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LETTER

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Reconstructing 120 years of climate change impacts on Joshua tree flowering

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Abstract

Quantifying how global change impacts wild populations remains challenging, especially for species poorly represented by systematic datasets. Here, we infer climate change effects on masting by Joshua trees (*Yucca brevifolia* and *Y. jaegeriana*), keystone perennials of the Mojave Desert, from 15 years of crowdsourced observations. We annotated phenophase in 10,212 geo-referenced images of Joshua trees on the iNaturalist crowdsourcing platform, and used them to train machine learning models predicting flowering from annual weather records. Hindcasting to 1900 with a trained model successfully recovers flowering events in independent historical records and reveals a slightly rising frequency of conditions supporting flowering since the early 20th Century. This reflects increased variation in annual precipitation, which drives masting events in wet years—but also increasing temperatures and drought stress, which may have net negative impacts on recruitment. Our findings reaffirm the value of crowdsourcing for understanding climate change impacts on biodiversity.

KEYWORDS

climate change, demography, masting, participatory science, *Yucca brevifolia*, *Yucca jaegeriana*

INTRODUCTION

Climate change is altering the phenology and productivity of plant populations worldwide, with implications for the stability of natural communities, ecosystem services, and food security (Cleland et al., 2007; Franklin et al., 2016; Franks et al., 2014; Parmesan & Yohe, 2003; Pearse et al., 2017). Climate-driven changes in the timing and intensity of plant reproduction can be examined using space-for-time substitutions, 'resurrection' experiments comparing plants grown from stored seed to contemporary populations (Franks et al., 2014), and phenology states preserved in herbarium records and historical documents (Willis et al., 2017) or as revealed by crowdsourcing initiatives (Fuccillo Battle et al., 2022). However, it remains challenging to reconstruct any element of plant populations' demographic responses to shifting climates, especially across the full geographic ranges of species poorly represented in historical records and research collections.

Species distribution models (SDMs) are a key tool for understanding how populations respond to environmental change (Elith & Leathwick, 2009; Merow et al., 2011; Sweet et al., 2019). The most common SDM methods use presence-absence records, or presence records with randomly drawn pseudo-absences, to identify suitable climate for a focal species. Presence-based SDMs provide only limited insight into a species' condition on the landscape, however, because 'presence' may mean anything from a single dying individual to a dense and growing population. Proposed methods to model population growth could better reflect this nuance, but require

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greater effort in data collection, model specification, and computational resources (Evans et al., 2016; Merow et al., 2014a; Morin & Thuiller, 2009; Snell et al., 2014).

Joshua trees (*Yucca brevifolia* Engelm. and *Y. jaegeriana* (McKelvey) L.W. Lenz; Figure 1a) are a case study in the limits of understanding population conditions through presence-based SDMs. Sister species of arborescent monocots endemic to the Mojave Desert of the southwestern United States, Joshua trees are strongly identified with the region in the popular imagination. They are the largest plants in most communities where they occur, providing food and habitat for many Mojave species (Peattie, 1950; Rowlands, 1978; Smith et al., 2023). Presence-based SDMs project that much of Joshua trees' current range will be unsuitable under future climates (Cole et al., 2011; Dole et al., 2003)—but while temperatures have risen substantially in the Mojave over the last century, evidence of Joshua tree populations' responses to this change remain elusive (U.S. Fish and Wildlife Service, 2023; Smith et al., 2023). Surveys in Joshua Tree National Park, at the trees' southern range limit, find reduced seedling recruitment consistent with projected habitat losses (Barrows & Murphy-Mariscal, 2012; Sweet et al., 2019), but no study has obtained range-wide data on Joshua tree populations' demographic condition.

Changing climate may impact Joshua trees' life cycle from germination to senescence (DeFalco et al., 2010; Esque et al., 2015; Harrower & Gilbert, 2018; Reynolds et al., 2012), but a particularly tractable focus is their flowering. Like other long-lived desert perennials,

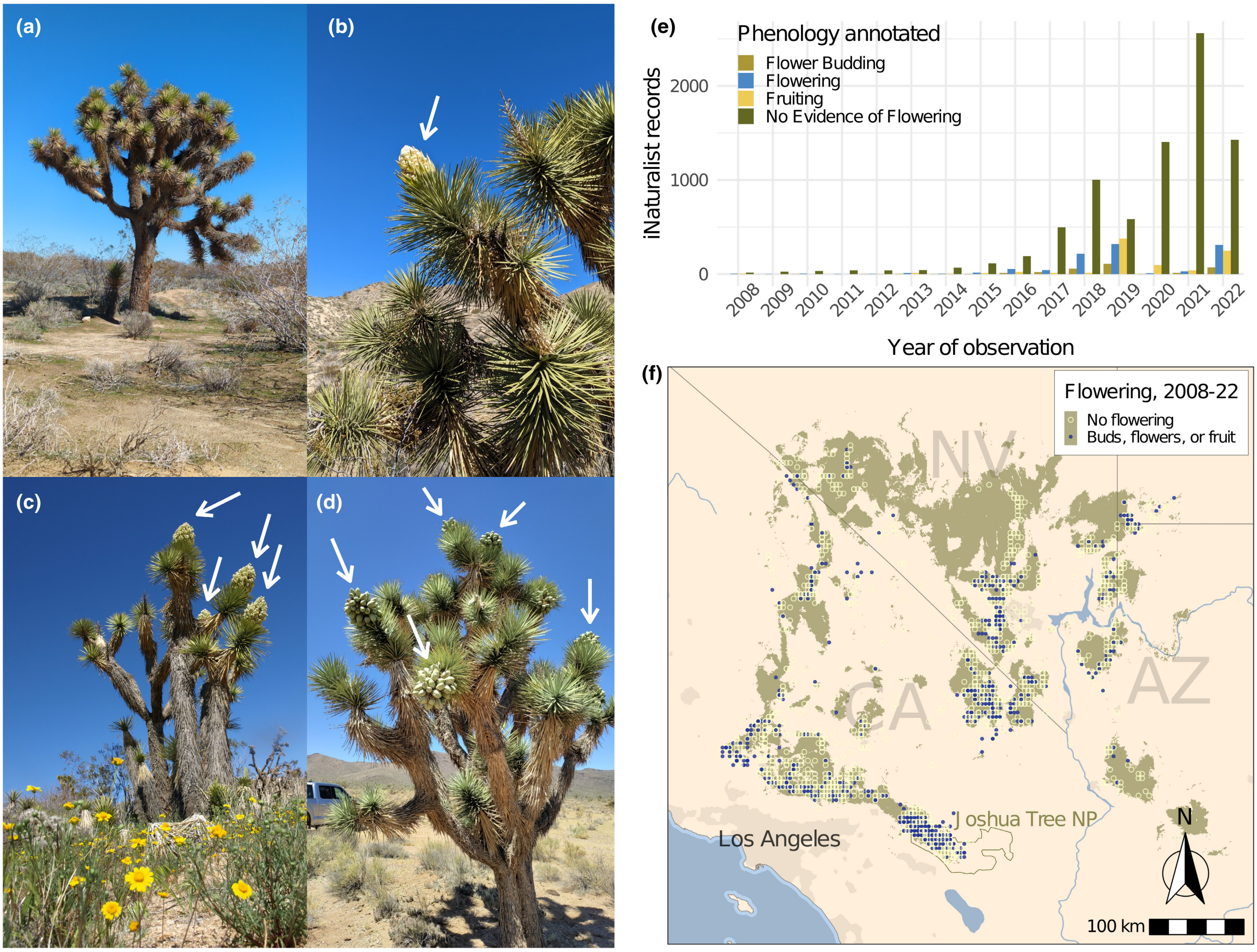

FIGURE 1 Joshua tree flowering activity recorded in crowdsourced observations. Joshua tree phenology can be diagnosed from images attached to geo-referenced observations in the iNaturalist database: (a) western Joshua tree (*Yucca brevifolia*) with no evidence of flowering in March 2023 (iNaturalist record 150083178 by user 'brewbooks'); (b) western Joshua tree with flowers budding (arrow) in March 2023 (record 150101172 by user 'mat_bristol'); (c) western Joshua tree with open flowers (arrows), in March 2008 (record 114881910 by user 'gregg29'); (d) eastern Joshua tree (*Y. jaegeriana*) with fresh green fruit (arrows) in May 2022 (record 127293323 by user 'karinp111'). (e) Total counts of 'research-grade' records of Joshua trees on the iNaturalist platform, by year of observation and diagnosed phenology status (thinner coloured bars) and proportion of records in each year indicating flowering (i.e. showing buds, flowers, or fruits; wide grey bars). (f) Locations of phenology records from all years in (e), rasterized to a 4 km grid (green shading, Joshua tree habitat modelled by Esque et al. (2023); open white points, grid cells with no evidence of flowering; solid blue points, cells with observations of buds, flowers, or fruit). Base map polygons from the Natural Earth public-domain database (naturalearthdata.com).

Joshua trees vary widely in their flowering intensity from year to year. This may reflect both variation in resource availability and adaptation to seed predation (Pellmyr & Segraves, 2003; Waitman et al., 2012)—flowering in response to annual weather variation should synchronize mass-flowering masting events to maximize seedling survival by overwhelming seed consumers (Koenig, 2021; Zwolak et al., 2022). Residents and tourists in the Mojave take great interest in Joshua tree flowering (James, 2013; McKinney, 1988; Overholt, 1932), but no one has systematically studied its environmental triggers. Popular hypotheses suggest Joshua trees mast in response to a wet year after one or more dry years (Downey, 1997; McKinney, 1988), that they flower *en masse* as a stress response (James, 2013), or that winter frost stimulates flowering (Brenskelle et al., 2021; Rodgers, 2023). All these hypothesized flowering triggers—precipitation, drought, and winter freezing—are shifting as global climate changes (Smith et al., 2023). Identifying which factors drive Joshua tree flowering would let us infer how Joshua trees are responding to recent climate change, in places and times that have not been available to direct observation.

Modelling Joshua tree flowering responses to annual weather variation would, ideally, draw on observations over multiple years at locations across the Mojave. Despite Joshua trees' ecological and cultural import, however, systematic records of their flowering are sparse. Joshua trees are challenging to preserve as herbarium specimens and therefore poorly represented in research collections; and available time-series observations in natural populations cover relatively small spans of time and geography (USA National Phenology Network, 2024). A solution may lie in the emerging practice of crowdsourcing. Crowdsourced natural history observations, collected opportunistically by volunteer contributors to ‘citizen science’ or ‘participatory science’ projects (Cooper et al., 2021; Ellwood et al., 2023), offer broader geographic and temporal coverage than directed efforts by working scientists (Amano et al., 2016; Dickinson et al., 2010; Panter et al., 2020). Crowdsourcing can produce data comparable to expert-collected observations (Aceves-Bueno et al., 2017; Callaghan et al., 2020; but see Tiago et al., 2017), especially when used with appropriate quality controls (Fuccillo et al., 2015; Kosmala et al., 2016; Panter et al., 2020).

Because of their cultural prominence and high visibility on the landscape, Joshua trees are well-represented on the iNaturalist crowdsourcing platform (inaturalist.org). Contributors to iNaturalist upload geo-referenced images to create occurrence records for species in the images. Joshua trees' morphology makes the diagnosis of species identity and phenology status from these images straightforward: they bear flowers in large panicles at the end of branches, so flowers and fruits are distinguishable at a distance (Figure 1a–d). Prior studies of *Yucca* species, including Joshua trees, characterized climate drivers of phenophase timing using iNaturalist records (Barve et al., 2020; Brenskelle et al., 2021), and we inferred the same data would support modelling variation in the occurrence, rather than the timing, of flowering.

Here, we draw on these crowdsourced records to reconstruct more than 120 years of Joshua tree reproductive activity. We annotated phenology status in images attached to more than 10,000 iNaturalist observations of Joshua trees, covering 15 years and much of the species' range (Figure 1e,f). With these records, we modelled the relationship between flowering and weather using Bayesian additive regression tree (BART) methods (Carlson, 2020; Carlson et al., 2022). We then used a trained BART model to hindcast flowering activity from historical weather records, back to the year 1900. Our hindcast aligns with independent historical records of Joshua tree flowering, and it predicts that flowering frequency has increased over the 20th Century, from a median of once every 5 years to more than once every 4 years. This trend is driven by warming winter temperatures and greater inter-annual variation in precipitation, which are likely to reduce seedling survival even as they boost flowering (Esque et al., 2015; Reynolds et al., 2012). Moreover, putative climate refugia in higher elevation and northerly regions have not necessarily seen increased flowering. These results provide new insight into climate change impacts on Joshua tree population health, and they parallel the effects of climate change on masting by other species. They also demonstrate the utility of crowdsourcing for understanding populations' responses to environmental change.

MATERIALS AND METHODS

Yucca brevifolia, the western Joshua tree, and *Y. jaegeriana*, the eastern Joshua tree, are parapatrically distributed with a narrow contact zone in central Nevada (Godsoe et al., 2008; Lenz, 2007; Pellmyr & Segraves, 2003). They differ in vegetative and floral morphology, and associate with different species of specialized pollinating *Yucca* moths (Godsoe et al., 2009). Nevertheless, the two species hybridize (Smith et al., 2021; Yoder et al., 2013), and occupy overlapping climates (Esque et al., 2023; Godsoe et al., 2009). We therefore treat eastern and western Joshua trees as a single population in the present study, though we also examine each separately as a point of comparison.

Data compilation

We queried iNaturalist for observations of Joshua trees (as *Y. brevifolia*; iNaturalist treats eastern and western Joshua trees as subspecies), located within the Mojave Desert and meeting the platform's standard for ‘research-grade’ data—having an attached image, high-precision location data, and species identity confirmed by at least two contributors, with no contradicting identifications. We used the images attached to each record to validate species identity and to annotate phenophase in iNaturalist's internal annotation system. We used code modified from the `rinat` package (Barve & Hart, 2022) to download phenophase-annotated records through the iNaturalist API. (A prior study of *Yucca* by Barve et al. (2020) similarly draws on iNaturalist, but we developed our own protocol to obtain records from a longer time frame and use annotation tools built into the platform.) We binned records by year and binary evidence of flowering—whether they showed no evidence of flowering, or else buds, flowers, or fruits—and aggregated records to the 4 km-square grid of the PRISM database of spatially interpolated weather records (PRISM Climate Group, Oregon State University, 2014). To maximize confidence in our data, we restricted analysis to 2008, the year iNaturalist launched, through 2022, the last full year available at the time of analysis.

Joshua trees flower in February through April; across the Mojave, most precipitation arrives during winter, though summer monsoons contribute more in the east. We defined a 'growing year' from April of 1 year through March of the next. Because we expected that Joshua trees flower in response to year-over-year variation in precipitation, as seen in other masting desert perennials (Meyer & Pendleton, 2015), we compiled candidate predictors from the PRISM database covering 2 years prior to observed flowering (Table S1): specifically, total precipitation in the growing year leading up to observation (Y0), 1 year prior (Y1), and 2 years prior (Y2), as well as maximum and minimum temperatures and vapour pressure deficit (VPD) in the growing year before observation (Y0). We also considered year-over-year differences in total precipitation over 2 years (Y0–Y1 and Y1–Y2), and contrasts in temperature and VPD over 1 year (Y0–Y1).

Predictor selection and model training

We modelled flowering as a binary, whether or not evidence of flowering (buds, flowers, or fruit) was recorded in a given year and location (e.g. as in Figure 1f). To model relationships between weather and flowering, we used Bayesian additive regression tree methods (BARTs; Chipman et al., 2010). BARTs are a classification and regression tree machine learning method with powerful capabilities for ecological data analysis, particularly dealing with potential confounding from sampling heterogeneity (Carlson, 2020; Carlson et al., 2022; Dorie, 2023; Tan & Roy, 2019; Figure 1e). BARTs perform comparably to similar algorithms like boosted regression trees, but make uncertainty more explicit in model estimation (Becker et al., 2022).

We selected predictors, trained BART models, and analysed results using methods in the `dbarts` (Dorie, 2023) and `embarcadero` (Carlson, 2020) packages for R (R Core Team, 2022). We selected predictors by training models of varying complexity (summing across 10, 20, 50, 100, 150, or 200 trees) and tracking the frequency with which simpler models dropped each candidate predictor. Predictors more likely to be included in the simplest models have greater predictive power, and we retained these for final model training (Chipman et al., 2010). We also used a stepwise BART model training utility implemented in `embarcadero`, which compares model fit while systematically removing predictors.

We trained a model using the most informative predictors, and then examined the effects of inter-annual sampling heterogeneity using leave-one-out cross-validation by observation year. We also trained a random-intercept (RI) BART model using the same predictors as the original model, plus a RI effect of observation year, which formally controls for inter-annual heterogeneity in flowering prevalence. We tested the concordance of the RI model with the original model by comparing their predictions for 2008–2022 across the full species range. Finally, to examine differences between *Y. brevifolia* and *Y. jaegeriana*, we used their well described geographic distributions to assign records to species (none were in the hybrid zone; Esque et al., 2023; Godsoe et al., 2009) and trained single-species models with the divided data.

Hindcasting flowering activity

To hindcast flowering, we used a trained BART model to predict flowering from PRISM records going back to 1895 (PRISM Climate Group, Oregon State University, 2014). We classified hindcast probabilities as predicting flowering or no flowering using a cutoff identified in model training to minimize false-positives and maximize true-positives (supplementary methods, Figure S2; Carlson, 2020). We summarized hindcast probabilities of flowering and predicted flowering years over 1900 to 2022 by masking prediction layers to a high-resolution map of Joshua tree habitat (Esque et al. (2023); Figure 1f). We examined trends within 4 km-square grid cells in the species' ranges by estimating correlations between the hindcast probability of flowering and the year for each cell, and by comparing the number of predicted flowering years over the first three decades of the 20th century (1900–1929) and the most recent three decades (1990–2019). To visualize drivers of changes in flowering from 1900–1929 to 1990–2019, we compared mean predictor values and predicted flowering years in each period, for each cell.

Validation with historical records of flowering

To validate hindcast predictions, we compared them to records of flowering in times and locations beyond the coverage of the iNaturalist database, back as far as 1913. These records represent substantially different search efforts than iNaturalist observations, but they provide independent points of comparison to our hindcast.

We compiled 357 formal records, which included specific dates of observation and geographic coordinates, from field notes by two coauthors (CIS and RY), study site descriptions from published research (St. Clair & Hoines, 2018), herbarium records (California Consortium of Herbaria, 2024; Texas and Oklahoma Regional Consortium of Herbaria, 2024), and the USA National Phenology Network Database (USA-NPN; USA National Phenology Network, 2024; Figure S6; more detail in Supplemental methods: Formal validation records). We compared our hindcast predictions with these formal records by, first, determining whether the hindcast predicted a significantly higher probability of flowering in years and locations where the formal records indicated flowering, compared with years and locations where they indicated no flowering. Second, we calculated AUC (the area-under-the-curve statistic, reflecting the frequency of correct classifications) for model predictions in years and locations represented by the formal records.

We also compared hindcast predictions with informal records in historical newspaper accounts of Joshua tree flowering obtained from the ProQuest digitized news database (proquest.com; search for "'Joshua tree" AND (flower* OR bloom*)'). These reports did not provide geographic coordinates but let us identify boundaries for described locales. In total, we found 22 accounts describing flowering as intensive or poor (17 intensive, 5 poor; supplementary methods, Table S2). We compared the hindcast with each newspaper account by averaging the hindcast probability of flowering for the year of the account within the bounding polygon for the locale described in the account (Table S2).

RESULTS

Crowdsourcing yields thousands of high-quality flowering records

We validated and annotated 10,212 iNaturalist records for Joshua trees from 2008 to 2022 (Figure 1e). Binning records by year and aggregating them to the 4 km-square grid of PRISM data yielded 2632 records (Figure 1f). The spatial and temporal distribution of these data reflect the iNaturalist contributor community as well as Joshua trees' ecology. Sampling density increased by orders of magnitude with participation in iNaturalist, from 26 records in 2008 to 2644 in 2021 (Figure 1e, narrow bars), though the prevalence of flowering did not significantly change over time (Figure 1e, wide grey bars; product–moment correlation between year and proportion of records indicating flowering=0.03, $p=0.83$). Observations were at the highest density in and around Joshua Tree National Park, less common in wilderness areas in western Arizona, and absent from a region occupied by restricted U.S. Air Force and Department of Energy facilities west of Las Vegas (Figure 1f). As a consequence, more records are from the range of the western Joshua tree (1460 gridded records for *Y. brevifolia* vs. 1172 for *Y. jaegeriana*).

Climate triggers predict flowering activity

Predictor selection and stepwise model training identified six predictors as most informative for differentiating the presence and absence of flowering in our training data: Y1–Y2 and Y0–Y1 contrasts in precipitation (Δ_{Y1-2}PPT and Δ_{Y0-1}PPT), maximum VPD in Y0 (MaxVPD$_{Y0}$), Y0–Y1 contrast in minimum VPD (Δ_{Y0-1}MinVPD), minimum temperature in Y0 (MinTemp$_{Y0}$), and Y0–Y1 contrast in maximum temperature (Δ_{Y0-1}MaxTemp; Figure 2a). A model trained on the 2008–2022 flowering records with these six predictors had high performance based on a fully randomized out-of-bag draw (AUC=0.84).

To explore the impacts of inter-annual heterogeneity in sampling (Figure 1e, coloured bars), we performed leave-one-out cross-validation by observation year; across 15 years in our dataset, the model was moderately successful at predicting observations in the left-out year (mean AUC ± SE = 0.60 ± 0.05 across all 15 observation years). To formally control for inter-annual heterogeneity in observations, we trained a second model with observation year included as a RI effect (Carlson et al., 2022; Dorie, 2023). This RI model had AUC=0.80, and AUC=0.59 ± 0.04 in leave-one-out cross-validation. Compared across the species' range, predicted probabilities of flowering from the original model and the RI model were overwhelmingly positively correlated in every year of observation (minimum Spearman's rho=0.66, median 0.91; $p<10^{-6}$ in all years). The two models agreed in 84% of classified predictions ($\chi^2_{df=1} = 18{,}226$, $p<10^{-6}$), with the original model predicting flowering when the RI model did not in 12% of predictions, and the RI model predicting flowering when the base model did not in 4%. Moreover, RI estimates from the RI model show no trend in parallel with increasing sampling density (Figure S4), consistent with the lack of a trend in the prevalence of flowering (Figure 1e, grey bars). These results indicate there is no systematic bias created by the greater number of iNaturalist contributions in more recent years. Finally, models separately trained on records from the ranges of each Joshua tree species produced results in alignment with the original two-species model (SI, Supplemental methods). Thus, we used the original model trained on data from both species' ranges, without the RI effect, for all subsequent analyses.

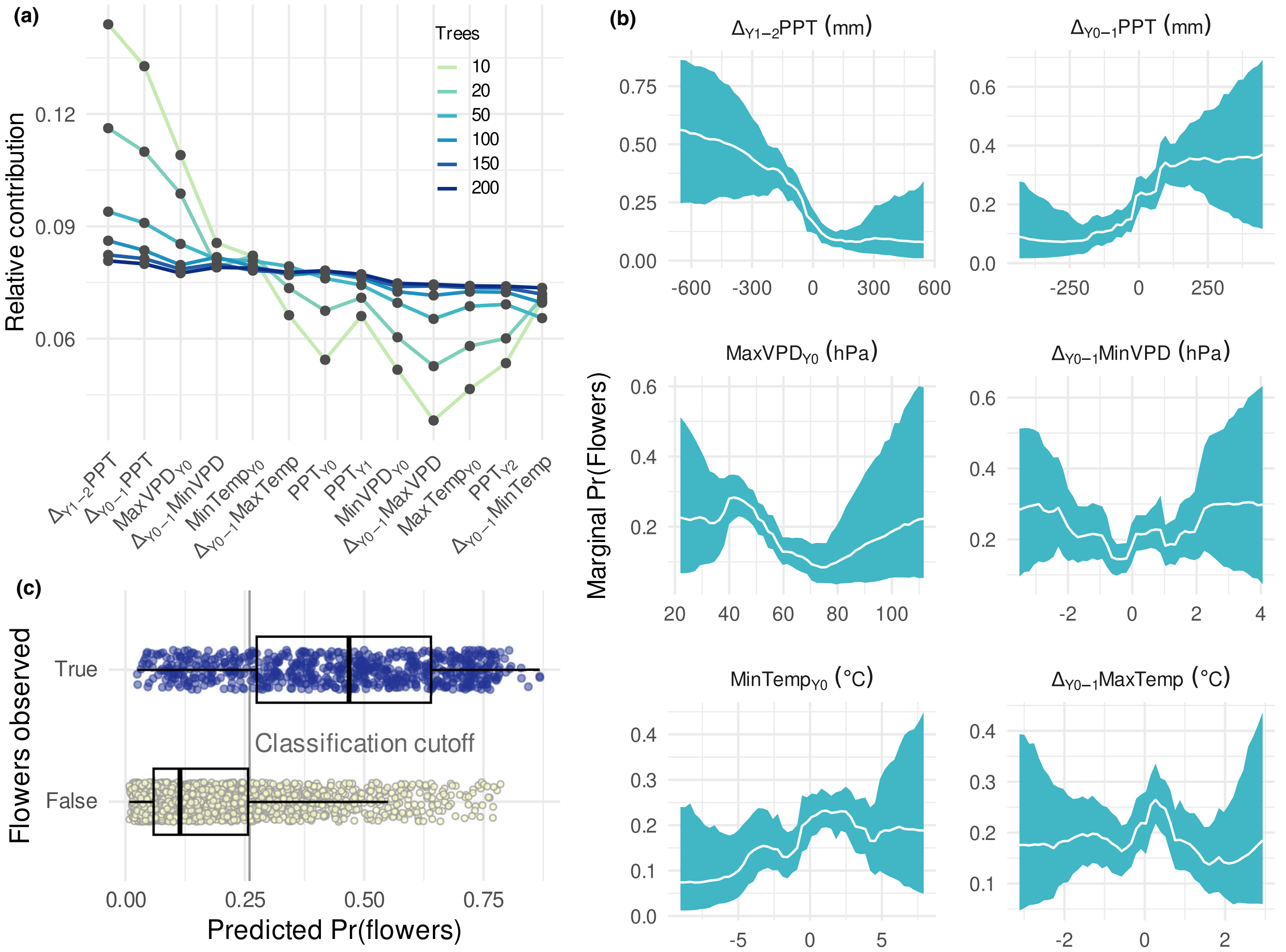

FIGURE 2 BART predictor selection, estimated predictor effects, and model accuracy. (a) Relative contributions of candidate predictors in models with decreasing complexity (regression tree count) identify the six left-most predictors as meaningfully predicting flowering activity (Carlson et al., 2022). (b) Partial effects of the top six environmental predictors in the final trained model (white line, median; shaded area 95% density interval across trees). (c) Modelled probability of flowering versus observed flowering in the full training dataset (AUC = 0.84) vertical line marks the classification cutoff with best discrimination (SI, Supplemental methods; Figure S1), box-and-whisker plots give median (centre bar), 25th and 75th percentile (lower and upper hinges) and smallest and largest values within 1.5 × the interquartile range of the median (whiskers) for predicted Pr(flowers).

Predictor effects match biological expectations

Our model finds flowering is more likely when the year leading up to flowering (Y0) is wetter than the previous year (Y1), and when that previous year was drier than 2 years prior to flowering (Y2; Figure 2b, Δ_{Y0-1}PPT and Δ_{Y1-2}PPT, respectively); this is consistent with masting in response to a year-over-year increase in precipitation. The model also finds flowering is more likely when maximum VPD is lower in the year leading up to flowering, and when minimum VPD has been relatively stable since the prior year (Figure 2b, MaxVPD$_{Y0}$ and Δ_{Y0-1}MinVPD), consistent with lower drought stress leading up to flowering. Finally, flowering is more likely when the minimum temperature in the year leading up to flowering is above freezing, and when the maximum temperature has been relatively stable since the prior year (Figure 2b, MinTemp$_{Y0}$ and Δ_{Y0-1}MaxTemp). This aligns with observations suggesting Joshua trees flower more intensively in historically warmer locations (St. Clair & Hoines, 2018), and that their distribution is limited by winter low temperatures (Dole et al., 2003; Rowlands, 1978), though it contradicts speculation that freezing triggers flowering (Brenskelle et al., 2021; Rodgers, 2023). Spatial projection of predictors' partial effects in individual years further illuminates these interpretations. In 2019, 58% of all records indicate flowering, and year-over-year precipitation contrasts contribute strongly to flowering (Figures 1e, 3a,b). In the following year, 2020, just 7% of records indicate flowering, and the same precipitation contrasts make much weaker contributions (Figures 1e, 3c,d). This pattern holds across all years of observation (Figures S9–S23).

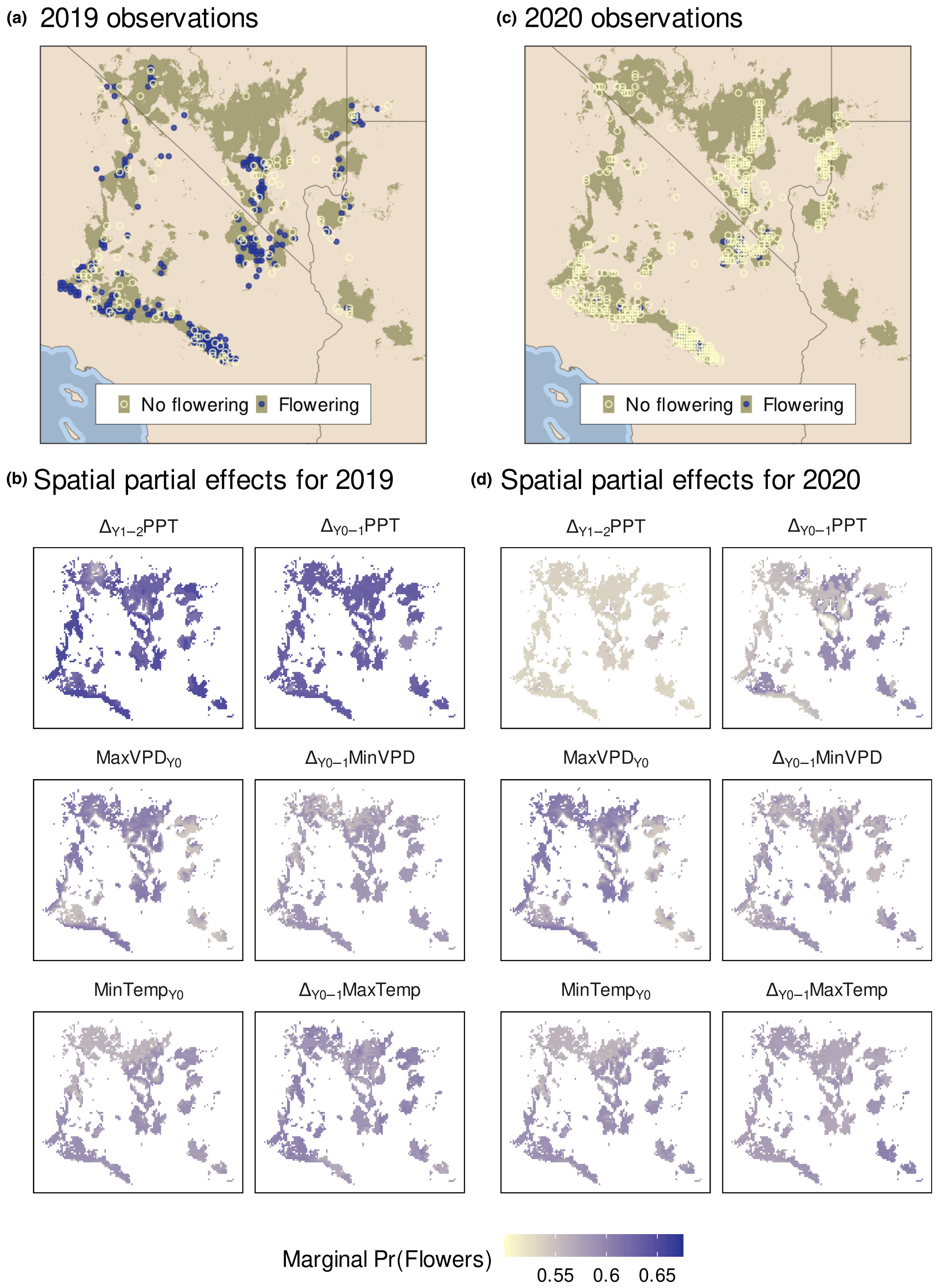

FIGURE 3 Spatial partial predictor effects in the trained model reflect flowering frequency in individual years of observation. (a) Training data for 2019, a year in which 67% of records indicate flowering. (b) Spatial partial effects of the six predictors in the final trained model, for conditions in 2019. (c) Training data for 2020 when 6% of records indicate flowering. (d) Spatial partial effects of predictors for conditions in 2020. Panels in b and d present values in a 4 km grid masked to the species distribution polygon in a and c. Figure S6. summarizes values for each predictor in each year of observation; Figures S7–S21 give training observations and spatial partial predictor effects for all observation years.

Hindcast flowering aligns with historical records

To reconstruct Joshua tree flowering since the early 20th Century, we used our working model to predict flowering from historical weather records (PRISM Climate Group, Oregon State University, 2014). Across the species' ranges (Figure 1f), the hindcast predicts a median of 30 flowering years from 1900 to 2022 (95% density from 5 to 57 flowering years), approximately once every 4 years. The hindcast generally matched observations of flowering in formal validation records dating back to 1913, which we assembled from field notes, the published literature (St. Clair & Hoines, 2018), herbarium records (California Consortium of Herbaria, 2024; Texas and Oklahoma Regional Consortium of Herbaria, 2024), and the USA-NPN database (USA National Phenology Network, 2024), as well as informal records from newspaper accounts (Figure 4; Supplemental methods, Table S2). The hindcast predicted a significantly higher probability of flowering in places and years when formal validation records indicated flowering (Figure 4b; two-sample *t*-test with $df=79.0$, $p<10^{-5}$), and had AUC = 0.70 when classifying them using the best discrimination cutoff identified in model training (Supplemental methods). The hindcast probability of flowering was also significantly higher in years and locales corresponding to 17 newspaper accounts of intense flowering, compared with 5 accounts of poor flowering, dating back to 1924 (Figure 4c; Table S2; *t*-test with $df=15.9$, $p<10^{-3}$).

Hindcasting reveals trends in flowering

Our hindcast reflects changes in climate from 1900 to 2022 and thereby suggests how this change impacted Joshua tree flowering. We first examined trends in flowering within grid cells in the species' ranges by estimating correlations between year and hindcast probability of flowering for each cell. The median correlation (Spearman's ρ) between year and hindcast probability of flowering was 0.05 (95% density −0.05 to 0.17), with a positive trend ($\rho>0$) in 80% of cells. Overall, this is consistent with a rising predicted probability of flowering since the year 1900. We then compared the number of flowering years predicted in 1900–1929 and 1990–2019. Across the species' range, the hindcast predicted a mean of 1.6 more flowering years in 1990–2019 compared with 1900–1929 (median of 2 more years; 95% density from 3 fewer to 6 more; Figure 5b). The median frequency of flowering in the early period was about once every 5 years, rising to more than once every 4 years in the recent period.

This increase in predicted flowering arises from changes in the climate triggers identified by our BART modelling. Compared with 1900–1929, the period of 1990–2019 saw greater year-over-year precipitation and VPD differences, as well as warming minimum temperatures (Figure 5c); increased flowering frequency follows from the partial effects of these predictors (Figure 2c; Figure 3). Regions showing increased flowering also show rising maximum VPD, consistent with increasing aridity

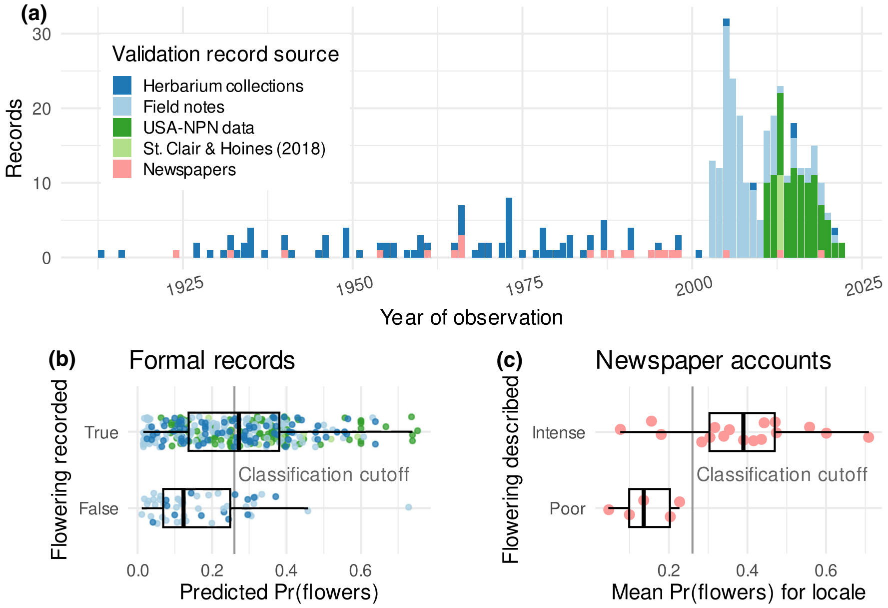

FIGURE 4 Formal and informal independent validation records align with hindcast predictions. (a) Validation records by source and year of observation. (b) Formal validation records (from herbaria, field notes, USA-NPN data, and St. Clair and Hoines (2018)) grouped by whether they recorded flowers in a given location and year, versus predicted probability of flowering from the base model hindcast for that location and year. (c) Informal records (from newspaper accounts) grouped by the quality of flowering described, versus predicted probability of flowering from the base model hindcast for the year of publication, averaged over the locale described (Supplemental methods, Table S2). Point colours in (b) and (c) follow coding in (a); classification cutoff and boxplot parameters as in Figure 2c.

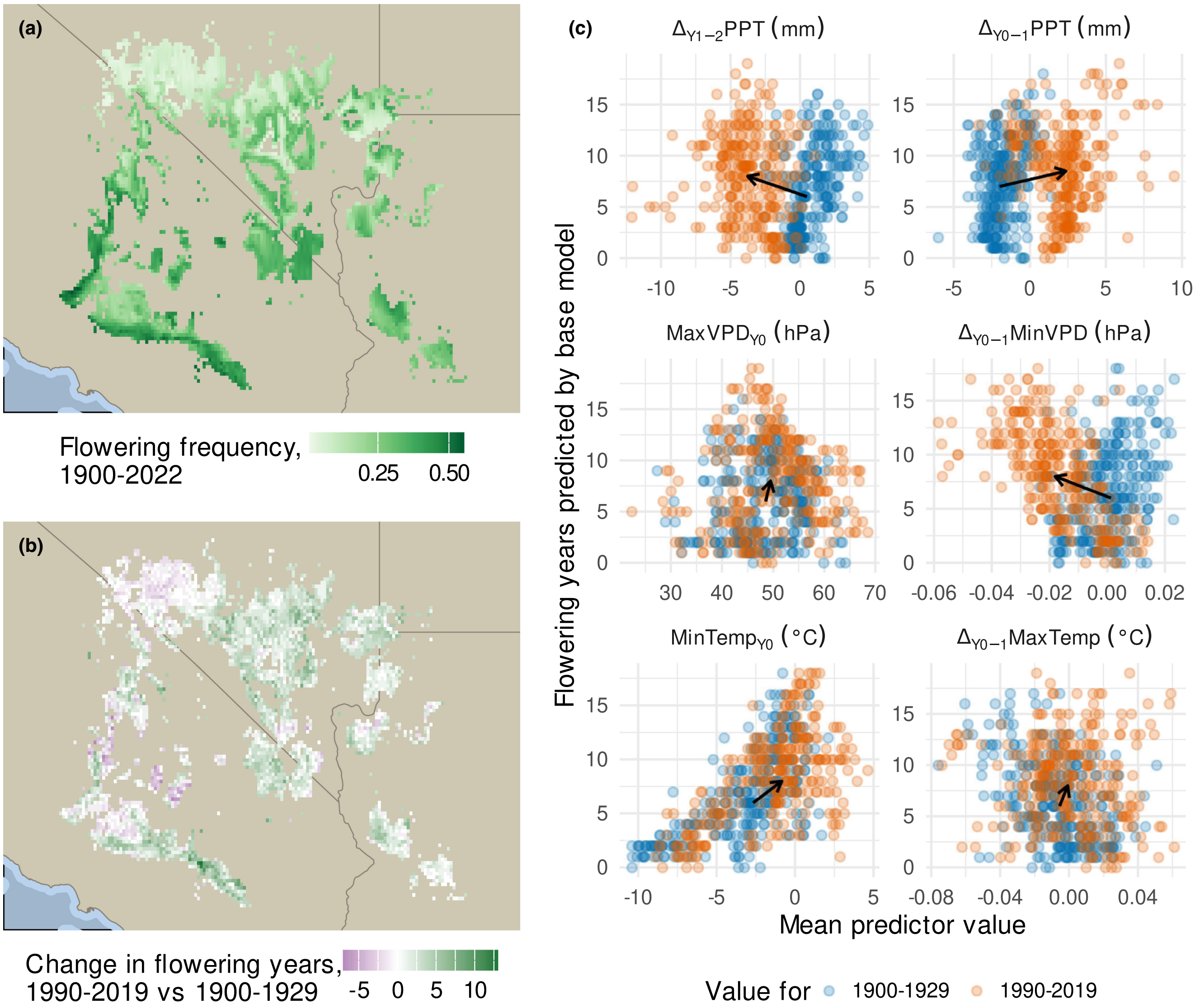

FIGURE 5 Hindcast frequency of flowering years reflects climate change since 1900. (a) Frequency of hindcast flowering years predicted over the full 1900 to 2022 study period, for 4 km-square grid cells masked to the species distribution polygon in Figure 1f. (b) Difference in flowering year frequency, 1990–2019 compared with 1900–1929, predicted by the base model. Positive values (green shading) indicate more predicted flowering years in the recent period. (c) Mean values for the six predictor variables versus flowering years predicted by the base model in 300 randomly drawn grid cells, over the period 1900–1920 (blue points) or 1990–2019 (orange points), with arrows linking the median values for the earlier period to median values for the recent period to indicate direction and magnitude of change. Compare to predictor partial effects in Figure 2b.

(Figure 5c), and this pattern is less obviously derived from the partial effect of maximum VPD (Figure 2c). It may instead reflect the correlation of VPD variation with precipitation and temperature drivers of increased flowering. The magnitude of change in maximum VPD between the two time periods is much smaller than the change in other predictors, but it does mean populations where we find greater increases in flowering face greater drought stress.

Predicted changes in flowering frequency varied with elevation and latitude, but were not necessarily as expected. Higher elevation and more northerly regions are a priori climate refugia, where Joshua trees may have more resources for reproduction (Morelli et al., 2016), but elevation and latitude have complex interactions with climate in the topography of the Mojave: prospective refugia for Joshua trees have been identified at high elevations in Joshua Tree National Park, near the species' southern range limit (Sweet et al., 2019). The hindcast does predict greater increases in flowering frequency at a higher elevation, but the correlation is not statistically significant (product–moment correlation = 0.02, $p = 0.14$). Meanwhile, change in predicted flowering years is significantly negatively correlated with latitude (cor = −0.08, $p < 10^{-6}$). This appears to be driven by stability or a slight decline of flowering frequency in the northwestern Mojave, and strongly increased flowering frequency in high-elevation sites in the southwest (Figure 5b). These trends may be consistent with increased flowering driven by warmer winter temperatures in historically cooler, wetter regions (Figures 2b, 5a) while flowering is stable or decreasing in historically drier regions that already see lower flowering frequency (Figure 5a).

DISCUSSION

Climate change impacts on global ecosystems are already pervasive, but quantifying those impacts remains challenging for many species. We applied readily available crowdsourced data to describe how 20th century climate trends have shaped reproductive activity by keystone species of the Mojave Desert. Our BART models trained on crowdsourced records of Joshua tree flowering identify biologically realistic climate drivers of flowering (Figure 1a,b), and our working model can then hindcast flowering activity to reconstruct long-term trends and recover flowering events in independent historical records (Figure 4). The hindcast suggests flowering has become somewhat more frequent since 1900, but this trend varies geographically, with decreased flowering in some putative climate change refugia (Figure 5). Our analyses provide new insight into Joshua tree population health, a major source of uncertainty in recent assessments of the species for endangered species protection (U.S. Fish and Wildlife Service, 2023). They also demonstrate the potential of crowdsourced data for examining population processes over wide geographic regions.

Joshua tree population status in changing climate

Our analyses identify drivers of Joshua tree masting, revealing how climate trends over the last century may have impacted Joshua tree populations. However, flowering is only one component of the populations' demographic health. Germination, seedling survival, and growth may not respond to the same climatic drivers as flowering, or may not respond in the same way. Our hindcast finds flowering frequency has likely increased as a result of growing inter-annual variability in precipitation and temperature (Figure 5c), and these trends may threaten survival and growth even as they boost flowering. Joshua tree seedling survival is highly sensitive to annual precipitation and must overcome heavy herbivory (Esque et al., 2015; Reynolds et al., 2012). Herbivory is even worse in drought years when Joshua trees provide a browse of last resort (DeFalco et al., 2010; Esque et al., 2015). Although range-wide data are lacking, there is reduced seedling recruitment in warmer, drier microclimates within Joshua Tree National Park, consistent with the expected effects of warming (Barrows & Murphy-Mariscal, 2012; Sweet et al., 2019).

Joshua trees' reliance on specialized *Yucca* moth pollinators may present another way in which more frequent flowering could fail to translate into greater recruitment (Godsoe et al., 2008; Pellmyr & Segraves, 2003). Yucca moths' responses to climate variation are largely unknown. Short-term studies suggest the moths are less active in cooler, high-elevation climates (Harrower & Gilbert, 2018; Rowlands, 1978), and if this is borne out, increased Joshua tree flowering in high-elevation climate refugia may often prove fruitless. To the extent flowering is part of population viability, our analyses can help identify emergent climate refugia for Joshua trees—but viability assessment must consider all aspects of Joshua trees' biology.

Masting dynamics and climate change

Joshua trees have multiple features associated with masting reproductive strategy, facing wide annual variation in resource availability (Figure S1) and substantial seed predation (Kelly & Sork, 2002; Meyer & Pendleton, 2015). Synchronized flowering may satiate not only seed-caching rodents, which are Joshua trees' primary means of seed dispersal (Waitman et al., 2012), but also the seed-feeding, brood-pollinating *Yucca* moths that are their sole pollinators (Pellmyr & Segraves, 2003). Masting more effectively satiates invertebrate seed predators than vertebrates (Zwolak et al., 2022), and Joshua trees flowers, fruits, and seeds are a food source for numerous insects beyond their pollinators (Smith et al., 2011; Terrill et al., 2019).

We identify climate predictors of Joshua tree masting and trends driven by those predictors that echo studies of masting and reproductive effort in other long-lived plants. In blackbrush (*Coleogyne ramosissima*), masting is driven by precipitation in the year prior to the year of flowering (Meyer & Pendleton, 2015); we similarly find year-on-year contrasts in precipitation, rather than total precipitation, are the most informative predictors of Joshua tree flowering (Figures 2b, 3). We also find rising winter temperatures are associated with increasing frequency of Joshua tree flowering (Figure 5b). Saguaro cactus (*Carnegia gigantea*), beech (*Fagus sylvatica*), and multiple oaks (*Quercus* spp.) flower more intensively in warmer years, or show increasing frequency of masting with warming average temperatures (Caignard et al., 2017; Övergaard et al., 2007; Renzi et al., 2019; Shibata et al., 2020). Inter-annual variation in seed production is increasing globally, potentially consistent with greater variability in climate drivers of masting (Pearse et al., 2017).

Crowdsourcing observations of population processes

Our analyses are enabled by the availability of crowdsourced Joshua tree observations, which expand the geographic and temporal scope of previously published data. Crowdsourcing is increasingly recognized as a valuable source of biodiversity, ecology, and demography data (Brenskelle et al., 2021; Fink et al., 2023; Gaier & Resasco, 2023; Pernat et al., 2021; Tiago et al., 2017; Wilson et al., 2020). Coordinated projects such as the USA-NPN *Nature's Notebook* program have characterized advancing spring phenology (Crimmins & Crimmins, 2022; Fuccillo Battle et al., 2022); while the iNaturalist platform, from which we draw our data, dramatically expands occurrence records for many taxa without (necessarily) directing contributors' sampling (Di Cecco et al., 2021).

The broader geographic coverage enabled by crowdsourcing is a key advantage for our analysis. Our training data cover a longer period than the median time-series study of masting (Hacket-Pain et al., 2022), and their geographic scope is substantially broader. Studies of masting typically track many individuals at just one or a few locations over the study period; after aggregating iNaturalist records to the 4 km grid of weather data, we obtain more than 2600 location-year observations of flowering activity. For comparison, the USA-NPN records of Joshua tree flowering track phenophase in hundreds of trees at 16 unique locations over a 12-year period; these amount to 108 location-year observations in our modelling framework (not all locations are represented in all years; Figure 4a; USA National Phenology Network, 2024).

Crowdsourcing observations may introduce both obvious and subtle biases in the resulting data, but these can be addressed by careful validation and testing (Barve et al., 2020; Di Cecco et al., 2021; Fuccillo et al., 2015). Our data benefit from Joshua trees' visual distinctiveness and the high visibility of their flowers and fruits (Figure 1a–d). Prior assessments have found high accuracy in crowdsourced phenophase records for less distinctive taxa (Fuccillo et al., 2015), and we reviewed records for species identity and phenophase as a key part of data compilation. The temporal and spatial distribution of our data is shaped by the geographic distribution of iNaturalist contributors and growing participation in the platform (Figure 1e,f). However, prevalence of flowering has not changed over the 15-year period of our training data (Figure 1e), and a model including a RI effect of observation year does not find RI effects with a temporal trend (Figure S3). Further, our hindcast aligns with records of flowering from historical sources covering years and locations beyond those represented in iNaturalist (Figure 4; Figure S6).

Modelling species' dynamic responses to climate

Finally, our analyses are proof of concept for a new approach to modelling species' habitat requirements. Modelling species' habitats to project their distributions into times and places that cannot be directly observed is a mainstay of modern ecology, but most methods for such modelling address only presence or absence on the landscape, not population status (Elith & Leathwick, 2009; Merow, Dahlgren, et al., 2014). Incorporating measures of population growth into habitat modelling requires substantial effort (Merow et al., 2011; Merow, Latimer, et al., 2014; Merow, Smith, et al., 2014). However, many other plant taxa, especially long-lived perennials such as Joshua trees, have flowers and fruits that can be diagnosed from casually collected images. We find such data can identify biologically realistic climate drivers of reproductive activity, and reconstruct past reproductive events reported in independent records. Going forward, this approach may provide a richer view of populations' responses to global change.

AUTHOR CONTRIBUTIONS

JBY conceived and planned the project; JBY and AA annotated crowd-sourced observations; CIS and RY provided independent records of flowering; JBY, LAD, TCE, and DFS consulted on predictor selection, and JBY and CJC developed and conducted model training and analysis; JBY drafted the manuscript, and all authors reviewed, edited, and approved the final text.

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CONFLICT OF INTEREST STATEMENT

The authors state that they have no conflict of interest in the present work.

DATA AVAILABILITY STATEMENT

Code for acquisition and management of iNaturalist and PRISM data, model training, hindcasting, and all analysis is available on Dryad, DOI: https://doi.org/10.5061/dryad.9kd51c5rr.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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