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A dynamic and hierarchical spatial occupancy model for interacting species

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Running headline: A dynamic and hierarchical spatial occupancy model for interacting species

1 Abstract

Occupancy models are currently being developed in two major directions: to account for spatial structure and species interactions. As interacting species (e.g., predators and prey) often operate at different spatial scales, including nested spatial structure might be especially relevant in models for interacting species. Here we bridge these two model frameworks by developing a spatially hierarchical two-species occupancy model. The model is dynamic, i.e. it estimates initial occupancy, colonization and extinction probabilities - including probabilities conditional to the other species' presence. With a simulation study, we demonstrate that the model is able to estimate parameters without bias under low, medium and high average occupancy probabilities, as well as low, medium and high detection probabilities. We further show the model's ability to deal with sparse field data by applying it to a spatially hierarchical camera trapping dataset on a mustelid-rodent predator-prey system. The field study illustrates that the model allows estimation of species interaction effects on colonization and extinction probabilities at two spatial scales. This creates opportunities to explicitly account for the spatial structure found in many spatially nested study designs, and to study interacting species that have contrasted movement ranges with camera traps.

Keywords: co-occurrence, multi-scale, occupancy, predator-prey, spatial, species interactions

2 Introduction

Occupancy models have become increasingly popular among ecologists (Bailey *et al.*, 2014; Guillera-Arroita, 2017) since being introduced to the ecological community by MacKenzie *et al.* (2002). In the seminal work by MacKenzie *et al.* (2002), the model estimated occupancy probability over multiple sites was assumed to be spatially independent (MacKenzie *et al.*, 2002). However,

this assumption is rarely met in the field (Johnson *et al.*, 2013), and failing to account for spatial structure will lead to overconfidence in estimated uncertainties and might even reverse the sign of the estimated slope of relationships (Guélat & Kéry, 2018). Alternative ways to account for spatial structure in occupancy models include adding a spatial covariate for the parameter of interest (occupancy, colonization or extinction) (Bled *et al.*, 2011; Eaton *et al.*, 2014; Yackulic *et al.*, 2014), or incorporating the spatial component in the dynamical part of dynamic occupancy models (i.e., models that explicitly estimate change over time). The latter can be done by including both short distance and long distance dispersal in the colonization and extinction functions (Sutherland *et al.*, 2014; Broms *et al.*, 2016).

However, many ecological data sampling designs exhibit a hierarchical spatial structure to highlight that processes may be multi-scaled or are advantageous due to logistics or necessary for ecological reasons (e.g., simultaneously monitoring of multiple species that function at different spatial scales) (Baumgardt *et al.*, 2019). A nested spatial structure is often also found in meta-analysis (Rich *et al.*, 2017; Davis *et al.*, 2018). Multi-scale occupancy models that have been recently developed enable analyses of data from designs with a hierarchy of spatial scales (Nichols *et al.*, 2008; Aing *et al.*, 2011; Mordecai *et al.*, 2011; Kéry & Royle, 2015; Smith & Goldberg, 2020), and these can be extended to dynamic versions to estimate colonization and extinction probabilities (Tingley *et al.*, 2018).

A parallel development of occupancy models -dynamic multi-species models- addresses how interacting species influence each others occupancy patterns over time (Rota *et al.*, 2016; MacKenzie *et al.*, 2017; Fidino *et al.*, 2019; Marescot *et al.*, 2020). These models have great potential to increase our knowledge of species interactions. However, interacting species in general, and predators and prey in particular, often move at different spatial scales (de Roos *et al.*, 1998; Fauchald *et al.*, 2000). It would therefore be useful to incorporate the multiple spatial scales of the interacting species to these models, but we are not aware that such dynamic occupancy model exists to date.

Here we build on dynamic multi-species models by MacKenzie *et al.* (2017) and Fidino *et al.*

(2019), as well as a dynamic and spatially hierarchical occupancy model by Tingley *et al.* (2018) to develop a spatially hierarchical dynamic two-species occupancy model. In this model, initial season occupancy, colonization and extinction probabilities are estimated at two spatial scales, i.e. both at site level and at a regional level, spanning a cluster of sites. After describing the model, we perform a simulation study to investigate potential bias and precision under different scenarios. Finally, we exemplify the usefulness of this approach for real data, by applying the model to a spatially hierarchical camera trapping dataset of a mammalian predator-prey system.

3 Methods

3.1 Data structure and latent ecological states

The spatial setup and model structure for this spatially hierarchical occupancy model is illustrated in Figure 1. Compared to the classical occupancy model, we have added an additional spatial level so that we have $b \in \{1,...,B\}$ blocks, each of which contains $k \in \{1,...,K\}$ sampling sites. Each sampling site is surveyed over $t \in \{1,...,T\}$ sampling occasions (hereafter primary occasions). Each primary occasion is sampled J times, $j \in \{1,...,J\}$ being the index of the survey (hereafter secondary occasion). For each secondary occasion, a species is either recorded as observed or unobserved.

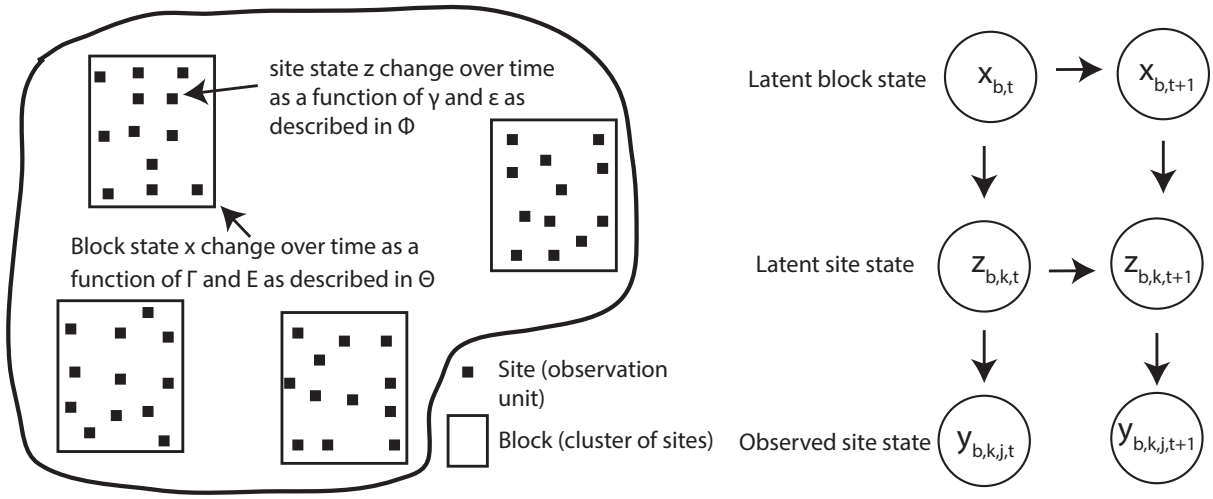

Figure 1: Conceptual diagram of the data and model structure. The panel on the left describes the two-level spatially hierarchical structure, the data sampling and state variables (probabilities) with clusters of sites nested in 4 blocks. γ and ε is site level colonization and extinction probabilities respectively with Φ being the site transition probability matrix. Γ and E are the block level colonization and extinction probabilities respectively with Θ being the block level transition probability matrix. The diagram on the right shows conditional dependencies between the state variables in the model. The index b indicates a given block, k a given site, t a given primary occasion and j a given secondary occasion.

Following MacKenzie *et al.* (2017) we describe the state of each site during each primary occasion with a latent variable z. Considering a two species model, any given site can then either be unoccupied (U), occupied by species A only (A), occupied by species B only (B) or occupied by both species A and B (AB). However, in this model we also consider an ecological process on the block level by describing a latent block state, x, that can take on any of the same four states as the latent site level state (U, A, B, or AB).

3.2 Transition model

After initial states have been modelled as a random categorical variable (see Appendix S1 for details), transitions between states are modelled with the transition probability matrices Θ for the

block level and Φ for the site level, with the latter depending on the block state. For simplicity it is assumed that the transition parameters (colonization and extinction) are equal for all sites, blocks and time steps. It is assumed that the site colonization (γ) and extinction (ε) is dependent on the site state in the previous time step (z_{t-1}) and the block state in the same time step ($x_{b,t}$). The latter is assumed because site-level colonization is only possible whenever the given species is already present in the block. Because site transition probabilities are dependent on the block state in the same time step, it is possible that both a block and sites within that block are colonized in the same time step. However, because it is assumed that the sites do not sample all available habitat within the block, block extinction is assumed to be independent of site extinction. Hence the model allow blocks to remain occupied even when all sites within that block go extinct. We note that feedback from site to block level could easily be added by making the block-level extinction parameters dependent on the site-level, i.e., the block goes extinct for species A when all sites within that block have gone extinct, even though it is not included here.

The transition probability matrix (Θ) for blocks (b) can be written as

$$\Theta = \begin{array}{cc} & \text{To state} \\ & \begin{array}{cccc} U & A & B & AB \end{array} \\ \text{From state} \begin{array}{c} \text{U} \\ \text{A} \\ \text{B} \\ \text{AB} \end{array} & \begin{pmatrix} (1-\Gamma_A)(1-\Gamma_B) & \Gamma_A(1-\Gamma_B) & (1-\Gamma_A)\Gamma_B & \Gamma_A\Gamma_B \\ E_N(1-\Gamma_{B|A}) & (1-E_A)(1-\Gamma_{B|A}) & E_A\Gamma_{B|A} & (1-E_A)\Gamma_{B|A} \\ (1-\Gamma_{A|B})E_B & \Gamma_{A|B}E_B & (1-\Gamma_{A|B})(1-E_B) & \Gamma_{A|B}(1-E_B) \\ E_{A|B}E_{B|A} & (1-E_{A|B})E_{B|A} & E_{A|B}(1-E_{P|N}) & (1-E_{A|B})(1-E_{B|A}) \end{pmatrix} \end{array} \tag{1}$$

The full model for both block- and site-level states can then be written as

$$\begin{aligned} x_{b,t}|(x_{b,t-1},\Gamma,E) &\sim \text{Categorical}(\Theta_{x_{b,t-1},\bullet}) \text{ for } t=2,....,T \\ z_{k,b,t}|(x_{b,t},z_{k,b,t-1},\gamma,\varepsilon) &\sim \text{Categorical}(\Phi(x_{b,t})_{z_{k,b,t-1},\bullet}) \text{ for } t=2,....,T. \end{aligned} \tag{2}$$

The indices $x_{b,t-1}$ describe a specific row in Θ and $z_{k,b,t-1}$ a specific row in Φ. The site-level transition matrix $\Phi(x_{b,t})$ matrix has a similar structure to Θ but has a dependency on the block-level state (Fig. 1); it is described in full in Appendix S1.

3.3 Detection model

It is assumed that detection of each species is independent of detection of the other species. For simplicity, it is also assumed in the simulation study that the detection probability is constant over sites, blocks and temporal occasions. However, note that a temporal covariate is added to the detection model in the empirical case study (see related section below). Let p_A and p_B be the detection probabilities of species A and B at a given site, the detection probability matrix (λ) can then be defined as

$$\lambda = \begin{array}{cc} & \text{Observed state} \\ & \begin{array}{cccc} U & A & B & AB \end{array} \\ \text{True state} \begin{array}{c} U \\ A \\ B \\ AB \end{array} & \begin{pmatrix} 1 & 0 & 0 & 0 \\ 1-p_A & p_A & 0 & 0 \\ 1-p_B & 0 & p_B & 0 \\ (1-p_A)(1-p_B) & p_A(1-p_B) & (1-p_A)p_B & p_Ap_B \end{pmatrix} \end{array} \tag{3}$$

where

$$y_{k,b,j,t}|(x_{b,t}, z_{k,b,t}) \sim \text{Categorical}(\lambda_{z_{k,b,t},\bullet}) \tag{4}$$

with $z_{k,b,t}$ being the chosen row of the detection matrix (λ) to draw the observed state.

If the ecological context requires, it is possible to estimate detection probabilities dependent on the detection of other species (Miller *et al.*, 2012; Fidino *et al.*, 2019), or alternatively, for limited data the detection probability matrix could be simplified further by estimating an independent detection probability for each observable category (Marescot *et al.*, 2020).

3.4 Simulation study

We conducted a simulation study to evaluate the performance of our model by examining potential bias and variance of colonization, extinction, and detection parameter estimates. The spatiotemporal structure of the simulated data was largely inspired by our empirical case study (see section below for a more detailed explanation). Hence we simulated data for 4 blocks (clusters of sites) with 12 sites within each block. We chose weeks as primary occasions and days within each week as secondary occasions. We simulated data for 50 weeks (approximately one year). The chosen parameters values were also inspired by the predator-prey case study (e.g. $E_A < E_B$. See all parameter values in Appendix S1). To investigate how contrasting scenarios affect bias of parameters, we simulated data from 6 different sets of parameter values. We made 3 scenarios with varying detection probability and 3 scenarios with a varying proportion of occupied sites (for details, see Appendix S1). For each scenario, we simulated and analyzed 50 replicate datasets. The models were analyzed in a Bayesian framework using the JAGS software (Plummer, 2003) with the `jagsUI` package (Kellner, 2015) in `R` (R Core Team, 2019). After a 1000 step adaptation phase and a burn-in of 0, the model was run for 5000 iterations with a thinning of 10. Convergence

was assessed by having a $\hat{R}$ <1.1 for all key parameters (Gelman *et al.*, 2013) and from graphical investigation of traceplots for all parameters.

3.5 Empirical case study

To illustrate the real-world applicability of our model, we used a camera trap dataset from the long-term monitoring program COAT (Climate-ecological Observatory of the Arctic Tundra). The camera trapping program targets small rodents and their small mustelid predators, both of which form a functional group. Here we consider that prey (group A) are rodents (grey-sided vole *Myodes rufucanus*, tundra vole *Microtus oeconomus* and Norwegian lemming *Lemmus lemmus*) while predators (group B) are mustelids (stoat *Mustela erminea* and least weasel *Mustela nivalis*). The camera traps, described by Soininen *et al.* (2015), are active year-round in arctic tundra habitats (70°20'N 29°38'E). The sampling design has a spatially hierarchical structure, where sites (camera traps), are spaced >300m apart but clustered in blocks of 11 to 12 cameras covering two different habitats, snowbeds and hummock tundra (see Appendix S1). This corresponds to movement ranges of rodents and mustelids, so that sites represent independent samples of rodent presence, whereas blocks represent independent samples of mustelid presence. Mustelids almost only occurred in the snowbed habitat, hence we chose to focus only on these sites, reducing number of cameras to 5 or 6 per block. The dataset consists of a total of 8 blocks.

All images of the two functional groups (i.e. rodents and mustelids) were identified by means of an algorithm for automatic classification of camera trap images. The MLWIC R-package (Tabak *et al.*, 2019) was used to train the algorithm (see Appendix S1 for more details). The resulting dataset describes, for each primary occasion (day), if each functional group was detected or not. The four states of sites and blocks thus correspond to U = none of the species are observed, A = only rodents observed, B = only mustelids observed, or AB = both rodents and mustelids are observed. To analyze this data, we included all weeks from the monitoring commenced in 2015,

making a total of 203 weeks. This resulted in inclusion of missing data since more then half of the sites were only observed for the last 47 weeks.

When analysing these data, we generally tried to make as little changes as possible to the model used in the simulation study. However, this study system has a strong seasonality that we needed to account for. To do this, we used a binary covariate defining summer as between 1st of July and 1st of November while the remaining months were defined as winter. This variable was then included as a covariate on detection probabilities (p_A and p_B) through a logit-link function. The model was analyzed similarly to the simulation model. However, to reach convergence with the real dataset we needed 20 000 steps of adaptation, a thinning of 20 and to run the model for 250 000 iterations.

4 Results

4.1 Simulation study

All colonisation and extinction probabilities at both spatial scales were estimated without bias (Fig. 2). The block level extinction probabilities (E_A, E_B, E_{AB} and E_{BA}) had more variability between the model runs than other parameters (Fig. 2). Both detection probabilities (p_A and p_B) and initial season occupancy probabilities ($\psi_{t=1}$) were also estimated without any apparent bias, and with low between-model variability for all data scenarios (see Appendix S1).

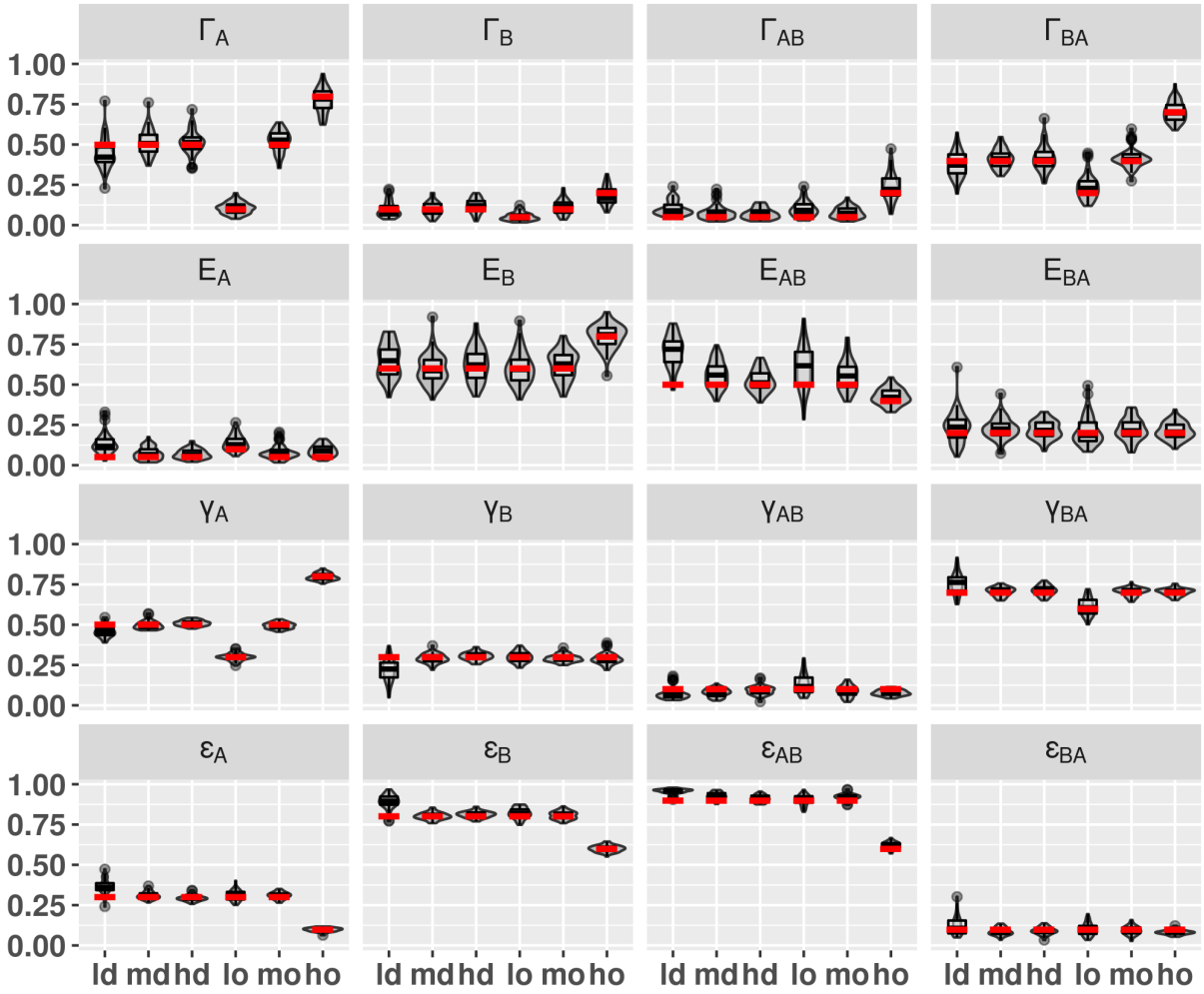

Figure 2: Violin plot and boxplot of the posterior means of site and block colonization (γ and Γ) and extinction probabilities (ε and E), from 50 simulation replicates. The red bar indicates the true parameter values. The x-axis displays the 6 different data scenarios: low, medium and high detection probability (ld,md,hd) and low, medium and high occupancy probability (lo,mo,ho).

4.2 Empirical case study

Rodents generally had a higher detection probability than mustelids (see Appendix S1). Both functional groups (i.e. rodents and mustelids) were less detectable during winter, but the seasonal effect were much stronger for the mustelids with detection probability close to zero during winter. Block

colonization probabilities for both rodents (A) and mustelids (B) were estimated to be close to zero (Fig. 3). For mustelids, the block colonization probability increased when rodents were already present in the block. While block extinction probability of rodents were estimated with low uncertainty, the other block extinction probabilities were estimated with larger uncertainties and might be unidentifiable using this dataset. At the site level, the parameter estimates of colonization probability of both rodents and mustelids indicate, as expected, a strong predator-prey interaction. Colonization probability of rodents became 5 times lower with the presence of mustelids, while the rodent extinction probability became 6 times higher with mustelids present. Colonization probability of mustelids was higher when rodents were present. Mustelids also seem to have a higher extinction probability when small rodents were present compared to when they were absent. The latter is unexpected considering the hypothesized predator-prey interaction. However, notice the large uncertainties (displayed in Fig. 3).

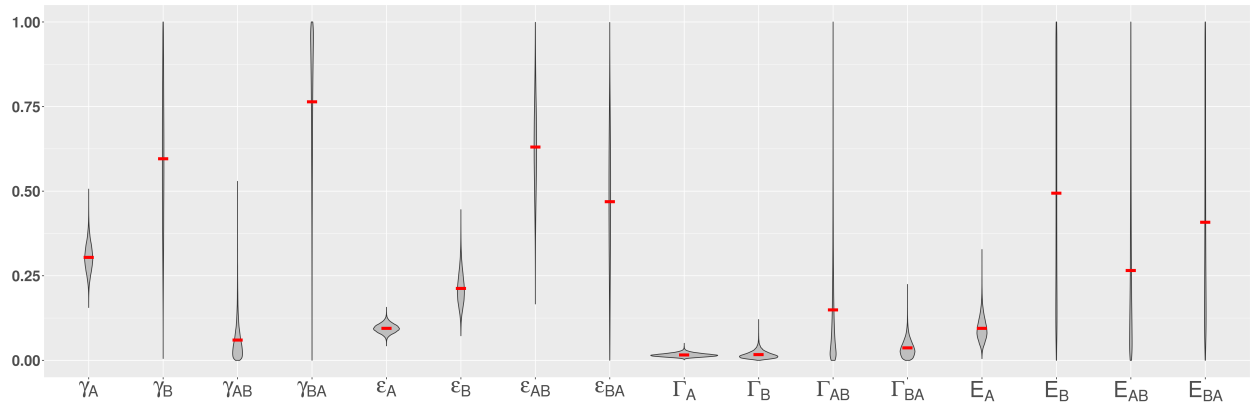

Figure 3: Violin plot of the estimated posterior distribution of site and block colonization (γ and Γ) and extinction probabilities (ε and E) from the case study. A denotes small rodents and B denotes small mustelids. Red bars indicate posterior mean.

5 Discussion

We have constructed a dynamic and spatially hierarchical occupancy model for interacting species. The model estimates initial occupancy, colonization and extinction parameters of interacting species in systems with two spatial levels, i.e., sites and blocks (cluster of sites). The dependency between levels is implemented through a block-state-dependent transition matrix for the site level, i.e., colonization of a site within a block is only possible if the species has previously colonized the block. Through simulations, we have shown that this model is able to produce unbiased estimates of colonization and extinction parameters under different scenarios of average presence and detection. The model was also fitted to an empirical case study with more demanding data, including issues such as missing data and seasonal variability.

We find the current extension of the dynamic multi-species occupancy framework to nested spatial scales useful for two reasons. First, it is possible to explicitly account for spatial structures found in many spatially nested study designs. Second, it makes it possible to investigate the joint colonization and extinction dynamics of species pairs that have contrasting movement ranges, where the daily movement range of one species (e.g., the predator) is equivalent to the dispersal distance for another species (e.g., the prey). Hence, this work helps to bridge the gap between the separate developments of spatial dynamic occupancy models (Tingley *et al.*, 2018) and dynamic multi-species occupancy models (MacKenzie *et al.*, 2017).

While the simulation study shows that all model parameters are generally estimated without bias, some parameters have a relatively large between-simulation variation (Fig. 2). This seems to be most pronounced in the block-level parameters, which might be due to the fact that all observations are done at site level, so that block-level parameters depend on the reconstruction of two latent states. In addition, the simulations also suggest that between-simulation variation is larger in block level extinction parameters (E) than in block level colonization parameters (Γ). This is likely to be because this model only includes a direct feedback between the spatial levels for the

colonization process. While we have done so to provide an ecologically realistic model for the case study (mustelids can be present at the block level yet "extinct" at all sites), one could include more feedback between the block and site level (e.g., block-level extinction probability is set to one when all sites within a block are empty).

Our real world case study incorporates some of the classical empirical challenges that ecologists have to deal with. The dataset has a high proportion of missing data and detection probability differs between the functional groups. In addition, the dataset comes from an ecosystem with both strong seasonality and multi-year cyclicity, which likely affects the detection, colonization and extinction probabilities. Moreover, we use functional groups instead of species, potentially adding noise in the dataset. Also, we treated blocks as if they were identical, which is likely to be an oversimplification. Even without addressing these challenges specifically in the model, with the exception of a seasonal covariate on detection probability, the model seems to be able to identify most parameters. However, it is evident that some parameters are estimated with large uncertainties, to a degree where limited ecological inference can be made (Fig. 3). Our empirical case study appears thus to constitute the minimal data requirements for this model. The block parameters that seem to be unidentifiable in the case study (E_B, E_{AB} and E_{BA}) are the same parameters that also had less precision in the simulation study (see discussion above). It is likely that a longer time series would increase parameter precision (Guillera-Arroita *et al.*, 2014). However, the model gave clear evidence of a strong predator-prey interaction between mustelids and rodents (Hanski *et al.*, 1993; Norrdahl & Korpimäki, 2000). Most of the current observational evidence for this hypothesis comes from indirect observations (snow tracks and winter nests) (Gilg *et al.*, 2003; Korpela *et al.*, 2014), and we provide here evidence from direct observations at commensurate spatial and temporal scales to those of theoretical models. Overall we argue that the model shows great potential to provide new knowledge about ecological interactions on multiple spatial scales, even with challenging ecological data.

To conclude, we developed a dynamic and hierarchical spatial occupancy model for interacting

species, which estimates initial occupancy, colonization and extinction probabilities on two spatial levels as well as detection probabilities without bias. Our model worked well on a challenging real world case study, and helped shed light on a predator-prey interaction between two species moving at two nested spatial scales. Furthermore, the model can easily be extended to include both temporal and spatial (on both spatial levels) covariates on initial occupancy, site colonization and extinction, block colonization and extinction and detection probabilities. The model also has potential to be extended to more species or spatial levels, however this has to be studied in more detail and preferably with additional simulation studies.

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7 Author contributions

Eivind F. Kleiven: Conceptualization (equal); Data curation (supporting); Formal analysis (lead); Investigation (equal); Methodology (equal); Project administration (lead); Software (lead); Validation (equal); Visualization (lead); Writing - original draft (lead): Writing - review & editing (lead). **Frederic Barraquand**: Conceptualization (equal); Formal analysis (supporting); Investigation (equal); Methodology (equal); Project administration (supporting); Software (supporting); Validation (equal); Visualization (supporting); Writing - original draft (supporting); Writing - re-

view & editing (equal). **Olivier Gimenez**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Validation (supporting); Visualization (supporting); Writing - review & editing (equal). **John-André Henden**: Conceptualization (equal), Formal analysis (supporting); Methodology (supporting); Writing - review & editing (equal). **Rolf A. Ims**: Conceptualization (equal), Funding acquisition (lead); Investigation (equal); Writing - review & editing (equal). **Eeva M. Soininen**: Conceptualization (equal); Data Curation (lead); Funding acquisition (lead); Investigation (equal); Project administration (supporting); Visualization (supporting); Writing - original draft (supporting); Writing - review & editing (equal). **Nigel G. Yoccoz**: Conceptualization (equal), Funding acquisition (lead); Formal analysis (supporting); Methodology (supporting); Writing - review & editing (equal).

8 Data Availability

All data and code used in this manuscript are available at UiT Open Research Data (doi.org/10.18710/ZLW59W).

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