Sample size considerations for species co-occurrence models

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Abstract

The multi-species occupancy model of Rota *et al*. (2016) is widely applied for inferences about interactions in the occurrence of different species, but convergence and estimation issues under realistic sample sizes are common. We conducted a simulation study to evaluate the ability to recover co-occurrence estimates using standard and penalised likelihood under varying sample size and interaction scenarios while increasing model complexity in two dimensions: the number of interacting species and the number of covariates. We demonstrate that the ability to quantify interactions in species occupancy using these models is highly sensitive to sample size and interaction strength. Even in the simplest scenario, there is high bias and low coverage in natural parameters (used for inference) for sample sizes below 400 sites. Strong co-occurrence is detected consistently above 400 sites, but weak co-occurrence is never consistently detected even with 3000 sites. We demonstrate that mean predictive ability is less affected by sample size and complexity, with low bias in derived probabilities at 100 sites. We caution the use of these models for inference in small datasets or when co-occurrence is expected to be weak, but show they are suitable to detect strong co-occurrence in larger datasets and generate predictions of site occupancy states.

Keywords: Camera trapping, Multi-species occupancy models, Occupancy modelling, Penalised likelihood, Power analysis, Species co-occurrence, Species interactions

Introduction

Quantifying and predicting species-habitat and species-species associations is fundamental to ecology, where such processes underpin species distributions and biodiversity (Linnell and Strand 2000). When studying factors affecting species distributions, it is common practice to discretize study areas into distinct sites and record whether or not a species is present in each (i.e., site occupancy: MacKenzie et al. 2002; Kéry and Royle 2015). Occupancy models are now routinely used to study spatial distributions, especially in low-density populations (MacKenzie et al. 2002, 2005; Burton et al. 2015). In its simplest form, the classical occupancy model accounts for the imperfect detection of the true occupancy state by combining two distinct probability models: (1) a state model for the underlying ecological variable of interest: occupancy, and (2) an observation model linking imperfect detection data to the latent state (MacKenzie et al. 2002). Although associations with habitat features are fundamental to understanding spatial distributions, accounting for non-independence in the occupancy of two or more species potentially arising from avoidance or attraction of one species towards another is increasingly of interest (Burton et al. 2015; Rota et al. 2016). Quantifying species co-occurrence using occupancy models is challenging, requiring either strong assumptions of interaction direction (Waddle et al. 2010) or prohibitively large data sets (MacKenzie et al. 2004). Recently, however, a multi-species occupancy model for two or more interacting species was proposed (Rota et al. 2016, ‘co-occurrence’ model from here). This framework offers the unique ability to explicitly quantify whether the presence of one species affects the occupancy (or detection) of another, over and above the effect of covariates included in the model (Rota et al. 2016; Kéry and Royle 2020), and perhaps most interestingly, whether these species associations vary over space (Rota et al. 2016; Twining et al. 2022).

The co-occurrence model was developed and motivated using empirical data from 1906 camera trap sites across 42,556 trap days (Rota et al. 2016) - a level of effort that the vast majority of studies applying the model fail to replicate (see Appendix). This is concerning given that even standard single-species occupancy models show significant bias and low precision with small sample sizes (Guillera-Arroita et al. 2010), suggesting extensions that increase model complexity are likely subject to similar sample size-related performance concerns. Moreover, convergence and estimation issues have already been highlighted for the co-occurrence model in smaller data sets (Clipp et al. 2021; Lauret et al. 2023). In these cases, a penalized likelihood approach has been developed (Clipp et al. 2021) which constrains unreasonably large parameter estimates and allows more complex models to be applied to smaller datasets. The trade-off for the variance reduction is, however, estimator bias and unreliable standard errors (Clipp et al. 2021). The effects of sample size and model complexity on model performance in general, and the degree of bias when penalised likelihood is used, has not been investigated in sufficient detail, despite several suggestions that estimation issues can exist (Kéry and Royle 2020). Given the rapid adoption of multispecies co-occurrence models and a corresponding widespread tendency to interpret statistical associations from these models as biological interactions (Blanchet et al. 2020), this is an important and potentially problematic knowledge gap.

Here, using an extensive simulation study, we evaluate co-occurrence model performance by testing the ability to recover known co-occurrence patterns under different sample sizes ($N = 20$ to $N = 3000$ sites) and co-occurrence scenarios (interaction strength and direction). We first test sample size-based performance under the simplest parameterization of the model (i.e., a null model with two interacting species). We then increase model complexity in two dimensions: the number of interacting species and the number of covariates on the species interaction term. For

each scenario, we implement both standard and penalised likelihood approaches to directly compare the inference-prediction trade-off.

Methods

Multi-species occupancy model description

We first provide an overview of the multi-species occupancy model for two or more interacting species (Rota et al. 2016, i.e., the 'co-occurrence' model). In the standard occupancy model, across $j = 1, \ldots, J$ sampling occasions at $i = 1, \ldots, N$ sites, the detection (y_{ij} = 1) or non-detection (y_{ij} = 0) of a species is modelled as a Bernoulli random variable, conditional on the underlying (latent) occupancy state (z_i), where $z_i = 1$ if the species is present and $z_i = 0$ if it is absent (MacKenzie et al. 2002). In the multispecies extension, each site is occupied or unoccupied by each of S species and can therefore take on one of 2^S possible states. The site occupancy state ($\mathbf{z}$) is then a vector of length 2^S describing the true state of a site and is modelled as a multivariate Bernoulli random variable with the expected probability vector $\boldsymbol{\psi}$ (Rota et al. 2016; Kéry and Royle 2020). With two species (A, B), a site has 4 possible states: both are absent [00]; A is present and B is absent [10]; A is absent and B is present [01]; and both are present [11]. The corresponding state vectors are $z_i = \{1,0,0,0\}$, $z_i = \{0,1,0,0\}$, $z_i = \{0,0,1,0\}$, and $z_i = \{0,0,0,1\}$, respectively (Rota et al. 2016). In the 2 species case, the probability mass function of the bivariate Bernoulli distribution can be represented as a set of 3 'natural parameters' which can be modelled as a function of covariates:

$$
\begin{aligned}
f_1 &= log\left(\frac{\psi_{10}}{\psi_{00}}\right) = \boldsymbol{X}'_{\alpha}\boldsymbol{\alpha} \\
f_2 &= log\left(\frac{\psi_{01}}{\psi_{00}}\right) = \boldsymbol{X}'_{\beta}\boldsymbol{\beta} \\
f_{12} &= log\left(\frac{\psi_{11}\psi_{00}}{\psi_{10}\psi_{01}}\right) = \boldsymbol{X}'_{\gamma}\boldsymbol{\gamma}
\end{aligned}
\tag{1}
$$

These natural parameters (f's; Equation 1) have a biological interpretation in terms of the log odds of occupancy: f_1 and f_2 are termed 'first-order' natural parameters and represent the log odds of species occurrence conditional on the absence of all other species included in the model; f_{12} is termed the 'second order' natural parameter and is the change in the log odds of species occurrence when the other interacting species is present, relative to when it is absent (Rota et al. 2016). There is, therefore, total pairwise independence between the occupancy of two species when $f_{12} = 0$, whereas $f_{12} \neq 0$ indicates non-independence in species occurrence above and beyond the effects of covariates included in the (first order) model. In total, models can have up to $2^S - 1$ natural parameters. However, in practice, it is common to only model pairwise interactions and set any natural parameter above second-order to zero (Kéry and Royle 2020). All natural parameters can be modelled as a function of covariates for inference on which features influence species occurrence (f_1, f_2) and co-occurrence (f_{12}). From these natural parameters, the expected state-specific probabilities ψ_{00}, ψ_{10}, ψ_{01}, ψ_{11} can be recovered using the multinomial logit link function (Rota et al. 2016). These probabilities (ψ's) are referred to as the general parameters of the model. Predictions of both the marginal occupancy probabilities (probability of species presence irrespective of occupancy of the others) and conditional occupancy probabilities (probability of species presence conditional on the presence or absence of the others) can be derived from the general parameters using basic probability rules (Rota et al. 2016).

Simulation study

We evaluated the performance of the co-occurrence model by simulating co-occurrence data and fitting the model, considering a total of 13 scenarios of increasing sample size and model complexity. We first explored the sample size effect using the simplest model structure with two interacting species and no covariates (null model), considering all six combinations of interaction strength (strong, moderate, weak) and sign (negative, positive). We then considered a further three scenarios increasing the number of species from $S = 2$ to $S = 3, 4, 5$, assuming constant interactions (network complexity). When adding more species to the network, we limited the maximum order of interactions to two (i.e. pairwise) as is common in the literature (Rota et al. 2016) and varied the pairwise interaction strength to ensure simulated data did not result in observations of all zeros or ones (i.e. complete separation). Finally, we considered four additional scenarios with two interacting species, increasing the number of covariates from 0 to 5 (covariate complexity). All covariates were continuous random variables from a standard normal distribution ($X \sim N(0,1)$).

In Equation 1, we defined a strong interaction as $\gamma_0 = \pm 1$, moderate as $\gamma_0 = \pm 0.6$, and weak as $\gamma_0 = \pm 0.2$. We assumed the same log-odds of single species occupancy within each scenario, where $\alpha_0 = \beta_0 = -0.4$ when the interaction was positive and $\alpha_0 = \beta_0 = 0.1$ when the interaction was negative. This ensured comparable marginal occupancy probabilities ($\psi_1 = \psi_2 \approx 0.5$) between each scenario, avoiding patterns of systematic biases from either too many or few instances of single species occurrence or co-occurrence effecting parameter identifiability.

For each scenario, we simulated and analysed 100 co-occurrence datasets with three $J = 3$ visits and sample size (i.e., number of sites N) increasing from 20 to 2980 ($exp(3) \rightarrow exp(8)$ in increments of $exp(.5)$). The range of N was chosen to reflect the range of sample sizes used when

applying the co-occurrence model, from data scarce ($N = 20$) to data-rich ($N \approx 3000$). We discarded simulated datasets that had no observations for any of the species. We fit the co-occurrence model to simulated data using both log-likelihood (LL) and penalized likelihood (PL) methods in the *unmarked* package (Kellner et al. 2023) using the `occuMulti` and `optimizePenalty` functions for LL and PL, respectively. For PL methods, we estimated the optimal penalty value ($\hat{\lambda}$) using the default settings of the fitting function, except when the standard likelihood approach failed to estimate the Hessian matrix. In these cases, we selected the optimal penalty value using cross-validation over a sensible range of penalty values as per Clipp et al. (2021).

We assessed the co-occurrence model performance based on percent relative bias and the coverage rate of the natural parameters (f's), general parameters (ψ), species-specific marginal probabilities (e.g., ψ_A) and conditional occupancy probabilities (e.g. $Pr(Z_A = 1|Z_B = 1)$). Finally, we calculated the power (i.e. inverse false positive rate) to detect a statistically significant interaction ($f_{12} \neq 0$) under a convention of type-I error rate of $\alpha < 0.05$. We report results using only models that both converged and had identifiable parameter estimates (see Table S3 for a summary of the frequency of convergence issues). All code for simulating data and model fitting is available at `https://osf.io/puvck/?view_only=e31f362d9d2d49c5806ce9b46f6d2034`.

Results

Null model for two species: sample size effects

We encountered no convergence issues in the null model scenarios and, therefore, only report results using the log-likelihood approach, noting results using penalised likelihood were consistent. We observed a clear effect of both sample size and interaction strength, but not interaction direction, on the power to recover the correct interaction coefficient (Figure 1). Under this simplest model parameterisation, the power to estimate the interaction parameter, and hence correctly infer co-occurrence, was unimpressive: power of 95% was only reached at around 400 sites with strong interactions, around 1000 sites with moderate interactions, and was not reached, even with 3000 sites, when interaction strengths are weak (Figure 1).

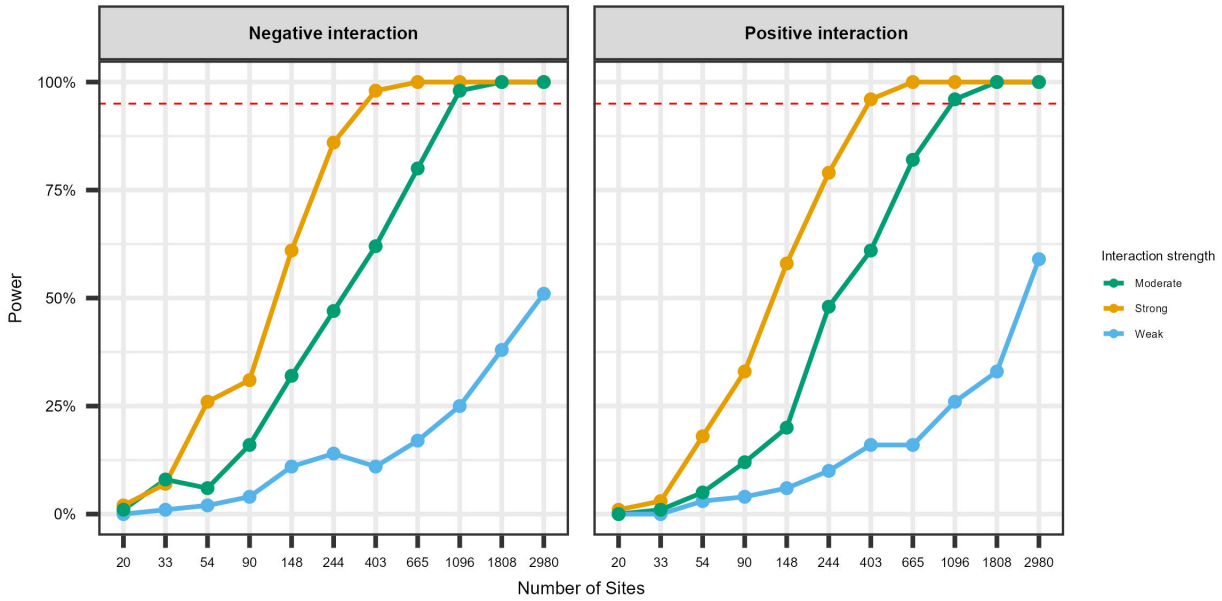

Figure 1: *Power of the co-occurrence model to detect strong, moderate and weak significant interactions under increasing sample size*

Sample size, but not interaction strength or direction, induced parameter bias (Table 1). Using 5% as a nominal threshold for acceptable bias, we observed sample size-related bias in natural parameters (i.e., f_1, f_2, f_{12}) where at least 400 sites were required to reliably estimate natural parameters from the null model. In contrast to the high sample size requirements of the natural parameters, the general parameters (ψ) were estimated without bias at around 100 sites (Table 1). Unbiased estimates of marginal and conditional occupancy probabilities were achieved at 50 sites when interactions were weak and 150 sites when interactions were strong (Table S1).

Table 1: *Mean % relative bias of natural (f_1, f_2 & f_{12}) and general ($\psi_{00}, \psi_{10}, \psi_{01}$ & ψ_{11}) parameters for the two species null model under combinations of sample size and interaction strength scenarios. White indicates mean %RB is equal to or lower than nominal 5% and, to aid visualisation, intensity of the red indicates increasing bias. The sample size required to achieve below 10% bias is larger for natural ($N > 403$) than general ($N > 33$) parameters.Positive and moderate strength scenarios are not shown as they follow similar patterns (see Table S2).*

		Natural			General			
N	Strength	f_1	f_2	f_{12}	ψ_{00}	ψ_{10}	ψ_{01}	ψ_{11}
20	Weak	48.1	217.9	-56.9	-6.4	-11.4	-4.0	23.4
33		242.2	214.5	81.9	-10.8	3.6	0.1	6.7
54		116.8	86.0	58.0	-4.3	2.5	0.8	0.7
90		6.5	24.5	-11.0	-1.1	-1.6	-0.3	3.1
148		37.3	5.2	20.4	-0.4	2.5	-1.1	-1.0
244		30.1	38.5	13.3	-2.4	0.0	0.9	1.4
403		15.4	7.1	-3.5	-1.2	0.2	-0.7	1.7
665		-3.1	5.7	-4.8	-0.4	-0.7	0.1	0.9
1096		6.1	4.7	1.8	-0.4	0.1	0.0	0.3
1808		10.4	3.0	0.5	-0.6	0.4	-0.4	0.6
2980		-3.5	-3.0	-5.1	0.1	-0.3	-0.2	0.5
20	Strong	523.3	545.2	158.3	-12.9	2.0	2.6	17.4
33		411.2	351.6	55.7	-9.9	4.2	1.9	7.2
54		104.7	87.3	15.8	-4.7	2.5	0.4	3.2
90		15.6	1.4	-3.1	0.1	-0.6	-1.8	5.7
148		12.4	25.6	2.1	-1.0	-0.7	0.8	1.9
244		-4.1	-34.5	-2.9	1.4	0.6	-2.4	1.4
403		16.7	39.6	4.2	-1.8	-0.4	1.9	0.4
665		7.5	17.7	1.4	-0.8	-0.2	0.8	0.5
1096		1.3	9.5	1.4	-0.3	-0.2	0.6	-0.2
1808		-5.9	-2.7	-0.6	0.3	-0.3	0.0	0.2
2980		-9.1	-1.6	0.0	0.5	-0.5	0.3	-0.6

Network complexity

The increased network models performed poorly at very low sample sizes and exhibited frequent convergence issues (Table S3), so we present results incorporating more species from > 50 sites. Under standard log-likelihood estimation, the complexity, or size, of the network did not affect the overall power relationship to correctly estimate the interaction strength (Figure 2) or the bias

in natural parameters (Table 2). Rather, consistent with the results from the simpler model (Figure 1), power and bias were related to sample size and interaction strength. The benefits of penalised likelihood to increase the power of detecting species interactions were apparent at low sample sizes (< 200) but their effects diminished with more than 200 sites (Figure 2). Log likelihood estimates eventually converged on minimal relative bias, but penalised likelihood estimates continued to show bias of over ten percent even with 3000+ sites in natural (Table 2). As with the null models for two species, bias in the general parameters and derived occupancy probabilities for all species was low, even where 5 species were included in the network (Figure S1, S2).

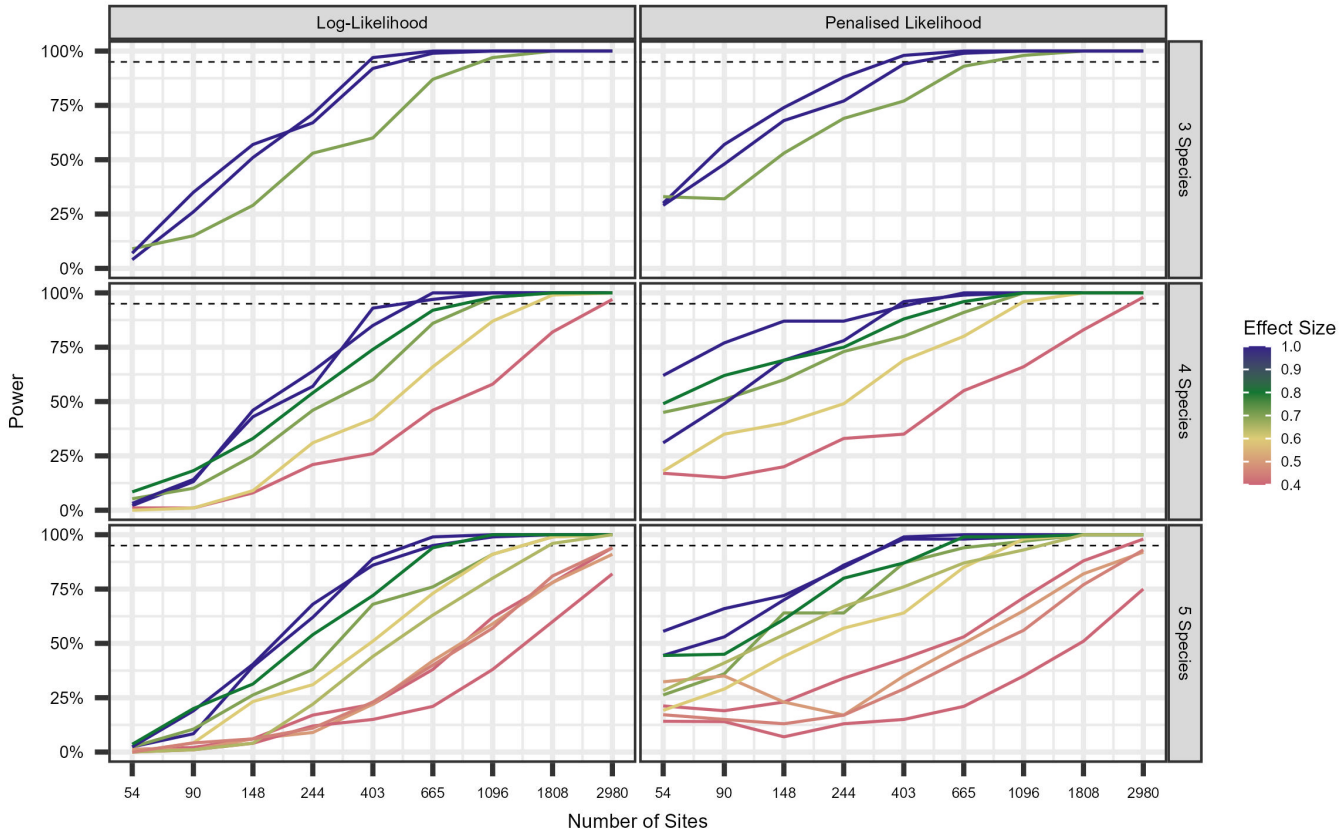

Figure 2: *Power of the co-occurrence model to detect a significant interaction term with increasing network complexity (3-5 species). Each line represents one pairwise interaction term (e.g. with 4 species there are 6 pairwise terms, with 5 species there are 10 pairwise interaction terms) and each term is coloured by the strength.*

Table 2: *Comparison of the relative bias (RB; in %) of natural parameters in the scenario of 4 interacting species under normal (LL) and penalized (PL) likelihood estimation methods. Natural parameter bias results for 3 and 5 species can be visualised in Figure S3.*

		1st Order				2nd Order					
N	Likelihood	f_1	f_2	f_3	f_4	f_{12}	f_{13}	f_{14}	f_{23}	f_{24}	f_{34}
54	LL	272.7	75.4	199.8	169.2	228.0	110.6	143.3	118.6	120.0	39.6
90		4.6	-0.2	89.3	-2.1	65.9	47.7	-97.3	34.6	86.8	55.6
148		64.6	35.1	18.5	1.6	24.6	-4.6	22.9	18.1	2.4	6.7
244		9.7	-3.0	5.0	8.1	5.0	6.7	-0.2	0.0	16.2	2.0
403		8.4	29.4	2.0	8.2	-2.1	-1.3	1.9	5.7	3.6	-4.2
665		5.1	2.6	2.3	7.2	-0.6	-0.6	8.6	2.8	6.6	1.8
1096		-2.8	4.6	2.4	3.3	0.5	2.9	-1.7	0.4	4.7	-0.3
1808		-3.3	5.1	2.3	2.1	-1.1	1.0	-1.8	1.0	4.6	2.4
2980		0.9	-9.8	-2.1	1.8	1.7	0.6	3.1	-3.3	-0.1	-0.7
54	PL	-60.2	29.4	-52.5	-59.4	-39.4	-35.1	-39.2	-41.2	-68.7	-31.1
90		-89.2	-65.6	-38.6	-58.0	-24.4	-2.6	-83.2	-50.8	-11.8	-6.4
148		-21.1	-14.2	-42.1	-27.2	-18.8	-18.0	-15.7	-28.6	-24.7	-19.7
244		-24.0	-19.2	-27.9	-10.6	-15.8	-4.2	-13.1	-23.8	-6.4	-10.4
403		-15.2	6.4	-22.2	-4.9	-14.5	-6.7	-9.9	-14.2	-9.3	-11.3
665		-9.8	-12.8	-13.4	-0.9	-8.4	-3.8	0.9	-10.3	-1.2	-2.7
1096		-13.0	-5.3	-8.6	-2.2	-5.2	0.6	-5.9	-8.6	-1.2	-3.4
1808		-9.9	-2.4	-5.1	-1.2	-4.6	-0.3	-4.6	-5.2	1.1	0.3
2980		-4.0	-13.7	-6.5	-0.3	-0.8	-0.1	1.0	-7.0	-2.1	-1.9

Covariate complexity

Increasing complexity through the addition of more covariates on the interaction effects did not affect the power to correctly estimate interaction strengths, or the bias in natural and general parameter estimates. For a given effect size, the relationship between power and sample size was the same, regardless of the number of covariates (Figure 3). This pattern was true also for bias (Table 3). The benefits of penalised likelihood to increase power and reduced bias were apparent at low sample sizes (< 200) but consistent with the network complexity scenarios, their benefits diminished with more than 200 sites.

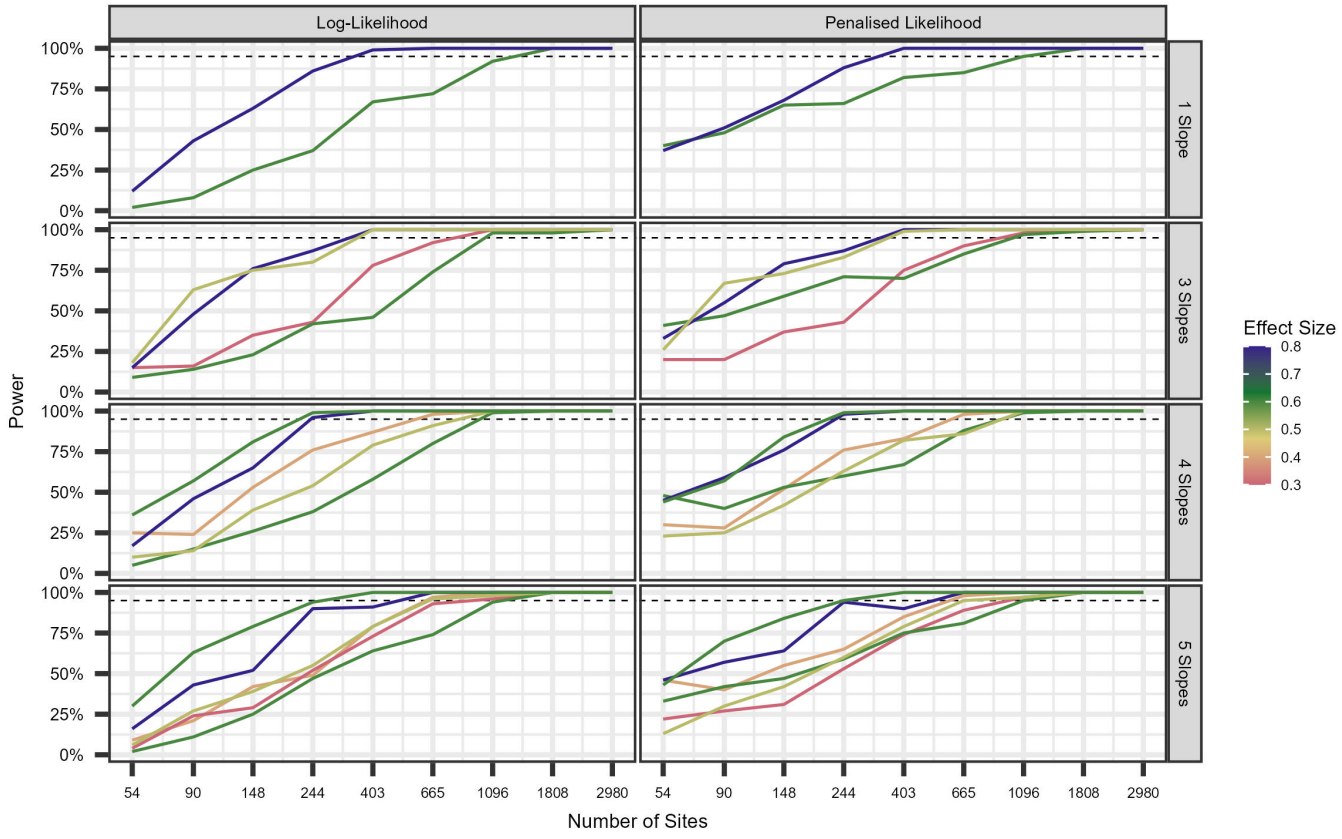

Figure 3: *Relationship between the Power (%) and sample size for the slope regression coefficient and second order natural parameters for scenarios with increasing covariate number.*

Table 3: *Effect of sample size (N) on the relative bias (RB; %) for the regression coefficient estimates (intercepts, e.g.* α_0*, and slopes, e.g.* α_1*) for the 1st (*f_1 *and* f_2*) and 2nd order (*f_{12}*) natural parameters, for the five slope scenario using standard (LL) and penalized (PL) estimation methods. PL estimates show lower RB in the smallest Ns but fail to reach nominal RB* $\leq$ *5% until the highest sample size, especially for 2nd order parameters (*γ*). The standard LL approach reaches nominal RB after N* $\geq$ 665*. The same pattern is observed for the other slope scenarios (Table S4-6). Results for general and dervied parameters are also consistent (Figure S3, S4).*

		1st Order					2nd Order		
N	Likelihood	α_0	α_1	α_2	β_0	β_1	γ_0	γ_1	γ_2
54	LL	1972.0	550.7	23.7	-1.9	25.5	-456.7	-126.0	89.3
90		-2.0	11.7	12.7	-1.7	21.8	45.7	29.7	20.1
148		-5.3	12.2	8.3	-1.4	10.5	17.4	12.7	8.0
244		-12.1	4.4	9.5	-15.0	3.1	20.8	13.7	3.3
403		-4.6	4.0	0.3	-6.4	-3.9	7.2	-0.1	4.6
665		4.2	-0.6	0.3	2.3	0.1	-1.8	2.5	3.3
1096		-4.3	-1.0	0.1	-3.5	0.3	3.5	1.7	-2.8
1808		3.6	2.1	0.5	2.9	1.9	-1.9	0.6	-0.2
2980		0.3	0.1	0.0	-3.3	-2.0	2.6	0.8	1.5
54	PL	-9.3	-6.2	-17.9	-34.2	-38.2	42.6	-17.6	0.9
90		-4.6	-8.8	-25.4	-26.0	-21.2	-43.4	-41.6	-42.1
148		0.3	-1.0	-9.8	-14.7	-15.2	-33.8	-35.5	-31.9
244		-3.3	1.0	-6.4	-19.1	-11.6	-21.3	-21.8	-23.4
403		1.5	1.8	-7.8	-9.3	-12.5	-20.9	-22.2	-15.4
665		6.4	-0.2	-5.0	0.3	-5.4	-20.9	-13.4	-9.3
1096		-0.8	-0.8	-3.0	-3.4	-3.2	-9.3	-7.5	-10.8
1808		6.1	2.3	-1.2	2.9	-0.2	-10.4	-5.5	-5.5
2980		2.2	0.3	-1.2	-3.2	-3.2	-2.8	-2.8	-1.6

Discussion

The development of accessible remote sensing methods such as camera traps and autonomous recording units that simultaneously monitor multiple species has greatly enhanced the feasibility of investigating species co-occurrence and its determinants from observational data at scale (Burton et al. 2015; Kerry et al. 2022). This has resulted in the rapid uptake of co-occurrence models, aiming to detect a non-independence in the occurrence of different species over and beyond additional habitat effects (Kéry and Royle 2020; Devarajan et al. 2020). Although it is widely reported these dependencies are purely statistical associations (Rota et al. 2016; Blanchet et al. 2020), there is still a tendency to interpret statistical associations in occurrence states as reflective of biological interactions (Twining et al. 2022; Parsons et al. 2019), where the link between the two is non trivial (Thurman et al. 2019; Freilich et al. 2018).

By evaluating the performance of the recently developed co-occurrence model under a range of what we consider to be biologically representative scenarios, we identify several important considerations when drawing inferences about ecological processes using this model. Our simulations for two interacting species have predominantly highlighted the high sample size requirements for detecting species co-occurrence, and that model performance is dominated by the strength of the interaction. Regardless of the expected underlying patterns of avoidance or attraction, we therefore demonstrate a key consideration for inferring co-occurrence using such models is first an appreciation of the expected value of statistical interaction in species occurrence states (i.e. f_{12}, Rota et al. (2016)).

Increasing model complexity over and above the sample size and interaction strength effects did not affect inference, i.e., reliable inference is more sensitive to the number of sites and the strength of the interaction of interest than the number of species or covariates considered. We

note that we considered only second-order interactions here, but feel this is appropriate given that this is recommended best practice (Rota et al. 2016; Clipp et al. 2021). This suggests that if sample sizes are sufficient, complex models can be fit to detect strong interactions in occupancy states, but high sample sizes are always needed to detect small associations regardless of model complexity. We further demonstrate that, while the ability to draw inferences about the factors affecting species co-occurrence relationships is compromised by low sample sizes (N < 400 sites), unbiased estimates of marginal and conditional occupancy probability can be achieved using smaller samples (N > 100 sites). This balance between prediction of occupancy probabilities and inference on specific biotic and abiotic effects is key, where an appreciation of the goals of model application is vital. When using these models to predict site occupancy probabilities, penalised likelihood fitting frameworks have already been developed (Clipp et al. 2021) and here we explicitly demonstrate how the trade-off between enhanced prediction with penalised likelihood and increased parameter bias varies across sample sizes, showing strong benefits at N < 400 sites. We note that the model structures tested in this study represent a subset of complexity, where a key benefit of these models in untangling species-species and species-habitat effects is where multiple species and covariate effects can be included in a single framework. In these cases, we expect our general results to hold true, with greater benefits of using a penalised likelihood as more convergence issues arise (Clipp et al. 2021).

Despite wide application across a range of sampling scenarios from e.g. 40 sites (Carricondo-Sanchez et al. 2019) to >2000 (Mandeville et al. 2024), practical guidance on fitting multi-species models, including considerations for model selection and interpretation, are still lacking. We encourage further investigation into methods to improve inference ability in smaller sample size scenarios, including the use of informative priors in a Bayesian framework which can

reduce issues with boundary estimates in similar contexts (Fidino et al. 2019). Limited data from cameras can also be combined with additional data generated for example by point-counts or transects using integrated models (Lauret et al. 2023). Further, while our study assumed a constant sampling effort of J = 3 occasions, it would be of interest to explore if increased sampling occasions reduces sample size requirements (Guillera-Arroita et al. 2010).

In this study, we provide an important first step on the link between observational data and ecological inference on biotic and abiotic determinants of species distributions. When applying these models, it is important to have an idea of the expected statistical interaction strength to be to be confident statistical associations can be recovered. Only then, researchers can consider what these associations may reflect in terms of biological interactions between species, on which an emerging literature exists (Blanchet et al. 2020; Thurman et al. 2019; Freilich et al. 2018). Although the Rota et al. (2016) model is unique in allowing associations to vary as a function of covariates, we note that other co-occurrence models such as the species interaction factor (SIF) model of McKenzie (MacKenzie et al. 2004) have been widely discarded in the multi-species literature due to high sample size requirements (Kerry et al. 2022). Our results suggest that high sample size requirements are features of species co-occurrence models, and we believe it would be interesting to revisit SIFs with the renewed sample sizes considered here in mind.

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Literature Cited

Blanchet, F. G., Cazelles, K., and Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, 23(7):1050–1063.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., and Boutin, S. (2015). Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of applied ecology*, 52(3):675–685.

Carricondo-Sanchez, D., Odden, M., Kulkarni, A., and Vanak, A. T. (2019). Scale-dependent strategies for coexistence of mesocarnivores in human-dominated landscapes. *Biotropica*, 51(5):781–791.

Clipp, H. L., Evans, A. L., Kessinger, B. E., Kellner, K., and Rota, C. T. (2021). A penalized likelihood for multispecies occupancy models improves predictions of species interactions. *Ecology*, 102(12):e03520.

Devarajan, K., Morelli, T. L., and Tenan, S. (2020). Multi-species occupancy models: Review, roadmap, and recommendations. *Ecography*, 43(11):1612–1624.

Fidino, M., Simonis, J. L., and Magle, S. B. (2019). A multistate dynamic occupancy model to estimate local colonization–extinction rates and patterns of co-occurrence between two or more interacting species. *Methods in Ecology and Evolution*, 10(2):233–244.

Freilich, M. A., Wieters, E., Broitman, B. R., Marquet, P. A., and Navarrete, S. A. (2018). Species co-occurrence networks: can they reveal trophic and non-trophic interactions in ecological communities? *Ecology*, 99(3):690–699.

Guillera-Arroita, G., Ridout, M. S., and Morgan, B. J. (2010). Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution*, 1(2):131–139.

Kellner, K. F., Smith, A. D., Royle, J. A., Kery, M., Belant, J. L., and Chandler, R. B. (2023). The

unmarked R package: Twelve years of advances in occurrence and abundance modelling in ecology. *Methods in Ecology and Evolution*, 14(6):1408–1415.

Kerry, R. G., Montalbo, F. J. P., Das, R., Patra, S., Mahapatra, G. P., Maurya, G. K., Nayak, V., Jena, A. B., Ukhurebor, K. E., Jena, R. C., et al. (2022). An overview of remote monitoring methods in biodiversity conservation. *Environmental Science and Pollution Research*, 29(53):80179–80221.

Kéry, M. and Royle, J. A. (2015). *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and Static Models*. Academic Press.

Kéry, M. and Royle, J. A. (2020). *Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 2: Dynamic and advanced models*. Academic Press.

Lauret, V., Labach, H., David, L., Authier, M., and Gimenez, O. (2023). Using integrated multispecies occupancy models to map co-occurrence between bottlenose dolphins and fisheries in the gulf of lion, french mediterranean sea. *Oikos*, 2023(11):e10270.

Linnell, J. D. and Strand, O. (2000). Interference interactions, co-existence and conservation of mammalian carnivores. *Diversity and Distributions*, 6(4):169–176.

MacKenzie, D. I., Bailey, L. L., and Nichols, J. D. (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*, 73(3):546–555.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J., and Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8):2248–2255.

MacKenzie, D. I., Nichols, J. D., Sutton, N., Kawanishi, K., and Bailey, L. L. (2005). Improving inferences in population studies of rare species that are detected imperfectly. *Ecology*,

86(5):1101–1113.

Mandeville, C. P., Finstad, A. G., Kålås, J. A., Stokke, B. G., Øien, I. J., and Nilsen, E. B. (2024). Interspecific competition impacts the occupancy and range limits of two ptarmigan species along the elevation gradient in norway. *Wildlife Biology*, page e01197.

Parsons, A. W., Rota, C. T., Forrester, T., Baker-Whatton, M. C., McShea, W. J., Schuttler, S. G., Millspaugh, J. J., and Kays, R. (2019). Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. *Journal of Applied Ecology*, 56(8):1894–1904.

Rota, C. T., Ferreira, M. A., Kays, R. W., Forrester, T. D., Kalies, E. L., McShea, W. J., Parsons, A. W., and Millspaugh, J. J. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, 7(10):1164–1173.

Thurman, L. L., Barner, A. K., Garcia, T. S., and Chestnut, T. (2019). Testing the link between species interactions and species co-occurrence in a trophic network. *Ecography*, 42(10):1658–1670.

Twining, J. P., Sutherland, C., Reid, N., and Tosh, D. G. (2022). Habitat mediates coevolved but not novel species interactions. *Proceedings of the Royal Society B*, 289(1966):20212338.

Waddle, J. H., Dorazio, R. M., Walls, S. C., Rice, K. G., Beauchamp, J., Schuman, M. J., and Mazzotti, F. J. (2010). A new parameterization for estimating co-occurrence of interacting species. *Ecological Applications*, 20(5):1467–1475.