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Review

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

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Since their introduction over 20 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 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. Based on these findings we highlight aspects of the modelling process that merit closer attention, such as the possible impacts of low complexity and missing drivers of heterogeneity on model performance, the uncertainties around robust and appropriate model selection techniques for different contexts, and the need for trusted and reliable tools for model assessment and evaluation.

Keywords: covariate selection, hierarchical model, imperfect detection, occupancy, range dynamics, species distributions

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Introduction

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

Irrespective of its importance, 'occupancy' – broadly referring here to the presence of a species in a given area and time period – has proven to be a persistently difficult quantity to estimate in practice. This difficulty arises from the challenges inherent in modelling complex and dynamic natural systems with incomplete data, exacerbated by the fact that it is often hard to determine whether a species is truly absent from a site or whether it was simply not detected. It is well-established that imperfect detection of organisms results in biased estimation of occupancy, particularly when detectability is not uniform in space or time (Gu and Swihart 2004, Lahoz-Monfort et al. 2014). Despite this fact and the ubiquity of imperfect detection in field data, historically many common models have not made adjustments for detection (Kellner and Swihart 2014). Another limitation of many models currently in use (such as conventional correlative species distribution models) is a lack of suitability for predicting to new locations and time periods when species ranges are shifting, as in biological invasions and climate change driven range shifts (Dormann 2007, Elith et al. 2010).

In recent years, awareness of these issues 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 accounting for imperfect detection (Box 1). In doing so, DOMs provide answers to common issues in occupancy estimation while requiring relatively simple-to-collect detection/non-detection data (Guillera-Arroita 2017, Briscoe et al. 2019). This balance between complexity and feasibility makes DOMs an appealing option for addressing many applied questions relating to species range dynamics.

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, www.r-project.org). In the Bayesian context, resources such as Kéry and 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 (Royle and Link 2006, Miller et al. 2011), model multiple states beyond occupied and unoccupied (Nichols et al. 2007), jointly estimate occupancy for multiple species (Dorazio et al. 2010, Devarajan et al. 2020), and incorporate spatially explicit occupancy dynamics (Heard et al. 2013, Broms et al. 2016). 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 (Farley et al. 2018, Altwegg and Nichols 2019). 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 and Donovan 2019, Lahoz-Monfort and 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 were 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.

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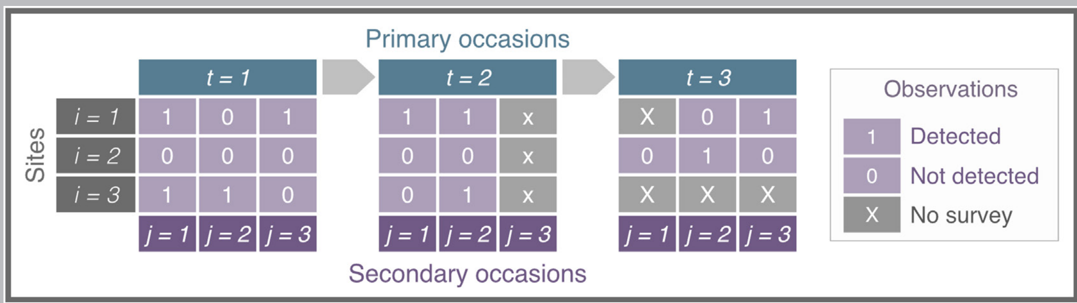
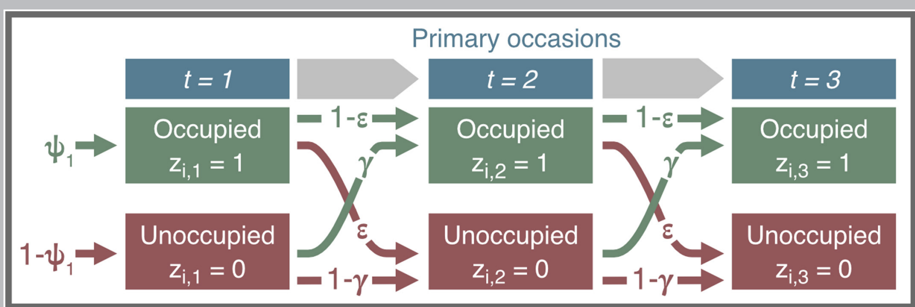
Box 1. An introduction to dynamic occupancy models.

DOMs are hierarchical models that link observed detection/non-detection data with the underlying latent process of changing site occupancy (MacKenzie et al. 2017, Kéry and Royle 2021). 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.

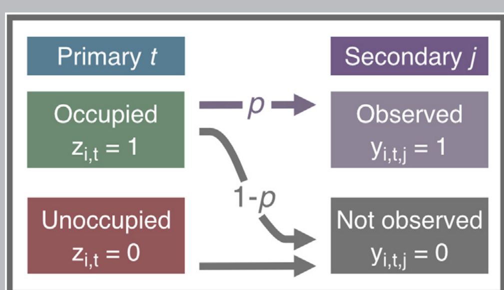
Input data: To separate these two processes DOMs require hierarchical data inputs. Occupancy is estimated at independent sites (*i*) during discrete, time-bound intervals termed 'primary occasions' (*t*). Within primary occasions, multiple observations are made at the same sites during independent 'secondary 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. 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: 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 ψ_1, such that $z_{i,t=1} \sim \text{Bernoulli}(\psi_1)$. In subsequent primary occasions changes in site occupancy are Markovian, determined by the site's state in the previous primary occasion and probabilities of colonisation γ and extinction ε, such that $z_{i,t} \sim \text{Bernoulli}\,(z_{i,t-1}(1-\varepsilon) + (1 - z_{i,t-1})\gamma)$.



Observation sub-model: The detection process relates the observed data y to the latent occupancy states z. 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. Detection at a site is determined by a Bernoulli trial with detection probability *p*, conditioned on the site being occupied in primary occasion *t* such that $y_{i,t,j} \sim \text{Bernoulli}\,(z_{i,t} \times p)$.



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In their original formulation, DOMs estimate four parameters of interest: initial occupancy (ψ_1), colonisation (γ), extinction (ε), 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: 1) sites are closed to changes in true occupancy state within each primary occasion, 2) occupancy at each site is independent of other sites, 3) observations within each primary occasion are independent of each other, 4) no false positive detections occur, and 5) key sources of heterogeneity (including in detectability) are modelled (MacKenzie et al. 2017).

Material and 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 26 July and 29 July 2024. The first query included all articles from 2004 to 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 the 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: 1) 'estimating parameters', where authors expressed interest in estimates of site occupancy, colonisation, extinction, or detection probabilities; 2) 'testing relationships', where authors examined predefined hypothesised relationships between covariates and model parameters; 3) 'identifying drivers', where authors more broadly explored covariates associated with model parameters; 4) 'predicting temporally', where authors predicted site occupancy under future conditions; 5) 'predicting spatially', where authors predicted site occupancy to unsurveyed locations; and 6) 'developing methods', where authors introduced, tested, or demonstrated aspects of DOMs.

Study systems

We recorded the approximate geographical location and spatial scale 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. We also recorded details on taxa modelled for each study system, with a 'taxon' defined as a grouping of organisms with a unique detection history. These often corresponded to individual species, although some articles modelled subspecies and others lumped multiple species into a single grouping for modelling. Details collected on these for each dataset included the number of discrete taxa modelled, their general categorisation (birds, mammals, herptiles, invertebrates, or 'other'), and their conservation status. A taxon was denoted as threatened if it was 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 subspecies that 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 were 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

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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 the 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 (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 and 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

Full details on the articles included in this review are provided in the Supporting information. In total, 92 articles were included, fewer than the 100 possible articles due to a deficit of qualifying papers in the first stratum. 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 (Fig. 1).

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 (Fig. 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*. Thirty-five percent of studies took a more exploratory approach to identifying possible drivers of occupancy, such as in Huber et al. (2017)'s study which examined dozens of habitat covariates for wood warbler *Phylloscopus sibilatrix* occupancy. Thirty-six percent of articles used DOMs specifically to obtain estimates of occupancy parameters, both for single species of high conservation interest and for broader community assemblages of species (Ahumada et al. 2013, Scott and Rissler 2015). While only 17% of articles used their DOMs to make predictions, the proportion of articles pursing 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 reviewed focused on methods development, representing continued focus on extending and testing DOMs.

Studies fitting DOMs were produced by authors from various sectors: while 79% of studies included at least one affiliate of an academic institution, 59% included a government affiliate, 28% a non-governmental organisation affiliate, and 12% an affiliate of a private company. Sixty-three percent of studies had cross-sector authorship with affiliations from at least two categories.

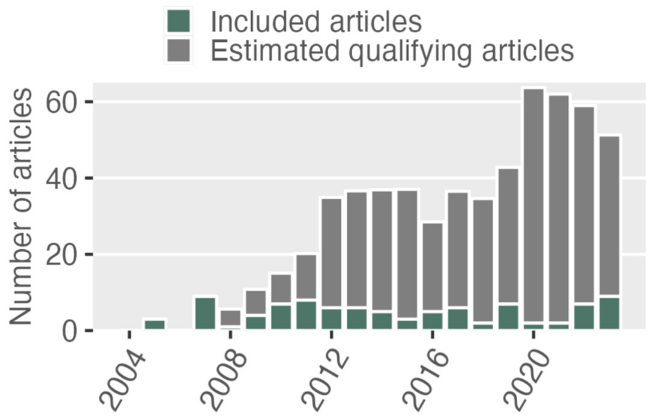

Figure 1. Bars indicate the estimated number of articles fitting dynamic occupancy models (DOMs) in each year, with green representing the articles included in our review and grey projecting the remaining qualifying articles. Projections were calculated using the number of unprocessed articles remaining in each year multiplied by the acceptance rate of the corresponding stratum: 12% of queried articles from 2004 to 2007; 24% from 2008 to 2011; 42% from 2012 to 2015; 35% from 2016 to 2019; and 57% from 2020 to 2023.

Study systems

Our review included DOMs fit using data collected on all continents bar Antarctica (Fig. 3a), although a majority of

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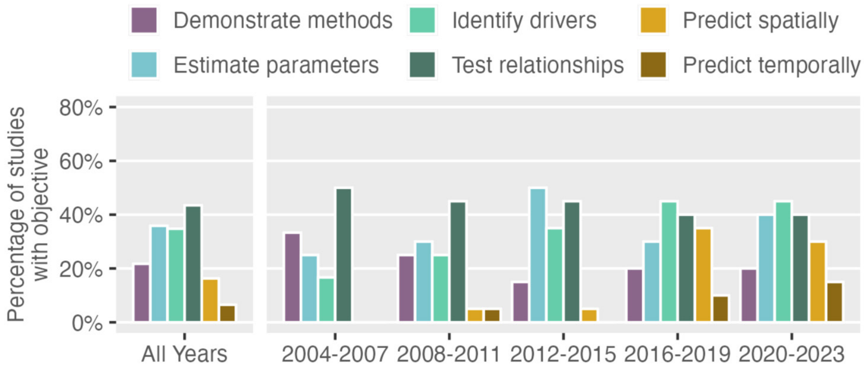

Figure 2. Bars represent the percentage of articles which pursued each of six non-exclusive research objectives. These objectives include articles which demonstrated methods for dynamic occupancy models (DOMs), estimated model parameters, identified drivers of occupancy dynamics, tested hypothesised 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).

articles used data from the USA. Study areas varied considerably in size – the smallest example came from a study of insect occurrence in a rainforest plot of less than one square kilometre (Basset et al. 2023), where the largest spanned the entire eastern half of the USA in a study of avian range shifts (Clement et al. 2019).

Most studies focused on vertebrate taxa (Fig. 3c), 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 changes in lichen occupancy, the spread of chronic wasting disease, and mosquito dynamics (Belinchón et al. 2017, Mores et al. 2020, Cook et al. 2022). The vast majority of studies modelled terrestrial species, though there were 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 (Fig. 3d). Thirty-four percent of studies fit independent models to multiple species (Otto and Roloff 2012, Peach et al. 2019), whereas 12% used explicitly multi-species extensions of DOMs. The latter group included hierarchical models which fit hundreds of species in a single implementation with species-level effects (Dorazio et al. 2010, Hendershot et al. 2020), as well as explicit interaction models which estimated conditional occupancy, colonisation, extinction, and detection probabilities (Lesmeister et al. 2015, Fidino et al. 2019).

Observations and data collection

The detection/non-detection data required for DOMs were collected using various survey methods across reviewed studies (Fig. 3e): 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 (Zuckerberg et al. 2011, Warrier et al. 2020). Datasets ranged considerably in size, with the smallest including observations at just 10 sites and the largest including over 6000 (Fig. 3f); 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 in a case-study using bird data to test model assumptions (Valente et al. 2017) to over sixty years in a long-running butterfly monitoring study (Strien et al. 2011), with a median duration of eight years. The number of primary occasions ranged from 2 to 189 (median six 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 themselves, with one study using surveys conducted by Joseph Grinnell in 1908 to model century-long changes in occupancy (Riddell et al. 2021).

Covariates and complexity

The most common covariates considered for use in DOMs addressed aspects of habitat and land cover (Fig. 4). Thirty-five percent of studies incorporated covariates for site geometry and connectivity, such as habitat patch size or distance

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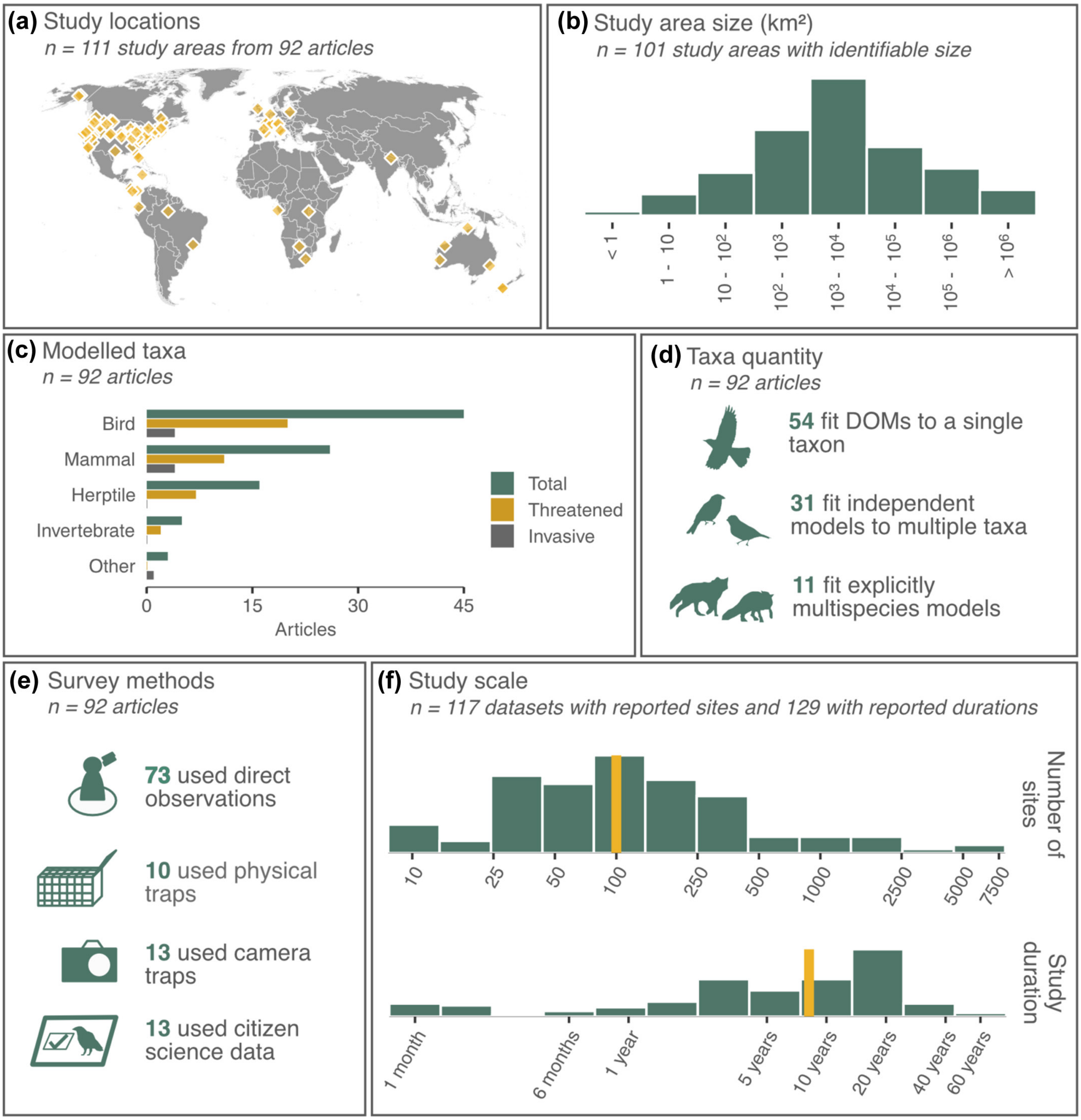

Figure 3. A summary of the research contexts in reviewed applications of dynamic occupancy models (DOMs). (a) The approximate locations of the study areas where data were collected. (b) Spatial extent of the study areas, defined as the area of inference within which all surveys were conducted. (c) Number of articles that fit models to each taxa category. Taxa were considered 'threatened' if indicated by authors or if they were 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 that used each method to capture detection/non-detection data. Categories are non-exclusive, and citizen science data are a subset of 'direct observations'. (f) The number of sites and study duration for each dataset used to fit DOMs – gold lines indicate medians.

to other sites. Often these were included as simple covariates on colonisation or extinction, such as the distance to other sites or landscape habitat connectivity metrics (Duggan et al. 2011). Alternatively, more complex parameterisations explicitly modelled colonisation or extinction as a spatial process dependent on patch size or the distance to occupied sites (Risk et al. 2011, Heard et al. 2013, Broms et al. 2016). Several studies also included biotic interactions with other species as covariates, often where the target taxon was threatened by invasive species. These covariates effectively

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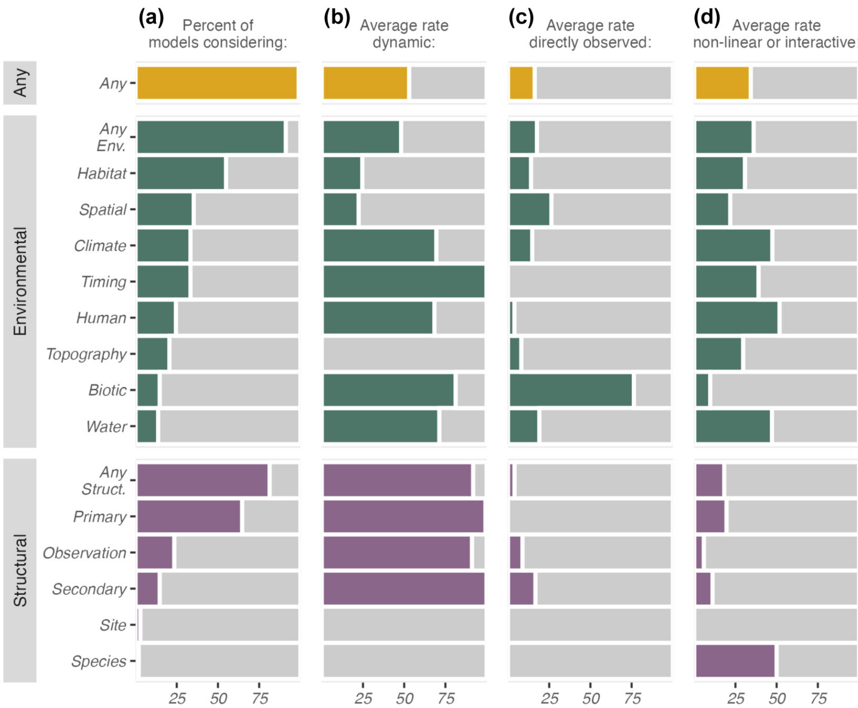

Figure 4. Attributes of the covariates considered for inclusion in dynamic occupancy models (DOMs). Columns represent the percentage of studies that tested at least one covariate in a category on any model parameter (a), and the average percentage of covariates in each category that were (b) time-varying, 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 were 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 expanded definitions and analysis code, see the Supporting information.

incorporate species interactions in DOMs without requiring more complex multi-species model extensions.

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 existing sources like remotely sensed datasets (70% of environmental covariates); this varied depending on the category of covariate (Fig. 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% of the environmental factors and 94% of the structural factors considered for colonisation, extinction, and detection (which may vary over time) were dynamic covariates. Covariates related to climate or weather were the most frequently dynamic category (Fig. 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 (Fig. 5). Note that this does not represent the number of covariates included in the final model formulation used for inference. The median number of covariates considered varied by parameter, with transition probabilities (colonisation and extinction) more likely to have a broader range of environmental covariates considered compared to initial occupancy and detection. The

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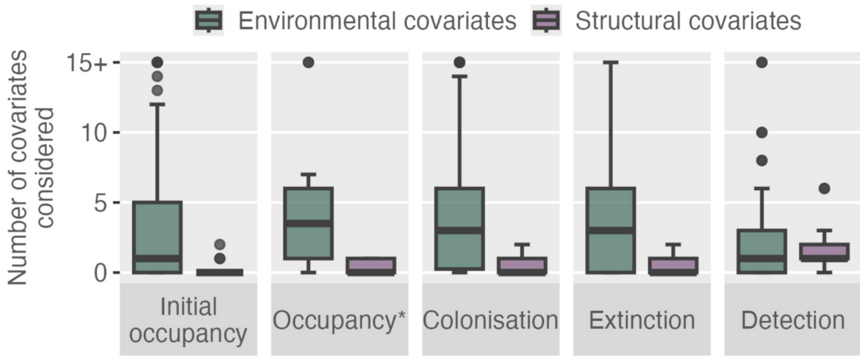

Figure 5. The number of covariates considered for each core parameter across all distinct modelling workflows in our sample. A covariate is defined here as a distinct variable considered for inclusion, with linear, non-linear, and interactive forms of the same factor counted as a single covariate. Covariates 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 dynamic occupancy models (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.

lack of any covariates considered for initial occupancy in 37% of studies is particularly notable, as is the observation that 30% of modelling workflows considered no environmental covariates for detection probability.

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. Two 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 and Anderson 2004).

Those Bayesian models that 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

Table 1. A summary of modelling practices in dynamic occupancy model (DOM) subset by framework (maximum likelihood or Bayesian). Some studies include multiple distinct modelling workflows (n = 102 workflows across 92 articles). Two models included in the 'All models' column were neural network based and fell into neither the MLE nor Bayesian categories. The model selection methods represented in this table are non-exclusive and some articles employed multiple approaches.

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

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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 Markov chain Monte Carlo (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 (Fig. 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 numbers of sites, the upper quartile contained more sites than in previous strata (Fig. 6a). The median number of covariates considered per parameter has also continually increased since the early years of DOMs, from 1.75 covariates in 2004–2007 to 4.75 in the 2020–2023 stratum (Fig. 6b).

While Bayesian models were included in all strata of our sample, there was a marked increase in their frequency in the most recent stratum (Fig. 6c). This may in part be explained by the publication of accessible resources such as Kéry and 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 (Fig. 6d). 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 (Fig. 6e).

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 (Table 2).

Aligning models with ecological expectations

Choosing appropriate covariates to fit realistic models and address research questions is a challenging task, requiring not only robust domain knowledge but also a clear understanding of what the different components of DOMs represent in context. A key finding of our review was the considerable variation in the data used for DOMs, where a study area could be local- or continental-scale, a site could be defined variously as a discrete habitat patch or a grid cell in continuous space, and a primary occasion could be days or decades long. Each of these factors (as well as the focal species' life history traits) shape what 'occupancy' and 'detection' represent for a given study. Understanding this nuance is necessary to align the covariates considered for DOMs with corresponding ecological processes.

A conventional definition of occupancy as the probability that a species is present within a site across a primary occasion requires compliance with the closure assumption, such that a species is always available for detection at occupied sites. Whether this is reasonable depends on the spatial extent of each site relative to the movement of individuals during a primary occasion, with cases where sites are discrete features equivalent to individual home ranges (Fig. 7a) or where they cover more area than home ranges (Fig. 7b-i) more likely to meet the assumption. Conversely, if sites are much smaller than individual home ranges it is less likely that a site will remain consistently occupied and that closure will be met. In such cases occupancy should be interpreted as the probability that a site is used by the species for at least some portion of the primary occasion (Fig. 7b-iii).

While much earlier research emphasised how closure violations bias estimates of occupancy and recommended means to avoid them (Rota et al. 2009, Kendall et al. 2013, Otto et al. 2013, MacKenzie et al. 2017, Valente et al. 2017), more recently authors have begun to consider how closure violations alter model interpretation rather than treating them as a problem to be solved (Efford and Dawson 2012, Goldstein et al. 2024, Valente et al. 2024). In our review, we did not determine whether individual studies best aligned with the conventional or site-use definitions of occupancy, although a recent review on single-season models found that potential closure violations are not discussed in the majority of cases (Goldstein et al. 2024). We do note that our sample was dominated by mammals and birds, often mobile species which are less likely to remain within a site for a long time period and fulfil closure assumptions. Looking forward,

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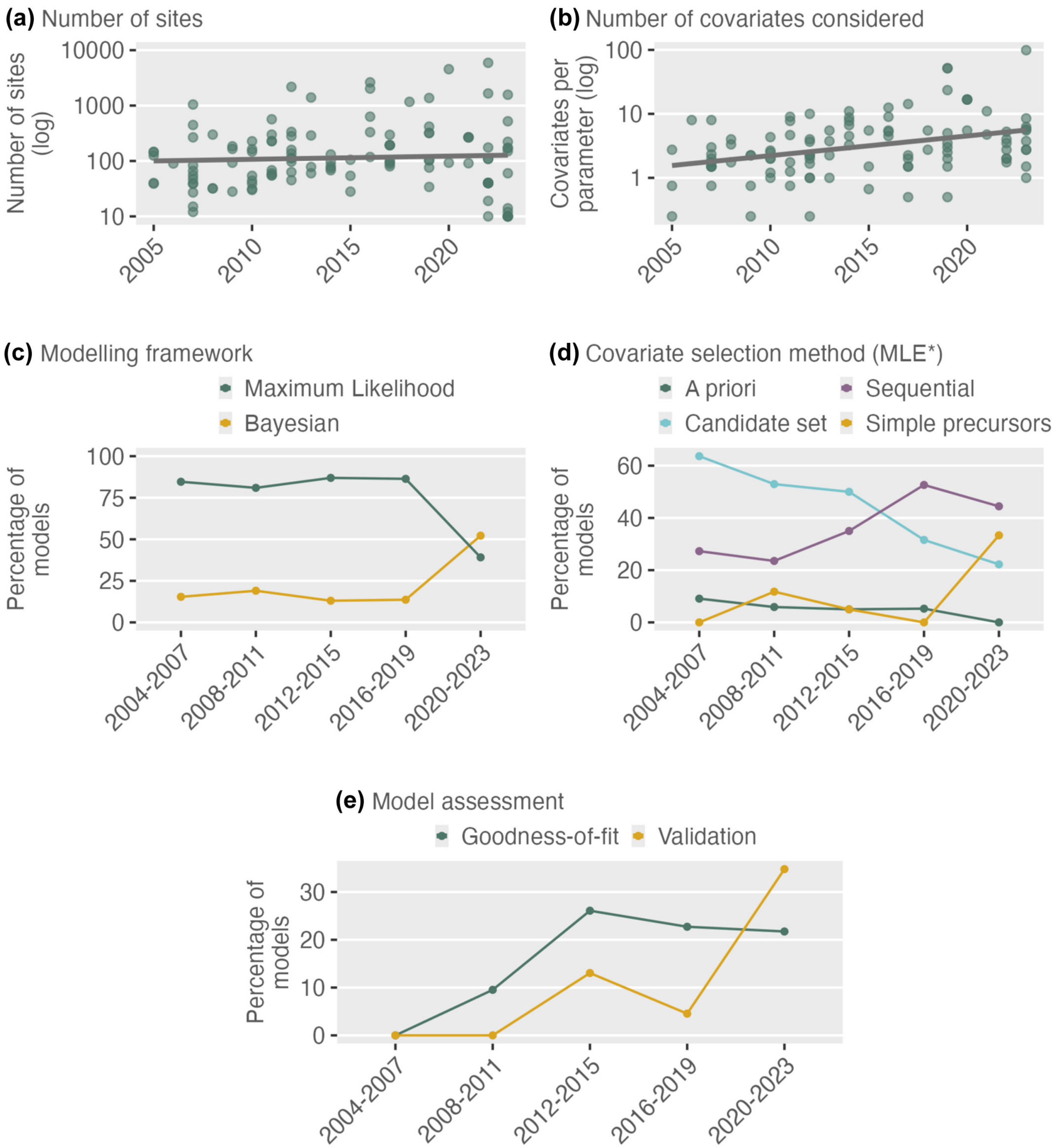

Figure 6. Key trends in applications of dynamic occupancy models over the study period. (a) The number of sites modelled in each dataset, presented on the log scale. (b) The number of covariates considered per model parameter in each modelling workflow, presented on the log scale. (c) The percentage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

studies using autonomous detectors like camera traps or acoustic monitors are also likely to require site-use interpretations of occupancy due to small detection ranges (Wood and Peery 2022). These methods also raise interesting questions on how to best delineate primary occasions in continuous data, a topic which has recently been explored in works including Valente et al. (2024)'s comparisons of occupancy estimates at varying time-scales and Erickson-Harris et al.

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Table 2. A summary of recommendations for current users of dynamic occupancy models (DOMs) and priorities for further research.

Topic	Recommendations	Priorities
Defining occupancy and detection	• Explicitly state context-dependent definitions of occupancy and detection probabilities	• Develop guidelines for delineating primary occasions in continuous data
Covariates for model parameters	• Choose relevant covariates for colonization and extinction, aligned with the temporal scale of changes in occupancy • Ensure that key drivers are also considered for initial occupancy, particularly when making spatial predictions • Ensure that environmental aspects of detection are reflected in candidate covariates	• Assess how missing drivers of heterogeneity on one parameter affect estimates of the other parameters and model predictions
Complexity and covariate responses	• Align covariate responses with hypothesised relationships, testing non-linear responses or interactions where appropriate	• Explore the best ways to include greater complexity in covariate responses, such as splines and machine learning based methods • Assess influence of covariate quantity and response complexity on predictive performance and uncertainty
Model selection	• For all objectives, ensure reported methods are comprehensive • When testing hypotheses, include clear rationale for covariate inclusions, such as by creating directed acyclic graphs. Some authors recommend constraining candidate sets or avoiding covariate selection altogether • Consider all models with similar support • 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	• Identify best approaches to model selection for various objectives while limiting computational costs • Compare performance of emerging Bayesian methods for model selection
Model assessment	• Available goodness-of-fit tests should be conducted and reported • 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	• Existing goodness-of-fit tests should be further validated • Additional research on methods for performance evaluation in hierarchical models is necessary

(2025)'s proposed method for testing alternative primary occasion durations. As possible interpretations of occupancy widen, it is increasingly important that authors provide clear, study-dependent definitions for the term to clarify assumptions and support interpretation for readers unfamiliar with the study system.

A clear understanding of how the spatial and temporal scale of sampling relates to the ecology of the species and model components is also important for selecting relevant covariates for detection. For example, where closure is unfeasible or unlikely, studies can better model heterogeneity in detection by including covariates that capture potential variation in the probability that individuals of the target species are within the detection radius during surveys (Mordecai et al. 2011). Likewise, variation in abundance between sites can affect detection (Royle 2006), and covariates that capture these patterns should be considered if variation is likely (Fig. 7a-ii, bi-ii). Significantly, most DOMs included in our review considered few (median = 3) covariates on detection. 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 (McClintock et al. 2010, Lahoz-Monfort et al. 2014).

Similar care should be taken when considering covariates for the components of the occupancy sub-model to ensure that they correspond with the ecological realities that they represent. Notably, our review found that many studies did not consider any covariates for initial occupancy, such that all sites were considered equally likely to be occupied in the first primary occasion. Unless a study is conducted at very small extents or study sites are truly uniform in their initial suitability, one would expect some amount of non-random variation in occupancy probability – and as seen in our review, many DOMs are applied at large spatial scales across significant habitat gradients. While the initial occupancy parameter represents only a snapshot of occupancy in one primary occasion and may not be of interest in and of itself, it does meaningfully contribute to the overall model likelihood (particularly in models with only a few primary occasions). Neglecting to account for heterogeneity in the initial occupancy state may adversely affect predictive performance or estimates of other model parameters; in tests of predictions using DOMs, Briscoe et al. (2021) posit that a constrained covariate pool for parameters including initial occupancy was likely partially responsible for poor spatial predictive performance. Regarding colonisation and extinction, it is interesting to note that over 50% of environmental covariates considered for transition probabilities in our review were static terms like long-term climate averages. While static covariates can provide useful information on habitat suitability that can persistently influence transition probabilities throughout a study period, dynamic covariates that vary across primary occasions are increasingly available and can provide greater nuance on how species respond to fluctuations in environmental conditions.

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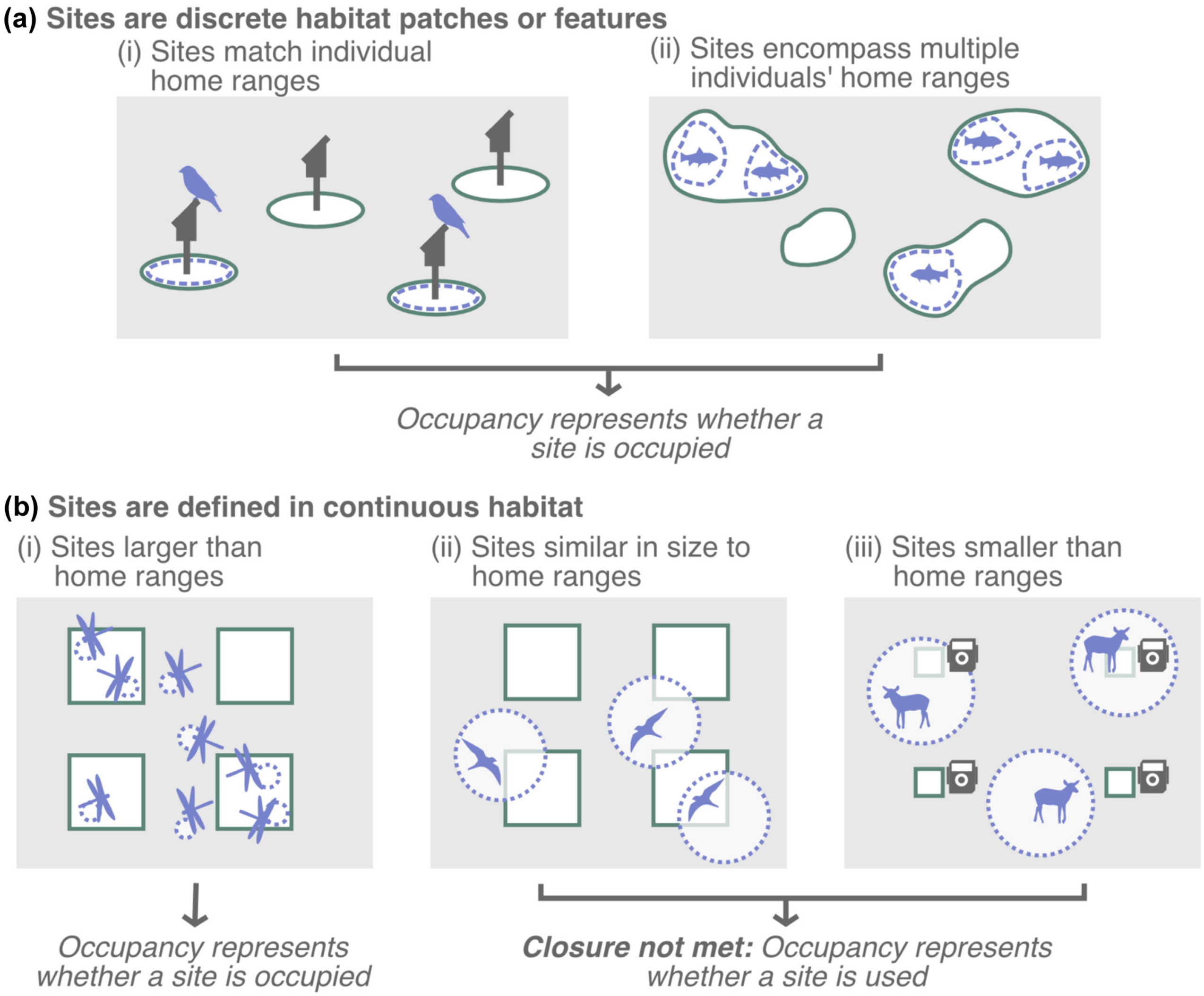

Figure 7. An overview of how the size of a site relative to the focal species' home range during a primary occasion can result in differing definitions of site occupancy. In (a), where a site represents a discrete habitat patch, occupancy typically represents whether a site is occupied during a primary occasion. 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. 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.

For all parameters, the consequences of unmodelled heterogeneity on model outputs remains an understudied aspect of DOMs, despite ongoing acknowledgements that this is an area meriting further research (MacKenzie et al. 2006, 2017). Simulation studies exploring, for example, how missing covariates on detection or initial occupancy may influence estimates of other parameters in DOMs, would help to inform where this may be of concern and guide model-building practices.

Capturing complex ecological relationships

Relationships between environmental factors and species occurrence are often expected to be non-linear or interactive – consider the theoretical relationship of any species to temperature, for example, where optimal suitability will generally fall somewhere between upper and lower critical limits given sufficiently large spatial scales. Despite the presumed frequency of these non-linear and interactive relationships in nature and the ease of implementation in tools for fitting DOMs, our review found that most studies considered only linear relationships between candidate covariates and modelled parameters. The scarcity of these more complex covariate responses stands in contrast with common practice in correlative species distribution models (SDMs), where research has suggested that allowing for non-linear and interactive relationships can yield improved spatial predictions of occupancy (Valavi et al. 2023). While frequency of these response types in SDM may be attributable to their ease of implementation in common tools like MAXENT and BRTs (Elith et al. 2008, Merow et al. 2013), the wider use of more complex responses may also be attributed to SDM's frequent application across relatively large geographic extents which might encompass

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the full species niche, where environmental relationships may be expected to be non-linear. With the use of DOMs at similarly large scales, perhaps these relationships should be considered more often given ecological theory and existing research on SDMs (Guisan et al. 2006, Austin 2007). While overfitting models can be a concern even when using covariate selection methods which penalise excessive complexity, omitting realistic forms also has consequences for model performance – appropriate model evaluation (currently rare; see below) can detect issues around overfitting and support finding a balance between generality and ecological realism.

While current approaches easily accommodate polynomial responses and interactions, ongoing research into other ways to incorporate complex relationships between occupancy and the environment may lead to improvements in spatial predictions (an increasingly popular use-case for DOMs). Machine-learning based approaches such as Joseph (2020)'s novel neural-network DOMs allow for exponentially higher levels of complexity, as do emerging methods marrying hierarchical models and generalised additive models (Pedersen et al. 2019, Rushing et al. 2019). Further expansion of these methods and other possibilities like BRTs (Hutchinson et al. 2011) may provide new options where data are abundant and spatial predictions are a priority, and development of tools to ease their implementation may facilitate their uptake.

Covariate selection

Methods used for covariate selection were particularly varied in reviewed DOMs, with a wide range of approaches used in both MLE and Bayesian frameworks and little consensus on the best techniques. Covariate selection is a particularly challenging task for DOMs relative to other common models for occupancy estimation, as testing alternative covariates across multiple parameters can result in a rapidly expanding pool of candidate models. Consider that while testing all combinations of six covariates for a simple correlative SDM would require fitting just 64 models, possible combinations of six covariates on each of DOMs' four parameters would require 16 million models, making exhaustive comparison computationally unfeasible and necessitating some approach to select covariates by exploring a smaller number of possible models.

The few papers that have addressed covariate selection in occupancy models have largely focused on AIC-based methods, which aim to identify models that are useful for prediction by selecting for fit while penalising complexity (Chakrabarti and Ghosh 2011). In a comparison of static occupancy models fit with three AIC-based approaches using simulated data, Doherty et al. (2012) found that while each method achieved similar predictive performance, estimates of covariate weights varied. They advise model averaging to mitigate this effect, but acknowledge that this effect is likely to be even larger in more complex models such as DOMs. More recent work by Morin et al. (2020) using static and dynamic 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 are themselves caused by multiple 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 (Tredennick et al. 2021, Arif and MacNeil 2022, Bolker 2024, Popovic et al. 2024). 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 and Massey 2023). These firmer views on causal inference are not universal, and authors including Nichols and Cooch (2025) have defended the use of predictive models (including DOMs) coupled with thoughtful and constrained model selection as useful tools for inference, while noting the importance of carefully considering relationships amongst covariates.

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

Studies fitting models within a Bayesian framework were much less likely to employ any form of model selection, perhaps reflecting the fact that Bayesian model selection for DOMs remains somewhat underexplored. In one of the few comparative studies on model selection for Bayesian occupancy models, Stevens and Conway (2019) found that models selected using the logarithmic scoring rule rather than WAIC or DIC produced better performing models for prediction. As the use of Bayesian DOMs increases, promising methods including regularisation priors (Park and Casella 2008), reversible-jump MCMC, and extensions of novel efficient Bayesian variable selection methods (Griffin et al.

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2020) merit future research on their suitability for use with these models. Hooten and Hobbs (2015)'s guide to Bayesian model selection in ecology also remains a valuable general resource for possible methods in this space. Looking beyond ecological research, advances in the broader literature on hidden Markov models may also be transferable to DOMs and support further improvements in building and testing these models.

Model assessment

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 (MacKenzie et al. 2017, Kéry and Royle 2021). Available options include MacKenzie and Bailey (2004)'s approach developed for single-season occupancy models based on parametric bootstrapping, which has been adapted to DOMs and implemented in the 'AICcModAvg' and 'unmarked' R packages (Kellner et al. 2023, Mazerolle 2025). In Bayesian implementations, posterior predictive checks offer means to assess model fit (Gelman 2014). Kéry and Royle (2021) apply ideas from the capture–recapture literature to suggest posterior predictive checks aimed at separately assessing fit in the static and dynamic components of DOMs, comparing between observed and expected detection frequencies per site and season to test the static component and between observed and expected numbers of transitions to test the dynamic component. Broms et al. (2016) discuss approaches to model assessment for Bayesian single-season multi-species occupancy models, with insights that may also be applicable to DOMs. Currently, no goodness-of-fit test enjoys widespread acceptance and existing methods require further empirical testing to determine their sensitivity to departures from model assumptions. Further developments, such as tests that can assess the fit in each of the processes modelled (initial occupancy, extinction, colonization, detection) and tools for graphical model checking (spatially or as a function of covariates; Warton et al. 2017) will be valuable. In the meantime, authors should continue to conduct and report goodness-of-fit tests using existing tools.

Going beyond model fit, studies interested in making spatial or temporal predictions require more substantial forms of model evaluation to quantify predictive performance (Araújo et al. 2005, Guisan and Thuiller 2005). As with other hierarchical models, evaluation for DOMs can be somewhat uncertain compared to settings where perfect detection can be assumed. In DOMs, the primary response variable of interest (species occupancy) is a latent variable where the true state is not perfectly known. Predictive performance evaluation is typically based on observed occupancy data, where a DOM is used to compute the probability of observing the species and this is compared with the field data. As these data confound the occupancy and detection processes, the ability to determine how well the latent process is predicted is somewhat restricted. Nonetheless, in the absence of data that allow independent assessment of the performance of the different parts of the model, evaluation of the ability to predict the observed state is preferrable to no evaluation at all. Where sufficient data exist, users should set aside a portion of data for testing model performance (Briscoe et al. 2021), and where this is not possible should consider cross-validation methods (available in the 'unmarked' and 'ubms' packages; Kellner et al. 2022, 2023).

Conclusions

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

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Author contributions

Saoirse Kelleher: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original

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draft (lead); Writing – review and editing (equal). **Gurutzeta Guillera-Arroita**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Jane Elith**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Natalie J. Briscoe**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal).

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Data availability statement

All data and analysis code are available in the Supporting information.

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Supporting information

The Supporting information associated with this article is available with the online version.

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