Gillson & Ekblom (2009) plot relationships between vegetation (arboreal and grass pollen) and (1) sedimentary $\delta^{15}\text{N}$ and (2) charcoal to depict threshold and quadratic associations, respectively. This allows the grassland–savanna transition to</p>

<p>shift</p>	<p>be explained in terms of a switch between nutrient/grazing limited and water/disturbance limited ecologies</p> <p>Willis et al. (2010) use phase plots to illustrate the rate of change over time in the abundance of key pollen taxa in Madagascan coastal forests to differentiate periods of relative stability prior to perturbation from post-disturbance trajectories and to represent the differing extent of recovery in two community types</p> <p>Seddon et al. (2011) use scatterplots to indicate the presence of alternative stable states (mangroves and microbial mat) in the lagoon system, with the main ecological change (alternative stable state threshold) inferred from a stable isotope mixing model showing shift in mangrove vs. microbial carbon inputs</p> <p>Bhagwat et al. (2012) use scatterplots to show variations over time in the relationship between forest: grass ratio (proxy for threshold changes in vegetation cover) and abiotic factors (monsoon intensity, soil erosion, fire). Redundancy analysis was used to assess how much variation in vegetation cover is explained by these variables. The strength of the association was assessed using (1) correlation coefficient (Pearson's r) and (2) quantile regression in recognition that relationships are unlikely to be stable over time and with different levels of vegetation cover (e.g. higher resilience to erosion and fire when tree cover is low)</p>
<p>Regime shift, breakpoint analysis</p>	<p>Rühland et al. (2013) apply two-segment, piecewise linear regression to identify critical values (i.e. breakpoints; Andersen et al. 2009, Toms & Lesperance 2003) in timeseries data for temperature, sea-surface temperature and diatoms to estimate the timing of threshold responses in subarctic lakes</p> <p>Zhang et al. (2015) identify significant breakpoints (critical transitions, regime shifts) in palaeoecological and socio-economic timeseries from sequential analysis of mean values using sequential Student's t-test (Rodionov 2004) and F-statistics (Andersen et al. 2009). A large number statistically significant breakpoints were identified, depending on timeseries duration and cut-off length. This was applied with a linear autoregressive model to test the hypothesis that breakpoints are an inherent feature of the timeseries. Early warning signal metrics were also applied (see below)</p> <p>Serrano et al. (2016) use the regime shift algorithm (Rodionov 2004, Andersen et al. 2009) to detect discontinuities in estuarine geochemical and sedimentary timeseries as signals of staged deterioration and regime shift associated with loss of seagrass</p>
<p>Superposed epoch analysis (SEA) to</p>	<p>Blarquez & Carcaillet (2010) use SEA to examine plant macrofossil influxes before and after fires, interpolated to a constant time-step of 15 years. This required data sorting in time windows relative to fire events to compare responses</p>

<p>assess sensitivity</p>	<p>between time windows & detect deviations from background. Fire return intervals were determined using CharAnalysis (Higuera et al. 2009). This allowed quantification of the minimum mean fire return interval (threshold) required for the study woodland to reach a resilient late successional stage</p> <p>Morris et al. (2015b) apply SEA to simulated datasets to test the null hypothesis that variability in biogeochemical proxies post-disturbance is greater than levels expected by chance and hence determine the sensitivity of a proxy to disturbance magnitude and duration, sample size and resolution</p>
<p>Dissimilarity & discontinuity analyses to assess regime shift</p>	<p>Figuroa-Rangel et al. (2010) detected significant differences in cloud forest assemblage (metrics: rarefaction, rate of change) and environmental variables using optimal splitting and one-way analysis of variance (ANOVA). Resilience (no state change) was inferred from high differences in rate of change (chord distance) but non-significant rarefaction differences among zones</p> <p>Spanbauer et al. (2016) apply Bayesian classification and regression tree models (BCART) to characterize size distribution of diatoms as means of detecting discontinuities in timeseries. Non-metric multidimensional scaling (NMDS) and ANOSIM were applied to assess whether the structure of discontinuities was impacted by regime shift &/or periods of instability identified by Spanbauer <i>et al.</i> (2014; see below). They identify discontinuity analysis as a conservative early warning signal</p>
<p>Early warning signals (EWS) of regime shift</p>	<p>Zhang et al. (2015) test for increased variance in timeseries as an indicator of critical slowing or flickering prior to regime shift (Dakos et al. 2012). This was applied alongside breakpoint analysis (see above)</p>
<p>Slow warning signals of regime shift</p>	<p>Spanbauer et al. (2014) compared univariate EWS (see above) with Fisher information (FI) and multivariate metrics of regime shift (redundancy analysis, principal coordinates of neighbour matrices analysis) in a diatom assemblage. FI characterises change in complex systems by collapsing variables into a single timeseries index based on the probability of a sample belonging to quasi-stable state. Unlike EWS, neither FI nor multivariate models require a priori knowledge of system behaviour and allow detection of slow system changes associated with loss of resilience preceding a regime shift</p>

Discussion

Defining resilience

Despite steady growth in the number of palaeoecological papers using the term ‘resilience’ (Fig. 1), 61% of the studies reviewed here did not identify which definition they were using and some of these made only passing use of the word. We considered that a further 14% indirectly defined the term through the use of descriptors associated with resilience theory (Table 1). For example, a number of studies discuss ‘persistence’ and therefore imply that they are discussing ecological resilience, not engineering resilience (Perry et al. 2009, Roche et al. 2011, Collins et al. 2013, Aranbarri et al. 2014). In this respect the palaeoecological literature follows a similar pattern to that seen in ecological research more generally: Myers-Smith et al. (2012) found that 66% of 234 ecology papers published between 2004 and 2011 did not identify which definition of resilience they applied. Perhaps some palaeoecologists, like ecologists more generally, feel that ‘resilience’ is a mature concept in no need of explicit definition, but the varied palaeoecological usage identified in this review indicates the opposite.

The consequent lack of clarity in palaeoecological discussions of resilience is a problem for several reasons. Without clear definitions, it is difficult to compare studies meaningfully or to draw general conclusions (Brand & Jax 2007, Cote & Darling 2010, Myers-Smith et al. 2012). This will make it difficult to address overarching research questions such as the priority questions listed in our introduction. By misapplying terminology related to processes, we risk perpetuating the misconception that palaeoecology is more concerned with describing patterns than with understanding the underlying mechanisms (Willis & Bhagwat 2010). And if we are unclear or inconsistent in how we use resilience terms, we are less able to engage constructively with ecologists and practitioners (e.g. Standish et al. 2014, Hodgson et al. 2015, Spears et al. 2015, Yeung & Richardson 2016).

Our proposed remedy is that palaeoecologists should be careful to (1) characterise as precisely as possible the disturbance regime in their study system, (2) explain how the ecosystem response (or lack thereof) to disturbance has been measured, and (3) explain how the causal mechanisms connecting disturbance to ecological response have been evaluated or inferred. These three components jointly comprise a ‘response model’ (Fig. 4), that is, an explicit statement of the anticipated relationships between proxies, disturbances and resilience properties (Carpenter et al. 2001, Myers-Smith et al. 2012, Hodgson et al. 2015). A response model should provide the necessary conceptual (heuristic) and measurable (quantitative) framework for assessing long-term ecosystem resilience. Only a minority of papers in this review identified or hypothesised a response model (e.g. Woodroffe 2007, Eppinga et al. 2009, Gillson & Ekblom 2009, Sayer et al. 2010, McLauchlan et al. 2014, Lopez-Merino et al. 2012). Calls for more explicit definition of response models have also been made recently in the fields of ecology and socio-ecology (e.g. Oliver et al. 2015, Angeler & Allen 2016, Cumming & Peterson 2017).

In the sections below we discuss the three elements of a response model further, before identifying outstanding issues and opportunities for future work. Throughout, we use

outbreaks of insect pests and insect-borne pathogens in forests during the Holocene to illustrate some key considerations associated with our proposed resilience response model (Table 3). Existing studies in this area have not yet explicitly applied resilience concepts, but it is an emerging topic of interest (Morris et al. 2017), and it provides a useful example because the ecosystem responses involved range from engineering (recovery) to ecological (reorganisation) resilience (Davis 1981, Waller 2013), and the data reflect many of the challenges associated with palaeo-resilience analysis, particularly *post hoc* application to existing datasets. Observed forest dieback events also provide insight into the pattern, scale and drivers of pest and pathogen outbreaks which can inform palaeoecological hypotheses and response models (e.g. Peglar 1993, Brunelle et al. 2008, Morris et al. 2013).

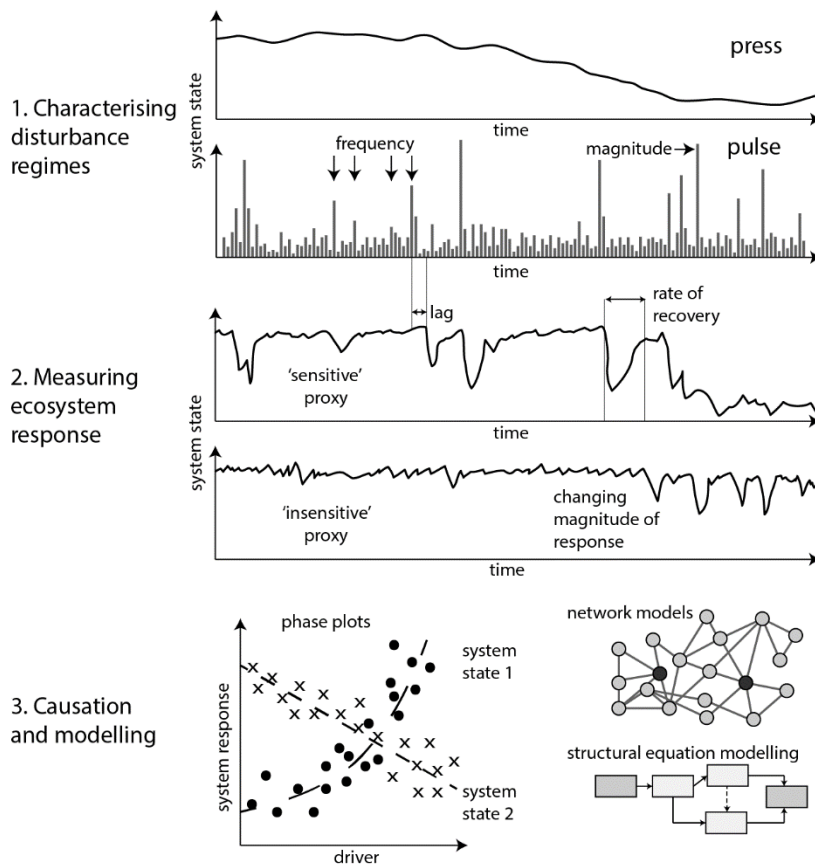


Figure 4. Response model for characterising resilience in timeseries, including an assessment of (1) disturbance regime, including pulse and press perturbations, (2) the ecosystem or proxy response, such as recovery rate and regime shift, and (3) an evaluation of causal relationships. The resolution and proxies may determine which definition or resilience and therefore which analytical methods are most appropriate at each of these stages

Table 3. Key methodological concerns and resilience attributes associated with insect pests and insect-borne pathogens in Holocene forests. See also Waller (2013: table 2) for general criteria advanced to support disease hypotheses

<p>Characterising the disturbance regime</p>
<p>Disease-driven disturbance regimes are challenging to identify: insect pest species are identifiable but their remains are relatively scarce in narrow-diameter cores (Morris et al. 2015a); presence of a fungal pathogen within insect vectors remains unproven (Waller 2013); parasitic fungal spores may represent secondary infection of stressed trees rather than the primary disease mechanism (Innes et al. 2006) and many are probably too fragile to survive (Waller 2013)</p> <p>Alternative proxies needed to detect disease dynamics, e.g. host to non-host pollen ratios (Morris & Brunelle 2012), fungal infection in spruce needles as proxy for disease stress (Jasinski & Payette 2007), or tree-ring data on growth impacts of disease (Payette et al. 2000, Sherriff et al. 2011)</p>
<p>Measuring ecosystem response and type of resilience</p>
<p>Initial impact: multi-site evidence of rapid, synchronous and widespread pollen reduction in host species (Davis 1981, Waller 2013), evaluated by comparing the size of the response with mean pollen variability (Peglar 1993) or host to non-host pollen ratio in outbreak and non-outbreak periods (Morris 2013, Morris et al. 2013)</p> <p>Chronological or spatial modelling can be used to assess the synchronicity or scale of impact (Parker et al. 2002, Caseldine & Fyfe 2006)</p> <p>Engineering resilience may be inferred from gradual or lagged host recovery (<i>Tsuga</i>: Davis 1981; <i>Ulmus</i>: Caseldine & Fyfe 2006; <i>Picea</i>: Brunelle et al. 2008)</p> <p>Ecological resilience may be indicated by partial host recovery with compositional change (e.g. due to migration, competition and growth-release in canopy or understorey taxa) (<i>Tsuga</i>: Davis 1981, Allison et al. 1986), permanent decline (<i>Ulmus</i>: Parker et al. 2002), or alternate stable state dynamics (<i>Picea-Cladonia</i> forest: Jasinski & Payette 2005)</p>
<p>Establishing causal interactions</p>
<p>Inferring causality: the fossil occurrence of insect remains with host pollen decline (spruce bark beetle: Brunelle et al. 2008), although co-occurrence is not universal (Morris & Brunelle 2012); the rare instance of insect remains, pollen decline and secondary fungal pathogen in host needles, indicating stress (Jasinski & Payette 2007)</p> <p>Modern analogue approach: Holocene incidence shows a comparable rate of host pollen reduction to modern disease impact, ideally with the remains of the inferred insect pest or fungal vector (Allison et al. 1986, Peglar 1993, Morris et al. 2013); causal explanations rely on high-resolution analysis of laminated sediments or recent sediments with secure chronological controls to demonstrate the comparability of past and recent events</p> <p>Informal hypothetical approach: qualitative comparison of competing explanations using multiple timeseries or sources of evidence, e.g. for climate, human activity (Davis 1981, Parker et al. 2002)</p>

Quantitative hypothesis-testing using modelling: GLMM used to compare pollen and catchment (erosion and nutrient availability) responses during endemic and outbreak phases (Morris et al. 2013)

Multiple proxies: inferences rely on multiple lines of evidence to identify outbreaks (Morris et al. 2013, Waller 2013), and to test potential interacting or alternative mechanisms, including climate variability as a trigger for pest or pathogen outbreaks (Latalowa et al. 2013), and human activity facilitating pathogen dispersal and impacts (Parker et al. 2002), or disease-fire interactions as a mechanism that maintains alternative stable states (Jasinski & Payette 2005)

Anomalous cases can support broader or temporally-specific explanations: e.g. insect remains with no pollen response in pre-elm decline sediments may indicate significance of interacting factors (Clark & Edwards 2004); the unusual persistence of *Ulmus* in western Ireland is interpreted as an absence of the pathogen, insect host or of susceptible host ecotypes on the western range margin of elm (Lamb & Thompson 2005)

Response model

Characterising disturbance regimes

McLauchlan et al. (2014: 106) pointed out that “[u]nderstanding long-term ecosystem resilience to disturbance requires a full characterization of disturbance regimes - the agent or mechanism of disturbance, as well as the magnitude, severity, and return interval”. In proxy systems, this is challenging: not all disturbances are equally amenable to quantification, particularly where multiple, interacting factors are inferred (e.g. burning, grazing and nitrogen availability; Gillson & Ekblom 2009, McLauchlan et al. 2014, Jeffers et al. 2015). Fire is one of the most commonly cited disturbance factors in palaeo-resilience papers (and in the ecological literature more generally; e.g. Millar & Stephenson 2015), and illustrates how far we can reasonably characterise a past disturbance regime in the palaeoecological record under more or less ideal circumstances. Metrics for quantifying fire regimes are well-established (e.g. CharAnalysis, Higuera et al. 2009) and have been widely used to identify individual fire events and quantify the fire return interval (e.g. Carcaillet et al. 2010, Crausbay et al. 2014, Lynch et al. 2014, Oris et al. 2014, Burjachs & Exposito 2015). The ability to analyse fire return intervals quantitatively in relation to a biotic response allows disturbance frequency and ecosystem recovery rates (‘engineering resilience’) to be estimated and compared between studies (e.g. Blarquez et al. 2012). Many other pulse disturbance events, including insect pest outbreaks, are less suited to this type of analysis due mainly to taphonomic constraints on insect preservation and recovery, for example (Table 3; Morris et al. 2015a).

Even with palaeofire studies, there are limits to the types of resilience we can readily explore. Repeated burning (disturbance) may eventually tip an ecosystem over a threshold, e.g. from forest to grassland. In this context, identifying fire events and return intervals remains useful, but limits us to considering ‘pulse’-resilience (to individual or episodic disturbance events) rather than ‘press’-resilience (to more gradual, longer-term forcing); and the interactions between different disturbance mechanisms remain challenging to explore (e.g. effects of disease on fuel load and fire frequency; Jasinski &

Payette 2007, Waller 2013; interactions between climate and disease outbreaks: Sherriff et al. 2011, Latalowa et al. 2013). It also remains difficult to address ‘ecological resilience’, as there is no universally applicable proxies or methods for quantifying the magnitude of many disturbance events (Cole et al. 2014). As a result, alternative methods of identifying disturbance regimes may need to be considered, as has occurred in efforts to identify Holocene outbreaks of forest pests and pathogens (e.g. Morris & Brunelle 2012). These examples illustrate the need to be specific about the disturbance regime and type of resilience that is being or can be studied using a particular proxy.

Measuring ecosystem response

The multitude of factors involved in ecosystem change can make it difficult to know what to measure in order to assess resilience, even in contemporary ecological studies (Oliver et al. 2015, Allen et al. 2016). This problem is compounded by the constraints of the proxy data that palaeoecologists rely on. For instance, pollen data are better suited to reconstructing large changes in the composition of a vegetation assemblage – switches from one quasi-stable state to another – than to measuring precisely the degree of stress that a system is experiencing (cf. Morris et al. 2015b). Given these constraints, the recovery rate of a palaeo-community following a (large) disturbance offers the most straightforward metric of engineering resilience (Cole et al. 2014). The use of recovery rate as a resilience metric assumes that systems are in equilibrium with prevailing conditions, which palaeoecologists know to be rarely, if ever, strictly true (Jackson 2006). Nonetheless, differences in the rate of recovery between sites can be used to assess which factors determine ecosystem sensitivity (Seddon et al. 2014b). Catchment and disturbance differences may, for instance, be useful for understanding why rates and levels of lake system recovery can range from rapid and complete, to slow and limited (Heiri et al. 2003, Donohue et al. 2010, Hillbrand et al. 2014, Barreiro-Lostres et al. 2015, Miras et al. 2015, Cvetkoska et al. 2016).

An apparent *lack* of response to disturbance – that is, stability, complacency or insensitivity of a proxy after a perturbation – could indicate a high level of ecological resilience in a system, an interesting result in itself (Bhagwat et al. 2012). A lack of response can be particularly instructive if stabilising or buffering factors can be identified (e.g. Balmford 1996, Perry et al. 2008, Carcaillet et al. 2010), but critical evaluation of the data is usually needed in order to be certain that the apparent complacency is not just an artefact of the insensitivity of palaeo-proxies or methods (Morris et al. 2015b).

Increasing sensitivity to perturbations or changes in recovery rate through time can signal a shift in tolerance limits, such as a transition from engineering to ecological (potentially threshold-type) resilience. For instance, in tropical forests, a non-linear relationship between disturbance frequency and the rate of recovery (e.g. a reduction in recovery rate with increasingly frequent disturbance) suggests that there are limits to the capacity of the forests to recover from disturbance (Cole et al. 2014). An understanding of how rates of recovery change through time in different ecosystems, and why system responses shift from recovery to reorganisation, would be a useful contribution from palaeoecology: ecological studies rarely address *why* different responses may emerge over time (e.g. Scheffer et al. 2001, Standish et al. 2014, Mori 2016). This requires studies that evaluate

how and why the resilience of an ecosystem can vary between sites, or change over time at a single site, which in turn requires clear and repeatable, ideally quantitative techniques for measuring regime change and recovery rates. Appropriate techniques are increasingly available: 16% of the studies reviewed applied quantitative tools to detect significant shifts in assemblage behaviour, including algorithms for detecting early warning signals and regime shift in timeseries (Fig. 4, Table 2).

We would not suggest that a quantitative approach is always essential, but it holds some advantages. It can encourage collaboration with ecology and environmental sciences, where there is a strong focus on quantitative metrics of resilience (Angeler & Allen 2016, Thomas 2016). Quantification can also be used to help test process-based questions and conduct comparative analyses in palaeoecology (e.g. Jeffers et al. 2011, Streeter & Dugmore 2014, Randsalu-Wendrup et al. 2016), which is a key aim of the PAGES Resilience Working Group (Seddon et al. 2014a). It may be no coincidence that, in our review, quantitative papers were more likely than qualitative ones to include a clear definition of ‘resilience’.

A key finding from multi-proxy studies, particularly quantitative analyses, is that ecosystem resilience is rarely adequately captured by a single metric, because the biotic and abiotic components that contribute to system resilience have different sensitivities, response rates and thresholds (e.g. Zhang et al. 2015). Ecological studies have reached similar conclusions, identifying a need to apply resilience metrics to multiple indicators and to consider resilience at species and ecosystem levels in order to derive more robust assessments (Angeler & Craig 2016, Burthe et al. 2016).

Causation and modelling

In the discussion above we have argued that precisely-defined and quantified studies, if not a prerequisite for assessing palaeo-resilience, can at least encourage clarity regarding the mechanisms that stabilise and restructure ecological and socio-ecological systems (Seddon et al. 2014a). However, demonstrating the existence of a causal mechanism linking disturbance and response is a fundamental problem in palaeoecology, as it often is in environmental science more generally (e.g. Hodgson et al. 2015, Cumming & Peterson 2017). It is fundamentally difficult to identify the processes of ecosystem response to disturbance simply by studying patterns of change in the past.

We suggest two ways in which response models may be used to explore the mechanisms of ecosystem resilience. Firstly, a response model can be used as a heuristic to set out potential explanatory relationships and feedbacks that may influence resilience, especially in *post hoc* applications of resilience theory to existing datasets or in systems which are poorly understood. For example, in the case of insect pest outbreaks, observed spatial variations in the timing and extent of the European mid-Holocene elm decline were used to develop hypotheses about causality, especially the interactions between disease, climate and human activity, and the potential for disease resistance in different populations of elms (Parker et al. 2002, Lamb & Thompson 2005). Similarly, Jasinski and Payette (2005) hypothesized two response models: one in which disease, fire and post-fire succession overcome species adaptive mechanisms that allow recovery from fire

disturbance, leading to alternative stable state forest communities; and another where a climate-mediated shift in fire regime leads to forest loss. These two models were then tested using palaeoecological data.

A second way in which response models can be used to frame palaeoecological resilience studies is to use numerical models of ecosystem behaviour, which incorporate hypothesised causal relationships explicitly, in conjunction with palaeoecological data. These include statistical and simulation models. One line of argument is to hypothesize a (conceptual) response model, attempt to simulate it using a numerical model, then test the combined model predictions using palaeoecological data. Another approach is to analyse palaeoecological datasets using statistical models which can identify non-random relationships between variables and estimate effect sizes. In this review, examples of numerical models used to assess potential causal relationships range from statistical two-way interaction models using phase space or scatter plots and non-linear regression (Gillson & Ekblom 2009, Seddon et al. 2011), to network models such as structural equation modelling (Lamentowicz et al. 2015), and simulation models based on ecophysiological tolerances (Cowling et al. 2014, Henne et al. 2015).

A strongly quantitative analytical approach is not always feasible. However, quantitative approaches could improve our understanding of which characteristics of a system and of a disturbance regime provide the best indicators of resilience (e.g. van de Leemput et al. 2017). This is particularly relevant where models of long-term behaviour are used to project future responses under climate change scenarios (e.g. Henne et al. 2015).

Scale and Resilience

One of the key concerns in understanding ecological resilience is scale, in terms both of space and time. Ecosystem responses to disturbance can vary across scales and are often conditioned by cross-scale interactions, where slow and fast variables interact to determine a system's proximity to critical thresholds (Peterson et al. 1998, Gunderson & Allen 2010, Hughes et al. 2013). Our discussion so far has assumed that the spatial and temporal resolution afforded by the sites and samples under study are appropriate to the temporal and spatial scales of the organisms (proxies) and processes under investigation. When this is the case, palaeoecology is well-placed to study the cumulative impact of slow and fast processes, to differentiate quasi-stable, self-regulating systems from those which are characterised by alternative stable states, and to examine response diversity across environmental gradients (e.g. Zhang et al. 2012, Oris et al. 2014, Jovanovska et al. 2016).

Few of the studies that we reviewed specifically considered whether the temporal sampling resolution was sufficient to support the inferred mechanism, or to reliably estimate response or recovery times (e.g. Cole et al. 2014, Morris et al. 2015b). Sedimentation rates and analytical choices, including sampling resolution and sample aggregation, can significantly affect our interpretation of palaeoecological data (Velghe et al. 2012, Macken and Reed 2014). For example, sampling resolution and the duration of a disturbance event affect the likelihood of differentiating between sensitivity and tolerance when examining biogeochemical responses to disturbance using proxies preserved in lake

sediments (Morris et al. 2015b). This issue is also evident in studies of tree disease, where comparisons of the rate of pollen reduction in modern tree disease outbreaks and prehistoric declines in tree pollen demonstrate that the rates of some prehistoric events are consistent with a hypothesis of pathogenic attack (and that recovery took centuries or millennia: Allison et al. 1986, Peglar 1993); detecting such an abrupt change required extremely well resolved data, given that disease outbreaks can last only a few years. Low sampling resolution can also constrain some quantitative approaches used to assess resilience, such as early warning signal metrics (Thomas 2016). Temporal resolution should therefore be an important consideration when selecting what form of resilience may be detectable and which resilience metrics are appropriate to the study system. Unevenly-spaced sampling and random variation may also generate noise that obscures the signal of system behaviour (Carstensen et al. 2013, Connor et al. 2017); such influences may only be detected by careful analysis of the consequences of methodological choices, e.g. using simulated datasets.

Resilience is inherently spatial, affected by the spatial extent of the perturbation and by spatial heterogeneity (Peterson et al. 1998, Gunderson & Allen 2010). These spatial aspects may be overlooked by single-site studies. Although a wide range of palaeoecological proxies has been used to address resilience, pollen analysis was the most common technique in the papers we reviewed. Palynology involves a spatially amalgamated signal of catchment vegetation, so sites with a large pollen source area, such as lakes, may be insensitive to the finer-grained disturbances that can influence community resilience in heterogeneous systems. The spatial resolution of the dataset must be compatible with the scale of inferred impacts. For instance, multi-site analysis may be needed to test the role of climate, disturbance and disease as causal mechanisms where regional gradients in resilience or local-level catastrophic events are hypothesized to exist (Jasinski & Payette 2005). Other proxies than pollen analysis are often intrinsically better suited to assessing finer-grained disturbances and their influence on community resilience, including the contribution of species diversity to local-scale ecological resilience and differences in resilience between components of a system (Angeler & Allen 2016). For example, biological proxies such as testate amoebae or macrofossils in peat bogs are likely to represent community responses on small spatial scales (e.g. Lamentowicz et al. 2008, Magnan et al. 2012, Blundell & Holden 2015).

Applying multiple proxies can strengthen palaeo-resilience analysis by providing evidence for how interactions between system components (e.g. across trophic levels) influence resilience. Palaeolimnological studies, particularly on small lakes, have proven to be productive in establishing how cross-scale trophic interactions affect ecosystem resilience (e.g. Madgwick et al. 2011, Velghe et al. 2012, Zhang et al. 2012). For instance, using plant macrofossil, pollen and diatom records, Sayer et al. (2010) identified a slow, internally-driven shift from macrophyte to phytoplankton dominance as a consequence of eutrophication, without the need to invoke an external perturbation to precipitate a transition between alternative state states. Such cross-scale interactions have received little attention in palaeo-resilience studies to date.

A growing number of studies use networks of sites to address resilience at the landscape scale. For example, multi-site studies using pollen and limnological proxies can identify asynchronous responses and differential sensitivity to disturbance between communities and along environmental gradients (e.g. Virah-Sawmy et al. 2009, Figueroa-Rangel et al. 2010, Oris et al. 2014). Such diverse species responses to environmental change are critical to ecosystem resilience (Elmqvist et al. 2003). This is particularly the case in socio-ecological systems, for example, when regime shift is recorded in several large lakes, but the shift is not yet detectable in regional socio-economic indicators. Rather than indicating a complacent or resistant system, the relatively slow and cumulative effects of social and economic pressures may be eroding broader ecosystem resilience (Zhang et al. 2015). Palaeoenvironmental databases such as the Global Pollen Database and Neotoma are likely to enable further such larger-scale analysis to take place (e.g. Cole et al. 2014, Whitehouse et al. 2014).

Conclusions

Resilience has become an important topic within theoretical ecology with significant applications in environmental management. Our review demonstrates that palaeoecology is making a significant contribution to our understanding of ecosystem resilience. However, we have also identified a number of ways in which the conceptualisation and investigation of resilience in palaeoecology could be improved. We make three recommendations:

1. Palaeoecologists should use ‘resilience’, and terms associated with it such as ‘sensitivity’, as precisely as possible. In particular, we should differentiate between ‘engineering’ and ‘ecological’ resilience. This applies to efforts to characterise disturbance mechanisms and to analyses of ecological responses to perturbations.
2. Palaeoecological resilience studies could be improved by defining a clear response model. Some of the most exciting advances in recent years have come from studies that integrate quantitative modelling with palaeoecological research. Data-model comparisons hold the potential to yield insights into the causal mechanisms that underpin ecosystem responses to disturbance, and to improve the ability of ecological models to adequately represent shifts in ecosystem resilience on a broad range of temporal and spatial scales.
3. Issues around temporal and spatial scaling should be considered explicitly during the project design stage. Cross-scale interactions are a particularly important aspect of resilience theory and careful attention to scale in palaeoecological research could illuminate the ways in which connectivity within a system contributes to resilience.

Declaration of Conflicting Interest

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