Increasing woodland density in the western US over the last 200 years was driven by long-term plant demography rather than Euro-American settlement

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Abstract

Recent increases in woody plant density in dryland ecosystems around the world are often attributed to land use changes such as livestock grazing, but evidence to support these hypotheses is mixed and the demographic processes underlying past changes in woody plant abundance are poorly understood. After examining tree age structures from woodlands across the western US using demographic models, we found little evidence of increasing per-capita tree establishment rates following Euro-American settlement, suggesting that modern increases in woodland density were been driven by long-term growth in tree populations. Contrary to common interpretations, we found that tree establishment rates have mostly declined, not increased, since Euro-American settlement, and in fact establishment rates are currently at their lowest rates since at least 1600, possibly linked to warming temperatures.

Main Text

One of the most evident ecological changes in many dryland ecosystems over the last 200 years has been increasing density and distribution of woody vegetation (*1*, *2*). Collectively referred to as woody encroachment or expansion, increases in woody plant density have significantly impacted ecosystem processes and services, including global carbon cycling and hydrology (*3*, *4*). Evidence of increasing woody plant density and cover has been found in several archives, including packrat middens, tree-ring establishment records, historical photos, modern field observations, and more recently, remote sensing (*5*, *6*). In the western US, tree-ring-derived age structures show dry woodlands, particularly pinyon-juniper woodlands, dominated by trees that largely established after the mid-1800's (*7*). Because this timing also coincides with the period of widespread Euro-American settlement in the region, the increase in establishment has usually been attributed to anthropogenic mechanisms, such as wildfire suppression and livestock grazing, or to changes in environmental conditions that coincide with Euro-American settlement (e.g. increasing atmospheric CO_2)(*5*). However, evidence supporting these hypotheses has generally not been conclusive or pervasive enough to explain regionwide increases in tree establishment(*1*, *8*). For example, wildfire suppression is often cited as a mechanism underlying increases in woodland density, but data on wildfire regimes indicate many pre-settlement pinyon-juniper woodlands were likely characterized by infrequent, high-severity fires, rather than frequent, low-severity fires that would have regularly reduced young tree density (*8*). Similarly, impacts of overgrazing by domestic livestock are also commonly invoked to explain increasing woodland density, but sites with no livestock grazing history have seen similar increases in tree establishment (*9*, *10*). As a result, directly attributing increasing woody plant

density in both the western US and globally to specific external drivers remains a challenge (*1*, *8*, *11*).

Demographic rates, and in particular the processes that control plant establishment (seed production, germination, and survival at early life stages), are critical in controlling rates of plant population growth (*12*). If hypothesized changes in abiotic or biotic conditions were responsible for a sudden increase in woody plant density, we would expect this to be associated with an increase in the per-capita establishment rate (new trees established per existing tree) sufficient to account for the observed increasing density of woody plants (*13*). For example, if high-frequency, low-severity fires previously killed seedlings and maintained low tree density, as has been observed in some ponderosa pine-dominated ecosystems (*14*), then fire exclusion would lead to a sudden increase in seedling survival and thus per-capita establishment rates. However, population growth is a non-linear, multiplicative process and thus rapid increases in population density and establishment over time are possible even if the underlying demographic rates remain constant, unchanged by environmental conditions (Fig. 1). Multiplicative population growth could create the false appearance of a sudden increase in woody plant density driven by changing environmental conditions, especially when a population experiences prolonged periods of growth after colonizing new habitat or recovering from past disturbance (*15*). This component of vegetation change is often overlooked but can be readily quantified using population models. Thus, determining the demographic and population processes behind increasing woody plant density is essential to understanding its causes (*16*).

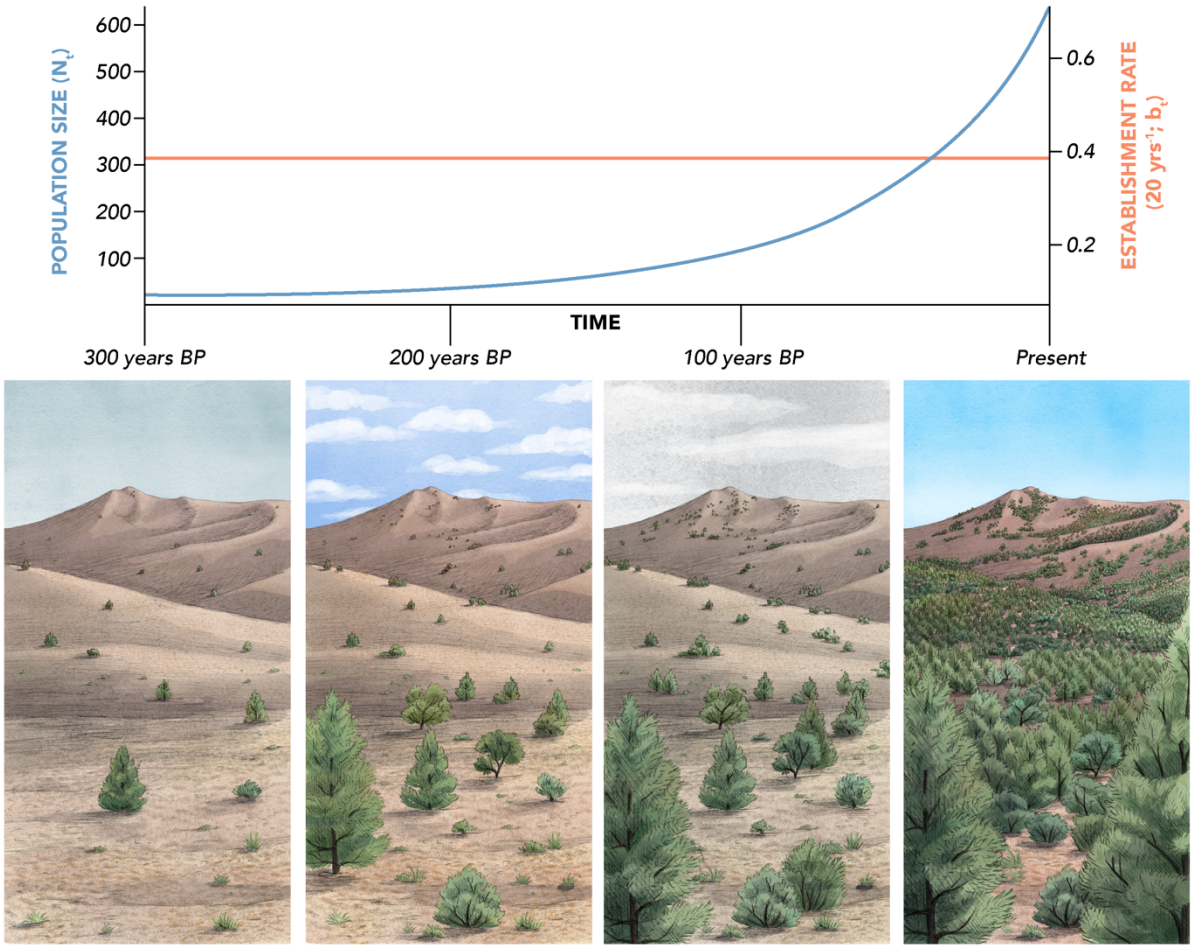

Figure 1. Increasing establishment under a constant establishment rate. Because new establishment (B_t) is the product of both population size (N_{t-1}) and per-capita establishment rate (b_t; $B_t = b_t N_{t-1}$) in a growing population the amount of new establishment will increase over time even if the underlying establishment rate is constant. One could view the rapid increase in establishment and population size as evidence of a change point and link the increase in establishment to an external driver. However, analysis of the underlying demographic mechanisms will find no change in per-capita establishment rates (orange) has occurred. Increased establishment is driven by the reproductive potential of larger populations. BP indicates "before present". (Illustration by Alex Boersma)

Here, we reexamine the drivers of widespread increases woody plant density by calculating empirical per-capita establishment rates (hereafter "establishment rates") prior to and following

Euro-American settlement in pinyon-juniper woodlands of the western US. Woodlands dominated by pinyon pine and juniper trees are among the most widespread forest types in the US, covering over 40 million hectares, and the most abundant remaining old-growth forest type in the US, representing nearly one-third of all old growth forest area (*17*). While increases in density of pinyon-juniper woodlands have been widely noted, the causes and management of increasing woodland density are often controversial (*8*, *18*). Despite the lack of conclusive evidence, the notion that increasing tree density and extent in western woodlands originated from Euro-American settlement remains prevalent in the scientific and land management literature. Such interpretation has motivated extensive vegetation treatments, often framed as restoration, to remove pinyon-juniper woodlands (*19–21*). At the same time, these woodlands have also experienced widespread mortality that has been attributed to climate change, either directly as drought stress (*22*) or indirectly as a result of insect outbreaks and increased wildfire activity (*23*).

One key aspect that was missing in previous interpretations of increasing woodland density is a quantification of the role of demographic and intrinsic population processes (*16*). To address this, we used published age structure data from 28 populations at 23 sites in the Great Basin and Colorado Plateau, US (Fig. S1; Table S1) to calculate establishment rates prior to and following Euro-American settlement. We evaluated the impact that changing establishment rates after 1850 had on observed woodland density increases, and then evaluate the relationship between establishment rates and climate conditions over the last 400 years. Extensive age structure data from stands that predate settlement are rare in savannas and woodlands, making pinyon-juniper

woodlands an ideal case study to evaluate establishment rates prior to and following Euro-American settlement.

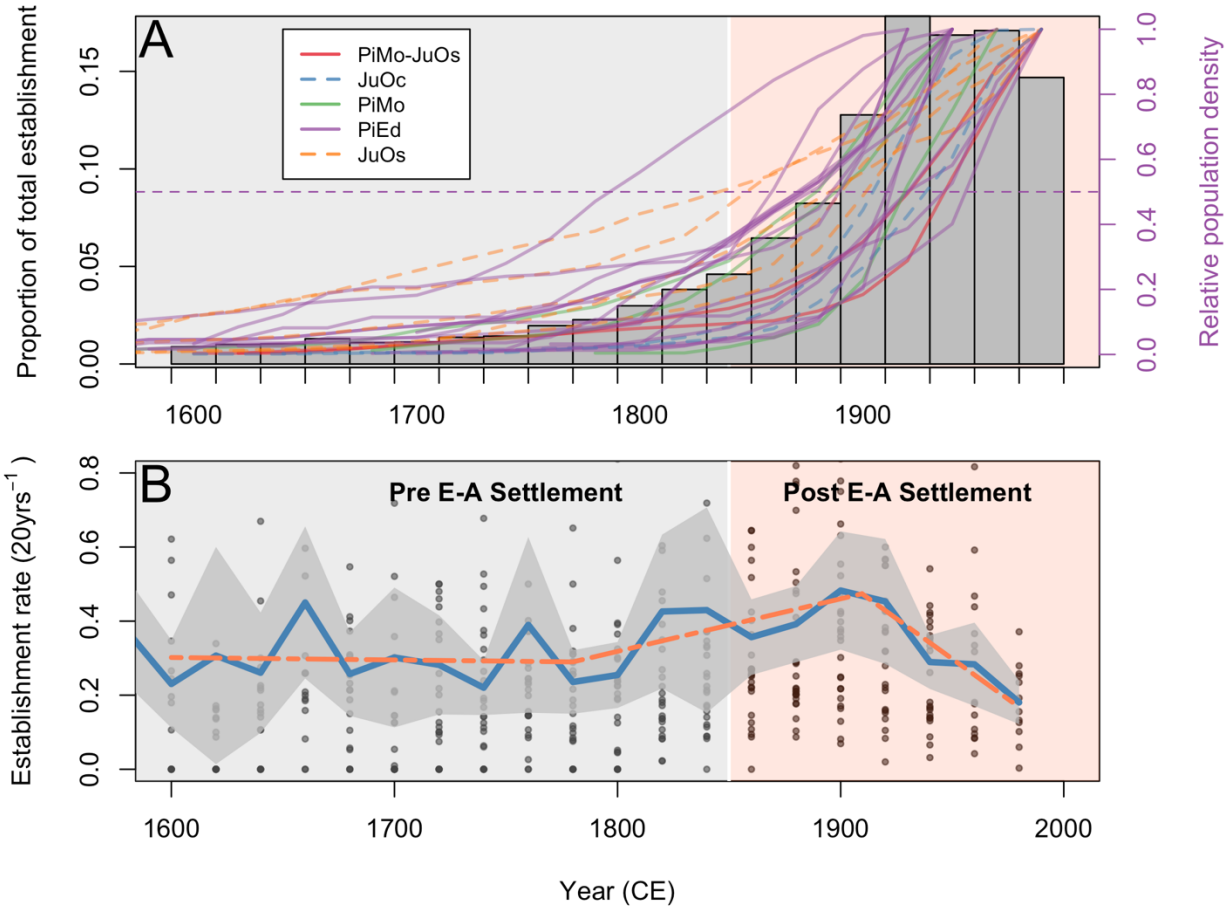

Figure 2. Tree establishment rates since 1600. (A) Proportion of total establishment occurring in each 20-year interval averaged across 28 populations and population density (i.e. cumulative establishment) in each population broken down by species. Dashed horizontal line indicates 50% of total. Speices in legend are mixed stands dominated by *Pinus monophylla,* with a minor *Juniperus osteosperma* component (PiMo-JuOs), *Juniperus occidentalis* (JuOc), *Pinus monophylla* (PiMo), *Pinus edulis* (PiEd), and *Juniperus osteosperma* (JuOs). (B) Per-capita establishment rates for each population (points), 20-year average (blue) and 95% confidence interval (grey), and results of segments regression (dashed orange). In all panels background color indicates before or after

Euro-American Settlement, with the division in 1850. For clarity, (B) is zoomed to show long-term average, the entire timeseries dataset is in Fig. S2.

Impacts of Euro-American settlement on tree establishment

Age structure data showed a regional trend of increasing pinyon-juniper tree establishment and density during the late 1800s and early 1900s, with more than half of trees establishing after 1850 in all but two populations (Fig. 2A). We found, however, that establishment rates between 1860-1900 generally fell within the pre-settlement range of variability (Fig. 2B), suggesting that rapid increases in density associated with Euro-American settlement were primarily driven by steady tree population growth rather than anthropogenic or environmental changes to underlying establishment rates. In contrast, we found that the largest change that has occurred since Euro-American settlement is a decline in tree establishment rates over the 20th century, which recently were at their lowest rates in at least 400 years.

Prior to 1600 average establishment rates were highly variable, fluctuating between 0.00 and 1.18 new trees per existing tree every 20 years (Fig. S2). Around 1600 average establishment rates dropped to 0.23 new trees per existing tree every 20 years but then increased to 0.45 in 1660, the second period in the last 400 years, before briefly stabilizing at ~0.25 between 1680 and 1740 (Fig. 2B). In the late-1700s, average establishment rates began gradually increasing until 1920, punctuated by periods with higher establishment rates prior to 1850. The results of segmented regression further corroborated this modest upward trend in establishment (Table S2). Although the total number of establishing trees per 20-year period more than tripled, we found only a modest increase in average tree establishment rates following Euro-American settlement, beginning at 0.35 in 1860 and peaking at 0.48 in 1900 (Fig. 2A,B). Segmented regression

indicates no detectable change in establishment rate patterns during the period of Euro-American settlement (approx. 1840-1860), with a continuation of the upward trend that began in the late 1700's. The largest change in establishment rates since Euro-American settlement occurred following ~1920, when both the 20-year average and segmented regression indicated establishment rates began to decline (Table S2). By the late 20th century tree establishment rates had reached their lowest level in 400 years, 0.18 new trees per existing tree every 20 years.

To better quantify the mechanisms explaining observed increases in establishment following Euro-American settlement, we separated contributions to establishment resulting from multiplicative population growth alone from contributions of changing establishment rates. We did so by comparing two simulations: one that maintained a constant establishment rate from the year 1860 (the "multiplicative growth" model), and the other using the observed establishment rates from 1860-1940, the post-settlement period. We find that multiplicative population growth consistently explained the majority of observed establishment increases (70-100%) across decades (Fig. 3A,B). Overall, multiplicative population growth with a constant establishment rate alone accounted for 85% of the total observed establishment in the period from 1860-1940 (Fig. 3C). Hence, changes in establishment rates due to anthropogenic or other environmental drivers are not needed to explain the rapid increases in establishment and population density after 1850.

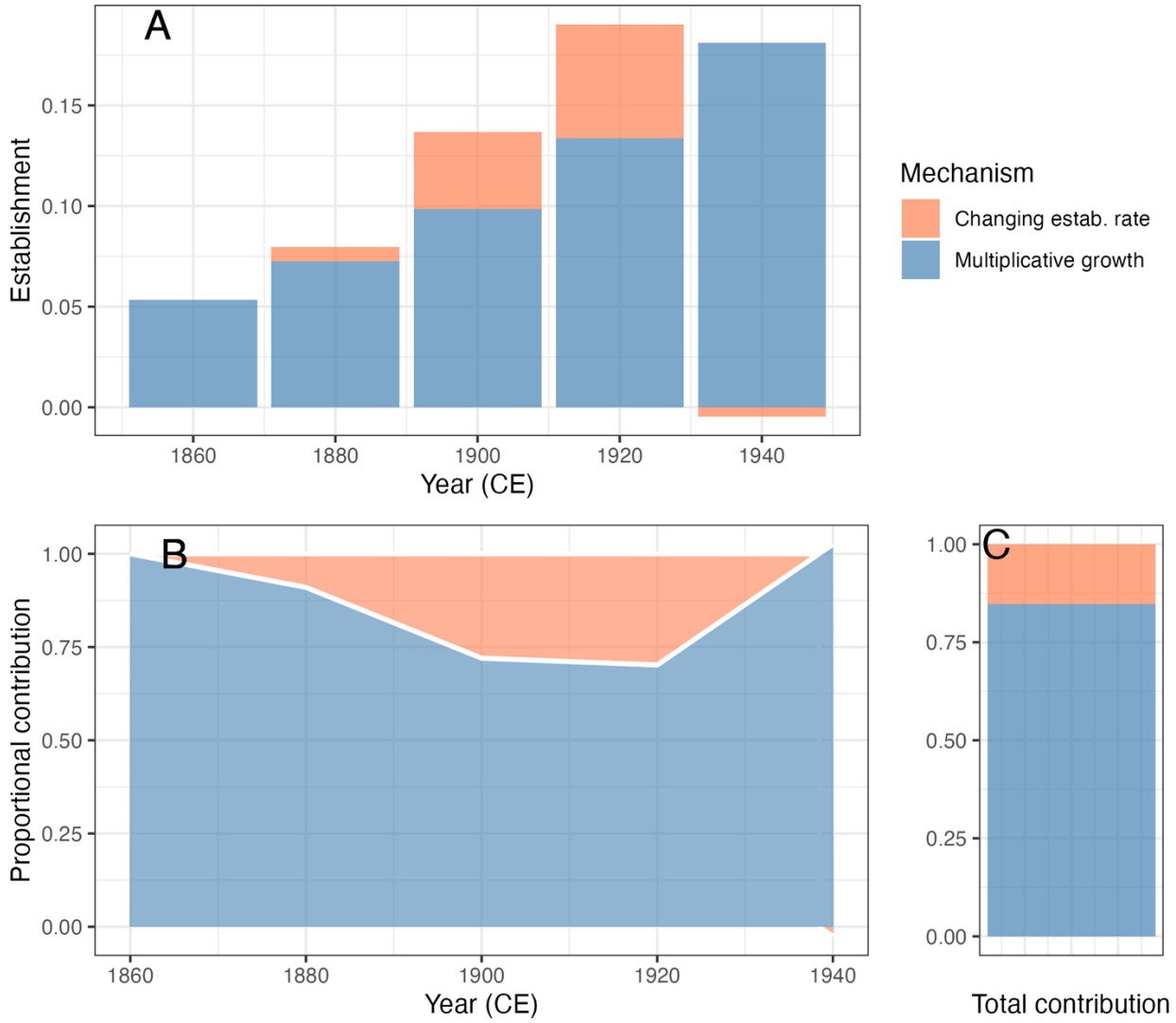

Figure 3. Decomposition of tree establishment following Euro-American settlement by mechanism. (A) Stacked bars with establishment in 20-year intervals decomposed into contributions of changing per-capita establishment rates (orange) and multiplicative population growth (blue) into total establishment in that interval (blue+orange). Negative values for changing establishment rate in 1940 (Panel A &B) indicate declines in establishment rates from 1860 and thus changing establishment rates would lower the establishment from what would be expected with constant multiplicative growth. (B) Relative proportional contribution of each mechanism, and (C) the contribution of each mechanism to total observed establishment summed across all intervals.

Robustness of establishment rate estimates

Pinyon pine and juniper species are known to have high survival rates, ~90 to >99% per 20 years (*24*), however our assumption of 100% survival could influence our interpretation of establishment rates. To test this, we calculated establishment rates after accounting for the impacts of survival under two additional scenarios: 1) constant survival rate of 90% per 20-year interval (comparable to observed rates in pinyon species), and 2) 100 simulated survival rate time series generated using a random walk model. While changing survival rates altered the magnitude of inferred establishment rates, we found that patterns and trends in per-capita establishment rates remained essentially unchanged under disparate survival scenarios (Fig. 4, Fig. S3). Establishment rate estimates remained similar in the face of disparate survival scenarios because, when mortality occurs, observed age structures underestimated both past establishment (i.e. many of the established plants were not still present to be censused), and past population size. Similarly, reproductive lags in young trees did not change overall establishment rate results (Fig. S4, S5).

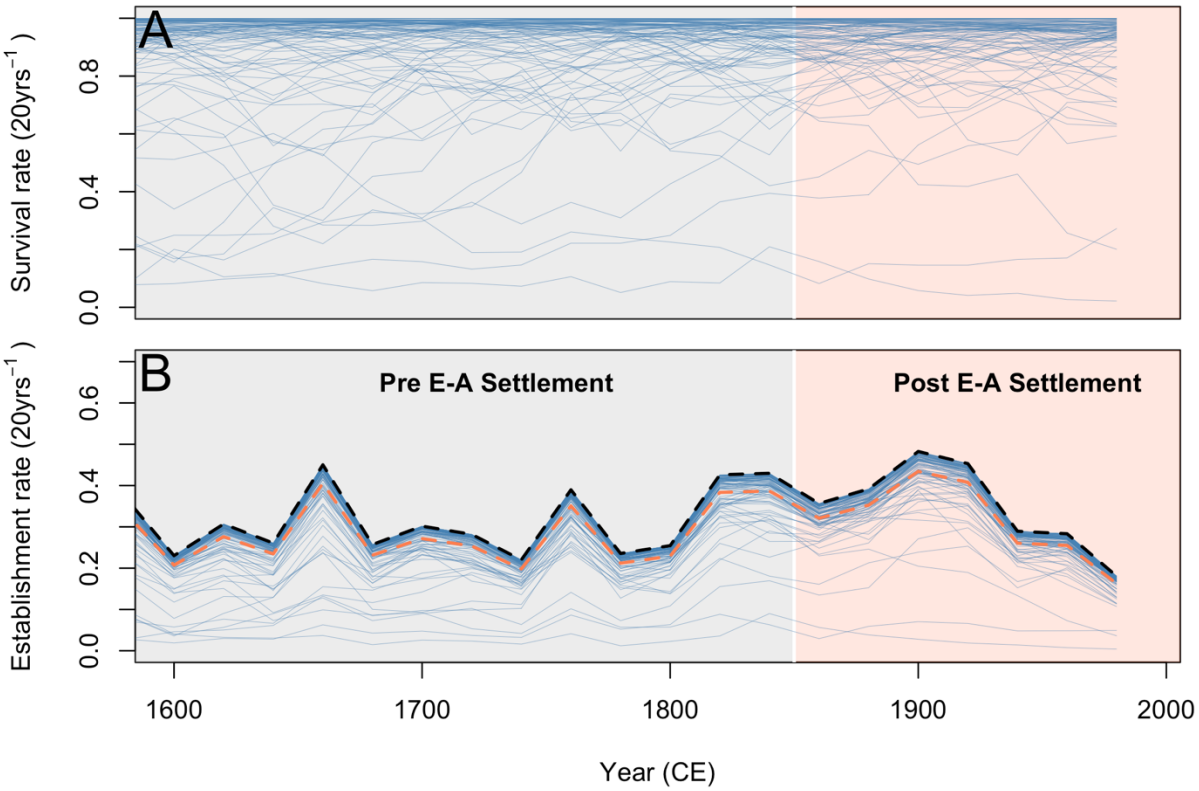

Figure 4. Impacts of survival rates on estimated per-capita establishment rates. (A) 100 randomly generated survival timeseries. (B) Estimated per-capita establishment rates given each of the survival scenarios in panel A. Dashed black and orange line indicates establishment rates with constant 100% and 90% survival, respectively.

Long-term drivers of woody plant abundance

We find little evidence to support the hypothesis that the acute effects of Euro-American settlement drove observed increases in tree establishment and density after 1850. Still, woodland density has likely been increasing for at least the last 400 years. Such sustained population growth was most likely driven by late Holocene climate and disturbance conditions, as shown by paleoecological records in the western US (*25–27*). The period from 900 to 1400 was associated

with region-wide increases in drought and wildfire activity and with declining presence of forests and woodlands, the extent of which may exceed any conditions in the modern era (*7*, *27*, *28*). Paired archaeological and paleoecological data also indicate a major change in land use by Indigenous peoples of the Great Basin and Colorado Plateau, including a decline in agriculture and fire prevalence around 1400 (*25*). Woodland contraction prior to 1500 may have created an ideal setting for sustained range-wide woodland tree population increases and range expansion when climate conditions changed towards cooler-wetter conditions and cultural fire practices changed (Fig. S2b*; 32*). This hypothesis is further supported by pollen and midden data from the western US which indicate tree abundance began to increase well before Euro-American settlement (*5*, *29*). Wildfire continues to play an important role in structuring pinyon-juniper woodlands. However, unlike other ecosystems known for frequent, low-severity fires, fire regimes in pinyon-juniper woodlands have generally been characterized by infrequent, high-severity fires (fire rotations of 400+ years), and several of the sites included in our study from the Colorado Plateau region show no evidence of fires in the last 400 years (*30*, *31*). As a result, fire exclusion in pinyon-juniper woodlands is unlikely to explain accelerating increases in tree density immediately following settlement (*8*).

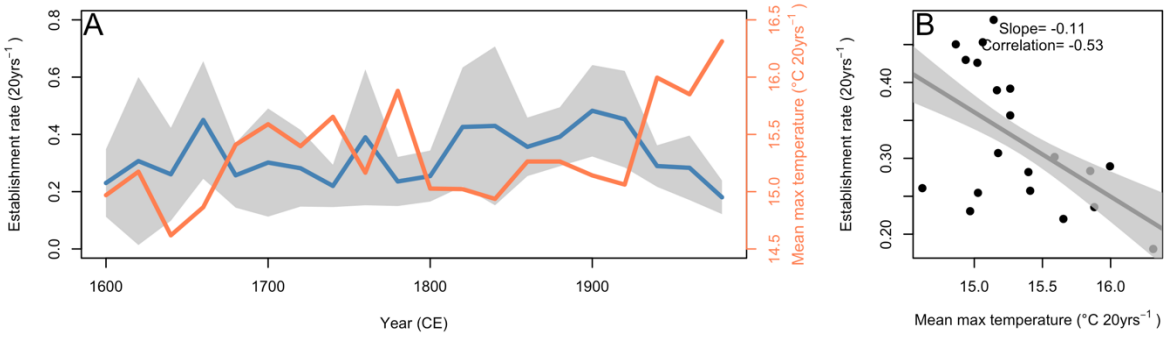

Figure 5. Relationship between temperature and per-capita establishment rates since 1600. (A) Time series of mean annual maximum temperature over 20 years and mean establishment rates since 1600. (B) Regression of mean annual maximum temperature and establishment rates in 20-year intervals from 1600 to 1980 indicating a negative relationship (*p=0.016*).

We find that the dominant trend since Euro-American settlement is declining, not increasing, tree establishment rates, and establishment rates are currently at their lowest level in at least 400 years. To better understand the drivers of this decline, we used temperature and precipitation reconstructions from the Colorado Plateau to explain average establishment rates (*32*). We found a negative relationship (*p=0.016*) between maximum annual temperatures and establishment rates since 1600, while total annual precipitation had a weakly positive relationship with establishment (*p=0.68*; Fig. S6). The 1930's were a period of drought and anomalously warm conditions throughout much of the western US, and have been subsequently followed by increasingly warm temperatures and extreme drought attributed to anthropogenic climate change (*28*). Our results suggest that climate change has likely helped drive the unprecedented decline in tree establishment rates we observe, matching other impacts of changing climate from contemporary studies (*33*, *34*). Our finding that declines in tree establishment rates began in the

first half of the 20th century suggests that impacts of a warming climate on forest and woodland health may have begun to emerge earlier than previously reported (*35*).

While we find a significant relationship between increasing temperatures and declining establishment rates, we cannot rule out the possible influence of other confounding factors. First, declining establishment rates could simply represent density-dependence as stands reach their carrying capacity. However, this is unlikely since establishment rate declines have been observed across a range of stand densities and ages (*7*). Second, the forced removal of Indigenous peoples from homelands in the Great Basin and Colorado Plateau could also have contributed to declining tree establishment rates. Indigenous peoples of this region have long been stewards of pinyon-juniper ecosystems, and removal of this traditional management may have led to declines in woodland health including increased pest and pathogen load (*36*). Regardless of the underlying mechanism, finding that woodland establishment rates are at their lowest rate in at least 400 years provides important, and previously unrecognized, context for understanding the dynamics of these ecosystems, as woodlands are currently experiencing recruitment declines unprecedented since the medieval warm period despite continuing to increase in density and extent.

Increases in woody plant density and extent have been noted in many dryland ecosystems across the world (*2*). Our results suggest that intrinsic population processes could help explain the rapid change of dryland ecosystems from low, but seemingly stable levels of woody plant density, to increasingly dense woody vegetation. Age structure data on dryland woody plants over the last several hundred years are rare outside of the southwest US but data do suggest similar

mechanisms may be operating in other regions. Estimated age structures from a savanna site in southern Texas, US (*37*), show rapid increases in tree density in the 20th century despite per-capita establishment rates that fall well within the range of variability from 1770-1900 (Fig. S7), suggesting multiplicative population growth could explain rapid increases in woody plant density. Fossil pollen data from Ethiopia and the Chihuahuan desert indicate declines in woodland abundance during the medieval climate anomaly, followed by the recovery of woody vegetation beginning during the little ice age (*38*, *39*). Research from African savannas also suggest that historic legacy and contingency, and not current environmental conditions, may be the primary driver of extant woody plant abundance (*40*). Demographic approaches can be used to better identify where and when anthropogenic forces may have altered historic vegetation dynamics. For example, in Arizona ponderosa pine forests, declines in wildfire frequency following Euro-American settlement are well documented in tree fire scars (*14*). Unlike pinyon-juniper woodland sites, analysis of tree-ring age structures do indicate a rapid, unprecedented increase of per-capita tree establishment rates during this period (Fig. S8, (*14*)) providing further evidence that fire exclusion has been a driver of tree density increases in southwest ponderosa pine ecosystems.

Our findings have important broader implications for understanding how environmental change alters ecosystem structure and dynamics. Our results illustrate how population vulnerability to climate changes can hide in plain sight. Tree establishment is a less visible indicator of declining forest health than mortality, but can be highly sensitive to climate conditions (*41*). We found the potential vulnerability of pinyon-juniper woodlands to climate change began to emerge 100 years ago with the initiation of declining establishment rates. However, despite declines in

establishment rates, population growth has continued throughout this period. Antecedent conditions that enabled long-term population growth may have masked the emerging trend of declining tree establishment rate. Given that establishment rates are nearing their lowest level in 400 years, we may be entering a period when population growth can no longer be maintained, and range contraction may be more likely (*34*, *42*).

Our research also provides a cautionary tale for ecologists studying anthropogenic influence in ecological processes, particularly those associated with singular past events like Euro-American colonization and settlement in North America. Settlement activities have undoubtedly changed the structure and function ecosystems, including the introduction and spread of invasive species and the widespread removal of native vegetation(*43*, *44*). However, impacts of settlement occur against the backdrop of long-term changes in climate and historical legacies that are critical to understanding the modern distribution and abundance of species but are often not readily apparent today (*16*, *26*). As a result, recent observed shifts in woody plant density and cover may coincide with changing environmental conditions during that period, but may not be causally linked. Focusing on the link between environmental conditions and the underlying processes that drive vegetation change (e.g. long-term demographic rates), rather than the patterns (e.g. cover, density) can help resolve this mismatch. Disentangling the causes of historical vegetation change can be challenging, and it can lead ecologists to seek explanations that invoke complex interactions among global change agents. However, our study highlights the need to compare such hypothesized models of change with simpler and often more parsimonious explanations, including neutral models of population dynamics in the absence of external drivers such as climate changes, fire regime shifts, or land-use change.

Materials and Methods

Demographic background

It is helpful to begin with a little background. Changes in population size over time can be described by

$$N_t = N_{t-1} + B_t - D_t \qquad (1)$$

Where N_t is the population size at time t, B_t is the number of individuals establishing in the population and D_t is the number of deaths. But this simple formulation fails to capture the compounding, multiplicative nature of population growth. Each new individual established will eventually have an opportunity to reproduce if they survive, further expanding the population and increasing establishment. So, it is more useful to express population change in per-capita establishment (b_t) and survival rates (s_t):

$$N_t = s_t N_{t-1} + b_t N_{t-1} \qquad (2)$$

If we assume $s_t = 1$ in all years (as is often implicitly assumed in interpretations of age structures in pinyon-juniper woodlands; we will revisit this later) then the observed age structure provides a perfect record of past establishment and total population size. The number or relative proportion of trees of a given age (B_t, i.e. each bar in Fig. 2A) represents $b_t N_{t-1}$, the product of both the per-capita establishment rate and the population size. Thus, we can observe greater establishment by either having a larger population size or increasing the average number of

offspring per individual. As long as establishment rate (b_t) exceeds the mortality rate ($1 - s_t$) the number of establishing individuals is expected to increase over time simply because each successive cohort contributes more reproductive potential, even if s_t and b_t are constant. Because population size itself influences the total amount of establishment, demographers look at changes in per-capita establishment (b_t), not total establishment (B_t) to identify the impacts of changing conditions such as changes in disturbance, climatic conditions, and other abiotic and biotic drivers (*12*, *13*). It's worth noting that authors of previous pinyon-juniper studies often refer to $b_t N_{t-1}$ as the establishment rate, but in those cases, this is the number of new trees per unit time, not the demographic rate (new trees per existing tree per unit time). If changes in climate, disturbance, or other abiotic and biotic conditions were driving the acceleration of establishment (B_t), this would be reflected by an increase in the per-capita establishment rate (b_t). Rearranging equation 2, the per-capita establishment rate for any period can be empirically calculated as:

$$b_t = \frac{N_t}{N_{t-1}} - s_t \tag{3}$$

Age Structure Data

To understand how per-capita establishment rates have changed over time we digitized and collated age structure data from existing studies. Studies included those previously known to the authors and additional published articles, reports, and theses identified as including age structure data using Google Scholar and Web of Science searches with combinations of the phrases "pinyon", "piñon", "juniper", "age structure", and "establishment". Papers that only sampled large trees, or in other ways incorporated a biased sampling of age structure, were not used.

Because we extracted data from graphs, we could not use papers where graphs were impossible to interpret and extract data with confidence. In addition, any study that aggregated tree establishment dates into intervals greater than 20 years was not included because of lack of temporal resolution. Because we are interested in how establishment rates have changed prior to and after Euro-American settlement, we did not include suitable age structures from studies where all trees established after 1800. This resulted in datasets from 28 populations at 23 sites (some sites have more than one species measured) from 10 separate studies (Table S2). Data points were extracted from published figures using Web Plot Digitizer (*45*), an online application for extracting data from scientific figures. Each extracted point included a very small amount of numerical error associated with digitization. Because in each dataset establishment years were aggregated into 10- or 20-year bins, we were able to correct numerical digitization errors in years of establishment. The numerical errors in establishment amount data were small (Fig. S9). Each study calculated tree ages within stand plots or transects using standard dendrochronology approaches and aggregated trees into 10-or 20- year cohorts. 12 of the datasets did not age the smallest trees in the stand (e.g. no trees smaller than 3 cm diameter were aged); in these datasets we did not use any tree establishment data after the 1940-1960 interval so as to not artificially lower establishment rates because of missing trees. Two datasets did not include trees < 4cm diameter, but already excluded data in their reporting after 1950 to account for missing small trees (*10*). Datasets spanned a diversity of geographic locations in the Great Basin and Colorado Plateau (Arizona, California, Colorado, Idaho, Nevada, and Utah; Fig. S1) and species including *Pinus monophylla* (PiMo), *Pinus edulis* (PiEd), *Juniperus osteosperma* (JuOs), *Juniperus occidentalis (*JuOc*)*, and mixed stands dominated by *Pinus monophylla,* with a minor *Juniperus osteosperma* component (PiMo-JuOs).

With these age structures we calculated the historical population sizes of each location as

$$N_t = \sum_{i=1}^{t} B_i \tag{4}$$

Here B could be the actual number of trees established, or the number of trees relative to the total number of established trees; either metric is appropriate for demographic analyses. As previously, we assumed 100% survival (we will revisit this assumption soon). This resulted in estimates of population dynamics over time in each location (Fig. 2A). We then used eq. 3 to calculate per-capita establishment rates in each location over time (Fig. 2B), again assuming $s_t = 1$.

To directly compare all datasets at the same time scale we aggregated 10-year datasets to 20-years by summing establishment in two 10-year intervals. In some cases, 10-year datasets did not end on the full 20-year interval, and only quantified establishment during the first 10 years (e.g. 1960-1969) of the 20-year interval (1960-1979). In these cases, the last 10 years of the dataset were not included in the analysis avoid underestimates of establishment (e.g. using 10 years of data for a 20-year interval).

We calculated the mean per-capita establishment rate (and 95% Confidence Interval) for each 20-year interval. We also performed segmented regression to identify and quantify major changes in per-capita establishment rates over time using the "segmented" package in R (*46*).

Segmented regression identifies the location and slope of change points in a response variable given a fixed number of change points. We performed segmented regression between the estimated establishment rates in all plots (response variable) and interval year (explanatory variable) with one to four change points. Change points numbers beyond four were not estimable.

We used 1850 as the division between pre- and post-Euro-American Settlement in the region following the 1847 founding of Salt Lake City, Utah and the 1849 California Gold Rush.

Correcting for survival

Age structure data may provide imperfect records of past establishment because survival may not be 100%, in which case some trees will have died long before being recorded. While we can't know with certainty what past survival rates were, we can test how realistic survival rates would alter our inference about establishment rates over time. To do this we tested two scenarios: constant, and randomly varying survival rates. We did this as: 1) A constant survival rate of 0.90 over each 20-year interval. This is comparable to the current survival rates of *Pinus monophylla* and *Pinus edulis* (*34*), while juniper species typically have higher survival; 2) simulated survival rate time series using a forward and reverse random walk starting at logit(0.95), that was then inverse-logit transformed to the 0-1 scale.

We corrected observed establishment numbers for past survival by accounting for the cumulative survival cohort from when the establishment occurred in interval, t, to the time of observation ($tmax$) as:

$$B_t = B_t^* * s_{t+1} * s_{t+2} \dots * s_{tmax} \qquad (5)$$

Here B_t is again the observed number of established individuals in interval, t. B_t^* is the true number of individuals that established in that interval.

This can be rearranged to calculate the true number of individuals and simplified as

$$B_t^* = \frac{B_t}{\prod_{i=t+1}^{tmax} s_i} \qquad (6)$$

In other words, the true number of individuals that established in a past year, B_t^*, is the observed number of establishing trees at that time corrected for the cumulative survival rate of that cohort from the time of establishment to the observation. Finally, we calculated the true population size at any time N_t^* as

$$N_t^* = B_t^* + s_t N_{t-1}^* \qquad (7)$$

Delayed reproduction

Time to first reproduction for pinyon and juniper can vary by species and site, but can take multiple decades. This could impact inferred per-capita establishment rates because not all members of the population would be contributing to new tree establishment. To understand how delayed reproduction would have impacted our inferred per-capita establishment rates we calculated per-capita establishment rates assuming a 40-year lag in reproduction. To do this we created a simple structured population model where we separated the population into those contributing to reproduction and those contributing to survival.

$$N_t = s_t N_{t-1} + b_t N_{t-lag} \qquad (8)$$

Here N_t is the population size at interval, t, and N_{t-lag} is the population size at an interval in the past corresponding to the lag. This can be rearranged as

$$\frac{N_t - s_t N_{t-1}}{N_{t-lag}} = b_t \qquad (9)$$

Assuming the survival rate is equal to 1, this simplifies to

$$\frac{N_t - N_{t-1}}{N_{t-lag}} = b_t \quad (10)$$

$N_t - N_{t-1}$ is equal to the number of newly established trees observed in an interval, B_t, thus the per-capita establishment rate is

$$b_t = \frac{B_t}{N_{t-lag}} \qquad (11)$$

In other words, the per-capita establishment rate is the number of newly established trees at t divided by the population size at $t - lag$.

Decomposing contributions to establishment

To quantify the role of multiplicative population growth relative to changing per-capita establishment rates we decomposed the amount of establishment due to each source from 1860-1940, the post-settlement period. We quantified the role of multiplicative growth by simulating population growth and establishment starting at a population size of 0.15 (typical of the relative population sizes in 1860) over the period of 1860-1940 at a fixed per-capita establishment rate equal to the average rate in 1860. This quantified the amount of establishment we would expect if no change in establishment rates had occurred. We then repeated this simulation, but with varying per-capita establishment rates, using the average establishment rate for each 20-year interval from Fig. 2. This quantified the amount of establishment we would expect with both

multiplicative growth and changing per-capita establishment rates after 1860. The difference in establishment between these two simulations is the contribution of changing per-capita establishment rates to overall establishment. Consistent with calculations of establishment rates in Fig. 2, survival was assumed to be 1. Changing the starting population size shifted the total amount of establishment, but has no impact on the relative contribution of multiplicative population growth vs. changing per-capita establishment rates. The choice of what baseline establishment rates to use for comparison (1840 vs. 1860, etc) modestly shifted the relative contributions of the two processes, but the qualitative result that multiplicative growth can explain most of the observed establishment was robust.

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Acknowledgments

We thank the authors that generated the data used in this work, which made this research possible. We thank Peter Adler for helpful feedback on earlier versions of this manuscript. This research was funded by the USDA National Institute of Food and Agriculture, the Nevada Agricultural Experiment Station, and by the USDA Forest Service, Rocky Mountain Research Station. The findings and conclusions in this publication are those of the authors and should not be considered to represent any official USDA determination or policy.

Author Contributions: RKS: Conceptualization, Data Curation, Formal Analysis, Writing. EP: Data Curation, Formal Analysis, Writing. FB, AU, PJW: Writing.

Data and materials availability: Data and R code to reproduce all analyses are available on GitHub at https://github.com/bobshriver/PJStructure.