Received: 24 May 2023 | Accepted: 5 December 2023

DOI: 10.1111/2041-210X.14275

Methods in Ecology and Evolution

RESEARCH ARTICLE

"Fractional replication" in single-visit multi-season occupancy models: Impacts of spatiotemporal autocorrelation on identifiability

Jeffrey W. Doser[1,2] | Sara Stoudt[3]

[1]Department of Integrative Biology, Michigan State University, East Lansing, Michigan, USA

[2]Ecology, Evolution, and Behavior Program, Michigan State University, East Lansing, Michigan, USA

[3]Department of Mathematics, Bucknell University, Lewisburg, Pennsylvania, USA

Correspondence
Jeffrey W. Doser
Email: doserjef@msu.edu

Funding information
Bucknell University's Department of Mathematics Distinguished Visiting Professor Program

Handling Editor: Xingfeng Si

Abstract

1. Understanding variation in species occupancy is an important task for conservation. When assessing occupancy patterns over multiple temporal seasons, it is recommended to visit at least a subset of sites multiple times within a season during a period of closure to account for observation biases. However, logistical constraints can inhibit re-visitation of sites within a season, resulting in the use of single-visit multi-season occupancy models. Some have suggested that autocorrelation in space and/or time can provide "fractional replication" to separately estimate occupancy probability from detection probability, but the reliability of such approaches is not well understood.
2. We perform an extensive simulation study to assess the reliability of estimates from single-visit multi-season occupancy models under differing amounts of spatial and temporal autocorrelation ("fractional replication"). We assess model performance under both correctly specified models and multiple forms of model mis-specification, and compare estimates from single-visit models to models with varying amounts of within-season replication. We also assess the reliability of single-visit models to estimate occupancy probability of ovenbirds (*Seiurus aurocapilla*) in New Hampshire, USA.
3. We found less bias in estimates from single-visit occupancy models with long-range spatial autocorrelation in occupancy probability compared to short-range spatial autocorrelation when the model is correctly specified. However, under certain forms of model mis-specification, estimates from single-visit multi-season occupancy models were biased and had low coverage rates regardless of the characteristics of the "fractional replication". In contrast, models with varying amounts of additional replication were robust to model mis-specification.
4. Our findings suggest that "fractional replication" cannot replace true replication in terms of occupancy probability identifiability and that researchers should consider the potential inaccuracies when using single-visit multi-season occupancy

Jeffrey W. Doser and Sara Stoudt contributed equally to this work.

models. We show that a little true replication can go a long way with even 10% of sites being revisited within a season leading to reasonably robust estimates even in the presence of extreme model mis-specifications. When possible, we recommend performing multiple within-season visits to at least a subset of spatial locations or integrating single-visit data with other data sources to mitigate reliance on parametric assumptions required for reliable inference in single-visit multi-season occupancy models.

KEYWORDS
autocorrelation, identifiability, model mis-specification, species distribution models

1 | INTRODUCTION

Species are influenced by a combination of abiotic and biotic processes that interact across local to macroscales to determine species distributions (MacArthur, 1972). Global change is contributing to population declines and range shifts across species and taxa at alarming rates (Rosenberg et al., 2019), with factors such as climate change (e.g. Spooner et al., 2018), habitat loss (e.g. Hallworth et al., 2021) and disease (e.g. Zipkin et al., 2020) having prominent roles. As such factors influence species and taxa across local, regional and macroscales, ecologists are increasingly interested in assessing patterns in species distributions across large spatial regions and time periods (Rollinson et al., 2021). Species distribution models (SDMs) provide a set of tools for ecologists to quantify where species occur across space and time (Guisan & Zimmermann, 2000). Data on whether or not a species was detected across a set of locations (hereafter detection-nondetection data) provide the ability to quantify species distributions without restrictive assumptions that are required to estimate species distributions using data that only contain information on where species occur (i.e. presence-only data; Yackulic et al., 2013). When modelling detection–nondetection data, it is crucial to account for imperfect detection, or the failure to observe a species during sampling when it is in fact present, as ignoring such biases in the data collection can result in biased estimates of species distributions (MacKenzie et al., 2002) and their relation to environmental covariates over space and time (Kéry & Schmidt, 2008).

Occupancy models are a specific type of SDM that explicitly account for imperfect detection by separately modelling the true, ecological process (i.e. occupancy) from the observation (i.e. detection) process in a hierarchical or multi-level framework (MacKenzie et al., 2002; Tyre et al., 2003). In order to separately estimate occupancy probability from detection probability, multiple surveys, or visits, are typically required for at least a subset of locations during a period of "closure" in which the true occupancy status of the species of interest is assumed to be constant. However, the additional time and resources it requires to perform multiple visits at survey locations can be prohibitively costly in many monitoring programs, particularly when monitoring across large spatiotemporal regions (von Hirschheydt et al., 2023). Determining the balance between the number of spatial locations that are surveyed versus the number of temporal replicates performed at a given location should be determined as part of the survey design phase (Guillera-Arroita et al., 2010; MacKenzie & Royle, 2005; Wood et al., 2019) and often depends on the specific objectives of the monitoring program (Guillera-Arroita & Lahoz-Monfort, 2012). Given the variation in monitoring programs and their objectives, simulation studies are often the most viable solution to determine an adequate balance of surveyed sites versus temporal replicates to meet specific objectives (DiRenzo et al., 2023; Kéry & Royle, 2021).

Due to the logistical and financial costs of performing multiple surveys at sites within a period of closure, researchers have explored the use of alternative approaches to disentangle occupancy from detection, including the use of spatial sub-sampling (e.g. MacKenzie & Royle, 2005; Sadoti et al., 2013), a time-to-first-detection protocol (Garrard et al., 2008) or a multiple-observer approach (MacKenzie & Royle, 2005). Further, there has been considerable interest in the use of single-visit occupancy models, which seek to disentangle occupancy from detection with only a single visit to each site (Lele et al., 2012). Such models require continuous covariates that separately influence occupancy probability and detection probability to disentangle estimates of occupancy from those of detection. However, the reliability of these approaches to separately estimate occupancy probability from detection probability is widely debated in statistical ecology (Knape & Korner-Nievergelt, 2015; Solymos & Lele, 2016). Such discussions often focus on identifiability or the requirement that equivalent observable distributions imply the same values of a property of interest. In particular, many have cautioned against the use of single-visit approaches as their identifiability is sensitive to the choice of link function and other parametric assumptions (Knape & Korner-Nievergelt, 2015; Stoudt et al., 2023). Recently, mathematical arguments have been made that suggest single-visit models can only provide information on the relative probability of presence (Wang et al., 2022; Wang & Stone, 2019), while others show single-visit data can contribute useful information when combined with other data sources (Doser, Leuenberger, et al., 2022; Lauret et al., 2021).

Single-visit approaches are particularly attractive when seeking to understand occupancy patterns over both space and time. When studying occupancy patterns and/or trends over multiple seasons, general recommendations are to follow the "robust design" in which sites are sampled over a set of seasons in which occupancy is allowed to change (i.e. primary time periods) and then within each season at least a subset of sites is visited multiple times during a period of population closure (i.e. secondary replicates; Kéry & Royle, 2021). The aforementioned logistical constraints are potentially more problematic in multi-season analyses as there are now multiple temporal levels of sampling at any given site. Further, many historical, long-term monitoring programs initiated prior to the development of occupancy models, such as breeding bird atlases and other national scale monitoring programs, only sample a site once per season. Developing statistically robust approaches to analyse such datasets that provide long time-series of species population dynamics is an important task for understanding global change effects on biodiversity. Recently, a variety of single-visit methods have been proposed explicitly for modelling spatiotemporal patterns in occupancy over multiple seasons (Hepler et al., 2018; Peach et al., 2017). These approaches are promising as spatial and temporal autocorrelation within and among sites between seasons may provide a form of "fractional replication" that can help distinguish occupancy from detection probability (Bellier et al., 2016; Hepler et al., 2018; Hines et al., 2010; section 4.7 in Kéry & Royle, 2021), similar to identifiability of process error from observational error in state-space models (e.g. Auger-Méthé et al., 2016). Such investigations show that when the model is correctly specified, it can recover estimates of occupancy and detection probability given a large enough dataset. Data points that are highly correlated in space and/or time are similar enough to provide partial replication to one another, and models are then able to borrow strength across these single visits. However, since many of the critiques of single-visit approaches hinge on parametric assumptions within the model specification, additional assessments of multi-season occupancy models under different forms of model mis-specification are needed to provide a more complete assessment of such "fractional replication" and whether they can reliably be used with single-visit data.

Here we perform an extensive simulation study to assess how different amounts of spatial and temporal autocorrelation (hereafter "fractional replication") influence the reliability of estimates from single-visit multi-season spatial occupancy models. We perform simulations using both correctly specified models and four different forms of model mis-specification, providing a more complete assessment of single-visit multi-season spatial occupancy models and their reliability when parametric assumptions may be broken. Additionally, we compare model performance of single-visit models to models with a subset of sites visited twice (so-called "mixed" designs; von Hirschheydt et al., 2023), all sites visited twice, and all sites visited five times to compare how different amounts of fractional replication and model mis-specification impact estimates under single-visit and multiple-visit approaches. As an empirical assessment of the reliability of single-visit approaches, we compare occupancy probability estimates of ovenbirds (*Seiurus aurocapilla*) across Hubbard Brook Experimental Forest in New Hampshire, USA using varying amounts of replicated data. We hope this investigation will help inform data-collection and modelling decisions to ensure that inference drawn from statistical models using the resulting data are accurate and reliable under best case scenarios but are also robust to inevitable model mis-specification.

2 | MATERIALS AND METHODS

Here we describe a multi-season spatial occupancy model as implemented in the function `stPGOcc` in the `spOccupancy` R package (Doser, Finley, et al., 2022). Alternative approaches exist to model occupancy dynamics across space and time, such as dynamic occupancy models (MacKenzie et al., 2003) and alternative formulations of multi-season spatial occupancy models (Hepler et al., 2018; Rushing et al., 2019). However, we focus our simulations and case study on the subsequently described model as it is easily implemented via user-friendly and computationally efficient software and similar approaches have been used in a variety of recent applications (e.g. Diana et al., 2023).

2.1 | Multi-season spatial occupancy model

Let $z_t(\boldsymbol{s}_j)$ denote the presence (1) or absence (0) of a species of interest at site j with spatial coordinates $\boldsymbol{s}_j$ during primary time period (i.e. season) t, with $j = 1, \dots, J$ and $t = 1, \dots, T$. We model $z_t(\boldsymbol{s}_j)$ according to

$$z_t(\boldsymbol{s}_j) \sim \text{Bernoulli}(\psi_t(\boldsymbol{s}_j)), \tag{1}$$

where $\psi_t(\boldsymbol{s}_j)$ is the occupancy probability at site j during season t. We model $\psi_t(\boldsymbol{s}_j)$ as a function of space and/or time-varying covariates as well as random effects to account for spatial and temporal autocorrelation. More specifically, we have

$$\text{logit}(\psi_t(\boldsymbol{s}_j)) = \boldsymbol{x}_t(\boldsymbol{s}_j)^\top \boldsymbol{\beta} + \text{w}(\boldsymbol{s}_j) + \eta_t, \tag{2}$$

where $\boldsymbol{\beta}$ are the effects of space and/or time varying covariates $\boldsymbol{x}_t(\boldsymbol{s}_j)$, $\text{w}(\boldsymbol{s}_j)$ is a spatial random effect and η_t is a temporal random effect. The temporal random effect η_t accounts for temporal autocorrelation in occupancy probability that is not explained by the covariates $\boldsymbol{x}_t(\boldsymbol{s}_j)$. We model η_t using a first-order autoregressive (i.e. AR(1)) covariance structure in which we estimate a temporal variance parameter σ^2_T and a temporal correlation parameter ρ. More specifically, the covariance between any two time points t and t' is $\sigma^2_T \rho^{|t-t'|}$.

The spatial random effect accounts for residual spatial autocorrelation in occupancy probability that is not explained by the covariates $\boldsymbol{x}_t(\boldsymbol{s}_j)$. We envision $\text{w}(\boldsymbol{s}_j)$ as arising from a zero-mean spatial Gaussian process, such that

$$\text{w}(\boldsymbol{s}) \sim \text{Normal}(0, \Sigma(\boldsymbol{s}, \boldsymbol{s}', \boldsymbol{\theta})), \tag{3}$$

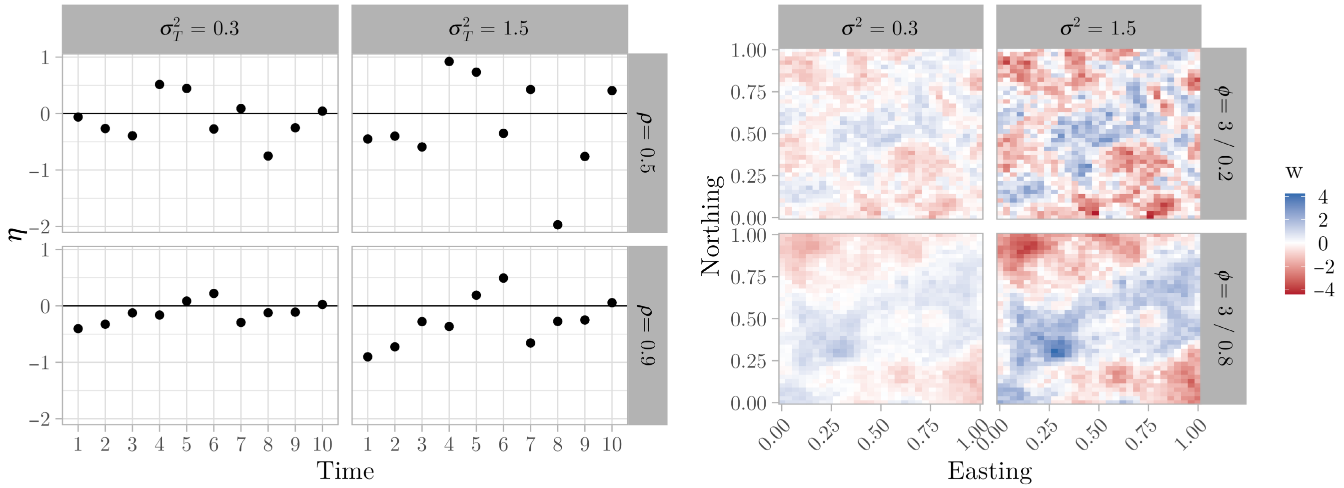

FIGURE 1 Effects of simulation parameter values for the temporal variance (σ_T^2) and the temporal correlation (ρ) parameters on temporal autocorrelation (left) and effects of simulation parameter values for the spatial variance (σ^2) and spatial decay (ϕ) parameters (right) on spatial autocorrelation.

where $\Sigma(\boldsymbol{s}, \boldsymbol{s}', \boldsymbol{\theta})$ is a $J \times J$ spatial covariance matrix with values that depend on the distances between any pair of sites $\boldsymbol{s}$ and $\boldsymbol{s}'$ and a set of parameters $\boldsymbol{\theta}$ that determine the pattern of spatial autocorrelation according to a spatial correlation function. Here, we use an exponential correlation function such that $\boldsymbol{\theta} = \{\sigma^2, \phi\}$, where σ^2 is a spatial variance parameter controlling the magnitude of $\mathbf{w}$ across space and ϕ is a spatial decay parameter controlling the range of spatial dependence. For computational efficiency, we model $\mathbf{w}$ using nearest neighbour Gaussian processes (NNGPs; Datta et al., 2016), an efficient alternative to the full Gaussian process that provides nearly identical inference. See Doser, Finley, et al. (2022) for further details.

Let $y_{t,k}(\boldsymbol{s}_j)$ denote the detection (1) or nondetection (0) of the species of interest at site j during season t during visit k for a total of $k = 1, \dots, K_{t,j}$ visits within some smaller time period when the closure assumption is reasonable. Note that the number of surveys can vary across different site/season combinations (i.e. not all sites need be surveyed in a given season). To account for imperfect detection, we model $y_{t,k}(\boldsymbol{s}_j)$ conditional on the true latent occupancy status $z_t(\boldsymbol{s}_j)$ following

$$y_{t,k}(\boldsymbol{s}_j) \mid z_t(\boldsymbol{s}_j) \sim \text{Bernoulli}(p_{t,k}(\boldsymbol{s}_j) z_t(\boldsymbol{s}_j)), \tag{4}$$

where $p_{t,k}(\boldsymbol{s}_j)$ is the probability of detecting the species at site j during visit k given the species is truly present at the site in season t. We model detection probability as a function of site and/or observation-level covariates according to

$$\text{logit}(p_{t,k}(\boldsymbol{s}_j)) = \mathbf{v}_{t,k}(\boldsymbol{s}_j)^{\top} \boldsymbol{\alpha}, \tag{5}$$

where $\boldsymbol{\alpha}$ is a vector of regression coefficients (including an intercept) that describe the effect of site and/or observation covariates $\mathbf{v}_{t,k}(\boldsymbol{s}_j)$ on detection. When only one visit is obtained at each site j during each season t (i.e. $K = 1$), the aforementioned model becomes a single-visit multi-season spatial occupancy model.

2.2 | Simulation studies

We used simulation to assess the identifiability of occupancy probability and detection probability in single-visit multi-season occupancy models with varying amounts of "fractional replication". We compared identifiability of single-visit models to three models with varying amounts of replication (e.g. 10% of sites visited twice, all sites visited twice, all sites visited five times) to assess the relative benefits of "fractional replication" compared to standard replication (i.e. multiple visits). We assessed model performance in scenarios where the model was correctly specified, as well as four mis-specification scenarios in which we varied the functional form (i.e. the link function) between occupancy/detection probability and covariates when simulating the data. These simulations allowed us to understand identifiability patterns in the potentially likely scenario that our model does not perfectly represent the true data-generating processes.

2.2.1 | Simulation Study 1: Impacts of "fractional replication"

We performed a simulation study to understand how differing characteristics of spatial and temporal autocorrelation ("fractional replication") influenced identifiability of single-visit multi-season spatial occupancy models compared to models with differing amounts of replication. Here we assume the model is correctly specified, such that the true occupancy status of the species is simulated exactly following Equations 1–3. In a second step, we simulate detection–nondetection datasets with different amounts of replication following Equations 4 and 5.

More specifically, we generated occupancy of a simulated species over $T = 10$ primary time periods and a study region comprised of $J = 1200$ sites, which were distributed evenly along a

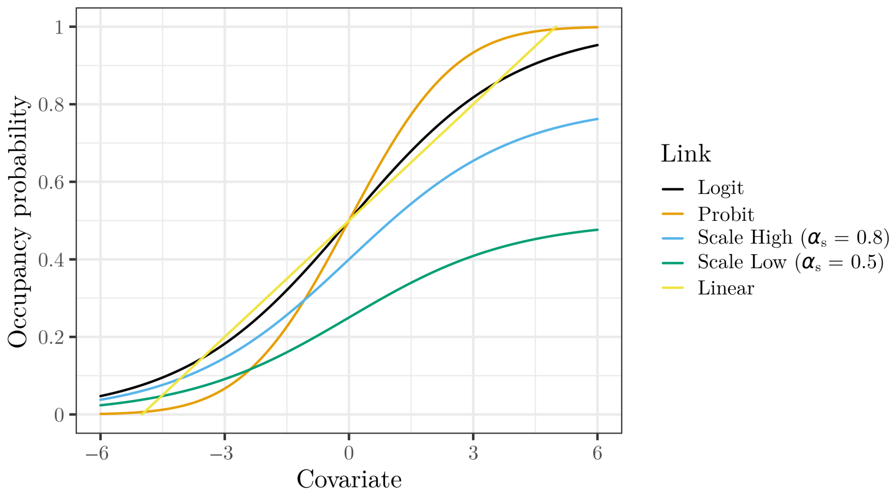

FIGURE 2 Functional forms of the five link functions used in the simulation studies. The "Scale High" and "Scale Low" functions correspond to a scaled logistic function with scale parameter α_s set to 0.8 and 0.5, respectively.

30×40 unit grid, analogous to a systematic sampling design. We simulated occupancy of the species at each site and primary time period following Equations 1 and 2, where we assumed occupancy probability was a function of an intercept $(\beta_0 = 0)$, a single covariate that had a moderate positive effect on occupancy probability $(\beta_1 = 0.5)$, and separate spatial $(\mathrm{w}(\mathbf{s}_j))$ and temporal (η_t) random effects. We varied the two parameters (σ^2 and ϕ) that governed the spatial autocorrelation and the two parameters (σ_T^2 and ρ) that governed the temporal autocorrelation to compare model performance under different "fractional replication" scenarios. Figure 1 shows the effect of the simulated parameter values on the resulting temporal random effects ($\boldsymbol{\eta}$) and spatial random effects ($\mathbf{w}$). Specifically, we varied the spatial variance parameter σ^2 to either low (0.3) or high (1.5) values, corresponding to small and large variability in occupancy probability across space, respectively. We set the spatial decay parameter ϕ to either high (3 / 0.2) or low (3 / 0.8), which corresponds to short range and long range spatial autocorrelation, respectively. More specifically, because we simulate data along a unit grid, $\phi = 3/0.2$ corresponds to an effective spatial range of 20% of the study area, while $\phi = 3/0.8$ corresponds to an effective spatial range of 80% of the study area (Figure 1, right panel). We set the temporal variance parameter (σ_T^2) to either low (0.3) or high (1.5), which influenced the magnitude of variability in the random effects. For the temporal correlation parameter (ρ), we set the correlation to low (0.5) or high (0.9), which influenced the amount of correlation in the resulting temporal random effects (Figure 1, left panel). All combinations of these parameter values resulted in 16 different "fractional replication" scenarios.

We generated 100 detection–nondetection datasets with 5 visits per site for each of the 16 "fractional replication" scenarios, resulting in a total of 1600 simulated datasets. Detection probability was simulated as a function of an intercept $(\alpha_0 = 0)$ and a single observational-level covariate that had a moderate negative effect on detection probability $(\alpha_1 = -0.5)$. We simulated all occupancy and detection covariates as arising from a normal distribution with mean zero and standard deviation one. We subsequently subset each of the complete datasets to compare model performance under four differing amounts of replication. More specifically, we compared models fit with (1) one visit per site (i.e. single-visit design); (2) 10% of sites visited twice within a season, with all other sites visited once (i.e. mixed design); (3) all sites visited twice (i.e. double-visit design); and (4) all sites visited five times (i.e. five-visit design, the full dataset). For each dataset and amount of replication, we fit a Bayesian multi-season spatial occupancy model using Markov chain Monte Carlo (MCMC) with the `stPGOcc` function in `spOccupancy` using default vague prior distributions (see Doser, Finley, et al., 2022 for details on default prior settings).

For comparison with the single-visit multi-season occupancy model, we also fit a logistic regression model with spatial and temporal autocorrelation that completely ignored detection probability. We fit this model using single-visit data, as such a model is often viewed as an alternative to fitting a multi-season single-visit occupancy model when there is no within-season replication. The model followed exactly Equations 1–3, except we treated the detection–nondetection data $y_{t,k}(\mathbf{s}_j)$ as the true occupancy status in Equation 1 and did not account for detection probability as in Equations 4 and 5. We fit this model using the `svcTPGBinom` function in `spOccupancy`.

We ran each model for 25,000 iterations with a burn-in period of 15,000 iterations and a thinning rate of 10, resulting in a total of 1000 samples from the posterior distribution. We assessed convergence of a subset of simulations under all 16 "fractional replication" scenarios by using the potential scale reduction factor (Brooks & Gelman, 1998) and visual assessment of traceplots calculated from three MCMC chains with divergent starting values. This indicated that these MCMC settings were sufficient to achieve convergence and adequate mixing of the MCMC chain for the latent occupancy probabilities $(\psi_t(\mathbf{s}_j))$. We compared model performance across the different scenarios by calculating occupancy probability average bias (i.e. estimated value minus true simulated value) and coverage rates of 95% credible intervals (i.e. the percentage of the true occupancy probabilities contained within the 95% credible interval).

2.2.2 | Simulation Study 2: Impacts of "fractional replication" under model mis-specification

In this simulation study, we assessed single-visit multi-season spatial occupancy model performance under the same set of 16 "fractional replication" scenarios, but we now assessed performance under four model mis-specification scenarios to provide a more robust assessment of single-visit multi-season spatial occupancy models and their ability to disentangle occupancy from detection. Specifically, we varied the link function used to relate occupancy and detection probability to covariates when generating the simulated datasets (Figure 2). We subsequently fit the multi-season spatial occupancy model described in Section 2.1 to each dataset, which uses a logit link function to relate both occupancy and detection. Following Stoudt et al. (2023), by exploring parameter estimates when this parametric assumption is not met, we can assess how identifiability of single-visit multi-season spatial occupancy models is dependent on parametric assumptions. We consider four mis-specified forms of the functional relationship between occupancy (and detection) and covariates: (1) probit, (2) scaled logistic bounded at 0.8, (3) scaled logistic bounded at 0.5 and (4) linear. The probit function is linearly related to the logit function across most of the range $[0, 1]$ but has shorter tails at the range bounds compared to the logit (Figure 2). The scaled logistic has a similar sigmoidal form between occupancy probability and covariates as the logit function but asymptotes at a maximum value determined by a scale parameter, α_s. This approximates a scenario where the conditions needed for a species to almost certainly appear at a site are not met in the sampling region. Such a situation can occur when the sampling region does not contain the entirety of a species' range and thus the ideal habitat of the species may not be present in the sampling region. We assess model performance in a scenario where occupancy is bounded at 0.5 and 0.8. The linear functional relationship assumes a linear relationship between occupancy probability and covariates, with simulated parameter values ensuring probabilities fall between zero and one. Note that in each scenario, the functional relationships are used for both occupancy and detection probability. However, for the scaled logistic scenario, the scale parameter on detection is equal to $\frac{1}{\alpha_s}$. This makes the product of occupancy and detection identifiable but multiple data-generating processes have the same observable distributions yet imply differing average occupancy and detection probabilities. We consider the probit mis-specification to be relatively mild and the scaled logistic mis-specification to be increasingly extreme as the scaling parameter decreases. We expect the linear mis-specification to be somewhere in between in terms of assumption violation extremeness.

For each of the 4 mis-specification scenarios, we explored model performance under the same 16 "fractional replication" scenarios and 4 replication scenarios described in Simulation Study 1. We also fit a logistic regression model using single-visit data as described in Simulation Study 1 as a potential alternative to the multi-season single-visit occupancy model. All parameter values were assigned the same values as in Simulation Study 1, with the only difference being the link functions used to simulate the data. For the linear link function, we used different parameter values for the regression coefficients and variance parameters to ensure the majority of the occupancy and detection probability values fell between zero and one ($\beta_0 = 0.5$, $\beta_1 = 0.1$, $\alpha_0 = 0.5$, $\alpha_1 = 0.1$, $\sigma^2 = \{0.005, 0.02\}$, $\sigma_T^2 = \{0.005, 0.02\}$). We fit the multi-season spatial occupancy model using a logit link function as described in Section 2.1 to each of the simulated datasets, with all MCMC criteria and model performance criteria identical to Simulation Study 1.

2.3 | Ovenbird case study

As an exploration of how single-visit multi-season spatial occupancy models perform on an empirical dataset, we applied single-visit and multiple-visit multi-season spatial occupancy models to estimate occupancy probability of ovenbirds across Hubbard Brook Experimental Forest (HBEF), a 3600 ha northern hardwood forest in New Hampshire, USA (Rodenhouse & Sillett, 2021). Observers annually record the numbers of all bird species at 50 m radius point count surveys across 373 sites, most of which are surveyed three times per breeding season since 1999. Here we used detection–nondetection data from 2010 to 2018. We compared estimates from 11 models with varying amounts of within-season replication to assess the sensitivity of model estimates under varying amounts of replication. The 11 models varied from using a maximum of 1 visit per site within a season to using a maximum of 3 visits per site within a season (i.e. the full data set). Note that the dataset was unbalanced (i.e. not all sites were surveyed every year and not all sites were surveyed three times in a year when they were surveyed). All models included the same covariates on occupancy probability and detection probability. We modelled occupancy probability as a function of linear and quadratic effects of elevation, a linear effect of annual breeding season (i.e. May–June) total precipitation, a linear effect of annual maximum breeding season temperature (i.e. May–June), a spatial random effect following Equation 3, and an AR(1) temporal random effect. Precipitation and temperature were calculated using the Parameter-elevation Regression on Independent Slopes Model (PRISM; Daly et al., 2008). We modelled detection probability as a function of linear and quadratic effects of ordinal date and a linear effect of the time of day the survey occurred.

We fit all models using MCMC via the `spOccupancy` package (Doser, Finley, et al., 2022), specifying vague priors for all model parameters (Supplemental Information S1). For all models, we ran three chains, each with 40,000 iterations with a burn-in period of 20,000 and a thinning rate of 20, resulting in a total of 3000 samples from the posterior distribution. Convergence was assessed using the potential scale reduction factor (Brooks & Gelman, 1998) and effective sample size calculated using the `coda` package (Plummer et al., 2006).

3 | RESULTS

3.1 | Simulation Study 1

Single-visit multi-season spatial occupancy models showed low bias across all 16 "fractional replication" scenarios when models were correctly specified. Scenarios with long-range spatial autocorrelation (i.e. low ϕ, Columns 3–4, Figure 3) had less bias compared to models with short-range spatial autocorrelation (i.e. high ϕ, Columns 1–2, Figure 3). This can be seen by more curvature in the solid line in the first two columns of Figure 3, with large occupancy probabilities being underestimated and small occupancy probabilities being overestimated. Further, the precision of average absolute bias in occupancy probability across the 100 simulations was higher under long-range spatial autocorrelation compared to short-range spatial autocorrelation (Supplemental Information S1, Figure S5 black lines). This can also be seen by the wider spread of the grey lines (representing variability across simulations) in the first two columns of Figure 3. Scenarios with high spatial variability (Columns 2 and 4, Figure 3) generally had higher bias than scenarios with low spatial variability (Columns 1 and 3, Figure 3), although this pattern was less evident when there was long-range spatial autocorrelation. The effects of temporal autocorrelation were less evident across the different scenarios and had minimal impacts on bias (compare across rows within a column, Figure 3). When temporal variance was high, there was more variability in estimates across simulations compared to scenarios with low temporal variance (grey lines in Rows 1–2 vs. Rows 3–4 in Figure 3). The same general patterns were found for "mixed" design models, double-visit models, and five-visit models (Supplemental Information S1, Figures S6–S8). Under all "fractional replication" scenarios, estimated occupancy probabilities

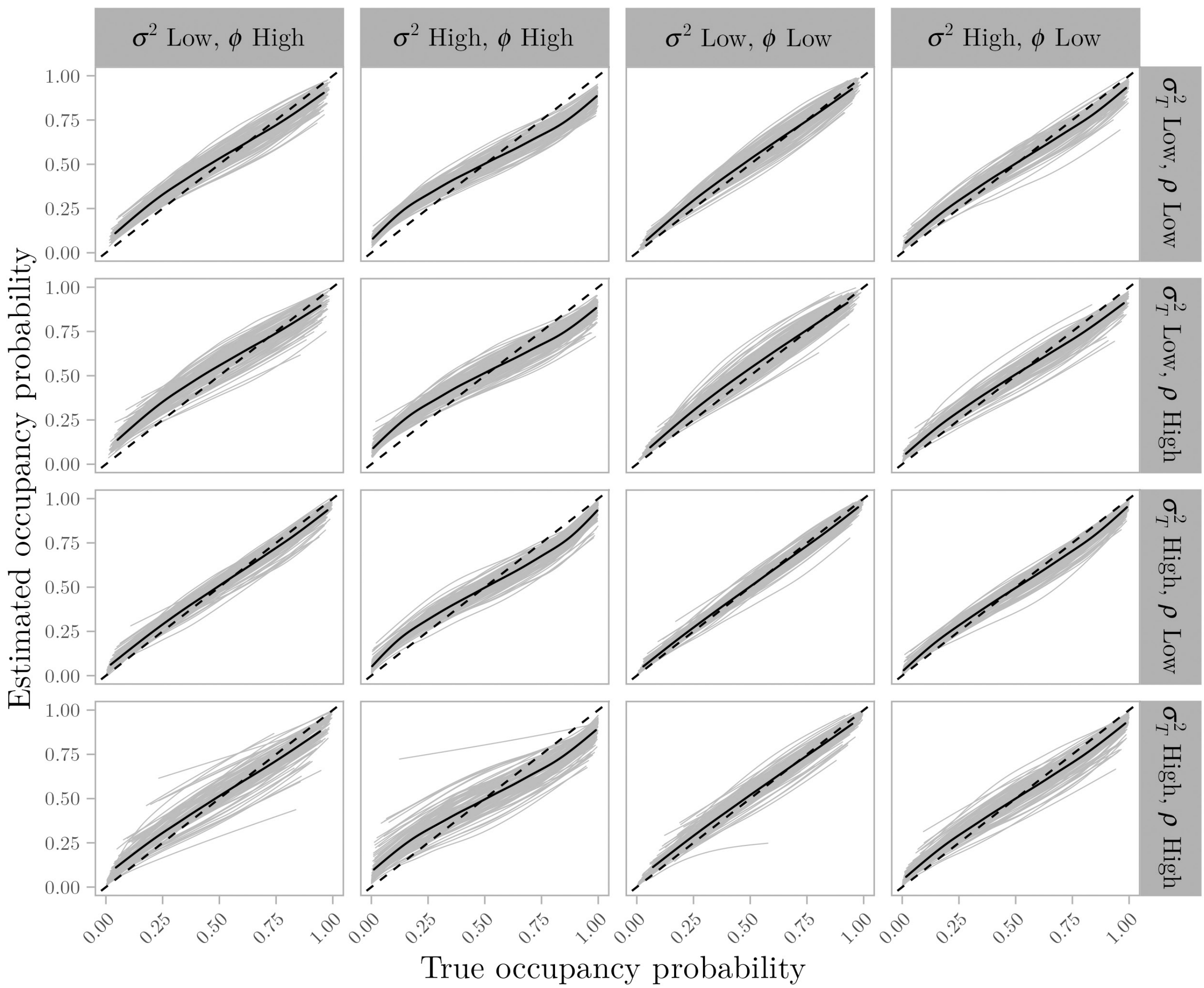

FIGURE 3 Accuracy of estimated occupancy probabilities in single-visit occupancy models with a logit link function under differing scenarios of spatial and temporal autocorrelation. The solid lines are smooth curves estimated using cubic splines that relate the estimated occupancy values to the true values. Estimates become more unbiased as the solid lines approach the one-to-one line (the black dashed line). Each solid grey line represents a single simulation, with the solid black line being the mean across all simulations.

from a logistic regression model ignoring imperfect detection had large-magnitude negative bias (Supplemental Information S1, Figures S3 and S4).

3.2 | Simulation Study 2

Under most forms of model mis-specification, estimates from single-visit multi-season spatial occupancy models had bias that was substantially higher compared to estimates from models with any amount of replication (Figures 4 and 5, and Supplemental Information Figures S1 and S2). This can be seen by the coloured lines (representing results from different model mis-specification scenarios) deviating greatly from the black line (representing results from the correctly specified model). Regardless of the amount of replication, all models were relatively robust to probit mis-specification, with average bias being comparable to the correctly specified scenario (compare orange lines to black lines in Figures 4 and 5). Under the two scaled-logistic mis-specification scenarios and the linear mis-specification scenario, single-visit models had substantial bias and low coverage rates (Table 1). For example, occupancy probabilities were overestimated in both scaled-logistic cases (the blue and green lines lie completely above the dashed line in Figure 4), more so for the scenario scaled more extremely (green more off of the line than blue). The linear mis-specification can both under and overestimate occupancy probabilities depending on the autocorrelation scenario (the yellow lines change patterns across the grid in Figure 4). Coverage rates decline based on the extremeness of the model mis-specification with the scaled-logistic being the most troublesome and the linear mis-specification being less so. In contrast to the correctly specified scenario, the amount and type of "fractional replication" did not have any effect on single-visit model estimates when the true link function was scaled-logistic or linear, suggesting that "fractional replication" cannot overcome a lack of identifiability when the model is mis-specified. Estimates from "mixed design", two-visit, and five-visit multi-season spatial occupancy models showed more robustness and less bias in all mis-specification scenarios (Figure 5 and Supplemental Information Figures S1 and S2, S4–S6), and coverage rates for the scaled logistic and linear mis-specification scenarios were far closer to the nominal 95% compared to the single-visit models. Each coloured line (representing a different model mis-specification) in Figure 5 is much closer to the dashed line (representing the truth), and systematic over or underestimation no longer occurs. Importantly, within any mis-specification scenario, incorporating even a small number of additional visits as done in the "mixed design" simulations resulted in larger improvements in bias compared to any changes observed across "fractional replication" scenarios. Noticeably, estimates from a logistic regression model ignoring imperfect detection had substantial negative bias that was more extreme than the bias in single-visit multi-season occupancy models (Supplemental Information S1, Figures S3 and S4).

3.3 | Ovenbird case study

Estimates of occupancy probability and detection probability from single-visit models were substantially different compared to estimates from models with any amount of replication (Figure 6). The single-visit model predicted high detection probability (mean = 0.90) and moderate occupancy probability (median = 0.43), but estimates quickly changed and generally stabilized after incorporating even small amounts of replication. This is evidenced by the clear elbows in the curves shown in Figure 6 when changing from a single-visit model (the leftmost point) to mixed design models. Differences were most evident in the intercepts for both occupancy and detection probability but were also observed to a lesser extent for covariate effects.

4 | DISCUSSION

As conservation and management require an understanding of the environmental drivers that influence population dynamics across space and time, there is an increasing need for reliable statistical tools that can leverage widely available, cost-effective data sources, such as single-visit detection–nondetection data. Here we performed an extensive simulation study to assess how different amounts of spatial and temporal autocorrelation (i.e. "fractional replication") influenced the reliability of estimates from single-visit multi-season spatial occupancy models. We found that long-range spatial autocorrelation can reduce bias in estimates from single-visit occupancy models when the model is correctly specified. However, we showed that under certain forms of model mis-specification, single-visit multi-season spatial occupancy models often had high bias and low coverage rates regardless of the characteristics of the "fractional replication", while models with varying amounts of additional replication (i.e. "mixed design" with 10% of sites visited twice within a season, two visits at each site, five visits at each site) were robust to model mis-specification. These results are consistent with studies looking at model mis-specification in single-season single-visit occupancy models (Knape & Korner-Nievergelt, 2015; Stoudt et al., 2023) and suggest that the "fractional replication" obtained in multi-season occupancy models by sharing information across space and time cannot substitute true replication.

For single-visit models that were correctly specified, we found higher accuracy (i.e. lower bias) in estimated occupancy probability values when the effective spatial range was long (e.g. ϕ was low; Figure 3). When the effective spatial range is long relative to the size of the study region and average distance between sites, the correlation in occupancy probability between sites is large and the model structure is able to "share information" across space. This pattern suggests that a cluster sampling design in single-visit monitoring programs could be used to induce "fractional replication" between sites that are close together and reduce bias in estimated occupancy probability values. For example, Pacifici et al. (2016) used a

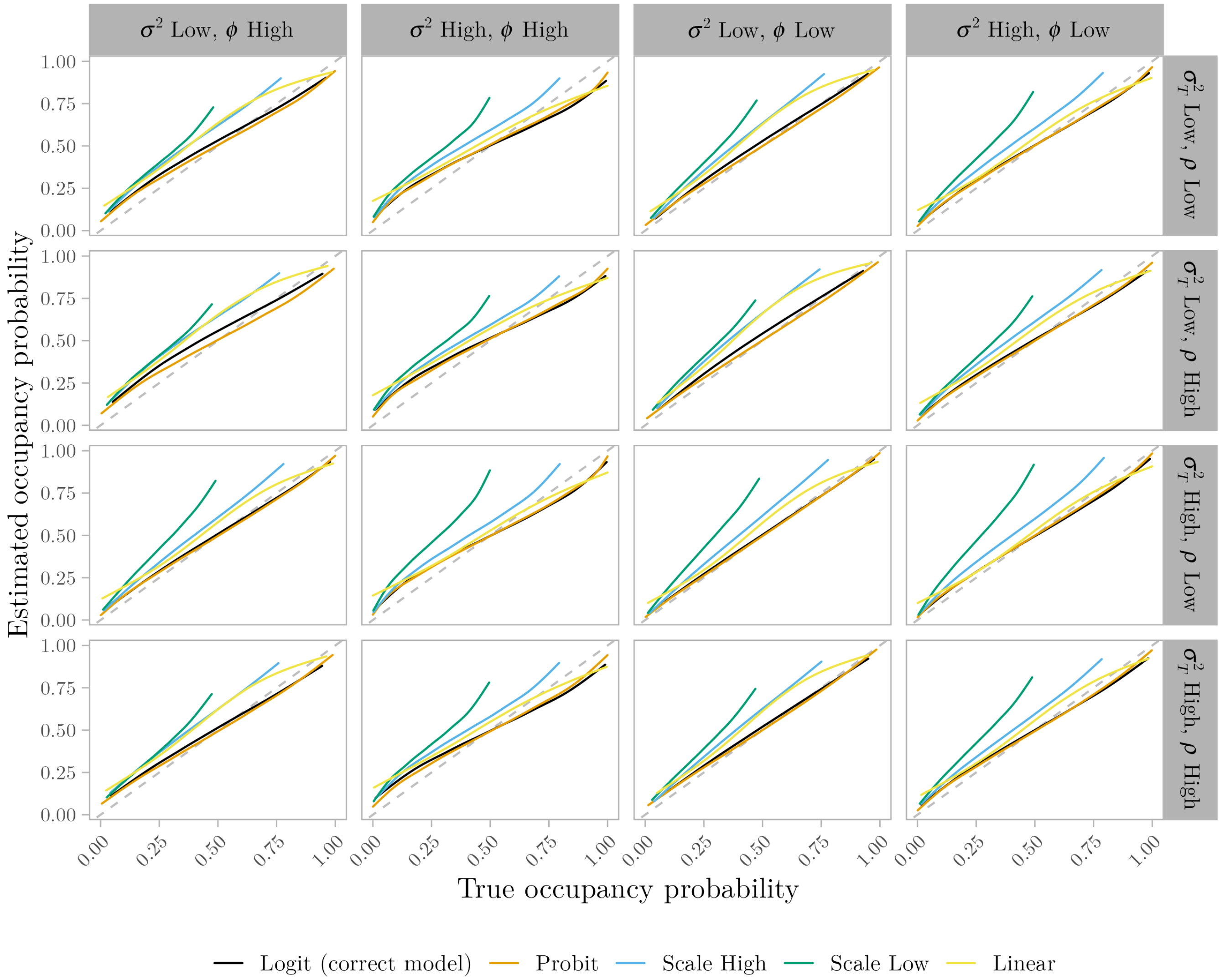

FIGURE 4 Accuracy of estimated occupancy probabilities in single-visit occupancy models under differing scenarios of spatial and temporal autocorrelation. Colours correspond to estimates under a correctly specified model and four different mis-specification scenarios. The "Scale High" and "Scale Low" functions correspond to a scaled logistic function with scale parameter α_s set to 0.8 and 0.5, respectively. The solid lines are smooth curves estimated using cubic splines that relate the estimated occupancy values to the true values. Estimates become more unbiased as they approach the one-to-one line (the grey dashed line). Each solid line corresponds to the mean across 100 simulations for the corresponding link function.

spatially-adaptive cluster sampling design and found it reduced bias in occupancy estimates for rare species. Here we used a systematic grid sampling design to generate our simulated data sets. Future simulation studies could explore the use of alternative sampling designs and their effects on occupancy probability identifiability.

We found that bias was substantially lower when using data from a "mixed design", where only a subset of sites were visited multiple times within a given season (von Hirschheydt et al., 2023; Figure 5). In our simulations, we simulated data such that 10% of sites within each season were surveyed twice, which suggests that a little true replication can go a long way in terms of improving the reliability of occupancy probability estimates. We assumed the repeat visits were randomly distributed across sites and seasons. Future simulation studies could assess the reliability of "mixed" designs when there is a non-random spatial and/or temporal pattern in the sites and/or seasons in which multiple visits are performed. This could provide insight on the use of multi-season occupancy models with historic data sets where initial sampling seasons did not have any within-season replication.

When the models were correctly specified (Simulation Study 1), both single-visit models and multiple-visit models generally had low bias and adequate coverage rates across all "fractional replication" scenarios. All models were relatively robust to model mis-specification in the form of a probit link function, with bias generally comparable to the correctly specified scenario, while coverage intervals were slightly below the nominal 95%. This is a result of difficulty in estimating the shorter tails of the probit link compared to the logit link (Figure 2). The robustness of all models to model mis-specification in the form of a probit link function is due to the similar shape of the probit link to the logit link.

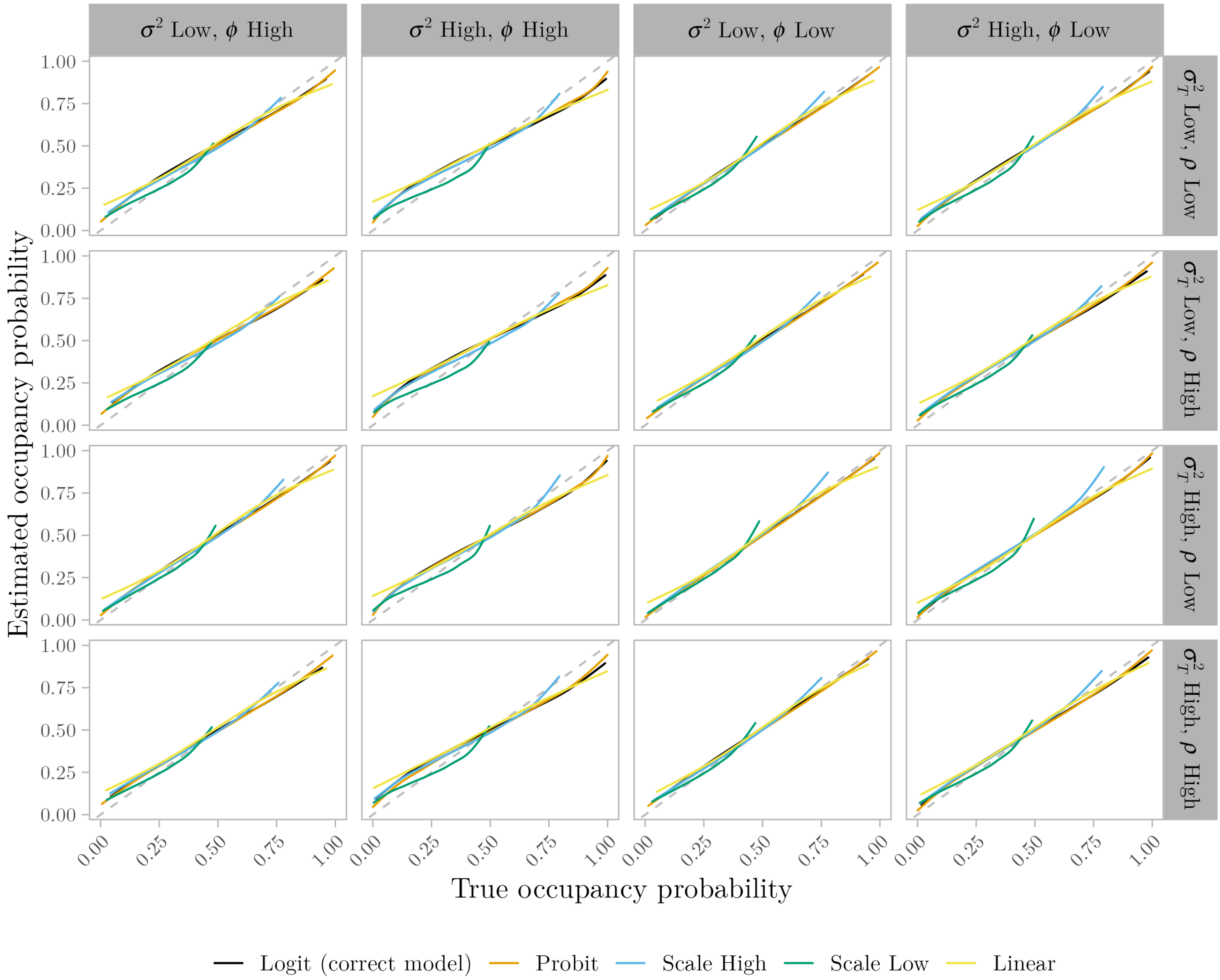

FIGURE 5 Accuracy of estimated occupancy probabilities in "mixed" design occupancy models under differing scenarios of spatial and temporal autocorrelation. In these models, 10% of locations had two visits within a season and the remaining 90% had one visit. Colours correspond to estimates under a correctly specified model and four different mis-specification scenarios. The "Scale High" and "Scale Low" functions correspond to a scaled logistic function with scale parameter α_s set to 0.8 and 0.5, respectively. The solid lines are smooth curves estimated using cubic splines that relate the estimated occupancy values to the true values. Estimates become more unbiased as they approach the one-to-one line (the grey dashed line). Each solid line corresponds to the mean across 100 simulations for the corresponding link function.

TABLE 1 Coverage rates for single-visit, mixed (i.e. 10% of sites with two visits, all others with one visit), double-visit, and five-visit multi-season spatial occupancy models under differing types of model mis-specification. Coverage rates are defined as the percentage of occupancy probabilities $(\psi_t(\mathbf{s}_j))$ contained within the 95% credible interval, averaged across 100 simulations within each of 16 different spatiotemporal autocorrelation scenarios.

Visits	Logit	Probit	Scale High	Scale Low	Linear
Single	96	91	83	64	87
Mixed	96	91	95	93	95
Double	96	90	95	92	95
Five	96	90	94	92	94

However, coverage rates for single-visit models under scaled logistic or linear model mis-specification, which are more severe forms of mis-specification relative to the presumed logit link, were well below 95%, regardless of the characteristics of the "fractional replication". Importantly, coverage rates for all multiple-visit models were much closer to the 95% nominal coverage rate under these same scenarios (Table 1). These results suggest that the accuracy of single-visit multi-season occupancy models is dependent on the true functional form of the relationship between occupancy and covariates, and that different amounts of "fractional replication" cannot overcome severe mis-specification of this relationship. As a result, the accuracy of such models will decrease as the functional form of the relationship becomes more different from the assumed

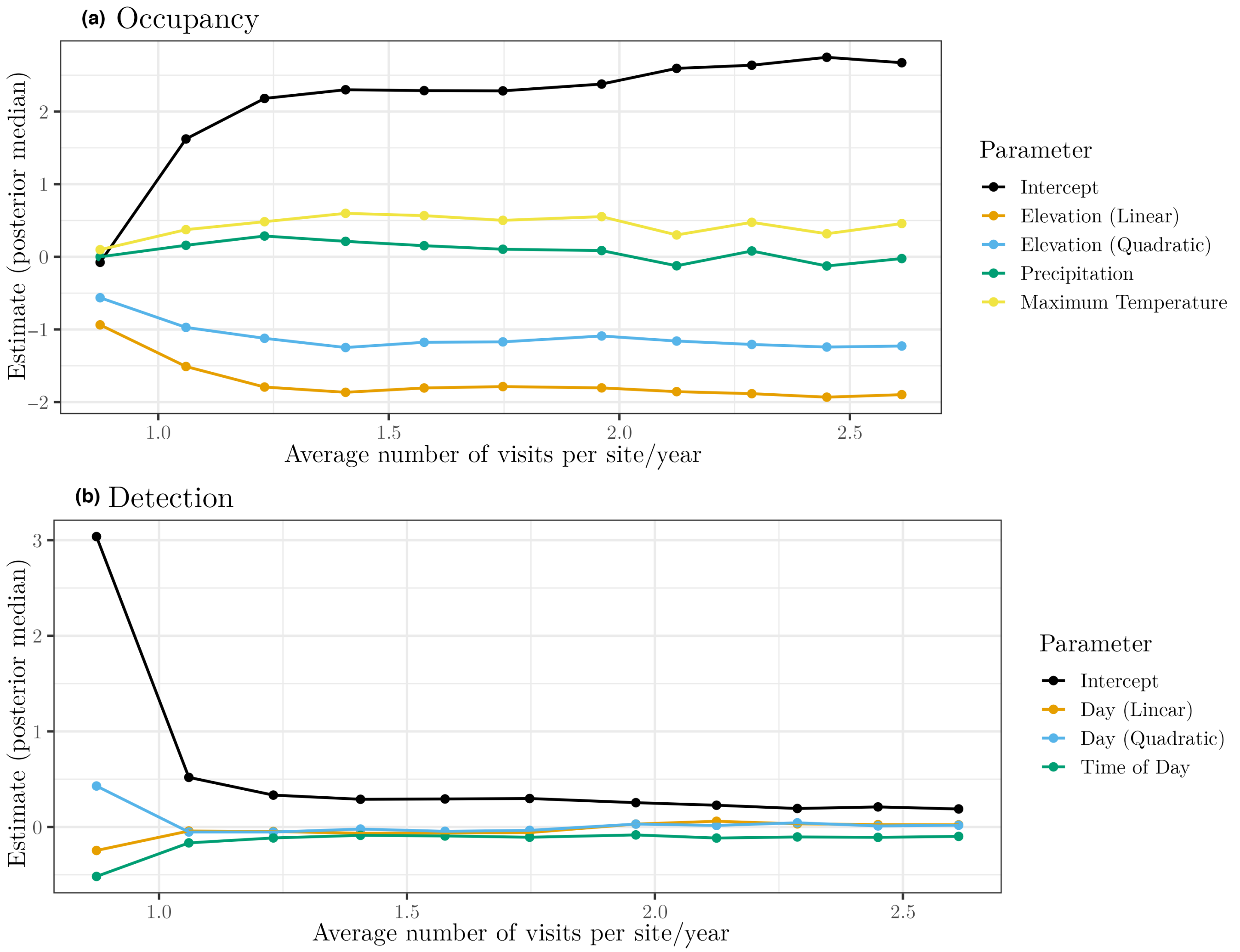

FIGURE 6 Model estimates (posterior medians) of occupancy (a) and detection (b) parameters from 11 multi-season spatial occupancy models that were fit using varying amounts of within-season replication. Note because not all sites were sampled each year, the average number of visits per site/year for the single-visit model is less than one.

logistic form. Given the complexity of true species-environment relationships, it is unlikely they follow the simple parametric form (i.e. logistic) assumed by the multi-season occupancy models we consider here. For practitioners interested in fitting single-visit multi-season occupancy models, we echo the recommendations of Phillips and Elith (2013), Knape and Korner-Nievergelt (2015) and Stoudt et al. (2023) to be aware of the parametric assumptions these models require for accurate inference and to consider how defensible such assumptions are for the given application.

Compared to the effects of spatial autocorrelation, we found smaller effects of temporal autocorrelation on resulting bias and uncertainty in occupancy probability estimates under single-visit and multiple-visit approaches (Figures 3 and 5). In particular, we found minimal effects of the degree of temporal autocorrelation (ρ) on the bias in estimated occupancy probability values, which differed from our expectation that bias would be lower under scenarios with a higher degree of temporal autocorrelation. This pattern could arise for two reasons. First, we tested model performance with datasets that were sampled over a 10 year period. Temporal autocorrelation could have larger impacts on bias for data sets comprised of a longer time series (e.g. 30 seasons; Hepler et al., 2018). Second, here we assessed one specific form of multi-season occupancy model, in which temporal autocorrelation in occupancy probability was explicitly separate from spatial autocorrelation (i.e. a separable spatiotemporal autocorrelation function). Alternative multi-season occupancy models with nonseparable spatiotemporal autocorrelation functions or a hidden Markov model structure (i.e. dynamic occupancy models) may reveal different patterns (Hepler et al., 2018; Peach et al., 2017).

More broadly, our results reinforce the importance of simulation studies that consider model performance under both correctly specified scenarios and under different forms of model mis-specification to more completely assess the reliability of a proposed modelling framework (Dennis et al., 2019; DiRenzo et al., 2023). We found generally reasonable performance of single-visit multi-season spatial occupancy models when data were simulated following the exact form of the model (Simulation

Study 1). These results agree with previous studies that assessed different approaches to model spatiotemporal patterns in occupancy over multiple seasons when the model is correctly specified (Hepler et al., 2018; Peach et al., 2017). However, it was only when assessing models under different forms of model mis-specification (Simulation Study 2) that we found bias in single-visit models as a result of the strong reliance on parametric assumptions. Thus, we strongly recommend researchers developing novel statistical models, or applying them in novel ways, to quantify their robustness to model mis-specification when assessing their ability to recover parameters of interest (DiRenzo et al., 2023).

We cannot directly assess the reliability of single-visit multi-season occupancy models with empirical data since we never know the true form of the functional relationship between occupancy/detection probability and covariates. However, we showed in our ovenbird case study that estimates of occupancy and detection probability from a single-visit model were substantially different to estimates from models with any amount of replication (Figure 6). Estimates of the effective spatial range across all models indicated fine-scale spatial autocorrelation relative to the size of the study area (Supplemental Information S1, Table S1). Based on our simulation results, we may expect single-visit models to provide more similar estimates to multiple-visit models in empirical datasets when there is long-range spatial autocorrelation in the data. Importantly, we also found that as the amount of replication increased, model estimates tended to stabilize around a single value, suggesting the models were approaching the "true" values based on the data at hand. These findings support our conclusions from the simulation study that the parametric assumptions required of single-visit multi-season occupancy models may lead to misleading inferences.

In light of our results, we provide three recommendations for practitioners seeking to study spatiotemporal patterns in occupancy probability over space and time using data with limited within-season replication. These recommendations explicitly acknowledge that practitioners will differ in their ability to collect new data and/or use additional data sources, and that some individuals may only have single-visit data available to use.

1. *Use a "mixed" design approach.* While single-visit models showed bias under multiple forms of model mis-specification, this bias was substantially reduced under a "mixed" design (von Hirschheydt et al., 2023) in which only 10% of sites were visited twice within a season. Thus, even small amounts of within-season temporal replication can drastically reduce the requirement of parametric assumptions for reliable inference in multi-season occupancy models, although more replication may be needed for inconspicuous species where detection probability is low. When possible, we recommend allocating resources to perform within-season replicate surveys at a subset of sites. The exact amount of replication needed to achieve a given level of accuracy and precision can be assessed using simulation studies following the approach used in von Hirschheydt et al. (2023) for single-season occupancy models and the functionality provided in user-friendly `R` packages such as `spOccupancy` (Doser, Finley, et al., 2022) and `unmarked` (Fiske & Chandler, 2011; Kellner et al., 2023).
2. *Combine multiple data sources in an integrated model.* Single-visit data can be combined with other detection-nondetection data sources in integrated occupancy models (Doser, Leuenberger, et al., 2022; Lauret et al., 2021) or with other data types in integrated species distribution models (Koshkina et al., 2017; Miller et al., 2019) to reduce the potential biases in single-visit models when parametric assumptions are not met. Such approaches leverage the information present in additional data sources to separately estimate the ecological process of interest (i.e. occupancy) from observational biases (i.e. detection).
3. *Understand the potential inaccuracies when using single-visit multi-season models.* We generally caution against the use of single-visit multi-season occupancy models due to the bias present when parametric assumptions are not met. However, when this is the only data source available and additional data collection is not possible (e.g. if using historical data), single-visit multi-season occupancy models will likely result in less bias than logistic regression models that ignore imperfect detection entirely, as we found in our simulation studies (Supplemental Information S1, Figures S3 and S4). When using single-visit models, we strongly encourage practitioners to understand the assumptions they are making and the potential impacts this can have on their resulting analysis. In such situations, we stress the importance of performing simulation studies and sensitivity analyses based on the available data at hand to understand the reliability of the model.

Understanding patterns in species distributions over space and time is crucial for effective conservation and management. Here we performed an extensive simulation study to assess how differing amounts of "fractional replication" influence the reliability of estimates from single-visit multi-season spatial occupancy models, a potentially cost-effective approach for monitoring species distributions over large spatiotemporal regions. We showed that while "fractional replication" can reduce bias in estimates under ideal scenarios when the model is correctly specified, it cannot eliminate bias when the model is mis-specified and parametric assumptions are not met. Our analysis and resulting recommendations should help inform data collection and modelling decisions when seeking to fit multi-season occupancy models with limited amounts of within-season replication.

AUTHOR CONTRIBUTIONS

Jeffrey W. Doser and Sara Stoudt conceived the ideas, designed methodology, analysed the data and contributed to the writing and revising of the manuscript. Both give final approval for publication.

ACKNOWLEDGEMENTS

Thank you to Perry de Valpine who passed along an announcement about multi-season functionality in the `spOccupancy` package (2022-07-20) to Sara Stoudt. In this message, the idea of "fractional" replication was mentioned and the idea of considering the

identifiability of this scenario was planted. This paper was supported by funding from Bucknell University's Department of Mathematics Distinguished Visiting Professor Program.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to report.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14275.

DATA AVAILABILITY STATEMENT

All data and code used in the manuscript are available at https://doi.org/10.5281/zenodo.10234982 (Doser & Stoudt, 2023).

ORCID

Jeffrey W. Doser https://orcid.org/0000-0002-8950-9895
Sara Stoudt https://orcid.org/0000-0002-1693-8058

REFERENCES

Auger-Méthé, M., Field, C., Albertsen, C. M., Derocher, A. E., Lewis, M. A., Jonsen, I. D., & Mills Flemming, J. (2016). State-space models' dirty little secrets: Even simple linear Gaussian models can have estimation problems. *Scientific Reports*, *6*(1), 26677. https://doi.org/10.1038/srep26677

Bellier, E., Kéry, M., & Schaub, M. (2016). Simulation-based assessment of dynamic N-mixture models in the presence of density dependence and environmental stochasticity. *Methods in Ecology and Evolution*, *7*(9), 1029–1040. https://doi.org/10.1111/2041-210X.12572

Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, *7*(4), 434–455. https://doi.org/10.1080/10618600.1998.10474787

Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., Curtis, J., & Pasteris, P. P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, *28*(15), 2031–2064. https://doi.org/10.1002/joc.1688

Datta, A., Banerjee, S., Finley, A. O., & Gelfand, A. E. (2016). Hierarchical nearest-neighbor Gaussian process models for large geostatistical datasets. *Journal of the American Statistical Association*, *111*(514), 800–812. https://doi.org/10.1080/01621459.2015.1044091

Dennis, B., Ponciano, J. M., Taper, M. L., & Lele, S. R. (2019). Errors in statistical inference under model misspecification: Evidence, hypothesis testing, and AIC. *Frontiers in Ecology and Evolution*, *7*, 372. https://doi.org/10.3389/fevo.2019.00372

Diana, A., Dennis, E. B., Matechou, E., & Morgan, B. J. T. (2023). Fast Bayesian inference for large occupancy datasets. *Biometrics*, *79*, 2503–2515. https://doi.org/10.1111/biom.13816

DiRenzo, G. V., Hanks, E., & Miller, D. A. (2023). A practical guide to understanding and validating complex models using data simulations. *Methods in Ecology and Evolution*, *14*(1), 203–217. https://doi.org/10.1111/2041-210X.14030

Doser, J. W., Finley, A. O., Kéry, M., & Zipkin, E. F. (2022). spOccupancy: An R package for single-species, multi-species, and integrated spatial occupancy models. *Methods in Ecology and Evolution*, *13*(8), 1670–1678. https://doi.org/10.1111/2041-210X.13897

Doser, J. W., Leuenberger, W., Sillett, T. S., Hallworth, M. T., & Zipkin, E. F. (2022). Integrated community occupancy models: A framework to assess occurrence and biodiversity dynamics using multiple data sources. *Methods in Ecology and Evolution*, *13*(4), 919–932. https://doi.org/10.1111/2041-210X.13811

Doser, J. W., & Stoudt, S. (2023). Code and data for "Fractional replication" in single-visit multi-season occupancy models: Impacts of spatio-temporal autocorrelation on identifiability. *Zenodo* https://doi.org/10.5281/zenodo.10234982

Fiske, I., & Chandler, R. (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, *43*(10), 1–23. https://doi.org/10.18637/jss.v043.i10

Garrard, G. E., Bekessy, S. A., McCarthy, M. A., & Wintle, B. A. (2008). When have we looked hard enough? A novel method for setting minimum survey effort protocols for flora surveys. *Austral Ecology*, *33*(8), 986–998. https://doi.org/10.1111/j.1442-9993.2008.01869.x

Guillera-Arroita, G., & Lahoz-Monfort, J. J. (2012). Designing studies to detect differences in species occupancy: Power analysis under imperfect detection. *Methods in Ecology and Evolution*, *3*(5), 860–869. https://doi.org/10.1111/j.2041-210X.2012.00225.x

Guillera-Arroita, G., Ridout, M. S., & Morgan, B. J. T. (2010). Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution*, *1*(2), 131–139. https://doi.org/10.1111/j.2041-210X.2010.00017.x

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, *135*(2–3), 147–186. https://doi.org/10.1016/S0304-3800(00)00354-9

Hallworth, M. T., Bayne, E., McKinnon, E., Love, O., Tremblay, J. A., Drolet, B., Ibarzabal, J., Van Wilgenburg, S., & Marra, P. P. (2021). Habitat loss on the breeding grounds is a major contributor to population declines in a long-distance migratory songbird. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1949), 20203164. https://doi.org/10.1098/rspb.2020.3164

Hepler, S. A., Erhardt, R., & Anderson, T. M. (2018). Identifying drivers of spatial variation in occupancy with limited replication camera trap data. *Ecology*, *99*(10), 2152–2158. https://doi.org/10.1002/ecy.2396

Hines, J. E., Nichols, J. D., Royle, J. A., MacKenzie, D. I., Gopalaswamy, A., Kumar, N. S., & Karanth, K. (2010). Tigers on trails: Occupancy modeling for cluster sampling. *Ecological Applications*, *20*(5), 1456–1466. https://doi.org/10.1890/09-0321.1

Kellner, K. F., Smith, A. D., Royle, J. A., Kéry, M., Belant, J. L., & Chandler, R. B. (2023). The unmarked R package: Twelve years of advances in occurrence and abundance modelling in ecology. *Methods in Ecology and Evolution*, *14*(6), 1408–1415. https://doi.org/10.1111/2041-210X.14123

Kéry, M., & Royle, J. A. (2021). *Applied hierarchical modleing in ecology analysis of distribution, abundance and species richness in R and BUGS, volume 2: Dynamic and advanced models*. London Elsevier, Academic Press.

Kéry, M., & Schmidt, B. (2008). Imperfect detection and its consequences for monitoring for conservation. *Community Ecology*, *9*(2), 207–216. https://doi.org/10.1556/ComEc.9.2008.2.10

Knape, J., & Korner-Nievergelt, F. (2015). Estimates from non-replicated population surveys rely on critical assumptions. *Methods in Ecology and Evolution*, *6*(3), 298–306. https://doi.org/10.1111/2041-210X.12329

Koshkina, V., Wang, Y., Gordon, A., Dorazio, R. M., White, M., & Stone, L. (2017). Integrated species distribution models: Combining presence-background data and site-occupancy data with imperfect detection. *Methods in Ecology and Evolution*, *8*(4), 420–430. https://doi.org/10.1111/2041-210X.12738

Lauret, V., Labach, H., Authier, M., & Gimenez, O. (2021). Using single visits into integrated occupancy models to make the most of existing monitoring programs. *Ecology*, *102*(12), e03535. https://doi.org/10.1002/ecy.3535

Lele, S. R., Moreno, M., & Bayne, E. (2012). Dealing with detection error in site occupancy surveys: What can we do with a single survey? *Journal of Plant Ecology*, *5*(1), 22–31. https://doi.org/10.1093/jpe/rtr042

MacArthur, R. H. (1972). *Geographical ecology: Patterns in the distribution of species*. Princeton University Press.

MacKenzie, D., & Royle, J. A. (2005). Designing occupancy studies: General advice and allocating survey effort. *Journal of Applied Ecology*, *42*(6), 1105–1114. https://doi.org/10.1111/j.1365-2664.2005.01098.x

MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., & Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, *84*(8), 2200–2207. https://doi.org/10.1890/02-3090

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8), 2248–2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

Miller, D. A., Pacifici, K., Sanderlin, J. S., & Reich, B. J. (2019). The recent past and promising future for data integration methods to estimate species' distributions. *Methods in Ecology and Evolution*, *10*(1), 22–37. https://doi.org/10.1111/2041-210X.13110

Pacifici, K., Reich, B. J., Dorazio, R. M., & Conroy, M. J. (2016). Occupancy estimation for rare species using a spatially-adaptive sampling design. *Methods in Ecology and Evolution*, *7*(3), 285–293. https://doi.org/10.1111/2041-210X.12499

Peach, M. A., Cohen, J. B., & Frair, J. L. (2017). Single-visit dynamic occupancy models: An approach to account for imperfect detection with Atlas data. *Journal of Applied Ecology*, *54*, 2033–2042. https://doi.org/10.1111/1365-2664.12925

Phillips, S. J., & Elith, J. (2013). On estimating probability of presence from use–availability or presence–background data. *Ecology*, *94*(6), 1409–1419. https://doi.org/10.1890/12-1520.1

Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News*, *6*(1), 7–11.

Rodenhouse, N. L., & Sillett, T. S. (2021). Valley-wide Bird Survey, Hubbard Brook Experimental Forest, 1999–2016 (ongoing). https://doi.org/10.6073/pasta/faca2b2cf2db9d415c39b695cc7fc21

Rollinson, C. R., Finley, A. O., Alexander, M. R., Banerjee, S., Dixon Hamil, K.-A., Koenig, L. E., Locke, D. H., DeMarche, M. L., Tingley, M. W., Wheeler, K., Youngflesh, C., & Zipkin, E. F. (2021). Working across space and time: Nonstationarity in ecological research and application. *Frontiers in Ecology and the Environment*, *19*(1), 66–72. https://doi.org/10.1002/fee.2298

Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., Stanton, J. C., Panjabi, A., Helft, L., Parr, M., & Marra, P. P. (2019). Decline of the north American avifauna. *Science*, *366*(6461), 120–124. https://doi.org/10.1126/science.aaw1313

Rushing, C. S., Royle, J. A., Ziolkowski, D. J., & Pardieck, K. L. (2019). Modeling spatially and temporally complex range dynamics when detection is imperfect. *Scientific Reports*, *9*(1), 1–9. https://doi.org/10.1038/s41598-019-48851-5

Sadoti, G., Zuckerberg, B., Jarzyna, M. A., & Porter, W. F. (2013). Applying occupancy estimation and modelling to the analysis of atlas data. *Diversity and Distributions*, *19*(7), 804–814. https://doi.org/10.1111/ddi.12041

Solymos, P., & Lele, S. R. (2016). Revisiting resource selection probability functions and single-visit methods: Clarification and extensions. *Methods in Ecology and Evolution*, *7*(2), 196–205. https://doi.org/10.1111/2041-210X.12432

Spooner, F. E., Pearson, R. G., & Freeman, R. (2018). Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Global Change Biology*, *24*(10), 4521–4531. https://doi.org/10.1111/gcb.14361

Stoudt, S., de Valpine, P., & Fithian, W. (2023). Non-parametric identifiability in species distribution and abundance models: Why it matters and how to diagnose a lack of it using simulation. *Journal of Statistical Theory and Practice*, *17*(39), 1–26. https://doi.org/10.1007/s42519-023-00336-5

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K., & Possingham, H. P. (2003). Improving precision and reducing bias in biological surveys: Estimating false-negative error rates. *Ecological Applications*, *13*(6), 1790–1801. https://doi.org/10.1890/02-5078

von Hirschheydt, G., Stofer, S., & Kéry, M. (2023). "Mixed" occupancy designs: When do additional single-visit data improve the inferences from standard multi-visit models? *Basic and Applied Ecology*, *67*, 61–69. https://doi.org/10.1016/j.baae.2023.01.003

Wang, Y., Samarasekara, C. L., & Stone, L. (2022). A machine learning method for estimating the probability of presence using presence-background data. *Ecology and Evolution*, *12*(6), e8998. https://doi.org/10.1002/ece3.8998

Wang, Y., & Stone, L. (2019). Understanding the connections between species distribution models for presence-background data. *Theoretical Ecology*, *12*(1), 73–88. https://doi.org/10.1007/s12080-018-0389-9

Wood, C. M., Popescu, V. D., Klinck, H., Keane, J. J., Gutiérrez, R., Sawyer, S. C., & Peery, M. Z. (2019). Detecting small changes in populations at landscape scales: A bioacoustic site-occupancy framework. *Ecological Indicators*, *98*, 492–507. https://doi.org/10.1016/j.ecolind.2018.11.018

Yackulic, C. B., Chandler, R., Zipkin, E. F., Royle, J. A., Nichols, J. D., Campbell Grant, E. H., & Veran, S. (2013). Presence-only modelling using MAXENT: When can we trust the inferences? *Methods in Ecology and Evolution*, *4*(3), 236–243. https://doi.org/10.1111/2041-210x.12004

Zipkin, E. F., DiRenzo, G. V., Ray, J. M., Rossman, S., & Lips, K. R. (2020). Tropical snake diversity collapses after widespread amphibian loss. *Science*, *367*(6479), 814–816. https://doi.org/10.1126/science.aay5733

SUPPORTING INFORMATION

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

Figure S1. Accuracy of estimated occupancy probabilities in double-visit occupancy models under differing scenarios of spatial and temporal autocorrelation.

Figure S2. Accuracy of estimated occupancy probabilities in five-visit occupancy models under differing scenarios of spatial and temporal autocorrelation.

Figure S3. Accuracy of estimated occupancy probabilities in a logistic regression model that ignores imperfect detection under differing scenarios of spatial and temporal autocorrelation.

Figure S4. Bias of estimated occupancy probabilities in logistic regression models that ignore imperfect detection under differing scenarios of spatial and temporal autocorrelation.

Figure S5. Bias of estimated occupancy probabilities in single-visit occupancy models under differing scenarios of spatial and temporal autocorrelation.

Figure S6. Bias of estimated occupancy probabilities in "mixed" design occupancy models under differing scenarios of spatial and temporal autocorrelation.

Figure S7. Bias of estimated occupancy probabilities in double-visit occupancy models under differing scenarios of spatial and temporal autocorrelation.

Figure S8. Bias of estimated occupancy probabilities in five-visit occupancy models under differing scenarios of spatial and temporal autocorrelation.

Table S1. Parameter estimates (posterior medians) for all occupancy parameters from the 11 models fit with differing amounts of within-season replication for the ovenbird case study.

How to cite this article: Doser, J. W., & Stoudt, S. (2023). "Fractional replication" in single-visit multi-season occupancy models: Impacts of spatiotemporal autocorrelation on identifiability. *Methods in Ecology and Evolution*, *00*, 1–15. https://doi.org/10.1111/2041-210X.14275