PNAS RESEARCH ARTICLE | ECOLOGY

Oak masting breaks down in a highly fragmented, pollen-limited landscape

Ian S. Pearse[a,1], Jill H. Baty[b], Mario B. Pesendorfer[c,d], Robert Olson[e], and Walter D. Koenig[f]

Edited by Richard S. Ostfeld, Cary Institute of Ecosystem Studies, Millbrook, NY; received November 21, 2025; accepted March 11, 2026

Masting, the production of variable and synchronous seed crops, is common among wind pollinated trees, and periodic pollen limitation is thought to be an important component of the process of masting. However, little is known either about the dynamics of mast seed production or pollen limitation in isolated trees. We tracked seed production of valley oak (*Quercus lobata*) over 11 years in a highly fragmented landscape in California's Central Valley in which many trees lacked conspecific neighbors within 500 m. We found that oaks with closer neighbors produced more acorns on average than oaks with fewer neighbors. Consistent with theories linking mast seeding and pollination, the isolation effect was most apparent in the highest seed production years. While individual trees showed substantial interannual variation in seed production, we observed little synchrony in seed production among individuals compared to intact oak populations throughout California. Our results indicate that highly fragmented populations suffer signs of pollen limitation and do not produce synchronous seed crops. Fragmentation, alongside climate change, is a dimension of global change that interrupts the typical seed production dynamics of trees.

masting | fragmentation | isolation | synchrony | quercus

Significance

Mast seeding, boom and bust seed production, has rippling effects throughout forest food webs These variable seed crops rely on interannual differences in flower production and pollination. We hypothesized that fragmentation, an important aspect of global change in forests, alters seed production dynamics of masting trees because it increases pollen limitation. Our study uses long-term data to demonstrate that isolation disrupts the process of masting in oaks. Our study suggests that fragmentation can have profound effects on seed production dynamics and points to a line of mechanistic research linking pollen limitation and mast seeding.

Mast seeding, the production of seed crops with high interannual variability and synchrony among trees, is a common and important process in forests globally (1–3). Masting dynamics drive fluctuations in many animals that consume tree seeds (4) and can have large and often unexpected consequences on the dynamics of forest food webs (5, 6). At the same time, seed production dynamics set the stage for forest regeneration and can have large effects on how forests recover from disturbances such as fires (7–9). Masting behavior is typically tied to interannual variation in weather, fluctuations in the internal resources of trees, and pollen limitation (1, 10–13).

Pollen limitation is an important process in models of masting because it can synchronize reproduction among individuals within populations (14–16). Two models that explain masting behavior involve periodic pollen limitation. In the pollen coupling model, interannual variation in the seed production of individuals is caused by the accumulation and expenditure of resources, and reproduction becomes synchronized within a population because pollen limits seed production in years in which fewer individuals set flower (15). This hypothesis has accumulated empirical support in systems such as the perennial forb, *Astragalus scaphoides* that reproduces episodically and exhibits pollen limitation during years of crop failures, which are not necessarily tied to variation in environmental conditions (16, 17). The environmental veto model suggests that seed production can be linked to pollination, but contrasts with the pollen coupling hypothesis by stating that environmental conditions periodically disrupt the processes of flowering, pollination, or seed development (1, 18). This hypothesis has support in systems such as oaks (genus *Quercus*) that produce mast seed crops correlated with annual weather conditions promoting pollination (11, 13, 18, 19). Because pollen limitation increases when there are fewer individuals with which to mate, both hypotheses predict that seed production dynamics should be influenced by the density of conspecifics. Specifically, we expect that periodic pollen limitation should be greater for individuals with fewer nearby pollen donors. Both models of masting suggest that pollen limitation due to isolation could desynchronize seed production, resulting in trees that produce seed crops on their own schedule. In the pollen coupling model, this is because pollen limitation due to isolation may decouple the relationship between the investment in large flower crops and the amount of pollen received by another tree; and in the environmental veto hypothesis, this may occur because pollen limitation due to isolation may limit seed production even in years in which environmental conditions allow it.

Fragmentation causes pollen limitation in many plants (20), but there are no prior studies that explore how it affects masting dynamics. Indeed, while masting plants are disproportionately wind pollinated (21, 22), there are few studies demonstrating how

Author affiliations: [a]U.S. Geological Survey, Fort Collins Science Center, Fort Collins, CO 80526; [b]City of Fort Collins, Dept Planning and Development, Fort Collins, CO 80524; [c]Universität für Bodenkultur Wien, Dept Forest Ecology, Vienna 1180, Austria; [d]Smithsonian's National Zoo and Conservation Biology Institute, Washington, D.C. 20008; [e]Net Contents Consulting, Los Altos, CA 94022; and [f]Hastings Natural History Reservation, University of California Berkeley, Carmel Valley, CA 93924

Author contributions: I.S.P., J.H.B., and W.D.K. designed research; I.S.P., J.H.B., M.B.P., R.O., and W.D.K. performed research; I.S.P. analyzed data; and I.S.P. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Copyright © 2026 the Author(s). Published by PNAS. This article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

[1]To whom correspondence may be addressed. Email: ipearse@usgs.gov.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2533900123/-/DCSupplemental.

Published May 11, 2026.

Downloaded from https://www.pnas.org by UC Berkeley on May 11, 2026 from IP address 128.32.10.230.

fragmentation or isolation affect pollen limitation in wind pollinated trees (23). However, there is evidence that such trees experience wind pollen limitation episodically, as would be expected based on two hypotheses linking mast seeding and pollination: the nonmutually exclusive, Pollen Coupling and Environmental Veto hypotheses (24–26). While there is clear evidence that wind-dispersed pollen can travel great distances (27, 28), there is also evidence that less dense stands of oaks growing in a savannah habitat produce fewer acorns, consistent with greater pollen limitation with fewer neighboring conspecifics (29). Fragmentation is happening throughout forests globally, and its consequences for seed production are poorly understood. Highly fragmented landscapes offer a situation in which we can test how isolation affects long-term seed production dynamics of trees.

We conducted a long-term (11-year) survey of annual seed production of valley oaks (*Quercus lobata*) in a highly fragmented agricultural landscape in the Central Valley of California. Valley oak, a California endemic, is one of the dominant tree species throughout low elevation habitats in the state. It is the only oak species common in the Central Valley prior to 1900 where it grew along riparian corridors and in savannah habitats (30, 31). Since that time, agriculture has been the dominant land use in the Central Valley, and the historical distribution of valley oak has become highly fragmented, often with single trees or small groves persisting in isolation (Fig. 1). At the same time, valley oak is commonly planted in urban areas and conserved along agricultural margins (32), giving it a patchy distribution in which some trees are highly isolated while others grow as part of larger stands. Valley oak is a masting species, and its seed production dynamics have been studied extensively in natural stands of oaks throughout California (33–36). From that work, we know that valley oak produces episodic large acorn crops that are synchronous at both the population and at large spatial scales (33, 35). Annual weather and resource dynamics are both thought to influence masting dynamics because acorn crops are positively correlated with years with warm springs and negatively correlated with the prior year's acorn crop (25, 37, 38). Pollination is strongly implicated in this process because valley oak is periodically pollen limited (24) and because warm springs result in more synchronous flowering (11). Despite this long history of research, nothing is known about seed production of valley oaks in highly fragmented landscapes.

We mapped oak trees in a 335-km^2 area in California's Central Valley and surveyed seed production of focal trees within the area chosen to span a gradient of isolation from conspecifics (Fig. 2). We used this dataset alongside concurrent measurements of acorn production in ten intact valley oak stands throughout California to address three related questions. 1) How does isolation affect the seed production dynamics of valley oaks? 2) Does pollen limitation due to isolation limit seed production more during large reproduction years when other constraints on seed production are likely relaxed? 3) Does fragmentation reduce reproductive synchrony?

Results

Description of Oaks and Seed Production. We mapped a total of 2,231 valley oak trees in rural areas of Yolo County (Fig. 2) and inferred a density of 1.8 valley oaks * hectare^{-1} in urban areas. In rural areas, trees were patchily distributed along roads and in fields, field margins, near houses, and in small forest fragments. We observed a range of seed production among individual trees and among years, in which 2017 was notably a seed crop failure for most trees within the population (Fig. 3).

How Does Isolation Affect the Seed Production Dynamics of Valley Oaks? Of the five measures of isolation, inverse distance to the nearest neighbor and squared inverse distance to the nearest neighbor were most predictive of long-term average seed production of valley oak trees (*SI Appendix*, Table S1). The explanatory power of these two variables was indistinguishable based on a criterion of ΔAIC < 2. Isolated oaks (those with a

Fig. 1. An isolated valley oak in an alfalfa field during the 2020 survey. Photo by Walt Koenig.

Downloaded from https://www.pnas.org by UC Berkeley on May 11, 2026 from IP address 128.32.10.230.

Downloaded from https://www.pnas.org by UC Berkeley on May 11, 2026 from IP address 128.32.10.230.

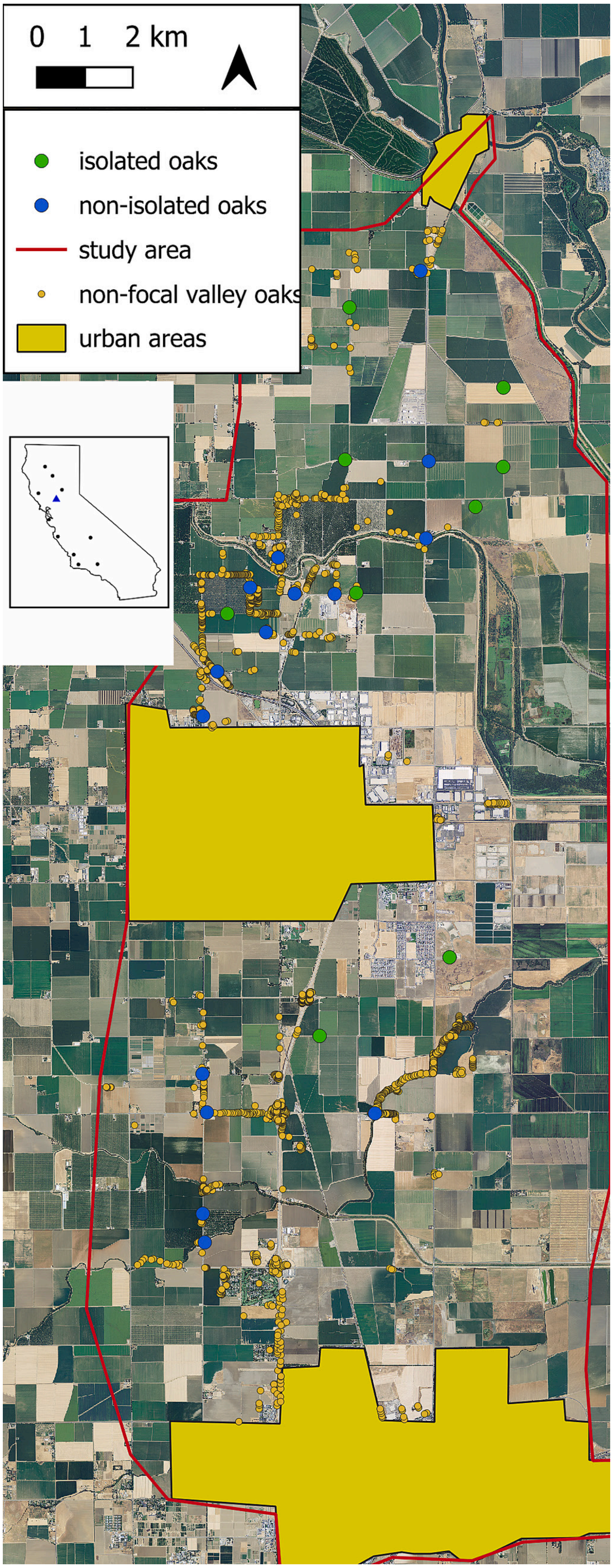

Fig. 2. Locations of valley oaks in Yolo County, California, USA. Locations of valley oaks in rural landscapes were mapped manually, and within urban areas, we assumed an average density of 1.2 valley oaks/hectare. The base layer is from the U.S. Department of Agriculture National Agricultural Imagery Program (USDA 2012). Inset map shows position of fragmented population (blue triangle) and ten nonfragmented oak populations in which seed production dynamics were measured (black dots) within California.

lower inverse distance to a nearest neighbor) had lower long-term average seed production than oaks with closer neighbors ($\beta = 13.1$, $F = 8.9$, $R^2 = 0.29$, $P = 0.006$). Long-term average seed production rapidly declined with a distance to the nearest neighbor at roughly 100 m (inverse distance; Fig. 4). The coefficient of variation (CV_i) of seed production was marginally greater in more isolated oaks with lower inverse distance to a nearest neighbor ($\beta = -11.3$, $F_{1,18} = 3.7$, $R^2 = 0.17$, $P = 0.07$).

Does the Effect of Isolation Depend on Mast Seed Crop Years? The effect of isolation depended on the population-level average seed production of a given year (Table 1). In years of high average seed production, trees with close neighbors produced larger seed crops than isolated trees ($\beta = 19.2$, $F = 13.1$, $R^2 = 0.37$, $P = 0.002$). However, in years of small average seed crops, the effect of isolation was less apparent and only marginally significant ($\beta = 6.9$, $F = 3.5$, $R^2 = 0.13$, $P = 0.08$).

Does Fragmentation Reduce Reproductive Synchrony in Valley Oaks? Trees within the fragmented Yolo population had a wide range of distances to nearest neighbors, ranging up to 1,240 m (*SI Appendix*, Fig. S1). In contrast, in one nonfragmented oak population (Hastings Natural History Reservation in central coastal California) with mapped oak individuals, the most isolated trees had nearest neighbors at 94 m (*SI Appendix*, Fig. S1). Consequently, in contrast to the fragmented population, we observed no effect of isolation on seed production in the nonfragmented site (*SI Appendix*, Fig. S2). Trees within the fragmented population produced seed crops that were not synchronous with one another, such that population-level synchrony of seed production (S) was substantially lower for the fragmented population than seed production in any other of 10 valley oak populations studied in California (Table 2). The isolated oaks (those lacking conspecific neighbors within 100 m) showed no significant cross-correlation in seed production ($S = 0.02$), while nonisolated trees showed weak synchrony ($S = 0.21$) over the study period.

We found no evidence to support the alternative hypothesis that low synchrony (S) of seed production in the fragmented population was due to greater geographic area of that population. Within the isolated population, distance between focal trees did not affect the cross-correlation in seed production dynamics (Mantel test; $r = -0.05$, $P = 0.71$), indicating that synchrony was lacking based on both distant and nearby trees. Likewise, in nonfragmented populations, reproductive synchrony was unrelated to the mean distance among oaks within a population, a measure of geographic area of the population ($n = 10$, $r = -0.36$, $P = 0.28$).

Because valley oaks in the fragmented population individually had exceptionally variable seed crops (CVi) but also had exceptionally low synchrony with one another (S), the population-level variability of seed production (CVp) was low but within the range of other valley oak populations. Likewise, long-term average seed production at the fragmented site was relatively low but within the range of other valley oak populations.

Discussion

Global forests are changing rapidly in many different ways (39), but we have a limited understanding of how global change is affecting seed production dynamics (40, 41). Climate change, particularly increased summer temperature, has dampened variability of seed production in European beech forests (*Fagus sylvatic*), likely because trees are receiving warmer summer environmental cues for reproduction nearly every year (42, 43). In piñon pine

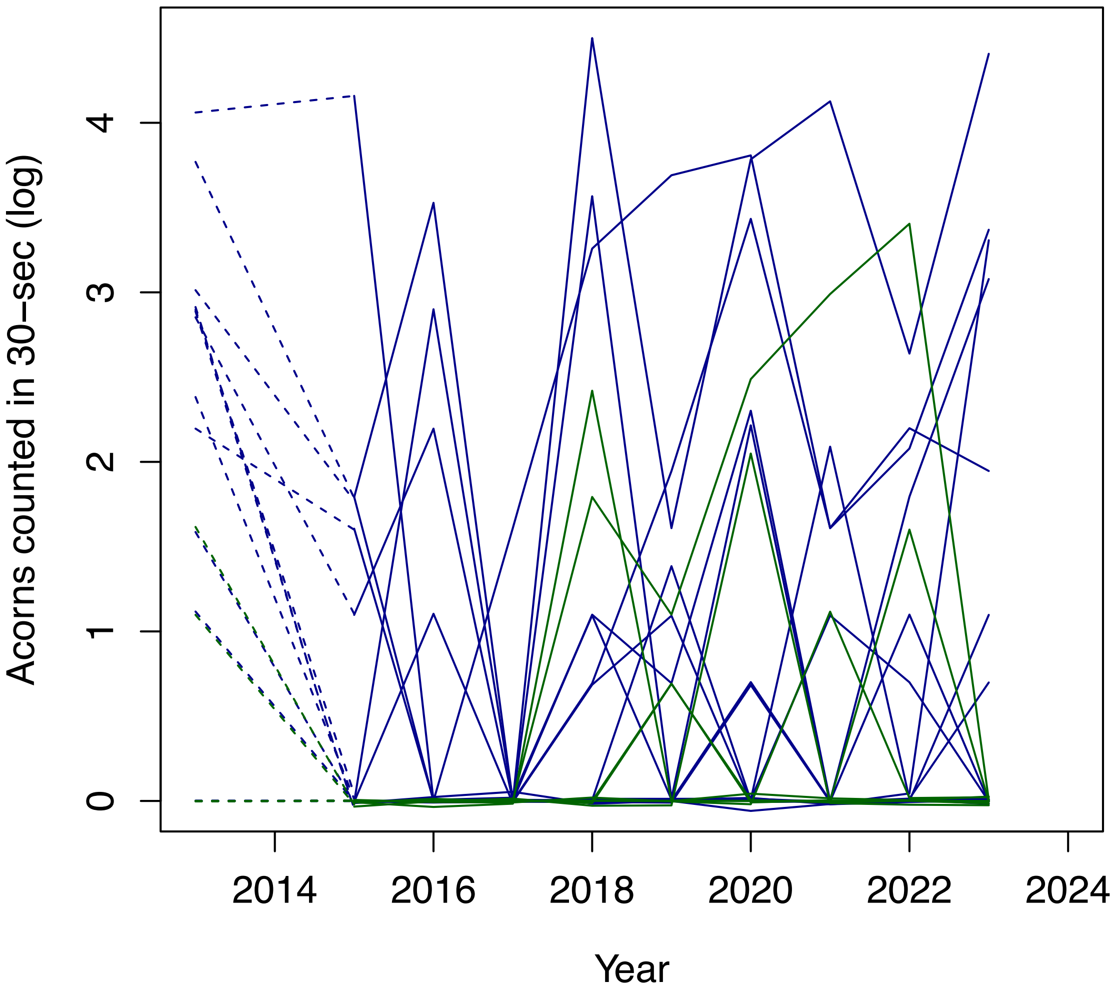

Fig. 3. Annual acorn production of 24 focal oak trees in Yolo County, CA from 2013 through 2023. Green lines are isolated trees (distance to nearest conspecific neighbor >100 m), and blue lines are nonisolated trees. Dashed lines indicate missing data for 2014. Points are jittered slightly along the y-axis to better visualize time series.

Downloaded from https://www.pnas.org by UC Berkeley on May 11, 2026 from IP address 128.32.10.230.

(*Pinus edulis*), large-scale droughts have reduced reproduction and caused more variable reproduction in recent years (44, 45), a trend consistent with longitudinal patterns of other tree species (46). Our study suggests that fragmentation is an important aspect of global change that can have profound effects on seed production dynamics by not only reducing seed production but also by desynchronizing seed crops within forest stands.

Our results are consistent with isolated trees in highly fragmented landscapes experiencing pollen limitation and therefore producing smaller seed crops on average than trees with closer neighbors. Until recently it was unknown whether oaks experienced pollen limitation, because wind-borne pollen can travel great distances (23). However, more recent studies have experimentally demonstrated periodic pollen limitation in valley oak (24, 47)and *Quercus ilex* (26), suggesting a general phenomenon.

Pollen limitation by isolation is also consistent with other lines of evidence in oak trees. Blue oak (*Quercus douglasii*) trees in low-density savannas produced smaller acorn crops than blue oaks in higher-density stands, though this pattern was only apparent in a population-wide high-reproduction year (29). The relevant distance that predicted acorn production in Knapp et al.'s study was 80 m, consistent with the distance from neighbors at which oaks in our study produced substantially lower long-term seed crops.

Estimates of the overall distance of pollen dispersal from oaks can be very large (48). However, estimates of effective pollination distances based on paternity estimates of offspring tend to be lower and more variable. In bur oak (*Quercus macrocarpa*), the average pollination distance within the tree stand was 75 m (49), although a large number of pollination events occurred from outside of the stand, likely at considerable distances (27, 28, 50). Pollination distances in valley oak have similarly varied considerably among studies (51, 52).

Isolation likely has other long-term effects on the genetic health and fitness of forest stands. For example, isolated stands of silver fir (*Abies alba*) produce a lower portion of viable seeds than trees from nonisolated stands, consistent with lower genetic diversity of paternity (53). Additional research could help reconcile the observations that wind-borne pollen can travel great distances, but pollen limitation and loss of genetic diversity can still occur in oaks and other wind pollinated plants. Mechanisms such as female choice and selective abortion of ovules fertilized by common fathers could help rectify these seemingly paradoxical observations (54).

Our results are also consistent with hypotheses proposing that pollination is a key factor synchronizing reproduction in masting trees (1, 12, 15). In our study, nonisolated trees produced large seed crops predominantly in years when the population-level average seed production was also high. In contrast, isolated trees produced relatively small acorn crops in most years. A mechanism that may be driving this pattern is periodic pollen limitation of reproduction in nonisolated trees and consistent pollen limitation in isolated trees. In nonfragmented forest stands, seed

Fig. 4. A negative relationship between the distance to nearest neighbor and the average acorn production of valley oak trees in Yolo County, CA calculated over the five highest high population-level seed production years. No relationship was observed between distance to the nearest conspecific neighbor and acorn production in the 5 lowest population-level seed production years. The trend line is the best fit model of acorn production = 1/distance to nearest conspecific.

crop failures are highly synchronous, even when the years of highest reproduction vary considerably among individuals (55). Our study suggests that fragmentation may increase the chances of seed crop failure for isolated trees even in years when other trees produce a seed crop. This same process, where a decreased mean seed production corresponds to an increase in the number of complete crop failures for isolated trees, likely causes the apparent marginal increase in variability of seed production of individuals (CVi).

Periodic pollen limitation is often implicated as a mechanism of masting in oaks, predominantly as an “environmental veto” of seed production in years when environmental conditions do not favor pollination (11, 12, 18, 25). In valley oak, years of low seed production are correlated with spring weather that desynchronizes reproduction within oak populations (11), likely resulting in pollen limitation. Models suggest that coordinated pollination failure is necessary for reproduction in this system to be synchronous (25, 56), and pollen limitation is observed experimentally (24). Similarly, in Holm oak (*Quercus ilex*), years of periodic pollen limitation correspond to years with long flowering periods and low seed crops (26).

In pedunculate oak (*Quercus robur*), greater seed production corresponds to years with greater aerial pollen collections (13, 57). However, the effects of pollen flow on seed production appear to be contingent on other factors as well, including the investment of trees in female flowers and environmental conditions (19). Pollination appears to be generally important for seed production dynamics in oaks; our results add fragmentation as a factor potentially disrupting pollination dynamics.

As is often the case in heavily altered landscapes, fragmentation is not the only effect of human activity on oak woodlands at our study site. The study was conducted during a particularly dry 5-year period (58). During these years, groundwater extraction lowered water tables throughout the Central Valley (59), and depletion of soil moisture led to subsequent die-offs of trees in surrounding areas (60). While this drought likely affected seed production at our site, it is unlikely to have disproportionately affected isolated trees or the fragmented population of oaks compared to others, as the isolated oak trees were spread throughout the study area and interspersed with stands of nonisolated oaks.

Conclusion

Isolated oaks in a fragmented landscape produced fewer and more variable acorn crops than nonisolated trees. We observed very low reproductive synchrony, one of the most important characteristics of mast seeding, among trees within the fragmented oak population, whereas other oak populations in California produced synchronous acorn crops over the same time frame. Our study suggests that fragmentation can result in large changes to the seed production dynamics of forests.

Materials and Methods

Study Site and Mapping Oaks. We conducted the study in Yolo County, California. The study area was mostly agricultural fields with a variety of annual and orchard crops, and it also encompassed three urban areas: Davis, Woodland, and Knight’s Landing (Fig. 2).

Within the study area, we identified the location of all rural trees using National Agricultural Imagery Program aerial imagery (61). We then drove along public roads to identify rural trees that were valley oaks, using binoculars to identify trees embedded in agricultural areas. The overall density of oaks in rural areas was 0.07 valley oaks hectare^{-1}. In urban areas, we could not see all trees to determine the species, so we instead estimated the density of valley oaks in those areas based on the following information. Total tree density of the urban areas was estimated as 73 trees hectare^{-1}, the average tree density in Sacramento, California (62). We then estimated the percentage of trees that were valley oaks (1.6%) as that percentage on city-owned properties in Woodland, CA, in a comprehensive list of tree plantings (63), resulting in a density of 1.2 valley oaks · hectare^{-1}. We created randomly distributed point locations of valley oaks at this density in each of the three urban areas within the study area. This approach assumes an even distribution of valley oaks in urban areas.

From the total list of rural oak trees, we chose 12 individuals that were in the upper 10% of distance to a nearest neighbor (distance to nearest neighbor >100 m), and then randomly drew 12 individuals from the remaining distribution of distance to nearest neighbor (<100 m). We replaced trees that were either inaccessible, whose nearest neighbor was an urban tree, or that was closer to the study

Table 1. ANOVA of interactive effects of isolation (inverse minimum distance to a conspecific) and annual population-level seed production on annual acorn production [acorns counted/30 s (log)] of individual valley oaks

Predictor	df	Sum Sq	F value	*P* value
Isolation	1	0.01	0.01	0.98
Annual population-level seed production (APSP)	1	0.76	0.75	0.39
Isolation*APSP	1	14.90	14.60	<0.0001
Error	235	239.60		

df = degrees of freedom.

Downloaded from https://www.pnas.org by UC Berkeley on May 11, 2026 from IP address 128.32.10.230.

Table 2. Comparison of Yolo County oaks with other populations of valley oak in CA

Site	Timeframe	Mean	kCVp	CVp	CVi	S	N Trees
Yolo oaks (all)	2013–2023	0.65	0.48	0.56	1.93	0.12	24
Yolo oaks (isolated)	2013–2023	0.26	0.67	0.9	2.46	0.02	9
Yolo oaks (not isolated)	2013–2023	0.88	0.48	0.56	1.7	0.21	15
Hastings	1980–2024	1.84	0.45	0.50	1.03	0.41	88
Jasper	1989–2024	1.15	0.56	0.68	1.45	0.38	39
Pozo	1989–2024	1.61	0.57	0.69	0.97	0.62	25
Sedgwick	1994–2024	1.67	0.51	0.59	0.95	0.37	26
Tower House	1994–2024	1.83	0.51	0.59	1.02	0.50	19
Dye Creek	1994–2024	1.70	0.53	0.63	1.07	0.56	20
Liebre Mountain	1999–2024	2.02	0.58	0.71	1.06	0.68	16
Hopland	1999–2024	2.03	0.51	0.59	0.81	0.61	11
Kaweah Oaks	1999–2024	0.76	0.76	1.15	2.05	0.36	32
Sierra Foothills	2001–2024	1.80	0.54	0.63	0.77	0.50	18

Isolate oaks were those whose nearest conspecific was >100 m. CVi = average coefficient of variation of individual tree seed production; S = population-level synchrony, CVp = population-level coefficient of variation of seed production; kCVp = Kvålseth-standardized CVp; Mean = long-term mean seed production.

boundary than any neighboring trees with others from the same distribution class. Three trees initially identified as "distant" were found, within the first year of study, to have neighboring valley oaks closer than 100 m, resulting in a slight imbalance toward nonisolated trees. This resulted in 24 focal trees for the study. All mapping and geospatial analyses were conducted using qGIS v. 3.40.9 (64).

Measuring Reproduction. We assessed acorn crops of each focal tree in the fragmented population from 2013 to 2023, excluding 2014 because of logistical constraints, following the methods of Koenig et al. (65). Two observers positioned at different vantage points near a focal tree counted acorns for 15 s. Acorn counts were summed as the number of acorns counted per 30 s sample (66). We measured acorn crops of valley oaks at 10 additional sites throughout California using the same method of timed acorn counts (35).

Statistical Analysis. We calculated isolation for each focal valley oak in the fragmented population based on five alternative estimates. These included 1) distance to nearest neighbor, 2) inverse distance to nearest neighbor, 3) squared inverse distance to nearest neighbor (the scalar of local pollen diffusion), 4) the summed inverse distance to all valley oaks in the study area, and 5) the average of the squared inverse distance to all valley oaks in the study area. Equations for the five estimates, where D = distance to each of the n valley oaks in the study area, were as follows:

$$(1)\quad MinimumDistance\left(D_M\right) = minimum(D)$$

$$(2)\quad InverseDistanceNearest = \frac{1}{D_M}$$

$$(3)\quad SquaredInverseDistanceNearest = \frac{1}{{D_M}^2}$$

$$(4)\quad SummedInverseDistance = \sum_{i=1}^{n} \frac{1}{D_i}$$

$$(5)\quad SummedSquaredInverseDistance = \sum_{i=1}^{n} \frac{1}{{D_i}^2}$$

We calculated two summaries of seed production dynamics for each focal valley oak: the long-term mean of log-transformed acorn counts (long-term average) and the coefficient of variation of seed production of log-transformed acorn counts of individual trees (CV_i). We assessed which metric of isolation was most associated with long-term seed production by comparing linear models in which each of the five isolation metrics predicted acorn production using Akaike information criterion (AIC; *SI Appendix*, Table S1). We then assessed the effect of inverse distance to nearest neighbor on long-term average seed production and CVi. We tested whether isolation disproportionately affected seed production in mast years using a linear model in which annual seed production of an individual tree (log-transformed) was predicted by the interaction between inverse distance to the nearest neighbor and the population-wide average of seed production for a given year. To tease apart the interaction between population-level seed crop size and isolation, we then separately assessed the effect of isolation on seed crops only considering the upper and lower 50% of seed production years. We predicted that isolation would affect seed production disproportionately in large seed production years because pollen would still be limiting for isolated trees in years thought to have favorable pollination conditions. In poor seed production years, we expected that all trees would produce small seed crops irrespective of isolation. We conducted an identical analysis of the interactive effects of inverse distance to a nearest neighbor and population-level seed crop size for the one nonfragmented oak population ("Hastings") for which we had mapped all mature valley oaks (*SI Appendix*, Fig. S3).

We calculated population-wide estimates of seed production dynamics from the entire fragmented population, from only the most isolated of trees within that population (distance to nearest neighbor >100 m) and least isolated trees (distance to nearest neighbor <100 m), and from each of the 10 additional populations of valley oak trees surveyed throughout California. We calculated the long-term average seed production as the average log-transformed acorn count of all trees in the population over all years of the study. We calculated the population-wide coefficient of variation of seed production (CVp) as the coefficient of variation of annual average log-transformed acorn counts within the population, and likewise calculated Kvålseth-standardized CV (kCV, 67) as a more robust measure of population-level variability. We calculated the average individual-level coefficient of variation of seed production (CVi) as the average coefficient of variation of annual seed production (log-transformed) for each tree in the population. Finally, we calculated the population-level synchrony in reproduction (S) as the average Pearson's correlation coefficient between seed production time series of each pair of valley oaks within each population.

Because reproductive synchrony decreases with distance (35) and oak populations in the study differed in geographic size, we tested the alternative hypothesis that oak sites with larger area were less synchronous because they were spread over a larger area. We first tested whether pairwise synchrony of reproduction decreased with distance between trees in the isolated population using a Mantel test. Then we tested, using Pearson's correlations, whether nonfragmented populations with greater average distances between oak trees had less synchronous reproduction. We refer to results as significant at the $\alpha = 0.05$ and marginally significant at $\alpha = 0.1$. All statistics were calculated in R v. 4.4.1. (68).

Data, Materials, and Software Availability. Seed crops spatial data have been deposited in U.S. Geological Survey Science Base (66).

ACKNOWLEDGMENTS. We thank Jean Knops, Tomika Hagiwara, Patrick Grof-Tisza, Soren Pearse, and Asa Pearse for help counting acorns as well as Katharine Ullmann, Cass Swett, Thor Harris, Eric LoPresti, Jenny Van Wyk, Jonathan Wooley, and Betsy Harbert for letting us stay with them while counting acorns. We apologize to Bill Carmen for giving him bad directions to the trees in 2014. Marion Pearse helped count acorns in 2023 and hindered counting acorns in 2013 while being born and slightly thereafter. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Downloaded from https://www.pnas.org by UC Berkeley on May 11, 2026 from IP address 128.32.10.230.

1. I. S. Pearse, W. D. Koenig, D. Kelly, Mechanisms of mast seeding: Resources, weather, cues, and selection. *New Phytol.* **212**, 546–562 (2016).
2. M. B. Pesendorfer *et al.*, The ecology and evolution of synchronized reproduction in long-lived plants. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **376**, 20200369 (2021).
3. M. Bogdziewicz *et al.*, Evolutionary ecology of masting: Mechanisms, models, and climate change. *Trends Ecol. Evol.* **39**, 851–862 (2024).
4. M. Bogdziewicz, R. Zwolak, E. E. Crone, How do vertebrates respond to mast seeding? *Oikos* **125**, 300–307 (2016).
5. R. S. Ostfeld, C. D. Canham, K. Oggenfuss, R. J. Winchcombe, F. Keesing, Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. *PLoS Biol.* **4**, e145 (2006).
6. T. J. Michaud, I. S. Pearse, H. Kauserud, C. J. Andrew, P. G. Kennedy, Mast seeding in European beech (*Fagus sylvatica* L.) is associated with reduced fungal sporocarp production and community diversity. *Ecol. Lett.* **27**, e14460 (2024).
7. V. S. Peters, S. E. Macdonald, M. R. Dale, The interaction between masting and fire is key to white spruce regeneration. *Ecology* **86**, 1744–1750 (2005).
8. D. Ascoli *et al.*, Climate teleconnections synchronize *Picea glauca* masting and fire disturbance: Evidence for a fire-related form of environmental prediction. *J. Ecol.* **108**, 1186–1198 (2020).
9. I. S. Pearse, A. P. Wion, A. D. Gonzalez, M. B. Pesendorfer, Understanding mast seeding for conservation and land management. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **376**, 20200383 (2021).
10. D. Kelly *et al.*, Of mast and mean: Differential-temperature cue makes mast seeding insensitive to climate change. *Ecol. Lett.* **16**, 90–98 (2013).
11. W. D. Koenig, J. M. Knops, W. J. Carmen, I. S. Pearse, What drives masting? The phenological synchrony hypothesis. *Ecology* **96**, 184–192 (2015).
12. M. Bogdziewicz, M. A. Steele, S. Marino, E. E. Crone, Correlated seed failure as an environmental veto to synchronize reproduction of masting plants. *New Phytol.* **219**, 98–108 (2018).
13. É. Schermer *et al.*, Flower phenology as a disruptor of the fruiting dynamics in temperate oak species. *New Phytol.* **225**, 1181–1192 (2020).
14. Y. Isagi, K. Sugimura, A. Sumida, H. Ito, How does masting happen and synchronize? *J. Theor. Biol.* **187**, 231–239 (1997).
15. A. Satake, Y. Iwasa, Pollen coupling of forest trees: Forming synchronized and periodic reproduction out of chaos. *J. Theor. Biol.* **203**, 63–84 (2000).
16. E. E. Crone, E. Miller, A. Sala, How do plants know when other plants are flowering? Resource depletion, pollen limitation and mast-seeding in a perennial wildflower. *Ecol. Lett.* **12**, 1119–1126 (2009).
17. E. E. Crone, L. Polansky, P. Lesica, Empirical models of pollen limitation, resource acquisition, and mast seeding by a bee-pollinated wildflower. *Am. Nat.* **166**, 396–408 (2005).
18. M. Bogdziewicz *et al.*, Environmental veto synchronizes mast seeding in four contrasting tree species. *Am. Nat.* **194**, 246–259 (2019).
19. E. Fleurot *et al.*, Reconciling pollen limitation theories: Insights from temperate oak masting. *Ecol. Lett.* **27**, e70009 (2024).
20. T. M. Knight *et al.*, Pollen limitation of plant reproduction: Pattern and process. *Annu. Rev. Ecol. Evol. Syst.* **36**, 467–497 (2005).
21. D. Kelly, V. L. Sork, Mast seeding in perennial plants: Why, how, where?. *Annu. Rev. Ecol. Syst.* **33**, 427–447 (2002).
22. I. S. Pearse, J. M. LaMontagne, M. Lordon, A. L. Hipp, W. D. Koenig, Biogeography and phylogeny of masting: Do global patterns fit functional hypotheses? *New Phytol.* **227**, 1557–1567 (2020).
23. W. D. Koenig, M. V. Ashley, Is pollen limited? The answer is blowin'in the wind. *Trends Ecol. Evol.* **18**, 157–159 (2003).
24. I. S. Pearse, W. D. Koenig, K. A. Funk, M. B. Pesendorfer, Pollen limitation and flower abortion in a wind-pollinated, masting tree. *Ecology* **96**, 587–593 (2015).
25. M. B. Pesendorfer, W. D. Koenig, I. S. Pearse, J. M. Knops, K. A. Funk, Individual resource limitation combined with population-wide pollen availability drives masting in the valley oak (*Quercus lobata*). *J. Ecol.* **104**, 637–645 (2016).
26. M. Bogdziewicz, M. Pesendorfer, E. E. Crone, C. Pérez-Izquierdo, R. Bonal, Flowering synchrony drives reproductive success in a wind-pollinated tree. *Ecol. Lett.* **23**, 1820–1826 (2020).
27. J. Buschbom, Y. Yanbaev, B. Degen, Efficient long-distance gene flow into an isolated relict oak stand. *J. Hered.* **102**, 464–472 (2011).
28. K. J. Craft, M. V. Ashley, Pollen-mediated gene flow in isolated and continuous stands of bur oak, Quercus macrocarpa (Fagaceae). *Am. J. Bot.* **97**, 1999–2006 (2010).
29. E. E. Knapp, M. A. Goedde, K. J. Rice, Pollen-limited reproduction in blue oak: Implications for wind pollination in fragmented populations. *Oecologia* **128**, 48–55 (2001).
30. Geographical Information Center, *The Central Valley Historic Mapping Project* (California State University, Chico, CA, 2003).
31. S. Mensing, The paleohistory of California oaks. Gen Tech Rep PSW-GTR-251 Berkeley CA US Dep. *Agric. For. Serv. Pac. Southwest Res. Stn.* **35–47**, 35–47 (2015).
32. Yolo County, *Oak Woodland Conservation and Enhancement Plan* (Yolo County, Woodland, CA, 2007)
33. W. D. Koenig, R. L. Mumme, W. J. Carmen, M. T. Stanback, Acorn production by oaks in central coastal California - Variation within and among years. *Ecology* **75**, 99–109 (1994).
34. W. D. Koenig, J. M. H. Knops, W. J. Carmen, M. T. Stanback, Spatial dynamics in the absence of dispersal: Acorn production by oaks in central coastal California. *Ecography* **22**, 499–506 (1999).
35. W. D. Koenig, J. M. Knops, Large-scale spatial synchrony and cross-synchrony in acorn production by two California oaks. *Ecology* **94**, 83–93 (2013).
36. W. D. Koenig, A brief history of masting research. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **376**, 20200423 (2021).
37. W. D. Koenig, J. M. H. Knops, W. J. Carmen, M. T. Stanback, R. L. Mumme, Acorn production by oaks in central coastal California: Influence of weather at three levels. *Can. J. For. Res.-Rev. Can. Rech. For.* **26**, 1677–1683 (1996).
38. I. S. Pearse, W. D. Koenig, J. M. Knops, Cues versus proximate drivers: Testing the mechanism behind masting behavior. *Oikos* **123**, 179–184 (2014).
39. S. Trumbore, P. Brando, H. Hartmann, Forest health and global change. *Science* **349**, 814–818 (2015).
40. A. Hacket-Pain, M. Bogdziewicz, Climate change and plant reproduction: Trends and drivers of mast seeding change. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **376**, 20200379 (2021).
41. V. Journe *et al.*, Weather drivers of reproductive variability in perennial plants and their implications for climate change risks. *Nat. Commun.* **16**, 9226 (2025).
42. M. Bogdziewicz, D. Kelly, P. A. Thomas, J. G. Lageard, A. Hacket-Pain, Climate warming disrupts mast seeding and its fitness benefits in European beech. *Nat. Plants* **6**, 88–94 (2020).
43. J. J. Foest *et al.*, Widespread breakdown in masting in European beech due to rising summer temperatures. *Glob. Change Biol.* **30**, e17307 (2024).
44. M. D. Redmond, F. Forcella, N. N. Barger, Declines in pinyon pine cone production associated with regional warming. *Ecosphere* **3**, 1–14 (2012).
45. A. P. Wion, I. S. Pearse, M. Broxson, M. D. Redmond, Mast hindcasts reveal pervasive effects of extreme drought on a foundational conifer species. *New Phytol.* **246**, 450–460 (2025).
46. I. S. Pearse, J. M. LaMontagne, W. D. Koenig, Inter-annual variation in seed production has increased over time (1900–2014). *Proc. R. Soc. B Biol. Sci.* **284**, 20171666 (2017).
47. W. D. Koenig *et al.*, Stabilizing selection for within-season flowering phenology confirms pollen limitation in a wind-pollinated tree. *J. Ecol.* **100**, 758–763 (2012).
48. S. Schueler, K. H. Schlünzen, Modeling of oak pollen dispersal on the landscape level with a mesoscale atmospheric model. *Environ. Model. Assess.* **11**, 179–194 (2006).
49. B. D. Dow, M. V. Ashley, High levels of gene flow in bur oak revealed by paternity analysis using microsatellites. *J. Hered.* **89**, 62–70 (1998).
50. B. D. Dow, M. V. Ashley, Factors influencing male mating success in bur oak. *Quercus macrocarpa*. *New Forests* **15**, 161–180 (1998).
51. V. L. Sork *et al.*, Pollen movement in declining populations of California Valley oak, *Quercus lobata*: Where have all the fathers gone?. *Mol. Ecol.* **11**, 1657–1668 (2002).
52. S. T. Abraham, D. N. Zaya, W. D. Koenig, M. V. Ashley, Interspecific and intraspecific pollination patterns of valley oak, *Quercus lobata*, in a mixed stand in coastal central California. *Int. J. Plant Sci.* **172**, 691–699 (2011).
53. J. Harmel *et al.*, Silver fir seed quality varies with habitat fragmentation, stand age, and abiotic conditions across Austria. *J. Appl. Ecol.* **63**, 70349 (2026).
54. K. J. Craft, J. S. Brown, A. J. Golubski, M. V. Ashley, A model for polyandry in oaks via female choice: A rigged lottery. *Evol. Ecol. Res.* **11**, 471–481 (2009).
55. J. Szymkowiak *et al.*, Geography of masting creates greater synchrony in seed scarcity than in seed abundance. *Proc. Natl. Acad. Sci.* **122**, e2518918122 (2025).
56. W. D. Koenig, J. M. Knops, M. B. Pesendorfer, D. N. Zaya, M. V. Ashley, Drivers of synchrony of acorn production in the valley oak (*Quercus lobata*) at two spatial scales. *Ecology* **98**, 3056–3062 (2017).
57. É. Schermer *et al.*, Pollen limitation as a main driver of fruiting dynamics in oak populations. *Ecol. Lett.* **22**, 98–107 (2019).
58. P. Ullrich *et al.*, California's drought of the future: A midcentury recreation of the exceptional conditions of 2012–2017. *Earths Future* **6**, 1568–1587 (2018).
59. P.-W. Liu *et al.*, Groundwater depletion in California's Central Valley accelerates during megadrought. *Nat. Commun.* **13**, 7825 (2022).
60. M. L. Goulden, R. C. Bales, California forest die-off linked to multi-year deep soil drying in 2012–2015 drought. *Nat. Geosci.* **12**, 632–637 (2019).
61. USDA/FSA, Aerial photography field office, USDA-FSA-APFO NAIP MrSID Mosaic–Yolo County. (2012), https://www.fpacbc.usda.gov/geospatial-services.
62. D. J. Nowak, D. E. Crane, Carbon storage and sequestration by urban trees in the USA. *Environ. Pollut.* **116**, 381–389 (2002).
63. City of Woodland, Woodland Urban Tree Map (2025), https://cityofwoodland.maps.arcgis.com/apps/instant/basic/index.html?appid=7b6311e7840445c98c98dfec81bd2eb0 [Accessed Jul 15, 2025].
64. QGIS.org, QGIS Geographic Information System v. 3.40.9. *QGIS Association* (2028), http://www.qgis.org.
65. W. D. Koenig, J. M. H. Knops, W. J. Carmen, M. T. Stanback, R. L. Mumme, Estimating acorn crops using visual surveys. *Can. J. For. Res.-Rev. Can. Rech. For.* **24**, 2105–2112 (1994).
66. I. S. Pearse, J. H. Baty, M. B. Pesendorfer, R. Olson, W. D. Koenig, Reproduction and locations of oaks in Yolo County, California, USA from 2013-2023. U.S. Geological Survey data release. https://doi.org/10.5066/P1ACVVBE. Deposited 15 April 2026.
67. J. R. Lobry, M.-C. Bel-Venner, M. Bogdziewicz, A. Hacket-Pain, S. Venner, The CV is dead, long live the CV!. *Methods Ecol. Evol.* **14**, 2780–2786 (2023).
68. R Core Team, R: A Language and Environment for Statistical Computing v4.5.1 (2025), https://www.r-project.org/.

Downloaded from https://www.pnas.org by UC Berkeley on May 11, 2026 from IP address 128.32.10.230.