PNAS RESEARCH ARTICLE | ECOLOGY

Long-term tree population growth can predict woody encroachment patterns

Robert K. Shriver[a,1], Elise Pletcher[a], Franco Biondi[a,2], Alexandra K. Urza[b,2], and Peter J. Weisberg[a,2]

Affiliations are included on p. 8.

Edited by Donald Ort, University of Illinois at Urbana Champaign, Urbana, IL; received November 21, 2024; accepted March 31, 2025

Recent increases in woody plant density in dryland ecosystems—or "woody encroachment"—around the world are often attributed to land-use changes such as increased livestock grazing and wildfire suppression or to global environmental trends (e.g., increasing atmospheric carbon dioxide). While such changes have undoubtedly impacted ecosystem structure and function, the evidence linking them to woody encroachment is mixed, and the underlying processes are not fully understood. To clarify the role of demographic processes in changing woody plant abundance, we conducted a meta-analysis of tree age structures from 29 woodland populations across the interior western United States, estimating per-capita tree establishment rates over the last several hundred years using demographic models. We found only limited evidence of increases in per-capita tree establishment rates following 19th-century Euro-American settlement. On the contrary, our results showed that observed age structures dominated by young trees, often cited as evidence of woody encroachment driven by anthropogenic processes, can be largely predicted by a null model based only on steady, multiplicative tree population growth. Moreover, we demonstrated that tree establishment rates in the last century have mostly declined rather than increased, and they are currently at their lowest rates since at least 1600 CE. Our results suggest that a large part of modern increases in woodland tree establishment and density may in fact be a result of long-term population increases, and failing to consider the demographic processes underlying population growth can lead to an overestimation of settlement effects on stand structure.

demography | null model | pinyon–juniper woodlands | range dynamics | woody encroachment

Significance

Increasing presence of woody plants in dryland ecosystems, also known as "woody encroachment," is commonly attributed to anthropogenic land-use changes such as livestock grazing and wildfire suppression. However, empirical evidence to support these external drivers has not uncovered a unifying mechanism. We test whether plant demographic processes could be responsible for woody encroachment using tree-ring data from pinyon and juniper woodland populations in the western United States. Our results indicate that woody encroachment patterns can largely be predicted by a null model based only on steady tree population growth. Modern increases in woodland density, which are typically viewed as a natural resource management problem, may therefore be a result of long-term population expansion and recovery.

One of the most evident ecological changes in many dryland ecosystems over the last 200 y has been increasing density and distribution of woody vegetation (1, 2). Collectively referred to as woody encroachment or expansion, such changes 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 (5–7). In the western United States, tree-ring-derived age structures show dry woodlands, particularly pinyon–juniper woodlands, dominated by trees that largely established after the mid-1800s CE (8–10). 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 recent Euro-American settlement (e.g., increasing atmospheric CO_2) (8, 11). However, evidence supporting these hypotheses has generally not been conclusive or pervasive enough to explain regionwide increases in tree establishment (11). For example, wildfire suppression and exclusion are often cited as a mechanism underlying increases in woodland density, but data on wildfire regimes indicate that many presettlement 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 (11–13). Similarly, impacts of overgrazing by domestic livestock are also commonly invoked to explain increasing woodland density, but sites with little livestock grazing history have seen similar increases in tree establishment (9, 10). As a result, directly attributing increasing woody plant density to specific external drivers remains a challenge (11, 14).

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 (15). 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 a notable increase in the per-capita establishment rate (i.e., new

Preprint server: This manuscript has been deposited on bioRxiv with a CC-BY-NC-ND 4.0 license 10.1101/2024.04.07.588197.

Author contributions: R.K.S. designed research; R.K.S. and E.P. performed research; R.K.S. and E.P. analyzed data; and R.K.S., E.P., F.B., A.K.U., and P.J.W. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence may be addressed. Email: rshriver@unr.edu.

[2]F.B., A.K.U., and P.J.W. contributed equally to this work.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2424096122/-/DCSupplemental.

Published May 1, 2025.

trees established per existing tree) (16). However, population growth is a multiplicative process, and thus, rapid increases in population density and net 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, recent increase in the rate of establishment driven by changing environmental conditions, especially when a population experiences prolonged periods of growth after colonizing new habitat or recovering from past disturbance (17). 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 for understanding its causes (18).

Pinyon–juniper woodlands are among the most widespread forest types in the United States, covering over 40 million hectares, and the most abundant remaining old-growth forest type in the United States, representing nearly one-third of all old growth forest area (19). While range expansion and increases in density of pinyon–juniper woodlands have been widely noted, the causes and management of increasing woodland density are often controversial (11, 20). Although evidence to support it has been mixed, the conclusion that increasing tree density and extent in western woodlands originated from Euro-American settlement is common in the scientific and land management literature. Such interpretation has motivated extensive vegetation treatments, usually framed as ecological restoration, to remove pinyon–juniper woodlands (21, 22). At the same time, these woodlands have also experienced widespread mortality that has been attributed to climate change, either directly as drought stress (23) or indirectly as a result of insect outbreaks and increased wildfire activity (24).

One key aspect missing from previous interpretations of increasing woodland density is a quantification of the role of demographic and intrinsic population processes (18). In this study, we used published age structure data from pinyon pine and juniper populations in the Great Basin and Colorado Plateau, western United States (Fig. 2*A* and *SI Appendix*, Tables S1 and S2), to calculate empirical per capita-establishment rates (hereafter "establishment rates") prior to, during, and after Euro-American settlement. We then evaluated the impact that changing establishment rates had on observed woodland age structures and density increases by comparing these increases to a null model that used only constant, average presettlement establishment rates from each population. Extensive age structure data documenting woody encroachment from stands that predate settlement are rare, making pinyon–juniper woodlands an ideal case study.

Results and Discussion

Tree Establishment Rates. Our literature search yielded data from 32 populations, of which 29 established prior to 1800, thus allowing for comparison of establishment rates prior to and during the Euro-American settlement period. Age structure data from the 29 pre-1800 populations indicated a trend of increasing pinyon–juniper net establishment and density during the late 1800s and early 1900s CE, with more than half of existing trees establishing after 1860 CE in 23 of the 29 populations (Fig. 2*B* and *SI Appendix*, Table S2). As was found in those published studies,

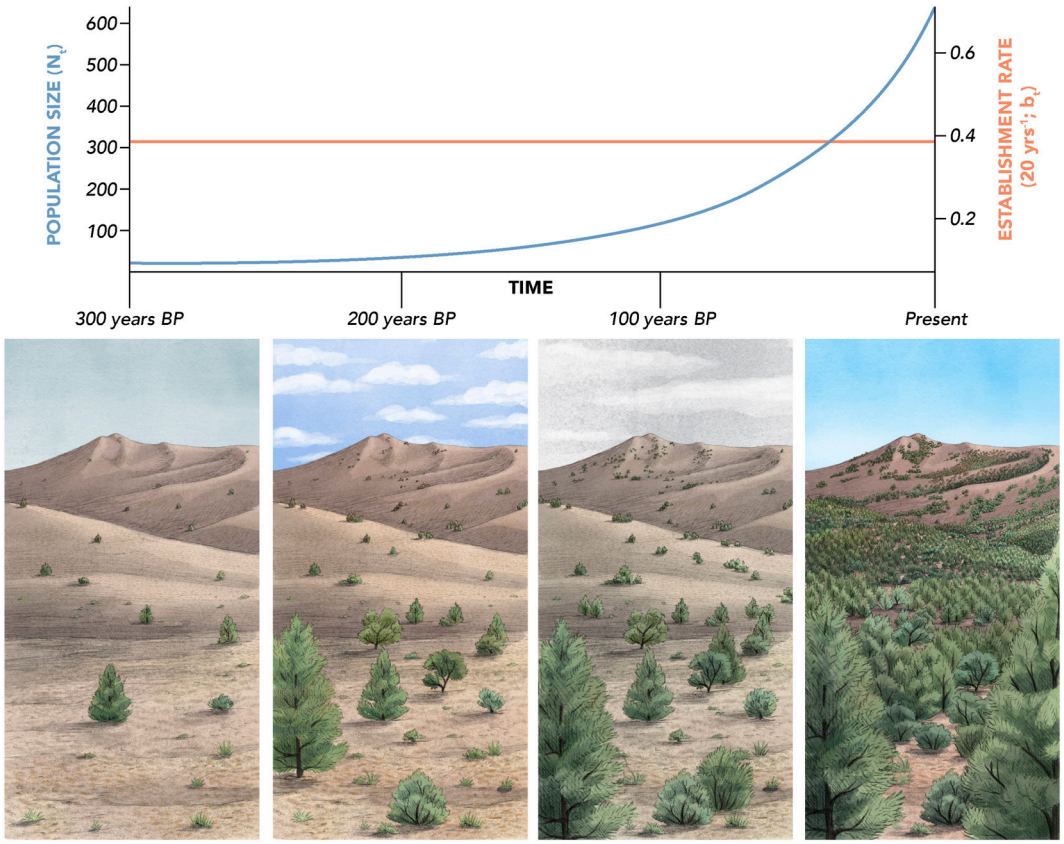

Fig. 1. Increasing establishment under a constant establishment rate. Because new establishment (B_t) is the product of both population size (N_{t-1}) and per-capita establishment rate (b_t; $B_t = b_t N_{t-1}$), in a growing population, the amount of new establishment will increase over time even if 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 that no change in per-capita establishment rates (orange) has occurred. Increased establishment is instead driven by the reproductive potential of larger populations. BP indicates "before present." (Illustration by Alex Boersma).

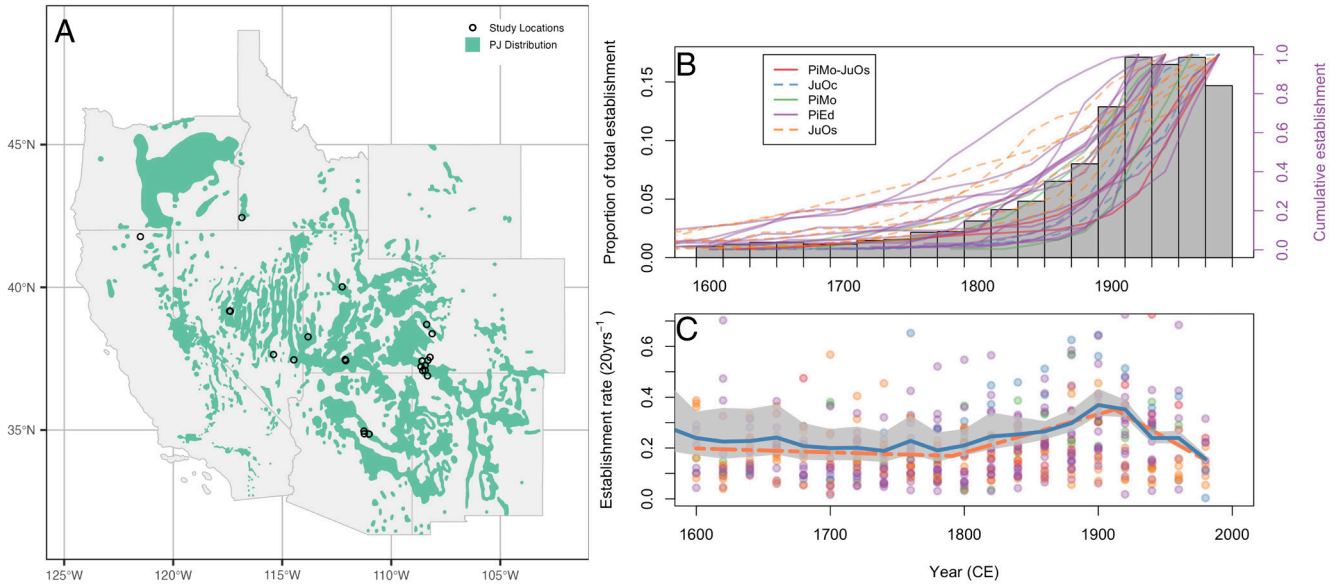

Fig. 2. Tree establishment rates since 1600 CE. (*A*) Map of sites in which age structure data exist (points) overlayed on the range pinyon–juniper in the western United States. (*B*) Proportion of total observed establishment occurring in each 20-y interval averaged across 29 pre-1800 populations and cumulative observed establishment in each population broken down by species. Species acronyms 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). (C) Per-capita establishment rates for each of the 29 pre-1800 populations (points), posterior median estimate for 20-y average (blue) and 95% credible interval (gray), and the best fit segmented regression (dashed orange). The entire timeseries dataset is shown in *SI Appendix*, Fig. S2.

far greater net tree establishment occurred in the 19th and 20th century than in previous periods (*SI Appendix*, Fig. S1). However, these unprecedented levels of net establishment were often not associated with unprecedented per-capita establishment rates. We found that while establishment rates during the recent period of Euro-American settlement (1860 to 1900 CE) were greater than in decades directly preceding settlement, they generally fell within the historic range of variability both on average and for individual sites (Fig. 2*C* and *SI Appendix*, Figs. S2 and S3).

Prior to 1600 CE, average establishment rates were highly variable, fluctuating between 0.12 and 0.47 (0.004-1.69 95% CI) average per-capita establishment rate per 20-y interval (*SI Appendix*, Fig. S2). Following approximately 1600 CE average establishment rates became more certain. Establishment rates dropped from 0.47 (0.31 to 0.78 95% CI) in 1520 to 0.24 (0.17 to 0.37 95% CI) per 20-y interval by 1660 CE, before briefly stabilizing at ~0.20 between 1680 and 1740 CE (Fig. 2*C*). In the late-1700s CE, average establishment rates gradually increased until 1920 CE. The results of segmented regression further corroborated this modest upward trend in establishment rates (*SI Appendix*, Table S3). Although the net number of establishing trees per 20-y period tripled from 1820 to 1900 CE on average, we observed a more modest increase in average per-capita tree establishment rates from 0.25 in 1820 CE (0.19 to 0.34 95% CI) to 0.37 in 1900 CE (0.33 to 0.43 95% CI) (Fig. 2 *B* and *C*). The best-fit segmented regression shows no detectable change in establishment rate patterns during the Euro-American settlement period (approx. 1860 to 1900 CE), with a continuation of the upward trend that began in the late 1700s CE. The largest recent change in establishment rates occurred after ~1900 CE, when both the 20-y average and segmented regression indicated establishment rates began to decline (*SI Appendix*, Table S3). As a consequence, by the late 20th-century average tree establishment rates had reached their lowest level in 400 y, i.e., 0.16 (0.14 to 0.17 95% CI) per 20-y interval. While considerable variability existed in establishment rates across species and sites, most (~80%) populations did not experience a notable increase in establishment rates during the settlement period despite large increases in net tree establishment (*SI Appendix*, Figs. S1 and S3). In addition, we found only one pinyon–juniper population with a high probability (>0.95) of establishment rates during the settlement period exceeding the presettlement period (*SI Appendix*, Fig. S4).

While establishment rates during the Euro-American settlement period generally fell within the historic range of variability, average establishment rates did increase across the late 1800s. To better quantify the degree to which increases in establishment rates explained observed increases in net tree establishment found in age structure data, we separated contributions to net establishment resulting from steady multiplicative population growth alone from contributions of changing establishment rates. We did so by comparing two simulations for each of the 29 pre-1800 populations: one used the observed establishment rates for each population during 1600 to 1980 CE (i.e., "changing establishment rates"), while the other was a null model that used the average, presettlement establishment rate for each population (1600 to 1840 CE was used for this "constant establishment rate").

We found that multiplicative population growth with a constant establishment rate alone consistently predicted most of the observed net establishment increases across decades and sites. Overall, in ~2/3 of the populations, 70% of the variation in net establishment was explained by the constant establishment rate (Fig. 3 *A* and *B*). Hence, steady, long-term population growth can explain much of the postsettlement observed increases in net establishment and density. However, multiplicative population growth alone did not always predict observed temporal variability in net establishment for an individual population, indicating that anthropogenic or environmental drivers likely still played an important role at the local scale. For example, the greatest underprediction of net establishment occurred in the 1900 and 1920 intervals, with increases in recruitment beyond constant levels in ~1/3 of population, indicating that settlement and the early 20th-century pluvial may be responsible for increases in establishment in a subset of populations (25) (Fig. 3*C* and *SI Appendix*, Fig. S5). Over- and underpredictions of individual population

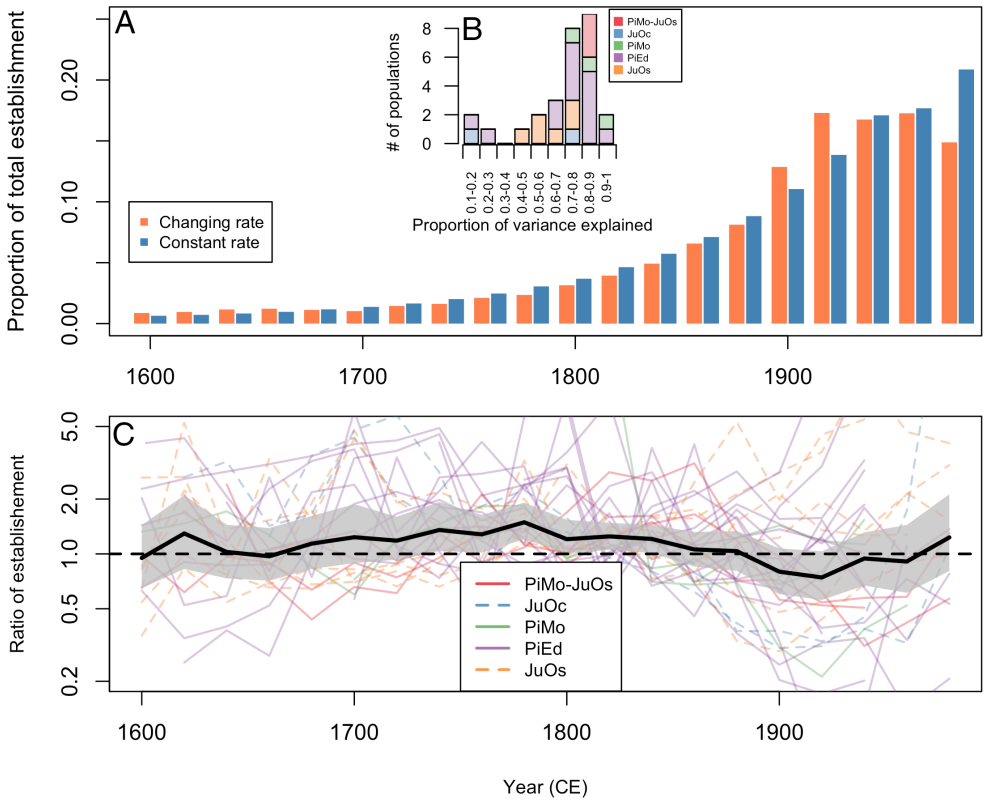

Fig. 3. Predictability of tree establishment patterns. (*A*) Bars representing average expected establishment in 20-y intervals across all populations expected from changing per-capita establishment rates (orange) and multiplicative population growth with a constant establishment rate (blue). (*B*) Proportion of variance in establishment explained by constant establishment rates in each population, colored by species. (*C*) Ratio of establishment ($\frac{Constant}{Changing}$) between each mechanism for each population in each 20-y interval. The solid black line indicates posterior estimate and 95% CI for the median. Values of 1 (dashed black line) indicate that the amount of establishment is the same under either mechanism, whereas values below 1 indicate that changing establishment rates would be expected to lead to greater establishment.

net establishment were found throughout the 400-y period, indicating that in some populations, exogenous drivers may have led to declines rather than increases in net establishment relative to a constant rate, while in others, constant establishment rates would underestimate net establishment. Averaging this over- and underprediction may in part explain the close correspondence between net establishment expected from multiplicative population growth and the changing establishment rates across all populations (Fig. 3*A*). Still, even without population-specific information, presettlement establishment rates typically predicted 75% or more of the observed population-level net establishment in a given 20-y interval during the postsettlement period (Fig. 3*C* and *SI Appendix*, Fig. S5). Therefore, not considering the demographic processes underlying population growth could lead to overestimating and/or misinterpreting the impacts of recent land-use and environmental changes.

Robustness of Establishment Rate Estimates. Tree-ring-derived age structure data can suffer from a "fading record" problem, where data reliability, and thus ecological inference, declines further into the past (18). Trees that were previously present in a population may have died before being observed, and probability of missing trees is likely to increase as we move further back in the historic record. As a result, tree survival could affect inference of past establishment, but our Bayesian inference approach allowed us to test this possibility and to account for uncertainties due to survival rates in estimates of establishment rates. Overall, despite high uncertainty in estimates of past survival rates, establishment rate estimates were typically well constrained and accurately identifiable (Fig. 4 and *SI Appendix*, Figs. S6 and S7). While uncertainty in establishment rates increased with time since present (Fig. 4*B* and *SI Appendix*, Figs. S3 and S6*B*), estimates of survival rates derived from posterior distribution samples varied independently from establishment rates, showing that uncertainties about survival rates had little impact on our estimates of establishment rates (Fig. 4*C* and *SI Appendix*, Fig. S7). Establishment rate estimates most likely remained similar in the face of disparate survival scenarios because, when mortality occurred, observed age structures underestimated both past establishment (i.e., many of the established plants were not yet present to be censused) and past population size, and the two underestimates canceled one another when calculating per-capita establishment.

Long-Term Drivers of Woody Plant Abundance. Our results indicate that long-term population growth can predict a substantial portion of postsettlement net tree establishment increases in pinyon–juniper woodlands and that tree density may have actually been increasing for at least the last 400 y. Such sustained population growth was likely enabled by late Holocene conditions, as shown by paleoecological records from the western United States (26–28). The period from 900 to 1500 CE 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 (8, 28–31). Paired archaeological and paleoecological data from the Great Basin and Colorado Plateau region also indicate that fuelwood harvesting, agriculture, and cultural fire practices may have led to further declines in pinyon–juniper abundance and extent prior to 1500 CE (26, 32, 33). Woodland harvesting and contraction prior to 1500 CE would have created a large

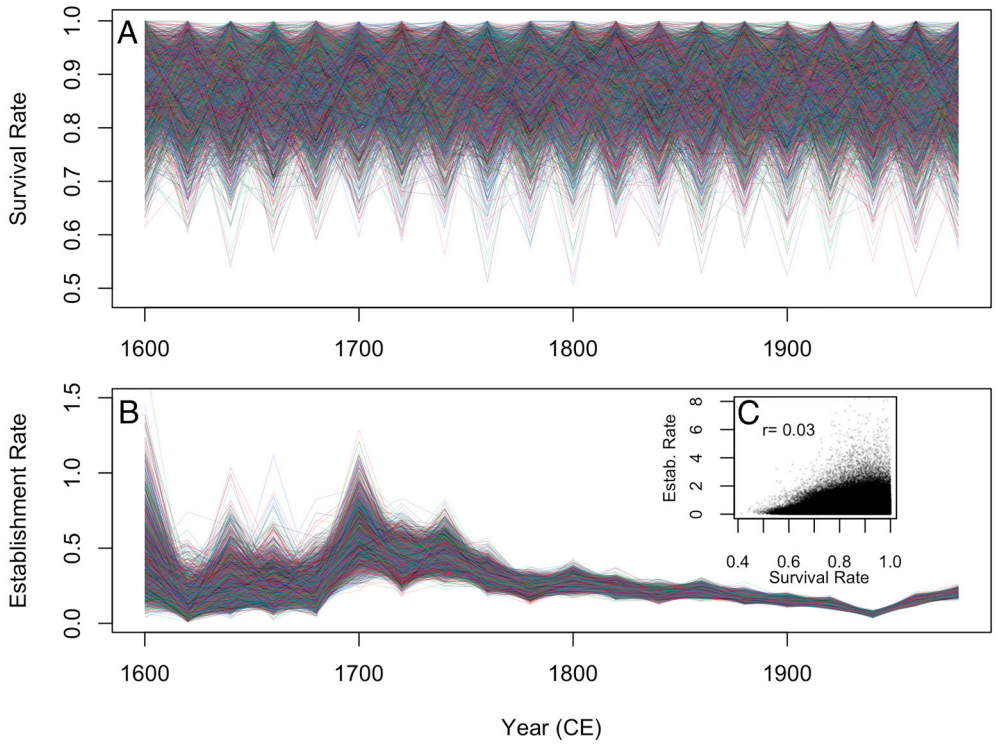

Fig. 4. Impacts of survival rates on estimated per-capita establishment rates. (*A*) Lines representing individual posterior draws for survival rates for a single population illustrating wide variability. (*B*) Lines representing individual posterior draws for establishment rates for the same population illustrating well-constrained estimates. (*C*) Correlation of survival and establishment rate posterior draws in all populations illustrating low correlation.

unfilled niche space for pinyon–juniper woodlands, providing ideal conditions for sustained range-wide tree population increases and range expansion once climate became cooler and wetter and cultural practices changed (*SI Appendix*, Fig. S2*B*); (34). This hypothesis is further supported by pollen and midden data from the western United States, which indicate tree abundance began to increase well before the 19th century, as well as by evidence of general range expansion of pinyon and other dryland tree species throughout the last 500 to 1,000 y (5, 30, 34, 35). Pinyon–juniper woodlands have undergone several periods of growth, expansion, and migration throughout the Holocene, often punctuated by periods of contraction (5, 27, 30, 36). The period of range expansion since 1600 CE may then represent the latest instance of this range expansion-contraction dynamic.

Woody encroachment occurs through both increasing tree density within a tree species' existing range (i.e., infilling or densification) and expansion via dispersal beyond historic range limits (37), and both infilling and expansion have been widely observed in pinyon–juniper woodlands (7, 38). The low-frequency, high severity fires that generally characterize pinyon–juniper woodlands (fire rotations of 400+ y) are unlikely to have maintained low tree density by "thinning from below" in existing populations (11), but more frequent high-severity fires in grasslands and shrublands could have still played an important role in setting tree range limits. Thus, fire exclusion and other settlement activities may have allowed for the expansion of woodlands even if they did not play a dominant role for infilling in the existing range (39). Our approach can characterize changes in establishment rates for populations that predate settlement but cannot speak to the processes that could have allowed for dispersal and range expansion. Analysis of establishment rates from three postsettlement populations found that rates of tree establishment in the expanded range were initially above average for pre-1800 populations, but still comparable to several established populations, and that establishment rates peaked in the early 1900s CE and have since been declining (*SI Appendix*, Fig. S3). Observations of initially high establishment rates in these postsettlement populations could indicate that expansion is being "pulled forward" by higher establishment rates at the low-density expansion edges (40, 41).

We found that the dominant trend since 1900 CE across presettlement populations is declining, not increasing, tree establishment rates, and average establishment rates are currently at their lowest level in the past 400 y. The 1930s CE were a period of drought and anomalously warm conditions throughout much of the western United States, and have been subsequently followed by variable, but generally warming temperatures and extreme drought attributed to anthropogenic climate change (29). Previous research from higher elevation forests in the western United States has found declines in tree survival across the 20th century and hypothesized that climate change was a likely cause (42). Our results and other contemporary studies in pinyon–juniper woodlands (43, 44) suggest that climate change may be a factor contributing to the unprecedented decline in tree establishment rates we observed. Declining establishment rates in infilling populations could also simply represent density dependence as stands reach their carrying capacity, although declining establishment rates have been observed across a range of stand densities and ages (8). Regardless of the underlying mechanism, finding that woodland establishment rates are at their lowest rate in at least 400 y provides important, and previously unrecognized, context for understanding the dynamics of woodland ecosystems.

Increases in woody plant density and extent have been noted in many dryland ecosystems across the world (2). Our results suggest that failure to consider the demographic processes underlying population dynamics may lead to overestimating the impacts of recent anthropogenic and environmental changes on increasing woody plant abundance. Hence, 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 dominated primarily by young plants. Age structure data on dryland woody plants over the last several 100 y are rare outside of the southwest United States, but similar mechanisms may be operating in other regions. For instance, estimated age structures from a savanna site in southern Texas, United States (45), show rapid increases in tree density in the 20th century as well as age structures similar to those found in pinyon–juniper woodlands suggesting multiplicative population growth could help explain rapid increases of woody plant density in that ecosystem too. Fossil pollen data from the Chihuahuan desert and Ethiopia indicate declines in woodland abundance during the medieval climate anomaly (~950 to 1250 CE), followed by the recovery of woody vegetation beginning during the little ice age (~1400 to 1700 CE) (46, 47).

In a contrasting example, establishment data from a ponderosa pine population in northern Arizona indicate per-capita establishment rates were highly unprecedented during the Euro-American settlement period (>20x increase)(48), far exceeding the observed establishment rate increases in any pinyon–juniper population (*SI Appendix*, Figs. S3 and S8). What differs for this ponderosa pine population that makes changing establishment rates during Euro-American settlement so clear? First, net tree establishment rapidly increased by 1 to 3 orders of magnitude, from approximately 0 to 20 trees per 20 y to 500- >13,000 trees per 20 y in the early 1900s. An increase in net establishment far more abrupt and greater in magnitude than in any pinyon–juniper population (*SI Appendix*, Fig. S8*B*). Second, unlike many pinyon–juniper woodlands, high-frequency, low-severity fires are thought to have historically maintained low tree density in ponderosa pine-dominated ecosystems of the southwest United States, and increases in per-capita establishment rates at this site closely coincide with declines in fire frequency from fire scar records(48), directly linking density increases to the well-documented mechanism of fire exclusion. We present here a Bayesian framework that accounts for survival uncertainty, but even simpler calculations can help identify the degree to which per-capita establishment rates may differ from net establishment. For example, assuming that all trees have survived, age structures provide a full record of population histories, and thus, the per capita establishment rates can be approximated as the net establishment for an interval (B_t) divided by the sum of all the trees that had established up until that point ($\sum_{i=1}^{t-1} B_i$), $B_t / \sum_{i=1}^{t-1} B_i$. Overall, this ponderosa pine case study shows establishment rate increases are detectable by our approach and clarifies when we expect to find a clear signal in increasing establishment rates from age structure data.

Our findings have important implications for the management and restoration of pinyon–juniper woodlands, one of the most widespread vegetation types in the United States. Removing pinyon and juniper trees and promoting ecosystem services provided by grasslands and shrublands has become an increasingly high priority for land management agencies, often based on the assumption that greater woodland density and extent over the last 200 y represent an unnatural phenomenon (49, 50). We suggest that the processes driving much of the recent increases in woodland density may not be historically unprecedented, but rather a continuation of population recovery and expansion that initiated at least 400 y ago, possibly following major changes in western North American forests caused by drought, wildfire, and shifts in Indigenous land use (28, 29, 32). As a result, management practices that counter woody encroachment by removing trees or other policies that focus on local scales likely cannot address the underlying regional drivers of increasing tree density in these ecosystems. Since widespread increases in woody plant density may still alter the provision of important ecosystem services or habitats for species of concern (21), it is crucial to consider the underlying processes driving increasing woody plant density as well as the consequences of greater woody plant density for ecosystem processes and services. Bearing in mind likely future scenarios of climate and disturbance, management should carefully consider the possibility of future woodland decline and contraction. Given that pinyon–juniper establishment rates are nearing their lowest level in 400 y and that widespread mortality has occurred in the Southwest United States, we may be entering a period when population growth can no longer be maintained, and range decline and contraction may be more likely (44, 51).

Our research also provides a cautionary tale for ecologists studying how anthropogenic factors influence ecological processes, particularly those associated with Euro-American settlement in the western United States. Human activities have undoubtedly changed the structure and function of ecosystems, including the introduction and spread of invasive species and the widespread removal of native vegetation (52, 53). At the same time, 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 (18, 27). As a result, recent observed shifts in woody plant density and cover may coincide with changing environmental conditions during the settlement period, but may not be causally linked. While no approach, including our own, can categorically exclude human settlement or other drivers of historic vegetation change, our results do show that failure to consider processes underlying plant population dynamics can lead us to overestimate their importance when examining observational data alone. Thankfully, approaches do exist to begin isolating the effects of long-term population growth from other exogenous drivers. The most straightforward approach is to focus on the processes that generate observed age structures, including per-capita establishment rates, rather than net establishment numbers. 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. Our study highlights the need to compare such hypothesized models of change with simpler and often more parsimonious explanations, including null models of population dynamics in the absence of external drivers such as climatic changes, wildfire regime shifts, or land-use changes.

Materials and Methods

Demographic Background. Our methods are based on classical population ecology theory, so it is helpful to begin with a little background. Changes in population size over time can be described by

$$N_t = N_{t-1} + B_t - D_t, \quad [1]$$

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):

$$N_t = s_t N_{t-1} + b_t N_{t-1}, \quad [2]$$

Net establishment, the number of trees of a given age, (B_t, i.e., each bar in Fig. 2*B* and *SI Appendix*, Fig. S1), represents $b_t N_{t-1}$, the product of both the per-capita establishment rate and the population size. Thus, we can observe greater net

establishment by either having a larger population size or increasing the average number of offspring per individual. As long as the 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 amount of net establishment, demographers look at changes in per-capita establishment (b_t), not net establishment (B_t) to identify the impacts of changing conditions such as changes in disturbance, climatic conditions, and other abiotic and biotic drivers (15, 16). It is worth noting that authors of previous pinyon–juniper studies often refer to b_tN_{t-1} as the establishment rate (8, 54), 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 net establishment (B_t), this would be reflected by an increase in the per-capita establishment rate (b_t). Rearranging Eq. **2**, the per-capita establishment rate for any period can be empirically calculated as

$$b_t = \frac{N_t}{N_{t-1}} - s_t. \quad [3]$$

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 y was not included because of lack of temporal resolution. This resulted in datasets from 32 populations at 23 sites (some sites have more than one species measured) from 10 separate studies (*SI Appendix*, Tables S1 and S2). Of the 32 datasets, 29 were from populations that established prior to 1800, allowing for comparison of establishment rates prior to and following Euro-American settlement. These 29 pre-1800 populations are used throughout the paper to better understand the processes driving infilling within pinyon–juniper populations.

Data points were extracted from published figures using Web Plot Digitizer (55), 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-y bins, we were able to correct numerical digitization errors in years of establishment. The numerical errors in establishment amount data were small (*SI Appendix*, Fig. S9). Each study calculated tree ages within stand plots or transects using standard dendrochronology approaches and aggregated trees into 10-or 20- y cohorts. 13 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 to 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 (9). In cases where authors did not provide exact geographic coordinates for studies locations were determined based on written descriptions and study maps. Datasets spanned a diversity of geographic locations in the Great Basin and Colorado Plateau (Arizona, California, Colorado, Idaho, Nevada, and Utah; Fig. 2*A*) 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). Populations used in this study cover a wide range of climate conditions experienced in the pinyon–juniper range, as determined by the presence of our five focal species within US Forest Service Forest Inventory and Analysis plots (*SI Appendix*, Fig. S10). However, warmer, drier sites are somewhat underrepresented.

To directly compare all datasets at the same time scale, we aggregated 10-y datasets to 20-y by summing establishment in two 10-y intervals. In some cases, 10-y datasets did not end on the full 20-y interval, and only quantified establishment during the first 10 y (e.g., 1960 to 1969) of the 20-y interval (1960 to 1979). In these cases, the last 10 y of the dataset were not included in the analysis to avoid underestimates of establishment (e.g., using 10 y of data for a 20-y interval). In cases where authors reported relative establishment (e.g., proportion of trees in each age cohort, trees in a standardized area), establishment values were converted back to tree counts using reported sample sizes or search areas. This step was necessary for our Bayesian inference approach where uncertainty depends, in part, on the number of individuals sampled.

Establishment Rate Inference. We used a Bayesian inference approach to estimate establishment rates in each population. This approach allowed us to account for full uncertainty in unknown survival rates and population size (s_t, N_t) when estimating establishment rates (b_t).

Population size at each time step was determined by Eq. **2**

$$N_t = s_tN_{t-1} + b_tN_{t-1},$$

where N_0, the number of founder trees before first recorded tree, was treated as an unknown parameter with prior *Normal*(50, 10). This prior distribution chosen to represent that survey data was unlikely to have captured the true initiation of the population because either the oldest tree was not sampled or died before sampling occurred. In practice, a noninformative prior [*Uniform*(1,1000)] [*Uniform(1,1000)*], does not alter general results but does tend to assume the first aged tree is the initiation of each population, leading to a modest increase in per-capita establishment rates early in a population history (*SI Appendix*, Fig. S11). Thus, *Normal*(50, 10) is a conservative prior that slightly lowers establishment rates prior to Euro-American settlement to account for uncertain population age.

The underlying population dynamics model (Eq. **2**) was then connected to observed establishment data in each population as

$$B_t \sim Poisson(B^*_t * s_{t+1} * s_{t+2} \cdots * s_{tmax}), \quad [4]$$

where B_t is the observed number of individuals that established at time t, and B^*_t is the true number of individuals that established (b_tN_{t-1}) corrected for the cumulative survival of that cohort from establishment to observation. Given observations of average decadal survival rates from 95% to >99% in pinyon–juniper species (56), we used a truncated normal informative prior for all intervals and populations of $s \sim Normal(0.95, 0.1)T[0, 1]$. This prior still allowed for considerable uncertainty in survival rates that aligns with current observed variability ranging from 50% to near 100% survival (e.g., Fig. 4). Establishment rates were given noninformative uniform priors. Because the Poisson distribution can only accommodate integers, and digitized establishment numbers often included small numerical errors that resulted in noninteger values, digitized establishment numbers were rounded to the nearest integer for model fitting. Models were fit to each population independently using "rstan" (57). Sampling algorithm was run for 2,000 iterations (1,000 of which was warmup) and model convergence was checked visually and using r-hat statistics (r-hat <1.1).

To test the ability of our modeling approach to recover underlying establishment rates, we simulated 100 establishment datasets over 30-time intervals using randomly generated, known survival and establishment rate values, and then fit the model described above to test whether posterior estimates of establishment rates align with the true values. The ability of our model to recover true establishment rates was calculated by using the correlation between true establishment rate values and estimated posterior median establishment rate values, RMSE between true and estimated establishment rate values across time periods (lower values indicate higher accuracy), and coverage. Coverage calculates the proportion of the true establishment rate values that fall within credible intervals, with the expectation that a well-developed, accurate model should recover the true value in its 95% credible interval approximately 95% of the time. Results indicated that while uncertainty in establishment rates increased with time since present, true establishment rates were identifiable, with a correlation of 0.78 between posterior median establishment rates and true values (*SI Appendix*, Fig. S6*A*). Across simulated datasets, RMSE was highest earliest in the timeseries (1.31), but declined rapidly nearing the present (0.03) (*SI Appendix*, Fig. S6*B*). Even when establishment rate estimates were less precise, true values were still accurately contained within posterior distributions as indicated by coverage values near 0.95 throughout the timeseries (*SI Appendix*, Fig. S6*C*).

We calculated the posterior distribution of the average per-capita establishment rate for each 20-y interval (posterior median and 95% credible interval are

displayed) using the posterior draws from all populations. We also used segmented regression to identify and quantify major changes in per-capita establishment rates over time with the "segmented" package in R (58). 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 posterior median establishment rates in all plots (response variable) and interval year (explanatory variable) with one to four change points and calculated AIC scores to determine the best fit model. Finally, we calculated the posterior probability that establishment rates observed during the Euro-American settlement period exceeded establishment rates prior to Euro-American settlement (i.e., >0.95 probability). To test the sensitivity of our results to the 1860 settlement threshold we also repeated this analysis using 1840 and 1880.

Decomposing Contributions to Establishment. To quantify the role of multiplicative population growth relative to changing per-capita establishment rates in driving age structures, we simulated expected net establishment in each 20-y interval from 1600 to 1980. We quantified the role of multiplicative growth by simulating population growth under a constant establishment rate, using the mean of the observed establishment rate from 1600 to 1840 intervals for that population. This quantified the net amount of establishment we would expect if no change in establishment rates occurred, and multiplicative population growth alone was responsible for observed dynamics. The year 1860 (i.e., after the 1840 to 1859 interval) was chosen at the pre–post settlement breakpoint given that most studies indicated 1860 was the approximate time of settlement (*SI Appendix*, Table S2). We acknowledge that settlement did not occur as a discrete event and settlement intensity was likely not constant, however differing settlement breakpoints did not alter general results (*SI Appendix*, Fig. S4). Future archeological and archival work could help narrow the timing and intensity of settlement at each site.

We then repeated this simulation, but with varying per-capita establishment rates, using the observed establishment rate for each 20-y interval from each population. This quantified the net amount of establishment we would expect with both multiplicative growth and changing per-capita establishment rates. Similar to Fig. 2*B* and *SI Appendix*, Fig. S1, expected observed establishment was then calculated as the survivorship of each 20-y cohort to observation. We relativized to the total for each population and simulation to allow for direct comparison across populations in Fig. 2*B*, while *SI Appendix*, Fig. S5 shows the total (unrelativized) net establishment for each population. The difference in net establishment between these two simulations is the contribution of changing per-capita establishment rates to overall establishment. In all cases, simulations accounted for and incorporated survival rate and establishment rate uncertainty by iterating over the draws from the posterior distribution for each population. The proportion of variance in establishment explained in each population (Fig. 3*B*) was calculated as the square of the Pearson correlation coefficient (r^2) of the total establishment amounts in each 20-y interval for each population. The proportion of net establishment within a population in each 20-y interval (Fig. 3*C*) was determined by the ratio of establishment predicted with constant establishment rates relative to changing establishment rates. Because the ratios are non-normally distributed, a simple average would skew toward larger values, making it appear as though constant rates predict more establishment. Therefore, we used the median to represent the central tendency.

Data, Materials, and Software Availability. Data and R code to reproduce all analyses are available on Zenodo at https://doi.org/10.5281/zenodo.15132862 (59).

ACKNOWLEDGMENTS. We thank the authors who 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 United States Department of Agriculture (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 affiliations: [a]Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV 89557; and [b]Rocky Mountain Research Station, United States Department of Agriculture Forest Service, Reno, NV 89557

1. N. N. Barger *et al.*, Woody plant proliferation in North American drylands: A synthesis of impacts on ecosystem carbon balance. *J. Geophys. Res. Biogeosciences* **116**, G00K07 (2011).
2. N. Stevens, C. E. R. Lehmann, B. P. Murphy, G. Durigan, Savanna woody encroachment is widespread across three continents. *Glob. Change Biol.* **23**, 235–244 (2017).
3. A. Ahlström *et al.*, The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink. *Science* **348**, 895–899 (2015).
4. A. P. Schreiner-McGraw *et al.*, Woody plant encroachment has a larger impact than climate change on dryland water budgets. *Sci. Rep.* **10**, 8112 (2020).
5. R. F. Miller, P. E. Wigand, Holocene changes in semiarid pinyon-juniper woodlands. *BioScience* **44**, 465–474 (1994).
6. K. g. Roques, T. g. O'Connor, A. r. Watkinson, Dynamics of shrub encroachment in an african savanna: Relative influences of fire, herbivory, rainfall and density dependence. *J. Appl. Ecol.* **38**, 268–280 (2001).
7. S. K. Filippelli *et al.*, Monitoring pinyon-juniper cover and aboveground biomass across the Great Basin. *Environ. Res. Lett.* **15**, 025004 (2020).
8. R. F. Miller *et al.*, The ecology, history, ecohydrology, and management of pinyon and juniper woodlands in the great basin and northern colorado plateau of the western United States. *Gen Tech Rep RMRS-GTR-403 Fort Collins CO US Dep. Agric. For. Serv. Rocky Mt. Res. Stn.* **284**, P403 (2019).
9. N. N. Barger, H. D. Adams, C. Woodhouse, J. C. Neff, G. P. Asner, Influence of livestock grazing and climate on pinyon pine (pinus edulis) dynamics. *Rangel. Ecol. Manag.* **62**, 531–539 (2009).
10. F. Biondi, M. Bradley, Long-term survivorship of single-needle pinyon (*Pinus monophylla*) in mixed-conifer ecosystems of the Great Basin, USA. *Ecosphere* **4**, 1–19 (2013).
11. W. H. Romme *et al.*, Historical and modern disturbance regimes, stand structures, and landscape dynamics in piñon–juniper vegetation of the Western United States. *Rangel. Ecol. Manag.* **62**, 203–222 (2009).
12. W. L. Baker, D. J. Shinneman, Fire and restoration of piñon–juniper woodlands in the western United States: A review. *For. Ecol. Manag.* **189**, 1–21 (2004).
13. M. L. Floyd, D. D. Hanna, W. H. Romme, Historical and recent fire regimes in Piñon–Juniper woodlands on Mesa Verde, Colorado USA. *For. Ecol. Manag.* **198**, 269–289 (2004).
14. S. R. Archer *et al.*, "Woody plant encroachment: Causes and consequences" in *Rangeland Systems: Processes, Management and Challenges, Springer Series on Environmental Management*, D. D. Briske, Ed. (Springer International Publishing, 2017), pp. 25–84.
15. J. Ehrlén, W. F. Morris, Predicting changes in the distribution and abundance of species under environmental change. *Ecol. Lett.* **18**, 303–314 (2015).
16. W. F. Morris, J. Ehrlén, J. P. Dahlgren, A. K. Loomis, A. M. Louthan, Biotic and anthropogenic forces rival climatic/abiotic factors in determining global plant population growth and fitness. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 1107–1112 (2020).
17. K. D. Bennett, Postglacial population expansion of forest trees in Norfolk UK. *Nature* **303**, 164–167 (1983).
18. T. W. Swetnam, C. D. Allen, J. L. Betancourt, Applied historical ecology: Using the past to manage for the future. *Ecol. Appl.* **9**, 1189–1206 (1999).
19. K. A. Pelz *et al.*, Quantifying old-growth forest of United States Forest Service public lands. *For. Ecol. Manag.* **549**, 121437 (2023).
20. A. J. Belsky, Viewpoint: Western juniper expansion: Is It a threat to arid Northwestern ecosystems? *J. Range Manag.* **49**, 53–59 (1996).
21. S. Baruch-Mordo *et al.*, Saving sage-grouse from the trees: A proactive solution to reducing a key threat to a candidate species. *Biol. Conserv.* **167**, 233–241 (2013).
22. J. R. Reinhardt *et al.*, Quantifying pinyon–juniper reduction within North America's sagebrush ecosystem. *Rangel. Ecol. Manag.* **73**, 420–432 (2020).
23. R. C. Mueller *et al.*, Differential tree mortality in response to severe drought: Evidence for long-term vegetation shifts. *J. Ecol.* **93**, 1085–1093 (2005).
24. W. R. L. Anderegg *et al.*, Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytol.* **208**, 674–683 (2015).
25. C. A. Woodhouse, K. E. Kunkel, D. R. Easterling, E. R. Cook, The twentieth-century pluvial in the western United States. *Geophys. Res. Lett.* **32**, 7 (2005).
26. V. A. Carter *et al.*, Legacies of Indigenous land use shaped past wildfire regimes in the Basin-Plateau Region, USA. *Commun. Earth Environ.* **2**, 1–9 (2021).
27. S. T. Gray, J. L. Betancourt, S. T. Jackson, R. G. Eddy, Role of multidecadal climate variability in a range extension of pinyon pine. *Ecology* **87**, 1124–1130 (2006).
28. W. J. Calder, D. Parker, C. J. Stopka, G. Jiménez-Moreno, B. N. Shuman, Medieval warming initiated exceptionally large wildfire outbreaks in the Rocky Mountains. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 13261–13266 (2015).
29. C. A. Woodhouse, D. M. Meko, G. M. MacDonald, D. W. Stahle, E. R. Cook, A 1,200-year perspective of 21st century drought in southwestern North America. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 21283–21288 (2010).
30. K. N. Weppner, J. L. Pierce, J. L. Betancourt, Holocene fire occurrence and alluvial responses at the leading edge of pinyon–juniper migration in the Northern Great Basin USA. *Quat. Res.* **80**, 143–157 (2013).
31. T. W. Swetnam, J. L. Betancourt, Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *J. Clim.* **11**, 3128–3147 (1998).
32. J. L. Betancourt, T. R. Van Devender, Holocene vegetation in chaco canyon New Mexico. *Science* **214**, 656–658 (1981).
33. D. G. Wyckoff, Secondary forest succession following abandonment of mesa verde. *Kiva* **42**, 215–231 (1977).
34. M. R. Lesser, S. T. Jackson, Contributions of long-distance dispersal to population growth in colonising Pinus ponderosa populations. *Ecol. Lett.* **16**, 380–389 (2013).
35. M. E. Lyford, S. T. Jackson, J. L. Betancourt, S. T. Gray, Influence of landscape structure and climate variability on a late holocene plant migration. *Ecol. Monogr.* **73**, 567–583 (2003).
36. K. L. Cole, J. F. Fisher, K. Ironside, J. I. Mead, P. Koehler, The biogeographic histories of Pinus edulis and Pinus monophylla over the last 50,000 years. *Quat. Int.* **310**, 96–110 (2013).

37. Y. Zhou *et al.*, Woody encroachment happens via intensification, not extensification, of species ranges in an African savanna. *Ecol. Appl.* **31**, e02437 (2021).
38. P. J. Weisberg, E. Lingua, R. B. Pillai, Spatial patterns of pinyon–juniper woodland expansion in central Nevada. *Rangel. Ecol. Manag.* **60**, 115–124 (2007).
39. J. M. Bauer, P. J. Weisberg, Fire history of a central Nevada pinyon–juniper woodland. *Can. J. For. Res.* **39**, 1589–1599 (2009).
40. T. Drees, B. M. Ochocki, S. L. Collins, T. E. X. Miller, Demography and dispersal at a grass-shrub ecotone: A spatial integral projection model for woody plant encroachment. *Ecol. Monogr.* **93**, e1574 (2023).
41. E. L. Schultz, S. K. Filippelli, J. C. Vogeler, R. K. Shriver, Density-dependent dynamics help explain the simultaneous expansion and decline of woodlands in the western US. *For. Ecol. Manag.* **546**, 121359 (2023).
42. P. J. van Mantgem *et al.*, Widespread increase of tree mortality rates in the Western United States. *Science* **323**, 521–524 (2009).
43. M. D. Redmond, F. Forcella, N. N. Barger, Declines in pinyon pine cone production associated with regional warming. *Ecosphere* **3**, art120 (2012).
44. R. K. Shriver, C. B. Yackulic, D. M. Bell, J. B. Bradford, Dry forest decline is driven by both declining recruitment and increasing mortality in response to warm, dry conditions. *Glob. Ecol. Biogeogr.* **31**, 2259–2269 (2022).
45. S. Archer, Have southern texas savannas been converted to woodlands in recent history? *Am. Nat.* **134**, 545–561 (1989).
46. A. Brunelle, T. a. Minckley, J. Delgadillo, S. Blissett, A long-term perspective on woody plant encroachment in the desert southwest, New Mexico, USA. *J. Veg. Sci.* **25**, 829–838 (2014).
47. G. Gil-Romera, H. F. Lamb, D. Turton, M. Sevilla-Callejo, M. Umer, Long-term resilience, bush encroachment patterns and local knowledge in a Northeast African savanna. *Glob. Environ. Change* **20**, 612–626 (2010).
48. J. N. Mast, P. Z. Fulé, M. M. Moore, W. W. Covington, A. E. M. Waltz, Restoration of presettlement age structure of an arizona ponderosa pine forest. *Ecol. Appl.* **9**, 228–239 (1999).
49. M. M. Rowland, L. H. Suring, R. J. Tausch, S. Geer, M. J. Wisdom, Characteristics of western juniper encroachment into sagebrush communities in central Oregon. *Gd. US Dep. Agric. For. Serv. Pac. Northwest Res. Stn. Gd. For. Range Sci. Lab.* **23**, 129513235 (2008).
50. S. L. Morford *et al.*, Herbaceous production lost to tree encroachment in United States rangelands. *J. Appl. Ecol.* **59**, 2971–2982 (2022).
51. M. E. K. Evans *et al.*, Tree rings reveal the transient risk of extinction hidden inside climate envelope forecasts. *Proc. Natl. Acad. Sci. U.S.A.* **121**, e2315700121 (2024).
52. D. Pimentel, L. Lach, R. Zuniga, D. Morrison, Environmental and economic costs of nonindigenous species in the United States. *BioScience* **50**, 53–65 (2000).
53. F. Samson, F. Knopf, Prairie conservation in North America. *BioScience* **44**, 418–421 (1994).
54. R. Miller, R. Tausch, R. Tausch, D. Johnson, S. C. Sanderson, *Age Structure and Expansion of Piñon-juniper Woodlands: A Regional Perspective in The Intermountain West* (Fort Collins, CO: U.S. Dept. of Agriculture, Forest Service, Rocky Mountain Research Station, 2008).
55. Ankit Rohatgi, Webplotdigitizer. (2022). Deposited 2022.
56. R. K. Shriver, C. B. Yackulic, D. M. Bell, J. B. Bradford, Quantifying the demographic vulnerabilities of dry woodlands to climate and competition using rangewide monitoring data. *Ecology* **102**, e03425 (2021).
57. J. Guo *et al.*, rstan: R Interface to Stan (2024). Deposited 5 March 2024.
58. V. M. R. Muggeo, Segmented regression models with break-points/ change-points estimation (with possibly random effects) (2024).
59. R. Shriver, Data and code associated with Shriver et al. 2025, Long-term tree population growth can predict woody encroachment patterns. Zenodo. https://doi.org/10.5281/zenodo.15132862. Deposited 3 April 2025.