INVITED PERSPECTIVE

Vegetation, environment, and time: The origination and termination of ecosystems

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Abstract

Terrestrial ecosystems originate when particular plant species attain dominance at specific locations under specific environmental regimes. Ecosystems terminate, gradually or abruptly, when the dominant species or functional types are replaced by others, usually owing to environmental change or severe and irreversible disturbance. Assessing whether current ecosystems are sustainable in the face of future environmental change can be aided by examining the range of environmental variation those ecosystems have experienced in the past, and by determining the environmental conditions under which those ecosystems arose. The range of environmental variation depends on the time scale at which it is assessed. A narrow time span (e.g. 200-300 years) may underestimate the range of variation within which an ecosystem is sustainable, and it may also underestimate the risk of major transformation or disruption of that ecosystem by environmental change. Longer time spans (e.g. 1000-2000 years) increase the range of variation, by encompassing a larger sample of natural variability as well as non-stationary variability in the earth system. Most modern ecosystems disappear when the time span is expanded to 10 000-15 000 years owing to secular changes in earth's climate system. Paleo-ecological records can pinpoint the time of origination of specific ecosystems, and paleo-environmental records can reveal the specific environmental changes that led to development of those ecosystems and the range of environmental variation under which those ecosystems have maintained themselves in the past. This information can help identify critical environmental thresholds beyond which specific modern ecosystems can no longer be sustained.

Keywords: Climate variability; Ecosystem; Historical range of variation; Global change; Paleo-ecology; Vegetation dynamics; Vegetation management.

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Introduction

A close friend and colleague often accuses me of being a radical Gleasonian. I cannot disagree. I view plant communities as fluid associations contingent on prevailing environment, available species pool, and historical factors (e.g. Jackson & Overpeck 2000). On the other hand, I view ecosystems as entities possessing

particular attributes and processes that are repeatable in space and time, and believe that specific ecosystems in specific locations have a time of origination ('birth') and a time of termination ('death'). This would seem to identify me as a confirmed Clementsian. Before you conclude that I am inconsistent, if not schizophrenic, let me explain. Though Gleason and Clements held some contrasting views, they are not as incompatible as popular legend would have it. Ecosystems rise and fall in predictable fashion, but the mechanics are individualistic.

I define ecosystems on the basis of their dominant plant species, which by virtue of physiognomy and physiology impose any number of ecosystem functions under a given environment (Chapin et al. 2002; Lavorel & Garnier 2002; Chapin 2003; Díaz et al. 2004). The suite of dominant plant species that govern ecosystem properties represent individualistic responses of those species to the environment. An ecosystem arises when a particular group of dominants comes together under a particular environmental regime, and that ecosystem terminates or develops into some other ecosystem when one or more of those dominants disappears or is replaced by a new species with different functional traits. By this definition, secondary succession is subsumed within an ecosystem, as long as the successional trajectories and pathways remain the same.

My thesis in this essay is that we need to understand the circumstances under which modern ecosystems arose and the range of environmental variability they have experienced in order to determine how (or whether) they can be sustained in the face of rapid environmental change, now and in the coming decades. My thinking represents an extension of the 'historical range of variability' (HRV) concept (Kauffmann et al. 1994; Landres et al. 1999; Meyer et al. 2005), which has been applied to North American forest management. Variability in climate, disturbance regime, stand size- and age-structure, coarse woody debris, hydrology, nutrient flux, and other ecosystem properties in the centuries immediately preceding EuroAmerican occupation of the region is used to provide management targets – for timber harvest, grazing, fuel treatment, wildfire suppression (or not), controlled burns, and other activities – that can maintain biological diversity and ecosystem services. Others have critiqued the HRV concept from a paleoecological standpoint (Millar 1997; Millar & Woolfenden 1999; Swetnam et al. 1999). I take a different approach here, discussing how our perception of natural variability depends on the time scale being considered and noting the need to use the past to assess vulnerability of ecosystems to transformation or collapse. I begin by discussing some concrete examples of ecosystem origination and variability from the Bighorn Mountains of northern Wyoming.

Looking backward from the Bighorn Mountains

The western slope of the Bighorn Range in northern Wyoming is similar physiographically and ecologically to the Colorado Plateau country 800 km to the south. Massive beds of Paleozoic limestones and sandstones dip westward into the painted-desert terrain of the Bighorn Basin. Deep canyons are vegetated by *Juniperus osteosperma* woodlands and open *Pinus ponderosa* forests, like their counterparts in Utah and Arizona. In fact, these woodlands and forests share many attributes with their Colorado Plateau counterparts, including many subdominant plant species and animal species. Many ecosystem properties are also shared, owing to the influence of functional traits of the dominant species.

As the lower slopes give way to the glaciated granites of the high country, the Bighorn landscape takes on a Rocky Mountain appearance, with montane forests of *Pinus contorta*, subalpine forests of *Abies lasiocarpa*, *Picea engelmannii* and *P. glauca* x *engelmannii*, and extensive alpine tundra. These ecosystems have their own unique properties, shared with their counterparts in other ranges of the central Rockies.

All of the woodland and forest ecosystems of the Bighorns existed in the centuries before EuroAmerican arrival. Ecologists and managers tend to focus on the last 200 - 300 years in assessing historical variability. This is certainly large enough to encompass a wide range of conditions, as well as high- and mid-frequency patterns of variation. A century usually displays a higher range of variation than any individual decade within it. But by the same token, a millennium should incorporate a wider range of conditions than any individual century within it, and ten millennia should comprise variability exceeding that of any single millennium. Records at these longer time scales exist in the Bighorn region. Tree-rings in old-growth forests and woodlands contain records of demography, disturbance and climate variation spanning many centuries. Natural lakes in the glaciated high country contain 12 000-year sedimentary records of vegetation change and fire history that can be extracted by study of pollen and charcoal. And caves and crevices in the canyon country contain fossil woodrat middens, which have 'snapshot' macrofossil records of past floristic composition of surrounding vegetation, ranging from the past few hundred years at some sites to the past 30 000 years at others.

Tree-ring records of precipitation variability during the past 750 years indicate that the Bighorn region experienced drought episodes in the late 13th and late 16th centuries far more severe than any of the past four centuries (Gray et al. 2004). These droughts undoubtedly had significant ecological effects (primary productivity, mortality, pest outbreaks, wildfires)

(e.g. Swetnam & Betancourt 1998; Swetnam et al. 1999; Gray et al. 2006). The extreme events of the 13th and 16th centuries were probably not severe enough to obliterate any of the major ecosystems of the Bighorns. Fossil pollen records from the subalpine forests indicate that the dominant forest types have been intact for several millennia (Baker 1983). Macrofossil records from woodrat middens in the Ponderosa pine and juniper woodlands indicate little or no compositional change in the past thousand years (Lyford et al. 2002, 2003; Jackson et al. 2002; Norris 2006), though we cannot assess changes in density or age-structure. Excepting recent human disturbance, ecosystems of the Bighorn region have been subject to greater natural variation during the past 750 years than the past 200 years, but the qualitative features of the landscape have not changed substantially in this time. Similarly, major vegetational patterns of the Colorado Plateau region have not changed substantially in the past thousand years (Betancourt 1990; Anderson 1993; Anderson et al. 1999; Weng & Jackson 1999). Thus, the similarities between the western Bighorns and the Colorado Plateau have persisted for the past several centuries.

If we were to compare the Bighorn region with the Colorado Plateau 5000 years ago, many of the ecological similarities would vanish. *Juniperus osteosperma* woodlands and *Pinus ponderosa* forests were widespread on the Colorado Plateau at that time, as they are today. But *P. ponderosa* was completely absent from the Bighorn region then, and *J. osteosperma* was restricted to a handful of widely scattered sites, rather than the extensive woodlands today. Temperature and precipitation regimes in the region were different from today, and thus vegetation composition and pattern, particularly at lower treeline, were also different. *Juniperus scopulorum* was the dominant woodland shrub, and forests upslope were comprised of *Pinus flexilis* and *Pseudotsuga menziesii*, with no *Pinus ponderosa*. Although the subalpine forest dominants – *Pinus contorta*, *Abies lasiocarpa*, *Picea glauca* x *engelmannii* - were the same as today's (Baker 1983), charcoal evidence from adjacent regions suggest that fire regimes within these forests were very different, (Millspaugh et al. 2000; Brunelle et al. 2005), owing to the prevailing climate patterns of the time. Viewed over the past 5000 years, the range of natural variability expands to encompass environmental regimes incapable of supporting some of the key modern dominants of the region, leading to ecosystems that do not exist today, and substantially altered ecosystem properties in some of those that have persisted.

If the time scale is expanded to the past 15 000 years, the range of variation increases dramatically. Most of the modern ecosystems of the Bighorn region vanish or are transformed into ecosystems with fundamentally different combinations of dominants by 10 000 years ago. Paleo-ecological records permit some glimpses of the extent of change. Packrat middens from low-elevation sites in Bighorn Canyon and the Bighorn Basin indicate woodlands dominated by *Pinus flexilis*, *Juniperus scopulorum*, and *J. communis* before 9000 years ago (Lyford et al. 2002; S.T. Jackson, J.L. Betancourt & M.E. Lyford unpubl.). *Picea pungens*, a montane/riparian species absent from the entire Bighorn region today, occurred during the last glacial maximum. Direct fossil evidence of *Pinus contorta* is absent from pre-Holocene records of the Bighorn region as well as other parts of the central Rockies. The species seems to have persisted during the glacial periods in isolated pockets on the flanks of these ranges (Jackson et al. 2005), in contrast to its widespread dominance today. Late-glacial pollen assemblages from the subalpine forests of the Bighorns (Burkart 1976) and other ranges of the central Rockies (Baker 1983; Whitlock 1993; Fall et al. 1995) indicate open vegetation, with extensive *Artemisia*, *Picea* spec., and *Pinus* subgenus *Strobus*. In the central Rockies, the latter taxon includes *P. flexilis*, which is today locally dominant near lower treeline, and *P. albicaulis*, which is absent from the Bighorn region, occurring in mountain ranges 200 km west. The dominant *Picea* species may well have been the boreal *P. glauca*; populations occur today in low-elevation riparian corridors of the Bighorns (S.T. Jackson pers. obs.), as well as mountains of northwest Wyoming (http://www.rmh.uwyo.edu). These vegetational changes, as well as evidence for glacial advances and retreats in the mountains (Davis 1988; Pierce 2004), permafrost features on the valley floors (Mears 1987), and dune movements in adjacent regions (Stokes & Gaylord 1993; Forman et al. 2001), all indicate high-magnitude environmental and ecosystem variation since the last glacial period.

Environmental variability and time: Two general properties

If we were to plot the total or cumulative range of variation for an environmental variable in a given region, especially a climatic variable – annual or seasonal temperature means or extremes, annual or seasonal precipitation, drought severity or duration – as a function of the time-interval over which we assessed the variation, we might expect to see two general patterns (Fig. 1). First, the range of variation in environment (and in consequent ecosystem properties) would increase as the time scale expanded. Second, the relationship would not necessarily be linear or curvilinear, but would exhibit a 'sloping staircase' pattern, where periods of slow, gradual
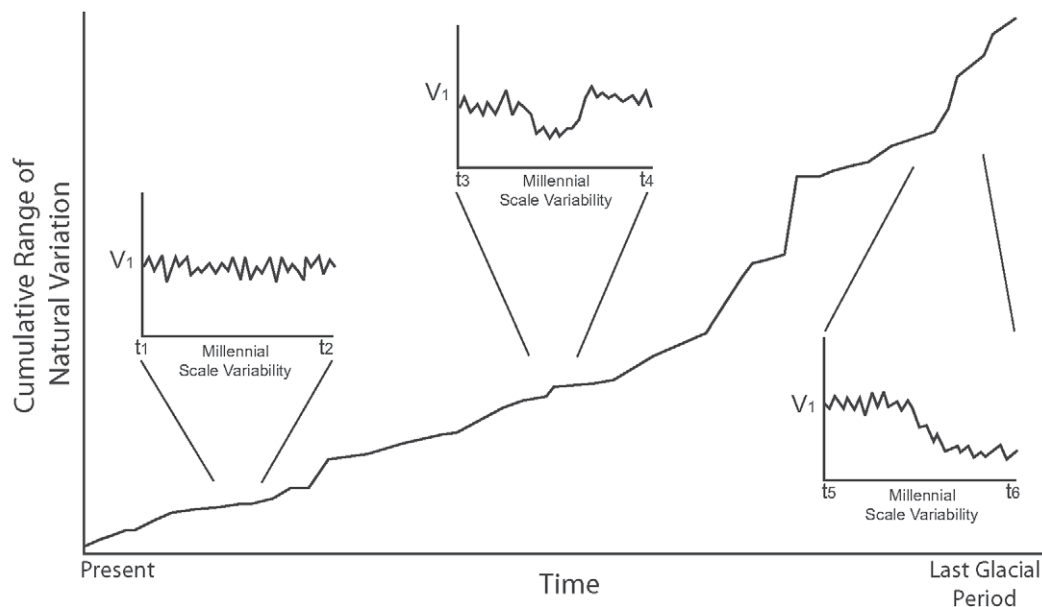
Fig. 1. Conceptual diagram showing the cumulative range of environmental variability experienced within a region plotted as a function of timescale, starting from the present and expanding retrospectively to the last glacial period. The range of variation estimated during the last 100 years is substantially smaller than that within the last 1000 years. The range of variation will continue to increase as the timescale expands to incorporate the entire Holocene (last 10 000 years), the late-glacial (10 000-15 000 years ago), and the last glacial maximum (21 000 yrs ago). The general patterns would continue across successively larger timespans (beyond 30 000 yrs) as a wider array of earth-system states was incorporated into the sample. The range of variability in ecosystem attributes, including composition of dominant species, plant-functional types, physiognomy, and ecosystem properties should vary in rough proportion to the range of environmental variability at a site. The topology of this relationship may vary among sites, and may also vary for different 30 000-year intervals of earth history.

The insets show non-cumulative environmental variation (e.g., annual temperature or precipitation) plotted as a function of time for selected 1000-year intervals to illustrate the patterns of cumulative variation. The left inset shows quasi-stationary climate variability, during which cumulative variability will increase very slowly. A high-magnitude climate excursion (e.g., an unusually severe and prolonged drought (Booth et al. 2005) or a transient temperature anomaly (Barber et al. 1999; Shuman et al. 2002) will lead to a step-change in cumulative variation (middle inset). An abrupt change in climatic regime, resulting in a major, persistent shift in means and/or mode of variability (Anon. 2002), will also lead to a step-change increase in cumulative variability (right inset).

increase in range of variation alternate with periods of rapid increase.

The steady increase in variability is in part a manifestation of the increasing sample size as the time-window increases. Because some elements of the climate system vary on time scales of decades to millennia, expanding the time scale encompasses a larger number of variations within a climate regime and different combinations of climate 'cycles' operating at different time scales. This sample-size effect is most prominent at relatively fine scales. For example, extending the time span from the past 300 years to the past 500 years in the Bighorn region adds the 16th century drought event as well as the unique variability regimes of the 17th and 18th centuries (Gray et al. 2004). These events and regimes may stem from interactions between high-frequency (annual ENSO) variation in the tropical Pacific and decadal to multidecadal variation in the North Pacific and North Atlantic (Gray et al. 2003, 2004; McCabe et al. 2004).

Accumulation of variability with time also results from the evolutionary nature of the earth system. Given sufficient time, especially more than a few centuries, major elements of the earth system undergo change – driven by such influences as solar variation, orbital change, tectonic activity, volcanism, and feedbacks among the atmosphere, oceans, ice sheets, and land surface. For example, Milankovitch variation in orbital parameters of the earth, which dictates the latitudinal and seasonal distribution of solar radiation, varies significantly at time scales of 3000 years and beyond, so high-magnitude climate change is inevitable at these time scales (Webb & Kutzbach 1998).

Even though many major components of the earth system – most notably Milankovitch forcing – change gradually, the earth-system response is often abrupt. Linear forcings are met with non-linear responses, in which atmospheric circulation patterns and variability regimes undergo rapid reorganization. Singular events

(volcanic eruptions, meltwater events) can also lead to abrupt, global-scale changes, either transient (e.g., the global events 8200 years ago (Barber et al. 1999) and 4200 years ago (Booth et al. 2005)) or persistent – e.g. the Younger Dryas Interval 12 800-11 600 years ago (Anon. 2002). Thus, environmental history consists of both high-frequency variability and low-frequency trends, punctuated by high-magnitude fluctuations and rapid shifts from one system-state to another, each with characteristic mean and variability regime (Mayewski et al. 2004).

Environmental variation, vegetation antiquity, and ecosystem properties

Every species has a fundamental niche, a characteristic envelope in environmental space bounded by thresholds beyond which individuals of the species cannot grow or reproduce successfully. Abundance of a species at a particular site is governed by its fundamental niche in the context of the local environment and the suite of other species growing at or near the site. Codominance or co-occurrence of two or more species requires that the respective fundamental niches intersect in the region of environmental space prevailing at a site (Jackson & Overpeck 2000). If ecosystems are defined by their dominant species, then every ecosystem has a characteristic envelope in environmental space. This envelope is defined by the individual environmental responses of the dominant species, and is a subset of the portion of environmental space where the fundamental niches of these species intersect. If the environment changes enough, a threshold for dominance, abundance, or even existence of one or more of the dominant species will be crossed, the species composition will change, and ecosystem properties will be altered – in other words, the original ecosystem will disappear and be replaced by a different ecosystem.

Environmental thresholds for maintenance of an ecosystem are often defined based on spatial placement of ecotones – for instance, the particular isotherms associated with the ecotone between *Pinus contorta* forests and *Picea/Abies* forests in the Bighorns could be used to define the environmental boundary between these ecosystems. Thus, if temperatures were to change, we might expect one ecosystem to replace the adjacent one along the ecotone (e.g. increased temperature would force upward expansion of *Pinus contorta* into territory occupied by *Picea/Abies* forest). This approach, however, has a potential pitfall: the environment is multivariate, environmental variables interact in their biotic influences, and future environmental changes will likely involve changes in suites of variables, as they have in

the past (Jackson & Overpeck 2000). As an example, the ecotone between *Pinus ponderosa* woodlands and *Juniperus osteosperma/J. scopulorum* woodlands in the western Bighorns has only existed for the past 1500-2000 years, and is contingent on the specific seasonal precipitation and temperature regimes that have prevailed in that period. These ecosystems are themselves recent features, developed only within the last 1000 to 6000 years. Similarly, the *Pinus contorta* and *Picea/Abies* ecosystems did not exist before ca. 10 000 years ago. Ecosystems and the intervening ecotones do not necessarily shift across the landscape like military fronts in a conventional war. In the face of multivariate environmental change, they dissolve and emerge in new configurations of species combinations, plant traits, consumer guilds, and disturbance regimes – with altered suites of ecosystem properties (Jackson & Overpeck 2000; Jackson & Williams 2004; Williams et al. 2004).

The shifting-boundary metaphor for ecosystem response to environmental change may be applicable to short time scales in periods of slow or gradual environmental change. Indeed, frontal behaviour during the past few centuries has been documented for many ecotones (e.g. Grimm 1983; Lloyd & Graumlich 1996; Allen & Breshears 1999). But periods of rapid environmental change, particularly regime shifts where atmospheric circulation patterns and/or variability regimes are altered, are likely to be accompanied by changes in species composition, and thus reconfiguration of ecosystems. Such ecosystem reconfiguration can also be driven by gradual environmental change in which key variables assume new combinations and gradients (Jackson & Overpeck 2000).

The antiquity of existing ecosystems can be assessed using paleo-ecological records of the constituent dominant species. Table 1 lists the age of origin and antecedents for a variety of ecosystems in the Bighorn region, the Interior West of the United States, and other parts of North America. It represents a selective sample, chosen to illustrate a few general lessons from the Late Quaternary.

First, all existing ecosystems have a finite time limit in the places where they occur, and all have been preceded by ecosystems different in species composition, plant-functional traits, and ecosystem properties. There are few or no spots on earth where ecosystems have existed unchanged for more than 12 000 years. Second, similar ecosystems, as defined by their dominant species, develop in different places, and at different times. For example, *Pinus ponderosa* forests and *Juniperus osteosperma* woodlands in the Colorado Plateau are several thousand years older than their counterparts in the Bighorn region (Table 1). Third, similar ecosystems had different antecedents in different places. *Pinus*

Table 1. Antiquity of selected modern North American ecosystems inferred from paleoecological records. Ecosystems are defined based on the dominant plant species as indicated from pollen and/or plant macrofossil data.

Modern ecosystem	Approximate age of origin (× 1000 a BP)	Antecedent ecosystem	Reference
Juniperus osteosperma woodland, Bighorn Basin, WY	2.8-1.0	*Juniperus scopulorum* woodland/steppe	Lyford et al. 2002, 2003
Pinus ponderosa forest, Bighorn Basin, WY	2.0-1.5	*Juniperus scopulorum/Pinus flexilis* woodland	Norris 2006
Pinus contorta forest, western Bighorn Mts., WY	< 10.5	*Picea* tundra/parkland	Burkart 1976; Baker 1983
Juniperus osteosperma woodland, SE UT	11.0-10.5	*Pseudotsuga menziesii/Pinus flexilis* woodland	Betancourt 1990
Pinus ponderosa forest, Kaibab Plateau, AZ	10.5	*Picea engelmannii/Picea pungens* woodland	Weng & Jackson 1999
Pinus contorta forest, Yellowstone Plateau, WY	10.5	*Picea* parkland and grassland	Whitlock 1993
Pinus contorta forest, SW Yukon Territory	3.0-2.5	*Picea* forest	MacDonald & Cwynar 1985
Montane parkland/grassland, Wind River Mts., WY	3.0-2.5	*Pinus contorta* forest	Lynch 1998
Pinus edulis/Juniperus osteosperma woodland, NE UT	0.8	*Juniperus osteosperma* woodland	Jackson et al. 2005
Pinus strobus/northern hardwoods forest, NE MI	1.0-0.8	Northern hardwoods/*Pinus strobus* forest	Booth & Jackson 2003
Picea rubens/P. glauca/northern hardwoods forest, C ME	1.0-0.8	Northern hardwoods/*Pinus strobus* forest	Schauffler & Jacobson 2002
Subalpine *Abies balsamea* forest, NY & NH	10.5-10.0	*Picea/Alnus* woodland	Spear et al. 1994; Jackson & Whitehead 1991
Subalpine *Picea rubens/Abies balsamea* forest, NY & NH	3.0-2.5	*Abies/Betula/Pinus* forest	Spear et al. 1994; Jackson & Whitehead 1991
Tsuga canadensis/northern hardwoods forest, W MA	3.0-2.5	*Quercus*/northern hardwoods forest	Whitehead & Crisman 1978; Shuman et al. 2004
Tsuga canadensis/northern hardwoods forest, N WI/MI	3.5-2.5	*Pinus strobus* forest	Davis et al. 1998

ponderosa forests in the Bighorn region were preceded by *Juniperus/Pinus flexilis* woodlands, while those in northern Arizona invaded *Picea* woodland and tundra-parkland. Thus, superficially similar ecosystems may have different properties, owing to different antiquity (time-dependent processes such as biogeochemical alterations, soil carbon and nutrient reservoirs) and to legacy effects of different antecedents.

A fourth observation is that different ecosystems arose at approximately the same time in different places. These instances represent regional to global-scale regime shifts in atmospheric circulation, leading to reconfiguration of climatic variables and widespread, synchronous transformation of ecosystems. This pattern is obviously not universal, but rapid regime-shifts in the earth system may be accompanied by widespread ecosystem transformation in diverse regions.

A critical question for ecosystem management in the face of global change is, 'how much environmental change can an ecosystem sustain before it is transformed into a different ecosystem?' Put another way, how much environmental change is required to alter the abundance of the dominant plant species? Are any key species vulnerable to population decline or extirpation? Are any minor local species, or potential invaders, poised to expand and transform ecosystem properties? A corollary question concerns ecosystem resistance to environmental change. History indicates that all ecosystems are sensitive to environmental change of the magnitude

experienced since the last glacial period (Table 1). Which are most likely to be transformed in the face of small changes? Which will be insensitive to future changes?

At first glance, the antiquity data of Table 1 might suggest that younger ecosystems – those whose dominants have been in a region only a short time – will be more sensitive to environmental change than older ecosystems. For example, the *Pinus contorta* forests of the Bighorns have persisted through the climatic changes and fluctuations of the entire Holocene, in contrast to the *P. ponderosa* forests, which did not occur (and presumably could not have occurred) in the regional climate before ca. 2500 years ago. Younger ecosystems might be closer to the environmental-tolerance thresholds of some or all of their constituent species, and so smaller changes might be required to convert them into other types of ecosystems.

Using antiquity alone to assess sensitivity to change is problematic, however, in that it does not incorporate information about the environment or its future trajectories. Climate might well change in a direction favouring younger ecosystems while approaching a threshold at which older ones might disappear. Furthermore, a regime-shift of sufficient magnitude might alter all ecosystems within a region, regardless of antiquity.

The paleo-ecological record can play a more useful role by identifying the environmental changes of the past that led to development of the ecosystems on the landscape today. What specific environmental changes

led to the establishment of *Pinus ponderosa* forests in the western Bighorns in the last 2000 years, and the widespread proliferation of *Juniperus osteosperma* woodlands in the eastern Bighorn Basin during the last 3000 years? What climate regime prevails in the Bighorn region now, for instance, that did not occur before 2000 or 3000 years ago? What was missing 3000+ years ago that prevented development of these ecosystems? Identification of the specific environmental changes that gave rise to specific ecosystems can help delineate the environmental boundaries of those systems, and hence provide some predictive power in assessing sensitivity to future change. Integration of empirical modeling of key species in environmental space with paleo-ecological and paleoclimatic records can contribute (e.g., Norris et al. 2006).

Such information would also be useful for older ecosystems (e.g., *Pinus contorta* and *Picea/Abies* forests), but equally important might be information about the nature and magnitude of environmental variability those ecosystems have experienced since they first developed in a region. What environmental variables have undergone significant change or variability within those ecosystems during the Holocene? What variables have remained more or less constant? It may well be the latter variables to which the ecosystem is most sensitive in terms of future change.

Ecosystem managers face a huge challenge in assessing ecosystem sustainability in the coming decades. Future environmental changes, including reorganizations of atmospheric circulation patterns, may drive wholesale ecosystem transformations, analogous to those 800-1000, 2500-3000, or 10 000-11 000 years ago. Paleo-ecological and paleoclimatological records can help determine the specific climate changes that drove the most recent changes, identify the nature and magnitude of past environmental changes that did *not* lead to eco-system reconfigurations, determine which ecosystems are at particular risk of climate-driven disruption in the coming century, and identify ecosystems that can be maintained under informed management. Advances in paleoclimate reconstruction and integration of paleoclimate data with synoptic climatology and climate dynamics should provide a clearer understanding of the climatic boundaries within which ecosystems can be maintained. Ecosystems will, of course, also be influenced by other forces, including invasive species, nitrogen and carbon fertilization, land use, and pathogens. Delineating the climatic boundaries of ecosystems using geohistorical records will nonetheless be critical in developing appropriate management strategies, and in deciding which ecosystems might be sustainable in a greenhouse world.

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