**Title:** Caching in: Tree masting influences populations of a declining avian seed disperser

Caching in: The importance of time and place for species interactions

Caching in: The importance of time and place in shaping seed dispersal interactions

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# Conflict of Interest

The authors declare no conflicts of interest.

# Author Contributions

AM-tK, APW, and KCR conceived the ideas; AM-tK, KO, and JSS developed statistical methods; AM-tK and KCR developed novel data layers and ran statistical models; AM-tK led the writing of the manuscript with support from APW and KCR. All authors contributed to the drafts and gave final approval for publication.

# Data Availability

Data and code for this paper are available on Zenodo (get up there!)

# Abstract

1. [Big picture and gaps]
2. [Methods]
3. [Results]
4. [Synthesis]

# Keywords

seed production, interannual climate variability, mutualism, *Pinus edulis*, *Gymnorhinus cyanocephalus*, resource availability, species interactions

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**1 Introduction**

Species interactions, including predation, herbivory, competition, and mutualisms, shape the functioning of every ecosystem (Tylianakis et al., 2008). Mutualist relationships are particularly threatened by environmental change across the globe as the loss of one interaction partner often leads to the co-extinction or functional extinction of the other partner, accompanied by the loss of ecological functions associated with mutualist interactions (Bascompte et al., 2019; Donoso et al., 2020; Valiente‐Banuet et al., 2015). For example, the loss of large-bodied seed dispersers reduces forest carbon storage (Brodie et al., 2025), and the global pollinator decline is likely to influence not only crop production (Burkle et al., 2013; Reilly et al., 2024), but also the structure and diversity of plant communities (Artamendi et al., 2024; Potts et al., 2010). Importantly, many mutualist interactions have non-instantaneous effects since past population and community dynamics likely shape present and future outcomes for ecosystem functioning (Essl,). Thus, understanding the current rewiring of mutualist interactions requires examining the temporal dynamics of populations and communities and how these shape interaction strength (Figueriedo et al)

In addition to temporal legacies, mutualism interaction strength is shaped by context in time and space and can even change direction (e.g., becoming consumptive) across contexts (Chamberlain, King and Marshall). How interactions vary across context is influenced by variation in fitness, resource availability, and competition (Liu and Gains, Langendorf et al.). This variation may be especially important for interactions like seed dispersal, where mutualisms can switch to consumptive interactions depending on seed availability (Bogdziewicz et al., 2020, Moore & Dittel, 2020; Sawaya et al., 2018). In marginal conditions (i.e. fewer resources, lower fitness individuals), seed dispersers spend more time foraging on patches of more readily-available resources and less time exploring their environments (Charnov, Barnett et al. 2007). This could mean that if patches of seeds are available in marginal conditions, seed dispersers will rely more heavily on those seeds, increasing dependencies between seed dispersers and seeds. Simultaneously, in optimal conditions that likely support larger seed disperser populations sizes, higher intraspecific competition may lead to more generalist foraging of individuals, thus reducing the dependency between seed dispersers and seeds of any particular plant species (King and Marshall, Sheppard et al.). These patterns can be built on predictive frameworks like optimal foraging theory, thus providing a general way to understand why and when mutualist interactions change in magnitude and direction (Chamberlain, Moore and Dittel, King and Marshall).

All seed dispersal interactions are likely dynamic in strength and direction through space and time. This dynamism is likely heightened in systems where seed dispersers depend on unreliable resources, such as interactions with masting plant species. Masting plants are those which, at the population level, produce a synchronous and abundant seed crop in particular years, usually due to cyclical climatic suitability and mediated by how much plants rely on animal-mediated pollination and dispersal (Pearse et al., 2016; Qiu et al., 2023). Masting leads to unreliable resources for seed dispersers since seeds are available in abundance some years and virtually absent in other years. Thus, masting plant species often have weaker mutualist interactions overall (Kelly and Sork). Seed dispersers and predators that rely on masting species often have a variety of temporal responses to seed availability, including anticipatory (e.g., “predictive”; Boutin et al., Wauters et al.) and lagged (e.g., “response”; Hallworth et al. 2024). Due to the variable availability of seeds, masting seed eaters rely on a variety of food sources (McKinnon et al., 2017; Simon et al., 2023) and have evolved behaviors that optimize finding seeds in patchy landscapes (e.g., flocking behavior and large-scale population movements, or “irruptions”, (Strong, Slagsvold and Wiebe).

A notable example of a mutualism between a masting species and seed disperser is the relationship between the two-needle pinyon pine *(Pinus edulis*) and the pinyon jay (*Gymnorhinus cyanocephalus*) in the western United States. In this close mutualism, pinyon jayscache seeds as a food resource across the landscape, which, in turn, can help to promote new regeneration of pinyon pine (Floyd, 1982; Ligon, 1978; Wiggins, 2005). Pinyon jays have been declining over the last several decades, but the cause of their decline likely involves a complex and unknown set of drivers, which could include climate, habitat change, and food resource availability (Boone et al., 2018; Van Lanen et al., 2023). Concurrently, two-needle pinyon pine has faced recent large-scale mortality events with limited regeneration and reduced seed production of the surviving trees (Breshears et al., 2005; Meddens et al., 2015, Redmond et al., 2018, Shaw et al., 2005, Redmond et al., 2012; Wion et al., 2025). This system is not unique – masting systems globally face changes in climate that shape masting dynamics that will likely alter seed dispersal interactions (Hacket-Pain and Bogdogowotiz 2021).

In this study, we look at the relationship between pinyon jay and two-needle pinyon pine across over a decade and the full range of two-needle pinyon (~55% of the range of pinyon jays; Figure X). This region has a wide range of baseline habitat suitability, and this decade had a wide range of climatic conditions (Boone et al., 2018; Van Lanen et al., 2023). We explicitly model the temporal dynamics of this mutualism; specifically, using a stochastic antecedent model to examine how populations of a seed disperser respond to resource availability and climate in time (Ogle et al. 2015). Importantly, these models simultaneously estimate anticipatory and lagged (e.g., “predictive” and “response”) effects and give each a relative contribution to overall patterns, thus allowing multiple hypothesized relationships to simultaneously hold (Zylstra). We leveraged 13 years (2010-2022) of eBird data on pinyon jay abundance spanning a large portion of its population range (Sullivan et al., 2009) and predicted pinyon pine seed availability for the same region (Southwest USA; Wion et al. 2025). Specifically, we address two key questions: 1) what are the relative contributions of anticipatory (“predictive”) and lagged (both “immediate” and “delayed response”) relationships between pinyon jay abundance and pinyon pine cone availability, and 2) how does the seed disperser relationship between pinyon jays and pinyon pine vary across a range of high to low quality habitat and climate conditions? Addressing these questions is not only crucial for conservation in this system but also builds a general framework for evaluating the temporal signals and context dependence of species interactions more broadly (Belitz et al., 2025).

# 2 Materials and Methods

### 2.1 Study region

Pinyon jays occur across the western US (California, Nevada, Utah, Arizona, Colorado, New Mexico, Idaho) (cite). In this study, we focused on the intermountain and southwest regions of the US where broad-scale information on two-needle pinyon cone production (as a proxy for seed production, referred to throughout as “pinyon”) was available (Wion et al., 2025). It is likely that pinyon jays rely on other species of pinyon pine (e.g., *P. cembroides, P. monophyla*) and other seed-producing species (e.g., oaks, *P. ponderosa*) for food and habitat across their range, but these tree species lack wide-scale estimates of seed production. This region represents ~55% of the total population range for pinyon jays and ranges in [elevation, other variables here?].

*2.2 Conceptualizing temporal relationships between pinyon pine and pinyon jays*

Previous studies have suggested that pinyon jays may “predict” cone availability as they see cones maturing (Ligon, 1978); while other work has documented birds nesting near cache sites from the previous year (Stotz & Balda, 1995). In addition, pinyon jays have delayed maturity, where individuals enter the breeding population several years after fledging (Marzluff and Balda 1988), meaning that pinyon seed resource pulses may have delayed effects on bird abundance. Thus, we developed our model with a temporal component that simultaneously incorporated three hypothesized temporal relationships between birds and cones: 1) “predictive” (anticipatory), 2) immediate “response” (birds spend time near cache sites from last year), and 3) “delayed response” (delayed population responses). Importantly, in our model, the relative importance of each of these hypotheses can be simultaneously evaluated (Tredinick, Zylstra). These predicted temporal relationships between pinyon jays and pinyon cone production can be found in Figure 1.

### 2.2 Data sources

We compiled data for birds and covariates from a variety of sources. Bird data came from eBird (Sullivan et al., 2009, more in Section 2.2.1 below). We used modeled cone hindcast estimates from a previous study (Wion et al. 2025, Section 2.2.2 below). Finally, to examine mediating effects of habitat and climate on jay-cone relationships, we compiled two variables describing habitat quality: pinyon basal area and North American Monsoon contributions (Branson 2008, Munson, Maurer); and two variables describing climate suitability (seasonal maximum temperature and precipitation; (Ligon, 1978; McDermott & DeGroote, 2016; Skagen & Adams, 2012; Stotz & Balda, 1995), Section 2.2.3).

*2.2.1 Bird abundance from eBird*

To estimate pinyon jay abundance in relation to seed abundance, we used data from eBird (Sullivan et al., 2009) from the four states of interest (Arizona, Colorado, New Mexico, and Utah). We chose to use eBird data because it has broad spatial and temporal coverage within the region of interest and equivalent spatial scale to link bird abundance and our climate covariates (4 km × 4 km grid cells). We downloaded all checklists and kept years with good checklist coverage for the region (2010-2022). We filtered checklists to areas supporting pinyon pine cover in the 2000s (see below in Section 2.2.3; Wilson et al., 2013).

eBird is participatory (“citizen” or “community”) science data, meaning that members from the public collect bird observation data and contribute to the eBird database. Thus, these data require filtering to ensure spatial and temporal consistency. We followed filtering methods suggested by the eBird database curators and similar studies (Robinson et al., 2018; Strimas-Mackey et al., 2023). Specifically, we selected data that represented only complete checklists (e.g., observers recorded all birds of all species observed, not just individuals of species of interest). We selected checklists from the nesting season (late February to early May; (Wiggins, 2005)) and included only observations from “stationary” and “traveling” protocols. We considered only the nesting season because this is a time of year during which birds are more stationary, so drivers of local bird abundance are easier to evaluate (Ligon, 1978; Wiggins, 2005). We also only included checklists with relatively similar effort: 1) collected in under five hours, 2) 0-5 km in distance, and 3) with ten or fewer observers.

Because of its participatory nature, eBird data has no control for sampling location, effort, or survey methods, so we also performed data subsampling steps following standard practices (Robinson et al., 2018). To do this, we first divided the study region into 4 km × 4 km grid cells to match the spatial scale of the covariates. We spatially sub-sampled eBird observations to include a set of checklists in each grid cell that represented relatively equal sampling effort across time and space. This meant we subsampled the number of checklists per grid cell based on the year with the fewest checklists per grid cell (2010; 4 checklists per cell). After filtering to this level, we still had fewer checklists overall in early years. Thus, we further reduced temporal bias by randomly subsampling checklists again so that we had equal sample sizes across years based on the year with the fewest checklists (*n* = 1,715 checklists in 2010). We then removed all checklists within 10 km of the exterior edges of the four states for which we had data (Arizona, Colorado, New Mexico, and Utah) since we had masked some other covariate layers to these states and observations near edges may have misrepresented values for pinyon basal area and cone production (see Sections 2.2.2 and 2.2.3). Of 833,834 checklists for the region in the nesting seasons between 2010-2022, we ran our model using data from 22,295 checklists (mean of 1.4 ± 0.01 s.e. checklists per grid cell in a specific year). We downloaded eBird data in May (Colorado and New Mexico) and June (Arizona and Utah) 2024 (Cornell Lab of Ornithology, 2024a, 2024b). In our final dataset, pinyon jays were observed in 600 checklists (2.7%). The maximum number of birds observed in one checklist was 350 (mean number of birds 0.42 ± 0.04 s.e.).

*2.2.2 Pinyon cone data*

For cone abundance data, we used annual cone production estimates for two-needle pinyon produced at a 4km x 4km gridded resolution by Wion et al (2025). More detailed methods on how cone availability was modeled are described in the original publication. While this model predicts cone availability, not seeds, the two are highly correlated in co-occurring pine species (e.g., *P. ponderosa* (Shepperd et al., 2006)). We used the cone production dataset both as a direct measure of pinyon seed availability and a proxy for the availability of other seeds eaten by pinyon jay (e.g., acorns, juniper berries) that respond to similar climate signals as pinyon pine, but with different temporal signals. Specifically, oaks and junipers produce seed one year after a good climate year; pinyon pine two years after (Parmenter et al., 2018).

*2.2.3 Habitat and climate covariates*

As an indicator of habitat structure, and to filter eBird observations to areas with pinyon pine, we derived yearly basal area of two-needle pinyon from 2010 to 2022 by combining basal area (BA) maps for this species from 2000-2009 (Wilson et al. 2013) and annual maps of tree cover from the Rangelands Analysis Platform (RAP, v.3.0) (Allred et al., 2021). We used the RAP canopy cover maps to annualize pinyon BA maps, and to project them forward in time using several steps. First, we aggregated RAP canopy cover for each year from a 30-m to a 250-m resolution (using the mean value) to align with the BA maps. Next, for each 250-m pixel, we divided pinyon basal area by percent canopy cover in that same location (i.e., the mean canopy cover from 2000 to 2009) to calculate the amount of pinyon BA represented by each unit of canopy cover (i.e., an expansion factor). Finally, we used these pixel-specific expansion factors and differences between 2000-2009 cover and the cover of a focal year (e.g., 2010) to adjust pinyon BA up or down in each pixel and year from 2010 to 2022 based on remotely sensed estimates of canopy cover. This approach allowed for both increases or decreases in pinyon BA during our study period based on patterns of ingrowth or mortality, respectively, and qualitatively aligned with patterns of forest change in different locations throughout the Southwest. For this study, we aggregated these 250-m grids to a 4-km resolution to align with other covariates.

As another habitat covariate, we calculated the percentage contribution of the North American monsoon to the region using 30-year 4km x 4km gridded monthly data from PRISM (CITE PRISM). Monsoon moisture is critical to dryland ecosystem productivity (Munson et al., Maurer et al. ) and can increase invertebrate abundance (pinyon jays rely on invertebrates during the nesting season, Ligon 1978, Branson 2008). We calculated the percentage of the 30-year monthly normal precipitation in each 4 x 4 km pixel falling in the months of July-September (i.e., the North American monsoon, referred to as “monsoonality” (Adams & Comrie, 1997)). Monsoonality values do not change over time for a pixel.

As climate covariates, we also extracted gridded monthly PRISM climate data for maximum temperature and precipitation, which are both relevant to jay biology (physiology and relative food availability) (Ligon, 1978; McDermott & DeGroote, 2016; Skagen & Adams, 2012; Stotz & Balda, 1995). Climate variables change through time for a given pixel and we combined monthly values into seasonal variables based on important periods in the pinyon jay life cycle (Wiggins, 2005). These included: 1) breeding season, 2) fledgling season (adults are caring for young), 3) early summer (bird behavior unknown), and 4) late summer through winter (caching seeds, potentially irrupting in search of seeds) (Wiggins 2005).

### 2.3 Modeling relationships between cones and birds

To explore relationships between pinyon jay abundance, pinyon cone production, and other covariates related to seed availability, habitat, and climate, we used an N-mixture model that included an observation process model for the pinyon jay survey (eBird) data and a biological process model that estimates latent jay “abundance” values (Royle, 2004). The observation process model includes covariates that describe variation in detection probabilities (e.g., survey conditions). The biological process model includes a likelihood that describes the biological drivers of latent pinyon jay abundance and includes the primary covariates of interest. Because were interested in temporal relationships between jay abundance and important covariates (e.g., cones, climate), we incorporated a stochastic antecedent model structure in the biological process model (Ogle et al., 2015). Specifically, we incorporated “predictive” (anticipatory) and “response” (both immediate and delayed) yearly time periods for cone availability. We also included lagged seasonal climate effects.

Replicate surveys within a closed time and location are required for successfully implementing N-mixture models which account for detection error (Royle et al., 2005). To use unstructured or semi-structured eBird data in this way (e.g., as a space-for-time substitution), checklists must represent locations across the range of potential covariate values (e.g., are not biased toward certain values of covariates of interest, (Hochachka et al., 2023)). We verified that checklists within our filtered dataset (see Section 2.2.1) met this assumption by comparing values for all covariates at locations with checklists to all gridded data available for those covariates (described more in Section 2.2.2 and 2.2.3).

### 2.3.1 Observation process model for pinyon jay abundance

In our model, observed count data from eBird checklists were used to estimate a “true” latent abundance, , that varies across space and time. eBird checklists are recorded with a geographical point location and often include information about travel distance of the observer (< 5km in our dataset after filtering). Thus, there is spatial uncertainty arising from two sources: 1) uncertainty in the location in which the survey was conducted (e.g., was the location recorded at the beginning, middle, or end of a survey and at what level of precision) and 2) uncertainty in the location along a survey at which pinyon jays were observed (e.g., it is unknown if birds were observed at the beginning, middle, or end of a walking survey). To account for this spatial uncertainty, we created circular buffers around each eBird checklist location based on the sampling distance for that checklist; this is, we defined the radius of the buffer circle as 1/2 of distance traveled for “traveling” checklists, or 0.5 km for “stationary” checklists. Then, we created a merged polygon (“sample polygon”) of all the checklists within a 4 km ×4 km grid cell for each year by merging the overlapping buffers of all checklists within a grid cell. Thus, the sample polygon and not the underlying 4 km ×4 km grid cell, is the spatial unit at which we estimated covariates shaping checklist level latent abundance, *N*.

Thus, for the observation process model, we define a likelihood for the observed eBird count data, *Y*, for checklist, , in blob, , and year, , based on a binomial distribution that accounts for the detection probability, *p*, and the latent true abundance of birds (“number of trials”) in the checklist:

We modeled the detection probability, *p*, for eBird data as a function of covariates that likely impact detection accuracy, including start time of the survey, duration of the survey, speed of the survey, and the number of observers for each checklist. Again, we filtered the available eBird data (see Section 2.2.1) to select checklists that represented similar effort. We implemented the following model for the logit-scale detection probability:

where  is intercept and each is the coefficient (effect) associated with each aforementioned covariate, *Xj* (*j* = 1, 2, … 4 covariates), that varies by checklist *c*, blob *i*, and year *t*. All covariates were standardized such that describes the baseline detection probability at average covariate values. We gave al coefficients for covariate effects and intercept vague normal priors.

### 2.4.2 Biological process model for pinyon jay abundance

Following standard assumptions for N-mixture models, we assumed that the latent abundance of jays in a checklist in a year, , followed a Poisson distribution with the expected abundance given by the intensity, (number of jays per area [km2]), multiplied by the sample polygon area, *Ac* (km2), associated with observed checklist *c* such that:

Furthermore, we modeled the log-scale as a function of environmental covariates that likely impact the abundance of pinyon jays across space and time:

In this formulation, covariates include only static or concurrent variables representing conditions occurring in sample polygon *i* and year *t*. These included the static covariate of monsoonality and concurrent covariate of pinyon pine basal area.

Conversely, represents covariates that integrate over past and/or future time periods and are defined using a stochastic antecedent structure (Ogle et al., 2015). In particular, each is defined as the weighted average of seasonal or yearly values for that covariate across a defined set of seasons or years. The weights for each covariate across all seasonal or yearly periods, *l*, , were assigned a Dirichlet prior, thus constraining the weights to sum to 1 across all periods (*l* = 1, 2, …, 5 for cones; *l* = 1, 2, …, 13 for climate variables). The weight for each time period indicates how important that covariate at time period *l* was to the overall effect; larger values of the weight denote higher importance of that season or year to that covariate effect.

The covariates for which we calculated weighted averages, to account for potential temporal effects (predictive or response for cones; lagged for climate) included seed (cone) production, maximum temperature, and precipitation. Seed (cone) production was considered on a yearly scale (cones production is considered on annual timescale) and included both predictive and response effects. Thus, we included cone production during the prior year and the concurrent year (both “predictive” time periods), and three years after the current year (“lagged” time periods, with two separate hypotheses of why they may shape jay abundance, Figure 1). Both temperature and precipitation were considered at a seasonal timescale and we only consider concurrent and lagged effects. The time periods were based on important seasonal biology for pinyon jays, including: breeding (February-April), feeding dependent young (May-June), summer foraging (July), fall and winter foraging, potentially with large-scale foraging movement, or irruption (August - January) (Wiggins 2005). For these climatic covariates, we considered 12 seasonal time periods into the past, that is the current breeding season to the breeding season three years ago. We also considered interactions between seed (cone) abundance and all other covariates (pinyon basal area, monsoonality, maximum temperature, and precipitation) to determine how the relationship pinyon jay abundance and cone abundance is mediated by other habitat and climate factors related to pinyon seed reliability and alternative food resources. We gave al coefficients for covariate effects and the intercept vague normal priors.

Finally, because sample polygons sometimes covered more than one 4 km × 4 km grid cell, we determined the percent of a sample polygon covering each grid cell and then calculated weighted average covariate values based on the covariate values of all overlapping grid cells multiplied by the percent of the sample polygons overlapping that cell. On average, polygons overlapped approximately two (mean = 2.13 ± 0.01 s.e.) grid cells, with a minimum of one grid cell and a maximum of nine cells for a single polygon.

### 2.4 Model implementation, convergence, and diagnostics

We implemented the above model in the Bayesian software JAGS (Plummer, 2003, version 4.3.0) using R (R Core Team, 2020, version 4.5.1) and the jagsUI wrapper package (Kellner, 2021, version 1.6.2). We prepared data using the here (Muller, 2020, version 1.0.1), tidyverse (Wickham et al., 2019, version 2.0.0), sf (Pebesma & Bivand, 2023, version 1.0.21), terra (Hijmans, 2020, version 1.8.54), readxl (Wickham & Bryan, 2015, version 1.4.5), exactextractr (Daniel Baston, 2019, version 0.10.0), spatialEco (Evans & Murphy, 2023, version 2.0-2), nngeo (Dorman, 2018, version 0.4.8), auk (Strimas-Mackey et al., 2017, version 0.8.2), lubridate (Grolemund & Wickham, 2011, version 1.9.4), prism (Hart & Bell, 2015, version 0.0.6), FNN (Beygelzimer et al., 2010, version 1.1.4.1), and data.table (Barrett et al., 2006, version 1.17.6) packages.

We initially implemented the model and simulated 4000 MCMC samples, which we used to determine the number of iterations (samples) needed to reach convergence and to sufficiently sample from the joint posterior distribution of all unknown parameters. We used the Raftery diagnostic (Raftery & Lewis, 1995) to determine the number of iterations needed and re-ran the model to obtain a sufficient number of iterations. We qualitatively assessed convergence of the MCMC sequences by inspecting trace, history, and autocorrelation plots generated with the mcmcplots package (Curtis, 2010, version 0.4.3). We quantitatively evaluated convergence using the raftery.diag() function in the coda package (Plummer et al., 1999, version 0.19.4.1); the MCMC sequences were deemed to have converged if the Gelman-Ruman statistic, , for all root nodes in the model was less than 1.1 (Gelman & Rubin, 1992). We assessed model goodness-of-fit by comparing observed eBird count data to predicted count data based on simulating count data (“replicated data”) from the Binomial distribution in equation X. We verified the lack of spatial autocorrelation in observed data by examining spatial patterns, or the lack thereof, in the residuals (observed – predicted counts) within each year via spline correlograms produced by the R package ncf (Bjornstad, 2008, version 1.3-2).

### 2.6 Out of sample model validation

To evaluate predictions outside of the data used to fit the model, we first removed the test data (22,295 checklists) from the available eBird checklist data (833,834 checklists). We performed the same set of steps for spatial and temporal stratification (Section 2.2.1 above) on the remaining checklists (811,539 checklists) for an additional 20,380 checklists that represented “out of sample” data. We predicted out of sample model fit using ~1000 posterior samples for covariate effects and intercepts from the test dataset and model. We then examined model replicative ability (RMSE and R2 between observed and predicted bird counts) of the test and out-of-sample datasets.

# 3 Results

*3.1 Modeled effects of seed availability*

Based on our fitted model (Figure X), pinyon jay abundance was positively correlated with cone availability ( = 0.95 [0.92, 0.98]). The importance weights of the years considered (two years before cones; three years after cones) indicate the greatest weight the year after cones ( = 0.64 [0.60, 0.67]) and some weight to two and three years after cones ( = 0.13 [0.07, 0.18] and 0.21 [0.17, 0.25], for two and three years after cones, respectively), though negligible weight for the years before cones ( = 0.01 [0, 0.03] and 0.01 [0, 0.06] for two and one years before cones, respectively). In other words, jay abundance in the spring breeding season had a strong, positive relationship with cone production in the prior fall. Abundances also remained higher in these same areas for up to three years after cone production.

*3.2 Mediating effects of habitat and climate*

Based on the interactions between cone availability and other covariates in our fitted model, the relationship between pinyon jay abundance and cone availability was stronger at higher values of precipitation ( = 0.60 [0.56, 0.66]) and maximum temperature ( = 0.37 [0.33, 0.40]). Conversely, the relationship between pinyon jay abundance and cone availability was weaker at higher values of pinyon basal area ( = -0.12 [-0.14, -0.11]) and monsoonality ( = -0.21 [-0.25, -0.19]).

*3.3 Other model effects*

All other covariates in the model had non-zero effects on pinyon jay abundance. Pinyon jay abundance was negatively related to precipitation ( = -2.62 [-2.72, -2.53]) and maximum temperature ( = -0.92 [-0.96, -0.88]). Pinyon jay abundance was positively associated with monsoonality ( = 0.51 [0.46, 0.56]) and pinyon basal area ( = 0.27 [0.25, 0.29]). All covariates were scaled in the model, so the relative magnitudes of these effects can be compared.

Important seasons for precipitation based on importance weights included, in order of importance: two years ago during fledging, three years ago during breeding, two years ago during breeding, and one year ago during fledging ( = 0.37 [0.35, 0.39]; 0.20 [0.18, 0.21]; 0.16 [0.14, 0.18]; 0.12 [0.10, 0.14], for each of those seasons, respectively). All other weights were not important (SI Figure 2). In other words, precipitation had a negative relationship with precipitation two breeding and fledging seasons ago, with some negative input from the fledging season last year and the breeding season three years ago. Important seasons for maximum temperature based on importance weights included: the breeding and fledging seasons two years ago ( = 0.60 [0.50, 0.69] and 0.34 [0.25, 0.44], for the breeding and fledging seasons, respectively). All other weights were not important (SI Figure 2). In other words, high temperatures during the breeding and fledging season two years ago had a negative effect on pinyon jay abundance.

*3.4 Model goodness-of-fit*

All parameters in the model converged with an 1.1 (SI Figure 1). The relationship between our observed data and replicated data produced by the model had a mean of 0.74 (SE: 0.0003). In general, the model under-estimated the highest counts but performed well on most other values (SI Figure 3). The RMSE for our in-sample (“test”) dataset had an average value of 3.25 (SE: 0.001) and the out-of-sample dataset had a value of 5.10 (SE: 0.0002; SI Figure 4). Thus, our model predicts slightly better to our in-sample (“test”) data than out-of-sample data, but neither are large on the scale of the count data (counts per checklist ranged from 0 - 350), suggesting good model fit and predictive capacity. We observed no strong spatial autocorrelation in residuals (SI Figure 5).

# 4 Discussion

[Main takeaways framed broadly]

[Temporal signal and why it matters for this and other interactions]

[Context dependence here in OFT and more broadly for other interactions]

[Gaps/Next steps]

[Broad takeaways – zoom out beyond mutualisms a bit more to talk about how important it is to model species interactions understanding their temporal signal and local context dependence]

Here, we demonstrated that pinyon jays have a strong, positive relationship with pinyon pine seed production across the US Southwest, indicating that food resource availability plays a critical role in the abundance and spatiotemporal trends of a declining avian species. Specifically, birds occurred in greater abundance near cache sites the year after high seed production years, with lagged effects that occur over at least two subsequent years. We also found that the relationship between pinyon jay abundance and seed availability is mediated by a suite of habitat and climate variables, including maximum temperature, precipitation, pinyon basal area, and the relative importance of the North American Monsoon (July-September). These interactive relationships suggest a combination of ecological effects, including a stronger relationship with seed availability following “stressful” climatic conditions during the nesting season and a weaker relationship with seed availability in more “suitable” habitat. Determining the relationship between pinyon jays and pinyon pine seed availability and how this relationship is shaped by climate and habitat context is an important step in recognizing potential mechanisms for pinyon jay population changes. We can build on these observations to understand how this important mutualism changes in magnitude or direction through space and time and build an approach for understanding seed dispersal mutualisms in general (Moore & Dittel, 2020).

In many systems with masting tree species, populations of seed predators are known to boom in synchrony with or following large masting events (e.g., (Boutin et al., 2006; Schnurr et al., 2002). This population growth has implications not only for seed predation and dispersal, but also other ecosystem functions and services (e.g., food web responses and disease dynamics (Bogdziewicz et al., 2016; Bregnard et al., 2021; Ostfeld & Keesing, 2000). While we did not observe a “predictive” or synchronous abundance response in pinyon jays (postulated in Ligon, 1978), we did observe that the effects of masting years in two-needle pinyon pine have lasting effects on population dynamics for at least three years (Figure 2). Further, we expect that these lagged responses are due to multiple mechanisms. The first, and stronger, mechanism (~63% of covariate importance weight) is that birds nest in the spring near cache sites from the previous fall (Stotz & Balda, 1995). The second, weaker, mechanism (13-21% of covariate importance weight), is likely a delayed population response from mast-year fledglings maturing to the breeding population (1.5-2 years after fledging; (Marzluff & Balda, 1988). Temporal delays are common in trophic interactions, including seed dispersal, though they are often discounted in food web and interaction network models (Yang et al., 2023). In any system, understanding these delayed responses and their mechanisms will aid in building better predictive models of species interactions (Poisot et al., 2015). Delayed effects may be particularly important to understand in systems with resource pulses (like masting), since they can link population fluctuations to proximal causes amidst the dynamics of systems with intrinsic boom and bust cycles (Clark et al., 2019).

Understanding the context dependence of species interactions helps predict current and future ecosystem states given ongoing anthropogenic changes (e.g., (Liu & Gaines, 2022; Polazzo et al., 2022). However, context dependent results are most useful if variation can be explained by consistent patterns or mechanisms (Catford et al., 2022). We found two predictable patterns in the context dependence of the relationship between pinyon jays and pinyon pine seeds. First, jays rely more on cones following climatic conditions that may be unfavorable for reproduction and population growth (lagged effects of temperature and precipitation, Figure 4 a and b; (Ligon, 1978; Marzluff, 1988). Second, jays rely less on cones in areas with more favorable habitat (higher pinyon pine basal area and higher North American Monsoon influence; Figure 4 c and d; (Boone et al., 2018; Johnson et al., 2016; Ligon, 1978; Neilson & Wullstein, 1983; Van Lanen et al., 2023). These patterns have implications for understanding the seed dispersal interaction between these two species and when it might change in direction or magnitude (Chamberlain et al., 2014). For example, jays may eat more seeds that they cache more quickly following stressful climatic conditions (weakening or shifting the mutualistic interaction); or they may eat fewer cached seeds in habitats with more food resources (strengthening the mutualistic interaction). The mediating effects of climate and habitat on seed dispersal in masting species may be more pronounced since seed dispersers have to be adaptable to pulses of resources when they become available (Clark et al., 2019).

This study highlights how seed dispersal mutualisms likely vary across space and time, especially in ecosystems where plant species mast. For one, climate and food availability interact over multiple years to impact the population dynamics of seed dispersers (Lira et al., 2019). Especially for declining species of dispersers, this temporal component can provide an evidence-based moving window with which to evaluate population trends (e.g., (Rouyer et al., 2011). Further, seed dispersers in masting systems have likely adapted unique strategies for surviving the boom and bust nature of these ecosystems, including wider diets and behaviors that support population persistence (e.g., sociality, irruptive movement (Strong et al., 2015)). This study demonstrates the importance of long-term and broad scale studies for understanding patterns shaping species interactions and how they shape ecosystems (Hughes et al., 2017; Liu & Gaines, 2022; Magurran et al., 2010). To understand the consequences of the temporal and spatial patterns shaping this mutualism, further studies can evaluate this system “from the plant’s perspective”. Specifically, under what climate and habitat conditions do pinyon jays serve as effective seed dispersers? Like many mutualisms, the benefit to pinyon pine may depend on context (Chamberlain et al., 2014; Moore & Dittel, 2020). [Understanding the context dependence of this mutualism is crucial giving the ongoing and future changes, including increased tree mortality and declining seed abundance, which will make it harder for pinyon jays to find seeds. Cite the stuff here from intro.]

Masting systems are defined by dynamic nutrient fluxes (CITE). These effects ripple out to impact whole food webs over the course of years (CITE). While seed dispersers that depend on masting species likely adapted to take advantage of seed resource pulses when they became available, many systems where masting is regulated by climate may face increased variability with climate change as seed production declines or as seed availability becomes more patchy with plant mortality events (CITE). Patterns in seed disperser populations and masting species rely on important feedbacks between interaction partners, with mutualistic interactions becoming predation when there are fewer seed resources (CITE). Like all mutualistic interactions, seed dispersal interactions are at great risk of disappearing with ongoing change across the globe due to processes such as co-extinction (Colwell et al., 2012; Dunn et al., 2009) and phenological mismatches. Building our understanding about the temporal dynamics and context dependence of seed dispersal interactions in masting systems is an important first step in understanding and curbing biodiversity loss in ecosystems across the planet.

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