SPECIAL FEATURE – ESSAY REVIEW
ECOLOGICAL CONSEQUENCES OF CLIMATE EXTREMES

Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary

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Summary

1. Abrupt changes and regime shifts are common phenomena in terrestrial ecological records spanning centuries to millennia, thus offering a rich opportunity to study the patterns and drivers of abrupt ecological change.

2. Because Quaternary climate changes also often were abrupt, a critical research question is to distinguish between extrinsic versus intrinsic abrupt ecological changes, i.e. those externally driven by abruptly changing climates, versus those resulting from thresholds, tipping points, and other non-linear responses of ecological systems to progressive climate change. Extrinsic and intrinsic abrupt ecological changes can be distinguished in part by compiling and analysing regional networks of palaeoecological records.

3. Abrupt ecological changes driven by spatially coherent and abrupt climate changes should manifest as approximately synchronous ecological responses, both among different taxa at a site and among sites. However, the magnitude and direction of response may vary among sites and taxa. Ecological responses to the rapid climatic changes accompanying the last deglaciation offer good model systems for studying extrinsic abrupt change.

4. When abrupt ecological changes are intrinsically driven, the timing and rate of ecological response to climate change will be strongly governed by local biotic and abiotic processes and by stochastic processes such as disturbance events or localized climatic extremes. Consequently, at a regional scale, one should observe ‘temporal mosaics’ of abrupt ecological change, in which the timing and rate of ecological change will vary among species within sites and among sites. These temporal mosaics are analogous to the spatial mosaics observed in ecological systems prone to threshold switches between alternate stable states. The early Holocene aridification of the North American mid-continent and the middle-Holocene aridification of North Africa may be good examples of temporal mosaics.

5. Synthesis. Past instances of extrinsic and intrinsic abrupt change are of direct relevance to global-change ecologists. The former allow study of the capacity of ecological systems to quickly adjust to abrupt climate changes, while the latter offer opportunities to understand the ecological processes causing abrupt local responses to regional climate change, to test tools for predicting critical thresholds, and to develop climate-adaptation strategies.

Key-words: abrupt change, alternate stable states, aridity, climate change, critical thresholds, palaeoecology and land-use history, Quaternary, regime shifts

Introduction

Abrupt ecological changes were a common phenomenon during the late Quaternary. Examples include the rapid shifts in the abundances of plant and aquatic species and community composition in response to abrupt millennial-scale climate variations and glacial terminations (Birks & Ammann 2000; Williams et al. 2002; Grimm et al. 2006; Yu 2007), the locally to regionally abrupt conversion of North Africa from grassland to desert during the middle Holocene (deMenocal et al. 2000; Liu et al. 2007; Kröpelin et al. 2008), the rapid declines
in tree density at the Minnesotan prairie–forest ecotone during the early Holocene (Umbanhowar et al. 2006; Williams, Shuman & Bartlein 2009), and the crash in hemlock population abundances in eastern North America c. 5500 years ago (Davis 1981; Bennett & Fuller 2002). These ecological regime shifts (sensu Folke et al. 2004), well-documented by a variety of palaeoecological records, offer a rich opportunity to study the patterns and drivers of abrupt ecological change.

Often, these abrupt ecological changes were driven by similarly abrupt climate changes, which were also frequent and widespread during the Quaternary (National Research Council 2002; Alley et al. 2003; Climate Change Science Program 2008). The climate system varies at all time-scales (McDowell, Webb & Bartlein 1990; Overpeck, Whitlock & Huntley 2003; White et al. 2010), from interannual to interdecadal phenomena, such as El Niño and the Pacific Decadal Oscillation, to the abrupt shifts in ocean and atmospheric circulation at millennial to glacial/interglacial time-scales (Alley et al. 2003). These abrupt climatic changes include both rapid shifts in the mean state of the climate system (e.g. the rapid warming at the termination of the Younger Dryas) and strong, but temporary, climatic extremes overlaid on longer-term trends (e.g. the North American megadroughts during the middle to late Holocene, Cook et al. 2004; Booth et al. 2005). Indeed, palaeoclimatologists working with palaeoecological records often operate with the implicit assumption that abrupt ecological changes are de facto evidence of abrupt climate change.

However, not all abrupt ecological changes necessarily derive from abrupt climate change. There is growing concern among global-change ecologists about the potential for ecosystems to non-linearly and abruptly respond to the accumulating forces of multiple anthropogenic drivers. The terminology varies subtly – ‘tipping points’, ‘ecological surprises’, ‘thresholds’, ‘regime shifts’, ‘critical transitions’, ‘bifurcations’, etc. (Holling 1973; Paine, Tegner & Johnson 1998; Scheffer & Carpenter 2003; Folke et al. 2004; Burket et al. 2005) – but the underlying concern is the same: ecosystems are complex and are governed by a mixture of external drivers, positive and negative feedback loops, and fast and slow processes. As a consequence, ecosystems can exhibit apparent stasis (or resilience) when subjected to an external forcing such as climate change or enhanced nutrient loadings, until an internal threshold is passed and the ecosystem rapidly undergoes a large and abrupt regime shift (Scheffer & Carpenter 2003; Folke et al. 2004; Smith et al. 2009), perhaps to a new stable state (Scheffer et al. 2001; Dearing 2008). Nonlinearities can also arise from feedback loops between ecological systems and other complex systems such as the atmosphere.

In this review, we pose the question: when is abrupt ecological change in palaeo-records directly forced by abrupt climate change, and when does it result from nonlinear responses of ecological systems to relatively small environmental forcings (Fig. 1)? Put another way, when do past abrupt ecological changes result from thresholds in ecological systems, the climate system, or the two coupled together (Maslin 2004)? This is a big question, too big to be encompassed by a single paper, so here we tackle it by developing two contrasting paradigms, and illustrate each with representative case studies. In the ‘extrinsic’ paradigm, abrupt ecological change is externally driven by abrupt climate change. Although nonlinearities might be present also in the ecological system response, a strong and rapid climatic forcing is the primary causative agent of the abrupt ecological change. Case studies of abrupt ecological shifts are drawn from the responses of plant communities to abrupt climate changes accompanying the last deglaciation. In the ‘intrinsic’ paradigm, climate forcing is progressive and gradual, although overlaid by higher-frequency variability, and abrupt ecological change is driven by internal threshold-type dynamics in the ecological systems. These internal dynamics are strongly governed by site-specific abiotic factors such as soil characteristics, groundwater regime and physiography, and by local biotic interactions such as competition, facilitation and disturbance, which together cause heterogeneous local responses to a common regional climatic forcing. Case studies for this second paradigm are drawn from the Holocene dynamics of semi-arid and arid ecosystems in central North America and North Africa as they responded to increasing aridity.

Not all system behaviour falls neatly into these two paradigms, but this delineation is a useful heuristic for thinking about past abrupt ecological changes. Moreover, extrinsic and intrinsic abrupt changes are both relevant to global-change ecologists, with different implications. Past instances of extrinsically driven abrupt change allow study of the adaptive capacity of ecological systems with respect to abrupt climate change, while abrupt changes due to intrinsic ecological processes provide insight into the physical and biological mechanisms that promote threshold-type dynamics in ecological systems. A critical challenge is to distinguish between extrinsic and intrinsic abrupt ecological changes in palaeo-records, given that climatic drivers of past ecological change are always imperfectly known. Here, we illustrate how regional networks of long-term ecological records can be used to discriminate between the spatio-temporal fingerprints of abrupt ecological change produced by extrinsic versus intrinsic processes. Examples of past abrupt changes offer rich opportunities to better understand the patterns and drivers of abrupt ecological change and thereby predict abrupt changes in contemporary ecosystems.

Defining abrupt change, regime shifts and thresholds

‘Abrupt’ change and regime shifts in ecological systems are seemingly simple concepts that can be defined in at least four fundamental ways. The first and broadest is “phenomenological”: abrupt change occurs when one or more variables in a system rapidly jump from one state to another, at rates that are rapid relative to background rates of change. ‘Variables’ are defined broadly and can include measures of ecosystem function (e.g. productivity), community metrics such as biodiversity or the abundance of individual species, and other state variables such as lake turbidity or lake level. If this new state is persistent, then the abrupt change has resulted in a ‘regime
Fig. 1. Extrinsic versus intrinsic paradigms of abrupt ecological change. Panels (a) and (f) represent a trend in an external driver (abrupt or gradual), while the other panels show the differential responses of three local ecosystems (sites) to the driver. In the extrinsic paradigm, abrupt ecological change is directly caused by an external driver such as climate, which is itself changing abruptly (a). Various ecological responses are possible [e.g. linear (b) and unimodal (d)]. However, the direction of ecological change may vary among sites for species with unimodal responses (e). In panel (b), sites 1–3 differ in their sensitivity to climatic forcing, with site 1 the most sensitive, while in panel (d), sites 1–3 differ in their position relative to a species' unimodal response curve. In the intrinsic paradigm, abrupt ecological change emerges from nonlinear dynamics that are internal to the responding ecological system. Possible nonlinear ecological dynamics include: a threshold-type response (g), a hysteresis response (i), and a unimodal response (k). All cases produce a temporal mosaic of abrupt ecological responses to a gradual linear forcing (f), in which the timing, rate, and direction of abrupt change are governed by the properties of the local system. Because in this example the climate forcing is a simple linear trend, systems with threshold-type and hysteresis behaviour (g, i) produce similar observed responses (h, j). In panels (g) and (i), sites 1–3 differ in their ecological resilience (Gunderson 2000) to climatic forcing, with site 1 the least resilient. In panel (k), sites are placed at different positions on a species' response curve, causing the local rates and direction of species' responses to vary among sites (l).

shift' in the system (Folke et al. 2004). This phenomenological definition allows statistical recognition of abrupt change using various forms of change-point detection analysis (Umbanhowar et al. 2006; Andersen et al. 2009), but does not consider the drivers of those rapid changes. Nor does this definition constrain the time-scale of abrupt change, except that for regime shifts the time-scale of the change must be short relative to the time-scales of the preceding and following persistent states.

The second definition is 'impacts-oriented': an abrupt change is defined as a large shift that occurs 'so rapidly and unexpectedly that human or natural systems have difficulty adapting to it' (National Research Council. 2002). This definition is narrower than the first one, because it constrains the
time-scale of abrupt changes and regime shifts to time-scales relevant to policymakers and most ecologists, i.e. those that occur within a few decades to a century at most. A third and closely related definition is ‘organism-based’: a change is abrupt if its duration is shorter than the average lifetime of an individual for a selected species. The fourth definition is ‘mechanistic’: an abrupt change in a system is one that does not smoothly follow the forcing but is rapid in comparison to it (Rahmstorf 2001; Alley et al. 2003; Scheffer & Carpenter 2003). This mechanistic definition is also narrower than the phenomenological definition, because it is limited to abrupt changes that emerge from thresholds, positive feedbacks or other nonlinear behaviour within the responding system. This kind of abrupt change is most worrisome for global-change ecologists and ecosystem managers (Groffman et al. 2006) because of the difficulty of predicting in advance when a system will pass a threshold. Identifying ‘tipping elements’ of the earth system (Lenton et al. 2008) and developing tools to predict the proximity of a system to a tipping point are major foci of complex-systems research (Rietkerk et al. 2004; Dakos et al. 2008; Scheffer et al. 2009; Brock & Carpenter 2010). Like the first definition, this mechanistic definition does not constrain the time-scale of abrupt change.

Usually, when working with ecological records that span centuries to millennia, one must work backwards from effects to causes. One observes abrupt changes in palaeoecological records, and seeks to understand the drivers of these changes. This paper therefore uses ‘abrupt change’ in its broadest and phenomenological sense (Definition 1), when referring to the abrupt changes empirically detected in palaeoecological records. We use ‘thresholds’ and ‘tipping points’ to refer to the mechanisms underlying some observed abrupt changes, i.e. to refer to processes within ecological systems that trigger abrupt responses to a small external perturbation (Definition 4). We limit the scope of this review by focusing on abrupt ecological changes that result in regime shifts, i.e. persistent new ecosystem states of function, structure, identity and feedbacks (Folke et al. 2004).

We then divide these abrupt changes and regime shifts into two sets: ‘extrinsic regime shifts’, in which the abrupt changes in an ecological system are externally driven by abrupt climate change (Fig. 1a–e), and ‘intrinsic regime shifts’, which emerge from internal nonlinear dynamics within an ecological system or from positive feedbacks between the ecological system and other linked systems (Fig. 1f–l). Nonlinear dynamics that can cause intrinsic regime shifts include simple critical thresholds (Fig. 1g), hysteresis (Fig. 1i), or unimodal species response curves (Fig. 1k). Because we seek to connect the abrupt changes in the past to the abrupt changes that may occur this century, we focus on past abrupt changes that last roughly a century or less. Both extrinsic and intrinsic processes can and often do operate in concert to produce abrupt ecological change – the operation of one does not exclude the other. Nevertheless, understanding the relative influence of extrinsic and intrinsic processes on ecological dynamics is essential to understanding the ecological impacts of future climate change (Maslin 2004).

Extrinsic regime shifts: ecological and evolutionary responses to abrupt climate change

In the first paradigm, abrupt ecological change is simply a direct response to abrupt climate change (Fig. 1a). Thus, ecosystem responses should be synchronous with or slightly lag behind the climate forcing and ecological responses should be detectable and approximately synchronous at many sites (Fig. 2e). Species abundances and ecosystem variables will differ in their responses to a given climatic forcing, depending on the shape of their response to climate (e.g. linear vs. unimodal, Fig. 1b,d), but site-specific differences will tend to be small relative to the overall rate and timing of the regional response. For species with unimodal distributions along environmental gradients (Fig. 1d), the rate and direction of ecological response may vary among sites (Fig. 1e, Shuman et al. 2002a), but the timing of change also should be regionally synchronous (Fig. 2e). Overall, a strong and coherent signal of the climatic event will still be detectable in the ecological responses of most sites.

Given the strong climatic forcing, critical research questions centre on the capacity of ecological systems to adjust to the new climatic regime. Populations and species will respond to climate variability at varying rates, with lag times that vary depending on the key ecological and evolutionary processes. These can be grouped into Type A ‘immediate’ processes, which operate relatively quickly, and ‘Type B ‘full’ processes, such as dispersal-limited species migration or rates of evolutionary adaptation, which result in lagged species responses to the new climatic regime (Webb 1986). Thus, a critical need is to assess the rates at which species can ecologically and/or evolutionarily adapt to abrupt climate change. For example, if climate change happens so abruptly that large-scale migration cannot occur, then to avoid extinction, species need to persist in situ via phenotypic plasticity or adapt to the new local climate regime (Aitken et al. 2008). Long ecological records thus provide insights into the capacity of species to migrate or otherwise respond to abrupt climate change.

To illustrate these points, we review ecosystem responses to several abrupt climate changes during the last deglaciation: the Bolling–Allerød (BA) warming (14 700 years ago) and the initiation and termination of the Younger Dryas (YD) (12 900–11 700 years ago) (Fig. 3). These events, particularly the YD, are among the best-studied events, both climatically and ecologically, of the Quaternary. Both events are classic examples of hemispheric to globally abrupt climate change and offer the opportunity to study the adaptive capacity of ecological systems under rapidly changing climate regimes. We focus primarily on plant communities of eastern North America, but refer to examples from other regions and taxa.

**BØLLING–ALLERØD AND YOUNGER DRYAS**

Several abrupt climatic events occurred during the transition from the Last Glacial Maximum to the current interglacial: abrupt warming at the start of the BA and end of the YD, and...
I. Extrinsic abrupt ecological change

II. Intrinsic abrupt ecological change

13.0 ka

GISP2

14 000 12 000 10 000 8 000

Cal yr. BP

Fig. 2. Schematics of two case studies of extrinsic versus intrinsic abrupt ecological change. In the example of extrinsically forced change, a large, widespread and rapid change in temperature (a), such as temperature changes at the onset and termination of the Bolling-Allerød and the Younger Dryas, cause abrupt ecological changes that are synchronous with or slightly lag the climatic changes (c). When the frequency of abrupt ecological change is assessed across many sites, ecological changes that are strongly forced by abrupt climatic change will show a strong spatial and temporal coherence (e). In the intrinsic case study, a long-term progressive trend (e.g. regional aridification) is overlain by significant higher-frequency variability such as droughts and megadroughts (Cook et al. 2008) or by step changes in the mean climate system (b), and abrupt ecological responses are strongly mediated by site-specific critical thresholds (d). These site-specific critical thresholds cause abrupt ecological changes to be distributed across the entire period of aridification. However, clusters of site-level abrupt change may result from extreme climate events, which may trigger many sites simultaneously (f).

Fig. 3. Time series of (a) oxygen isotope variations at the GISP2 Greenland ice core in Greenland (Grootes & Stuiver 1997) compared with (b) the timing of major ecological events in New England, USA, vegetation history (Shuman, Newby & Donnelly 2009): the maximum abundance of Picea, the Pinus decline, the rise in Fagus pollen abundance above 1%, and the mid-Holocene Tsuga decline.
ampliation of around 9 °C in less than 70 years from 14 670 to
14 600 years ago, as measured from the Greenland Ice Sheet
Project 2 (GISP2) ice core (Severinghaus & Brook 1999). The
YD followed the BA and was characterized by abrupt cooling and
warming during the onset and termination of the period at
12 900 and 11 700 years ago, respectively (Steffensen et al.
2008). At the start of the YD, atmospheric circulation over
Greenland and Europe may have changed within a single year
(Brauer et al. 2008), followed by cooling over several decades.
Warming at the end of the YD occurred even more rapidly
than cooling at the onset (Alley et al. 1993). On Greenland,
temperatures rose by roughly 15 °C, with about half of the
warming occurring over just a few decades (Dansgaard, White
& Johnsen 1989; Taylor et al. 1997; Severinghaus & Brook
1999; Alley 2000).

The precise drivers of these abrupt climate changes remain a
subject of intense palaeoclimatic research, but most explana-
tions invoke shifts in the rate of deepwater formation in the
North Atlantic and the resulting effects on heat transport by
Atlantic meridional overturning circulation (AMOC, Sever-
inghaus & Brook 1999; Alley 2000; Clark et al. 2002b; Mc-
manus et al. 2004; Carlson et al. 2007; Liu et al. 2009; Denton
et al. 2010). Climatic signals associated with the BA and YD
are seen most strongly in the North Atlantic and surrounding
regions (Shakun & Carlson 2010), but due to the links between
AMOC and the global atmospheric circulation, these events
are recorded in climate time series world-wide (Petet 1995;
Wang et al. 2001), although the manifestations vary globally
and include antiphased temperature changes between the
northern and southern high latitudes (Denton et al. 2010).

Here, we focus on records from the Northern Hemisphere
where the ecological effects of rapid temperature change
should be easiest to detect and quantify.

Many pollen records from eastern North America record a
sequence of vegetational events that clearly reflect the influ-
ence of BA warming, followed by cooling at the onset of the
YD, and warming at the termination of the YD (e.g. Mott
et al. 1986; Shuman et al. 2004; Gonzales & Grimm 2009).
As early as 1951, Deevey noted similarities between New
England vegetation history and the ‘Allerod oscillation’
between the Older Dryas and YD periods reported by Euro-
pean stratigraphers. He delineated a sequence of formal pol-
len zones for the New England region that has since been
demonstrated to correspond well with the climate history of
the late-glacial period (Deevey 1951; Shuman et al. 2004).
Further analyses of pollen records from New England have
shown that many ecological events occur synchronously
among sites and with known abrupt climatic events (Fig. 3),
consistent with the expectations of externally forced eco-
lological regime shifts (Fig. 2). In another example, the classic
BA–YD-Holocene signal is very clearly reflected in both the
isotopic climate signature (δ18O) and the late-glacial vegeta-
tion history at White Lake, NJ, USA (Yu 2007). Climatic
and ecological signals of the BA and YD may have been
delayed at White Lake by roughly 300–400 years after their
occurrence in other North Atlantic records (Yu 2007), but
within the site there is very little lag between climate change
and vegetation response. Indeed, responses to YD cooling
and warming were simultaneous within the sampling resolu-
tion (30–100 years), and there was a slight lag with BA warming
(c. 200 years) (Yu 2007).

Ecological records from New England and eastern Canada
confirm rapid and near-synchronous ecological responses to
climatic change at many different sites (Fig. 2e), as well as in
other taxa. In this system, there was

Intrinsic regime shifts: tipping points and temporal mosaics

In the second paradigm, a long-term progressive climatic trend is overlain by higher-frequency variability (Fig. 2b). Local ecosystems are differentially sensitive to climatic forcing, exhibiting different mixtures of linear and nonlinear responses (Figs 1g,i,k), and site-specific factors strongly govern the local ecological response. Spatial variations in high-frequency climatic events, such as droughts, and stochastic processes, such as fires and other disturbances, can determine when a system experiences a regime shift (Paine, Tegner & Johnson 1998). As a consequence, the rate and timing of ecological change varies widely among sites (Fig. 2d). However, at a regional scale, extreme climate events can simultaneously force multiple local systems past their tipping points, resulting in clusters of abrupt change (Fig. 2f).

A confident attribution of past abrupt ecological changes to internal tipping points is difficult in general and nearly impossible for single sites. Paired palaeoclimatic and palaeoecological records at individual sites can be highly suggestive, if they show abrupt ecological changes in the apparent absence of any abrupt climate changes. However, because the palaeoclimatic history at any single site is always imperfectly known, it is hard to rule out the possibility that abrupt ecological changes observed at that site were forced by an unknown but suddenly changing external driver (Fig. 1a).

Regional networks of high-resolution and well-dated palaeoecological records enable powerful assessments of the causes of abrupt ecological changes (Waller, Street-Parrot & Wang 2007; Fritz 2008; Kuper & Kröpelin 2008; Williams et al. 2010). Specifically, if locally abrupt ecological change is caused by systemic non-reversible thresholds that emerge from the interaction between regional climate forcing and site-specific factors (Fig. 1f–l), then one should observe a ‘temporal mosaic’ of local responses to the regional forcing:

1. differences in the timing of abrupt ecological change among sites (Fig. 2d),
2. variable rates of ecological change among sites, with some sites changing abruptly and others not and
3. variable rates of ecological change among taxonomic groups within a site, with some taxa changing abruptly and others not.

This may sound like a description of random noise (Blauw, Bennet & Christen 2010) or the localized dynamics of non-climatic processes, and in practice, temporal mosaics, caused by ecological tipping points that are driven by regional climate change, can indeed be difficult to distinguish from purely random or locally driven processes. However, two additional criteria for temporal mosaics aid this distinction:

4. the direction of the regime shifts must be replicated across sites such that the large majority of the local systems are shifting in the same direction (e.g. from a ‘wet’ state to a ‘dry’ state), even if the details of timing and rate vary among sites (Fig. 2d,f), and
5. the new state must be persistent, indicating that the progressive climate forcing has forced the ecological system past a critical threshold into a new stable regime (Scheffer & Carpenter 2003).

The concept of temporal mosaics is closely related to the spatial mosaics and patterning exhibited among sites within regional systems that are prone to threshold switches between alternate stable states (Rietkerk et al. 2004). Spatial mosaics occur when localized positive feedbacks create self-organized and locally homogenous systems within a regional spatial mosaic. Temporal mosaics occur when these spatial mosaics are subjected to a gradual external forcing, causing the relative balance of stabilizing and destabilizing feedbacks to shift. Because this balance is governed in part by local, system-specific factors, the timing and rate of change will vary among locations within the spatial mosaic, resulting in a temporal mosaic of site-level responses. Inter-site heterogeneity in the timing and rate of ecological change in palaeoecological records can also result from heterogeneous data quality, e.g. low temporal sampling resolution or low precision and accuracy in the chronological controls used to establish a time-scale for palaeo-records (e.g. Grimm, Maher & Nelson 2009). This alternative hypothesis, however, can be tested and potentially rejected by restricting the regional analysis to sites with well-constrained ages and by identifying differences in timing that are too large to be explainable by dating imprecision (Williams et al. 2010).

To illustrate the above points, we review case studies of systems characterized by locally to regionally abrupt regime shifts during periods of progressive long-term climate change. The first case study reviews the response of the Great Plains and surrounding ecosystems in central North America to increasing aridity during the early to middle Holocene, while the second case study reviews the response of the North African Sahara and Sahel to increasing aridity during the middle to late Holocene. These examples were chosen because semi-arid ecosystems provide some of the best examples of ecological thresholds, positive feedbacks and alternative stable states (Wang & Eltahir 2000; Sternberg 2001; van de Koppel & Rietkerk 2004), and locally to regionally abrupt changes are well-documented in these systems during the Holocene (e.g. Grimm 1983; deMenocal et al. 2000; Umbanhowar et al. 2006; Waller, Street-Parrot & Wang 2007; Williams, Shuman & Bartlein 2009).

Central North America

Central North America east of the Rocky Mountains is a moisture-limited system, characterized by a strong west-to-east gradient of increasing precipitation and soil moisture, and a suite of semi-arid ecosystems (Grimm 2001). Diverse ecological and physical systems in central North America have been strongly responsive to hydrological variations during the Holocene, including shifts in rates of tree growth (Cook et al. 1999); the abundance of C3 and C4 grasses (Nordt, von Fischer & Tieszen 2007) and other herbaceous taxa (Grimm 2001; Clark et al. 2002a); the position of the prairie–forest ecotone (McAndrews 2007).
fire frequency and biomass burnt (Clark 1988; Brown et al. 2005); lake levels, lake salinity and aquatic community composition (Laird et al. 1996, 2003; Shuman et al., 2002a); flood frequency and magnitude in fluvial systems (Knox 2000); and switches in aeolian systems between active and vegetation-stabilized (Forman, Oglesby & Webb 2001; Wolfe, Ollerhead & Lian 2002; Miao et al. 2007). The long-term hydrological trends for this region are well known: central North America became progressively drier until c. 8000–6000 years ago (timing varies within the region). It then became gradually wetter, reaching conditions similar to present, around 4000 years ago (Forman, Oglesby & Webb 2001; Nelson & Hu 2008; Williams et al. 2010). These trends are linked to the early Holocene peak in summer insolation (Fig. 4a), which increased summer temperatures and evaporative demand in the Great Plains (Kutzbach et al. 1998) and may also have suppressed summer precipitation by driving a dynamical shift towards regionally descending vertical air motion and clear-sky conditions (Harrison et al. 2003; Diffenbaugh et al. 2006). The retreat of the Laurentide Ice Sheet (and its collapse 8400 years ago) may also have promoted mid-continent warming by altering atmospheric circulation, moisture advection and the position of storm tracks (Shuman et al. 2002a; Shuman & Donnelly 2006). Higher-frequency drought episodes (with durations of decades to centuries) are superimposed upon these long-term trends (Woodhouse & Overpeck 1998; Clark et al. 2002a; Laird et al. 2003; Miao et al. 2007).

In response to these hydrological changes, the prairie–forest ecotone first shifted eastwards during the early Holocene, then westwards during the late Holocene, presumably in response to increasing moisture availability (Williams, Shuman & Bartlein 2009). These ecolonal dynamics were asymmetric, in that the early Holocene conversions of local ecosystems from forest to prairie were rapid (century-scale) while the late Holocene reforestation was gradual (millennium-scale) (Umbanhowar et al. 2006; Nelson & Hu 2008; Williams, Shuman & Bartlein 2009). At some sites, this asymmetry is also evident in δ18O, dust flux, sediment magnetic properties and other abiotic indicators of regional aridity (Nelson et al. 2006; Nelson & Hu 2006), which suggests that in some instances, rapid deforestation at the prairie–forest ecotone was directly caused by extrinsic climate change, perhaps linked to the collapse of the Laurentide Ice Sheet. However, the timing and rates of deforestation were heterogeneous in space and time (Grimm 1983; Camill et al. 2003; Nelson et al. 2006; Umbanhowar et al. 2006). For example, Sharkey Lake and Kimble Pond, in south-central Minnesota, both record decreasing abundances of arboreal taxa during the early Holocene and increasing charcoal influx, but at Sharkey Lake, the rate of charcoal influx is rapid and begins 8000 years ago, while at Kimble Pond, the increase is more gradual and begins a bit later, c. 7500 years ago (Camill et al. 2003). Rates of decrease in arboreal pollen abundances also are faster at Sharkey Lake than at Kimble Pond. Regional synthesizes of early Holocene fossil pollen records and other indicators of aridification show spatial variability in the timing of change, with a cluster at c. 8000 years BP (Fig. 4b, Williams et al. 2010).

The early Holocene dynamics of the prairie–forest ecotone thus appear to offer an example of a temporal mosaic, in which the often abrupt, but temporarily heterogeneous shift from forest to grassland is caused by strong positive feedbacks among fire, climate and vegetation that promote two alternate stable states within the same climate regime: a forested state, in which a low availability of dry fuels reduces fire severity and forest regeneration is not dispersal-limited, and a grasslands state, in which fires inhibit recruitment and encroachment of woody species and regeneration is further limited by dispersal limitation from scattered forest patches (Grimm 1983, 1984; Umbanhowar 2004). A progressive external forcing will shift the relative balance among positive and negative feedbacks, controlling rates of tree regeneration and fire regime and pushing these systems to new persistent states. Because the threshold for forest persistence will depend on the interaction between fire regime (heavily influenced by local factors and stochastic processes such as fire ignition), the spatial distribution of forest patches, and regional climate change, the timing and rate of deforestation will vary widely among sites (Fig. 1g,i,k, Grimm 1983; Camill et al. 2003; Umbanhowar 2004), as will the relative importance of direct climatic controls on vegetation versus indirect controls manifested via changes in fire regime (Nelson & Hu 2006). However, time-transgressive patterns may be observed within this temporal mosaic.

Fig. 4. Regional climate drivers of early Holocene aridification in the Great Plains, USA, and the spatiotemporal distribution of abrupt ecological responses (Williams et al. 2010). (a) Temporal trend in June, July, and August insolation for 40° N expressed as differences from present (solid line) (Berger & Loutre 1991) and the rate of change of the area of the Laurentide Ice Sheet (dashed line) (Dyke 2004, P. Clark, pers. comm.). (b) The temporal distribution of locally abrupt changes in central North America, including shifts in the relative abundances of C3 and C4 plants, shifts in tree cove density, and variations in lake level and salinity. (c) The same data as in (b), plotted against longitude, showing a west to east time-transgressive trend.


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because (i) the ecotone is situated on a moisture gradient, and so more arid sites may be nearer to a threshold than less arid sites (Williams, Shuman & Bartlein 2009; Williams et al. 2010), and (ii) as the ecotone shifts, the supply of tree seeds can change exponentially due to metapopulation dynamics at range margins (Levin & Clay 1984). Once the forest-to-grassland conversion is locally complete, the enhanced fire regime and reduced seed rain may prevent woody encroachment, even if climatic conditions are suitable for tree regeneration. Note that if this system was subjected to a large and abrupt external forcing (e.g. a widespread, severe and persistent drought), then the site-level responses could be essentially collapsed into a single synchronous regional-scale change (Fig. 1c,e). For example, post-fire succession from forest to grassland could be synchronized at decadal scales by a widespread, severe event.

Despite strong local-scale heterogeneity, spatial structure in the regional timing and patterns of ecological change can provide insights into the relationship between regional climate change and local response. For example, a synthesis of palaeoecological and palaeohydrological proxies from the Great Plains (Williams et al. 2010) shows that the timing of site responses to aridification was time-transgressive, with western sites beginning to dry before eastern sites. This time-transgression was also apparent in sites with abrupt responses to aridification (Fig. 4c), suggesting that the ecological resilience to aridification was lower for the more xeric western sites, causing them to pass their tipping points before eastern sites. (A possible alternate hypothesis is that the early Holocene decrease in moisture availability propagated eastwards in the central US causing an extrinsic forcing of abrupt change that was time-transgressive, Williams et al. 2010). Superimposed on this regional trend are a cluster of abrupt changes at c. 8000 years ago (Fig. 4b), which roughly corresponds to the collapse of the Laurentide Ice Sheet and the perturbation of the climate system with a meltwater pulse to the North Atlantic (Alley et al. 1997; LeGrande et al. 2006). In central North America, the collapse of the Laurentide Ice Sheet may have forced a step change of the climate system towards a drier state, through shifts in atmospheric circulation patterns and the paths of moisture transport (Shuman et al. 2002a). Thus, the overall picture from central North America is one of progressive aridification during the early Holocene, perhaps accelerated at times by extrinsically driven events such as the 8200 event, which resulted in a temporal mosaic of local response, with sites varying widely in the rate and timing of response.

NORTH AFRICA

The widespread shift of the Sahara from ‘green’ grassland to ‘brown’ desert (Claussen 1998) is perhaps the most drastic ecosystem transformation of the Holocene. In North Africa, the ‘African Humid Period’ began around 12,000 years ago and ended between 5000 and 3000 years ago (Gasse 2000; deMenocal et al. 2000; Waller, Street-Parrot & Wang 2007; Kuper & Kröpelin 2008) (Fig. 5). During the humid period, much of now-desert North Africa was covered by grasslands, Sahelian woodlands extended further north, lake levels were higher than at present, and prehistoric societies occupied lands that are now largely uninhabitable (Jolly et al. 1998a,b; Kohfeld & Harrison 2000; Kuper & Kröpelin 2008).

Holoceine aridification in North Africa was externally driven by precession of the Earth’s orbit, which has gradually weakened summer insolation from a peak 11,000 years ago to its current low. Insolation regulates land–ocean heating contrasts and hence the strength of the North African and other subtropical monsoons (Kutzbach 1981). The insolation-driven weakening of monsoonal summer precipitation likely was amplified by positive feedback loops between the atmosphere and the ocean (Kutzbach & Liu 1997) and the atmosphere and land surface (Ganopolski et al. 1998). Earth system models have predicted that the North African grasslands may have abruptly collapsed in response to gradual insolation forcing, either due to positive hydrological coupling between the land surface and the atmosphere (Ganopolski et al. 1998; Claussen 1998).
et al. 1999; Wang & Eltahir 2000) or by a threshold response of North African vegetation to precipitation variability overlaid on a progressive decrease in precipitation (Liu et al. 2007). Abrupt desertification is supported by many palaeocological and palaeoclimatic records from the region, most particularly by marine records from western North Africa that show abrupt increases in aeolian dust fluxes c. 5500 years ago (deMenocal et al. 2000). This evidence has led to a widespread view of North Africa as a classic example of a tipping element in the earth system capable of regionally catastrophic shifts between alternate stable state (e.g. Schefter et al. 2001; Lenton et al. 2008).

A fuller consideration of palaeoecological and palaeoclimatic records from north-western and north-central Africa, however, suggests that the regional history of desertification was considerably more complex than a simple synchronous and abrupt regional shift forced by positive biosphere–atmosphere couplings (Waller, Street-Parrot & Wang 2007; Kuper & Kröpelin 2008). Instead, local rates of response to aridification varied widely in rate and timing, both among sites and among different ecological communities at the same site (Fig. 5). For example, at Lake Yoó in northern Chad, the sequence of vegetation changes at the site strongly indicates that drying began around 5600 years ago and continued until 2700 years ago (Kröpelin et al. 2008). Several abrupt ecological events punctuated this progressive trend, such as abrupt shifts in chironomid and diatom assemblages between 4200 and 3900 years ago, consistent with a rapid salinization of the lake (Kröpelin et al. 2008), and rapid increases in Poaceae and Typha abundances 2700 years ago, consistent with further lake salinization and swamp expansion. At the Manga Grasslands in north-east Nigeria, multiple pollen records drawn from interdune swales show an abrupt onset of more arid conditions, but the timing varies among sites from 5150 to 3150 years ago (Waller, Street-Parrot & Wang 2007). Vegetation changes at Lake Tilla in Nigeria indicate that drying may have begun as early as 7600 years ago (Salzmann, Hoelzmann & Morczinek 2002). A regional synthesis of archaeological records from North Africa indicates that human depopulation began first in the north around 7300 years ago and progressed southward until around 3400 years ago (Kuper & Kröpelin 2008).

Thus, as in the Great Plains, the general pattern is a temporal mosaic of site-level responses to regional aridification, consisting of (i) a consistent shift among sites towards a more arid state with (ii) strong variations among (and within) sites in the timing and pace of change. Abrupt ecological changes are common, but highly variable in timing. The timing is too variable to be explainable by poor chronological precision. Thus, the available data strongly suggest that ecologically abrupt change in Holocene North Africa is governed not by positive atmosphere–vegetation feedbacks operating at the regional scale, but instead by local, site-specific thresholds (Kröpelin et al. 2008). As in central North America, the time-transgressive trend (here recorded in the archaeological data synthesis) suggests that tipping points for the more xeric northern sites were passed before the tipping points for more southern mesic sites (Kuper & Kröpelin 2008). Other regional syntheses of lake-level records suggest that the progressive aridification of North Africa may have been overlaid by episodes of pronounced drought, signalled by clusters of lake-level declines across sites (Gasse 2000). One such episode may have occurred 4200 and 4000 years ago (Gasse 2000), although recent reanalyses at Lake Botswunami, Ghana, suggest that the abrupt changes in lake hydrology may have occurred more recently, c. 3200 years ago (Russell, Talbot & Haskell 2003).

**Abrupt ecological changes in the past: implications for global-change research**

Most research on abrupt change during the Quaternary has had a palaeoclimatic emphasis, in which the primary goal is to understand the drivers of abrupt change within the earth system (Rahmstorf 2001; Alley et al. 2003; Schneider 2004; Claussen 2009). However, given the strong need to develop climate-adaptation strategies (Pielke et al. 2007), particularly for ecosystem managers (Groffman et al. 2006; Millar, Stephenson & Stephens 2007), there is increasing interest in using palaeo-records to understand the patterns and processes governing past abrupt ecological changes. Abrupt and intrinsic abrupt changes carry distinct implications for global-change ecologists. In the following sections, we discuss this in more detail.

**EXTRINSIC ABRUPT CHANGE AND REGIME SHIFTS**

The rapid climate changes accompanying the last deglaciation offer model systems for studying the response of species and ecosystems to abrupt climate change, with rates and magnitudes of climate change that are comparable to those projected for this century (Overpeck, Whitlock & Huntley 2003). Species respond to rapid climatic change in three ways: they can become extinct, persist in situ, and/or migrate to more suitable habitats (Aitken et al. 2008). As opposed to the well-known late Pleistocene extinctions in vertebrates (Barnosky et al. 2004; Burney & Flannery 2005), climate-driven extinctions were minimal in tree communities during the last deglaciation. Only one plant species in eastern North America is known to have become extinct since the last glacial maximum (*Picea crichi菲尔di*), although the cause of its extinction is unknown (Jackson & Weng 1999). Thus, the late-Quaternary fossil record generally suggests that rapid climate change alone does not trigger plant species extinctions (Botkin et al. 2007), although it is possible that other extinction events remain unrecognized.

Immediate in situ responses such as population expansion certainly occurred during the rapid, late-glacial climate oscillations. Some of the species that showed strong responses to the BA and YD climate oscillations (such as *Picea*) were already locally present, so much of the response observed in the pollen diagrams of single sites is likely due to in situ changes in population abundances. These suggest that demographic processes in plant populations are quite sensitive to abrupt climate change, with initial time lags measured on the order of decades (Ammann et al. 2000; Williams et al. 2002; Yu 2007). Addi-
tional high-resolution palaeoecological records would help constrain the timing and trajectory of local population responses to abrupt climate change.

A key policy question at present is whether species will be able to migrate fast enough to track current rates of climate change, or whether they will require assistance by transplanting populations outside their historic ranges (i.e. assisted migration, McLachlan, Hellman & Schwartz 2007). Migration was a primary response of plant species to past climate changes (Davis 1976; Williams et al. 2004), but estimates of past rates of plant and tree migration range widely, from < 0.1 km year\(^{-1}\) to 1 km year\(^{-1}\) (Pearson 2006). These estimates of tree migration rates during deglaciation encompass the spatial velocity of projected temperature change under the Intergovernmental Panel on Climate Change A1B emissions scenario (Loarie et al. 2009), estimated to have a mean rate of 0.42 km year\(^{-1}\) and rates that vary by biome (e.g. 0.35 for temperate broadleaved and mixed forests). Estimates of recent range shifts for some species exceed the mean rate (0.61 km year\(^{-1}\); Parmesan & Yohe 2003), but whether all species can sustain these rates is unclear, in part because not enough time has passed since the onset of anthropogenic climate change to accurately constrain estimates of range shifts.

Estimating past rates of migration from fossil pollen records is difficult because cryptic populations of rare species may go undetected (e.g. McLachlan, Clark & Manos 2005) while species with well-dispersed wind pollen are frequently found in pollen records outside their range limits. Further development of statistical methods of reconstructing tree distributions from fossil pollen data, with appropriate measures of uncertainty (Sugita 2007a; Sugita 2007b Paciorek & McLachlan 2009), would be useful. Additionally, there is a critical need to map the patterns and rates of plant migration and population expansion during periods of abrupt climate change. Most estimates of past migration rates are based on broad spatial and temporal scales (i.e. from the last glacial maximum to present), rather than focused on migrational responses to abrupt events such as the BA and YD. New networks of high-resolution and well-dated fossil pollen records are enabling more detailed analyses of plant migration (Seppälä et al. 2009).

Little work has been done on the role of evolutionary adaptation in facilitating local vegetation responses to rapid climatic change during deglaciation (but see Davis & Shaw 2001; Davis, Shaw & Etterson 2005), but studies of modern populations indicate that adaptation can and has operated on the time-scales (< 100 years) of the rapid changes discussed here (e.g. Bradshaw & Holzapfel 2006). Clearly, more work needs to be done with modern systems and perhaps using ancient DNA (e.g. Parducci et al. 2005) to test the limits of rapid evolutionary adaptation in the face of abrupt climate change.

**INTRINSIC ABRUPT CHANGE AND REGIME SHIFTS**

Global climate models project that anthropogenic global warming in this century will be accompanied by zonally patterned changes in precipitation, with subtropical regions such as the south-western USA expected to become increasingly arid (Seager et al. 2007). In the Holocene records from both central North America and North Africa, the characteristic pattern has been a highly heterogeneous mosaic of local ecological responses, with variations in the timing, rate, and even direction of change. The timing of local response is governed by a combination of site-specific physical factors, biotic interactions, and stochastic processes such as disturbances (Paine, Tegnér & Johnson 1998) or localized climatic extremes (Jentsch, Kreyling & Beierkuhnlein 2007). Some regional patterns emerge (e.g. systems in more xeric regions tend to pass thresholds earlier than systems in more mesic regions) but site-to-site heterogeneity is substantial.

This heterogeneity severely challenges efforts to adapt to 21st-century climate change, because abrupt changes appear to be a common phenomenon in these arid to semi-arid systems, and because of the difficulty of predicting the timing of local responses. Forest and woodland communities in western North America appear to be already experiencing the effects of recent climate changes, with widespread increases in rates of tree mortality (van Mantgem et al. 2009), localized regions with strong tree die-offs (Breshears et al. 2005), rapid shifts of ecotones (Allen & Breshears 1998) and pest outbreaks (Raffa et al. 2008). However, unequivocal attribution of these events to climate change is difficult, given the short duration of these ecological records and the multiplicity of possible drivers and interactions among drivers. The prospect of heterogeneous local responses to regional climate changes places a premium on developing extensive monitoring systems capable of detecting when ecological systems are approaching or passing tipping points.

A major research priority is to develop tools capable of predicting when a system may be approaching a critical threshold (Dakos et al. 2008; Scheffer et al. 2009; Brock & Carpenter 2010). Palaeoecological records are replete with examples of abrupt change, resulting from both extrinsic and intrinsic drivers, and hence can serve as a rich testing ground for critical-threshold detection tools. Critical-threshold predictors have been applied to palaeoclimatic time series and ecological systems (Scheffer et al. 2009), so it is a logical next step to begin applications to palaeoecological time series.

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