




# Statistical Reports

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## Accommodating the role of site memory in dynamic species distribution models

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**Abstract.** First-order dynamic occupancy models (FODOMs) are a class of state-space model in which the true state (occurrence) is observed imperfectly. An important assumption of FODOMs is that site dynamics only depend on the current state and that variations in dynamic processes are adequately captured with covariates or random effects. However, it is often difficult to understand and/or measure the covariates that generate ecological data, which are typically spatiotemporally correlated. Consequently, the non-independent error structure of correlated data causes underestimation of parameter uncertainty and poor ecological inference. Here, we extend the FODOM framework with a second-order Markov process to accommodate site memory when covariates are not available. Our modeling framework can be used to make reliable inference about site occupancy, colonization, extinction, turnover, and detection probabilities. We present a series of simulations to illustrate the data requirements and model performance. We then applied our modeling framework to 13 yr of data from an amphibian community in southern Arizona, USA. In this analysis, we found residual temporal autocorrelation of population processes for most species, even after accounting for long-term drought dynamics. Our approach represents a valuable advance in obtaining inference on population dynamics, especially as they relate to metapopulations.

**Key words:** colonization; extinction; hidden Markov occupancy model; imperfect detection probability; second-order Markov process; site history; site-occupancy model; species–environment relationship; temporal autocorrelation; turnover.

### INTRODUCTION

Determining species–environment relationships has long been a central theme in ecology (Grinnell 1917, Elton 1927). The quantification of such species–environment

relationships represents the core of modern species distribution modeling (e.g., Phillips et al. 2006) and predictive spatial modeling (e.g., Guisan and Zimmermann 2000, Anderson et al. 2002). One of the central tenets of this research is the recognition that patterns of site occupancy (quantified as the probability that a species occupies a site) are driven by spatial and temporal variation in biotic and abiotic factors. However, it can be difficult to understand and measure all of the relevant covariates a priori, which themselves are often spatiotemporally correlated (Ives and Zhu 2006, Hoeting 2009). Consequently, the non-independent error structure of correlated ecological data may lead to underestimating parameter uncertainty (Schabenberger and Gotway 2005), excluding important

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covariates during model selection (Hoeting et al. 2006), and generating inaccurate species occurrence maps (Lattimer et al. 2006). While ecologists have long recognized these issues (Hoeting et al. 2006), models that accommodate autocorrelation are infrequently applied to the estimation of population dynamics because it is often unclear how to accommodate for structural dependencies (but see Bled et al. 2011, Yackulic et al. 2012, Guélat and Kéry 2018).

To estimate population dynamics using site-occupancy data, researchers routinely use first-order dynamic occupancy models (hereafter FODOMs; MacKenzie et al. 2002, 2003; Tyre et al. 2003). First-order dynamic occupancy models are a class of state-space models in which the true state (occurrence) is observed imperfectly. In this instance, observation error is attributed to the inability to detect a species that is present at a site (i.e., a false negative). An important assumption of FODOMs is that dynamic processes, such as colonization and extinction, only depend on the current state of the site and that any variations are captured by fixed or random effects. In other words, these models assume a first-order temporal dependence structure, even though ecological data are often temporally correlated (Hoeting 2009). In the absence of fixed or random effects, FODOMs can produce biased parameter estimates, similar to the effects of unaccounted for spatial autocorrelation (Legendre 1993, Bled et al. 2011, Yackulic et al. 2012, Guélat and Kéry 2018).

The effects of temporal autocorrelation have important ecological implications. For example, temporal autocorrelation in habitat quality can influence site colonization probability (e.g., Bulluck et al. 2019, Che-Castaldo et al. 2019). In this case, some sites may be more likely to be occupied because of species' site fidelity or resource availability (e.g., Hoover 2003, Broderick et al. 2007); alternatively, some sites may not be colonized as readily because resources are depleted, predators are present, or habitat quality is poor (e.g., Leps et al. 2016). In both cases, temporal autocorrelation of species' site occupancy can be attributed to covariates pertaining to either spatial or temporal characteristics. However, predicting and quantifying which spatial or temporal characteristics influence population dynamics is not always possible.

Here, we extend FODOMs with a second-order Markov process to include site memory (i.e., site history) when covariates are not available (Fig. 1A). The process of site memory accommodates the phenomena of temporal dependency (e.g., Sollmann et al. 2015, Fay et al. 2020) and site heterogeneity by incorporating information on the state of site occupancy during previous seasons as a covariate on dynamic parameters. We investigate the performance of our modeling approach through a series of simulations, and we demonstrate its utility using a 13-yr data set of six amphibian species in southern Arizona, USA. Our model provides a useful framework for understanding site fidelity, habitat

preferences, and resource availability in ecological data sets when covariates are not available.

## METHODS

### Memory model

We modified the FODOM to include a second-order Markov process (i.e., the probability of occupancy in season  $t$  depends on the occupancy at season  $t - 1$  and  $t - 2$ ; Fig. 1A). Similar to other dynamic occupancy models, the data consist of species detection or non-detection at site  $i$  during survey  $j$  and season  $t$ .

For the first season, we define the occupancy of site  $i$ ,  $z_{i,1}$ , as a Bernoulli trial

$$z_{i,1} \sim \text{Bernoulli}(\psi)$$

where  $z = 1$  if the site is occupied, and 0 otherwise.  $z$  is a latent state variable and represents true site occurrence, and  $\psi$  is defined as the probability of occupancy.

For the second season, we define that the occupancy of site  $i$ ,  $z_{i,2}$ , depends on the occupancy of site  $i$  the previous season,  $t - 1$ , such that

$$z_{i,2} \sim \text{Bernoulli}(\mu_{i,1})$$

$$\mu_{i,1} = z_{i,1} \times (1 - \varepsilon_{i,1}) + (1 - z_{i,1}) \times \gamma_{i,1}$$

$$\text{logit}(\varepsilon_{i,1}) = \alpha_0$$

$$\text{logit}(\gamma_{i,1}) = \beta_0$$

where  $\varepsilon$  is the extinction probability (i.e., the probability that an occupied site at time  $t - 1$  becomes unoccupied at  $t$ ),  $\gamma$  is the colonization probability (i.e., the probability that an unoccupied site at time  $t - 1$  becomes occupied at  $t$ ), and  $\alpha_0$  and  $\beta_0$  represent the first-order effects of site occupancy ( $t - 1$ ) on current occupancy ( $t$ ).

After the second season (i.e.,  $t > 2$ ), the occupancy of site  $i$  depends on both the occupancy at site  $i$  during the previous season,  $t - 1$ , and the season before that,  $t - 2$ , such that

$$z_{i,t} \sim \text{Bernoulli}(\mu_{i,t-1})$$

$$\mu_{i,t-1} = z_{i,t-1} \times (1 - \varepsilon_{i,t-1}) + (1 - z_{i,t-1}) \times \gamma_{i,t-1}$$

$$\text{logit}(\varepsilon_{i,t-1}) = \alpha_0 + \alpha_1 \times z_{i,t-2}$$

$$\text{logit}(\gamma_{i,t-1}) = \beta_0 + \beta_1 \times z_{i,t-2}$$

Here,  $\alpha_1$  and  $\beta_1$  represent the second-order effects of site occupancy ( $t - 2$ ) on current occupancy ( $t$ ). Note that other covariates can be added to  $\varepsilon$  or  $\gamma$  using the logit-link function.

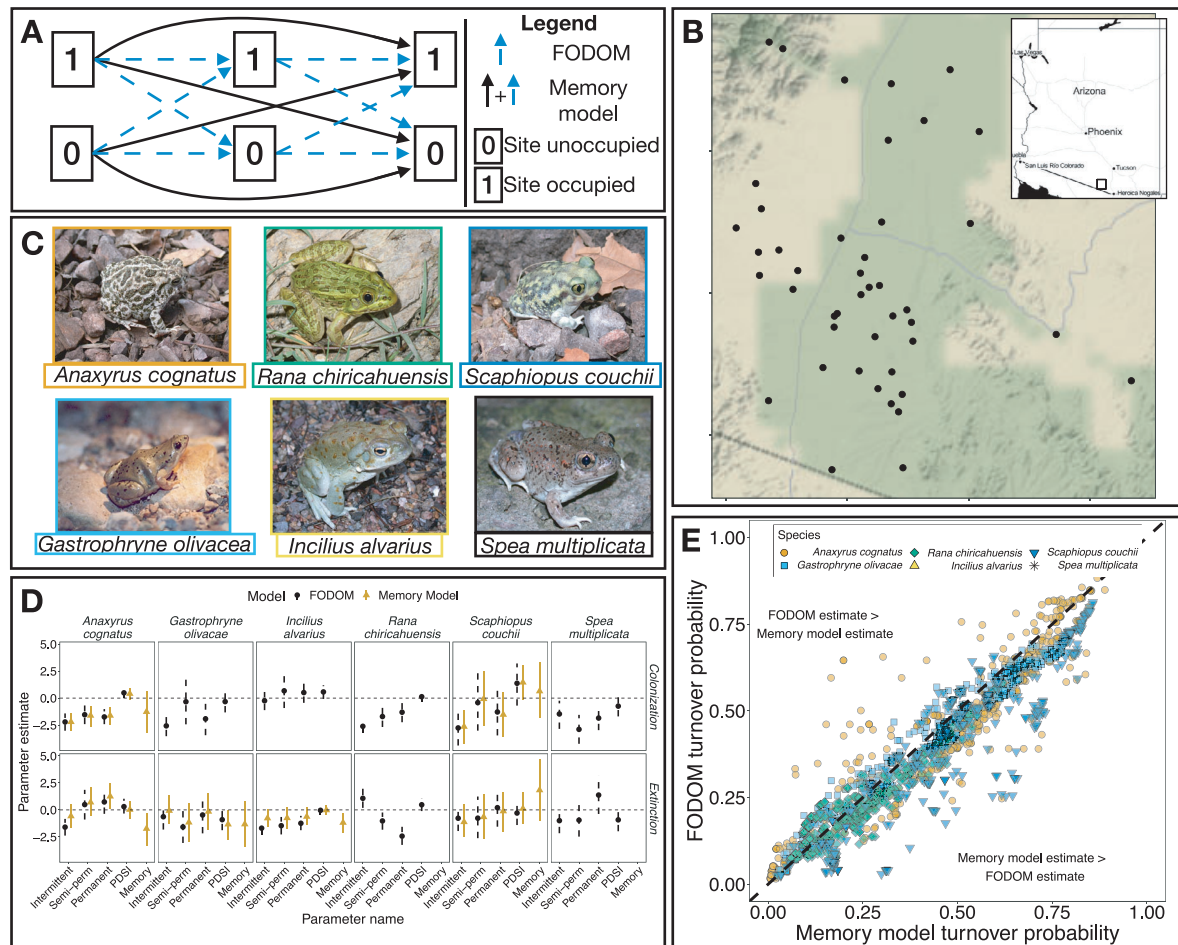


FIG. 1. (A) Summary of model structure and (B) the case study, where 44 sites were surveyed in Arizona, USA for (C) six amphibian species. In panel A, we depict the differences between the FODOM (blue dashed arrows only) and the memory model (black solid and blue dashed arrows). (D) We used these two models to estimate species colonization (top) and extinction (bottom). The plot depicts mean (point) and 90% CI (line range) parameter estimates on the logit scale. Covariates in the model include water body type (i.e., intermittent, permanent, semipermanent [semi]) and long-term drought dynamics (PDSI). (E) Last, we examined how turnover probabilities differed between the two models (FODOM vs. memory model). Values above the one-to-one line (dashed line) represent estimates that are higher for the FODOM than the memory model, whereas values below the one-to-one line represent turnover probabilities that are higher for the memory model than the FODOM. Photos: USGS ARMI ([https:// www.usgs.armi.gov](https://www.usgs.armi.gov)) or by the authors.

Last, we consider components related to the sampling process. Species observations at the  $i$ th site during the  $j$ th survey and  $t$ th year,  $y_{i,j,t}$ , are assumed to be Bernoulli random variables dependent on true site occurrence,  $z_{i,t}$

$$y_{i,j,t} \sim \text{Bernoulli}(p \times z_{i,t})$$

where  $p$  is the probability of detecting a species given it is present at a site ( $z_{i,t} = 1$ ). For an alternative explanation of the model, see Appendix S1. Code to simulate data can be found in the Dryad repository associated with this paper. For an alternative parameterization using a hidden Markov model, see Appendix S2. The model parameterization presented in the main text is a special case of this more general second-order hidden

Markov occupancy model, which can easily be extended to an  $N$ th-order Markov dependence.

### Simulation studies

We developed a series of simulations to (1) examine patterns of model accuracy, precision, and bias for a range of parameter values, (2) provide general sampling design guidelines when no information is known about parameter values, and (3) compare model performance when site memory and heterogeneity does and does not occur. To do this, we simulated data across a range of scenarios, study designs, and parameter values. We assumed independence and population closure for within-season sampling events (MacKenzie et al. 2002,

2003, Tyre et al. 2003). Parameters were drawn independently to guarantee ample coverage across parameter space (Appendix S3). All data sets were simulated with site memory unless otherwise mentioned. We analyzed data using a Bayesian approach with Markov chain Monte Carlo in R (R Core Team 2019) and JAGS (Plummer 2003; Appendix S3).

#### *Parameter accuracy, precision, and bias*

We examined patterns of model accuracy, precision, and bias for a range of parameter values. We generated 9,849 simulated data sets and analyzed them using the memory model. Then, we grouped the simulated data sets depending on their true parameter value (Appendix S4). We used post hoc linear models to examine patterns of parameter accuracy (i.e., how close are model estimates to true values?), precision (i.e., how large is the 95% credible interval?), and bias (i.e., what are patterns of over- vs. underestimation?). We defined accuracy as the log absolute error (Appendix S4), precision as the width of the 95% CI (Appendix S5), and bias as the difference between the model estimate and the true parameter value (Appendix S6). In each post hoc linear model, we used either accuracy, precision, or bias as the response variable, and log number of sites, surveys, and seasons as covariates. For more details, see Appendix S4, S5, and S6, code in Data S1: ModelS1.R and the Dryad repository associated with this paper.

#### *Sampling design guidelines*

To provide general sampling design guidelines when no information is known about the parameter values, we set out to determine the number of sites, surveys, and seasons that need to be sampled to achieve an acceptable threshold of absolute error. We used the same simulated data sets and model runs from above, but we did not group parameters by their true values. Again, we fit post hoc linear models to examine patterns of parameter accuracy, and we set an acceptable threshold of absolute error equal to either 0.1 or 0.01. We generated different combinations of number of sites and surveys sampled, and using these values, we solved for the number of seasons to be sampled to achieve the set level of acceptable error. Last, using these sampling designs, we plugged them into the precision and bias post hoc models to calculate predicted mean values for each metric (Appendix S7).

#### *Comparison between the memory model and FODOM*

To compare the performance of the memory model and FODOM, we ran the memory model and the FODOM side by side under three simulation scenarios (Data S1: ModelS1.R, S2: ModelS2.R). Under the first

scenario, we generated data *without* site memory and *without* site heterogeneity (total number of simulations = 9,911). Under the second scenario, we generated data *with* site memory and *without* site heterogeneity (total number of simulations = 9,849), and under the third scenario, we generated data *with* site memory and *with* site heterogeneity (total number of simulations = 9,915). Site heterogeneity was added as a site-level random-effect term to site occupancy ( $\psi$ ), extinction ( $\epsilon$ ), and colonization ( $\gamma$ ) probabilities using a logit-link function and a Gaussian distribution with mean = 0 and standard deviation = 1. With this specification, particular sites consistently had higher occupancy, extinction, and colonization probabilities than other sites.

To compare the performance of each model under each scenario to truth, we calculated the root mean squared error (RMSE) of turnover probabilities (Appendix S8). When site memory was used to generate the data (i.e., second and third scenarios), we also examined if the true magnitude of site memory (i.e., absolute values of  $\alpha_1$  and  $\beta_1$ ) influenced model accuracy (as defined above) of turnover probabilities (Appendix S8).

#### *Case study*

To test the utility and performance of the memory model, we applied it to a data set where 44 sites were surveyed for six species up to three times annually every year for 13 yr (2007–2019), except for one year (2018; Appendix S9, Appendix S10: Table S2). The study area was located on the Buenos Aires National Wildlife Refuge and the adjoining State Trust land to the west in Arizona, USA (Fig. 1B and C). Our goals were twofold. First, we sought to evaluate evidence for including a memory term in the statistical analysis, and second, we aimed to determine how our inference would have differed between the memory model and FODOM. Therefore, we describe a two-part analysis.

In the first part, we used indicator variable selection to evaluate evidence for adding a second-order memory term to species extinction and colonization probabilities (Hobbs and Hooten 2015). Then, using the resulting memory model from the first part, we compared parameter estimates between the memory model and the FODOM. We allowed all parameters to be species specific. We included water body type and the Palmer Drought Severity Index (PDSI) as covariates on colonization and extinction probabilities, which we expected to drive occupancy dynamics in this desert system. We expected that a pond might be colonized in a year with abundant precipitation (i.e., colonization event) and a pond would not persist occupied in a year with poor monsoon rains (i.e., extinction event). We also included wind speed, temperature, and water presence/absence as covariates on detection probability. We report posterior means and the 90% CI. For more details, see Appendix S9 and Data S3: ModelS3.R.



## RESULTS

*Parameter accuracy, precision, and bias*

In general, the memory model recovered fairly accurate (absolute difference between model estimated mean and true value =  $0.27 \pm 0.001$  [mean  $\pm$  SE] logit scale; Appendix S10: Fig. S1) and precise (mean width of 95% credible interval =  $0.19 \pm 0.001$  probability scale; Appendix S10: Fig. S2) parameter estimates with low bias (estimate – truth =  $-0.001 \pm 0.002$  logit scale; Appendix S10: Fig. S3). Our simulations show that the ability of the memory model to recover parameters (when site memory is present) is dependent on the true parameter values and the amount of available data (Appendix S10: Figs. S1–S3). Specific recommendations on sampling design depend on true parameter values (Appendix S10: Figs. S1–S3), but typically, model estimates were more accurate and precise when more sites and seasons were analyzed (Appendix S10: Figs. S1–S3).

*Sampling design guidelines*

Depending on the investigator's acceptable level of error for parameter estimates, we found that a variety of sampling designs can be used (Table 1). With these sampling designs, the average predicted precision across

parameters is between 0.27 and 0.60 on the probability scale, and the average predicted bias is between  $-0.004$  and  $0.003$  on the logit scale.

*Comparison between the memory model and FODOM*

The memory model on average predicted slightly lower turnover probabilities than the FODOM under each scenario (difference between memory model turnover probability and FODOM under first scenario =  $-0.001 \pm 0.001$  [mean  $\pm$  SE]; second scenario  $-0.004 \pm 0.001$ ; third scenario =  $-0.002 \pm 0.001$ ). We also found that the memory model predicted turnover probabilities more closely to truth than the FODOM, indicated by lower RMSE values (Fig. 2), except when data were simulated *without* site memory and *without* site heterogeneity (i.e., first scenario). However, even in this case, the RMSE values from the memory model were extremely low (i.e.,  $< 0.005$ ; Fig. 2), suggesting that the model still performs well. When data were simulated *with* site memory (i.e., second and third scenarios), parameter accuracy increased as the magnitude of the memory effects increased using the memory model, whereas parameter accuracy tended to decrease or remain constant as the magnitude of the memory effects increased using the FODOM (Appendix S10: Figs. S4, S5, Table S3).

TABLE 1. General sampling design guidelines to achieve an acceptable level of parameter error (i.e., absolute difference between the model estimate and true parameter value).

Sites	Surveys	Seasons	Average predicted mean	
			Precision	Bias
Acceptable error = 0.1				
20	2	7	0.60	0.0013
50	2	6	0.51	−0.0003
100	2	6	0.43	−0.0010
20	4	7	0.54	−0.0006
50	4	6	0.45	−0.0022
100	4	5	0.39	−0.0037
20	6	6	0.52	−0.0023
50	6	6	0.41	−0.0033
100	6	5	0.35	−0.0048
Acceptable error = 0.01				
20	2	12	0.53	0.0034
50	2	11	0.44	0.0021
100	2	11	0.36	0.0013
20	4	12	0.47	0.0015
50	4	11	0.37	0.0001
100	4	10	0.31	−0.0010
20	6	11	0.44	0.0000
50	6	11	0.34	−0.0010
100	6	10	0.27	−0.0021

*Notes:* Using these sampling designs, we calculated the average predicted mean precision and bias across dynamic parameters. Average predicted mean precision is on the probability scale, and the average predicted mean bias is on the logit scale. See Appendix S7 for details.

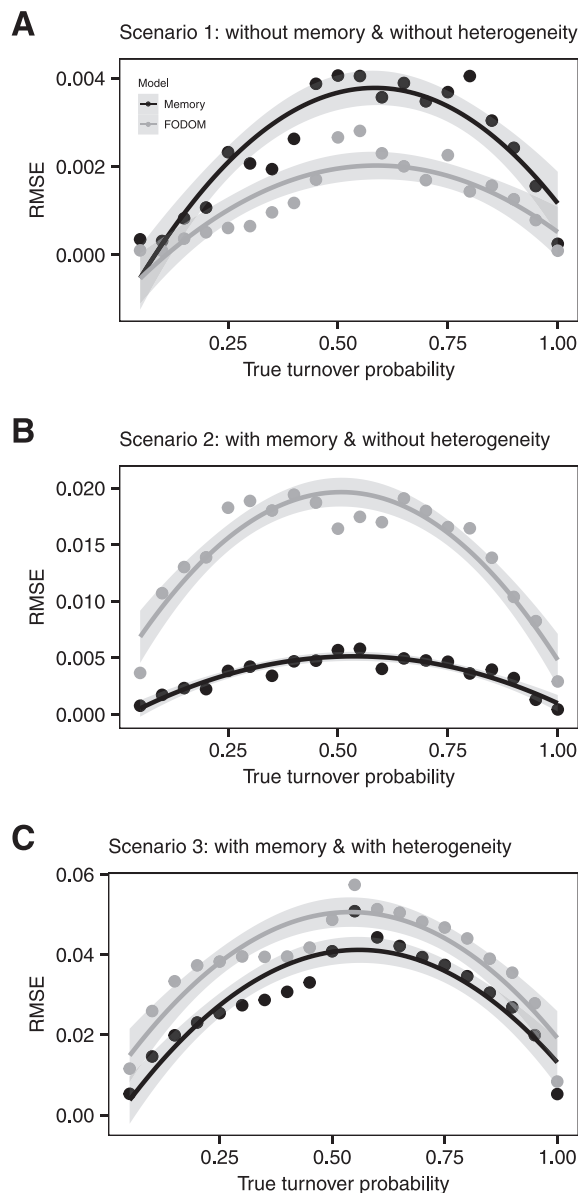


FIG. 2. Comparison of model accuracy with respect to truth. We calculated the root mean squared error (RMSE; y-axis) under scenarios where data were generated (A) without memory and without site heterogeneity, (B) with memory and without site heterogeneity, and (C) with memory and with site heterogeneity. The black line (fitted post hoc linear model with quadratic term) and points (RMSE estimates from simulations) show the performance of the memory model, whereas the gray line and points show the performance of the FODOM (see methods in Appendix S8).

### Case study

Although most parameter estimates were similar between the memory model and FODOM (Appendix S10: Tables S4, S5), we detected an effect of site memory for most species even after accounting for long-term

drought dynamics (Fig. 1D). Site occupancy two seasons prior decreased the extinction probability of three species (*Anaxyrus cognatus*, *Gastrophryne olivacea*, *Incilius alvarius*) and tended to increase the extinction probability of one species (*Scaphiopus couchii*; Fig. 1D). In contrast, site occupancy two seasons prior showed tendencies of decreasing the colonization probability of *A. cognatus* and increasing the colonization probability of *S. couchii* (Fig. 1D). Last, the FODOM predicted lower turnover probabilities by an average of  $0.03 \pm 0.01$  (probability scale; Fig. 1E) than the memory model.

### DISCUSSION

We demonstrate the improved inference of dynamic population processes, including colonization, extinction, and turnover probabilities, when temporal dependencies are accounted for using the memory model. The model accommodates temporal autocorrelation generated by site heterogeneity and only requires detection/non-detection data collected over multiple seasons across sites, with repeated surveys within each season.

The accuracy, precision, and bias of dynamic parameters estimated by the memory model depend on both true parameter values and the amount of available data (Appendix S10: Figs. S1, S2, S3). As with most other multi-parameter models, the model performed better with more data. When few sites were sampled ( $n = 5$ ), the model's parameter accuracy (average difference of 0.72 between truth and model estimate on the logit scale; Appendix S10: Fig. S1) and precision (95% CI was 0.58 on the probability scale; Appendix S10: Fig. S2) were poor. In general, the recommended number of seasons to sample will be greater either in the absence of covariates that explain temporal dependencies or if dynamic processes are second-order Markovian rather than first order. However, keep in mind that sampling effort should be allocated according to research objectives, where the sampling design is dictated by parameters of interest.

In our analysis of an amphibian community in Arizona, USA, we found that site memory influenced the site colonization and extinction probabilities of most species. In an effort to account for temporal dependencies in the data, we included the Palmer Drought Severity Index (PDSI) as a covariate on dynamics processes. However, we found residual temporal autocorrelation of population processes for most species, even after accounting for long-term drought dynamics. This suggests that there are other biotic or abiotic mechanisms not accounted for in the model that influence dynamic processes and that covariates may not always adequately capture temporal dependencies.

We also found that turnover probabilities across amphibian species estimated by the FODOM were on average lower than those estimated by the memory model (Fig. 1D), suggesting that site occupancy is more dynamic than previously predicted. In contrast, when data were simulated, we found that the memory model

estimated turnover probabilities lower than the FODOM and that the memory model typically outperformed the FODOM, as demonstrated by lower RMSE estimates (Fig. 2). In addition, when site memory and heterogeneity were present in the simulated data (i.e., third scenario), the memory model was able to accommodate the extra source of heterogeneity via the memory component (i.e.,  $\alpha_1$  and  $\beta_1$ ) more readily than the FODOM. Collectively, these results indicate that the memory model produces more reliable estimates of turnover probabilities than the FODOM, which could result in either more static or dynamic conclusions of species distributions than truth.

In practice, researchers should keep in mind several constraints and practicalities before employing the memory model. First, researchers should consider their goals and objectives, as well as considering if the memory model would improve their ecological inference. In general, our simulations suggest that the memory model typically outperforms the FODOM. Second, researchers should consider if covariates can adequately describe the source of temporal dependencies in the data. In the case where covariates are available, there may still be residual autocorrelation, where the magnitude of the residual autocorrelation may depend on the strength of the covariates driving the temporal autocorrelation. Last, along those same lines, users should consider the trade-offs in spending time and money collecting extra data (e.g., across sites and seasons) to fit the memory model vs. spending time a priori determining biologically meaningful covariates to measure and collect. For example, the run times for the memory model were on average three times greater than the FODOM (memory model =  $49.29 \pm 1.16$  minutes; FODOM =  $16.14 \pm 0.34$  minutes [mean  $\pm$  SE]). Future users of the memory model should base modeling decisions on the ecology of their system, results from simulation studies, and computational considerations.

We foresee the memory model being useful in a number of applications where inference is made difficult by processes operating over time, similar to the applications of memory in multistate mark-recapture models (e.g., Pradel 2005). For example, the memory model can be used to estimate species arrival or extinction times (e.g., Williamson 2006), decision rules associated with species site fidelity (e.g., Hoover 2003), habitat choice (e.g., Johnson and Gillingham 2008), resource availability (e.g., Johnson et al. 2010), examining species-environment relationships (e.g., De'ath 2002), applications to metapopulation turnover and lifetimes (e.g., Moilanen 2002), and identifying abiotic refugia (e.g., Keppel et al. 2015). Across all of these applications, species' life history, behavior, the environment, or their interactions influence population dynamics, making parameter estimation and inference difficult. By accommodating temporal dependencies and site heterogeneity, the memory model makes it possible to more easily account for memory processes using detection/non-detection data when

covariates are not available. Under each of these proposed applications, we also foresee the ability to more accurately predict and forecast species distributions. In this way, incorporating temporal autocorrelation in statistical models can more readily move us closer to accurately estimating population dynamics.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3315/supportinfo>

## OPEN RESEARCH

All data and code for analyses are available from Dryad (DiRenzo et al. 2021): <https://doi.org/10.5061/dryad.vdncjsxs7>