

# Twenty years of dynamic occupancy models: a review of applications and look towards the future

## Abstract

Since their introduction over twenty years ago, dynamic occupancy models (DOMs) have become a powerful and flexible framework for estimating species occupancy across space and time while accounting for imperfect detection. As their popularity has increased and extensions have further expanded their capabilities, DOMs have been applied to increasingly diverse datasets and research objectives in applied ecology. At the same time, technological advancements have resulted in massive increases in available data, offering both new opportunities and new challenges for users of DOMs. Given these developments, it is timely to examine common practices in building these models to understand the breadth of modelling approaches, determine potential vulnerabilities, and identify priorities for future research. We reviewed a sample of articles that have fit DOMs in the past 20 years, examining the contexts of their application and the approaches taken to the model building process. We find that these models have been used to pursue diverse objectives, based on datasets with wide-ranging spatial and temporal scales collected using a variety of survey methods. Our comparisons of modelling approaches indicate that many applications of DOMs considered relatively few covariates on key model parameters, as well as a tendency towards linear responses over more complex non-linear or interactive forms. Model selection techniques were largely idiosyncratic with little consensus on the best approaches, and model evaluation was rare across reviewed applications –

additionally, existing research on either of these subjects is limited. Based on these findings, we identify key areas of the modelling process which merit discussion and further investigation. Where possible we provide recommendations for current users of DOMs, and where uncertainties remain, we highlight key priorities for future research to support users in fitting the most reliable and useful models possible.

## Introduction

1 The description of patterns of species occupancy across landscapes has been a long-  
2 standing subject of ecological research (Humboldt, 1849). Estimates of how widespread a  
3 species is and where it occurs are the foundation of monitoring programs and important  
4 for assessing conservation status, while identifying potential drivers of occurrence can help  
5 inform potential management actions (MacKenzie & Reardon, 2013). Robust knowledge of  
6 the occupancy patterns of a species can also help us to predict where a species is most  
7 likely to occur, both under present conditions and in hypothetical future scenarios (Kéry et  
8 al., 2013).

9 Irrespective of its importance, 'occupancy' – broadly referring here to the presence of a  
10 species in a given area and time period – has proven to be a persistently difficult quantity  
11 to estimate in practice. This difficulty arises from the challenges inherent in modelling  
12 complex and dynamic natural systems with incomplete data, exacerbated by the fact that it  
13 is often impossible to determine whether a species is truly absent from a site or whether it  
14 was simply not detected. It is well-established that imperfect detection of organisms results  
15 in biased estimates of occupancy (Gu & Swihart, 2004; Lahoz-Monfort et al., 2014). Despite  
16 this fact and the ubiquity of imperfect detection in field data, many models in widespread  
17 use make no adjustments for detection (Kellner & Swihart, 2014). In addition to this  
18 limitation, many models currently in use (such as conventional correlative species  
19 distribution models) are ill-suited for predicting to new locations and time periods  
20 (Dormann, 2007; Elith et al., 2010). These shortcomings are particularly pronounced when  
21 modelling biological invasions and climate change driven range shifts, both of which are

management priorities that are increasingly commonplace in the Anthropocene (Bertelsmeier et al., 2013; Lenoir & Svenning, 2015).

In recent years, awareness of these obstacles to accurate occupancy estimation and the limitations of many popular methods has encouraged interest in a variety of process-explicit models better suited to these contexts (Briscoe et al., 2019). These include ‘dynamic occupancy models’ (DOMs), first introduced by MacKenzie et al. (2003) as an extension to earlier static site occupancy models (MacKenzie et al., 2002). In their simplest form DOMs use hierarchical observation data to estimate changing site occupancy over time while correcting for imperfect detection; an overview of the basic form and requirements of these models can be found in Box 1. By accounting for imperfect detection and explicitly modelling colonisation and extinction to describe changes in site occupancy DOMs provide answers to common issues in occupancy estimation and offer important advantages over other models (Guillera-Arroita, 2017). Alongside these advantages, they require only relatively simple-to-collect detection/non-detection data rather than the detailed demographic or abundance data required by other more process-explicit models (Briscoe et al., 2019). This balance between complexity and feasibility makes DOMs an appealing option for many applied ecologists.

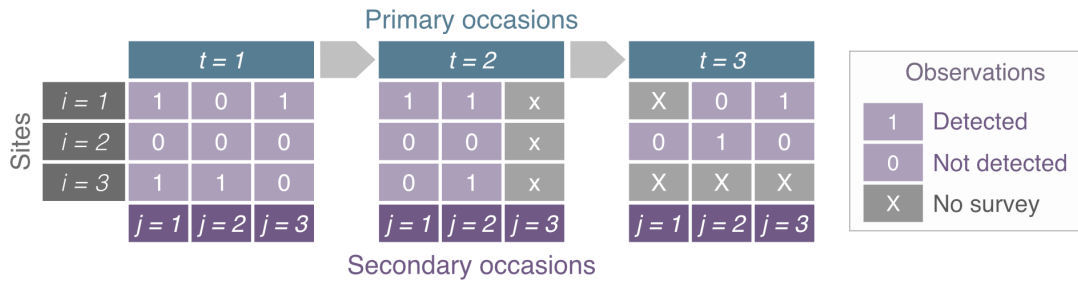
**Box 1: An introduction to dynamic occupancy models**

DOMs are hierarchical models that link observed detection/non-detection data with the underlying latent process of changing site occupancy. To do this, they contain two sub-models: one describing the ecological process of sites shifting between unoccupied and

occupied states over time, and one describing the observation process that records whether a species is detected during surveys given its presence at a site.

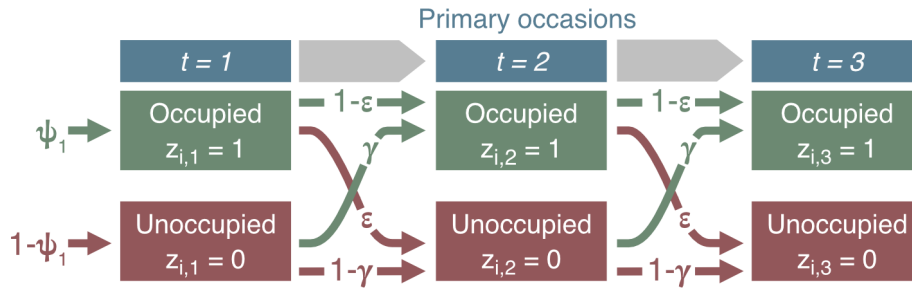
**Input data:** To separate these two processes DOMs require hierarchical data inputs.

Occupancy is estimated at independent sites ( $i$ ) during discrete, time-bound intervals termed ‘primary occasions’ ( $t$ ). Within primary occasions, multiple observations are made at the same sites during independent ‘secondary occasions’ ( $j$ ). For each observation, a species is either detected ( $y_{i,t,j} = 1$ ) or not ( $y_{i,t,j} = 0$ ), resulting in a three dimensional detection matrix as shown in the example below. It is not necessary for all primary occasions to contain the same number of secondary occasions, and missing observations at sites can be accommodated. While secondary occasions are most often represented as repeat observations, other options including same-visit replicates and spatial replicates may also be used (Guillera-Arroita, 2017).

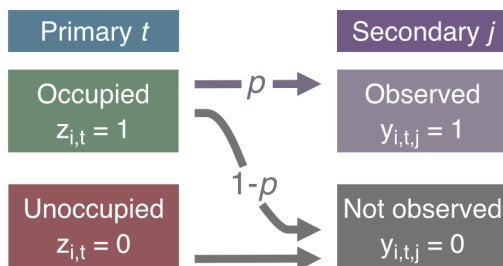


**Occupancy sub-model:** Changing site occupancy over time is described as a Markovian process as represented in the graphic below. In each primary occasion  $t$ , each site  $i$  may exist in either an occupied ( $z_{i,t} = 1$ ) or unoccupied state ( $z_{i,t} = 0$ ). In the first primary occasion, occupancy is determined by a Bernoulli trial with initial occupancy probability  $\psi_1$ , such that  $z_{i,t=1} \sim \text{Bernoulli}(\psi_1)$ . In subsequent primary occasions, site occupancy is

determined by the site's state in the previous primary occasion and probabilities of colonisation  $\gamma$  and extinction  $\epsilon$ , such that  $z_{i,t} \sim \text{Bernoulli}(z_{i,t-1}(1 - \epsilon) + (1 - z_{i,t-1}) * \gamma)$ .



**Observation sub-model:** The detection process relates the observed data  $\mathbf{y}$  to the latent occupancy states  $\mathbf{z}$  as shown in the below graphic. During any given secondary occasion  $j$  within primary occasion  $t$  at site  $i$ , observers will either observe ( $y_{i,t,j} = 1$ ) or not observe ( $y_{i,t,j} = 0$ ) the target species. The probability of observation is given as a Bernoulli trial with detection probability  $p$ , conditioned on the site being occupied in primary occasion  $t$  such that  $y_{i,t,j} \sim \text{Bernoulli}(z_{i,t} * p)$ .



In their original formulation, DOMs estimate four parameters of interest: initial occupancy ( $\psi_1$ ), colonisation ( $\gamma$ ), extinction ( $\epsilon$ ), and detection ( $p$ ). While we have represented each of these parameters as constants for simplicity, they are more often

modelled as time-dependent or estimated with respect to covariates. These covariates are typically incorporated via a logit link function, such that DOMs can be considered four interconnected generalised linear models.

Conventional DOMs make several important assumptions: i) sites are closed to changes in true occupancy state within each primary occasion, ii) occupancy at each site is independent of other sites, iii) observations within each primary occasion are independent of each other, iv) no false positive detections occur, and v) key sources of heterogeneity (including in detectability) are modelled.

For more detailed information on DOMs and related models, see (MacKenzie et al., 2017) and (Kéry & Royle, 2021).

Over the past two decades, continued research on DOMs and occupancy models more broadly has established a powerful and flexible modelling framework suitable for many common tasks in ecological research. Uptake of these models has been encouraged by the availability of freely available software tools for fitting DOMs, which include the program PRESENCE and the R package *unmarked* for fitting the models by maximum likelihood estimation (Hines, 2006; Kellner et al., 2023). In the Bayesian context, resources such as Kéry & Royle (2021) 's text on hierarchical modelling in JAGS and the *ubms* R package have helped to increase the accessibility of these implementations (Kellner et al., 2022). Various model extensions have further broadened DOMs' capabilities – these include models that can account for false positives (Miller et al., 2011; Royle & Link, 2006), model multiple states beyond occupied and unoccupied (Nichols et al., 2007), and jointly estimate occupancy for multiple species (Devarajan et al., 2020; Dorazio et al., 2010). For more

details on using these extensions, see reviews by Bailey et al. (2014) and Guillera-Arroita (2017).

Coinciding with these developments, recent years have seen substantial changes in how ecologists conduct their research. The amount of data available for modelling (including species detections as well as environmental data) has grown considerably over time due to a range of factors, including improvements to data sharing, new large-scale monitoring programs, and increased interest in citizen science efforts (Altwegg & Nichols, 2019; Farley et al., 2018). Technological advances have facilitated the widespread deployment of autonomous detection methods including camera traps and acoustic monitors, generating large quantities of observation data suitable for analysis with DOMs (Balantic & Donovan, 2019; Lahoz-Monfort & Magrath, 2021). At the same time, advancements in computing have made methods which may have been too computationally expensive in the past far more accessible for many. While these advances create exciting new opportunities, they also introduce new challenges for users who must navigate a complex model building process to produce useful and reliable models. Where researchers on related species distribution models have built a large body of literature on assessing various approaches to model building including covariate inclusion and model selection, comparatively little research on these topics has been published for DOMs despite additional complications in performing these tasks for hierarchical models (Guisan et al., 2017).

## Objectives

To understand how users have applied DOMs over the past two decades, we conducted an in-depth review of studies implementing these models since their introduction. We first



identify the research contexts where DOMs have been used, characterising the research objectives they have been applied to, the scale and characteristics of the study systems where data was collected, and the methods used to collect and format the data used to fit models. We then review approaches taken to the modelling process, including the nature of the covariates considered for inclusion and the form of their relationships in the model, the methods used for model selection, and the reporting of model assessment and evaluation. By jointly considering the research contexts to which DOMs are now applied and the approaches taken for model building and evaluation, we aim to highlight challenges in building DOMs, providing recommendations where possible and identifying priorities for future research where uncertainties remain.

## Methods

Our review was constrained to applications of the dynamic occupancy model of MacKenzie et al. (2003) and its extensions. To be included, articles must have fit models that met the following criteria:

- i. Used non-simulated, field-collected, detection/non-detection data.
- ii. Included data from multiple sites which could exist in at least two states, including an occupied and unoccupied state.
- iii. Included data from multiple primary occasions, between which sites change states conditional on the prior occasion's occupancy state and transition probabilities such as colonisation and extinction.

iv. Contained at least one parameter describing the detection process.

A pool of candidate articles was generated using two queries on Web of Science on July 26 and July 29, 2024. The first query included all articles from 2004-2023 which cited MacKenzie et al. (2003). To capture additional relevant articles that did not directly cite MacKenzie et al. (2003), a second query was generated to search articles in the same time-span matching the terms “*dynamic occupancy model\**”, “*multi-season occupancy model\**”, or “*occupancy dynamic\**”; articles including each of “*occupancy*”, “*colonization*”, “*extinction/persistence*”, and “*detection*”; and articles with the term “*occupancy*” located near “*dynamic*” in the title, key terms, or abstract. These queries resulted in 1469 articles: 897 retrieved only from the MacKenzie citations, 274 only from the keywords search, and 298 which appeared in both queries. To allow comparison of DOMs through time, we divided all articles across five four-year strata spanning 2004-2007, 2008-2011, 2012-2015, 2016-2019, and 2020-2023. From each stratum we randomly selected 20 articles for inclusion in the review. Articles that did not meet inclusion criteria were replaced from within their own stratum unless no articles remained. For each article we documented details on the research contexts, datasets, and modelling processes as outlined below.

## Research objectives

We allocated each article to research objective categories based on the aims stated in the text. The six non-exclusive categories included i) ‘estimating trends’, where authors expressed interest in estimates of site occupancy, colonisation, extinction, or detection probabilities; ii) ‘testing relationships’, where authors examined predefined hypothesised relationships between covariates and model parameters; iii) ‘identifying drivers’, where

authors more broadly explored covariates associated with model parameters; iv)  
'predicting temporally', where authors predicted site occupancy under future conditions; v)  
'predicting spatially', where authors predicted site occupancy to unsurveyed locations; and  
vi) 'developing methods', where authors introduced, tested, or demonstrated aspects of  
DOMs.

## Study systems

We recorded the approximate geographical location, spatial scale, and target taxa for each  
study system in the reviewed articles. In cases where a single article included DOMs fit to  
data from multiple study systems, we recorded details for each dataset that was analysed  
independently. A study system's spatial scale was defined as the intended area of inference  
containing all sites, measured to an order of magnitude to account for uncertainty in  
reporting. Details collected on target taxa included the total number of taxa modelled, their  
general categorisation (birds, mammals, herptiles, invertebrates, or 'other'), and their  
conservation status. Taxa were denoted as threatened if they were listed on the IUCN Red  
List of Species as of 2024 or if authors explicitly stated that they were threatened (IUCN,  
2024). This deference to authors' representation of conservation status was made to  
account for sub-species which lack listings or species which are of more local concern,  
although we acknowledge that in some cases conservation status may have changed since  
publication.

## Observations and data structure

For each article, we recorded how observation data was collected for use in modelling.  
Categories of survey methods included human observations, physical trapping, camera

traps, and acoustic monitors. Within these categories we also indicated whether any observations were collected by citizen scientists, either as part of structured survey programs or as more *ad hoc* observations. Details collected on each dataset's structure included the number of primary and secondary occasions, the time elapsed between the first and last survey, and the number of sites used for modelling.

## Covariates and complexity

We were interested in the types and quantities of the covariates considered by authors. To this end, we recorded all covariates considered in each study regardless of whether they were included in final models, acknowledging that not all covariates considered are always reported. Key traits of each covariate were recorded including a general categorisation (see supporting information), whether they were directly observed or remotely sensed, whether they were static or varied between primary occasions, and how they were represented in the model: as a linear response, a non-linear response, or part of an interaction with another covariate (James et al., 2021). In some cases, a single article included distinct modelling workflows with different candidate covariates. Covariates were recorded for each of these workflows independently.

## Model selection and assessment

Model selection procedures were sorted into non-exclusive categories including '*a priori*', where only one model was considered; 'candidate set', where a predefined set of models was considered; 'sequential', where covariates were selected parameter-by-parameter (e.g., fitting detection first, followed by initial occupancy and so on); and 'simple precursors', where covariate selection was preceded by tests with a simpler model

implementation such as a linear regression or single season occupancy model. We also indicated whether model averaging was used for multi-model inference Burnham & Anderson (2004). For each modelling workflow, we documented whether goodness-of-fit was tested and reported, and whether model performance was assessed by validation with either in-sample or out-of-sample data.

## Results

92 articles were included for this review, fewer than the 100 possible articles due to a deficit of qualifying papers in the first stratum (2004-2007). All review data is available in the supporting information. Based on the acceptance rates within each stratum and the number of unprocessed articles remaining for each year, an estimated 496 of 1152 unprocessed articles in our sample would have met inclusion criteria, with an apparent increase over time in the number of articles fitting DOMs (Figure 1).

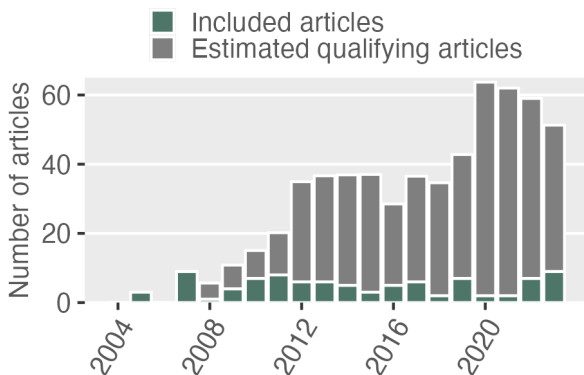


Figure 1: Bars indicate the estimated number of articles fitting DOMs in each year, with green representing articles included in our review and grey projected remaining qualifying

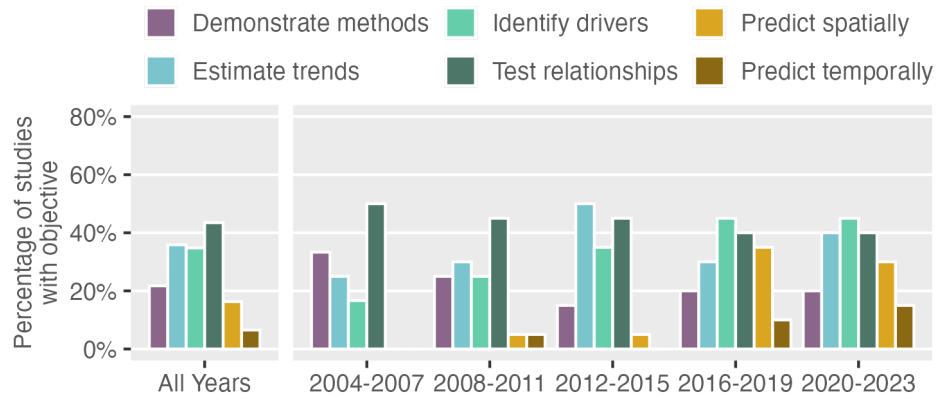
articles. Projections were calculated using the number of unprocessed articles remaining in each year multiplied by the acceptance rate of the corresponding stratum: 12% of queried articles from 2004-2007; 24% from 2008-2011; 42% from 2012-2015; 35% from 2016-2019; and 57% from 2020-2023.

## Research objectives

DOMs have been used to achieve varied research objectives, with no one category of objective representing over half of usage and 37% of studies having pursued multiple objectives simultaneously (Figure 2). The most frequent use of DOMs (44% of studies) was to test hypothesised relationships between environmental factors and species occupancy, often targeting core conservation priorities for their focal species as demonstrated by Olson et al. (2005) 's early study assessing the influence of barred owls (*Strix varia*) on the threatened spotted owl (*Strix occidentalis*). 35% of studies took a more exploratory approach to identifying possible drivers of occupancy, such as in Huber et al. (2017) 's study that examined dozens of habitat covariates for wood warbler (*Phylloscopus sibilatrix*) occupancy. An additional 36% of articles used DOMs to monitor trends in occupancy state through time, both for single species of high conservation interest and for broader community assemblages of species (Ahumada et al., 2013; Scott & Rissler, 2015). While only 17% of articles used their DOMs to make predictions, the proportion of articles pursuing this objective has increased in recent years. These studies tended to have a strong conservation focus, as with McGowan et al. (2020) 's projections of future occupancy for wetland birds under alternative management scenarios. Finally, 22% of the papers

188 reviewed focused on methods development, representing continued focus on extending  
189 and testing DOMs.

190 The applied nature of studies fitting DOMs is further reflected in their authorship: while  
191 79% of studies included at least one affiliate of an academic institution, 59% included a  
192 government affiliate, 28% an NGO affiliate, and 12% an affiliate of a private company. 63%  
193 of studies had cross-sector authorship with affiliations from at least two categories.



*Figure 2: Bars represent the percentage of articles which pursued each of six non-exclusive research objectives. These objectives include articles which demonstrated methods for DOMs, estimated trends in model parameters, identified drivers of occupancy dynamics, tested hypothesised relationships with the environment, made spatial predictions, and made temporal predictions. Percentages are given for each four-year stratum ( $n = 12$  articles for 2004-2007;  $n = 20$  for all other strata), as well as for all articles in the review sample ( $n = 92$ ).*



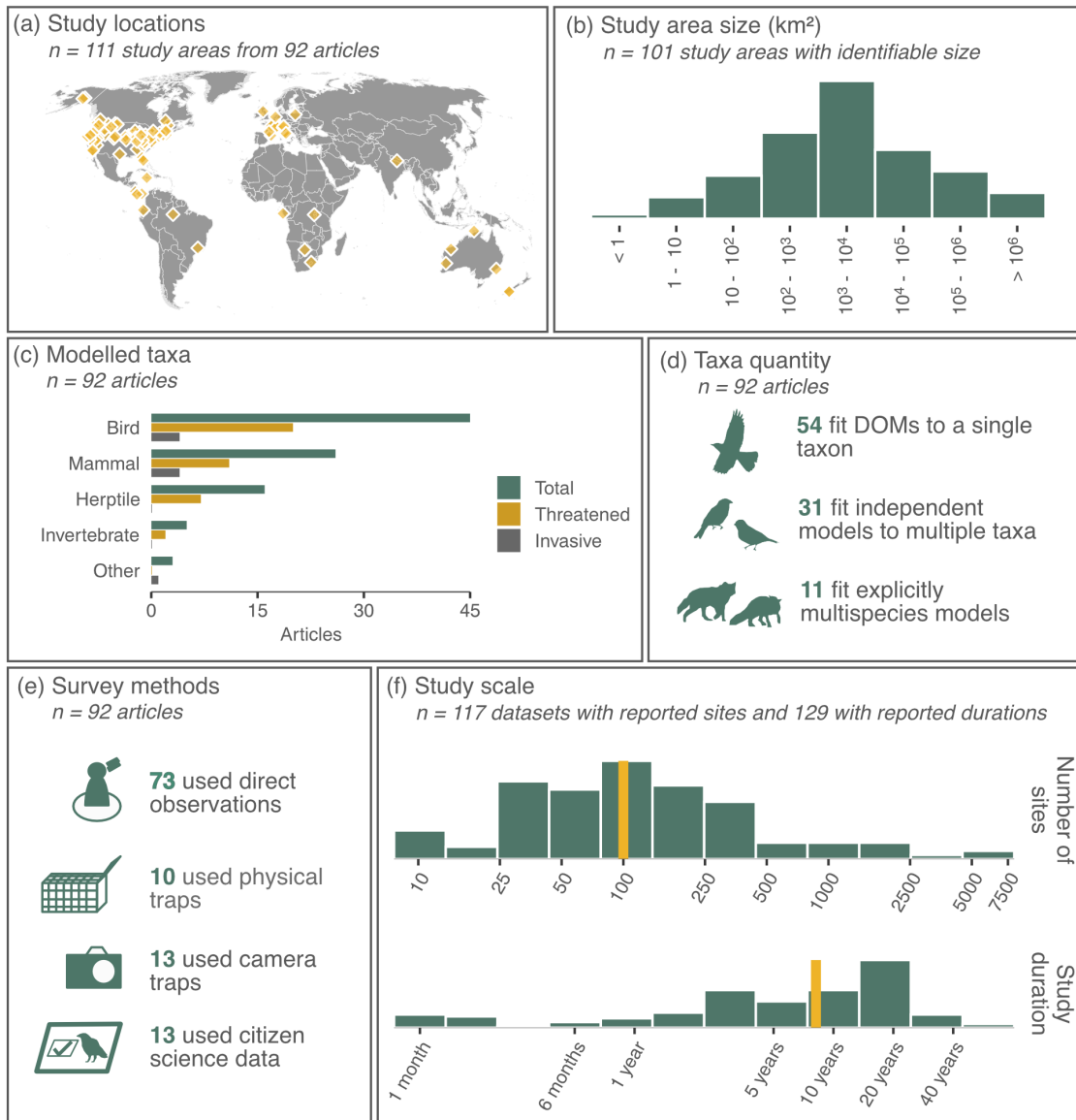
## Study systems

The study systems included in our sample were globally distributed: while a majority of articles used data collected in the United States of America, study systems spanned all continents except Antarctica (Figure 3 A). These study areas varied considerably in size, ranging from hyper-local to continental scales (Figure 3 B). The smallest study locality included in our sample explored insect occurrence in a rainforest plot less than one square kilometre, while the largest analysis modelled avian range shifts across the entire eastern half of the United States (Basset et al., 2023; Clement et al., 2019).

Most studies focused on vertebrate taxa (Figure 3 C), particularly birds and mammals. DOMs have been less frequently applied to non-animal organisms, perhaps due to a reduced emphasis on imperfect detection outside of the wildlife modelling community. However, there were exceptions, including studies that used DOMs to model decadal changes in lichen occupancy, the spread of chronic wasting disease, and mosquito dynamics (Belinchón et al., 2017; Cook et al., 2022; Mores et al., 2020). The vast majority of studies model terrestrial species, though there have been a limited number of studies on aquatic taxa including invasive salmon, Great Plains stream fishes, and whales (Falke et al., 2012; Fisher et al., 2014; Pendleton et al., 2022).

While most studies fit models for a single taxon (either a single species or multiple species lumped together), 44% fit models to multiple distinct taxa (Figure 3 D). 34% of studies fit independent models to multiple species (Otto & Roloff, 2012; Peach et al., 2019), whereas 12% used explicitly multi-species extensions of DOMs. The latter included hierarchical models which fit hundreds of species in a single implementation with species-level effects

216 (Dorazio et al., 2010; Hendershot et al., 2020) as well as explicit interaction models which  
217 estimated conditional occupancy, colonisation, extinction, and detection probabilities  
218 (Fidino et al., 2019; Lesmeister et al., 2015).



*Figure 3: A summary of the research contexts in reviewed applications of DOMs. a) The approximate locations of the study areas where data was collected. b) Spatial extent of the study areas, defined as the area of inference within which all surveyed points were contained. c) Number of articles that fit models to each taxa category. Taxa are considered ‘threatened’ if indicated by authors or they are listed on the IUCN Red List. d) The number of*

*taxa modelled as distinct groups in each application. Explicitly multi-species models include both hierarchical jointly estimated models and more interactive models. e) Number of articles using each method for capturing detection/non-detection data. These are non-exclusive, and citizen science data is a subset of 'direct observations.'* (f) *The number of sites and study duration for each dataset used to fit DOMs – gold lines indicate medians.*

## Observations and data collection

The detection/non-detection data required for DOMs was collected using various survey methods across reviewed studies (Figure 3 E): 79% of studies used direct observation data, 11% used live-trapping methods, and 14% used detections from camera traps. Within these categories, 10% of studies used citizen science data. Citizen science data included coordinated surveys at backyard bird-feeders as well as interviews with civilians on sightings of tiger (*Panthera tigris*) signs (Warrier et al., 2020; Zuckerberg et al., 2011). Datasets ranged considerably in size, with the smallest including observations at just 10 sites and the largest including over 6000 (Figure 3 F); the median dataset included 100 sites. The temporal scale of studies shows similar variability – time elapsed between the first and last survey ranged from under one month to over forty years (median 8 years), and the number of primary occasions ranged from 2 to 189 (median 6 occasions).

Notably, not all of these datasets were originally collected in a hierarchical structure with DOMs in mind. In these cases, authors formatted their data into a hierarchical format *post-hoc* using a variety of methods. Some defined primary occasions as arbitrary discrete time intervals, treating all surveys occurring within a window as secondary occasions; others defined sites as larger grid cells, treating any survey falling within the grid as a spatial replicate. For example, in the only application of DOMs to marine species in our sample, Pendleton et al. (2022) used aerial transects broken up into grid cells to observe whale occupancy. In another example with grid cells, Marescot et al. (2020) fit a multi-species model treating poachers as a taxon and using ranger reports from each cell to create detection histories. These manipulations permit use of data predating DOMs, with one

241 study using surveys conducted by Joseph Grinnell in 1908 to model century-long changes  
242 in occupancy (Riddell et al., 2021).

### 243 **Covariates and complexity**

244 The most common covariates considered for use in DOMs addressed aspects of habitat and  
245 land cover [Figure 4](#). 35% of studies incorporated covariates for site geometry and  
246 connectivity, such as habitat patch size or distance to other sites. Often these were included  
247 as simple covariates on colonisation or extinction, such as the distance to other sites or  
248 landscape habitat connectivity metrics (Duggan et al., 2011). Alternatively, more complex  
249 parameterisations explicitly modelled colonisation or extinction as a spatial process  
250 dependent on patch size or the distance to occupied sites (Broms et al., 2016; Risk et al.,  
251 2011). Several studies also included biotic interactions with other species as covariates,  
252 often where the target taxon was threatened by invasive species. These covariates  
253 effectively incorporate species interactions in DOMs without requiring the use of more  
254 complex explicitly multi-species models.

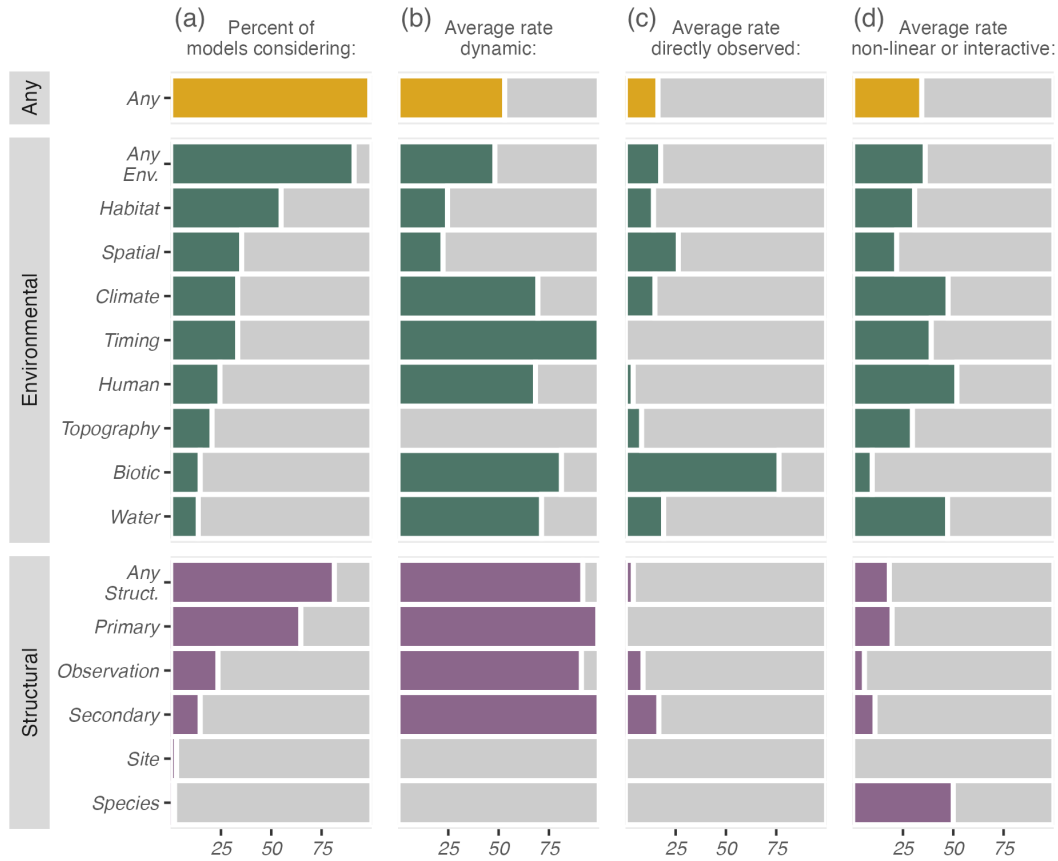


Figure 4: Attributes of the covariates considered for inclusion in DOMs. Columns represent the percentage of studies that tested at least one covariate in a category on any model parameter (a), and the average percentage of covariates in each category that were (b) time-varying, excluding covariates on initial occupancy, (c) directly observed at each site, and (d) considered with non-linear terms or interactions with other covariates. To avoid the dominance of studies considering large amounts of covariates in b-d, we first calculated the relevant percentage of covariates per study then took the mean. Covariates were classified as either environmental factors representing plausible ecological correlates of model

*parameters, or structural factors related to the model form or observational details that distinct from the environment. Environmental categories included 'Habitat' – land cover and habitat features; 'Spatial' – site dimensions and physical location; 'Climate' – weather and long-term climate; 'Timing' – chronology with ecological relevance; 'Human' – interaction with anthropogenic activity; 'Topography' – geologic features; 'Biotic' – any potential predator/prey/competitor interactions; and 'Water' – hydrologic features. Structural categories included 'Primary' – effect of the primary occasion; 'Observation' – observation method and characteristics; 'Secondary' – effect of the primary occasion; 'Site' – site-level effects; and 'Species' – species-specific effects. We also provide summaries across all covariate categories ('Any'), all environmental covariates ('Any Env'), and all structural covariates ('Any Struct.'). For more verbose definitions and analysis code, see supplementally materials.*

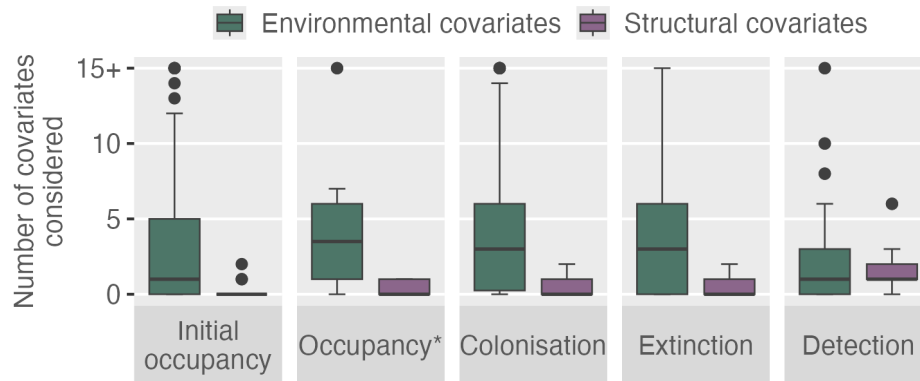


Covariate data for studies in our sample were either collected directly during surveys by researchers (an average of 30% of environmental covariates per study), or derived from pre-existing remotely sensed datasets (70% of environmental covariates); this varied depending on the category of covariate [Figure 4](#). Directly collected data often represented finer-scale factors like prey species occurrence or details of habitat structure, which can be difficult to measure remotely. An average of 43% percent of the environmental factors and 94% of the structural factors considered for time-varying parameters were dynamic covariates, with terms relating to climate or weather most frequently dynamic [Figure 4](#).

In conventional DOMs, covariates for each parameter are incorporated via a logistic regression (i.e., a linear regression through a logit link function; MacKenzie et al. (2017)). Statistical relationships between model parameters and covariates (e.g., between initial occupancy and its environmental covariates) are represented as linear terms unless more complexity is specified, although non-linear responses can be easily accommodated in DOMs by using polynomial transformations and interactions between covariates. Despite this, in our sample only 35% of articles tested one or more non-linear responses to an environmental covariate, with most studies representing all covariates as simple linear terms. Interactions between covariates were similarly rare, with only 24% of studies considering at least one interaction between terms.

The size of the covariate pool for each parameter varied substantially, with the number of covariates considered ranging from 0 (effectively modelling the parameter as a constant) to over 40 candidates on a single parameter ([Figure 5](#)). Note that this does not represent the number of covariates included in the final model formulation used for inference. The

277 median number of covariates considered varied by parameter, with transition probabilities  
278 (colonisation and extinction) more likely to have a broader range of environmental  
279 covariates considered compared to initial occupancy and detection. The lack of any  
280 covariates considered for initial occupancy in 37% of studies is particularly notable, as is  
281 the observation that 30% of modelling workflows considered no environmental covariates  
282 for detection probability.



*Figure 5: The number of covariates considered for each core parameter across all distinct modelling workflows in our sample. A covariate is defined here as a distinct variable considered for inclusion, with linear, non-linear, and interactive forms of the same factor counted as a single covariate. Covariates are either ‘environmental’, representing plausible ecological correlates of model parameters, or ‘structural’, relating to factors without direct ecological relationships. The ‘Occupancy\*’ category here corresponds with alternative parameterisations of DOMs that jointly estimate occupancy, colonisation, and detection with extinction being only a derived parameter; this contrasts with more popular initial occupancy/colonisation/extinction/detection parameterisations.*

## Model selection and assessment

The 92 articles in our sample included 102 distinct modelling workflows. Of these models, 76 were fit by maximum likelihood estimation (MLE) and 24 were Bayesian implementations. 2 models fell into neither category and instead used machine learning based methods (Joseph, 2020).

In most cases, the DOMs fit in a study did not use all covariates initially considered for inclusion: 80% of modelling workflows included some form of model selection approach to identify a final model or set of models to make inferences from Table 1. Approaches varied between the MLE and Bayesian implementations in our sample; where 95% of MLE models performed some manner of model selection, only 33% of Bayesian models did so, with the majority instead fitting a single model defined *a priori*. For MLE models the most popular and conventional approach to model selection (45% of models) involved the creation of a candidate set of models, where the best model(s) was selected according to the lowest AIC score. The next most popular method in MLE studies was to use sequential model selection methods (37% of models), where the structure for each model parameter was fit in sequence. For example, a protocol might have first identified the best structure for detection probability while holding the other parameters constant, before moving on to initial occupancy and so on until all parameters were fixed. The remainder of MLE studies (8%) used a variety of other approaches, such as fitting simpler models like single season occupancy models to identify the most informative covariates to use in a dynamic occupancy model. Across all MLE implementations, 47% of articles used multi-model inference by model-averaging with AIC weights (Burnham & Anderson, 2004).

*Table 1: A summary of modelling practices in DOMs subset by framework (maximum likelihood or Bayesian). Some studies include multiple distinct modelling workflows (n = 102 workflows across 92 articles). 2 models included in the 'All models' column were neural network based and fell into neither the MLE or Bayesian categories. The model selection methods represented in this table are non-exclusive and some articles employed multiple approaches.*

	MLE	Bayesian	All models
<i>Number of workflows</i>	76	24	102
<i>Median covariates considered per parameter</i>	3	2.12	2.75
<b>Covariate selection methods</b>			
<i>Percentage using any model selection approach</i>	95%	33%	80%
<i>Percentage comparing models in a candidate set</i>	45%	12%	36%
<i>Percentage using sequential model selection</i>	37%	0%	27%
<i>Percentage selecting covariates with simpler models</i>	8%	4%	7%
<i>Percentage using model-averaging</i>	47%	4%	36%
<b>Model evaluation conducted</b>			
<i>Percentage calculating goodness-of-fit</i>	20%	12%	18%
<i>Percentage assessing predictive performance</i>	4%	17%	7%

Those Bayesian models which did perform model selection took various approaches, with largely idiosyncratic methods across these studies. While direct comparison of model fit was rare amongst Bayesian methods, it is feasible – Urban et al. (2023) identified the best model from a Bayesian candidate set using the predictive performance on both in and out-of-sample validation data. Another approach used by Cook et al. (2022) fit a global model including all covariates, before removing each covariate where the 95% credible interval of the posterior distribution overlapped zero and refitting the reduced model. Ahumada et al. (2013) took a hybrid approach, where model selection was conducted by a sequential method fitting models by MLE before refitting the best structure as a Bayesian model. Finally, Brown et al. (2014) capitalised on the advantages of the Bayesian framework and used reversible jump MCMC routines to perform model selection during model fitting. Regardless of the implementation, assessment of model fit and model performance was rare amongst the articles in our sample. Only 18% of studies tested for goodness-of-fit, and just 7% calculated predictive performance with either in-sample or out-of-sample validation.

### **Temporal trends in applications of DOMs**

While our temporally stratified sample allows us to consider changes in how DOMs have been applied over the past two decades, modest sample sizes within strata necessitate caution in interpreting these results. Nonetheless, there are several clear trends we believe are worth noting (Figure 6). Firstly, recent strata saw changes in the number of sites modelled in each study. In our two most recent strata spanning 2016-2023, the range in the number of sites was noticeably wide. While models continue to be fit with small

327 numbers of sites, the upper quartile contained more sites than in previous strata (Figure 6  
328 A). The median number of covariates considered per parameter has also continually  
329 increased since the early years of DOMs, from 1.75 covariates in 2004-2007 to 4.75 in the  
330 2020-2023 stratum (Figure 6 B).

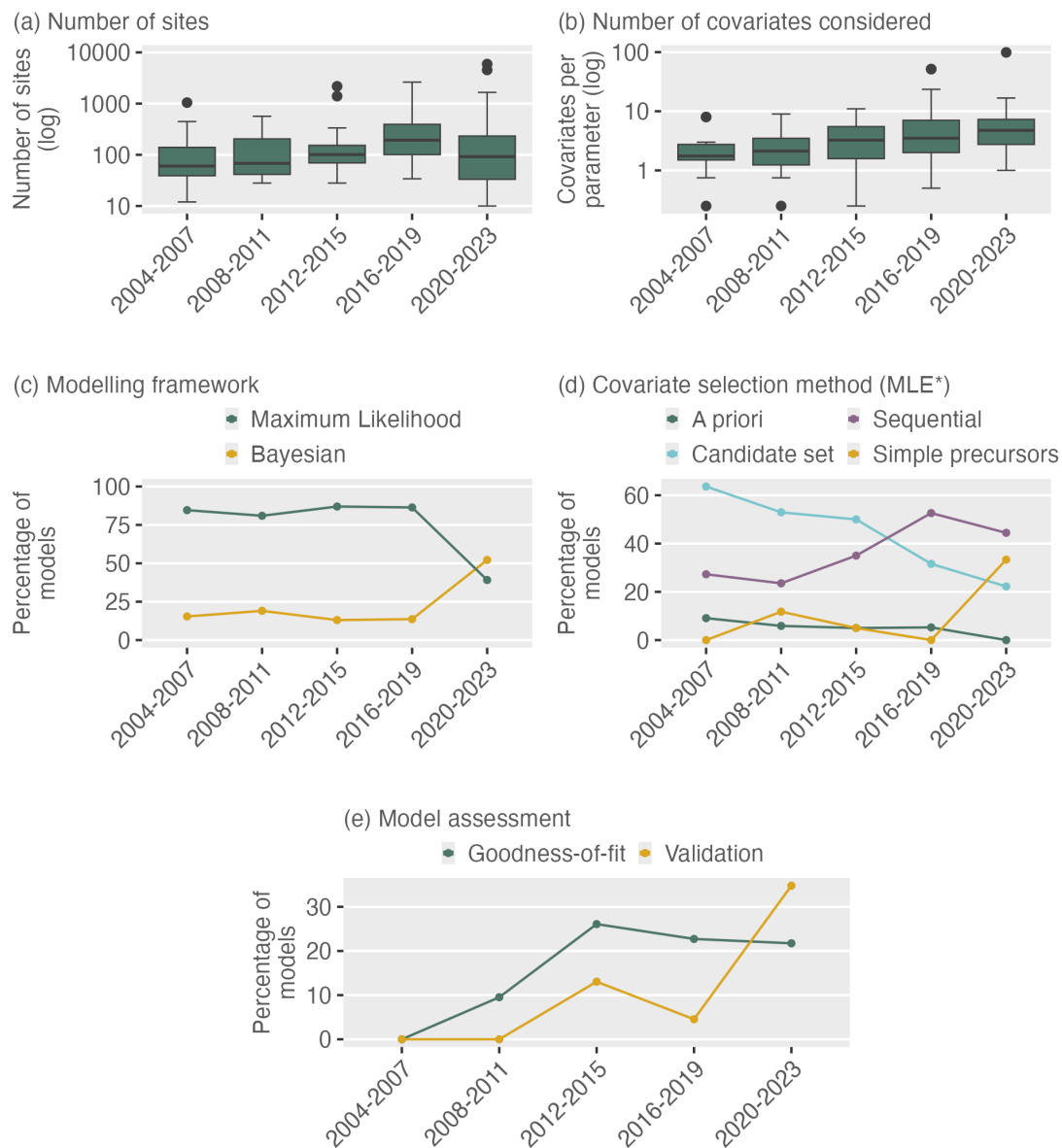


Figure 6: Key trends in applications of dynamic occupancy models over the study period. a) The number of sites modelled in each dataset, presented on the log scale. b) The number of covariates considered per model parameter in each modelling workflow, presented on the log scale. c) The percentage of models in each stratum fit in the maximum likelihood or



*Bayesian frameworks. d) The percentage of articles in each stratum that used each of four non-exclusive covariate selection strategies. This panel includes only articles which fit models via maximum likelihood. e) The percentage of articles in each stratum that reported goodness-of-fit testing and model validation (with either in or out of sample data).*

While Bayesian models were included in all strata of our sample, there was a marked increase in their frequency in the most recent stratum (Figure 6 C). This may in part be explained by the publication of accessible resources such as Kéry & Royle (2021), which includes chapters on fitting DOMs in JAGS with associated code. Within the MLE implementations, the most popular model selection methods have shifted over time. The number of studies using predefined sets of candidate models has gradually declined, contemporaneous with an increase in articles using sequential model selection methods (Figure 6 D). While there is evidence of improvement from earlier strata, goodness-of-fit testing and model validation using either in- or out-of-sample data remained uncommon even in more recent strata where tests were readily available in common R packages (Figure 6 E).

## Discussion

Over the past two decades dynamic occupancy models have been applied to an increasingly broad range of objectives and research contexts. As their popularity has grown and new tools have become available, authors have implemented DOMs with wide ranging amounts of data, at small and large spatial and temporal scales, using diverse data collection techniques. While each of these studies share the same underlying methodology, their approaches to implementation and interpretation vary considerably. The approach to building any type of model will necessarily depend on the character of the data available and on the priorities of the model-builder. This precludes any prescription of the 'best' way

to build DOMs; however, we believe that there are several areas of the modelling process that merit closer consideration by both those using and further developing these methods.

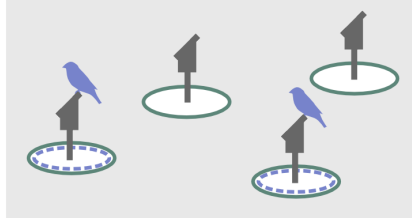
### Defining occupancy and detection

Building and interpreting DOMs requires a firm understanding of what probabilities of occupancy and detection conceptually represent for a given dataset. However, arriving at appropriate definitions for these terms can be a challenge. What site occupancy describes is dependent on a variety of factors, including the spatial extent of sites, the duration of primary occasions, the survey methods used, and the ways that each of these relate to the life history traits of the target species (Valente et al., 2024). Applications of DOMs in our review used data that varied across each of these axes, resulting in vastly different conceptions of occupancy and detection.

The appropriate definition of occupancy is closely related to the spatial extent of each site, relative to a species' home range within a primary occasion (Figure 7.) This relationship determines whether the closure assumption – which states that the occupancy status of sites does not change within primary occasions such that the species is always available for detection at occupied sites – is fulfilled. If this is the case, and assuming that the survey method can detect the species even if it occurs in only a portion of the site, occupancy parameters represent the probability that the species is present within a site across a primary occasion. Conversely, if the home range of species is not wholly contained within a site, occupancy must be interpreted as the probability that a site is *used* by the species for at least some portion of the primary occasion (Figure 7 bii-iii).

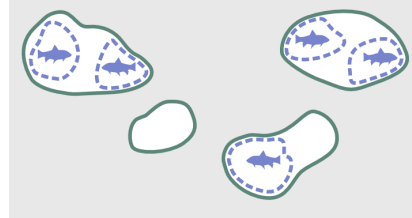
**(a) Sites are discrete habitat patches or features**

(i) Sites match individual home ranges



Occupancy = Abundance

(ii) Sites encompass multiple individuals' home ranges

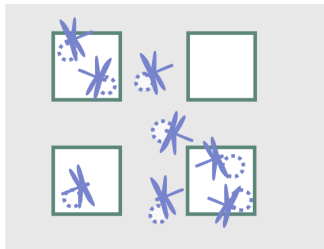


Occupancy  $\neq$  Abundance

Occupancy represents whether a site is occupied

**(b) Sites are defined in continuous habitat**

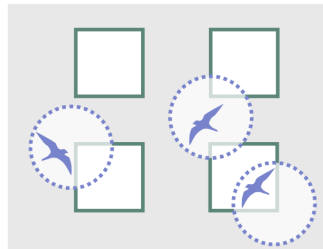
(i) Sites larger than home ranges



Occupancy  $\neq$  Abundance

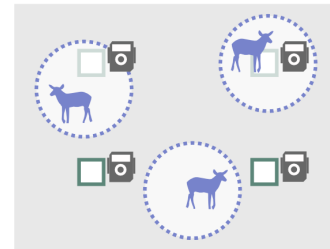
Occupancy represents whether a site is occupied

(ii) Sites similar in size to home ranges



Occupancy  $\approx$  Abundance  
(unless home ranges overlap)

(iii) Sites smaller than home ranges



Occupancy  $\neq$  Abundance

**Closure not met:** Occupancy represents whether a site is used

*Figure 7: An overview of how the size of a site relative to the focal species' home range during a primary occasion can result in differing definitions of site occupancy. In (a), where a site represents a discrete habitat patch, occupancy typically represents whether a site is occupied during a primary occasion. If each site corresponds with an individual's home range (a-i), as can occur with nest box surveys, occupancy is equivalent to abundance. If each site can contain multiple home ranges (a-ii) as with surveys of water bodies, this occupancy-abundance relationship is lost. In (b), where sites are defined in continuous*

*habitat, occupancy definitions are more variable. If sites are larger than the focal species home range (b-i), occupancy will still represent whether a site is occupied and will not relate to abundance (as in a-ii). Closure violations occur when individuals do not remain within a site for the full primary occasion (b-ii, b-iii). Here, occupancy represents whether a site is used during a primary occasion. If sites have a similar size to the species home range and home ranges do not overlap (b-ii), occupancy may retain some relationship with abundance. If sites are smaller than the home range (b-iii) as typically occurs with camera traps, the occupancy-abundance relationship is in general lost, although in some cases extrapolations may be possible for territorial species.*

The relationship between sites and home ranges also determines whether occupancy corresponds with abundance (Steenweg et al., 2018). In cases where each site corresponds with the home range of a single individual or pair, site occupancy may be fully equivalent to abundance. For example, this may be the case with many studies of spotted owls (*Strix occidentalis*), where sites typically include all possible owl territories in a region (Olson et al., 2005). Alternatively, where sites are larger than home ranges, occupancy will only approach abundance at low densities. Users of DOMs should be conservative when making inference on abundance, noting that it typically requires making strong assumptions beyond those required for estimating occupancy or site use.

Earlier occupancy model research was often focused on the conventional definition of occupancy which require compliance with the closure assumption. This work emphasised how violations of this assumption can bias estimates of model parameters, leading to overestimates of occupancy when sites are not consistently occupied within primary occasions due to non-random mortality or movement of individuals (Otto et al., 2013; Valente et al., 2017). These authors provide guidance for study designs to ensure closure, as well as tests and analysis-based solutions for cases where closure is violated (Kendall et al., 2013; MacKenzie et al., 2017; Rota et al., 2009).

More recently, authors have begun to consider closure violations less as a source of bias and more as a modifier to the definition of occupancy (Efford & Dawson, 2012; Goldstein et al., 2024; Valente et al., 2024), now representing site use. Many DOMs in our review would best fit this definition of occupancy: closure is often an unreliable assumption when modelling the mobile birds and mammals which dominate our sample, particularly when

sites do not align with species home ranges. When data is collected with autonomous units like camera traps or acoustic monitors, small detection ranges make violation of closure very likely, necessitating a definition of occupancy which represents the probability that a species uses habitat that overlaps with the unit's detection range during the primary occasion (Wood & Peery, 2022).

Alternative definitions of occupancy have knock-on effects for detection probabilities with important implications for model building and interpretation. 'Detection' is often described as the probability that a species is observed during a survey given that a site is occupied, depending largely on the ability of the observer to identify the species. However, in practice detection probabilities can include several other components – individual movement patterns can determine whether a species is even available for detection at occupied sites, behaviour alters the perceptibility of a species, and variation in abundance changes the number of individuals available for detection (Guillera-Arroita, 2017). Consider a study using acoustic monitors, where a species is considered detected if a call is identified within a one-day secondary occasion: the probability of detection would be contingent on the number of individuals in the area, whether any of them entered the recording range, whether they made any vocalisations, and whether human listeners or classifier software successfully identified the call. In this circumstance, detection would contain both ecological and observational components.

An unusual challenge arises when users seek to fit to DOMs to detection/non-detection data that is continuously recorded – this may occur with camera traps or acoustic monitors which can run for long time periods, or with data from citizen science portals that lacks

clearly delineated survey periods. In these situations, modellers must arbitrarily determine how to stratify detections into primary and secondary occasions (but note the availability of continuous detection models for secondary “occasions”; Emmet et al., 2021; Guillera-Arroita et al., 2011; Pautrel et al., 2024). The stratification of primary occasions affects the temporal scale at which occupancy is measured, with corresponding changes to the definitions of occupancy and detection. The appropriate duration of these occasions will of course depend on research objectives and the ecology of the target species (Chave, 2013), but guidelines for approaching this task in DOMs specifically would hold value for the increasing numbers of authors fitting models to this type of data.

In all cases we echo recommendations made to users of occupancy-detection models more broadly, that they establish clear definitions for both occupancy and detection that correspond to the target species’ biology and the structure of the data used for modelling (Goldstein et al., 2024). While this is a productive exercise for clarifying internal assumptions and guiding choice of covariates, including these definitions in published articles also provides transparency and supports interpretation for readers less familiar with the study system.

### Identifying covariates for each modelled parameter

The definitions of occupancy and detection should strongly inform decisions on the covariates that are considered for inclusion in DOMs. Hypothesised relationships between occupancy dynamics and the environment should correspond with the spatial and temporal scale at which the data was collected, noting that the underlying mechanisms that drive occupancy at different timescales are likely to differ for many species.



438 Our review found that many studies did not include any covariates on initial occupancy.  
439 However, unless a study is conducted at very small extents or study sites are truly uniform  
440 in their initial suitability, one would expect some amount of non-random variation in  
441 occupancy probability across any study system. As seen in our review, many DOMs are  
442 applied at large spatial scales across significant habitat gradients. Omission of the factors  
443 that drive occupancy biases spatial predictions in static SDMs (Barry & Elith, 2006), which  
444 the initial occupancy component of DOMs conceptually resembles. In tests of predictions  
445 using DOMs, Briscoe et al. (2021) posit that poor spatial predictive performance may have  
446 been the result of a constrained covariate pool for parameters including initial occupancy.  
447 Where spatial predictions are of interest, it is prudent for users of DOMs to consider  
448 sufficient covariates to capture the key drivers of occupancy in the first primary occasion –  
449 this may be less of a concern in cases where estimating trends in occupancy probability is a  
450 greater priority.

451 When choosing covariates for colonisation and extinction users should prioritise the  
452 factors most likely to be of importance in driving change *between* primary occasions. DOMs  
453 are generally first-order Markov models where occupancy probabilities are linked only to  
454 the preceding primary occasions; therefore, covariates should have some link to possible  
455 mechanisms of transition at this timescale. Interestingly, fewer than 50% of environmental  
456 covariates considered for transition probabilities in our review were time-varying. While  
457 some static covariates provide useful information on habitat suitability in general, dynamic  
458 covariates are increasingly available and can provide more nuance on how species respond  
459 to fluctuations in environmental conditions.

As previously mentioned, different definitions of detection probability can include aspects of species abundance, behaviour, and resource use which should be reflected in the choice of covariates considered for inclusion on this parameter. Most DOMs included in our review considered comparatively few (median = 3) covariates on detection, either environmental or structural. We encourage authors to consider fully how environmental factors might influence detection in their study system, and to avoid restricting these covariates to the occupancy dynamics parameters. Existing work on unmodelled heterogeneity in detection demonstrates a deleterious effect on estimates of occupancy probability in both SDMs and DOMs, highlighting the need for greater emphasis on this component of the model (Lahoz-Monfort et al., 2014; McClintock et al., 2010).

The consequences of unmodelled heterogeneity on model outputs generally remains an understudied aspect of DOMs, despite ongoing acknowledgements that this is an area meriting further research (MacKenzie et al., 2006; MacKenzie et al., 2017). Simulation studies exploring these scenarios would help to inform where this may be of concern and guide future research on model building practices. This includes explorations on how missing covariates on detection may influence estimates of other parameters in DOMs, particularly in cases where closure is violated and detection contains a large environmental component.

### Complexity in DOMs

One aspect of fitting DOMs meriting broader discussion centres on ‘model complexity,’ and how much must be incorporated into models to reliably estimate species occupancy under different contexts and use cases. Complexity is a broad term encompassing many aspects of

a model, including the number of covariates included, the form of their relationship to response variables, and the overall structure of the model (Merow et al., 2014). Opinions on simplicity versus complexity in ecological models are diverse - where some advocate for the simplest possible models, arguing that they are most generalisable; others insist that overly simple models cannot adequately represent the most important drivers in a system (Evans et al., 2013; Lonergan, 2014). By their nature, DOMs are somewhat more complex than simpler models for studying occupancy due to their hierarchical structure, which is necessary to control for detectability and to capture occupancy dynamics. Within this structure, however, further complexity is up to the modeller: one can choose how many covariates to consider for inclusion on parameters, and how to represent the nature of the relationship between those covariates and parameters. In the applications of DOMs in our review, average complexity was somewhat low along both of these axes – relatively few covariates per parameter were considered for inclusion, and the majority of studies did not consider non-linear responses nor interactions between covariates.

Research from correlative species distribution models (SDMs) indicates that allowing for more complex relationships can improve model performance in spatial predictions of occupancy (Valavi et al., 2023), an increasingly popular use-case for DOMs. Many common approaches for SDMs, such as MAXENT and Boosted Regression Trees, permit considerable flexibility in the shape of their covariate response curves and use of interactions, where supported by the data (Elith et al., 2008; Merow et al., 2013). Within DOMs, there are promising developments in methods for incorporating additional complexity, including Joseph (2020) 's novel neural-network occupancy model which allows for exponentially higher levels of complexity, potentially offering improved performance for prediction-

oriented studies. While no studies in our samples used these approaches, other means for flexible response shapes such as splines, BRTs, or machine learning based methods may offer other avenues for increased flexibility (Hutchinson et al., 2011; Joseph, 2020; Rushing et al., 2019). Further research on these methods may provide new options where spatial predictive performance is a priority.

The emphasis on more complex responses in SDMs may also be attributed to their frequent application across relatively large geographic extents which might encompass the full species niche, where environmental relationships may be expected to be non-linear. However, we found that many DOMs were also implemented across large spatial extents where non-linear responses might be expected. When this is probable, modellers should ensure that covariate responses are ecologically realistic and appropriately reflect the hypothesised relationships (Austin, 2007). Similar consideration should be given to interactions between covariates, given that these relationships are commonly expected based on ecological theory and that their exclusion can negatively impact model performance (Guisan et al., 2006). This is not to suggest that modellers should consider arbitrary non-linear responses or covariate interactions that are not grounded in ecological theory, but that they should remain open to more complexity where merited by the data and study system. While overfitting models can be a concern, many covariate selection methods (including AIC-based approaches and Bayesian regularisation) will penalise excessive complexity and appropriate model evaluation (currently rare – see below) can detect these issues.

## 526   Covariate Selection

527   Methods used for covariate selection were particularly varied in reviewed DOMs, with a  
528   wide range of approaches used in both MLE and Bayesian frameworks and little consensus  
529   on the best techniques. Covariate selection is a particularly challenging task for DOMs  
530   relative to other common models for occupancy estimation, as testing alternative  
531   covariates across multiple parameters can result in a rapidly expanding pool of candidate  
532   models. Consider that while testing all combinations of 6 covariates for a simple correlative  
533   SDM would require fitting just 64 models, possible combinations of 6 covariates on each of  
534   the DOMs four parameters would require 24 million models, making exhaustive  
535   comparison computationally infeasible. Limited research has been conducted on the  
536   advantages of different methods for covariate selection in DOMs, and there is unlikely to be  
537   a one-size-fits-all approach which will be appropriate for all possible objectives. However,  
538   it is important to consider the implications of the different model selection approaches in  
539   common usage and their suitability for various use-cases.

540   The few papers that have addressed covariate selection in occupancy models have largely  
541   focused on AIC-based methods, which aim to identify models that are useful for prediction  
542   by selecting for fit while penalising complexity (Chakrabarti & Ghosh, 2011). In a  
543   comparison of static occupancy models fit with three AIC-based approaches using  
544   simulated data, Doherty et al. (2012) found that while each method achieved similar  
545   predictive performance, estimates of covariate weights varied. They advise model  
546   averaging to mitigate this effect, but acknowledge that this effect is likely to be even larger  
547   in more complex models such as DOMs. More recent work by Morin et al. (2020) using

occupancy models fit to field data had similar findings, with sequential model selection approaches often failing to identify the lowest AIC model amongst exhaustive combinations. They recommend that modellers carry more candidate models through each stage in sequential selection processes to increase the probability that the top models are identified, given that exhaustive model selection may not be feasible for DOMs with moderate-large numbers of potential covariates.

The most common application of DOMs was to test hypothesised relationships. In recent years, work from the causal modelling community has critiqued aspects of model selection in cases where the principal research objective is to test pre-defined environmental relationships (Tredennick et al., 2021). Stewart et al. (2023) discuss this in the context of occupancy modelling, demonstrating the risks posed by certain ‘collider’ variables which have causal relationships with both occupancy and other covariates in the candidate set. Where these colliders are present, the top models selected by AIC may produce inaccurate estimates of focal covariates, even where they produce more accurate estimates of occupancy probabilities. As a result of these concerns, recent work has reinforced suggestions to limit or avoid covariate selection when inference on hypothesised relationships is the primary objective (Arif & MacNeil, 2022; Bolker, 2024; Popovic et al., 2024; Tredennick et al., 2021). These authors instead suggest a focus on more constrained model sets defined *a priori*, with careful consideration of the structural relationships between candidate covariates using tools such as directed acyclic graphs to clarify assumptions (Arif & Massey, 2023). These firmer views on causal inference are not universal, and authors including Nichols & Cooch (2024) have defended the use of predictive models (including DOMs) coupled with thoughtful and constrained model

571 selection as useful tools for inference, while noting the importance of carefully considering  
572 relationships among covariates.

573 Where inference on pre-specified hypotheses is not required, approaches to model  
574 selection may be more flexible. AIC-based model selection starting from a larger pool of  
575 candidate covariates is suitable for exploratory research, where the risk of bias in  
576 coefficient estimates and spurious correlations may be less of a concern (Tredennick et al.,  
577 2021). Prediction remains somewhat underexplored for DOMs, and further research is  
578 needed on the best techniques for fitting models for this purpose (Briscoe et al., 2021).  
579 While we discuss model evaluation in greater detail later in the discussion, model selection  
580 by cross-validation is a promising avenue where computationally feasible and is available  
581 via the R packages *ubms* and *unmarked* (Kellner et al., 2022, 2023; Yates et al., 2023).

582 Regardless of objective, Bayesian model selection for DOMs remains somewhat  
583 underexplored. Hooten & Hobbs (2015) 's guide to Bayesian model selection in ecology  
584 remains a valuable resource for possible methods for fitting and evaluating these models,  
585 and a range of promising methods including regularisation priors and reversible-jump  
586 MCMC merit future research on their suitability for use with DOMs (Park & Casella, 2008).  
587 In one of the few comparative studies on model selection for Bayesian occupancy models,  
588 Stevens & Conway (2019) found that models selected using the logarithmic scoring rule  
589 rather than WAIC or DIC produced better performing models for prediction. As the  
590 accessibility and popularity of Bayesian DOMs appears likely to continue to increase,  
591 further research and tool development in this space is necessary.

## Model assessment

Regardless of covariate selection protocol, it is important to determine whether a chosen model appropriately reflects the data and is suitable for its use case. However, current applications of DOMs report model assessment at rates lower than either single-season occupancy models or SDMs (Araújo et al., 2019; Goldstein et al., 2024). This is perhaps because model assessment methods and guidance remain underdeveloped for DOMs: few goodness-of-fit tests have been proposed, and those which do exist require more empirical assessment for greater acceptance. Currently, MacKenzie & Bailey (2004) 's approach for single-season occupancy models using a parametric bootstrap has been extended to DOMs and is implemented in the *AICcModAvg* and *unmarked* R packages – Kéry & Royle (2021) describe the test and present an alternative based on separately assessing fit to static and dynamic components of the model. In Bayesian implementations, posterior predictive checks offer means to assess model fit (Gelman, 2014). Broms et al. (2016) discusses various options for model assessment in Bayesian single-season multi-species occupancy models, with insights that may also be applicable to DOMs. While further tests and developments of these methods are necessary to solidify their use, current authors should to the best extent possible continue to conduct and report goodness-of-fit tests using existing tools regardless of their research objective.

Studies interested in making spatial or temporal predictions require more substantial forms of model evaluation to quantify predictive performance (Araújo et al., 2005; Guisan & Thuiller, 2005). As with other hierarchical models, model evaluation for DOMs can be difficult and somewhat uncertain compared to other model types, as the primary response



614 variable of interest (species occupancy) is a latent variable where the true state is generally  
615 not known. Predictive performance evaluation is thus typically based on *observed*  
616 occupancy data, where a DOM is used to compute the probability of observing the species  
617 and this is compared with the field data. This method confounds the occupancy and  
618 detection processes, restricting our ability to determine whether any variation is correctly  
619 apportioned to each of these processes.

620 While predictive performance should ideally be tested with independent datasets, this is  
621 generally not practicable with DOMs. Best practice should involve setting aside a portion of  
622 data for testing final models, where this is not possible, cross-validation should be  
623 considered to attain an estimate of performance. Validation of DOM predictions can be  
624 done by splitting datasets temporally and using latter years for evaluation or by setting  
625 aside sites (Briscoe et al., 2021). Site-based cross validation is included in several packages  
626 including *unmarked* and *ubms* (Kellner et al., 2022, 2023).

627 *Table 2: A summary of recommendations for current users of DOMs and priorities for further*  
628 *research.*

Topic	Recommendations	Priorities
<b>Defining occupancy and detection</b>	<ul style="list-style-type: none"> <li>• Explicitly state context-dependent definitions of occupancy and detection probabilities.</li> </ul>	<ul style="list-style-type: none"> <li>• Develop guidelines for delineating primary occasions in continuous data.</li> </ul>
<b>Covariates for model parameters</b>	<ul style="list-style-type: none"> <li>• Choose relevant covariates for colonization and extinction, aligned with the temporal scale of changes in occupancy.</li> <li>• Ensure that key drivers are also considered for initial occupancy, particularly when making spatial predictions.</li> <li>• Ensure that environmental aspects of detection are reflected in candidate covariates.</li> </ul>	<ul style="list-style-type: none"> <li>• Assess how missing drivers of heterogeneity on one parameter affect estimates of the other parameters and model predictions.</li> </ul>
<b>Complexity and covariate responses</b>	<ul style="list-style-type: none"> <li>• Align covariate responses with hypothesised relationships, testing non-linear responses or interactions where appropriate.</li> </ul>	<ul style="list-style-type: none"> <li>• Explore the best ways to include greater complexity in covariate responses, such as splines and machine learning based methods.</li> <li>• Assess influence of covariate quantity and response complexity on predictive performance and uncertainty.</li> </ul>
<b>Model selection</b>	<ul style="list-style-type: none"> <li>• For all objectives, ensure reported methods are comprehensive.</li> <li>• When testing hypotheses, include clear rationale for covariate inclusions, such as by creating directed acyclic graphs. Some authors recommend constraining</li> </ul>	<ul style="list-style-type: none"> <li>• Identify best approaches to model selection for various objectives while limiting computational costs.</li> <li>• Compare performance of emerging Bayesian methods for model selection.</li> </ul>

	<p>candidate sets or avoiding covariate selection altogether.</p> <ul style="list-style-type: none"> <li>• Consider all models with similar support.</li> <li>• Be aware that results of model selection are sensitive to implementation. When using sequential selection, test more models at each stage to avoid missing the best-performing model.</li> </ul>	
<b>Model assessment</b>	<ul style="list-style-type: none"> <li>• Available goodness-of-fit tests should always be conducted and reported.</li> <li>• Data should be reserved for out-of-sample validation wherever possible, and especially when prediction is an objective. If not feasible, in-sample validation should be performed and performance metrics reported.</li> </ul>	<ul style="list-style-type: none"> <li>• Existing goodness-of-fit tests should be further validated to ease concerns regarding their use.</li> <li>• Additional research on methods for performance evaluation in hierarchical models is necessary</li> </ul>

## 629 Conclusions

630 In the two decades since the publication of MacKenzie et al. (2003), use of dynamic  
631 occupancy models has increased and they have been applied to a broad range of data types  
632 and ecological and applied problems. This expansion can pose challenges in navigating the  
633 model building processes and aligning data, model and interpretations to produce useful  
634 outputs. Many of our recommendations thus simply implore users to take stock at key  
635 points to clarify their assumptions and expectations. With frequent use of DOMs for  
636 important problems such as managing critically endangered species, guiding public health  
637 decisions and tracking harmful invasive species, understanding the sensitivity of model  
638 outputs to decisions made in the model fitting process becomes increasingly important.  
639 Major uncertainties remain in key areas of the model development process including model  
640 selection and evaluation, with much of the existing guidance based on the static occupancy  
641 modelling literature (MacKenzie et al., 2017). Several of the research priorities we  
642 identified relate to increasingly common use-cases – such as generating spatial and  
643 temporal predictions, and modelling data derived from novel detection techniques.  
644 Targeted research and guidance specific to DOMs will be needed to ensure that the  
645 potential of these tools can be realised, and they can reliably inform conservation and  
646 management decisions.

## References

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- Ahumada, J. A., Hurtado, J., & Lizcano, D. (2013). Monitoring the Status and Trends of Tropical Forest Terrestrial Vertebrate Communities from Camera Trap Data: A Tool for Conservation. *PLOS ONE*, 8(9), e73707. <https://doi.org/10.1371/journal.pone.0073707>
- Altwegg, R., & Nichols, J. D. (2019). Occupancy models for citizen-science data. *Methods in Ecology and Evolution*, 10(1), 8–21. <https://doi.org/10.1111/2041-210X.13090>
- Araújo, M., Anderson, R. P., Márcia Barbosa, A., Beale, C. M., Dormann, C. F., Early, R., Garcia, R. A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R. B., Zimmermann, N. E., & Rahbek, C. (2019). Standards for distribution models in biodiversity assessments. *Science Advances*, 5(1), eaat4858. <https://doi.org/10.1126/sciadv.aat4858>
- Araújo, M., Pearson, R., Thuiller, W., & Erhard, M. (2005). Validation of species-climate impact models under climate change. *Global Change Biology*, 11, 1504–1513. <https://doi.org/10.1111/j.1365-2486.2005.01000.x>
- Arif, S., & MacNeil, M. A. (2022). Predictive models aren't for causal inference. *Ecology Letters*, 25(8), 1741–1745. <https://doi.org/10.1111/ele.14033>
- Arif, S., & Massey, M. D. B. (2023). Reducing bias in experimental ecology through directed acyclic graphs. *Ecology and Evolution*, 13(3), e9947. <https://doi.org/10.1002/ece3.9947>
- Austin, M. (2007). Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling*, 200(1), 1–19. <https://doi.org/10.1016/j.ecolmodel.2006.07.005>
- Bailey, L. L., MacKenzie, D. I., & Nichols, J. D. (2014). Advances and applications of occupancy models. *Methods in Ecology and Evolution*, 5(12), 1269–1279. <https://doi.org/10.1111/2041-210X.12100>
- Balantic, C., & Donovan, T. (2019). Dynamic wildlife occupancy models using automated acoustic monitoring data. *Ecological Applications*, 29(3). <https://doi.org/10.1002/eap.1854>
- Barry, S., & Elith, J. (2006). Error and uncertainty in habitat models. *Journal of Applied Ecology*, 43(3), 413–423. <https://doi.org/10.1111/j.1365-2664.2006.01136.x>
- Basset, Y., Butterill, P. T., Donoso, D. A., P. A. Lamarre, G., Souto-Vilarós, D., Perez, F., Bobadilla, R., Lopez, Y., Alejandro Ramírez Silva, J., & Barrios, H. (2023). Abundance, occurrence and time series: Long-term monitoring of social insects in a tropical rainforest. *Ecological Indicators*, 150, 110243. <https://doi.org/10.1016/j.ecolind.2023.110243>
- Belinchón, R., Harrison, P. J., Mair, L., Várkonyi, G., & Snäll, T. (2017). Local epiphyte establishment and future metapopulation dynamics in landscapes with different spatiotemporal properties. *Ecology*, 98(3), 741–750. <https://doi.org/10.1002/ecy.1686>
- Bertelsmeier, C., Luque, G. M., & Courchamp, F. (2013). Increase in Quantity and Quality of Suitable Areas for Invasive Species as Climate Changes. *Conservation Biology*, 27(6), 1458–1467. <https://doi.org/10.1111/cobi.12093>

- Bolker, B. M. (2024). Multimodel Approaches Are Not the Best Way to Understand Multifactorial Systems. *Entropy*, 26(6), 506. <https://doi.org/10.3390/e26060506>
- Briscoe, N. J., Elith, J., Salguero-Gómez, R., Lahoz-Monfort, J. J., Camac, J. S., Giljohann, K. M., Holden, M. H., Hradsky, B. A., Kearney, M. R., McMahon, S. M., Phillips, B. L., Regan, T. J., Rhodes, J. R., Vesk, P. A., Wintle, B. A., Yen, J. D. L., & Guillera-Arroita, G. (2019). Forecasting species range dynamics with process-explicit models: matching methods to applications. *Ecology Letters*, 22(11), 1940–1956. <https://doi.org/10.1111/ele.13348>
- Briscoe, N. J., Zurell, D., Elith, J., König, C., Fandos, G., Malchow, A.-K., Kéry, M., Schmid, H., & Guillera-Arroita, G. (2021). Can dynamic occupancy models improve predictions of species' range dynamics? A test using Swiss birds. *Global Change Biology*, 27(18), 4269–4282. <https://doi.org/10.1111/gcb.15723>
- Broms, K. M., Hooten, M. B., Johnson, D. S., Altwegg, R., & Conquest, L. L. (2016). Dynamic occupancy models for explicit colonization processes. *Ecology*, 97(1), 194–204. <https://doi.org/10.1890/15-0416.1>
- Brown, J. L., Collopy, M. W., & Smallwood, J. A. (2014). Habitat fragmentation reduces occupancy of nest boxes by an open-country raptor. *Bird Conservation International*, 24(3), 364–378. <https://doi.org/10.1017/S0959270913000415>
- Burnham, K. P., & Anderson, D. R. (2004). *Model Selection and Multimodel Inference*. Springer. <https://doi.org/10.1007/b97636>
- Chakrabarti, A., & Ghosh, J. K. (2011). *AIC, BIC and recent advances in model selection* (P. S. Bandyopadhyay & M. R. Forster, Eds.; Vol. 7, pp. 583–605). North-Holland. <https://doi.org/10.1016/B978-0-444-51862-0.50018-6>
- Chave, J. (2013). The problem of pattern and scale in ecology: what have we learned in 20 years? *Ecology Letters*, 16(s1), 4–16. <https://doi.org/10.1111/ele.12048>
- Clement, M. J., Nichols, J. D., Collazo, J. A., Terando, A. J., Hines, J. E., & Williams, S. G. (2019). Partitioning global change: Assessing the relative importance of changes in climate and land cover for changes in avian distribution. *Ecology and Evolution*, 9(4), 1985–2003. <https://doi.org/10.1002/ece3.4890>
- Cook, J. D., Williams, D. M., Porter, W. F., & Christensen, S. A. (2022). Improved predictions and forecasts of chronic wasting disease occurrence using multiple mechanism dynamic occupancy modeling. *The Journal of Wildlife Management*, 86(7), e22296. <https://doi.org/10.1002/jwmg.22296>
- Devarajan, K., Morelli, T. L., & Tenan, S. (2020). Multi-species occupancy models: review, roadmap, and recommendations. *Ecography*, 43(11), 1612–1624. <https://doi.org/10.1111/ecog.04957>
- Doherty, P. F., White, G. C., & Burnham, K. P. (2012). Comparison of model building and selection strategies. *Journal of Ornithology*, 152(2), 317–323. <https://doi.org/10.1007/s10336-010-0598-5>

Dorazio, R. M., Kéry, M., Royle, J. A., & Plattner, M. (2010). Models for inference in dynamic metacommunity systems. *Ecology*, 91(8), 2466–2475. <https://doi.org/10.1890/09-1033.1>

Dormann, C. F. (2007). Promising the future? Global change projections of species distributions. *Basic and Applied Ecology*, 8(5), 387–397. <https://doi.org/10.1016/j.baae.2006.11.001>

Duggan, J. M., Schooley, R. L., & Heske, E. J. (2011). Modeling occupancy dynamics of a rare species, Franklin's ground squirrel, with limited data: are simple connectivity metrics adequate? *Landscape Ecology*, 26(10), 1477–1490. <https://doi.org/10.1007/s10980-011-9652-9>

Efford, M. G., & Dawson, D. K. (2012). Occupancy in continuous habitat. *Ecosphere*, 3(4), art32. <https://doi.org/10.1890/ES11-00308.1>

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, 1(4), 330–342. <https://doi.org/10.1111/j.2041-210X.2010.00036.x>

Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, 77(4), 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>

Emmet, R. L., Long, R. A., & Gardner, B. (2021). Modeling multi-scale occupancy for monitoring rare and highly mobile species. *Ecosphere*, 12(7), e03637. <https://doi.org/10.1002/ecs2.3637>

Evans, M. R., Grimm, V., Johst, K., Knuuttila, T., Langhe, R. de, Lessells, C. M., Merz, M., O'Malley, M. A., Orzack, S. H., Weisberg, M., Wilkinson, D. J., Wolkenhauer, O., & Benton, T. G. (2013). Do simple models lead to generality in ecology? *Trends in Ecology & Evolution*, 28(10), 578–583. <https://doi.org/10.1016/j.tree.2013.05.022>

Falke, J. A., Bailey, L. L., Fausch, K. D., & Bestgen, K. R. (2012). Colonization and extinction in dynamic habitats: an occupancy approach for a Great Plains stream fish assemblage. *Ecology*, 93(4), 858–867. <https://doi.org/10.1890/11-1515.1>

Farley, S. S., Dawson, A., Goring, S. J., & Williams, J. W. (2018). Situating ecology as a big-data science: Current advances, challenges, and solutions. *BioScience*, 68(8), 563–576. <https://doi.org/10.1093/biosci/biy068>

Fidino, M., Simonis, J. L., & Magle, S. B. (2019). A multistate dynamic occupancy model to estimate local colonization/extinction rates and patterns of co-occurrence between two or more interacting species. *Methods in Ecology and Evolution*, 10(2), 233–244. <https://doi.org/10.1111/2041-210X.13117>

Fisher, A. C., Volpe, J. P., & Fisher, J. T. (2014). Occupancy dynamics of escaped farmed Atlantic salmon in Canadian Pacific coastal salmon streams: implications for sustained invasions. *Biological Invasions*, 16(10), 2137–2146. <https://doi.org/10.1007/s10530-014-0653-x>

Gelman, A. (2014). *Bayesian data analysis*.

<https://research.ebsco.com/linkprocessor/plink?id=86df87c2-efc9-3fae-8c85-32142daec7af>

Goldstein, B. R., Keller, A. G., Calhoun, K. L., Barker, K. J., Montealegre-Mora, F., Serota, M. W., Van Scoyoc, A., Parker-Shames, P., Andreozzi, C. L., & Valpine, P. de. (2024). How do ecologists estimate occupancy in practice? *Ecography*, *n/a*(*n/a*), e07402.

<https://doi.org/10.1111/ecog.07402>

Gu, W., & Swihart, R. K. (2004). Absent or undetected? Effects of non-detection of species occurrence on wildlife habitat models. *Biological Conservation*, *116*(2), 195–203.

[https://doi.org/10.1016/S0006-3207\(03\)00190-3](https://doi.org/10.1016/S0006-3207(03)00190-3)

Guillera-Arroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities.

*Ecography*, *40*(2), 281–295. <https://doi.org/10.1111/ecog.02445>

Guillera-Arroita, G., Morgan, B. J. T., Ridout, M. S., & Linkie, M. (2011). Species Occupancy Modeling for Detection Data Collected Along a Transect. *Journal of Agricultural, Biological, and Environmental Statistics*, *16*(3), 301–317. <https://doi.org/10.1007/s13253-010-0053-3>

Guisan, A., Lehmann, A., Ferrier, S., Austin, M., Overton, J. Mc. C., Aspinall, R., & Hastie, T. (2006). Making better biogeographical predictions of species' distributions. *Journal of Applied Ecology*, *43*(3), 386–392. <https://doi.org/10.1111/j.1365-2664.2006.01164.x>

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, *8*(9), 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat suitability and distribution models: With applications in R*. Cambridge University Press.

<https://doi.org/10.1017/9781139028271>

Hendershot, J. N., Smith, J. R., Anderson, C. B., Letten, A. D., Frishkoff, L. O., Zook, J. R., Fukami, T., & Daily, G. C. (2020). Intensive farming drives long-term shifts in avian community composition. *Nature*, *579*(7799), 393–396. <https://doi.org/10.1038/s41586-020-2090-6>

Hines, J. (2006). *PRESENCE2 - software to estimate patch occupancy and related parameters*. USGS, Patuxent Wildlife Research Center.

Hooten, M. B., & Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. *Ecological Monographs*, *85*(1), 3–28. <https://doi.org/10.1890/14-0661.1>

Huber, N., Kéry, M., & Pasinelli, G. (2017). Occupancy dynamics of the Wood Warbler *Phylloscopus sibilatrix* assessed with habitat and remote sensing data. *Ibis*, *159*(3), 623–637. <https://doi.org/10.1111/ibi.12472>



- Humboldt, A. von. (1849). *Cosmos : a sketch of a physical description of the universe*.
- Hutchinson, R., Liu, L.-P., & Dietterich, T. (2011). Incorporating Boosted Regression Trees into Ecological Latent Variable Models. *Proceedings of the AAAI Conference on Artificial Intelligence*, 25(1), 1343–1348. <https://doi.org/10.1609/aaai.v25i1.7801>
- IUCN. (2024). *The IUCN red list of threatened species*. Version 2024-2. <https://www.iucnredlist.org>.
- James, G., Witten, D., Hastie, T., & Tibshirani, R. (2021). *An Introduction to Statistical Learning: with Applications in R*. Springer US. <https://doi.org/10.1007/978-1-0716-1418-1>
- Joseph, M. B. (2020). Neural hierarchical models of ecological populations. *Ecology Letters*, 23(4), 734–747. <https://doi.org/10.1111/ele.13462>
- Kellner, K. F., Fowler, N. L., Petroelje, T. R., Kautz, T. M., Beyer Jr., D. E., & Belant, J. L. (2022). ubms: An R package for fitting hierarchical occupancy and N-mixture abundance models in a Bayesian framework. *Methods in Ecology and Evolution*, 13(3), 577–584. <https://doi.org/10.1111/2041-210X.13777>
- 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>
- Kellner, K. F., & Swihart, R. K. (2014). Accounting for Imperfect Detection in Ecology: A Quantitative Review. *PLOS ONE*, 9(10), e111436. <https://doi.org/10.1371/journal.pone.0111436>
- Kendall, W. L., Hines, J. E., Nichols, J. D., & Grant, E. H. C. (2013). Relaxing the closure assumption in occupancy models: staggered arrival and departure times. *Ecology*, 94(3), 610–617. <https://doi.org/10.1890/12-1720.1>
- Kéry, M., Guisera-Aroita, G., & Lahoz-Monfort, J. J. (2013). Analysing and mapping species range dynamics using occupancy models. *Journal of Biogeography*, 40(8), 1463–1474. <https://doi.org/10.1111/jbi.12087>
- Kéry, M., & Royle, J. A. (2021). *Applied hierarchical modeling in ecology : analysis of distribution, abundance and species richness in R and BUGS. Volume 2, Dynamic and advanced models*. <https://research.ebsco.com/linkprocessor/plink?id=acdec215-f169-3c05-a996-ad3f64d6341e>
- Lahoz-Monfort, J. J., Guisera-Aroita, G., & Wintle, B. A. (2014). Imperfect detection impacts the performance of species distribution models. *Global Ecology and Biogeography*, 23(4), 504–515. <https://doi.org/10.1111/geb.12138>
- Lahoz-Monfort, J. J., & Magrath, M. J. L. (2021). A comprehensive overview of technologies for species and habitat monitoring and conservation. *BioScience*, 71(10), 1038–1062. <https://doi.org/10.1093/biosci/biab073>

Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts a global multidimensional synthesis and new research directions. *Ecography*, 38(1), 15–28.

<https://doi.org/10.1111/ecog.00967>

Lesmeister, D. B., Nielsen, C. K., Schaubert, E. M., & Hellgren, E. C. (2015). Spatial and temporal structure of a mesocarnivore guild in midwestern north America: Midwestern Carnivore Guild Structure. *Wildlife Monographs*, 191(1), 1–61.

<https://doi.org/10.1002/wmon.1015>

Loneragan, M. (2014). Data availability constrains model complexity, generality, and utility: A response to evans *et al.* *Trends in Ecology & Evolution*, 29(6), 301–302.

<https://doi.org/10.1016/j.tree.2014.03.005>

MacKenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, 9(3), 300–318.

<https://doi.org/10.1198/108571104X3361>

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., Andrew Royle, J., & 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](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)

[https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2006). *Occupancy Estimation and Modeling : Inferring Patterns and Dynamics of Species Occurrence*.

<https://pubs.usgs.gov/publication/5200296>

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2017). *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence*. Elsevier Science & Technology.

<http://ebookcentral.proquest.com/lib/unimelb/detail.action?docID=5124550>

MacKenzie, D. I., & Reardon, J. T. (2013). *Occupancy Methods for Conservation Management* (pp. 248–264). John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781118490747.ch11>

Marescot, L., Lyet, A., Singh, R., Carter, N., & Gimenez, O. (2020). Inferring wildlife poaching in southeast Asia with multispecies dynamic occupancy models. *Ecography*, 43(2), 239–250. <https://doi.org/10.1111/ecog.04536>

McClintock, B. T., Bailey, L. L., Pollock, K. H., & Simons, T. R. (2010). Unmodelled observation error induces bias when inferring patterns and dynamics of species occurrence via aural detections. *Ecology*, 91(8), 2446–2454. <https://www.jstor.org/stable/27860809>

McGowan, C. P., Angeli, N., Beisler, W., Snyder, C. W., Rankin, N. M., Woodrow, J., Wilson, J., Rivenbark, E., Schwarzer, A., Hand, C., Anthony, R. M., Griffin, R., Barrett, K., Haverland, A., Roach, N., Schneider, T., Smith, A. J., Smith, F., Tolliver, J., & Watts, B. D. (2020). Linking

monitoring and data analysis to predictions and decisions for the range-wide eastern black rail status assessment. *Endangered Species Research*, 43, 209–222.

<https://doi.org/10.3354/esr01063>

Merow, C., Smith, M. J., Edwards Jr, T. C., Guisan, A., McMahon, S. M., Normand, S., Thuiller, W., Wüest, R. O., Zimmermann, N. E., & Elith, J. (2014). What do we gain from simplicity versus complexity in species distribution models? *Ecography*, 37(12), 1267–1281.

<https://doi.org/10.1111/ecog.00845>

Merow, C., Smith, M. J., & Silander Jr, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, 36(10), 1058–1069. <https://doi.org/10.1111/j.1600-0587.2013.07872.x>

Miller, D., Nichols, J., McClintock, B., Grant, E., Bailey, L., & Weir, L. (2011). Improving occupancy estimation when two types of observational error occur: Non-detection and species misidentification. *Ecology*, 92, 1422–1428. <https://doi.org/10.2307/23035095>

Mores, G. B., Schuler-Faccini, L., Hasenack, H., Fetzner, L. O., Souza, G. D., & Ferraz, G. (2020). Site Occupancy by *Aedes aegypti* in a Subtropical City is Most Sensitive to Control during Autumn and Winter Months. *The American Journal of Tropical Medicine and Hygiene*, 103(1), 445–454. <https://doi.org/10.4269/ajtmh.19-0366>

Morin, D. J., Yackulic, C. B., Diffendorfer, J. E., Lesmeister, D. B., Nielsen, C. K., Reid, J., & Schaubert, E. M. (2020). Is your ad hoc model selection strategy affecting your multimodel inference? *Ecosphere*, 11(1), e02997. <https://doi.org/10.1002/ecs2.2997>

Nichols, J. D., & Cooch, E. G. (2024). Predictive Models are Indeed Useful for Causal Inference. *Ecology*.

Nichols, J. D., Hines, J. E., Mackenzie, D. I., Seamans, M. E., & Gutiérrez, R. J. (2007). Occupancy estimation and modeling with multiple states and state uncertainty. *Ecology*, 88(6), 1395–1400. <https://www.jstor.org/stable/27651247>

Olson, G. S., Anthony, R. G., Forsman, E. D., Ackers, S. H., Loschl, P. J., Reid, J. A., Dugger, K. M., Glenn, E. M., & Ripple, W. J. (2005). Modeling of Site Occupancy Dynamics for Northern Spotted Owls, with Emphasis on the Effects of Barred Owls. *The Journal of Wildlife Management*, 69(3), 918–932. [https://doi.org/10.2193/0022-541X\(2005\)069\[0918:MOSODF\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)069[0918:MOSODF]2.0.CO;2)

Otto, C. R. V., Bailey, L. L., & Roloff, G. J. (2013). Improving species occupancy estimation when sampling violates the closure assumption. *Ecography*, 36(12), 1299–1309. <https://doi.org/10.1111/j.1600-0587.2013.00137.x>

Otto, C. R. V., & Roloff, G. J. (2012). Songbird response to green-tree retention prescriptions in clearcut forests. *Forest Ecology and Management*, 284, 241–250. <https://doi.org/10.1016/j.foreco.2012.07.016>

Park, T., & Casella, G. (2008). The Bayesian Lasso. *Journal of the American Statistical Association*, 103(482), 681–686. <https://doi.org/10.1198/016214508000000337>

Pautrel, L., Moulherat, S., Gimenez, O., & Etienne, M.-P. (2024). Analysing biodiversity observation data collected in continuous time: Should we use discrete- or continuous-time occupancy models? *Methods in Ecology and Evolution*, 15(5), 935–950. <https://doi.org/10.1111/2041-210X.14314>

Peach, M. A., Cohen, J. B., Frair, J. L., Zuckerberg, B., Sullivan, P., Porter, W. F., & Lang, C. (2019). Value of protected areas to avian persistence across 20 years of climate and land-use change. *Conservation Biology*, 33(2), 423–433. <https://doi.org/10.1111/cobi.13205>

Pendleton, D. E., Tingley, M. W., Ganley, L. C., Friedland, K. D., Mayo, C., Brown, M. W., McKenna, B. E., Jordaan, A., & Staudinger, M. D. (2022). Decadal-scale phenology and seasonal climate drivers of migratory baleen whales in a rapidly warming marine ecosystem. *Global Change Biology*, 28(16), 4989–5005. <https://doi.org/10.1111/gcb.16225>

Popovic, G., Mason, T. J., Drobniak, S. M., Marques, T. A., Potts, J., Joo, R., Altwegg, R., Burns, C. C. I., McCarthy, M. A., Johnston, A., Nakagawa, S., McMillan, L., Devarajan, K., Taggart, P. L., Wunderlich, A., Mair, M. M., Martínez-Lanfranco, J. A., Lagisz, M., & Pottier, P. (2024). Four principles for improved statistical ecology. *Methods in Ecology and Evolution*, 15(2), 266–281. <https://doi.org/10.1111/2041-210X.14270>

Riddell, E. A., Iknayan, K. J., Hargrove, L., Tremor, S., Patton, J. L., Ramirez, R., Wolf, B. O., & Beissinger, S. R. (2021). Exposure to climate change drives stability or collapse of desert mammal and bird communities. *Science*, 371(6529), 633–636. <https://doi.org/10.1126/science.abd4605>

Risk, B. B., Valpine, P. de, & Beissinger, S. R. (2011). A robust-design formulation of the incidence function model of metapopulation dynamics applied to two species of rails. *Ecology*, 92(2), 462–474. <https://doi.org/10.1890/09-2402.1>

Rota, C. T., Fletcher Jr, R. J., Dorazio, R. M., & Betts, M. G. (2009). Occupancy estimation and the closure assumption. *Journal of Applied Ecology*, 46(6), 1173–1181. <https://doi.org/10.1111/j.1365-2664.2009.01734.x>

Royle, J. A., & Link, W. A. (2006). GENERALIZED SITE OCCUPANCY MODELS ALLOWING FOR FALSE POSITIVE AND FALSE NEGATIVE ERRORS. *Ecology*, 87(4), 835–841. [https://doi.org/10.1890/0012-9658\(2006\)87\[835:GSOMAF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[835:GSOMAF]2.0.CO;2)

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), 12805. <https://doi.org/10.1038/s41598-019-48851-5>

Scott, P. A., & Rissler, L. J. (2015). Integrating dynamic occupancy modeling and genetics to infer the status of the imperiled flattened musk turtle. *Biological Conservation*, 192, 294–303. <https://doi.org/10.1016/j.biocon.2015.10.004>

Steenweg, R., Hebblewhite, M., Whittington, J., Lukacs, P., & McKelvey, K. (2018). Sampling scales define occupancy and underlying occupancyabundance relationships in animals. *Ecology*, 99(1), 172–183. <https://doi.org/10.1002/ecy.2054>

- Stevens, B. S., & Conway, C. J. (2019). Identifying important military installations for continental-scale conservation of marsh bird breeding habitat. *Journal of Environmental Management*, 252, 109664. <https://doi.org/10.1016/j.jenvman.2019.109664>
- Stewart, P. S., Stephens, P. A., Hill, R. A., Whittingham, M. J., & Dawson, W. (2023). Model selection in occupancy models: Inference versus prediction. *Ecology*, 104(3), e3942. <https://doi.org/10.1002/ecy.3942>
- Tredennick, A. T., Hooker, G., Ellner, S. P., & Adler, P. B. (2021). A practical guide to selecting models for exploration, inference, and prediction in ecology. *Ecology*, 102(6), e03336. <https://doi.org/10.1002/ecy.3336>
- Urban, M. C., Nadeau, C. P., & Giery, S. T. (2023). Using mechanistic insights to predict the climate-induced expansion of a key aquatic predator. *Ecological Monographs*, 93(3), e1575. <https://doi.org/10.1002/ecm.1575>
- Valavi, R., Elith, J., Lahoz-Monfort, J. J., & Guillera-Aroita, G. (2023). Flexible species distribution modelling methods perform well on spatially separated testing data. *Global Ecology and Biogeography*, 32(3), 369–383. <https://doi.org/10.1111/geb.13639>
- Valente, J. J., Hutchinson, R. A., & Betts, M. G. (2017). Distinguishing distribution dynamics from temporary emigration using dynamic occupancy models. *Methods in Ecology and Evolution*, 8(12), 1707–1716. <https://doi.org/10.1111/2041-210X.12840>
- Valente, J. J., Jirinec, V., & Leu, M. (2024). Thinking beyond the closure assumption: Designing surveys for estimating biological truth with occupancy models. *Methods in Ecology and Evolution*, 2041–210X.14439. <https://doi.org/10.1111/2041-210X.14439>
- Warrier, R., Noon, B. R., & Bailey, L. (2020). Agricultural lands offer seasonal habitats to tigers in a human-dominated and fragmented landscape in India. *Ecosphere*, 11(7). <https://doi.org/10.1002/ecs2.3080>
- Wood, C. M., & Peery, M. Z. (2022). What does ‘occupancy’ mean in passive acoustic surveys? *Ibis*, 164(4), 1295–1300. <https://doi.org/10.1111/ibi.13092>
- Yates, L. A., Aandahl, Z., Richards, S. A., & Brook, B. W. (2023). Cross validation for model selection: A review with examples from ecology. *Ecological Monographs*, 93(1), e1557. <https://doi.org/10.1002/ecm.1557>
- Zuckerberg, B., Bonter, D. N., Hochachka, W. M., Koenig, W. D., DeGaetano, A. T., & Dickinson, J. L. (2011). Climatic constraints on wintering bird distributions are modified by urbanization and weather: Wintering birds, weather, food, and climate. *Journal of Animal Ecology*, 80(2), 403–413. <https://doi.org/10.1111/j.1365-2656.2010.01780.x>