Long-Term Tree Cover Dynamics in a Pinyon-Juniper Woodland: Climate-Change-Type Drought Resets Successional Clock

Michael J. Clifford,[1]* Neil S. Cobb,[2] and Michaela Buenemann[3]

[1]Earth and Environmental Science Department, Lehigh University, 1 West Packer Avenue, Bethlehem, Pennsylvania 18015, USA; [2]Merriam-Powell Center for Environmental Research, Department of Biological Sciences, Northern Arizona University, Peterson Hall, Box 6077, Flagstaff, Arizona 86011, USA; [3]Department of Geography, New Mexico State University, MSC MAP, P.O. Box 30001, Las Cruces, New Mexico 88003, USA

ABSTRACT

Woody vegetation has expanded in coverage over the past century in many places globally, exemplified by pinyon-juniper changes in the Southwestern United States. Extreme drought is one of the few non-management drivers besides fire that might reverse such cover changes, but this has not been well documented. Here, we assess 68 years of tree cover dynamics across an elevation gradient of a pinyon-juniper woodland using aerial photographs (1936 and 1959) and QuickBird imagery (2004). Canopy cover increased 32% from 1936 to the onset of a major drought (2002). The largest relative increase in canopy cover occurred from 1936 to 1959 at the higher elevations, but these gains were eliminated by fires occurring from 1959 to 2002, during which time lower elevations with low canopy cover exhibited the greatest relative increases. The 2002–2004 drought reduced canopy cover by 55%, which eliminated gains in cover that occurred since 1936. Relative tree cover loss was highest at low elevations with low tree cover, but absolute tree cover loss was greater in areas of high tree cover, which increased with elevation. The loss of more than half of the canopy cover during a 2-year drought period was much greater than losses due to fire or possible increases due to historic land use (for example, grazing). These results suggest that regional-scale climatic influences may be more important than land use legacies in controlling tree cover of these and perhaps other semiarid woodlands over longer time scales—notable given that similar episodes of tree mortality are projected in coming decades with climate change.

Key words: drought; climate change; pinyon-juniper woodland expansion; aerial photographs; QuickBird; die-off; mortality; fire; grazing; elevation gradient.

INTRODUCTION

Many woody vegetation types have increased in spatial extent and density over the past century. A particularly notable example of this is the expansion of pinyon-juniper woodlands throughout much of the arid and semiarid southwestern USA since the late 1800s (Yorks and others 1994; Van Auken

2000; Weisberg and others 2007). Expansion and infilling of woody vegetation in drylands has been attributed to grazing, fire suppression, historic climate change, and/or atmospheric CO_2 enrichment during the past century, with their relative roles often being difficult to untangle (Archer 1994; Harris and others 2003; House and others 2002; Van Auken 2000). Depending on whether the driving forces were mainly human or natural, increases in woody plant coverage are often distinguished between woody plant encroachment and natural succession, respectively (Yorks and others 1994; Van Auken 2000). Independent of what caused the shift in woody plant and grass dominance, much effort has focused on the reduction of tree densities and/or extent in an effort to return affected areas to a ''natural state,'' usually defined as pre-European (Aro 1971). However, research on the impact of climatic events on woody vegetation dynamics and the role climate plays in controlling woodland dynamics has been limited (Swetnam and Betancourt 1998; Breshears and others 2005; Shinneman and Baker 2009).

Climatically driven disturbance events such as drought, hurricanes, fire, or floods are a major source of vegetation changes, driving large-scale patch dynamics (Turner 1989; Malmstrom and Raffa 2000; Asner and others 2003), altering vegetation composition (Breshears and others 2005), and shifting ecotones (Allen and Breshears 1998; Dullinger and others 2004; Floyd and others 2004). In the Southwestern United States, droughts are major disturbance events and drive other disturbance events such as fire (Westerling and others 2006) and bark beetle outbreaks (Allen and Breshears 1998; Breshears and others 2005; Shaw and others 2005; McDowell and others 2008). Both impact ecosystem processes and can significantly alter future disturbance dynamics (Turner 1989; Kulakowski and others 2003). However, extreme events such as droughts are rarely cited as being important in woodland cover dynamics compared to fire and grazing, and are poorly understood in terms of their impact on those dynamics (for example, Van Auken 2000; Weisberg and others 2007; Bradley and Fleishman 2008). It is also unclear how woodland dynamics vary over elevation gradients (Allen and Breshears 1998; Adams and Kolb 2005), which is relevant to predicting vegetation changes in response to climate change (Kelly and Goulden 2008; Breshears and others 2008).

An extreme drought with anomalously warm temperatures characterized the Southwestern USA from 2002 to 2004 (Breshears and others 2005). This extreme drought precipitated pinyon ips bark beetle (*Ips confusus* LeConte) outbreaks, leading to 52% mortality of pinyon (*Pinus edulis* Engelm.) trees in our study area (Floyd and others 2009) and regional mortality from 10 to 90% (Breshears and others 2005; Shaw and others 2005). The warmer temperatures also likely exacerbated the pinyon mortality (Adams and others 2009). One-seeded juniper (*Juniperus monosperma* Engelm.), a co-dominant of pinyon in northern Arizona, also experienced significant mortality, but comparatively less (10%), because it was not affected by bark beetle attacks (Floyd and others 2009) as was the case for other woody species (Koepke and others 2010). Although a bark beetle outbreak was the proximate factor associated with pinyon mortality in our study area, we presume that the drought that led to the region-wide outbreak was ultimately responsible for all woody plant mortality. Therefore, all canopy loss in 2002–2004 will be referred to as drought mortality hereafter. Using remotely sensed data from 1936, 1959, and 2004, the objectives of this article are to: (1) map long-term (1936–2004) woodland cover dynamics along an elevation gradient in northern Arizona; (2) examine the role of fire, grazing, and drought in determining woodland cover dynamics; and (3) highlight the impact of the most recent drought-induced mortality event on resetting the woody plant successional clock and converting pinyon-juniper woodlands to juniper-dominated savannas.

METHODS

Study Area

The study area (21,193 ha) is located approximately 27 km north of Flagstaff, Arizona, on the north side of the San Francisco Peaks (Clifford and others 2008; Floyd and others 2009; Figure 1). It is dominated by pinyon-juniper woodland and bordered by grasslands at the lower and ponderosa pine (*Pinus ponderosa*) forest at the upper ecotones. The climate is characterized as a midlatitude steppe (BSk) climate (Köppen 1936). The elevation ranges from 1,740 to 2,480 m (mean = 2,029 m). Over 90% of the study area is administered by the federal government under the jurisdiction of the United States Forest Service (USFS).

Image Acquisition, Pre-Processing, and Classification

Hard copy panchromatic aerial photographs from 1936 and 1959 were obtained from the Museum of Northern Arizona and USFS, respectively.
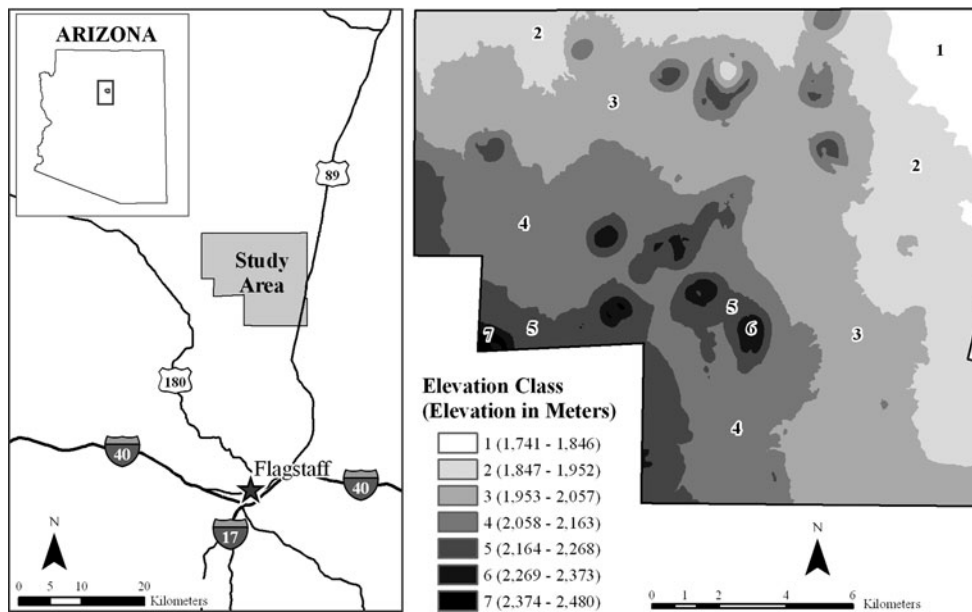
The photos were scanned and digitized at 1,200 dots per inch and compiled into a mosaic with a spatial resolution of 1 m. A 2004 QuickBird image was acquired through DigitalGlobe for June 2, 2004, the driest time of year when tree cover is most easily distinguished from herbaceous cover. The 2004 QuickBird image was used to quantify canopy cover both prior to the die-off event in 2002 and after the die-off event in 2004. We use this image for both tasks for two reasons: (1) the image was acquired immediately after the die-off period occurred, when live trees, dead trees, and herbaceous vegetation could be readily differentiated based on their unique spectral responses, especially in the near-infrared (NIR); and (2) other high-resolution imagery for the study area was not available for the time immediately prior to the die-off period. The NIR band of the QuickBird image was pansharpened from 2.4 to 0.62 m. Images were subsequently co-registered and subset to the area shared by all images (Figure 1).

All remotely sensed data sets were classified using a supervised classification technique (Carmel and Kadmon 1998; Anderson and Cobb 2004) and binary classification scheme. The classification differentiated between tree cover and intercanopy spaces comprised grasses, herbaceous dicots, and low-growing shrubs. Gray-level thresholds were used to classify canopy and intercanopy spaces in the panchromatic images (1936 and 1959), whereas NIR band thresholds were used to classify the QuickBird imagery into intercanopy spaces and (a) live and dead tree crowns (that is, ''2002 pre

die-off'' conditions) and (b) live tree crowns only (that is, ''2004 post die-off'' conditions). We did not attempt to distinguish between pinyons and junipers as both species have similar reflectance characteristics in the visible and NIR portions of the electromagnetic spectrum (Stimson and others 2005).

Accuracy Assessment of Classifications

The QuickBird-derived classifications were obtained by comparing percent canopy cover estimates collected in the field in 2002 and 2004 with percent canopy cover estimates from the 2002 pre- and 2004 post die-off classifications, respectively. An accuracy assessment was performed for each classified image. Comparisons between field and remotely sensed data were made in 18 randomly established field plots (Floyd and others 2009), each representing a belt transect 200 m × 10 m containing twenty 10 m × 10 m sub-plots. Each sub-plot was GPSed to less than 1 m accuracy and digitized to create a 10 m × 10 m polygon of the subplot. The classified QuickBird images were masked to the extent of these polygons, and canopy cover was obtained for each polygon. The image-derived canopy cover estimates were compared to the average canopy cover estimates from the field transect sub-plots. An accuracy assessment of the 1936 or 1959 classifications was performed by generating 100 random points on each image and visually comparing the computer-generated values at these points with cover characteristics on the original aerial photographs.

Elevation Gradient, Vegetation Change, and Pattern Analyses

We examined vegetation changes in the landscape over a 68-year period by using a 10-m digital elevation model, which we classified into seven elevation zones between 1,740 and 2,480 m with each zone comprising 105 m of relief (Figure 1). For each elevation zone, we calculated the amount of canopy cover for each year (for example, 1936, 1959, 2002 pre die-off, and 2004 post die-off). For the 2002 pre die-off and 2004 post die-off years, we calculated the average patch size and total patch number for each elevation zone, whereby patches were defined as contiguous "clumps" of foliage cover (that is, adjacent pixels of foliage). We only used the 2002 pre die-off and 2004 post die-off data for patch size and patch number analyses because the data were derived from the same image and the higher spatial and spectral resolution of the imagery allowed us to detect even small single tree patches.

To examine the change in canopy cover through time, each classified image was aggregated from 1-m pixels into 1-ha pixels. For each 1-ha pixel, we estimated canopy cover in percent (0–100%) by determining the percentage of 10,000 1-m pixels (that is, 10,000 m^2 = 1 ha) classified as canopy cover. Pixels of 1 ha were used to compensate for misregistration and misclassification errors, and to allow for continuous estimates of vegetation cover change, which provide more information than binary estimates of vegetation change from either canopy to intercanopy or vice versa. Canopy cover changes between years were assessed in three different ways:

(1) amount of canopy cover change:

$$x_i = a_i - b_i \qquad (1)$$

(2) rate of canopy cover change:

$$y_i = [(a_i - b_i)/b_i] \times 100 \qquad (2)$$

(3) percentage of canopy cover change:

$$z_i = (b_i/a_i) \times 100, \qquad (3)$$

where a_i is the canopy cover at time 1 (for example, 2002 pre die-off) and b_i the canopy cover at time 2 (for example, 2004 post die-off) at 1-ha pixel i, and x_i is the amount, y_i the rate, and z_i the percentage of canopy cover change at that 1-ha pixel. Therefore, canopy cover changes were assessed in absolute terms (equation (1)), as a rate (equation (2)), and in relative terms (equation (3)).

In addition, a series of regression analyses were performed on the 1-ha spatial resolution imagery to explore the relationships between 1936 and 2002 pre die-off canopy cover; 1936 canopy cover and rate of canopy cover change between 1936 and 2002 pre die-off; 2002 pre die-off canopy cover and amount of canopy cover change between 2002 pre- and 2004 post die-off; and 2002 pre die-off canopy cover and percentage of canopy cover change between 2002 pre- and 2004 post die-off.

Role of Fire and Historic Land Use on Woodland Canopy Cover

To determine if fire was a significant factor affecting canopy cover, we acquired digital spatial data layers of past historic fire distribution from the USFS. We then calculated canopy cover from the 1936 and 2002 pre die-off classifications based on all pixels both within these historically burned areas and in adjacent control areas (that is, non-burned) that were similar in size (for example, 6% of the landscape for burned and 10% of the landscape for non-burned) and elevation (mean = 2,180 m for burned and 2,166 m for non-burned) to the burned areas. Data were compared graphically to assess how fire impacted canopy cover from 1936 to 2002 pre die-off.

With the exception of a few small private inholdings where trees were cleared for pasture, all of the historic land use has been grazing by free-ranging cattle and sheep. We examined records for animal unit month (AUM) from the USFS for the Peaks Grazing Allotment (approximately 68,000 ha), which encompasses the entire study area. Grazing records did not specify where on the study area grazing was occurring; therefore, we could not directly assess the role of grazing by cattle or sheep in promoting tree establishment and expansion. However, we were able to document grazing levels from 1914 until present to determine if there was a qualitative relationship between grazing and expected changes in canopy cover (see Discussion).

RESULTS

Classification Accuracy Assessment

Based on 100 random points, the 1936 and 1959 images showed a 96 and 94% overall accuracy of the classifications, respectively. In the 1936 classification, 2% of the canopy reference points were misclassified as intercanopy and 2% of the intercanopy reference points as canopy. In the 1959 classification, 5% of the canopy reference points were misclassified as intercanopy and 1% of the

intercanopy reference points as canopy. The agreement of QuickBird imagery and field-derived estimates of canopy and intercanopy spaces was relatively high for both the 2002 pre die-off ($r^2 = 0.803$) and 2004 post die-off ($r^2 = 0.806$) conditions (for example, Kadmon and Harari-Kremer 1999; Ko and others 2009). The slope of the 2002 pre die-off classification was 1.33, indicating a slight over-estimation of canopy cover. The slope of the 2004 post die-off classification was 0.77, indicating a slight under-estimation of canopy cover. This would indicate differences between 2002 pre die-off and 2004 post die-off canopy cover are slightly less than we report here. However, tree canopy cover estimates obtained from ground transects ($n = 60$) in the area prior to and after the die-off event (see Floyd and others 2009) indicate agreement with our remotely sensed estimates and thus provide increased confidence in our Quick-Bird-derived estimates. According to the transects, pre die-off canopy cover was 14.6% and post die-off canopy cover 4.9%; according to the QuickBird image classifications, canopy cover was 14.1% in 2002 and 6.4% in 2004. Therefore, the pre and post die-off differences between the field and remotely sensed estimates were only 0.5 and 1.5%, respectively.

Rates and Patterns of Canopy Cover Change over Time and Elevation

There was a general increase in tree canopy cover from 1936 (9.5% canopy cover) to 2002 pre die-off (14.1% canopy cover) followed by a substantial decrease to 6.4% tree cover in 2004 post die-off (Figure 2). Only the highest elevation zone increased in canopy cover from 1936 to 2004 post die-off, although all other elevation zones

decreased in canopy cover from 1936. These changes are shown in the canopy cover maps for 1936, 1959, 2002 pre die-off, and 2004 post die-off (Figure 3) as well as a canopy cover change map for the 2002–2004 time period (Figure 4).

Nested within this general pattern were two different patterns of tree cover change, one during the 1936–1959 period and another during the 1959–2002 period. These two patterns, as well as the 2004 post die-off reduction, were depicted by standardizing the magnitude of changes through 1959, 2002, and 2004 to canopy cover levels of 1936 for seven elevation zones (Figure 5). From 1936–1959, few changes took place at lower and middle elevations, but a substantial increase in canopy cover occurred at higher elevations (2,200–2,400 m). However, these increases at higher elevations were lost from 1959 to 2002 pre die-off and are best explained by fires that primarily occurred there during this time (see section regarding fire below). Despite losses in canopy cover at higher elevations, overall canopy cover increased 1.2-fold during the 1959–2002 pre die-off period, with the largest increases occurring at lower elevations between 1,775 and 2,050 m. To put these patterns in a spatial perspective, we quantified the amount of study area that each of these seven elevation zones occupied. Over 80% of the study area was within elevation zones 2, 3, and 4 (1,800–2,100 m) and although the greatest relative increases and decreases occurred at the lowest and highest areas where pinyon-juniper woodlands occur, the greatest absolute changes occurred at these mid-elevations.

When we examined patch size, patch number, and canopy cover changes using 1-m pixels a number of patterns emerged. In 2002, both canopy cover and number of patches increased with
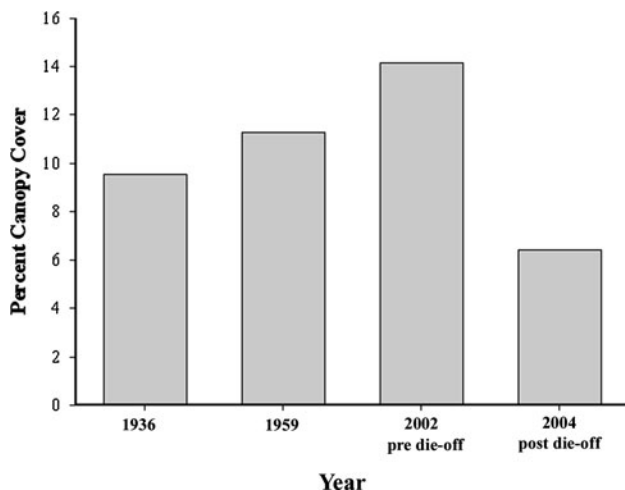

Figure 2. Change in canopy cover from 1936 to 2004. Canopy cover increase was linear ($r^2 = 0.99$) from 1936 to 1959 to 2002, but drought- and bark beetle outbreak-induced mortality in just 2 years after 2002 reset canopy cover levels to pre-1936 levels.
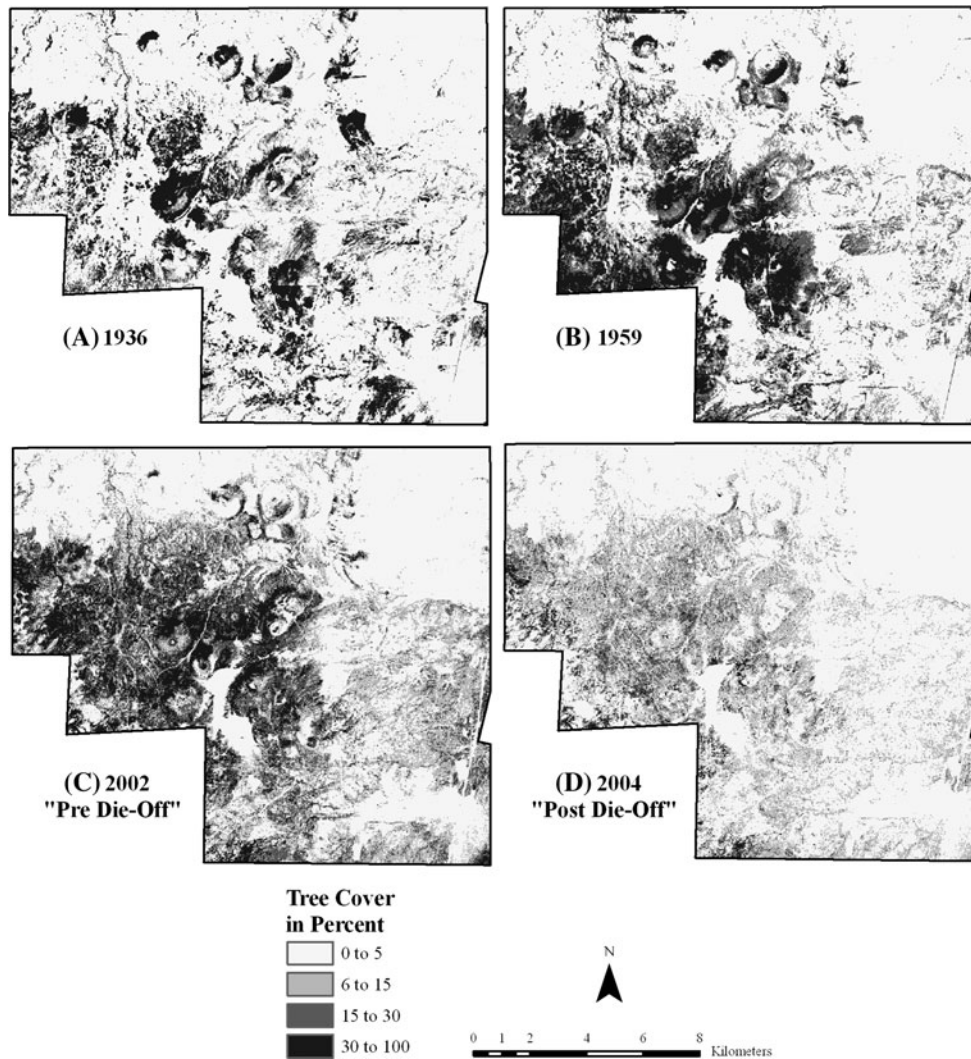
Figure 3. Change in canopy cover between 1936 and 2004. Maps represent percent canopy cover given a 30-m pixel size and grouped into four categories based on natural breaks in the data. Overall canopy cover was **A** 9.5% in 1936, **B** 11.3% in 1959, **C** 14% in 2002 (pre die-off), and **D** 6.4% in 2004 (post die-off).

elevation, suggesting a threshold pattern in canopy cover, with areas below 2,000 m having up to 12% cover and areas over 2,000 m in elevation having greater than 20% canopy cover (Figure 6A). The pattern of patch number was less pronounced than for canopy cover, and patch number decreased at the highest elevation where woodland mixes with ponderosa pine forest and crowns become fused leading to fewer (Figure 6B) and larger patches (Figure 6C). The drought had the effect of reducing canopy cover across the elevation gradient, especially at mid- to high-elevations (Figure 6A).

In comparing canopy cover and patch dynamics from 2002 pre die-off to 2004 post die-off, there was an overall pattern of increasing canopy cover and patch density (that is, patches per ha) with increasing elevation (Figure 6). An exception to this rule was the highest elevation zone where patch density decreased and patch size increased

greatly, which was due to increased canopy closure and tree density. The 2004 post die-off landscape showed a clear decrease in patch number and patch density compared to earlier years, but drought mortality caused mean patch size to remain stable.

The percentage of canopy cover change between 2002 pre- and 2004 post die-off (that is, the drought-induced percentage of tree mortality) was not dependent on canopy cover just before the die-off (Table 1). Canopy cover had a poor relationship to the percentage of mortality ($r^2 = 0.006$). However, areas with high cover lost more overall canopy cover than areas of low cover ($P < 0.001$, $r^2 = 0.873$), albeit not proportionally. This indicates that all areas in the study area incurred canopy loss from drought mortality, but that canopy mortality was not density dependent and that these areas may have lost more canopy cover simply because there was more cover to lose. Additionally, during
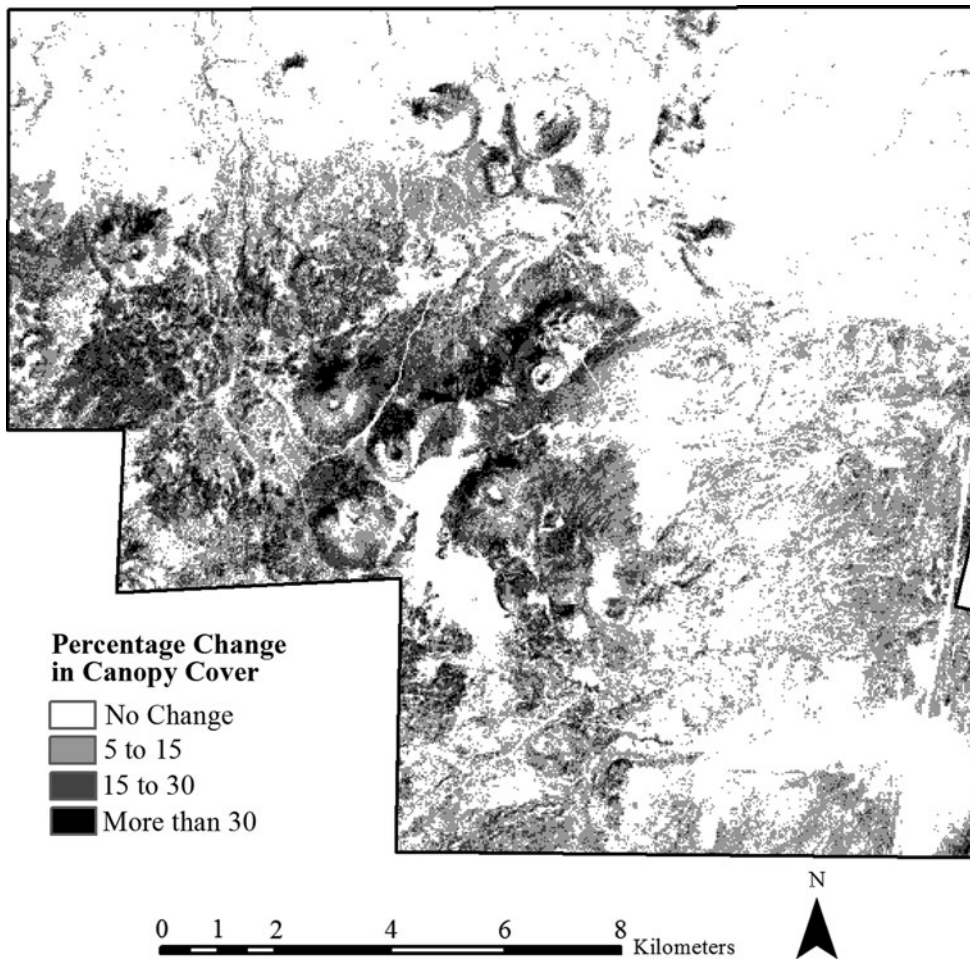
Figure 4. Change map showing the percent of change in canopy cover from 2002 pre die-off to 2004 post die-off.

the 66-year period of expansion, areas where canopy cover increased had lower canopy cover, whereas areas with high canopy cover in 1936 increased relatively little or remained stable during this time of woodland expansion (Table 1), possibly indicating dense areas in 1936 reached canopy cover equilibrium.

Fire Control on Tree Cover

Between 1936 and 2002 pre die-off, there were nine recorded fires that ranged in size from 9 to 900 ha (mean = 202 ha, median = 59 ha) and in total affected 6% of the study area. Fires were recorded beginning in 1931, with the earliest recorded fire in our study area occurring in 1948 and the latest in 1996. Fires were restricted to higher elevations (mean elevation of fires was 2,180 m; Figure 7), which characterize only a small proportion of the study area (Figure 1). Canopy cover of sites that burned at some point between 1936 and 2002 pre die-off was 10.9% in 1936. Unburned control sites had a similar cover in 1936 (11.7%) and a mean elevation of 2,166 m

(Figure 7). However, in 2002, canopy cover increased nearly 1.23-fold in unburned areas compared to burned areas at 16.3 and 21.1% canopy cover, respectively. We found no record of fires being suppressed in the study area during from 1936–2002.

DISCUSSION

Our results highlight how extreme climatic events (Breshears and others 2005; Weiss and others 2009) can rapidly reset woodland tree cover after a relatively long period of expansion and infilling (1936–2002). Our study supports the growing proposition that global climate-change-type drought can be a key factor in mediating woodland dynamics (Allen and Breshears 1998; Barger and others 2009; Huang and others 2010). We propose that extreme climate events such as drought can be more important drivers of long-term woodland cover dynamics than historic land use, and yet climate has previously received comparatively little attention as a driver of such dynamics (Adams and others 2009;
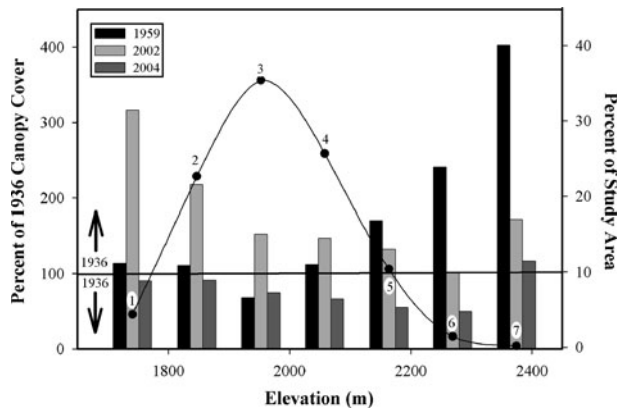
Figure 5. Change in percent canopy cover from 1936 to 2004 for seven elevation zones (*numbers* above bar graph correspond to zones in Figure 1). The *horizontal line* at 100% (left *y*-axis) indicates 1936 canopy cover levels. The *bars* show canopy cover changes (for example, 1959, 2002 pre die-off, and 2004 post die-off) relative to 1936 levels. *Solid circles* show the percentage of the study area encompassed by each elevation zone (right *y*-axis). Increases in percent canopy cover by 1959 were most prevalent at higher elevations but mostly eliminated by fire by 2002. Increases in canopy cover from 1959 to 2002 were most prevalent at lower elevations. Drought-induced mortality reduced cover at all elevations. Overall, the magnitude of canopy cover change was most extreme in the highest and lowest elevation zones, but these zones were smallest in areal extent. Most of the changes occurred in mid-elevations.

Allen and others 2010; Baker and Shinneman 2004; Romme and others 2009). However, we did not find any evidence of drought mortality from the 1950s drought, as was found in New Mexico (Allen and Breshears 1998). Increased tree cover due to fire suppression and overgrazing has been proposed to promote tree mortality during drought (Romme and others 2009), but we found no evidence to support this proposition. An important but unresolved issue is whether the drought impacts that we documented here are the first of a series of droughts linked to climate change (Breshears and others 2005; Adams and others 2009). If so, then this could be the beginning of a no-analog period (Overpeck and Udall 2010) leading to the transformation of woodlands to savannas and then possibly to grasslands or semi-arid deserts.

Elevation Gradient, Fire, and Grazing

Although significant drought-induced mortality occurred along the entire elevation gradient, four patterns were evident among high, medium, and low elevation zones; (1) high elevation stands experienced the greatest fluctuation in cover prior
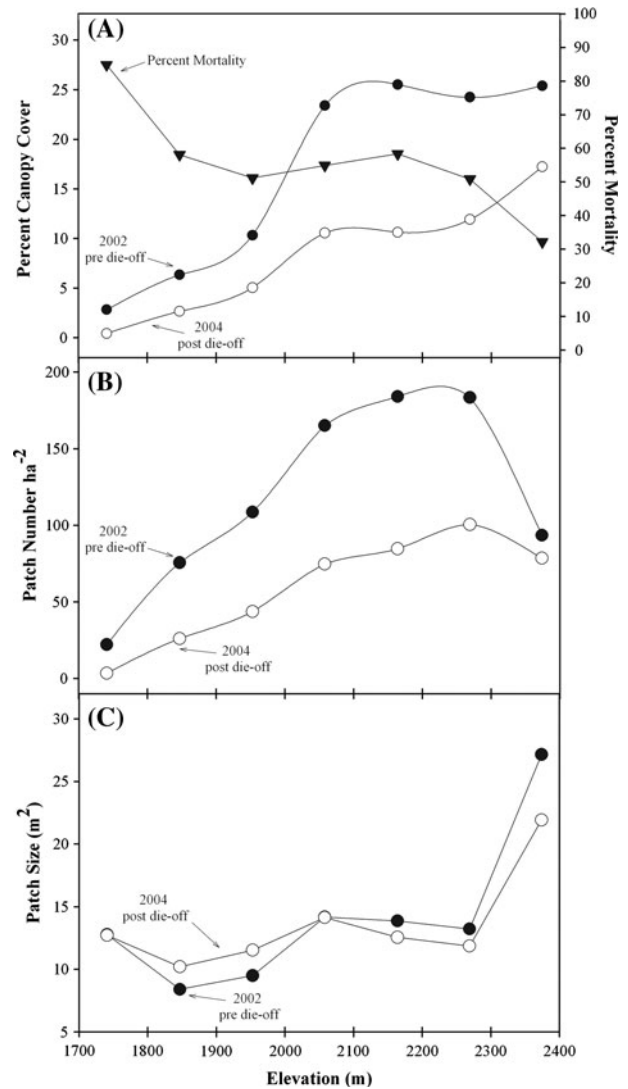

Figure 6. Drought- and bark beetle outbreak-induced patch dynamics across an elevation gradient. Canopy cover (**A**) and patch number (**B**) increased with elevation, whereas mortality decreased with elevation. Mortality significantly decreased canopy cover and patch number from 2002 pre die-off to 2004 post die-off. Mean patch size did not change from 2002 pre die-off to 2004 post die-off (**C**).

to the drought, (2) low elevation stands experienced the greatest change in cover due to the drought, (3) mid-elevation stands, which comprise 60% of the area, exhibited the smallest relative increases in cover prior to the drought, did not experience fire, and were more buffered against drought than lower elevations, and (4) although patch size was relatively stable, even after the die-off event, the number of patches decreased at all elevations, especially at mid-elevations (2,100–2,300 m).

Table 1. Relationships Between Canopy Cover and Cover Changes Through Time

| Predictor variable (x)	Dependent variable (y)	P	r^2	Line equation
2002 Pre die-off canopy cover	1936 Canopy cover	<0.0001	0.336	$y = a(1 - e^{-bx})$
Rate of canopy cover change from 1936 to 2002 pre die-off	1936 Canopy cover	<0.0001	0.323	$y = 11.156e^{-0.2901x}$
2002 Pre die-off canopy cover	Amount of canopy cover change from 2002 pre die-off to 2004 post die-off	<0.0001	0.873	$y = 1.7566 + 1.4586x$
2002 Pre die-off canopy cover	Percentage of canopy cover change from 2002 pre die-off to 2004 post die-off	<0.001	0.0006	$y = 0.5881 + -0.0005x$
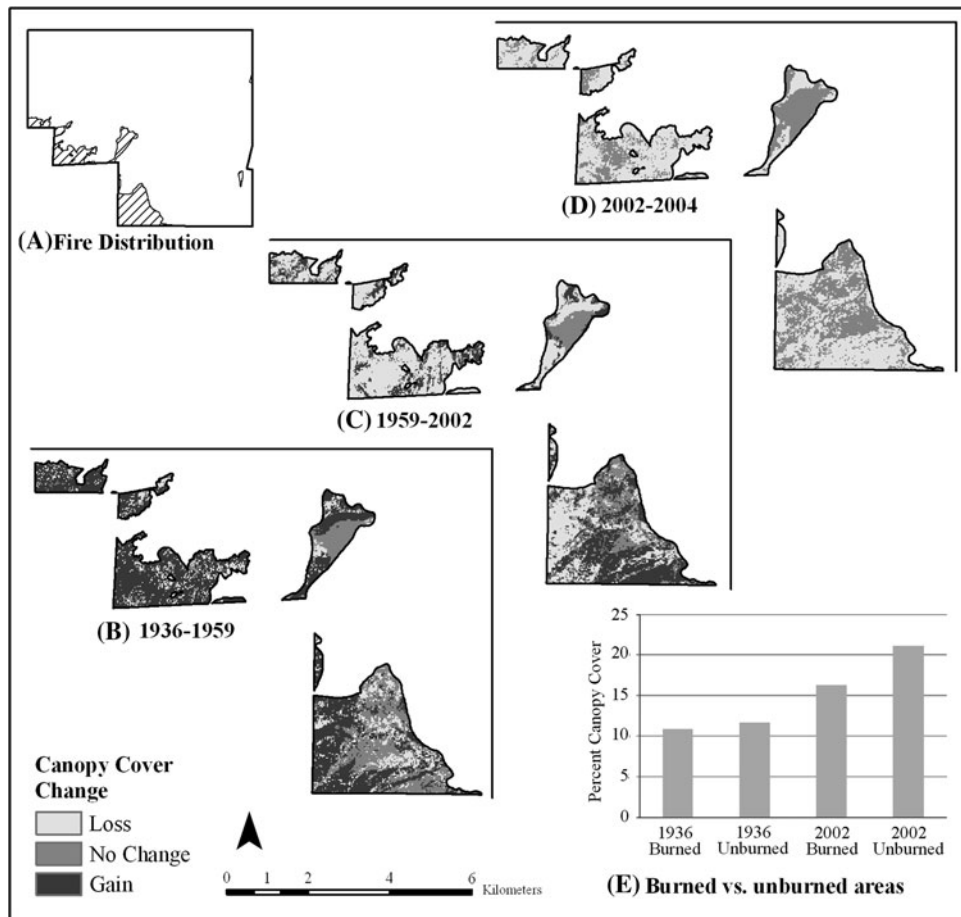
Figure 7. Historic fires reduced canopy cover and contributed to suppression of woodland expansion and infilling, but occurred in only 6% of the study area and reduced canopy cover less so than the recent drought and bark beetle outbreak. **A** Historic fires in the study area occurred near the ponderosa pine (*Pinus ponderosa*) forests in the upper elevations and to some extent in pinyon-juniper woodlands at lower elevations (compare with elevation map in Figure 1). Maps **B** through **D** show canopy cover gains and losses and areas of no change where fires occurred at one point or another between 1936 and 2002 (that is, historic fire distribution shown in **A**). **B** Canopy cover increased from 1936 to 1959. **C** Canopy cover decreased between 1959 and 2002 due to fire, and **D** canopy cover declined further due to drought. **E** Fire reduced the percent woodland cover between 1936 and 2002: in 1936, canopy cover was nearly identical in burned sites and unburned control sites (ca. 11%); in 2002, the canopy cover in burned sites was almost 5% lower (16.3%) than that of unburned control sites (21.1%).

Our ability to make predictions of ecological consequence regarding change in tree patches is limited to the degree that the spatial and spectral resolutions of the imagery are insufficient to distinguish between pinyon and juniper or to identify the number of trees in a patch. Our approach captured landscape heterogeneity at the finest possible spatial scale given our data and did not involve the definition of a potential arbitrary minimum patch size. We felt this approach was appropriate because of the many multi- and cross-scale interactions found in ecosystems (Turner 1989). Furthermore, by examining more than 1,600 trees with crown sizes at least 1 m^2 measured throughout the study area and adjoining woodlands [for more details, see Floyd and others (2009)], the mean crown size for all trees was 4.1 ± 0.02 m^2, indicating that the typical patch comprised two to four trees. Knowing the species composition and the development stage of individual trees comprising patches would greatly expand our ability to make predictions about future woodland dynamics. An ongoing ground-level study is documenting changes in patch composition and how those influence pinyon and juniper seedling establishment.

Concerning higher elevations (1,740–2,480 m), which comprise only 6% of our study area, canopy cover increased dramatically from 1936 to 1959, but was essentially lost between 1936 and 1959 due to high severity fires occurring near the woodland-ponderosa pine ecotone. Canopy cover in the burned upper ecotone was 5% lower than in similar unburned control areas, indicating fires inhibited some woodland infilling, but still allowed for increases in canopy cover since 1936. So, in upper ecotones where woodlands are adjacent to fire-dominated ecosystems, fire can have an important effect in reducing canopy cover. Fire in these areas may also explain the maintenance of woodland-forest ecotones as was found for a savanna-forest ecotone in South Dakota (Brown and Sieg 1999).

At lower elevations, canopy cover did not increase during the 1936–1959 period as we observed for the higher elevations. During the 1959–2002 period, when fires were occurring at higher elevations and reducing tree cover there, the canopy cover at lower elevations continued to increase, perhaps due to more favorable climatic conditions for seedling establishment and tree growth in the 1970s and 1980s (Swetnam and Betancourt 1998). Precipitation during the 1959–2002 period was considerably higher (55.9 ± 15.4 SD cm) than during the 1935–1959 period

(46.5 ± 12.4 SD cm) based on NOAA records for Flagstaff, Arizona.

There was an inverse relationship between elevation and tree cover fluctuations, with high and low elevations being much more dynamic than mid-elevations (Figure 5). This may indicate that mid-elevation woodlands are more in equilibrium and buffered against both fire and drought. Allen and Breshears (1998) documented significant changes in *Pinus ponderosa* at lower ecotones in response to drought. Likewise, we found the greatest relative change at the lower woodland–grassland ecotone. We did not find obvious shifts in ecotone boundaries. However, if we use the 10% tree cover as the cut off to distinguish woodland ($>10\%$) and savanna ($<10\%$) then most of our study area experienced a conversion from woodland to savanna (Figure 6A), which has important ecosystem consequences (Royer and others 2011).

The lack of historical and current data on grazing presents a challenge in assessing its role in vegetation dynamics. Sheep and cattle grazed the area at approximately 4,000 AUMs per year between the early 1900s and the 1980s, a number that thereafter declined to approximately 1,500 AUMs per year (Data from Coconino National Forest). The level of grazing at 4,000 AUM on the landscape is considered light (for example, 0.05 AUM ha^{-1}) compared to more heavily grazed areas (for example, >1.0 AUM ha^{-1}) (Buckhouse and Gifford 1976; Loft and others 1987; Willms and others 1988). We have never observed signs of overgrazing during field studies, which we have conducted in the area since 1985, and all grazing records indicate that grazing has been seasonal. Given these records and the current condition (for example, low erosion and high percentage grass and understory cover) of the study area, we conclude that grazing by livestock likely had a minimal impact on pinyon-juniper cover in the study area except on the few inholdings of private land.

Our findings support those of Barger and others (2009) in that climate, and not land use history, is the most important factor explaining woodland dynamics in our study area, and that some woodland fluctuations may have been wrongly attributed to grazing and fire suppression. Canopy cover was also less impacted by fire than by drought, suggesting that climate may have a more important role in controlling canopy cover and density than fire, especially over large areas and long time periods. Shinneman and Baker (2009) examined the role of multi-decadal drought and pinyon-juniper woodland establishment, demonstrating that both pinyon and juniper establishment since

1500 AD has been reliant on climatic fluctuations of the Pacific Decadal Oscillation and Atlantic Multidecadal Oscillation. Swetnam and Betancourt (1998) moreover concluded that old (for example, >400 years) pinyons from the Southwest are not abundant possibly due to extensive drought in the late 1500s and a potential associated tree mortality event.

Patterns of Infilling and Woodland Equilibrium

The pattern of infilling that we documented has also been found in other pinyon-juniper woodlands (Weisberg and others 2007). Specifically, the relative increase in tree cover was greatest in areas where canopy cover was low in 1936 (for example, 1–5%), whereas tree cover remained relatively stable in areas where cover was high in 1936 (>30%). However, the increase in tree cover in our study area was modest compared to long-term increases reported for other woodlands (Miller and Wigand 1994; Weisberg and others 2007; also see Romme and others 2009). The mechanisms that caused woodland expansion and increased density in northern Arizona are still unknown, but grazing remained relatively stable at relatively low intensities during the past century (see above) and fires occurred on only 6% of the landscape occupied by woodlands. Our results are consistent with the notion that climate may be more important in structuring pinyon-juniper woodlands rather than historical land use (Barger and others 2009) and that many woodland areas may be in a constant flux of recovery from droughts.

Our results do raise the question as to whether this or other pinyon-juniper woodland areas ever approach equilibrium (Breshears 2006). The drought-related mortality and fire at the higher elevations effectively reset cover to pre-1936 levels, and hence levels that would be more typical of a savanna (<10% tree cover) than a woodland. There were stands within the boundary of our study area that had attained tree cover over 40%, suggesting that this woodland area could reach cover values higher than those we documented in the absence of disturbance, as has been found for populations of *P. monophylla* (Bradley and Fleishman 2008). However, even peak canopy cover in our study area (14% in 2002) is still considered low for pinyon-juniper woodlands, and thus our study may not be representative of higher-cover woodlands. However, other higher canopy cover estimates for this woodland type (for example, Landfire, ReGAP) may be due to the inclusion of shrubs in cover assessments (Huang personal communication) or due to data- and methods-induced overestimates of regional percent cover (Huang and others 2009).

Density-Dependent Mortality

Understanding factors that mediate changes in tree density has important land management implications. Most of the pinyon-juniper woodlands on the Colorado Plateau occur on publicly owned and tribal lands. It has been suggested that high tree density in pinyon-juniper woodlands predisposes trees to bark beetle attack (Negron and Wilson 2003), thus providing a rationale for thinning projects to restore woodlands to a ''healthy'' condition where stands become more resilient to drought-related mortality. Consequently, there have been concerted efforts to thin or eliminate woodland trees because of the perceived unnatural characteristics associated with woodland infilling and expansion as a result of fire prevention and overgrazing (Romme and others 2009). However, we found that increasing amounts of canopy cover did not proportionally increase mortality, showing no density-dependent relationship between die-off and canopy cover. These results provide further support to the notion that high-density stands are not more susceptible to climate-change-type drought-related mortality than low-density stands (Floyd and others 2009; Ganey and Vojta 2011). Our findings differ from results of woodland studies in Nevada with lower mortality levels (for example, <10%; Weisberg and others 2007; Greenwood and Weisberg 2008). Other studies in northern Arizona conducted early in the drought (for example, during 2002) indicated that increased canopy cover or stand density should increase mortality (Negron and Wilson 2003; Santos and Whitham 2010). Santos and Whitham (2010) concluded that high-density stands lead to greater mortality, but they did not measure stand density, canopy cover, or basal area, and therefore our results are not comparable. Our intensive study complements the most extensive study to date examining the relationship between tree density and die-off (Floyd and others 2009). The results of our study and others highlight the complexities related to density-dependent mortality resulting in temporal and spatial variation among stands.

Ecosystem and Management Consequences of Tree Mortality

The rapidity of the mortality event documented here shows how quickly climatic and associated disturbances such as bark beetle outbreaks can reduce canopy cover. The loss of more than half of the overstory has strong implications for biogeochemical cycling, animal habitat, understory vegetation, woodland succession, and future disturbance dynamics (Breshears and others 1997; Kulakowski and others 2003; Breshears and others 2009a, b; Adams and others 2010). Near-ground solar radiation will increase in areas of high die-off (Royer and others 2011), lowering overall soil moisture resources in the landscape (Breshears and others 2009a, b), and further altering ecosystem processes (for example, Steltzer and others 2009). When canopy cover is reduced, understory grass cover may increase (Allen and Nowak 2008), altering future fire dynamics in drought-affected pinyon-juniper woodlands (Kulakowski and others 2003; Clifford and others 2008), which currently consist of a mixture of dead and live tree crowns.

A key question is whether this extreme event will be followed by increased tree recruitment leading to a slow increase in tree cover and re-establishment of pinyon-juniper woodland, or whether we are witnessing the beginning of ecosystem conversion to a more permanent juniper savanna-grassland. If climate change promotes warmer and drier droughts (Overpeck and Udall 2010), we expect the latter to occur. However, we have observed some juniper recruitment in our long-term plots, which suggest that at least, to date permanent ecosystem conversion to a juniper savanna-grassland is just as possible as a resetting of woodland succession.

It is important to note the scale of our study in relation to the regional drought-induced mortality event. This study included approximately 8 million trees distributed over 211 km^2 and, together with other regional studies (for example, Shaw and others 2005; Breshears and others 2005; Floyd and others 2009; Huang and others 2009), provides a robust mesoscale assessment of regional pinyon mortality. Based on USFS aerial survey data, over 71 million mature pinyon trees have died across approximately 115,000 km^2 of Southwestern pinyon-juniper woodlands, leading to the conversion of approximately 415 km^2 of canopy area into open grassland (Drought Impacts on Regional Ecosystems Network, http://www4.nau.edu/direnet/). Through studies like this and others (for example, Huang and others 2009), we are able to compile regional-scale inferences about the ecosystem impact of protracted droughts and associated disturbances under a changing climate (Allen and others 2010).

The relatively long expansion time of this woodland and the rapid die-off of canopy cover show the importance of climatic extremes in influencing disturbance events and hint at the ensuing ecological threshold that ecosystems may experience under future climates. Our results suggest this may be true with regard to decadal historical vegetation changes in the past century, not just longer centennial to millennial time scales (Betancourt and others 1991; Anderson 1993). These rapid, extreme climatic events may be more important than other historical factors at mediating woodland stand dynamics. With the current rate of increasing global temperatures, die-off events like the one described here will likely increase in frequency and vegetation changes will rapidly occur over large areas during relatively short time periods (Adams and others 2009; Allen and others 2010).

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