

# Modelling nonlinear responses of a desert rodent species to environmental change with hierarchical dynamic generalized additive models

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## ABSTRACT

Modelling abundance fluctuations of species is a crucial first step for understanding and forecasting system dynamics under future conditions. But, especially in multivariate response data, this can be hampered by characteristics of the study system such as unknown complexity, differently formed spatial and temporal dependency, non-linear relationships, and observation characteristics such as zero-inflation. This study aimed to explore how such challenges can be addressed by using hierarchical Dynamic Generalized Additive Models (DGAM) for multivariate count responses in a Bayesian framework while modelling multi-site monthly captures for the Desert Pocket Mouse (*Chaetodipus penicillatus*) over 23 years from a long-term study in Arizona, USA. By fitting models of increasing complexity and developing bespoke checking functions that captured targeted ecological aspects such as spatio-temporal dependence, we show how nonlinear dynamic models can be built to improve forecasts for multivariate count-valued time series.

We found strong evidence that accounting for non-linear and time-lagged effects of as much as 12 months improved model fit and forecasting performance. Evaluation of models for other species in geographically different habitats is essential for generalizing model strategies and insights into long-term abundance-environment relationships, while systematic comparisons will only be possible if multivariate modelling workflows account for the complexity of non-linear and lagged effects and potentially also other aspects such as biotic interactions.

## 1. Introduction

Informed species and habitat management is crucial to maintain ecosystem function and sustainability (Lindenmayer and Likens, 2009). This requires information on probable future states of populations, communities, and ecosystems in response to changing environmental conditions (Clark et al., 2001; Evans, 2012; Mouquet, 2012; Purves et al., 2013; Sutherland, 2006; Tallis & Kareiva, 2006). Applications include deriving information on future states of population viability (Clements, 1936; Dietze et al., 2018; Gleason, 1926; Godfray & May, 2014; Houlahan et al., 2017; Sutherland et al., 2013), exploration of community composition and functional dynamics (Petchey et al., 2015; Roy et al., 2014; Sutherland et al., 2007), and scenario-based assessments of risk arising from ecological stressors such as severe weather conditions or disease (Mace et al., 2008; Thomas et al., 2011). Long-term monitoring processes [e.g., National Ecological Observatory Network

(NEON), Terrestrial Ecosystem Research Network, International Long-Term Ecological Research, FLUXNET, Global Lakes Ecological Observatory Network (GLEON)] provide necessary historical data to begin addressing these goals (Clark et al., 2001; Lindenmayer and Likens, 2009). Even when quality monitoring takes place, deriving necessary information for all relevant ecological aspects is a challenging task, especially as it is challenging to collected data on different organisms and abiotic condition with matching protocols and the same routine (Oliver & Roy, 2015).

To make inferences about probable future states using these data, ecological forecasting models are needed. The field of near-term ecological forecasting has risen to meet these needs (Dietze et al., 2018). Despite the broad importance of long-term monitoring, predicting what ecosystems will look like in the future is difficult for several reasons. Ecological processes are noisy and difficult to observe (Green et al., 2004; Guisan et al., 2013). We often do not have a prior

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understanding of functional forms of relationships among ecological aspects. They can either change rapidly or with considerable time lags in response to multiple abiotic and biotic drivers (Akiner et al., 2016; Keirans & Durden, 2001; Kelehear et al., 2017; Medlock et al., 2015; Schaffner et al., 2013). Also, such relationships may be nonlinear. This makes it difficult to form forecasting model that adequately approximates the underlying data generating process. How can we infer these sources in a robust statistical model and derive information about future status?

When appropriate models are used to address the complexities of ecological data, the forecaster is still tasked with deciding how a model should be used. Identification of end users and their needs is crucial in developing ecological forecasting models (Carey et al., 2022; Dietze et al., 2018; Hobday et al., 2019). A clear set of goals is required to evaluate models against those goals (Dietze et al., 2018). These forecasting approaches are expected to be useful across other disciplines too (Gregory et al., 2012; Hooten & Hobbs, 2015; Williams & Hooten, 2016). There will not be any 'best' model for a forecasting scenario, as different models have their own advantages and disadvantages (Box et al., 1978; Gelman et al., 2020). A combined process of informed model assessment and exploration of alternative model structures (either separate models or variants of a single model) provides insight to test hypotheses and improve models (e.g., identifying time lags, feedbacks, and thresholds) (Dietze et al., 2018). Iterative processes are crucial in many ways to develop a predictive model (Carey et al., 2022; Dietze et al., 2018; Hobday et al., 2019; Tetlock and Gardner, 2015). Comparison of multiple modelling approaches is also useful to understand ecological processes, and situations in which each model is more effective (Harris et al., 2018; White et al., 2019). With the advancement of computational capabilities, such complex task of iteratively testing different models in terms of fit and forecasting capabilities can be handled under a principled modelling frameworks (Simmons and Holsingworth, 2002).

In this study, we used nonlinear models to analyse and forecast rodent species dynamics using capture rates data from a long-term monitoring study. We focused on captures for the desert pocket mouse (*Chaetodipus penicillatus*) from the Portal Project, an ecological monitoring study near Portal, Arizona (Ernest et al., 2018). These data have been widely used for research to understand dynamics of species fauna. For example, structural and compositional changes in rodent communities have been studied along with resource sharing by assessing the shape of rank abundance distributions concluding that a few key species are mostly responsible for changes in rodent community assemblage composition and overall rodent abundance fluctuations (Thibault et al., 2004). Lima et al. (2008) studied nonlinear dynamics of population sizes of two species of Kangaroo rats *Dipodomys ordii* and *D. merriami* based on impacts of seasonal rainfall (summer and winter) and intraspecific competition by means of logistic model. They found that rainfall in summer is more important than winter rainfall and that competition for resources can play a key role. But this study did not consider making inferences about other potential sources of temporal and spatial variation, such as plot, treatment, and temperature effects. Another study assessed impacts of seasonal annual cumulative precipitation, as a proxy of resource availability, on population dynamics of three guilds of desert rodents with distributed lag of precipitation up to order 2 (two previous seasons) through generalized linear models applied for seasonally aggregated data (Thibault et al., 2010). This study confirmed that precipitation affects both resource and consumer populations. But the impacts of other factors, especially temperature and environmental resources, were not considered in this study. Their model was also not capable for forecasting short term monthly captures since it was based on seasonal data.

Forecasting models developed around the Portal Project rodent data include a Poisson auto-regressive model, which was proposed for an automated forecasting system (White et al., 2019). Those models set a framework by which other forecast models can be compared. But

questions remain about how to systematically select the most suitable forms to model covariate relationships, and whether any additional sources of heterogeneity need to be considered. Another study applied three Bayesian time series models to forecast captures of the desert pocket mouse (Simonis et al., 2021). They found a first order autoregressive model to be the most suitable for short term forecasting compared to random walk and seasonal autoregressive models. But they also discussed the merits of probabilistic forecast evaluation, which they used to show that different models perform well under different scenarios/time periods. This study, however, did not consider impacts due to variations in plots, experimental treatments and impacts of those environmental factors found to highly affect species dynamics in other studies.

Here, we explore how accounting for features of multivariate time series of (animal) count data in recently developed dynamic generalised additive models (DGAMs) improves model fit and near-term forecasting accuracy. Using rodent capture data from 24 adjacent experimental plots exposed to differences in experimental setup and environmental conditions, we extended previous work by showing how novel DGAMs can be used to build multidimensional nonlinear functions that capture complex lagged climatic (minimum temperature, precipitation) and environmental effects (NDVI) while also modelling multi-site dynamics. We also explore how some alternative tailored posterior checking functions can be used to assess performance and identifying model failures.

## 2. Material and methods

### 2.1. Study Location and study species

The Portal Project is a long-term ecological study located in Chihuahuan Desert near Portal, Arizona (Ernest et al., 2018). This desert consists of a high biological diversity of grasses, plants, and animals with various type of water limited areas such as mountains, urban, and non-desert. There are 24 experimental (sampling) plots of size of 0.25 ha (50m\*50m) over an area of 20 ha which has been protected by a fence from cattle. Each experimental plot also has fence around and access through small gates of different sizes to selectively restrict access for rodent species. These plots were grouped into four treatment types according to presence/absence of gates and their sizes (removal, control, spectab, enclosure). Treatment 'removal' has gates to exclude all species of rodents (any rodents trapped on these plots are removed from the site). Control plots allow free passage for all rodents with larger gates (3.7 × 5.7 cm) and treatment 'spectab' has gates of size of 2.6 × 3.0 cm and this is to exclude Banner-tailed kangaroo rats (*D. spectabilis*), the largest kangaroo species only. Enclosure has gates of size 1.9 × 1.9 cm that block entry of dominant kangaroo rat species from the genus *Dipodomys*. These treatments are reinforced every month by removing all rodents that should not be on particular plots.

There are 49 trapping stations (stakes) permanently fixed in each plot in 7 rows and 7 columns with a distance of 6.5 m between any two adjacent stakes. The number of captures in each plot is recorded on a lunar monthly basis.

Our species of interest was the desert pocket mouse, *C. penicillatus*. Though the average lifespan of *C. penicillatus* is around one year, a few individuals survive more than one year. This nocturnal species is inactive during the winter period in southern Arizona. They can make burrow in many types of soils by chewing (Arnolf, 1942; Brylski and Patton, 2000). Leaves, seeds, grains, nuts and occasionally insects are the main food sources. Seeds are also stored in burrows and in dispersed caches throughout their territories. Although there is no direct evidence, this species probably acquires all the water it needs from its food (Arnolf, 1942; Brylski and Patton, 2000). Female adults give birth to up to seven offspring during period from early spring to the late summer (February to September) with an average gestation period of 23 days (Biota Information System of New Mexico, 2000; Utah Division of Wildlife

Resources, 2001). Young females may reach early sexual maturity.

## 2.2. Species captures rates time series and environmental predictors

Portal data has been made available in the R package ‘portalr’ in a GitHub repository (<https://github.com/weecology/PortalData>) and archived on Zenodo (Ernest et al., 2018). We extracted information on year, month, plot, treatment, number of traps in plot, and number of captures of *C. penicillatus* from Portal capture data from 1996 to 2018. Data prior to 1996 was excluded as experimental plant manipulation were done and PIT Tagging was not in practice prior to this year. Data from 2019, 2020, 2021, and 2022 were also excluded since COVID disruptions impacted the ability to sample.

A variable “time” was created to represent the sampling timepoint on a continuous time scale with values from 1 to 284 corresponding to the onset of each new moon cycle, with a time window of approximately one lunar month. Missing capture records were denoted as NA in the response variable. An aggregated response variable ( $Y_{\text{aggregate}}$ ) was calculated as the total number of observed trappings across all plots and treatments for each timepoint, which we used as an additional contributor to the likelihood in our models (see 2.4 section below). If any plot-level observations were NA during a particular timepoint, then the resulting aggregate also contained NA.

We used climatic and environmental data (minimum temperature, precipitation, and Normalized Difference Vegetation Index-NDVI) made available together with the capture data in the same R package. Precipitation and temperature have been collected hourly by an automated weather station located in the experimental site, which has been upgraded several times while NDVI has been collected through remote sensors (Ernest et al., 2018). Corresponding daily values such as average (e.g. for precipitation and temperature), minimum, and maximum (e.g. for temperature) have been calculated based on these hourly data, and monthly figures by taking averages of daily values accordingly (e.g. monthly minimum temperature is the average of daily minimum temperatures).

As our modelling framework did not allow for missing covariate values, we imputed a total of one missing observation for minimum temperature with posterior mean expectations from Generalized Additive Models (GAMs) fitted in the *mgcv* R package (Wood, 2017). We used smooth functions of year (represented with a thin plate regression of smooth term of order 12) and month (represented with a cyclic cubic regression spline smooth of order 10). For missing data in the variable treatment, the previous treatment was assumed to remain. Lagged values to an order of 12 months of minimum temperature, precipitation, and NDVI were considered as predictors in models. Prior to model fitting, data were split into training data and testing data sets. Data from 1996 to 2017 were used as training data and data in 2018 were used as testing data.

## 2.3. Data exploration

As shown in Fig.S2.1(A), the treatment ‘control’ was most common, followed by ‘exclosure’, ‘removal’ and ‘spectabs’, where treatment types changed over time on 13 out of 24 plots (Fig.S2.1(B)). As shown in Fig. S2.2(A), >2,000 zeros out of a total of 6,816 captures were recorded and this leads for over dispersion. A seasonal pattern in captures was observable within the year which gradually increases up to July-August and declines towards December (Fig.S2.2(B)). Minimum temperature gradually increased from less than 5 °C in January to about 20 °C to July before dropping again (Fig.S2.2(C)). Precipitation tended to decline from January to May from about 35 mm to 5 mm and then increased to about 70 mm by July before progressive declines towards the end of the year (Fig.S2.2(D)). NDVI tended to remain at low values during first seven months and last two months compared to its values between August and October (Fig. S2.2(E)). The onset NDVI (i.e. the greenup period) usually takes place one month after increases in precipitation.

Number of captures were correlated with minimum temperature and NDVI, but these patterns did not appear to be linear (Fig. S2.2(F, H)), and these climatic and environmental factors were somewhat correlated with each other (Fig. S2.2(I, J, K)).

## 2.4. Generalized additive modelling framework

We modelled the average of captures  $\theta_{it}$  for each plot  $i$  at a given time  $t$  based on the capture data  $Y_{it}$  and  $Y_{\text{aggregate},t}$  as:

$$Y_{it} \sim f_{Y_{it}}(\theta_{it})$$

$$\log(\theta_{it}) = S_1(x_1) + \dots + S_k(x_k) \quad (1)$$

$$Y_{\text{aggregate},t} \sim f_Y(\theta_{\text{aggregate},t})$$

$$\theta_{\text{aggregate},t} = \theta_{1,t} + \theta_{2,t} + \dots + \theta_{24,t} \quad (2)$$

Here,  $f$  represents an exponential probability distribution, and  $S_i$ 's represent smooth functions of covariates  $X$ , some of which can be multidimensional (i.e., tensor product smooths of multiple covariates, or possibly distributed lag nonlinear models that allow smooth functions of a covariate to change smoothly over increasing lags). The aggregate capture data  $Y_{\text{aggregate},t}$  contributes to the likelihood to enforce coherence of plot-level predictions (i.e., plot-level predictions at time  $t$  are allowed to vary, but the sum of their expectations should equal the expectation for the aggregated population-level prediction).

## 2.5. Model expansion and final model

As part of our workflow, we fitted seven models of increasing complexity with different combinations of predictors (plot treatment and environmental variables) and functional forms (e.g., lagged effects). The first five models used a Poisson distribution for the plot-level captures and the rest used a Negative Binomial distribution. Details of the first six models are given in supplementary-1 (S1). Diagnostics and checking functions described below were used for model evaluation. The compositional structure of the final model (given by Eq. (3)) is represented graphically in Fig. S2.8 and its specification is as follows.

$$y_{it} \sim \text{NegBinomial}(\mu_{it}, \emptyset)$$

$$\log(\mu_{it}) = \alpha_{\text{plot}[i]} + \alpha_{\text{treatment}[j]} + S_1(\text{mintemp}_{(\text{lag})}, \text{ndvi}_{(\text{lag})}) + S_2(\text{precipitation}) + Z_{it} \quad (3)$$

where,

$$i = 1, 2, \dots, 24, j = 1, 2, 3, 4$$

$\mu_{it} = E(y_{it})$ : is the expected (average) number of captures for plot  $i$  at time  $t$

$\alpha_{\text{plot}} \sim \text{Normal}(\mu_{\text{plot}}, \sigma_{\text{plot}}^2)$ : effect of plot  $i$  (random effect)

$\mu_{\text{plot}} \sim \text{Normal}(0, 1)$

$\sigma_{\text{plot}}^2 \sim \text{Exponential}(0.5)$

$\alpha_{\text{treatment}} \sim \text{Normal}(\mu_{\text{treatment}}, \sigma_{\text{treatment}}^2)$ : effect of treatment  $j$  (random effect)

$\mu_{\text{treatment}} \sim \text{Normal}(0, 1)$

$\sigma_{\text{treatment}}^2 \sim \text{Exponential}(0.5)$

$S_1(\text{mintemp}_{(\text{lag})}, \text{ndvi}_{(\text{lag})})$ : smooth function represents interaction effects of different lagged minimum temperature and NDVI (up to order of 12)

$\beta_1 \sim \text{MultiNormal}(0, \Sigma^{-1} \lambda)$ : coefficients in smooth function  $S_1(\text{mintemp}, \text{NDVI}, \text{lag})$

$S_2(\text{precipitation})$ : smooth function represents effects of precipitation.

$\beta_2 \sim \text{MultiNormal}(0, \Sigma^{-1} \lambda)$ : coefficients in smooth function  $S_2(\text{precipitation})$

$\Sigma^{-1} \sim$  basis expansion function (supplied by *mgcv* function)

$\lambda \sim \text{Normal}(30, 25)$

$\frac{1}{\emptyset} \sim \text{Exponential}(5)$

$Z_{it} \sim \text{MultiNormal}(0, K)$ : Gaussian Process latent trend component

$$K(t, t') = g_{GP}^2 \exp\left(-\frac{|t-t'|^2}{\rho_{GP}^2}\right)$$

$g_{GP} \sim \text{Normal}(0, 0.5)$

$\rho_{GP} \sim \text{InverseGamma}(1.49, 5.67)$

We used tensor product smooth terms to specify basis functions capturing interactions between lagged minimum temperature and lagged NDVI which represent the interaction between climatic (through minimum temperature) and environmental factors (through NDVI). As marginal basis functions, thin plate regression splines were used for lagged minimum temperature (with  $k=4$  basis functions) and for lagged NDVI (with  $k=3$  basis functions). For lags, cubic regression splines (with  $k=4$  basis functions) were used. To capture remaining variation, impacts of lagged precipitation were included as an equally weighted single index smooth function, equating to a rolling sum of precipitation in the previous 12 months. Their interactions with other variables considered were omitted to avoid overfitting. We used a shrinkage version of the thin plate spline ( $bs = 'ts'$ ) with a smoothing order of  $k = 5$ .

The Negative Binomial (NB) distribution was used to account for overdispersion (Boyard et al., 2011; Cat et al., 2017; Daniel et al., 2015; Qviller et al., 2014). We used an exponential distribution for the inverse of the overdispersion parameter,  $\phi$ , of NB. This prior put greater prior belief on large values of  $\phi$ , meaning it pulls toward a Poisson if support for overdispersion is limited.

A latent trend component was added to capture any remaining autocorrelation. We identified two strategies that could capture both overdispersion and autocorrelation. Under both Poisson distribution and NB, random walk (RW) or autoregressive model of order 1 (AR1) could be used as a jumpy trend while a smooth trend can be considered under Negative Binomial distribution. Their forecasts and assumptions about the data process are different. In Poisson, both autocorrelation and overdispersion are supposed to come from the same unmeasured process, but Negative Binomial assumes different processes. We used a smooth trend under NB as we believed trend was to be smooth and to avoid competition on dispersion in case of use of NB with RW or AR1. This was modelled with a Gaussian Process function with squared exponential covariance kernel. An informative prior on the length scale was used to ensure that trends were smooth.

Models were fitted with the *mvglam()* function in *mvglam* package in R (Clark and Wells, 2022). The use of informative priors generates a starting point for sparse data problems to make formal predictions with uncertainties, and then to iteratively refine these predictions as data become available (Dietze et al., 2018). Prior distributions for stochastic parameters were chosen to be weakly informative by relegating low prior probability on impossible values while still allowing for a wide range of functional forms. Hamiltonian Monte Carlo (HMC) was used to estimate posterior distribution with the CmdStan interface (Stan Development Team, 2021a). R 4.1.0 (R Core Team, 2021) was used for processing posterior distributions. Four parallel Markov chains were considered to evaluate model convergence, and to explore joint posterior distribution with estimated effective sample sizes per iteration, Rhat (ensuring no parameters had Rhats  $> 1.05$ ), and estimator bias in the form of HMC divergences.

## 2.6. Model evaluation strategy

We used Discrete Rank Probability Score (DRPS) for out of sample forecast and two alternative posterior checking functions applied to both training and testing data to scrutinise models in a targeted way. They helped us expand our model configurations to better meet our goals of capturing both temporal and spatial variation in captures within and across plots. For evaluating forecasting performance of the final model, we used forecasting errors (observed-predicted) and related measure such as their average and some graphical representations.

### 2.6.1. Mantel Method

This test compared the overall distributions of observed and predicted counts in each plot as a test of spatial realism. We first asked whether models could simulate distributions of captures that were similar to the observed spatial distribution using a Mantel correlation test. For this, we computed Manhattan distance matrices for pairwise comparisons of observed captures in each plot. We then computed a distance matrix for the expected captures and compared these two distance matrices with a Mantel test. Predictions that more accurately reflected the spatial distribution of observations resulted in higher Mantel correlation coefficients. This correlation was produced for each posterior draw, and they were summarised in a histogram.

### 2.6.2. Cophenetic Method

To assess each model's ability to produce realistic spatiotemporal predictions, we used a cophenetic distance-based test. For this test, we computed the Manhattan distance between vectors of all counts (predicted and observed) at each timepoint. Hierarchical clustering was then used to determine which capture vectors were most similar, and we computed the cophenetic distance between observed and predicted counts for each timepoint as a measure of prediction fit. This resulted in a vector of distances representing how well a model could predict variation in captures overtime and they were summarized in a histogram. For more details of these checking functions, refer to R codes in GitHub via the link given under the Data Availability section.

## 3. Results

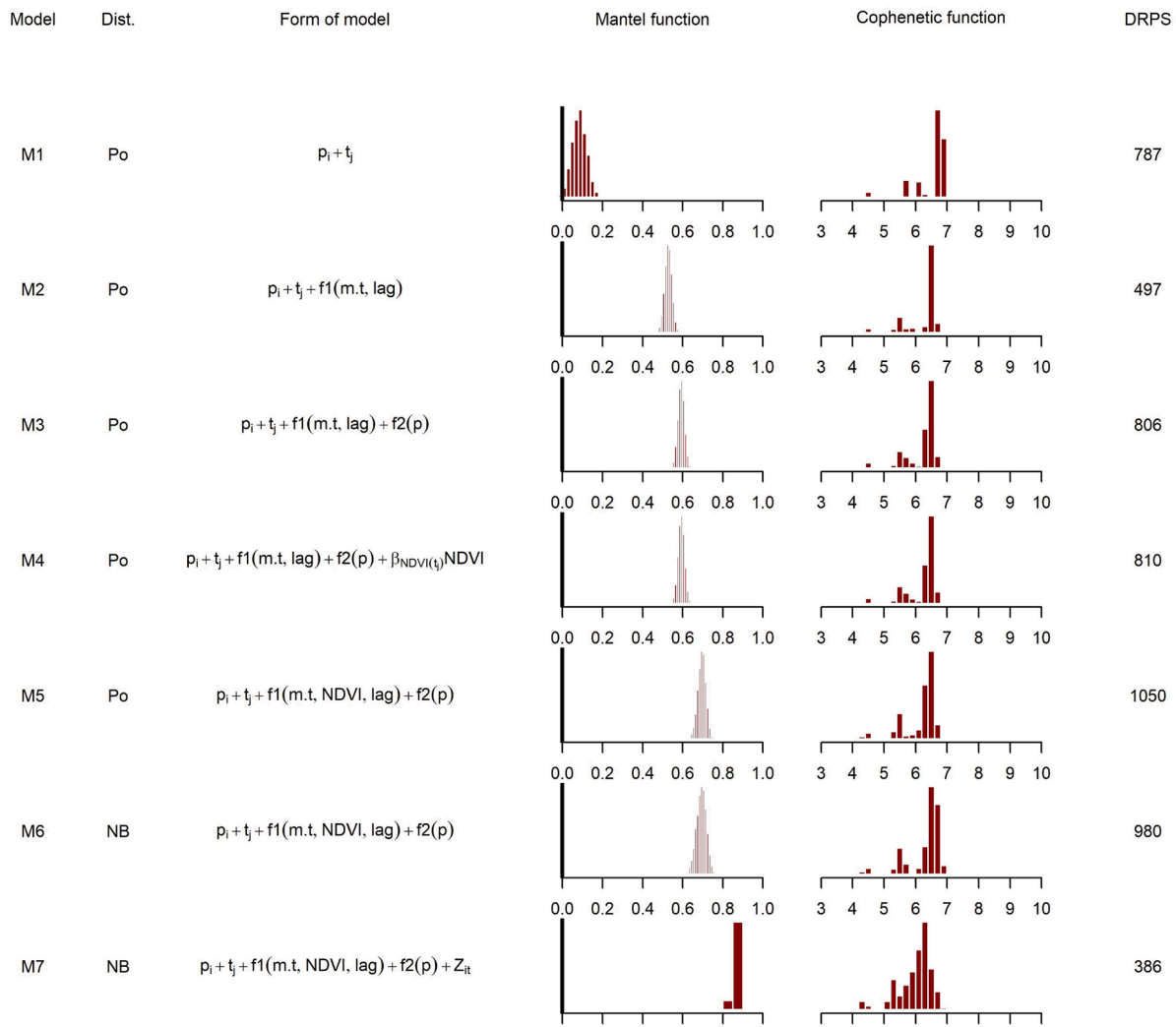
Our checking functions revealed considerable differences in model fit and forecasting quality (Fig. 1).

Shifts in the Mantel correlations (upward) and Cophenetic distances (downward) reflect the improved predictive performance due to newly added predictors (Fig. 1). All these models converged well with no major divergence issues and large effective sample sizes (Fig. S2.9). The three most evident improvements could be seen when models were upgraded with distributed lagged predictors (i.e., Model 2 vs 1, Model 5 vs 4 in Fig. 1) and when the trend was added (Model 7 vs 6 in Fig. 1). Addition of annual cumulative precipitation as a predictor to the model also improved model performance, indicated by an upward shift in Mantel function and slight downward shift in Cophenetic function (row 3 in Fig. 1). The final model gave the best performance according to both summary functions. Low values of total DRPS from models from 24 plots also confirmed the improvement of the model. However, some good models (e.g., model 5) produced higher DRPS. That could be due to higher variations in predictions in a few plots as this is the total of DRPS of model for each plot. We describe the key outcomes of the final model below.

### 3.1. Nonlinear environmental effects

Climatic factors (minimum temperature and precipitation) and environmental factors (NDVI) were considered using different structural forms, whereby our iterative model building process favoured nonlinear effects (Figs. 2 and 3).

Posterior checking functions supported the inclusion of a three-dimensional tensor product to capture lagged, nonlinear interaction effects between minimum temperature and NDVI. To better understand variation in partial impacts (conditional) of these interactions on the response (log of expected average captures), we simulated response values from the model 7 for different values of minimum temperature and NDVI while holding all other predictors constant. Interaction effects of minimum temperature and NDVI were complex and expected to vary across different lags (Fig. 2). Present captures are more influenced by minimum temperature and NDVI in 9-12 previous months (Figures 2(D, E)) than in recent months (0-6) as seen in Fig. 2 (A, B, C). The model expected to see more captures when both minimum temperature and



**Fig. 1.** Performances of seven models. Model numbers (M1-M7) are in the first column, while assumed distributions (Po-Poisson, NB-Negative Binomial) for response under each model are given in the second column. Form of each model, the opposite side of the response variable (log of mean captures), linear predictors, are in the third column (here,  $p_i$ =plot<sub>[i]</sub>,  $t_j$ =treatment<sub>[j]</sub>, m.t.=minimum temperature, lag=lags of 12 order,  $\beta$ =coefficient of random slope, NDVI=normalized difference vegetation index, p=precipitation,  $z_{it}$ =trend component). Distributions of Mantel correlation coefficients (higher is better) and Cophenetic distance (lower is better) for each model are shown in fourth and fifth columns respectively. Discrete Rank Probability Scores (DRPS) for the total number of captures in each out-of-sample timepoint are in the sixth column.

NDVI were high (lag 0), suggesting an immediate response in capture fluctuations to these drivers (Fig. 2(A)), while Fig. 2(C) and Fig. S2.2 also provide evidence that if temperature and NDVI were moderate (corresponding to spring or autumn conditions), low captures are to be expected six months later (corresponding to the following autumn and spring respectively).

Smaller number of captures can be expected when both minimum temperature and NDVI were moderate at time lags of 3-9 months (Figs. 2 (B, C, D)). According to Fig. 2(E), captures in a particular months in this year remain moderately with less variation for most of values of minimum temperature and NDVI in the same month of last year. Notably, 12-month lagged temperature and NDVI effects were markedly different from those from shorter time lags, exhibiting a strong decrease in capture rate for high NDVI values in combination with low minimum temperature values but an increase in capture rate for high NDVI values in combination with moderate minimum temperature values. These all show the significance of lagged distributed predictors in capturing the seasonality in species population fluctuations.

According to the final model, a nonlinear function was supported for capturing the effect of annual cumulative precipitation (Fig. 3(A)). When annual cumulative precipitation increased from 1 to 25 mm,

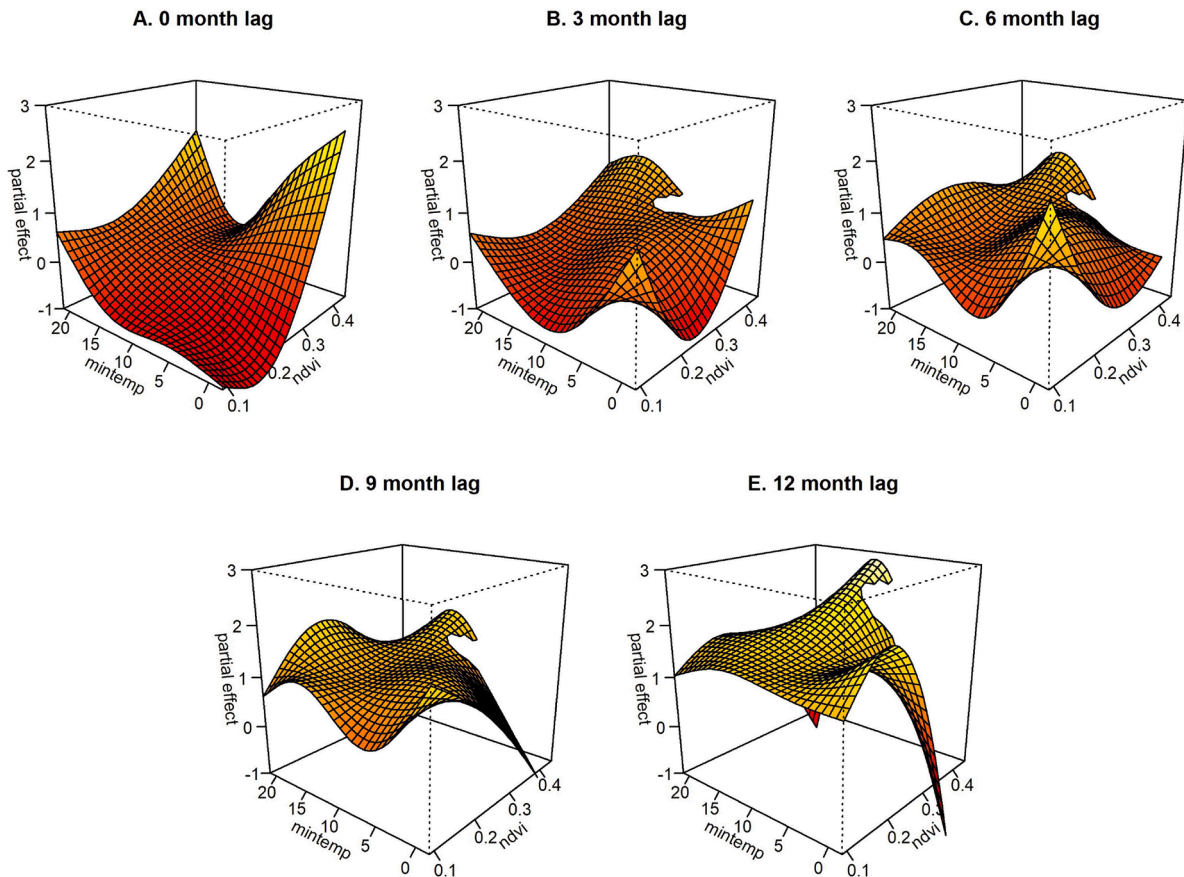
marginal captures are expected to decrease slightly, but then captures increase steadily up to about 85 mm. When it exceeds 85 mm, the number of captures is expected to decrease dramatically.

### 3.2. Hierarchical effects of plot and treatment

The role of random effects of sampling plots and treatments is also important in representing dynamics in number of rodent captures. Variation in their impacts is illustrated in Fig. S2.3 (A, B) for the first model and in Fig. 3 (B, C) for the final model. The final model did not find support for much heterogeneity in average captures across most of plots and treatments. That may be due to contribution of other model components such as the dynamic trend. However, according to the final model, average captures for plots (5,10) were lower than others while treatment 'removal' had the lowest average captures compared to other treatments (Fig. 3 (B, C)).

### 3.3. Dynamic latent trend

Latent trend components were included in the final model to capture unexplained temporal autocorrelation. The length scale values of the



**Fig. 2.** Posterior median expectations from Model 7 (including distributed lagged effects and trends) across different values of minimum temperature and NDVI under different lags. All other predictors were held constant when simulating from the model 7. Colour variation from dark red to light yellow represents the increment in expected captures.

underlying Gaussian process tended to be large (5-15), suggesting that there was considerable temporal dependence in captures when conditioning on covariate and plot/treatment effects (Fig. S2.10). This flexible trend allowed the model to produce robust probabilistic forecasts (Fig. 4 (A)). Fig. 4 (B) shows that the latent trend for plot 1 fluctuated over time. An increasing trend was estimated for early part of the study period. During 2005-2009, this trend drastically dropped and then rose gradually up to 2014, and then decline again. Fig. 4 (C) shows relative forecast uncertainty contributions by the GAM and trend components. In most of the forecasting horizon, uncertainty in the GAM component of the model represented more than 50 % of total forecast uncertainty. However, this proportion decreased gradually with length of forecasting horizon and trend captures that proportion. This also confirms the strong role of the trend component within the final model.

### 3.4. Forecasting performances and model diagnostics

To understand the model's performance in terms of forecasting at each timepoint within each sampling plot, we used posterior forecasting average residuals (observed-predicted) in raster plot setup with spatial (across plots) and temporal patterns. The majority of plots showed a mixture of overpredictions and underprediction throughout the training period (Fig. S2.11). However, there were periods when systematic patterns of over- or underprediction occurred. For example, in April 1997, Nov-Dec. in 1999, forecasts of most of experimental plots are having higher deviations from observed captures while low errors can be seen in period Oct. 1997-Jan. 1998. Some experimental plots have shown low forecasting error (e. g. 9, 23) and high forecasting error (e. g. plot 13) in most of time points as shown by side shadow plot. Forecasting errors vary across most timepoints in some plots (e. g. 2, 5, 12, 24).

Forecasts for the aggregate (total captures) series confirm that the final model most accurately replicated the dynamics of the observed data during the training and testing periods (Fig. S2.12). However, representation of zero captures by this model was lacking. On average, forecasting errors were negative, emphasizing that the model tended to overpredict (Fig. S2.13). Even though, slight trend is visible, as a whole, for captures of all sizes, forecasting errors remain at the same level.

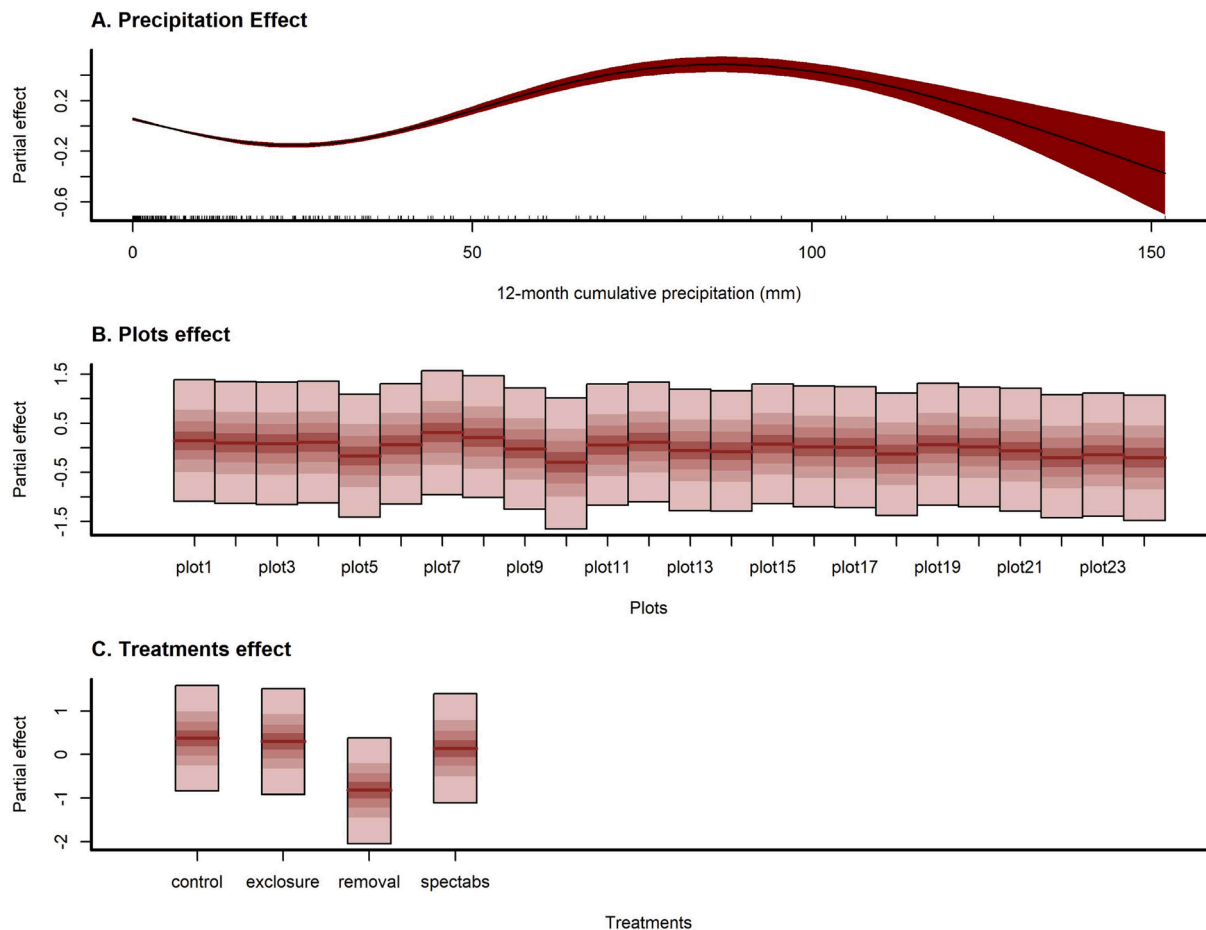
Plot-level estimates of overdispersion parameter were skewed but generally fell within a range 0-100, indicating there was support for using an over dispersed observation model (Fig. S2.14). Fig. S2.15(A) indicates constancy of model error for series 1. Remaining overdispersion of data is illustrated by deviation from straight line as shown in Fig. S2.15(B). Minor autocorrelation in residuals can be seen from Fig. S2.15(C). Further, both Fig. S2.15(C, D) provide evidence for uncaptured seasonal variation in data but their impacts are minor in magnitude.

## 4. Discussion

Our hierarchical dynamic generalized additive time series model that jointly captures lagged environmental effects through smoothed splines and unobserved temporal trends produced realistic parameter estimates and forecasts for capture rates of *C. penicillatus*.

### 4.1. Nonlinear lagged effects of climatic and environmental factor effects

Our work extends these findings by showing that nonlinear and delayed effects of such environmental drivers over time scales of as much as 12 months are important. While, minimum temperature and NDVI jointly impacted capture rates, their varied impact across different



**Fig. 3.** Partial effects of precipitation, plots, and treatments on number of captures (median) according to Model 7. A: Represents average partial effects (dark black line at the centre of confidence interval) of cumulated precipitation over 12 months period on number of captures and dark brown line is the average impact. B: Plot-level random intercepts. C: Treatment-level random intercepts. Both figures B and C are with 20 %, 40 %, 60 % and 90 % of quantiles around 50<sup>th</sup> quantile of effects from all draws for each plot.

time lags were as expected, given that temperature may impact *C. penicillatus* directly through altering foraging behaviour during extreme weather conditions and indirectly through climate effects on primary resource availability (i.e. fluctuations in rodent numbers that may be represented by changes in NDVI with time lags that present the time from abiotic exposure to biological responses across the food chain from primary resource production to rodent fecundity). Medium level of precipitation, for example, improve the growth of foods sources such as plants and seeds (Övergaard et al., 2007; Ernest et al., 2000; Vacchiano et al., 2017), and hence affecting survival and fecundity of *C. penicillatus* (Korslund and Steen, 2006). Such indirect effects may explain why it is important to account for lagged effects over several months to discover meaningful exposure-response relationships.

Distributed lags are not widely used in ecology, though ours is not the first study to highlight their usefulness in modeling ecological responses such as the lagged effect of climate on primary and secondary consumers (Gasparrini, 2011; Wells et al., 2016; Wood, 2017).

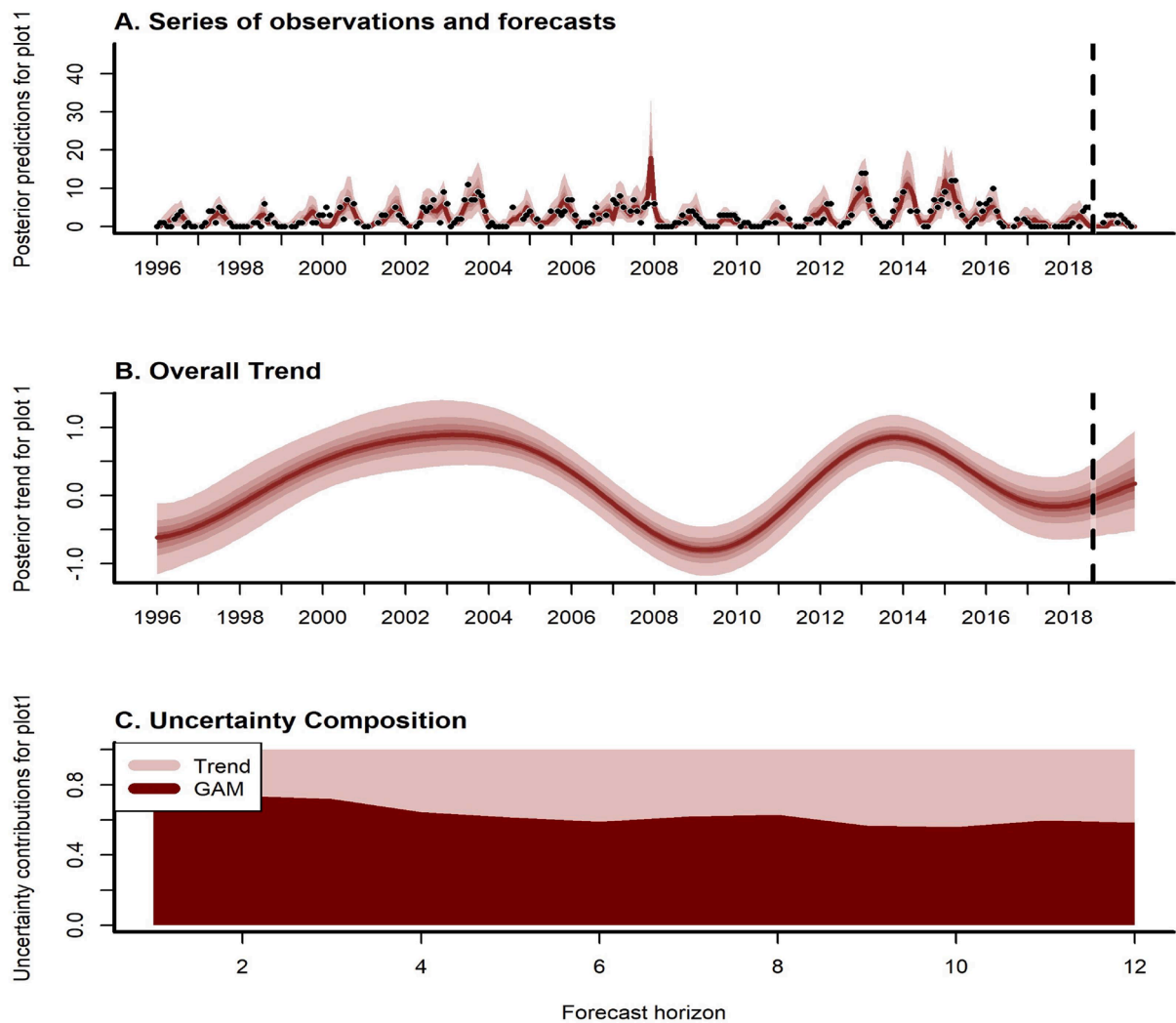
Minimum temperature and NDVI act as proxies for short-term drivers of activities of this species, likely representing the availability of resources and interacting species, that serve for example as prey and predator, provide shelter, or impact foraging conditions during extreme weather events such as drought or flooding. In fact, many rodent (e.g. agoutis) change their activities according to variation in temperature, food availability, and predation risk (Lambert et al., 2009; Suselbeek et al., 2014; Aronson et al., 1993; Oliveira-Santos et al., 2009). In general, *C. penicillatus* spends the daytime in underground burrows to protect from hot and dry air and come out at night for the food similar to

some other species (e.g. Lambert et al., 2009), and it is plausible to assume high temperature to decrease their activities (Váczsi et al., 2006). Possibly, this species reduces its activity during periods of bright moonlight, while high vegetation density should support higher levels of activity (Chidodo et al., 2019). Moreover, low winter temperatures, below the level this species can withstand means individuals stay in underground burrows in dormant state (hibernation) and are rarely captured.

The single productive season of *C. penicillatus* begins at the end of winter and female mice become pregnant throughout April. After about 4 weeks of gestation period, females give about 3-5 births in following months. As a result, fecundity and population growth in summer can be assumed to be the result of increased temperature and the environmental conditions several months early as relevant of how abiotic conditions affect primary resource availability and exposure-response relationships from foraging to reproduction.

Notably, in terms of the observable variation in capture rates, it is likely that both changes in individuals' activity rates as well as population growth are reflected in the capture data, which we believe does not necessarily impact the outcome of the forecasting exercise but does raise need for caution when interpreting the finding in terms of biological processes at work.

Minimum temperature, precipitation, and NDVI are subject to seasonal patterns with different time periods. These impacts of lags, seasonality and interactions could be behind these nonlinear impacts. Thibault & Brown, (2008) also have shown that seasonal patterns in climatic factors (e.g., rainfall) and extreme weather conditions (e.g.,



**Fig. 4.** Forecasts, trend, and uncertainty representation from Model 7 for sampling plot 1. A: Observed captures (dots) and posterior predictions (shaded ribbons). B: Posterior estimates of the overall trend component during period of training and testing data sets. In plots A and B, shaded ribbons are the bands that cover 20 %, 40 %, 60 % and 90 % of quantiles around 50<sup>th</sup> quantile of forecasts/trends from all draws. Left and right side of vertical dashed line represent training and testing data respectively. Time is in X-axis in months, but, only years are displayed. C: Present proportion of total uncertainty captured by GAM model (dark brown) and trend component (light area) during testing period (12 months in 2018), the testing period.

flood) bring nonlinear impacts on Kangaroo rodent community. NDVI is positively correlated with temperature at some stages (early, late) of growing season, while negatively and weakly correlated during mid of growing period (Wang et al., 2003). Changes (enclosure) in some rodent species capture rate impact on composition of plant communities in both grassland and shrubland and these impacts vary depending on seasons (Thibault et al., 2010). Seasonal production of vegetation (trees, shrubs, herbaceous plant) are responsible for fluctuation of several rodent species between years and geographical areas (Clement et al., 2009; Imholt et al., 2015; Reil et al., 2015).

#### 4.2. Other sources of systematic heterogeneity

We also found that pocket mouse capture rates vary across some plots and some treatments at different degrees. Though experimental plots are of the same size and experience effects of same climatic and environmental status, we can see a stochastic nature of colonisation of this species, which lead to minor but persistent difference across plots. This spatial variation in captures across plots may be due to restrictions of access of certain species through treatments, other characteristics of plots such as landscape, resources (plants, seeds), and effects from other species (e.g. prey, predatory). For example, colonization of Bailey's

pocket mouse in the site brought major impacts on usage of land and resources by the focal species (Bledsoe & Ernest, 2019; Diaz & Ernest, 2022).

Our analysis confirmed expectations of highest capture rates under the treatments 'control' and 'exclosure'. These plots are designed to either allow all rodents to freely colonize or to exclude some of the desert pocket mouse's key competitors (kangaroo rats). We also expected to see the fewest captures in the 'removal' plots, and again this expectation was confirmed by our analyses. However, only 'removal' showed reasonable differences from others in terms of estimates and their corresponding uncertainties. This also could be due to the stochastic nature of colonizations and interactions among species on individual plots, which may be why our plot-level random intercepts captured more of the systematic variation in captures than did the treatment-level intercepts.

#### 4.3. Dynamic trends to capture unmodelled temporal variation

Because we observed autocorrelation and unmodelled temporal variation in capture rates, a smooth dynamic trend was added to the model to capture this temporal variation. The trends components in our analysis tended to be non-linear and captured a large portion of



variation that were not captured by other components of the models.

Perhaps, this remaining non-linear temporal variation could be due to competitive interactions among species (Shimadzu et al., 2013). For example, Bailey's pocket mouse competes with *C. penicillatus*, (Ernest and Browns, 2001), while decline in kangaroo rats leads for a rise in pocket mice (*C. baileyi* and *C. penicillatus*) abundance (Thibault et al., 2004). Further, phenomenon such as droughts, prevalence of resources that handle prey (Shimadzu et al., 2013), changes of resources used in common (i.e., habitats) (Macchi et al., 2019; Melo et al., 2018) also could be behind remaining variation. Use of more relevant predictors will improve predictive power and accuracy in modelling non-linear relationships (Fuente et al., 2021; VanDerWal et al., 2009).

#### 4.4. The utility of iterative model expansion and checking functions

Iterative model building processes are important for selecting a model that best approximate the true data generating process. One way to do this is to fit and compare multiple models in a Bayesian framework (Gelman et al., 2020). But to identify model configurations that give reliable inference, we must evaluate whether an approximation is good or bad. Often this is done using information criteria such as DIC or BIC. However, we avoided these measures as identification of corresponding degrees of freedom of models became problematic because of the large number of random effects that were being regularized within our models. Moreover, it was not clear how these generic prediction measures relate to the specific goals of the analysis. Selecting models by using these criteria lacks a proper theoretical background and they are affected by the underlying estimation methods (Gasparrini & Leone, 2014; Obermeier et al., 2015).

Hence, we used alternative bespoke checking functions, and we demonstrate that they can identify directions for targeted model development. They were useful in evaluating models in terms of forecasting performance in individual series and in understanding magnitude of model representation of overdispersion and spatiotemporal variation in capture data across plots and time on overall capturing. Gaining feedback, improving self-experience in model building, and correcting models and methods iteratively is crucial in building a predictive capacity (Kahneman, 2013; Tetlock and Gardner, 2015), testifying quantitative predictions (Dietze et al., 2018), accelerated both basic and applied research (Murphy & Winkler, 1984; Shuman, 1989), improving forecasts and continuous decision-making (Carey et al., 2022; Dietze et al., 2018; Hobday et al., 2019). Comparison of forecasts from complicated model with a simple benchmark model is necessary (Harris et al., 2018; Lewis et al., 2022; Simonis et al., 2021).

Discussing model's performances for series of each experimental plot individually was not practical since there were 24 series. Hence, model's performances across all series were discussed together through the developed checking functions which evaluate prediction accuracy while capturing temporal and spatial variation. However, to exhibits how model performs within individual series, performances of model were discussed only for a few experimental plots (i.e., plots 1, 16).

Further, computational and manpower resources are needed for this sort of iterative Bayesian modelling (goes against time pressures in many applied settings). Generating predictions with large data set in spatio-temporal setup is computationally intensive (McDermott & Wikle, 2017).

#### 4.5. Avenues of future research

It is essential to study these impacts beyond *Chihuahuan* site (Oliver & Roy, 2015) as biodiversity, species abundance vary across ecosystems (Cárdenas et al., 2021); topography, habitat type modify effects of weather at local level and surrounding landscapes (Oliver et al., 2013). We considered only near-term prediction which provides opportunity to test models iteratively and update models quickly (Collins et al., 2013; Hobday et al., 2016; Loescher et al., 2017; Pouyat et al., 2010).

However, this study could be extended with forecasts over longer time window to better understand which model components are crucial for expanding forecasting windows (Adler et al., 2020, Benincà et al., 2008). Further, this could be extended with consideration of variability in sampling processes, random and systematic errors (Dietze et al., 2018), other species with their interaction as species are affected positively or negatively by other species (Lima et al., 2008). Use of abundance of multiple species in multivariate setup, spatial movements of treatment types over time also may be much useful in developing better forecasts.

## 5. Conclusions

Ecological forecasts are needed in applied conservation and many other areas. Our study demonstrates that model developers should consider nonlinear lagged effects when designing and critiquing probabilistic models. Considering systematic sources of variation is essential and hierarchical models play an important role in that process. We advocate a Bayesian based iterative workflow that includes building models with different complexity and structure and use as suite of checking functions rather than using DIC or BIC multi-model comparison criteria in order to fully account for dynamic abundance-covariate dynamics in complex real-world scenarios.

Information (sequence of models, their specifications, justification) of all other models fitted are in supplementary-1(S1) and other outputs are given in supplementary-2(S2).

### CRediT authorship contribution statement

**K.A.N.K. Karunarathna:** Conceptualization, Data curation, Formal analysis, Methodology, Validation, Visualization, Software, Writing – original draft. **Konstans Wells:** Methodology, Writing – review & editing. **Nicholas J. Clark:** Funding acquisition, Resources, Supervision, Writing – review & editing, Conceptualization, Data curation, Formal analysis, Methodology, Validation, Visualization, Software, Writing – original draft.

### Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Nicholas J. Clark reports financial support was provided by ARC DECRA Fellowship.

### Data availability

Portal data has been made available in the R package 'portal' in a GitHub repository (<https://github.com/weecology/PortalData>) and archived on Zenodo (<https://zenodo.org/records/1217619>). R codes of models are available from <https://github.com/kankkarunarathna/PortalAnalysis>.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2024.110648](https://doi.org/10.1016/j.ecolmodel.2024.110648).

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