

1 **Improving inference of metacommunity structure using**  
2 **multi-species occupancy models**

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<sup>7</sup> **Abstract**

<sup>8</sup> Blah blah blah

## 9 Introduction

Broadly speaking, the metacommunity concept seeks to understand how spatial patterns of community composition emerge as a product of both local (e.g. competition) and regional (e.g. dispersal) dynamics (Leibold et al. 2004, Holyoak et al. 2005, Chase 2005). To date, metacommunity research can be separated into two nearly distinct categories: mechanism-based approaches and pattern-based approaches. The mechanism-based approach employs mechanistic modeling or controlled experiments to generate and test hypotheses related to, for example, the coexistence of competitors across local sites (Holyoak et al. 2005, Cottenie 2005, Urban and De Meester 2009, Economo 2011, Logue et al. 2011, Pillai et al. 2011, Carrara et al. 2012). The pattern-based approach uses an inverse process, attempting to relate empirically observed patterns of species occurrences across a landscape to hypothesized biological processes (Leibold and Mikkelsen 2002, Presley and Willig 2010, Presley et al. 2010, López-González et al. 2012, Henriques-Silva et al. 2013, Meynard et al. 2013, Richgels et al. 2013, Erős et al. 2014). While both approaches have advanced understanding of community structure and its underpinnings, methodological improvements could facilitate a synthesis of these often disparate lines of research. Improving metacommunity analytic tools could therefore lead to a more complete understanding of community patterns and structuring mechanisms.

The pattern-based metacommunity approach, often referred to as the ‘elements of metacommunity structure’ (EMS) paradigm, utilizes observed occurrences of species among ‘patches’ of habitat in the metacommunity (e.g. field sampling sites). This data is typically compiled into a species-by-site incidence matrix and statistical analyses determine if the metacommunity exhibits any of twelve unique structures (Leibold and Mikkelsen 2002, Presley et al. 2010). Based on the specific structure observed, inferences are made as to how the metacommunity assembles along dominant environmental axes. However, the efficacy of this pattern-to-process approach depends heavily upon the quality of the observed data (Gotelli and Graves 1996). For instance, problems with species detection could lead to inaccurate incidence matrices and, therefore, inaccurate assessments of metacommunity structure. Fortunately, decades of advancements in occupancy modeling have led to powerful methods to deal with problems such as species detectability. Integrating occupancy modeling with the pattern-based EMS paradigm should improve our ability to assess metacommunity structure and our ability to infer structuring processes.

Occupancy modeling relies on repeated sampling surveys to distinguish between the probability of a species occurring at a site and the probability of a species being detected at a site in which it occurs (MacKenzie et al. 2002). These models also facilitate estimation of covariate effects on detection and occurrence probabilities. Recently, dynamic multi-species occupancy models have been developed for use with longitudinal data sets to better estimate metacommunity composition, such as alpha, beta and gamma diversity metrics, as well as species-, site- and time-specific covariate effects on occurrence probabilities (Dorazio et al. 2010, Burton et al. 2012). Dorazio et al. (2010) specifically identify a closer union of their modeling framework with metacommunity theory as a priority in the field. While the integration of occupancy modeling with metacommunity theory is nascent, there is enormous potential for this to improve the study of metacommunity dynamics.

In this article, we will highlight some of the difficulties with current EMS methods and emphasize how integrating EMS with occupancy modeling will help to resolve or ameliorate these issues. We will also illustrate unique advantages of occupancy modeling that will complement the EMS paradigm. First, we will begin by briefly reviewing the methods involved in the analysis of EMS and the structuring of multi-species occupancy models. Next, we will verbally outline various problems or advantages and couple these explanations with illustrative examples generated with simulated data sets. Our motivation for this article is to highlight the breadth of utilities gained by integrating these two approaches, rather than to explore any specific question or topic in full detail. We have also made our modeling and simulation code publicly available and fully annotated so that these methods can be appropriately and broadly utilized. We believe our approach will facilitate a more complete understanding of metacommunity structure and its underpinning mechanisms.

## Elements of metacommunity structure

The EMS paradigm follows a step-wise procedure to determine which of twelve potential metacommunity structures are exhibited by a data set of species occurrences observed across multiple sites. Although the procedure can determine that no orderly structure exists (i.e. random structure), most metacommunities seem to exhibit detectable structure (Leibold and Mikkelsen 2002). Here we briefly describe these methods, as others have done a more thorough job elsewhere (Leibold and Mikkelsen 2002, Presley et al. 2010).

First, species occurrence data are assembled into a site x species incidence matrix and this matrix is then ordinated, typically using reciprocal averaging. Ordination groups sites with common species assemblages and species with common distributions among sites, theoretically representing how species assemblages are structured along a dominant environmental axis (i.e. gradient). From the ordinated matrix, statistics are then calculated to summarize the three elements of metacommunity structure.

The first metric of metacommunity structure is coherence, which represents whether the majority of species in the metacommunity respond to the same environmental axis of variation as a cohesive unit, the foundation of structure. Coherence is estimated using the number of embedded absences in the ordinated matrix. Embedded absences occur in areas of the matrix where a species is absent in a site in which it would be expected to occur based on the ordination. The observed number of embedded absences are then compared to a null distribution of embedded absences generated from ~1000 simulated matrices (Figure 1).

If a metacommunity exhibits positive coherence, two more metrics are calculated to further describe the metacommunity structure: turnover and boundary clumping. Turnover represents how species composition changes along the theoretical environmental gradient, estimated using the number of species replacements observed in the ordinated matrix. Negative turnover (significantly fewer replacements than the null) is indicative of nested subsets, while positive turnover represents shifting composition along the gradient. Boundary clumping, estimated with Morisita's index, helps to further distinguish structures by determining if discernible groups of species form along the gradient. Additionally, if there is no significant turnover,

various quasi-structures are assigned to the metacommunity, depending on the trend observed in turnover and boundary clumping (*sensu* Presley et al. 2010).

After the metacommunity structure is discerned using the three metrics above, researchers typically seek to determine which environmental covariates might be driving the primary axis of variation in the ordinated community. This analysis takes various forms. In most cases, the ordination score of the primary axis is extracted for each sampled site. Then univariate correlation tests are run for each covariate of interest, and subsequently researchers theorize how significantly correlated covariates might be responsible for structuring the metacommunity (e.g. Henriques-Silva et al. 2013, Meynard et al. 2013). Another, related approach is to use, for example, canonical correspondence analysis to relate site compositions to multiple covariates simultaneously (e.g. López-González et al. 2012). A more recent approach is to combine one of these previously discussed analyses with a variance partitioning analysis to evaluate the relative contribution of classes of covariates, such as ‘local’ and ‘spatial’ or ‘abiotic’ and ‘biotic’ (Henriques-Silva et al. 2013) to species compositions across sites.

Although these methods have yielded various insights into the structuring of metacommunities, at each step of this process, there are problems that can arise due to the methods themselves, such as type I error inflation, or due to inherent issues in data quality, such as detection errors. Below, we will briefly describe the structure of multi-species occupancy models, which estimate detection and occurrence probabilities and associate these probabilities with covariates, all within the same model. After this, we will highlight various issues with the EMS paradigm that can be ameliorated using occupancy modeling.

## Multi-species occupancy models

Species occupancy models were developed to estimate a species’ probability of occurring within a site while correcting for the fact that species may go undetected in a survey. Occupancy models use data from multi-observation surveys, which allows us to disentangle detection and occurrence probabilities to better estimate true species occupancy. More recently, these models have been extended to multi-species and multi-timepoint (longitudinal) surveys. In these models, species-, site- and time-specific estimates of detection probability, occurrence probability and covariate effects can be estimated. Additionally, with longitudinal surveys, the probabilities of persistence at a site and colonization of previously unoccupied sites can be estimated. All of these models typically estimate parameters using Bayesian methods. Here, for simplicity, we will describe the structure of a single timepoint, multi-species occupancy model with multiple observations at each site over the single time period.

Let  $z_{i,k}$  represent the true occurrence of species  $i$  at site  $k$ , where  $z_{1,2} = 1$  means that Species 1 is present at Site 2. This true occurrence is estimated as a Bernouli trial with probability,  $\psi_{i,k}$ , the probability of occurrence:

$$z_{i,k} \sim \text{Bern}(\psi_{i,k})$$

The probability of occurrence,  $\psi_{i,k}$ , can be related to any number of covariates as follows:

$$\text{logit}(\psi_{i,k}) = \alpha_{i0} + \alpha_{i1}X_{k1} + \cdots + \alpha_{iC}X_{kC}$$

, where  $C$  is the number of covariates,  $\alpha_{ic}$  is the species-specific effect of covariate  $c$ ,  $\alpha_{i0}$  is the species-specific baseline occurrence probability, and  $X_{kc}$  is the site-specific value of covariate  $c$  at site  $k$ .

Multiple surveys are conducted at each site and compiled into a species-by-site matrix,  $Y$ . For example, if Species 1 is observed in five total surveys at Site 2,  $Y_{1,2} = 5$ . These observations, however, have inherent error in detectability. So, let  $\rho_{i,k}$  represent the species- and site-specific probability of detection. Again, the probabilities of detection can be influenced by site-level covariates. These covariates can be the same as or unique from the covariates influencing occurrence probabilities. Here we assume the same covariates:

$$\text{logit}(\rho_{i,k}) = \beta_{i0} + \beta_{i1}X_{k1} + \cdots + \beta_{iC}X_{kC}$$

The observed occurrences are thus binomially distributed, influenced by both the detection and occurrence probabilities and the number of surveys conducted at each site,  $J_k$ :

$$Y_{i,k} \sim \text{Binom}(J_k, z_{i,k}\rho_{i,k})$$

Depending on how many sites were sampled and how many species were observed, estimating all of these species- and site-specific parameters can be computationally expensive. In order to optimize parameter estimation, metacommunity-level hyperparameters are estimated in a hierarchical Bayesian model. Thus, species- and site-level parameters are drawn from the metacommunity-level distribution of parameter values.

## Difficulties with the EMS paradigm

### *Detection errors*

A large issue with occurrence data is that these data inherently suffer from problems with detection, and the EMS paradigm so far has not attempted to account for this problem. Detection error can influence the ordination of the community matrix, the calculated EMS metrics, and the accuracy of structural inference based on null matrices. For example, if species detection is imperfect, the calculated number of embedded absences from the ordinated matrix may be overestimated, which could lead to type II errors where metacommunities are incorrectly assigned random structures. Additionally, imperfect detection influences the form of null matrices, as most methods of null matrix generation utilize the raw data on row and/or column sums (Gotelli 2000). The occupancy modeling framework can circumvent this problem by estimating true occupancy of each species at each site,  $z_{i,k}$ .

With the Bayesian approach to occupancy modeling, Gibbs sampling is used to create a distribution of posterior estimates for each  $z_{i,k}$ . At each sampling iteration, the estimated  $z_{i,k}$  values can be assembled into an incidence matrix,  $Z_{iter}$ . Each  $Z_{iter}$  can then be ordinated to provide a distribution of incidence matrices that represent estimates of true occupancy states. In this way, we can generate a posterior distribution of metacommunity structure, rather than a single estimate for a given dataset.

For example, we simulated occupancy of 12 species at 75 sites, assuming 4 re-sampling visits per site using a simple occupancy model framework. We assigned metacommunity

hyperparameters for base-line occurrence and detection probabilities, assuming each was normally distributed (Figure 1). Species-specific probabilities were thus randomly drawn from these distributions. In order to achieve coherence, we assumed that species' overall occupancy probability was influenced by a single continuous covariate, distributed uniformly among sites. Species-specific covariate effects were also drawn randomly from a uniform distribution based on hyperparameters. For simplicity, we assumed did not assign covariate effects on detection probability. We then estimated posterior distributions for true occurrence of each species at each site,  $z_{i,k}$ , using a hierarchical Bayesian occupancy model, described above. Code and documentation for this and all following simulations can be found at ([github link](#)). We used R ([citation](#)) and JAGS (Plummer 2003), via the R package 'rjags', for all of our simulations and analyses. We used the R package 'metacom' for EMS analyses (Dallas 2014).

After we verified model convergence, we randomly sampled 200  $Z_{iter}$  from the full posterior sample. We chose to subsample the posterior for computational tractability. We then ordinated each  $Z_{iter}$  and overlayed these ordinated matrices to generate a heat map (Figure 2). This heat map allows us to see the range of likely ordinated matrices, given that some species are likely to go undetected during data collection. Next, for each of the 200 posterior matrices, we calculated the three elements of metacommunity structure using 1000 null matrix simulations for each  $Z_{iter}$ . In this way, we were able to generate Bayesian posterior estimates for the elements of metacommunity structure (Figure 3). **(Generate pie-chart-esque figure that shows how often different structures were assigned to  $Z_{iter}$ )**

This new approach to estimating elements of metacommunity structure allows us to more fully quantify and describe metacommunity structure, based on estimated true occurrence. This method will also allow us to fully explore the influence of detection on our ability to assign metacommunity structure. For instance, in our simulation, the ordinated matrix created with the raw data exhibits Clementsian structure (positive coherence, positive turnover, significant boundary clumping). However, when we observe the posterior distribution of EMS, we find that only 11.5% (23/200) of the ordinated  $Z_{iter}$  exhibit Clementsian structure; the rest exhibit Gleasonian structure. This simple example demonstrates how detection errors can influence inference of metacommunity structure and how occupancy modeling can help to shed more light on patterns based on Bayesian probability.

#### *Covariate effects*

Another issue with the EMS strategy that can be ameliorated by a merger with occupancy modeling is the way in which covariate effects are explored. As discussed above, many researchers extract the first ordination axis score for each sampled site and associate these scores to any number of site-specific covariates using multiple univariate correlation tests. This approach is flawed due to inflation of the overall type I error rate caused by conducting multiple tests. Additionally, regardless of the type of statistical test, using the ordination scores from a single axis could be leaving out valuable information, and these ordination scores are extracted from a matrix that is most likely flawed by detection error in the first place. Occupancy modeling helps to remedy these issues by estimating species-specific covariate effects on occurrence probability based on the raw data, not ordination scores. Then, using Bayesian model selection and model averaging, dominant covariates and their effects can be estimated without the need for multiple tests.

The influence of confounding covariate effects on detection and occurrence probabilities can also be explored within the occupancy modeling framework. For example, if a single covariate, such as vegetation density, has positive effects on species' occupancy but negative effects on species' detectability, how might this influence our ability to detect or accurately assign metacommunity structure? The simulation method described above could be used to explore this question in a future study by altering the correlation between the covariate's effect on each species' detection and occurrence probabilities and observing how metacommunity structure changes.

## Complementary features of occupancy modeling

### *Structuring mechanisms*

While introducing the EMS methods in their seminal paper, Leibold and Mikkelsen (2002) emphasize that the EMS paradigm can identify patterns, but cannot necessarily elucidate the processes that lead to pattern. However, multi-species occupancy modeling can complement the features of the EMS paradigm and help to better elucidate metacommunity structuring mechanisms. For example, metacommunities that exhibit Gleasonian and Clementsian structure are assumed to be structured differently based on species-specific responses to a dominant environmental gradient (Clements 1916, Gleason 1926, Gilpin and Diamond 1982). It is often stated that Gleasonian structure arises from idiosyncratic species responses, whereas Clementsian structure arises from groups of species that respond similarly to each other, but differently from other groups of species in the metacommunity. Alternatively, Clementsian structure could arise from negative associations between species pairs or groups that arise along the gradient (Gilpin and Diamond 1982). Still, these mechanistic interpretations of structure remain more or less speculative in the EMS paradigm. The occupancy modeling simulation framework that we described above can help us to understand under which conditions different metacommunity structures might arise.

We used simulation to explore how the distribution of species-specific covariate effects and the distribution of covariate values observed among sampled sites affect the resulting metacommunity structure. Again we simulated 12 species distributed across 75 sites, with 4 re-sampling surveys at each site. Base-line occurrence and detection probabilities were fixed across species. We, however, altered the distribution and range (hyperparameters) from which the species-specific covariate effects and site-specific covariate values were drawn (Tables 1 and 2). For each set of hyperparameter values, we simulated 10 incidence matrices, ordinated each one and determined the resulting metacommunity structure based on 1000 null matrices.

Importantly, we found that the range and distribution of site-specific covariate values sampled across the landscape can alter the observed metacommunity structure, independent of the species-specific covariate effects (Table 1). In other words, the selection of sampling sites in a study could alter the observed metacommunity structure in a way that may reflect statistical phenomena rather than biological ones, complicating inferences about structuring mechanisms. Furthermore, with our chosen set of parameter values, we were overall more likely to observe Clementsian structure than Gleasonian structure, even when species-specific covariate effects were drawn from a broader distribution and were essentially idiosyncratic



(Table 1). Additionally, we were able to produce nested structures when we forced covariate values to be only positive (or negative), even though covariate effects did not change from the Gleasonian/Clementsian examples (Table 2).

Our findings above suggest that under some circumstances metacommunity structure might arise from statistical phenomena in addition to or in place of biological processes. Similar to our findings, Locey and White (2013) explored the ‘feasible set’ of species area distributions (SAD) as constrained by total species richness and total abundance of species, showing that the ubiquitous hollow-curve SAD may be the result of a statistical phenomenon. Admittedly, our simulations did not attempt to encompass the entire feasibility space of the occupancy model, as this would require altering many parameters. However, this occupancy modeling simulation framework could be used as a type of sensitivity test to help us understand when structures might be generated by sampling issues versus biological processes.

### *Temporal dynamics*

With longitudinal metacommunity data becoming more and more available, an interesting question that arises is how does metacommunity structure vary across time points and what are the driving mechanisms for these changes. For example, Erős et al. (2014) explored how metacommunity structure of stream fishes changed over time and how this structure was influenced by environmental covariates. Dynamic occupancy modeling has a few complementary features that could aid in a more cohesive approach to studying such questions.

Occupancy modeling could be used to distinguish if changes in metacommunity structure are more related to changing covariate values at sites over time, whether the dominant structuring covariate changes identity over time (e.g. from altitude to pH), or if metacommunity structure changes due to idiosyncratic changes in how species respond to the same covariates over time. Additionally, Dorazio et al. (2010) showed how multi-species occupancy modeling can be used to estimate species- and time-specific covariates on detection, occurrence, colonization and persistence probabilities. Understanding colonization and persistence (i.e. extinction) dynamics could aid in inferring more specific mechanisms for metacommunity structural changes.

## **Discussion**

... Shortcomings... - Still relies on single axis ordination for metacommunity analyses - Sensitivity to priors for metacommunity parameter distributions? (e.g. I assigned some parameters from uniform distributions, but their priors were assumed to be normally distributed)

Our simulations are simple in many regards and future studies could more fully explore the sensitivity of metacommunity structure to various model assumptions. One important extension would be to determine the effects of discrete versus continuous covariates and the resulting patterns when both types of covariates influence occurrence probabilities. Additionally, we held our metacommunity size constant, in terms of the number of species and the number of sites sampled. It is well established that matrix size influences the power to detect patterns using null models (Gotelli and Graves 1996, Gotelli 2000), so understanding

the influence of these parameters in occupancy models will be important. For tractability, we unrealistically assumed that base-line occurrence and detection probabilities were fixed among species. Understanding how the distributions of these probabilities (and their species-specific covariance) influences overall metacommunity structure should be a leading question.

## Table and Figure Legends

Table 1. Metacommunity structures observed by varying the distributions of covariate values and species-specific covariate effects. Each set of parameters was independently simulated 10 times for 12 species among 75 sites with 4 re-sampling surveys each. The resulting incidence matrices were ordinated, and the EMS were calculated to discern metacommunity structure. All observed metacommunity structures from the 10 simulations were noted. Structures that are bolded were more represented in the sample. Species-specific covariate effects are on the logit scale.

Table 2. Generating nested subsets by altering covariate values. Simulations were conducted as in Table 1; however, we constrained covariate values to be only positive, resulting in predominately nested and quasi-nested structures. Structures that are bolded were more represented in the sample. Species-specific covariate effects are on the logit scale.

Figure 1. Flow chart that is followed to determine metacommunity structure. Text in gray boxes represents the metric used to estimate the corresponding element of structure (e.g. embedded absences are used to determine coherence). NS = non-significant based on simulated null matrices.

Figure 2. (a) The ordinated matrix from simulated occurrences and (b) the ordinated heat map generated from 200 ordinated  $Z_{iter}$  estimated with a hierarchical Bayesian occupancy model. Species-specific base-line occurrence probabilities and detection probabilities were both drawn from a normal distribution with mean=0.5 and SD=0.75. Species-specific covariate effects were drawn from a uniform distribution with high=1.5 and low=-1.5 (on the logit scale). Site-specific covariate values were randomly assigned from a uniform distribution with high=4 and low=-4.

Figure 3. Posterior distributions of the elements of metacommunity structure for our simulated metacommunity, based on 200 ordinated  $Z_{iter}$  shown in Figure 2. (a) Coherence normalized z-scores comparing the number of embedded absences to 1000 null matrices created in the R package ‘metacom’, using the default null generator method, ‘r1’. (b) Turnover z-scores comparing the number of replacements as in (a). (c) Estimated boundary clumping using Morisita’s index. Based on an  $\alpha = 0.05$ , all coherence measures were significantly positive, all turnover was significantly positive, but only 23/200 Morisita’s Index scores were significantly different than 1.

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