

Statistical power of dynamic occupancy models to identify temporal change: Informing the North American Bat Monitoring Program



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ABSTRACT

Dynamic occupancy models provide a flexible framework for estimating and mapping species occupancy patterns over space and time for large-scale monitoring programs (e.g., the North American Bat Monitoring Program (NABat), the Amphibian Research and Monitoring Initiative). Challenges for designing surveys using the dynamic occupancy modeling framework include defining appropriate derived trend parameters, and providing usable tools for researchers to conduct project-specific sample size investigations. We present a simulation-based power analysis framework for dynamic occupancy models that allows for the incorporation of the underlying environmental space (i.e., as covariates) within a specific study region to inform sample size estimation. We investigate two definitions of temporal trend: (1) a gradual, sustained (linear or nonlinear) change over a period of many years, and (2) an abrupt increase or decrease between two time periods. We draw upon pilot data collected following NABat protocols to inform assumed data generating values in a demonstration of our approach. Due to the complicated parameter structure of dynamic occupancy models, we emphasize the importance of visualizing simulated changes over time based on different parameter settings prior to conducting a power analysis. Our simulations revealed that the linearity of short-term trends (five years in our investigation) conferred higher power with lower sample size than longer trends where occupancy probabilities approached zero (ten years in our investigation). We provide an example of how to use our tools to conduct customized investigations using questions posed by NABat, and in doing so, we shed light on general guidelines that can be applied to programs monitoring species occupancy for other taxa. Importantly, we created an R package to execute our approach for informing program-, species-, and study-specific investigations aimed at identifying changes in species occupancy.

1. Introduction

Large-scale conservation monitoring programs pursue assessments of status and trends in species distribution for imperiled or invasive species (e.g., Jones, 2011; Noon et al., 2012; Loeb et al., 2015). To be successful in this pursuit, baseline estimates of required sample sizes for achieving stated program objectives must be established in the design phase and then updated as data from early sampling efforts become available. Using customized power analyses iteratively, as new information about the species of interest becomes available, can help programs avoid wasting time and money (e.g., Fig. 3 in Guillera-Arriola et al., 2010; Gerrodette, 1987), or worse, a complete loss of trust from

funding agencies (Marsh and Trenham, 2008; Reynolds et al., 2011). Ideally, a statistical power analysis will be crafted around a well-defined ecological objective that can be linked to estimable parameters within a statistical model.

A popular metric for geographically extensive monitoring programs is species occupancy (probability); this metric can be particularly useful for cryptic species whose abundances cannot be reliably measured (e.g., Jones, 2011; Noon et al., 2012; MacKenzie and Nichols, 2004). For example, the North American Bat Monitoring program (NABat; Loeb et al., 2015) augments count data with detection/non-detection data derived from recorded echolocation calls (Banner et al., 2018), because count data (e.g., mist netting, roost surveys) are difficult to collect

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across the extent of a species' range. For such monitoring programs, a general temporal trend objective is often stated, "to identify an $x\%$ change in species occupancy probability over a specified time period, such as five or ten years, with 80% power and Type I error less than 0.05;" hereafter, we use this definition for *temporal trend objective* and *trend*.

The dynamic occupancy modeling framework (e.g., MacKenzie et al., 2003; Royle and Kéry, 2007; Royle and Dorazio, 2008) provides a flexible and realistic way to address temporal trend objectives, however, there remains a need to guide practitioners on statistical power and sample size. Previous survey design guidance for dynamic occupancy models focused on optimizing the estimation of model parameters through the minimization of their root mean square errors (see Bailey et al., 2007; McKann et al., 2013), but did not investigate sample size requirements for temporal trend objectives directly (but see Mattfeldt et al., 2009). Additionally, with the exceptions of Ellis et al. (2014, 2015), power analyses or sample size calculations often ignore the potential influence of the underlying environmental space that will be surveyed and ultimately used as covariates to predict the probability of species occupancy at unsurveyed locations (species distribution maps).

Assessing power for trend objectives in a dynamic occupancy model is less straightforward than simply setting a specified effect size in a linear trend model based on relevant biological knowledge about the system (e.g., Starcevic et al., 2018; Wagner et al., 2013; Gerrodette, 1987) because of the model's complicated parameter structure (see Section 2.1). We propose and demonstrate that the best approach is to graphically assess the imposed trend for different specifications of dynamic occupancy model parameter values to understand the implied effect size, and to avoid using unrealistic trends in power analyses. In this work, we investigate the connection between temporal trend objectives and the parameterization used in a dynamic occupancy model to develop a simulation-based power analysis framework that can be broadly used by occupancy-based monitoring programs. Our approach also allows for the inclusion of real environmental covariate data, enabling us to investigate the potential influence of the underlying environmental space for different spatial extents within a specific region of interest.

Monitoring programs are often omnibus in the sense that inference is desired at different spatial extents and for multiple species. We created an R (R Core Team, 2018) package `dynOccupow` to execute our approach for informing program-, species-, and study-specific investigations aimed at detecting changes in species occupancy. Our package can be used to help researchers and/or managers weigh trade-offs among survey design elements that can be controlled (e.g., number of sites, visits, and years; desired power; maximum tolerance of Type I error) while accounting for elements that cannot be controlled like background variation inherent in the system (i.e., variation that cannot be accounted for through the experimental design or the statistical model). We use the context of NABat to provide an example of how to conduct customized investigations into survey design questions, and in doing so we shed light on general considerations for assessing change over time using dynamic occupancy models.

2. Methods

2.1. Dynamic occupancy models

Dynamic occupancy models (for an introduction see MacKenzie et al., 2006) assume a sampling framework where analysis units are defined by sites, which can either be a partition of the region of interest into equal-area spatial units (e.g., 10 km × 10 km grid cells), or by naturally occurring units such as ponds or lakes. Sites are defined such that it is reasonable to assume the species of interest either occupies or does not occupy the site for the duration of the season (i.e., occupancy is closed within season). During a visit, species observations arise

through either passive (e.g., acoustic detector, camera trap) or active (e.g., human observer) sampling, often aggregating many observation-level detection/non-detections into visit-level data. To account for imperfect detection, which occurs when the species is present at the site but missed during a visit, at least a subset of sites must be visited more than once during each sampling season. The repeated visits can either be spatial (multiple visits to a site during the same survey event), or temporal (multiple survey events to the same location in a site during the same sampling season, although see section 10.11 in Kéry and Royle (2016) for how the space-for-time substitution affects the interpretation of the detection parameter); for both types of visits, it must be reasonable to assume that observations from visits within a site result in independent detection/non-detection data. In addition to the independence and closure assumptions, the dynamic occupancy model assumes that the species cannot be detected if it is not present during the observation process, but see (Banner et al., 2018; Chambert et al., 2015, 2018; Miller et al., 2011) for models that can address misidentification errors.

2.1.1. Model specification for simulation and analysis

Large-scale monitoring programs aim to generalize inferences beyond survey locations by employing probabilistic sampling designs, which select n sites for monitoring from a spatial domain comprised of N total sites (indexed by $i = 1, \dots, n; n \ll N$). Our approach facilitates investigation of two probabilistic sampling designs: the simple random sample (SRS) and a spatially-balanced analog defined by the generalized random tessellation stratified (GRTS) algorithm (see Stevens and Olsen, 2004). We simulate and analyze detection/non-detection data according to the auto-logistic parameterization of the dynamic occupancy model described in Royle and Kéry (2007) and Royle and Dorazio (2008) (Eqs. (1)–(6), see Appendix A for simulation steps).

$$Z_{i,1} \sim \text{Bernoulli}(\psi_{i,1}) \quad (1)$$

$$\text{logit}(\psi_1) = \mathbf{X}_{t=1}\theta \quad (2)$$

$$Z_{i,t}|Z_{i,t-1} \sim \text{Bernoulli}(\pi_{i,t}) \text{ for } t \geq 2 \quad (3)$$

$$\text{logit}(\pi_{i,t}) = a_t + b_t z_{i,t-1} \quad (4)$$

$$Y_{j,t}|Z_{i,t} \sim \text{Bernoulli}(z_{i,t}p_{j,t}) \quad (5)$$

$$\text{logit}(\mathbf{p}_t) = \mathbf{W}_t\omega_t. \quad (6)$$

This model assumes that true occupancy status in site i during the first year, denoted $Z_{i,1}$, follows a Bernoulli distribution with probability of occurrence equal to $\psi_{i,1}$ (Eq. (1)). Logit-linear relationships between site-level covariates and true species occupancy during the first year ψ_1 are specified through Eq. (2), where $\mathbf{X}_{t=1}$ is a $n \times r$ matrix of r covariates, and θ is a $(r + 1) \times 1$ column-vector of partial regression coefficients representing assumed relationships. The occupancy status of site i in year t follows a Bernoulli distribution with probability equal to $\pi_{i,t}$ (Eq. (3)), which is calculated assuming that a site's occupancy status is dependent on the status of that site in the previous year (i.e., first order Markov process, Eq. (4)). The parameters a_t and b_t are directly related to site-specific colonization and extinction probabilities through $\text{logit}(\gamma_{t-1}) = a_t$ and $\text{logit}(\phi_{t-1}) = a_t + b_t$. The colonization probability, γ_t , is the rate at which unoccupied sites in year $t - 1$ become occupied in year t . Additionally, the rate at which occupied sites in year $t - 1$ become unoccupied in year t is the extinction probability, $\epsilon_t = 1 - \phi_t$, where ϕ_t is the survival probability of an occupied site in year $t - 1$ remaining occupied in year t . Site-level covariates could be included to account for heterogeneity in $\pi_{i,t}$, but force the computation of colonization and extinction probabilities to be done assuming covariate values are zero (or average values for standardized covariates), complicating interpretations. Thus, unless site-level covariates are changing over time, we recommend relating them to initial occupancy $\psi_{i,1}$ instead of the update probabilities ($\pi_{i,t}$). If site i is occupied, the probability of

detecting a species during visit j in year t is $p_{ij,t}$, and individual observations (detections/non-detections), denoted $Y_{ij,t}$, are also assumed to follow a Bernoulli distribution (Eq. (5)). When covariates are available, they can be included to account for heterogeneity in detection probabilities among sites, visits, and seasons through Eq. (6), where \mathbf{W}_t is a $(n \times J) \times (w + 1)$ matrix of w covariates and an intercept term and ω_t are partial regression coefficients representing assumed covariate-detection relationships.

2.1.2. Imposing, quantifying, and identifying temporal trends

Trends in species occupancy are defined by changes in annual occupancy probabilities over time, where annual occupancy probabilities are computed recursively using the colonization and extinction parameters, $\psi_{i,t} = \psi_{i,t-1}\phi_{t-1} + (1 - \psi_{i,t-1})\gamma_{t-1}$, for years $t = 2, \dots, T$. We extend the work of Bailey et al. (2007) and McKann et al. (2013) by directly investigating power for two derived trend parameters from dynamic occupancy models. The two trend parameters we investigate are based on a spatially explicit parameterization of MacKenzie et al. (2003) yearly growth rate, $\lambda_{i,t} = \psi_{i,t}/\psi_{i,t-1}$ ($t = 2, 3, \dots, T$), which characterizes inter-annual changes for subsequent years throughout a study. Let $\bar{\psi}_t$ be the average occupancy over all sites in year t , $\bar{\psi}_t = \frac{1}{n} \sum_{i=1}^n \psi_{i,t}$, and $\bar{\lambda}_t$ be the average growth rate for year t , $\bar{\lambda}_t = \bar{\psi}_t/\bar{\psi}_{t-1}$. Then, we define the average annual growth rate as the overall average of the average growth rates for years $t = 2, \dots, T$, $\lambda_{avg} = \frac{1}{T-1} \sum_{t=2}^T \bar{\lambda}_t$, which is similar to the linear trend parameter used in Ellis et al. (2014), Ellis et al. (2015), and Adams et al. (2013). Similarly, we define the total growth rate as the ratio of average occupancy in the last year to that in the first year $\lambda_{Tot} = \bar{\psi}_T/\bar{\psi}_1$. Total growth rate can be used to characterize the long-term step trend in occupancy since the initiation of the monitoring program (e.g., step-change as in Gerrodette, 1987; Seavy and Reynolds, 2007; Wagner et al., 2013).

Both trend parameters λ_{Tot} and λ_{avg} estimate net change, which can be thought of as a measurement of total change in a parameter arising from all sources (McDonald, 2003). Parameter values of less than one for λ_{avg} and λ_{Tot} indicate a net decrease in the total number of sites where the species occurs over the time interval of interest within the defined study region. Although an observed decrease in the total number of sites where the species occurs could be offset by individuals moving to better habitat outside the study region, in many cases, the decrease could represent a constriction in distribution that is often related to a declining population (see Noon et al., 2012; Holt et al., 2002; Tempel and Gutierrez, 2012; Gaston et al., 2000).

Both trend parameters assume approximately monotonic change in species occupancy over the duration of the study. The average annual growth rate makes the stricter assumption that the average yearly changes are similar (i.e., the trend is approximately linear). In our data simulation, the imposed effect size of the trend depends on annual occupancy probabilities, which are a function of the dynamic occupancy model parameters colonization and extinction and any assumed species-environment relationships with initial occupancy (Eqs. (1)–(6)). Therefore, the effect size (as per power analyses) for a temporal trend objective is indirectly set through the specification of dynamic occupancy parameter values and assumed species-environment relationships.

2.1.3. Conducting simulation-based power analyses

We created a fully-documented R (R Core Team, 2018) package, `dynOccuPow` (See Data S1 found in Appendix B), for simulating data under the auto-logistic parameterization of the dynamic occupancy model, fitting those data using the same model (i.e., an unbiased simulation-based approach) and assessing power to identify trends for the average annual change and the overall total change in occupancy. To conduct a power analysis, the user must specify a set of survey designs (e.g., n sites, J visits, T years in the study), assumed values for colonization and extinction probabilities ($\gamma_{(T-1) \times 1}$, $\phi_{(T-1) \times 1}$), assumed

relationships between initial occupancy and detection and associated spatially explicit covariates (θ and $\mathbf{X}_{t=1}$, ω_t and \mathbf{W}_t , respectively), and either a GRTS-based or SRS sampling design. Our approach assumes there are no missing observations, which if violated could result in sample size recommendations that are too liberal. Following survey design suggestions for multi-season studies from MacKenzie and Royle (2005) and Bailey et al. (2007), our approach also assumes the same n sites are visited each sampling season. Lastly, for simplicity, we assume the same number of visits to each site during each season, although a simple extension could accommodate different numbers of visits among surveyed sites (i.e., $J_{i,t}$ rather than J).

The package includes functions for visualizing imposed trends for a set of specified values for dynamic occupancy model parameters and study designs, user-friendly functions for fitting models within the Bayesian framework using `rjags` (Plummer, 2016), functions for checking convergence diagnostics for the Markov chain Monte Carlo (MCMC) samplers, and functions to generate and compare results from simulations from multiple different survey design scenarios (Supplement S2 found in Appendix B contains a detailed package tutorial). The models included in our package use weakly informative, normal priors with a mean equal to zero and variance equal to ten on all partial regression coefficients, which helps constrain the posterior distribution within the reasonable range of partial regression coefficient values on the logit scale, although this can be customized (see Supplement S2).

2.2. Example: monitoring for NABat

Many North American bat populations are declining due to habitat alteration, expanding wind energy industry, and white-nose Syndrome (WNS), which is a disease caused by the invasive pathogenic fungus *Pseudogymnoascus destructans* of Eurasian origin (O'Shea et al., 2016; Hammerson et al., 2017). Due to their cryptic and wide-ranging behavior, the probability of occurrence is a more appropriate interpretation of the occupancy parameter in the context of bat monitoring, so hereafter we refer to occurrence rather than occupancy in the context of NABat. A goal of NABat is early identification of changes in species occurrence (specifically declines) in the forty-seven North American bat species. Stationary acoustic bat detectors with ultrasonic microphones are used to collect detection/non-detection data for up to four nights during a season, where the season is defined as the summer active period (Loeb et al., 2015). These detectors record bat echolocation call files that are processed and classified to species using automated software, thus requiring human verification to remove misidentification errors prior to analysis (see Banner et al., 2018 and Reichert et al., 2018).

The NABat program is using a master sample to facilitate coordination and collaboration among partners (Irvine et al., 2018). The NABat master sample is a probabilistic design created by applying the GRTS algorithm to randomly order all 10 km \times 10 km grid cells in the contiguous United States (Talbert and Reichert, 2018). The grain size was chosen to accommodate the long nightly foraging distances and large home ranges of temperate bats during summer, making the occupancy framework reasonable for monitoring (i.e., closure and independence assumptions are reasonable, Loeb et al. (2015)). The NABat master sample is a spatially balanced ordered list of all grid cells and any consecutively numbered subset should be spatially balanced. As with many large-scale monitoring programs, power to identify changes in species occurrence probability is desired for different spatial subsets (e.g., management area like a National Forest, state, country, etc.). Within spatial subsets, the n grid cells with the smallest GRTS-order assigned values are selected for bat surveys.

We considered two spatial subsets of the master sample within the United States Forest Service, Region 9 (USFS-R9): USFS-R9 as a whole and National Forest (NF) land within USFS-R9 (Fig. 1; we also examined a similar subset in the Pacific Northwestern US, see Supplement

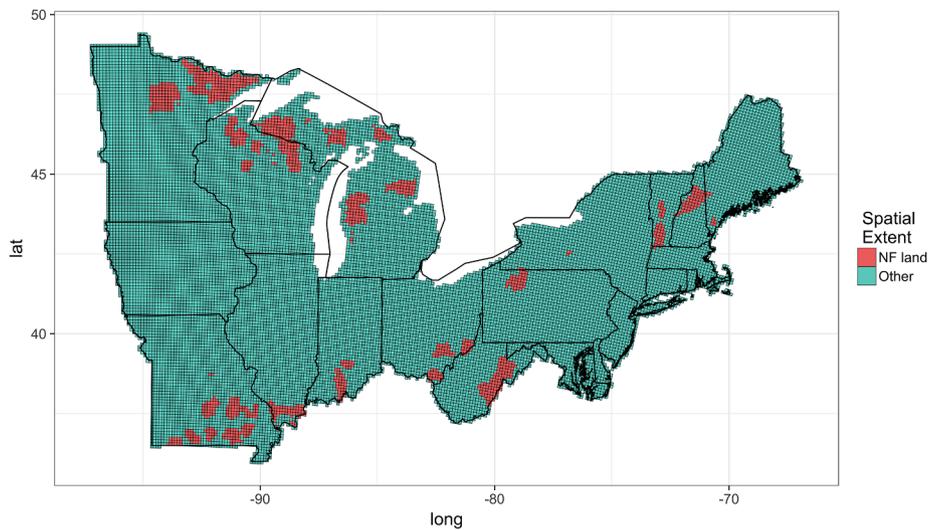


Fig. 1. United States Forest Service Region 9 with National Forest land indicated by salmon-colored grid cells. For scale, this region takes up about one quarter of the contiguous United States.

S2). We chose these two subsets because interest lies in inference for both extents. Additionally, the spatially explicit site-level covariate, percent forest cover, which has been shown to be related to occurrence for some bat species (e.g., the big brown bat, *Eptesicus fuscus*, Rodhouse et al., 2015; Kalcounis-Ruppell et al., 2005; Arnett and Hayes, 2009), was available for the entire region (provided by Eric Winters). Unsurprisingly, National Forest land is more forested than USFS-R9 as a whole (USFS-R9 5-number summary = (0, 8, 27, 58, 99)% vs. NF land 5-number summary = (5, 50, 65, 82, 99)%), thus comparing these spatial subsets allowed us to more generally consider how the environmental covariate space that is related to initial occupancy may affect power to identify trends in different spatial subsets (e.g., NF land vs. R9). We standardized percent forest cover to have a mean of zero and standard deviation of one with respect to the spatial subset of interest, which can help with convergence during model fitting (Royle and Dorazio, 2008).

We generated data for two types of species, a species with average initial occurrence and a species with high initial occurrence when percent forest cover was at its average value (i.e., percent forest = 0). For both species types, we used a value consistent with the estimated logit-linear relationship between occurrence probability and percent forest cover (all else constant) for the big brown bat from previous research, reflecting our best guess based on the available information. Specifically,

we used $logit(\psi_{i,1}) = 0 + 1.4perFor_i$ ($\theta = [0, 1.4]$) to generate initial occupancy for species with average initial occurrence, and $logit(\psi_{i,1}) = 1.4 + 1.4perFor_i$ ($\theta = [1.4, 1.4]$) for species with high initial occurrence. Based on pilot data from northern Wisconsin and the western Upper Peninsula of Michigan, we assumed both species types had constant detection probabilities of $p = 0.5$ ($\omega_t = [0]$); this was consistent for most species surveyed, but no covariate information was available to explain heterogeneity in detection probabilities. Similarly, we did not include spatio-temporal covariates for the colonization and extinction probabilities because we only had access to effectively static site-level covariates.

To reflect an imperiled population, we imposed a multiplicative decline in the survival rate for occurrence following $\phi_{t-1} = \phi_1 \times d^{t-2}$ ($t = 2, \dots, T$; $d = 0.9$), imposing an aggressive 10% yearly decline in the occurrence survival rate for the species of interest. Our approach is similar to that taken in Rodhouse et al. (2015) and reflects the kinds of declines induced by WNS (Frick et al., 2010) and wind turbine collisions (Frick et al., 2017) that have already been observed in parts of North America. We set $\phi_1 = 0.8$, and held colonization constant at 0.2 or 0.01 for $t = 2, \dots, T$ for both spatial subsets. We investigated the same combinations of colonization and extinction for the five- and ten-year studies, but for the ten-year studies, we only considered the larger spatial subset, USFS-R9. We chose these two constant levels for

Table 1
Species-specific parameter settings used in data generation for a simulation-based power analysis aimed to identify an aggressive decline in occupancy for survey lengths of five and ten years. Bold symbols and values denote vectors.

Subset	Species Type	$\theta_{(r+1) \times 1}$	$\gamma_{(t-1) \times 1}$	ϕ_1	d	$\omega_{(w+1), r \times 1}$	Study
USFS-R9	<i>High Initial Occurrence</i>						
	Negligible Colonization	[1.4, 1.4]	0.01	0.8	0.9	0	5,10 years
	Colonization	[1.4,1.4]	0.2	0.8	0.9	0	5,10 years
	<i>Average Initial Occurrence</i>						
	Negligible Colonization	[0,1.4]	0.01	0.8	0.9	0	5,10 years
	Colonization	[0,1.4]	0.2	0.8	0.9	0	5,10 years
NF	<i>High Initial Occurrence</i>						
	Negligible Colonization	[1.4, 1.4]	0.01	0.8	0.9	0	5 years
	Colonization	[1.4,1.4]	0.2	0.8	0.9	0	5 years
	<i>Average Initial Occurrence</i>						
	Negligible Colonization	[0,1.4]	0.01	0.8	0.9	0	5 years
	Colonization	[0,1.4]	0.2	0.8	0.9	0	5 years

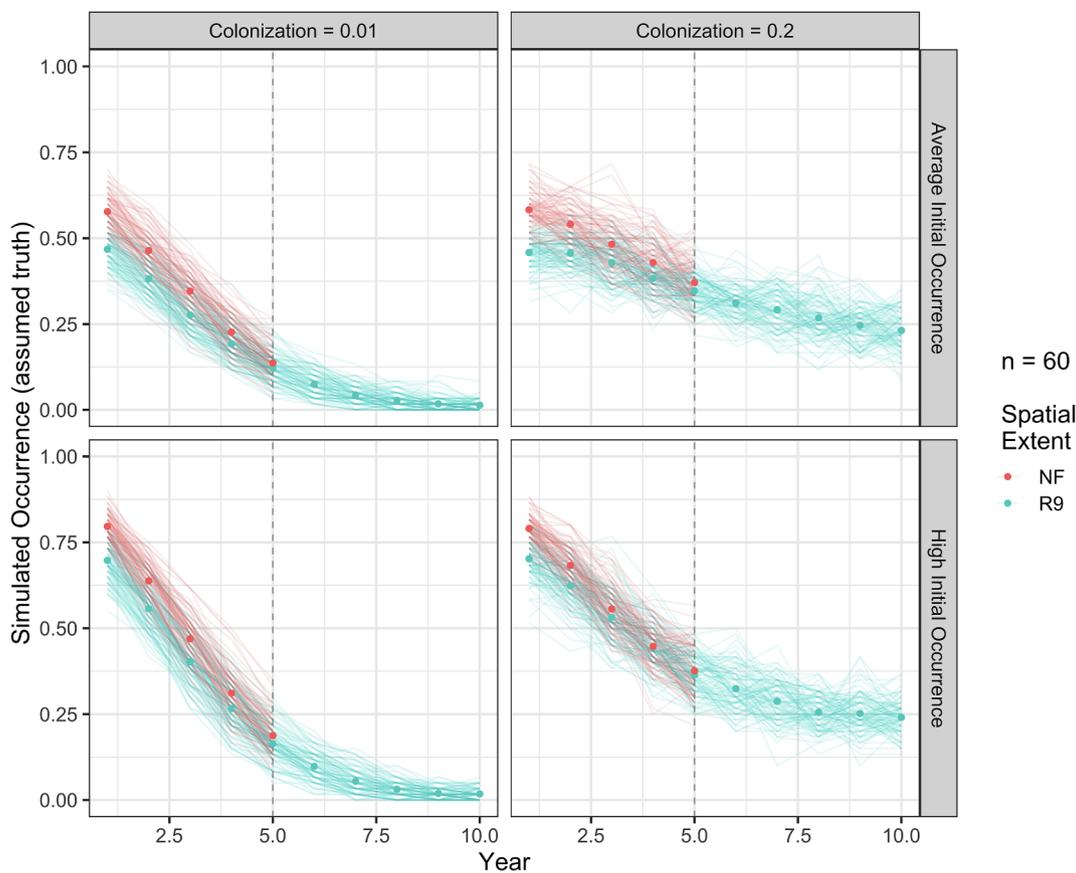


Fig. 2. Trends simulated according to twelve species- and survey-length-specific scenarios. Five-year and ten-year surveys are denoted by the vertical dashed line. Comparisons can be made between survey length (5 vs. 10 years), two different spatial subsets (NF land = salmon, USFS-R9 = blue), two levels of colonization (panels), and two levels of baseline initial occupancy (rows).

Table 2

Number of grid cells surveyed given different percentages of the total number of grid cells selected for two spatial subsets of interest, the USFS-R9 and the land in the region that is owned by the National Forests.

Spatial subset	1%	1.5%	2.1%	$n = 30$	$n = 40$	$n = 50$	$n = 60$	$n = 70$	$n = 80$	$n = 90$
USFS-R9	182	273	382	30	40	50	60	70	80	90
NF Land	15	22	30	–	40	50	60	70	80	90

colonization to get a sense for how the dynamics (i.e., colonization $\gg 0$) can affect the imposed trend, effect size, and consequently power (scenarios defined in Table 1). Mathematically, we cannot set colonization to 0 in the auto-logistic parameterization of the dynamic occupancy model, so the case where $\gamma = 0.01$ represents negligible colonization, implying very few of the unoccupied grid cells at the start of each year will become occupied during the next year (about 1 in 100), and resulting in an overall reduction in the number of sites occupied. Ecologically, when colonization is 0.01, we can think of a scenario where individuals are dying or leaving grid cells but not immigrating to new cells. Whereas, when colonization occurs ($\gamma = 0.2$), individuals are dying or leaving grid cells, but immigration to new cells is also happening within the defined spatial subset.

We were specifically interested in the sample size required to identify the decline scenarios shown in Fig. 2 for the two derived trend parameters (λ_{Tot} and λ_{Avg}). In our power analysis, we assumed a visit design with four visits to sites ($J = 4$) for all scenarios, which was based on recommendations provided for species with a detection probability of about 0.5 in McKann et al. (2013). We considered equal-intensity sampling (same percentage of grid cells surveyed) for the two spatial subsets: 1% of grid cells, 1.5% of grid cells, and 2.1% of grid cells (Table 2). We also investigated equal-effort or fixed sample sizes of

30, 40, ..., 90 grid cells regardless of the spatial subset's extent to represent the 30-grid-cell guideline from initial NABat recommendations (Loeb et al., 2015) up to a larger sample size of 90 grid cells, which has been feasible for regions in the western United States.

We generated one-hundred realizations of occurrence probabilities assuming the species-specific characteristics and duration of study described in Table 1, for a sample size of $n = 60$ (shown in Fig. 2). These simulated trend lines allow us to visualize how the combination of initial occurrence and colonization/extinction parameters interact to impose trends on occurrence over time, and the amount of variation among them sheds some light on relative effect sizes for each scenario. The scenarios we considered resulted in linear trends (Fig. 2, most five year scenarios), curvilinear trends (ten year scenarios), trends with large effect sizes (Fig. 2, colonization = 0.01, and most five year studies), and those with more modest effect sizes (Fig. 2, colonization = 0.2, average initial occupancy, ten year study). For larger n , we would expect the variability among the one-hundred simulated trends for each scenario in Fig. 1 to decrease, and for smaller n we would expect it to increase.

Using dynOccuPow we conducted simulation studies with 100 simulated datasets for each of the twelve scenarios specified in Table 1 for each n specified in Table 2 (datasets for $n = 60$ shown in Fig. 2). The

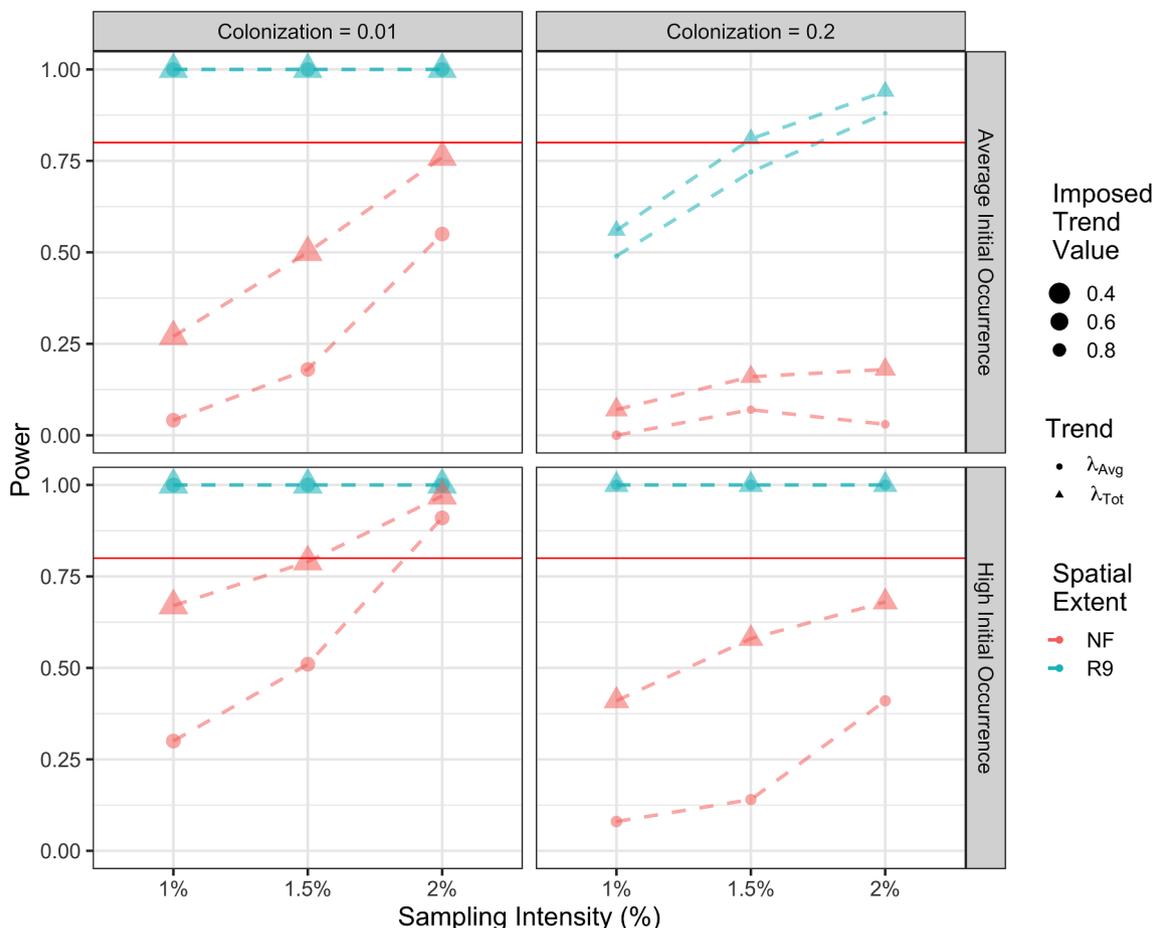


Fig. 3. Comparison of power (y-axis) to identify a decline in occurrence over five years using λ_{Tot} (triangles) and λ_{Avg} (circles) for equal-intensity sampling efforts (x-axis). Colors distinguish between spatial subsets (R9: blue; NF: salmon). The two levels of initial occurrence in the rows (top = Average Initial Occurrence, bottom = High Initial Occurrence). The sizes of the plotting characters are proportional to the true trend imposed during data generation; smaller values represent larger effect sizes, and are shown with larger plotting characters.

functions in our package use a Bayesian implementation of the autologistic dynamic occupancy model. We specified 3 independent chains for 10,000 iterations with a burn-in of 5000 to sample from the posterior distribution. We observed reasonable convergence of the MCMC samplers for all scenarios except for those where the average occurrence probability approached zero in latter years, which required larger sample sizes than the ones we investigated. We saved the MCMC draws from the posterior distribution, the posterior means, the posterior medians, the posterior standard deviations, and 95% credible intervals for all parameters of interest. Values of one for λ_{Tot} and λ_{Avg} represent no change in occurrence probability during the study. Power was computed as the proportion of realizations of data that, when analyzed, resulted in 95% credible intervals for λ_{Tot} and λ_{Avg} with upper and lower endpoints that both fall below one, the no-change value.

3. Results

In general, we observed higher power for both trend parameters with larger sample sizes (Figs. 3–5). This result was expected because, given the assumed detection probability of 0.5, we fixed the number of visits at a value that was sufficient for convergence of estimators from the dynamic occupancy model (McKann et al., 2013). Therefore, increasing the number of grid cells, holding all else constant, allowed for more precise estimation of annual species occurrences. We also observed higher power for the total growth rate than for the average annual growth rate in all scenarios (Figs. 3–5).

3.1. Comparing spatial subsets

3.1.1. Equal-intensity sampling

The geographic area for USFS-R9 is much larger than that defined by NF land within USFS-R9 (Fig. 1). Thus, there is a large disparity in sample sizes between the equal-intensity sample sizes for USFS-R9 and NF land. Specifically, USFS-R9 sample sizes are large (> 181) and tended to be well-powered for identifying net changes in occurrence, whereas sample size for NF land are small (< 30) and tended to be under-powered for most scenarios (Fig. 3). Lower colonization afforded higher power for both trend parameters in both spatial subsets (Fig. 3) with one exception. The exception was the scenario with high baseline initial occurrence in USFS-R9 (Fig. 3: bottom row, blue lines), which had approximately perfect power (out of 100 realizations) regardless of assumed colonization values. Furthermore, for both spatial subsets, the assumed value for baseline initial occurrence appeared to affect the power to identify changes in occurrence, with higher values of baseline initial occurrence affording more power (Fig. 3: top vs. bottom row). Most of the differences between the spatial subsets we observed in this comparison are due to the large disparity in sample sizes. Next, we consider equal-effort sample sizes for both subsets to address our question about how the species-environment relationship between percent forest cover and initial occurrence affects power.

3.1.2. Fixed-effort sampling

For the fixed-effort sample sizes, we observed higher power for all scenarios with lower colonization versus those with higher colonization

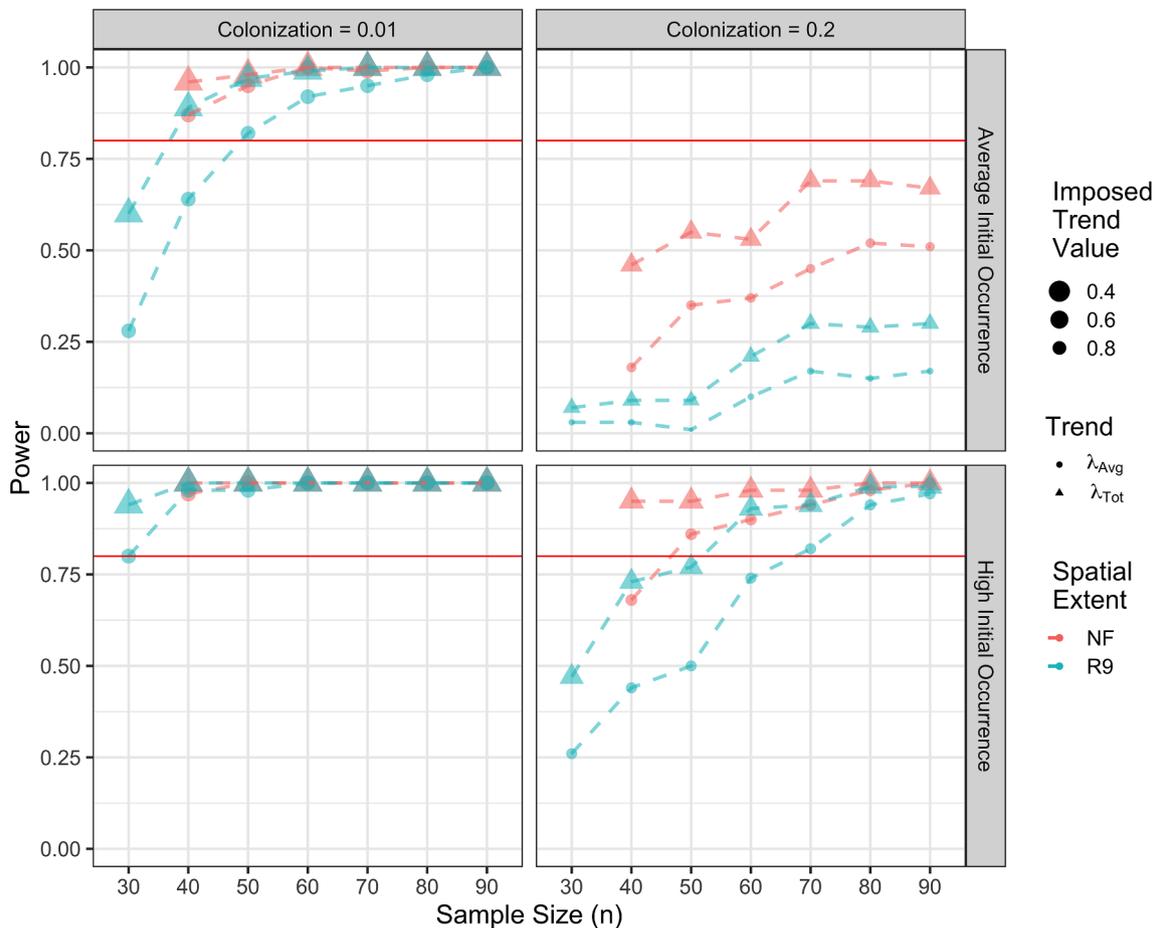


Fig. 4. Comparison of power (y-axis) to identify a decline in occupancy during a five year period using λ_{Tot} (triangles) and λ_{Avg} (circles) for fixed-effort sample sizes (x-axis). Colors distinguish between spatial subsets (R9: blue; NF: salmon). The two levels of initial occurrence in the rows (top = Average Initial Occurrence, bottom = High Initial Occurrence). The sizes of the plotting characters are proportional to the true trend imposed during data generation; smaller values represent larger effect sizes, and are shown with larger plotting characters.

(left panel vs. right panel, Fig. 4). We also observed more power from the fixed-effort sample sizes within NF land than those within USFS-R9. This result is likely due to a combination of the strong relationship assumed between initial occurrence and percent forest cover and the fact that the percentage of the spatial subset being sampled is higher in NF land than it is in USFS-R9. Specifically, for the fixed-effort sample sizes considered, the percentage of the total subset that was sampled ranged from 0.15% to 0.5% in USFS-R9 and from 2% to 6% in NF land. Additionally, the effect size of the imposed trend was larger in NF land than in USFS-R9, a direct result of the average percent forest cover being higher in NF land and driving up the average initial occurrence (≈ 0.8 vs. 0.75 in Fig. 2).

3.2. Comparing five and ten-year studies within USFS-R9

For the ten-year studies, the average annual growth rate (λ_{avg}) was insufficient for identifying trends. This insufficiency in power in the ten-year studies was directly tied to an assumption made by the average annual growth rate parameter; specifically, the assumption that changes in the ratios of average occurrence probability between subsequent years are constant. For the five-year studies, the assumption was reasonable because the trends reflected an approximately linear decline in occurrence (see Fig. 2). For the ten-year studies, however, the decline was curvilinear. Specifically, the ten-year decline appeared exponential when colonization was 0.01 and/or initial occurrence was high, and it appeared to be more cubic in nature when colonization was 0.2 and initial occurrence was average (Fig. 2); thus, the average annual

occurrence parameter was not appropriate for identifying the nonlinear trends.

We observed consistently higher power for the total growth rate (λ_{Tot}) coming from ten-year studies than we did for that from the five-year studies (Fig. 5, green triangles vs. purple triangles, right panel). Conversely, in the ten-year studies with negligible colonization, the total growth rate parameter exhibited insufficient power to identify the imposed trend regardless of the level of initial occurrence. This observation is despite the large effect size for the change in average occurrence between year one and year ten in these scenarios (see Fig. 2). This apparent contradiction is a direct result of the average occurrence probabilities in the later years (years 7+) being extremely close to zero, and thus requiring larger sample sizes for precise estimation. In other words, the simulated Y for these scenarios are too sparse (are mostly zeros) for the dynamic occupancy model to estimate the parameters (see Fig. 6) with the sample sizes we investigated and the sampler settings used (3 chains, 10,000 iterations, burn in of 5000, and thinned by 3). This relationship can be thought of as a *floor effect* that we would hope not to observe, as it corresponds to regional extinction of a species.

Lastly, we observed extremely high power for both trend parameters from the five year studies when colonization was low, regardless of initial occurrence. This is a direct result of the large effect size from these scenarios, which appear as the strong negative linear relationship and large change from the initial to the final average occurrence probability in the imposed trends in Fig. 2. Further, the imposed trend is linear for five-year studies, and the occurrence probability in the final

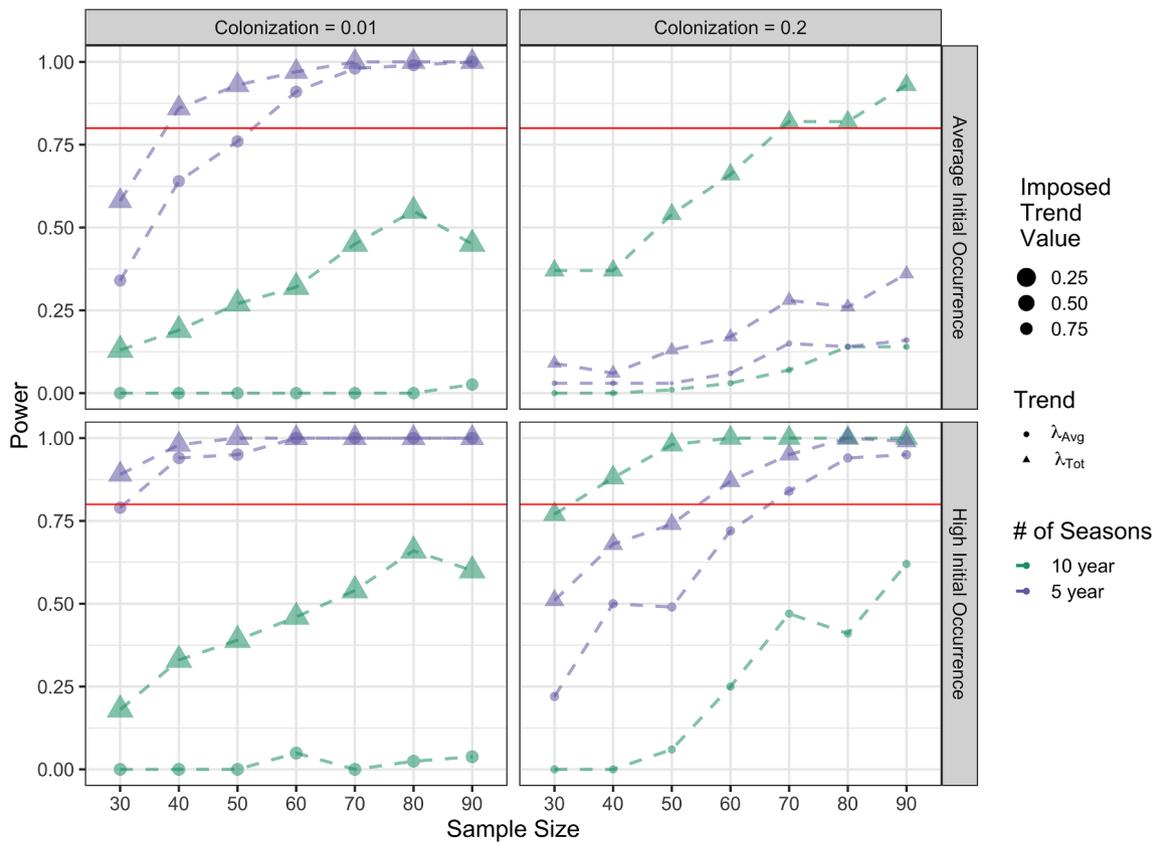


Fig. 5. Comparison of power (y-axis) to identify a decline in occurrence during a five year study using λ_{Tot} (triangles) and λ_{Avg} (circles) for fixed effort sample sizes (x-axis). Colors distinguish between lengths of studies (ten-year: green; five-year: purple). The two levels for colonization are shown in the panels (left = 0.2, right = 0.01), and the two levels of initial occurrence in the rows (top = Average Initial Occurrence, bottom = High Initial Occurrence). The sizes of the plotting characters are proportional to the true trend imposed during data generation; smaller values represent larger effect sizes, and are shown with larger plotting characters.

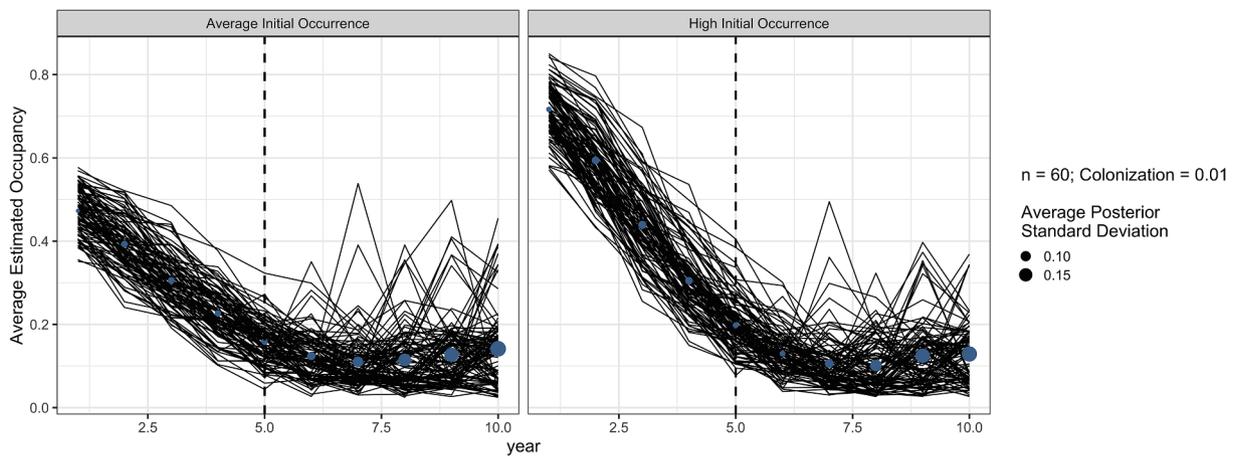


Fig. 6. Posterior mean occupancy is plotted versus year for each realization of data (each line), under the effectively no colonization scenarios with Average Initial Occurrence (left) and High Initial Occurrence (right) in a ten-year study. The vertical dashed line is at five years, differentiating five- and ten-year studies. Five-year studies in the power analysis were actually different realizations of data, but showed extremely similar results.

year was large enough that it could be estimated with low bias and high precision (Fig. 6, left of the dashed line, both plots).

4. Discussion

Dynamic occupancy models provide a flexible framework for simulating and analyzing detection/non-detection data that is reasonably consistent with monitoring programs designed to characterize changes in species distributions over time. Real ecological data may not be

consistent with the assumed model, and given the complicated parameter structure for trends within dynamic occupancy models, visualizing trends during the data-generation step of a simulation-based power analysis is important to ensure the imposed trends are reasonable approximations to what is expected for the species of interest (e.g., Fig. 2). Thus, simulation-based power analyses can provide good starting places for programs and can help refine survey design recommendations as new data become available.

We provide a tool for investigating two derived temporal trend

parameters and conducting simulation-based power analyses (`dynOccuPow`) such that measurable trend objectives can be articulated and met using dynamic occupancy models. We simulated and analyzed data using a dynamic occupancy model (i.e., an unbiased simulation-based approach), making the implicit assumption that survival and colonization rates and underlying species-environment relationships are the main drivers of how species distribution changes over time. Additionally, our approach assumes the grain size of analysis units, the timing or spatial location of visits, and the length of the season are defined such that it is reasonable to assume closure and independence of observations arising from visits within the same season. Considering whether or not the dynamic occupancy model is a reasonable framework for characterizing trend within the system of interest *prior* to using our approach for power analysis is critical. We use the bat monitoring program NABat as an example, which was designed so that data could be analyzed using occupancy models. In our example, we specifically considered between-season mortality via WNS, wind turbines, and habitat alteration that is reflected regionally in terms of net change in occurrence. We envision this framework to be broadly appealing for many species distributional change processes, and thus other geographically extensive occupancy monitoring programs in addition to NABat.

Unlike a typical power analysis, where the user sets the effect size for the parameter they wish to identify as an input (e.g., estimate and residual standard deviation for a linear trend parameter), the effect size for trend-detection objectives is a function of the model parameters specified by the user. The complicated structure of derived occupancy (or occurrence) and trend parameters motivated our development of visualization tools for plotting the trends induced by a set of species-specific values for colonization, extinction, initial occupancy, and detection probabilities. These tools can be used to translate prior information (e.g., results from analyzing pilot data or expert knowledge) into imposed trends, facilitating articulation and refinement of measurable program objectives. In the context of our example, we knew little about colonization and extinction probabilities for bats in USFS-R9, so we investigated a variety of decline scenarios for different survey lengths to characterize (as broadly as possible) potential declines.

We focused on differences in the estimated sample size required to achieve an 80% chance of identifying imposed trends within two spatial extents and for two lengths of studies based on 95% credible intervals for two derived trend parameters (λ_{Tot} and λ_{Avg}), using a dynamic occupancy model. Comparing fixed-effort sample sizes for NF land within USFS-R9 to all of USFS-R9, we highlighted the importance of assumed species-specific relationships between landscape covariates and initial occurrence. Namely, that the effect size for an imposed trend will be higher for the spatial subset that has, on average, higher values for a covariate that is strongly and positively associated with initial occurrence. We expect this relationship to hold in general, and we expect the inverse to hold as well. If covariate information is available for the sample frame (e.g., through a GIS layer), it can be used in the power analysis to generate realistic detection/non-detection data and address questions at different spatial extents. The ability to include actual covariate data into a power analysis and compare different spatial subsets within a region of interest is a unique feature of our approach.

The five- vs. ten-year scenarios revealed some interesting general results and cautionary guidelines for designing occupancy-based monitoring programs. Particularly, it is important to choose appropriate trend parameters for identifying changes in occupancy or occurrence, conditional on the characteristics of the trend imposed. That is, total growth rate λ_{Tot} is reasonable for monotonic change (linear or functional), but the average growth rate λ_{Avg} is only appropriate for linear changes. Additionally, although we would hope not to observe a rapid regional extinction (e.g., trends imposed by colonization = 0.01 in our ten-year study), the dynamic occupancy model will require infeasibly large sample sizes to identify the change with the total growth rate parameter due to the rarity of observed detections as occupancy

probabilities approach zero. Conversely, the model will be well-powered to identify an aggressive decline in the short run with the total growth rate parameter, suggesting that it is important to monitor species often (e.g., every 5 years). Ideally, data from continual monitoring could be used to update and inform species-specific assumed parameter values at many intervals to keep sample size estimates from power analyses current and reflective of the most up-to-date approximation of reality.

Survey design questions should be investigated on a case-by-case and species-by-species basis, using the foremost information (pilot data) available. In our example, we observed the sample size required to identify overall changes in occurrence increase for the higher colonization rate ($\gamma = 0.2$ vs. $\gamma = 0.01$). We also note that our pilot data were extremely limited with respect to the region of interest (i.e., detection data came from two northeastern states within a large area). In addition to obtaining more pilot data for estimating detection probabilities of bat species in the region, we recommend gathering data to obtain estimates of realistic colonization rates for bats in the region and updating the analysis accordingly.

5. Conclusion

Our tools can be used in an iterative fashion to evaluate and adjust objectives during initial design of monitoring programs, and to refine survey design recommendations during implementation. For example, in the case of NABat, no pilot data was available when the monitoring plan (Loeb et al., 2015) was written, so an initial sample size recommendation was based on existing survey design literature without conducting a formal power analysis; the recommendation was to survey at least 30 grid cells. In contrast, our refinement of the initial recommendations in light of pilot data show much more effort is needed to identify changes in species occurrence driven by a multiplicative decrease in survival rate. Although our results make use of limited pilot information, they are an improvement over the initial recommendations, highlighting the importance of collecting sufficient data to be used with tools like `DynOccuPow`, ultimately making the best use of monitoring resources.

Author contribution

K. Banner, K. Irvine, T. Rodhouse, and A. Litt conceived ideas and were involved in discussions regarding statistical methodology; K. Banner created the R package and vignette. K. Banner led the writing of the manuscript with significant support from K. Irvine, T. Rodhouse, and A. Litt. D. Donner contributed conceptually to spatial scaling discussions, contributed materials and resources to implement and collect field bat acoustic data, and provided the manually-vetted bat pilot data. All authors contributed critically to the drafts and gave final approval for publication.

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Appendix A. Data simulation details

Large-scale monitoring programs aim to generalize inferences beyond survey locations by employing probabilistic sampling designs, which select n sites for monitoring (indexed by $i = 1, \dots, n$) from a spatial domain comprised of N total sites ($n \ll N$). Our approach facilitates investigation of two probabilistic sampling designs: the simple random sample (SRS) and a spatially-balanced analog defined by the generalized random tessellation stratified (GRTS) algorithm (see Stevens and Olsen, 2004). Detection/non-detection data are simulated and stored in an array, $\mathbf{Y}_{n \times J \times T}$, where its elements represent visit-level detections from a survey of n sites (rows) with J visits to each site (columns) for a duration of T seasons (layers of $n \times J$ matrices). The data take on the values: $y_{ijt} = 1$ if the species was detected at least once during visit j to site i in season t , or $y_{ijt} = 0$ if undetected; our approach assumes no missing observations, which if violated could result in sample size recommendations that are too liberal. Following survey design suggestions for multi-season studies from MacKenzie and Royle (2005) and Bailey et al. (2007), we also assume the same n sites were visited each sampling season. Lastly, for simplicity, we assume the same number of visits to each site during each season, although a simple extension could accommodate different numbers of visits among surveyed sites (i.e., $J_{i,t}$ rather than J).

To generate \mathbf{Y} , we used a form of the auto-logistic parameterization described in Royle and Kery (2007) and Royle and Dorazio (2008). The model assumes a Markov dependence between the true occupancy of site i in year t , given its status in year $t - 1$ ($t = 2, 3, \dots, T$). The Markov dependence is specified through colonization and extinction parameters. The colonization probability, γ_t , is the rate at which unoccupied sites in year $t - 1$ become occupied in year t . Additionally, the rate at which occupied sites in year $t - 1$ become unoccupied in year t is the extinction probability, $\epsilon_t = 1 - \phi_t$, where ϕ_t is the survival probability of an occupied site in year $t - 1$ remaining occupied in year t . Following model specifications, our approach generates the initial occupancy state for each site, $z_{i,1} = 1$ if site i is occupied and $z_{i,1} = 0$ if site i unoccupied from a Bernoulli($\psi_{i,1}$) distribution. The model allows for logit-linear relationships between site-level covariates and species occurrence during the first year through $\text{logit}(\psi_i) = \mathbf{X}_{i=1}\theta$, where $\mathbf{X}_{i=1}$ is a matrix of covariates, and θ is a vector of partial regression coefficients representing the assumed relationships.

The occupancy statuses for subsequent years ($Z_{i,t}$, $t = 2, \dots, T$) are simulated sequentially, conditional on the previous year (Markov dependence), using the distribution specified by the model: $Z_{i,t} = 1 | Z_{i,t-1} \sim \text{Bernoulli}(\pi_{i,t})$. The yearly occupancy probabilities are calculated according to $\text{logit}(\pi_i) = a_i + b_i z_{i,t-1}$, where $\mathbf{z}_{i,t-1}$ is an $n \times 1$ vector representing the true occupancy status in year $t - 1$. The parameters a_i and b_i are related to site-specific colonization and extinction probabilities through $\text{logit}(\gamma_{t-1}) = a_i$ and $\text{logit}(\phi_{t-1}) = a_i + b_i$. Our approach accommodates the general form of the auto-logistic parameterization, which allows for site-level covariates on the update probabilities and is commonly used by practitioners (e.g., Rodhouse et al., 2012, 2015). However, the computation of the colonization and extinction probabilities must be done assuming covariate values are zero (or average values for standardized covariates), which can complicate interpretations. Therefore, unless the site-level covariates are changing over time, we recommend relating them to initial occupancy.

The final step in our data simulation approach uses the true occupancy status of site i in year t (simulated $Z_{i,t}$) and estimated detection probabilities to generate \mathbf{Y} . The probability of detecting a species during visit j in year t if site i is occupied is p_{ijt} and the individual observations y_{ijt} are simulated from a Bernoulli($z_{i,t} \times p_{ijt}$) distribution. When covariates are available, they can be included to account for heterogeneity in detection probabilities among sites, visits, and seasons through the logit-linear relationship, $\text{logit}(\mathbf{p}_i) = \mathbf{W}_i \omega_i$, where \mathbf{W}_i has dimensions $(n \times J) \times w$ and w is the number of covariates.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ecolind.2019.05.047>.

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