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Special Section

Vegetation Response to Early Holocene Warming as an Analog for Current and Future Changes

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Abstract: *Temperatures in southwestern North America are projected to increase 3.5–4 °C over the next 60–90 years. This will precipitate ecological shifts as the ranges of species change in response to new climates. During this shift, rapid-colonizing species should increase, whereas slow-colonizing species will at first decrease, but eventually become reestablished in their new range. This successional process has been estimated to require from 100 to over 300 years in small areas, under a stable climate, with a nearby seed source. How much longer will it require on a continental scale, under a changing climate, without a nearby seed source? I considered this question through an examination of the response of fossil plant assemblages from the Grand Canyon, Arizona, to the most recent rapid warming of similar magnitude that occurred at the start of the Holocene, 11,700 years ago. At that time, temperatures in southwestern North America increased about 4 °C over less than a century. Grand Canyon plant species responded at different rates to this warming climate. Early-successional species rapidly increased, whereas late-successional species decreased. This shift persisted throughout the next 2700 years. I found two earlier, less-extreme species shifts following rapid warming events around 14,700 and 16,800 years ago. Late-successional species predominated only after 4000 years or more of relatively stable temperature. These results suggest the potential magnitude, duration, and nature of future ecological changes and have implications for conservation plans, especially those incorporating equilibrium assumptions or reconstituting past conditions. When these concepts are extended to include the most rapid early-successional colonizers, they imply that the recent increases in invasive exotics may be only the most noticeable part of a new resurgence of early-successional vegetation. Additionally, my results challenge the reliability of models of future vegetation and carbon balance that project conditions on the basis of assumptions of equilibrium within only a century.*

Keywords: colonizing species, early Holocene, global warming, Grand Canyon, plant succession, vegetation change

Respuesta de la Vegetación al Calentamiento en el Holoceno Temprano como un Análogo para Cambios Actuales y Futuros

Resumen: *Se proyecta que las temperaturas en el suroeste de Norte América incrementen 3.5 a 4 °C en los próximos 60–90 años. Esto precipitará cambios ecológicos a medida que cambien los rangos de las especies como respuesta a los climas nuevos. Durante este cambio, las especies colonizadoras rápidas deberán incrementar, mientras que las especies colonizadoras lentas primero decrecerán, pero eventualmente se restablecerán en su nuevo rango. Se ha estimado que este proceso sucesional requiere de 100 a más de 300 años en áreas pequeñas, con clima estable, con una fuente de semillas cercana. ¿Cuánto tiempo más se requerirá en una escala continental, bajo clima cambiante, sin una fuente de semillas cercana? Consideré esta pregunta examinando la respuesta de ensambles de plantas fósiles del Gran Cañón, Arizona, al calentamiento rápido de magnitud similar más reciente que ocurrió al principio del Holoceno, hace 11,700 años. En ese tiempo, las temperaturas en el suroeste de Norte América incrementaron casi 4 °C en menos de un siglo. Las especies de plantas del Gran Cañón respondieron a este aumento de temperatura de tasas diferentes. Las especies*

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sucesionales tempranas incrementaron rápidamente, mientras que las sucesionales tardías decrecieron. Este cambio persistió durante los siguientes 2700 años. Encontré dos cambios previos, menos extremos, después de eventos de calentamiento rápido hace 14,700 y 16,800 años. Las especies sucesionales tardías predominaron solo después de 4000 o más años de temperatura relativamente estable. Estos resultados sugieren la potencial magnitud, duración y naturaleza de cambios ecológicos futuros y tienen implicaciones para los planes de conservación, especialmente los que incorporan suposiciones de equilibrio o que reconstruyen condiciones pasadas. Cuando estos conceptos son extendidos para incluir a los colonizadores sucesionales tempranos más rápidos, implican que los incrementos recientes de invasores exóticos pueden ser solo la parte más notable de una nueva resurgencia de vegetación sucesional temprana. Adicionalmente, mis resultados desafían la confiabilidad de los modelos de vegetación futura y balance de carbonos que proyectan condiciones con base en suposiciones de equilibrio durante solo un siglo.

Palabras Clave: calentamiento global, cambio de vegetación, especies colonizadoras, Gran Cañón, Holoceno temprano, sucesión vegetal

Introduction

Historic Successional Vegetation Change

Studies of vegetation changes in the 20th century often depict them within a conceptual framework of initial disturbance and resulting succession. These studies have generated a broad literature detailing ample mechanisms and a complex nomenclature describing abundant types of both disturbance and succession (e.g., Cowles 1899; Drury & Nisbet 1973; White & Pickett 1985; Glenn-Lewin et al. 1992; and many others). Within this conceptual framework, primary succession refers to changes taking place as plants colonize a new substrate lacking a developed soil such as a recently formed glacial moraine, a lava flow, or landslide. Secondary plant succession refers to changes typical of a disturbed area with a developed soil, a stable climate, and a readily available source of seeds for all species of all successional stages. Secondary succession is typified by the easily studied changes occurring in abandoned agricultural fields (old-field succession).

The time span required for secondary succession to run its course following a disturbance has been estimated for many vegetation types. This is typically represented by the regrowth of the original forest tree species in an area that was cleared for farming or by another disturbance. Hardwood species of the eastern deciduous forests of North America do not start to become abundant until 70–100 years after the disturbance (Christensen & Peet 1984) and likely require many more years to become dominant. Subalpine forests in Colorado require between 200 (mesic slopes) and 300 years (dry slopes) to fully reestablish after fire (Donnegan & Rebertus 1999). In semiarid regions it takes pinyon woodlands in northern Arizona over 215 years to mature following their removal (Tress & Klopatek 1987). These estimates are derived from small areas surrounded by mature forest or woodland vegetation that receive a steady influx of seeds from those species. These results, with longer successional response times in less-humid and less-fertile regions, are consistent with measurements of species turnover on multiple old-field sites (Prach et al. 1993).

Results of the few studies done on succession in arid lands suggest that these processes are much slower (Otto et al. 2006). A study of succession on dated debris flows in the Grand Canyon (Bowers et al. 1997) demonstrates that some species colonize and disappear within decades. Other species, such as creosote bush (*Larrea tridentata*), require several centuries to be recorded and become abundant only after millennia. Results of a study in a more severe, hyperarid desert farther south (McAuliffe 1988) suggest that creosote bush (*L. tridentata*) requires more than 400 years to reach its maximum density.

Here, I adopted the broad definition of Drury and Nisbet (1973), that succession is "...a predictable change in species composition over time." No specific pattern of succession or successional mechanism is necessarily implied because different species have different successional mechanisms. Furthermore, because I integrated data across a broad spectrum of times, climates and vegetation types, these predictable changes are represented as the abundance of plants from different successional classes, rather than particular species or assemblages. This concept is similar to that used in designating plant functional types (Neilson et al. 2005), except that species are instead classified as successional types. This approach allows integration of data from an adequate spatial scale and a sufficiently detailed chronology that the effect of climate shifts is evident on a scale of <250 years. I applied this successional perspective to a series of fossil plant assemblages from the Grand Canyon, Arizona that reflect previous times of rapid climate warming. My results suggest not only what may be the best past analog for future vegetation changes, but also yield another viewpoint on current ongoing ecological processes.

Equilibrium Assumptions

Many concepts in ecology and conservation planning incorporate assumptions of equilibrium within natural systems. Fundamental natural units such as communities, associations, or biomes are presumed to possess a natural and stable order that is perceived as "normal" and desirable. But closer examination almost always reveals

nature to be in a continual state of flux. It is only the pace and character of these changes that is variable. It is also typically assumed that once a disturbance has ceased, natural mechanisms will return the system to its predisturbance, and most desirable, state. Unfortunately, many of the current disturbances affecting natural systems—invasive species, increased atmospheric CO_2, and greatly altered climate—are one-way changes that will not be reverting to their predisturbance state. After a long and as-yet-undetermined amount of time, ecosystems should eventually adjust to these new conditions, but they will then be greatly displaced from their current locations and current intercommunity relationships. Yet most conservation plans still seek to recreate past, or maintain present, distributions and relationships even though the conditions that supported such things may never occur again.

Most models of projected future changes between now and a future climate with two times the amount of preindustrial CO_2, generally expected to occur 60–90 years from now, also incorporate assumptions of equilibrium at the association, community, or biome level. This limitation is fully acknowledged by many researchers (Neilson et al. 1998; IPCC 2007*b*). But to ecologists familiar with the rates of vegetation change in historical studies of things like old-field succession, this assumption of equilibrium in less than a century raises concerns. Because most secondary successions in a small area require 100 to over 300 years to complete under a stable climate with a nearby seed source, how will successional processes run their course on a continental scale in 60–90 years under a continuously changing climate without a nearby seed source?

To project future conditions, simplistic equilibrium models could be replaced by dynamic vegetation models that incorporate processes such as disturbance, succession, and migration (Woodward & Beerling 1997; Guisan & Thuiller 2005). But dynamic vegetation models need to be parameterized with data from scale-appropriate disturbance, succession, and migration events. Currently, migration models are often parameterized by extrapolation of anecdotal observations of a few recent dispersal events. Such observations cannot be reliably expanded to encompass entire landscapes because they represent an inappropriate spatial scale. The temporal scale of these data is also inappropriate for the greater continent-wide spatial scale required. Measurement of change across extreme spatial scales requires a greatly expanded temporal scale because the natural dynamics of the system extend so much longer than the typical period of study (Wiens 1989). Appropriate long-term landscape-scale data required for parameterizing dynamic vegetation models are only available from historical and paleoecological time series (Froyd & Willis 2008).

Paleoecological research on vegetation change over longer periods of time usually concentrates on shifts at the association, community, or biome level. It is almost always assumed that these species groupings reach equilibrium with their contemporaneous climate more rapidly than the sampling interval used. That is, any temporary or dynamic reshuffling of species in response to the change has run its course, leaving a stable vegetation type in equilibrium with climate. This is often an acceptable assumption considering that most climate shifts are comparatively gradual or minor and that many paleoecological records have comparatively poor temporal resolution. But equilibrium assumptions become misleading when applied to high-resolution data of the most severe climate shifts. A few researchers have considered the transient dynamics following a climate change or other disturbance (e.g., Davis 1986; Lischke et al. 2002; Bergman et al. 2005; Peros et al. 2008), but these interpretations are uncommon.

The assumption of perpetual equilibrium between vegetation and climate has been required for the reconstruction of paleoclimates from fossil vegetation. Rather than attributing fossil vegetation as a response to an earlier climate change, it has been assumed that any vegetation reflects its contemporaneous climate. That is, a period with early-successional species following a climate change has been interpreted as representing a period of climate favoring these species rather than any transient successional process put in motion by the earlier change. Because there was no independent verification of the precise timing of paleoclimatic changes, there was no easy way to objectively discriminate between the equilibrium and nonequilibrium interpretations. But over the last decade, newer geochemical data, from such things as stable isotopes and elemental ratios, have developed into paleoclimatic proxies with greater precision, detail, and reliability than biological proxies. As a result, paleoecologists can now question their equilibrium assumptions and are free to infer the ecological consequences of past climate changes that are independently reconstructed from geophysical climate proxies.

Changes on these increased spatial and temporal scales can be described within the same framework of disturbance and resultant succession applied by modern ecologists, albeit at broader scales. At these larger scales, a disturbance remains "...a relatively discrete event in time that causes abrupt change in (an) ecosystem..." (White & Pickett 1985), but in this context the terms *discrete* and *abrupt* are relative to the new scale. A major climate change occurring in a 200-year interval over a 10,000-year record is abrupt.

The Most Recent Event of Abrupt Climate Warming

To evaluate the possible effects of future climate changes on natural systems, detailed data from an analogous shift in the past are needed. But, because paleoecological data become less detailed through time, this period

needs to be as recent as possible. Permanent plots, aerial photography, historical data, and dendrochronology yield detailed information on historical changes over the last 50–1000 years (Egan & Howell 2001). But there were no events of rapid climate warming over this period comparable in magnitude with those projected for the next century. Warming events during the last 1000 years are reconstructed by most proxy data as <0.5 °C in magnitude (IPCC 2007*a*). In contrast, future changes for western North America are typically modeled to be between 3.5 and 4 °C over the next 60–90 years on the basis of the moderate A1B carbon-emission scenario (IPCC 2007*a*).

The last climate shift of similar magnitude to that expected over the next century occurred about 11,700 years ago (Overpeck et al. 2003) as the Younger Dryas period ended and the early Holocene began. This change has been measured with the greatest accuracy and precision on the Greenland Ice Sheet. A recent ice core suggests that this most rapid warming may have started as a switch in climate mode occurring during only 1–3 years, initiating warming over the subsequent 50 years (Steffensen et al. 2008). Furthermore, a similar step change in climate is recorded earlier, around 14,700 years ago. These rapid warming events are thought to have been caused by a sudden shift in the position of the Intertropical Convergence Zone, which affected such things as the wetting of low-latitude Asian deserts. As a result these changes were likely synchronous throughout at least the Northern Hemisphere, although different regions experienced different magnitudes of change.

Radiocarbon-dated terrestrial records from western North America are not nearly as detailed or as chronologically reliable as ice cores dated from annual layers. But these more regional records suggest a warming of >4 °C in winter minimum temperatures in the Grand Canyon (Cole & Arundel 2005) and an approximately 4 °C increase in mean annual sea surface temperature off the coast of northern California around 11,700 years ago (Barron et al. 2004). Oxygen isotope values from a sea core in the Santa Barbara Basin (Hendy et al. 2002) also suggest abrupt warming events around 11,700 and 14,700 years ago (Fig. 1d). A break in this sea core obscures the timing of an even earlier warming event that occurred between 16,800 and 15,700 years ago.

The relative recency of the warming events occurring 11,700 and 14,700 years ago ensures that there are abundant terrestrial paleoecological records demonstrating their effects. Better analogs for our incipient climate changes may exist in much older periods, but we are unlikely to find such detailed terrestrial records of their consequences. Some characteristics of these past events are dissimilar to the conditions that will accompany future warming, such as the geographic position and composition of ecosystems, the distribution of seasonal solar insolation, the atmospheric content of CO_2, and the presence or absence of introduced and extirpated species. Nevertheless, these periods stand out as the most recent examples of widespread warming of >3 °C that have taken place over a 50 to 200-year period.

The rates at which species migrated in response to the early Holocene warming are evident from geographic analysis of fossil data. Late-successional trees in the eastern deciduous forest and boreal forests of North America migrated northward at rates estimated from <100 m/year (McLachlan et al. 2005) to 300 m/year (Yansa 2006). Conversely, migration rates in the arid southwest seem to have been slower. Plant macrofossils of major species from packrat (*Neotoma* spp.) middens provide evidence that migration rates of many species ranged between 10 and 100 m/year following this sudden climate warming (K.C., unpublished data). For example, Colorado pinyon pine (*Pinus edulis*) was not found north of the westernmost Grand Canyon and Wupatki National Monument of northern Arizona during the latest Pleistocene (Cole 1990; Ironside 2006). Yet it did not reach its northern limit near the Utah-Wyoming border (Jackson et al. 2005), its northeastern limit at Owl Canyon, Colorado (Betancourt et al. 1991), or its eastern limit at Carrizo Canyon, Colorado (Anderson & Feiler 2009), until after 1300 years ago. Holocene fossil records along the way record a gradual migration between 11,700 and 1300 years ago at rate averaging 43 m/year (Cole et al. 2008*a*).

Methods

To allow comparison between ice cores, sea cores, radiocarbon dates, and modeling results, I converted past dates to a calendar-year scale (Stuiver & Reimer 1993), expressed as years before present (present is defined as 1950 AD). I analyzed a series of fossil plant assemblages from packrat middens collected within the Grand Canyon, Arizona, to quantify the changing number of species within the assemblages and the ratio of rapid- to slow-colonizing species. These analyses included 50 assemblages reported by Cole (1985) and an additional 31 assemblages collected during the last decade that were selected specifically to fill in temporal gaps in the prior midden series. To clarify changes happening during the Pleistocene–Holocene transition, I redated the assemblages younger than 14,000 years that had the least precise conventional radiocarbon ages with the newer accelerator mass spectrometry (AMS) (Van Devender et al. 1985) method to reduce their age uncertainty. This is critical because this statistical uncertainty of the age often expands during the conversion to a calendar-year chronology.

I chose perennial species within these assemblages for this analysis because these plants are easily identified to the species level and their presence in a midden assemblage is the most reliable. The characteristics of each species are described in the species summaries published

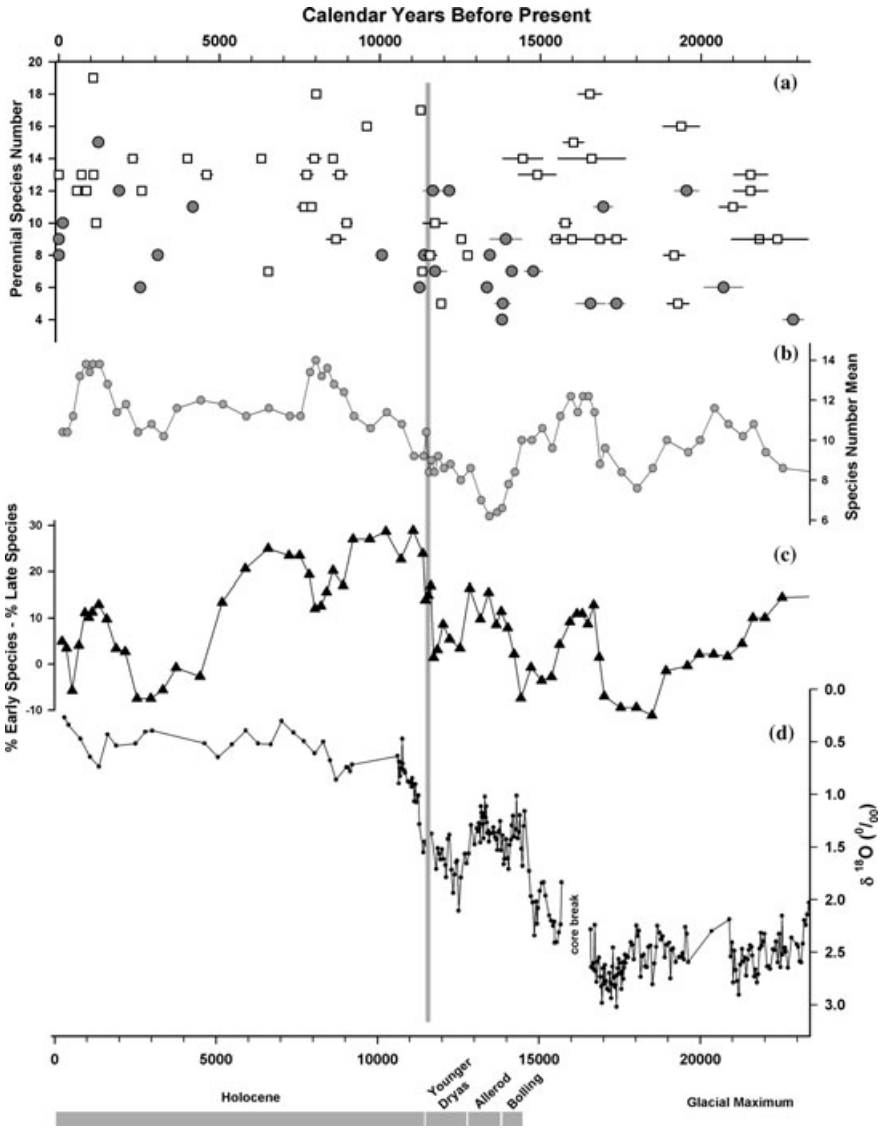

Figure 1. (a) Number of perennial species (trees, shrubs, and succulents) identified in 81 fossil packrat midden assemblages from the Grand Canyon, Arizona (filled circles, assemblages from 725 to 1220 m elevation; squares, assemblages from 1400 to 2020 m elevation). Potential calendar year range at 1 SD shown by bars. (b) Five-sample moving mean of the values in (a). (c) Five-sample moving mean of the percent early-successional minus percent late-successional species (Table 1) of total perennial species. (d) Foraminifera ^{18}O isotope series of N. pachyderma*, a proxy for temperature, from the ODP 893A sea core from the Santa Barbara Basin (modified from Hendy et al. 2002). Vertical gray bar shows the start of the Holocene at 11,700 years ago; major Northern Hemisphere climatic periods are shown at bottom.*

by the U.S. Department of Agriculture (USDA) Forest Service (2009). Because each species summary includes a specific section discussing successional status, each plant could be objectively categorized into three successional classes with this source. I classified species into three groups (Table 1): (1) early-successional, rapid-colonizing species reaching their peak abundance <100 years after disturbance; (2) late-successional, slow-colonizing species reaching their peak abundance >100 years after disturbance; and (3) species equally typical of early and late stages or with insufficient information. The majority of the species fell into group 3. I based the classification of three lower-elevation species not covered by the USDA database on Bowers et al. (1997).

Table 1 contains classifications of early and late species typical of high, middle, and low elevations where these middens were collected along a 1200-m gradient for both the Holocene and Pleistocene vegetation types of the Grand Canyon (Cole 1990). Classification of species by successional status rather than preferred climate zone, elevational range, or time period, allowed an integration of the data across time and space, which created a unique view of paleoecological change. Although Pleistocene fossils generally represent forests and many Holocene fossils represent woodlands or shrublands, successional status allowed consideration of trends in vegetation type that are independent from the complexities of different elevations, time periods, substrates, and slopes. Presumably, an abrupt continental-scale shift in climate would affect the successional status of all associations across the landscape simultaneously.

Results

There was considerable variability in the number of plant species throughout the fossil series (Fig. 1a), which

Table 1. Taxa representing early and late species from Grand Canyon macrofossil assemblages selected from U.S. Department of Agriculture Forest Service (2009) species summaries and Bowers et al. (1997).

Earliest successional species of Grand Canyon[a]	*Latest successional species of Grand Canyon*[b]
Encelia spp.	*Larrea tridentata*
Gutierrezia sarothrae/microcephala	*Ferocactus wislizenii*
Brickellia spp.	*Echinocactus polycephalus*
Agave utahensis	*Coleogyne ramosissima*
Happlopappus spp. (incl. *Isocoma)*	*Atriplex confertifolia*
Chrysothamnus viscidiflorus/C. nauseosus (incl. *Ericameria nauseosus)*	*Artemisia tridentata*
Atriplex canescens	*Krascheninnikovia lanata*
Rhus trilobata	*Pinus edulis*
Artemisia ludoviciana	*Pseudotsuga menziesii*
Cercocarpus montanus	*Picea pungens/engelmanii*
Ptelea trifoliata var. *pallida*	
Fraxinus anomala	
Holodiscus dumosus	
Robinia neomexicana	
Pinus flexilis	

[a] *Rapid disperser or initial colonizer of disturbed areas, invading and reaching maximum in less than 100 years.*
[b] *Slow disperser, reaching maximum over 100 years after disturbance.*

demonstrated the need for a large number of fossil assemblages for this type of analysis. However, longerterm trends became evident when the data were averaged into a five-sample moving mean (Fig 1b). Species number declined below its long-term mean through the Pleistocene–Holocene transition, as previously reported by Cole (1985). The percentages of rapid- versus slow-colonizing species, again averaged into a five-sample moving mean, were combined in a successional index by subtracting one curve from the other (Fig. 1c).

The successional index fluctuated throughout the 23,000 years (Fig. 1c). The largest and most persistent shift toward rapid-colonizing species started between 11,700 and 11,600 years ago and persisted through the mid-Holocene except for a smaller reversal around 8200 years ago. Other rapid increases occurred around 16,700 and 14,200 years ago. These two earliest increases, dated very roughly with less precise radiocarbon ages, persisted for 1200 and 1500 years, respectively. The most persistent periods of slow-colonizing species were from 18,700 to 16,700 and 4800 to 2200 years ago.

Discussion

Geophysical Climate Records and Succession

Results for the successional index correlated well with timing of the major temperature shifts affecting western North America during the last 23,000 years, as reconstructed from geophysical paleoclimate proxies such as the oxygen isotope series from a sea core taken in the Santa Barbara Basin (Fig. 1d; Hendy et al. 2002). The abrupt temperature increases at 11,700 and 14,700 years ago, both exceptionally well-quantified from the Greenland NGRIP ice core (Steffensen et al. 2008), were reflected in the abrupt increases in the successional index following these events (Fig. 1c). The similar rise in the successional index between about 17,000 and 16,600 years ago coincides with a sudden climate change of the H1 Heinrich event occurring at 16,800 years ago (Hemming 2004). This H1 event is likely the same warming event implied between 16,800 and 15,700 years ago around the break in the Santa Barbara Basin core (Fig. 1d). The largest and most persistent increase in the successional index in the Grand Canyon, started just after 11,700 years ago. The extent of this shift may have been accentuated by continually rising temperatures following the initial sharp increase. Quantified temperature series from terrestrial habitats for the early Holocene are less well documented than those showing the initial increase, but the records of Cole and Arundel (2005) and those from the Greenland Ice Sheet (e.g., Grootes & Stuiver, 1997) suggest that following the initial rapid increase in temperature around 11,700 years ago, temperatures then continued to rise even further at a slower rate over the next 1500 years. If so, it would be impossible to separate the delayed effects of the initial rapid temperature increase from the effects of the continuing more-moderate temperature increases in maintaining the high ratio of early-colonizing species in the Grand Canyon during the next 1500 years. This trajectory of a rapid initial temperature increase followed by continually rising temperatures in the early Holocene is analogous to future longer-term climates projected to occur during the next three centuries by most scenarios of future atmospheric CO_2 (IPCC 2007*a*).

The successional index from this record remained elevated (early-successional species dominated) for 5500 years following the warming at 11,700 years ago until about 6000 years ago. These high values were interrupted by the modest decline around 8200 years ago. The low point of this decline occurred, perhaps coincidentally, very close to the only major reversal of Holocene temperature 8200 years ago (Thomas et al. 2007). It is possible that this cooling event, and the subsequent warming reversal immediately following, could have extended the period of dominance by the early-colonizing species. If so, it would be more cautious to infer that the dominance of the early-colonizers in the Grand Canyon following the postglacial warming only lasted 2700 years, from 11,700 until just after 9000 years ago.

In contrast to the increases of the successional index that followed temperature increases, the lowest values of the index (late-successional species dominate) followed

periods of relative temperature stability that lasted 4000 years or more, such as after the glacial maximum and the late middle Holocene. There appeared to be no cooling events during the last 23,000 years that matched the warming events for magnitude and abruptness. Even the cooling at the start of the Younger Dryas period seems to have been more gradual (Steffensen et al. 2008) than these warming events.

Implications for Future Ecosystems

The 2700-year period of the highest ratio of early-colonizing species following the warming at 11,700 years ago strongly suggests that some vegetation responses to continent-wide disturbances do not rapidly equilibrate. These results duplicate model results reported by Lischke et al. (2002) that show "...vegetation [in the Swiss Alps] was in equilibrium with climate during long periods, but responded with lags at the time-scale of centuries to millennia caused by a secondary succession after rapid climatic changes such as at the end of Younger Dryas..." Lischke's and my results suggest that in the future these successional changes will be long lasting and will continue well beyond the horizon of most studies attempting to characterize the vegetation of 2100 AD by at least an order of magnitude.

The three periods of dominance by early-colonizing species following warming events around 16,800, 14,700, and 11,700 years ago required 1200, 1500, and 2700 years, respectively to equilibrate and seemed to reflect the severity of the initial event. In the arid shrublands to semiarid forests of the Grand Canyon, these changes are likely to be more prolonged than would be expected in humid environments (Prach et al. 1993; Otto et al. 2006) and represent only one region. Although my analyses incorporated data from throughout a study area of about 500 km^2, integration of data over an even larger spatial scale may be required to match an appropriate temporal scale for such a study (Wiens 1989).

My results also have implications for monitoring ongoing vegetation change. Familiar plant assemblages will change in unexpected ways, causing increases in rapid colonizers at the expense of slow colonizers. This change will not be evident to ecologists who have classified vegetation types with association (or community) approaches in which early-successional members are combined with late-successional members to characterize the same association type as is used in most vegetation-mapping efforts. These maps will not register any change if only the late-successional association members are eliminated because the early-successional association members will remain. To avoid this problem, vegetation must be either classified on the basis of individual species or varieties or with a successional approach that incorporates migrational or successional characteristics into the classification.

The popular approach of measurement of movement along local ecotones may also prove futile because the invasion of colonizers, and the mortality of existing species, likely will exceed the spatial scale of most studies, perhaps encompassing the entire study area simultaneously as was the case in the Grand Canyon 11,700 years ago. The number of native species in any one area will likely decrease as the slow-colonizing species become more restricted in their distributions. Theoretically, this loss of diversity could also affect animal species. Animal species adapted to recently disturbed or weedy communities would likely prosper.

An encouraging result of my analyses is that most extant plant species have previously survived a sudden climate warming that was at least similar in magnitude to the changes starting now, albeit without the current anthropogenic alterations on the landscape. The slow-colonizing species abundant today probably experienced a population bottleneck at the time but have successfully re-expanded since. This is the case for the pinyon pines in western North America (Cole et al. 2008*b*) and the oak species in Europe (Dumolin-Lapégue et al. 1997).

The number of fossil assemblages in my study is insufficient for assessing whether this early Holocene climate change resulted in extinctions of infrequent species. Although no extinctions are evident from the plant macrofossils in the assemblages, the data are probably comparable with measuring about 100 2000-m^2 plant plots across a broad landscape. Such a limited amount of sampling data will likely only represent the most frequent species on the landscape, those unlikely to be threatened with extinction. The well-known extinctions in the North American megafauna seem to be unrelated to this rapid warming event of 11,700 years ago. Most of these megafauna extinctions occurred around 1200 years earlier, as *Homo sapiens* became abundant and climates cooled at the start of the Younger Dryas period (Burney & Flannery 2005).

Implications for Exotic and Native Weedy Species

The successional concepts I explored have important implications for making projections about populations of weedy herbs and grasses that are the earliest successional species and typically the most rapid colonizers. The recent rapid spread of introduced species is easily documented because these species were not previously known from the new areas and every first appearance becomes a documented range expansion. However, a corresponding expansion of native weedy species outside their historical ranges is more difficult to verify. Historical ranges of widely distributed native herbs and grasses are poorly documented. In addition, year-to-year abundances of these species can be highly variable. Consequently, any new record of a native herb is usually considered a result

of more thorough collecting, rather than an actual range expansion.

The temporal population dynamics of exotic and native weedy species are similar, primarily reflecting the successional class and life form. They exploit the same ecological strategies, filling similar roles within communities (Meiners 2007). The results of this study imply that the current rapid increase in exotic weedy species may only be a part of larger ongoing ecological changes that remain unnoticed because early-colonizing native species are often ignored in studies of invasive species (Colautti et al. 2004).

Continent-Wide Succession

Thus far I have considered only rates of secondary succession. Primary succession often takes so long that it can only be estimated by comparing different-aged substrates, such as chronosequences of sand dunes. Henry Cowles first suggested the relationship between the age of sand dunes and their overlying vegetation along the southern edge of Lake Michigan (Cowles 1899). Following Cowles, Olson (1958) demonstrated that although most soil and plant development occurred during the first 1000–3000 years following dune stabilization, slower processes required as many as 10,000 years to fully run their course. Although soil development on sand dunes likely requires more time than more productive substrates, these rates of change may be more comparable with rates of change in arid and semiarid regions.

The continent-wide changes that could reasonably be expected from rapid and extreme climate shifts are not entirely analogous to either primary or secondary succession as they have been studied traditionally. Future changes will be unlike secondary succession because their extreme spatial scale will retard many plant species lacking mechanisms for rapid and wide dispersal. They will differ from primary succession because many developed soils will remain during the shift. But, the extreme turnover of dominant vegetation will likely increase erosion rates, exposing more primary substrate. Erosion did increase in arid regions following the early Holocene climate warming (McDonald et al. 2003).

An ecosystem disturbance remains recognizable to a historical ecologist a century after the event (Egan & Howell 2001). Natural disturbances such as fire and tornado blowdowns are reflected in species composition, and more severe disturbances resulting from substrate-altering events, such as landslides or farming, are even more evident. If local disturbances such as these can visibly influence plant composition a century after their occurrence, it seems unlikely that a continent-wide climate-driven disturbance would equilibrate even a century after the climate change reached a stable point, much less while it is still shifting. Both the paleoecological data presented here and the ecological evidence of small-scale historical disturbances imply that ecosystems could not adjust to such a climate perturbation for at least a millennium, or more likely, several millennia.

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