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

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Abstract

Occupancy models.

# Introduction

Ecologists are often asked to describe, explain, and predict where and when species occur on the landscape. Research on patterns of species occupancy dates back to the origins of the field, and continues to a priority in quantitative ecological research (Humboldt, 1849). Estimates of how widespread a species is and where it occurs are the foundation of monitoring programs and important for assessing conservation status, while identifying potential drivers of occurrence can help inform potential management actions (MacKenzie & 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).

While occupancy is a useful concept, it is also a challenging quantity to describe, measure, and estimate. The need to understand and quantitatively describe species occupancy has led to the development of several popular modelling approaches, including stochastic patch occupancy models commonly applied to study meta-population dynamics (Gutiérrez-Arellano et al., 2024), and species distribution models (SDMs) widely used to explore species occurrence at larger scales (Franklin, 2010). However, several factors can make occupancy difficult to estimate. For instance, simple presence/absence observations can be biased when species are detected imperfectly – this is often the case in wildlife field data, where it can be impossible to determine from a single observation whether a location is truly occupied or whether the species occurs but was not detected (Gu & Swihart, 2004; Lahoz-Monfort et al., 2014). Despite the ubiquity of imperfect detection in data collection, many models fit to presence/absence data make no adjustment for this source of bias (Kellner & Swihart, 2014). Another challenge for modelling occupancy is the difficulty in describing populations under non-equilibrium conditions, where a species’ occurrence pattern and relationship to its environment is in flux (Dormann, 2007; Elith et al., 2010). These conditions often occur during biological invasions and climate change driven range shifts, each of which are conservation priorities and increasingly common scenarios in the Anthropocene (Bertelsmeier et al., 2013; Lenoir & Svenning, 2015).

The site occupancy models first introduced by MacKenzie et al. (2002) set the foundation for a powerful framework for modelling presence/absence data while accounting for each of these challenges (Guillera-Arroita, 2017) . Drawing on principles from the mark-recapture literature, occupancy models use multiple resurveys of sites to estimate detection probabilities and correct for bias in estimates of site occupancy. Originally a static model, MacKenzie et al. (2003) extended this model for use in multiple time-steps by explicitly describing the process of changing occupancy via colonisation and extinction, relaxing assumptions of equilibrium and allowing description of patterns of site occupancy through time. For newcomers to DOMs, in [Box 1](#nte-Primer) we present a simple introduction to the basic model form as described in MacKenzie et al. (2003).

This dynamic occupancy model (DOM) balances complexity and feasibility, explicitly describing the key processes driving occupancy dynamics while requiring reasonably simple-to-collect presence absence/data instead of the detailed demographic or abundance data required by more process-explicit models (Briscoe et al., 2019). These features make the DOM an important tool, with uses including hypothesis testing of relationships between occupancy and the environment, explorations of the key drivers of occupancy, and even prediction of occupancy under future conditions (Briscoe et al., 2021; Kéry et al., 2013).

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| Note 1: An introduction to dynamic occupancy models |
| We give a minimal introduction to the canonical dynamic occupancy model as defined in MacKenzie et al. (2003). DOMs allow estimation of changes in site occupancy over time while accounting for imperfect detection. Data collection DOMs require hierarchical data to separate the occupancy and detection processes. Occupancy is measured in discrete, time-bound intervals termed *primary occasions*. Within each primary occasion *t*, multiple observations are recorded at the same sites. Importantly, all sites or primary occasions do not require the same number of observations and some number of missing observations are permissible.   Site occupancy sub-model Occupancy is described during discrete, time-bound intervals termed *primary occasions.* In each primary occasion *t,* each site *i* may exist in either an occupied (zi,t = 1) or unoccupied state (zi,t = 0). In the first primary occasion, occupancy is determined as a Bernoulli trial with initial occupancy probability 𝛙1, such that . In subsequent primary occasions, site occupancy is determined by the site’s state in the previous primary occasion and probability of colonisation 𝛄 and extinction 𝛆, such that . While we present each of 𝛙1, 𝛄, and 𝛆 as constants for simplicity, they may be estimated with respect to covariates which are typically included via a logit link.   Detection sub-model During any given survey *j,* observers will either observe (yi,t,j = 1) or not observe (yi,t,j = 0) the target species. In each survey, the probability of observing the target species at a site is given as a Bernoulli trial with detection probability *p,* conditional on the site being occupied, such that . This formulation assumes that no false positive detections exist; that is, observations are never recorded at truly unoccupied sites. As with the occupancy probabilities, *p* may also be estimated using covariates via a logit link.   Fitting DOMs DOMs are most often fit with maximum likelihood estimation, which identifies the values of 𝛙1, 𝛄, 𝛆, and *p* under which the observed data **y** are most probable. Common tools for fitting DOMs include PRESENCE, MARK, and the r package unmarked. DOMs may also be fit in a Bayesian framework, with available packages including ubms. |

DOMs make several key assumptions requiring careful consideration by model users, which we outline here as our reviews related aspects of model building.

1. **False positive detections do not occur**. While this assumption can be safely met in many studies, it is not necessarily guaranteed when working with more cryptic species or less reliable survey methods. McClintock et al. (2010) and Miller et al. (2015) comment on the bias induced when false positives occur and are not accounted for, highlighting the need to consider how certain detections truly are for any given study system. Significantly, even genuine detections of a species can be considered ‘false positives’ when they do not represent the intended definition of occupancy, such as detections of transient individuals when the intent is to estimate breeding occupancy (Berigan et al., 2019). Where this assumption can not reasonably be met, model extensions designed to account for false positive error should be considered (Miller et al., 2011; Miller et al., 2015; Royle & Link, 2006).
2. **Sites are closed to occupancy between seasons.** This requirement, best known as the ‘closure assumption,’ has also been subject to considerable discussion in terms of the bias introduced when it is violated (Otto et al., 2013; Rota et al., 2009). Closure is dependent not only on the life history of the species, but also on the definition of occupancy used by researchers — short seasons may represent dynamics more representative of species ‘use,’ and it can be difficult to distinguish local extinction from temporary emigration (Valente et al., 2017). Model extensions to relax the closure assumption have been developed, including approaches using staggered arrival and departure periods between sites (Kendall et al., 2013). A more pertinent approach for most studies, however, is careful consideration of the appropriate definition of occupancy under the survey design used (Steenweg et al., 2018).
3. **Heterogeneity in occupancy and detection is accounted for.** As with any approach for modelling species occurrence, it is assumed that DOMs appropriately capture variation in occupancy patterns and species detectability across the study system. Generally, this is achieved by allowing model parameters (ψ1, γ, ε, and ρ) to vary with respect to covariates representing the environmental factors which may be expected to influence these parameters. An important element of this assumption is that the likelihood of detection of a species can depend not only on the observability of the species, but also on factors like habitat suitability which influence species abundance and activity (Guillera-Arroita, 2017). While no model will fully account for the complexity inherent in patterns of species occupancy and detection, failure to capture key drivers is likely to introduce bias and confound inference made from model estimates (Barry & Elith, 2006). Compared to the first two assumptions mentioned, this aspect of DOMs has been less thoroughly discussed and comparatively little is known about how this latent heterogeneity can influence model performance.

Since its original description in MacKenzie et al. (2003), the DOM has been further developed with numerous model extensions and alternative formulations including aforementioned implementations accounting for false positives (Miller et al., 2011; Miller et al., 2015; Royle & Link, 2006), multiple states beyond occupied and unoccupied (Nichols et al., 2007), and jointly estimated multi-species models (Dorazio et al., 2010). For a comprehensive discussion of common extensions and their applications see Bailey et al. (2014) and Guillera-Arroita (2017), as well as Devarajan et al. (2020) for a more detailed review of multi-species occupancy models.

# Review methods

Methods.

# Results

Coverage.

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| Figure 1: Bars indicate the 92 articles included in our review as a proportion of the estimated number of published articles fitting DOMs, based on the qualification rate for articles in each strata. The proportion of articles included from each strata were as follows: 12% from 2005-2008; 24% from 2008-2011; 42% from 2012-2015; 35% from 2016-2019; and 57% from 2020-2023. |

Stamp collection.

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| Figure 2: A) Locations of study areas where data was collected for reviewed DOMs. B) Spatial extent of study areas, defined as the area of inference, within which all surveyed points were contained. C) Number of articles which fit models to each category of taxa. Taxa were considered ‘threatened’ if they are listed on the IUCN Red List, or if authors indicate that they are otherwise threatened. D) Explicitly multi-species models include both hierarchical, jointly estimated models as well as more interactive models. Some studies fit both independent and multi-species models, such that these values do not sum to our sample size. E) Survey methods used to collected presence/absence data. Note that some articles employed multiple detection methods, and that some methods (e.g., citizen bird counts) may fall into multiple categories. F) Quantity of sites where surveys were conducted and duration of studies. Yellow bars indicate median values for site quantity (100) and study duration (8.2 years). Study duration is defined as the time elapsed between the first and last survey. |

Covariates.

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| Table 1: All covariates considered for inclusion in a study were classified into mutually exclusive categories. We calculate the percentage of studies which include at least one covariate of a given category on any parameter, Initial Occupancy (ψ1), Occupancy (ψ), Colonisation (γ), Extinction(ε), and Detection (ρ). We also present the average percentage of covariates in a category which are dynamic (varying through seasons) and directly observed, as well as the percentage of articles which model each category of covariate with a non-linear relationship or as part of an interaction with another covariate.   |  | | Percentage of articles with covariate on parameters: | | | | | | Percentage which are: | | Articles representing this covariate with: | | | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | | Any | ψ1 | ψ | γ | ε | ρ | Dynamic | Directly observed | Non-linear relationships | Interactions between covariates | | Environmental covariates | **Habitat** *Aspects of habitat and land cover* | 55% | 41% | 25% | 43% | 46% | 28% | 24% | 33% | 12% | 25% | | **Spatial** *Site geometry, connectivity, or other spatial elements* | 35% | 22% | 31% | 33% | 30% | 11% | 30% | 39% | 22% | 25% | | **Phenology** *Time-varying elements distinct from sampling occasions* | 33% | 1% | 0% | 5% | 4% | 33% | 100% | 0% | 41% | 9% | | **Climate/Weather** *Climate, weather, and natural disasters* | 33% | 13% | 12% | 18% | 18% | 24% | 77% | 35% | 32% | 26% | | **Anthropogenic** *Relations to human activity* | 25% | 20% | 6% | 23% | 21% | 6% | 11% | 8% | 12% | 20% | | **Other environmental** *Other environmental covariate not otherwise listed* | 21% | 5% | 19% | 4% | 10% | 13% | 71% | 78% | 0% | 0% | | **Topography** *Elements of landscape topography* | 21% | 18% | 25% | 13% | 14% | 6% | 0% | 7% | 29% | 10% | | **Biotic interaction** *Interactions with other (non-plant) species* | 15% | 7% | 0% | 14% | 14% | 5% | 59% | 64% | 7% | 20% | | **Hydrology** *Aspects of hydrology, such as distance to water* | 14% | 8% | 25% | 14% | 11% | 4% | 37% | 33% | 29% | 21% | | **Any Environmental** | 91% | 62% | 94% | 74% | 73% | 70% | 43% | 30% | 33% | 26% | | Structural covariates | **Primary occasion** *Effect of the primary occasion* | 65% | 1% | 44% | 39% | 38% | 61% | 99% | 0% | 15% | 8% | | **Observation** *Details on the observation process* | 24% | 0% | 0% | 0% | 0% | 24% | 93% | 7% | 8% | 4% | | **Secondary occasion** *Effect of the secondary occasion* | 15% | 0% | 0% | 0% | 0% | 15% | 100% | 10% | 13% | 0% | | **Site effect** *Site-level effects* | 3% | 0% | 0% | 2% | 2% | 2% | 0% | 0% | 0% | 0% | | **Other structural** *Other structural covariate not otherwise listed* | 3% | 1% | 0% | 0% | 0% | 2% | 33% | 33% | 0% | 33% | | **Species effect** *Species-level effects* | 2% | 2% | 0% | 2% | 2% | 1% | 0% | 0% | 0% | 50% | | **Any Structural** | 81% | 3% | 44% | 41% | 40% | 80% | 94% | 4% | 16% | 8% | | All covariates | **All covariates** | 99% | 63% | 100% | 85% | 85% | 97% | 54% | 20% | 35% | 24% | |

More covariates.

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| Figure 3: The number of covariates considered for each parameter across all studies in our sample. ‘Occupancy’ given here represents the alternative parameterisation of the DOM which jointly estimates Occupancy for every season, Colonisation, and Detection, where Extinction is a derived parameter; this differs from the more popular Initial occupancy/Colonisation/Extinction/Detection parameterisation. Here, a ‘covariate’ is defined as each distinct covariate considered for inclusion. Linear and quadratic representations of the same covariate are counted as one covariate. |

Modelling summary.

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| Table 2: Modelling practices in dynamic occupancy models, subset by frequentist or bayesian implementations. The median covariate count presented here represents the median quantity of covariates considered for each model parameter across the studies in our review. The model selection methods represented in this table are non-exclusive and some articles employ multiple approaches. 2 models included in the ‘Overall’ column are neural network based and fall into neither the Frequentist or Bayesian categories.   |  | Frequentist | Bayesian | All models | | --- | --- | --- | --- | |  | | | | | Number of studies | 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 procedural 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% | |

Objectives.

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| Figure 4: A) Proportion of articles in each year-strata and across all years which match each of six non-exclusive objective categories. B) Quantity of covariates considered per parameter for models which pursued each objectives. |

More objectives.

# Discussion

Discussion.

# Conclusions

Conclusions.

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