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Phylogenetic occupancy models integrate imperfect detection and phylogenetic signal to analyze community structure

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Abstract. Biological communities are structured phylogenetically—closely related species are typically more likely to be found at the same sites. This may be, in part, because they respond similarly to environmental gradients. Accurately surveying biological communities is, however, made difficult by the fact that detection of species is not perfect. In recent years, numerous statistical methods have been developed that aim to overcome deficiencies in the species detection process. However, these methods do not allow investigators to assess phylogenetic community structure. Here, we introduce the phylogenetic occupancy model (POM), which accounts for imperfect species detection while assessing phylogenetic patterns in community structure. Using simulated data sets we show that the POM grants less biased estimates of phylogenetic structure than models without imperfect detection, and can correctly ascertain the effects of species traits on community composition while accounting for evolutionary non-independence of taxa. Integrating phylogenetic methods into widely used occupancy models will help clarify how evolutionary history influences modern day communities.

Key words: detectability; environmental gradient; hierarchical model; JAGS; phylogenetic generalized linear mixed effect model; phylogenetic diversity; phylogenetic occupancy model; trait-based.

Introduction

Evolutionary history shapes the composition of modern communities through processes such as character displacement and phylogenetic conservation of resource requirements. Uncovering these phylogenetic patterns will prove critical in answering key questions in evolution and ecology such as (1) do close relatives competitively exclude one another (MacArthur and Levins 1967, Helmus et al. 2007, Mayfield and Levine 2010, Bennett et al. 2013, Narwani et al. 2013), (2) to what degree do environmental conditions deterministically filter species (Helmus et al. 2010), and (3) do deterministic or historical forces dominate in shaping community composition (Cavender-Bares et al. 2009, Peay et al. 2012).

Some progress has been made in understanding how phylogenetic relatedness structures communities, both in simple experiments (Cadotte and Strauss 2011, Peay et al. 2012) and real-world communities (Bennett et al. 2013, Frishkoff et al. 2014). Generally it seems that individual communities are not random assortments of species but, instead, are phylogenetically clustered. In other words, species within a community are, on average, more closely related to one another than they are to species from outside the community (Vamosi et al. 2009). This pattern is generally interpreted as the effect of environmental determinism—closely related species respond to environmental gradients in similar ways and are thus associated with, or excluded from, local communities in concert.

Recently, model-based approaches for studying how phylogenetic relatedness influences community structure have gained traction over more traditional index based and null model methods (Ives and Helmus 2011). Null models generally proceed by shuffling species among communities and then asking, for example, whether species within communities are more closely related to one another than randomly selected pairs of species (Webb 2000). In contrast, model-based approaches estimate species' responses to an environmental gradient and then ask whether closely related species respond more similarly (Ives and Helmus 2011). The principle benefits of model-based approaches are that they (1) provide direct estimates of effect sizes; (2) allow prediction beyond the sample (to unmeasured sites with known environmental properties or to unmeasured species with known phylogenetic placement); (3) allow for nuisance variables to be easily accounted and controlled for; and (4) enable the use of model selection techniques. Together these features facilitate identifying species- or site-level traits that do (or do not) impact community structure.

Ives and Helmus (2011) initially introduced model based analysis of phylogenetic community structure through the phylogenetic generalized linear mixed effect model (PGLMM). The PGLMM explains variation in

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community structure (presence vs. absence) across sites and species, with the species effects partitioned between phylogenetic and non-phylogenetic components. Although the current model based approaches used to study phylogenetic structure of communities are powerful, they may be biased by the implicit assumption that species are perfectly detected and that rates of detection do not differ between species or sites. When working with field-collected community data, however, this is rarely the case. Failure to observe a species at a particular site occurs either because the species is not present, or because the species is present but evades detection. In many analyses this detection bias is ignored. However if probabilities of detection differ by species, by site, or across time periods, ignoring this bias can lead to spurious inferences about community structure (Iknayan et al. 2013).

Multi-Species Occupancy Models (hereafter referred to as MSOMs) are used when one wishes to make community-wide inferences, while acknowledging that not all species will be detected all the time (Iknayan et al. 2013). Failure to incorporate imperfect detection leads to downward biased estimates of occupancy, and such naïve estimates can result in incorrect inferences. For example, Tingley and Beissinger (2013) found that incorporating imperfect detection radically changed estimates of bird species richness in the Sierra Nevada. Without incorporating detection, it appeared that bird species richness was low in the early 20th century but increased by ~30% a century later. In fact, species richness declined by ~5% (which the authors attribute to climate change), but surveyors' abilities to detect species improved dramatically over that time period, nearly doubling (which they attribute to better sampling methodologies). Because they can disentangle processes that affect detectability (typically a nuisance parameter) from ones that affect occupancy (typically what researchers are actually concerned about), occupancy models are becoming increasingly important for community ecology and conservation (Iknayan et al. 2013). This class of models has been the focus of active research and development, allowing, for example, the effects of spatial autocorrelation and competition to be directly quantified and accounted for (e.g., Rota et al. 2016).

Current MSOMs do not, however, enable direct incorporation of phylogenetic information. Thus, investigators in the past have used indirect tests, such as including taxonomic families as fixed factors in analyses (Tingley and Beissinger 2013), or using a two-step procedure, first modeling occupancy probability and then testing for phylogenetic signals in these occupancies (Frishkoff et al. 2014). These alternatives are not ideal, because failure to directly incorporate phylogenetic non-independence can lead researchers to incorrect inferences regarding parameters of interest (Revell 2010).

Here we develop an extension of the MSOM that allows for direct inclusion of phylogenetic data (hereafter the 'phylogenetic occupancy model', POM; see Fig. 1 for schematic of basic model design). Our main focus in doing so is to estimate the similarity of species' responses to an environmental gradient. Development of MSOMs that

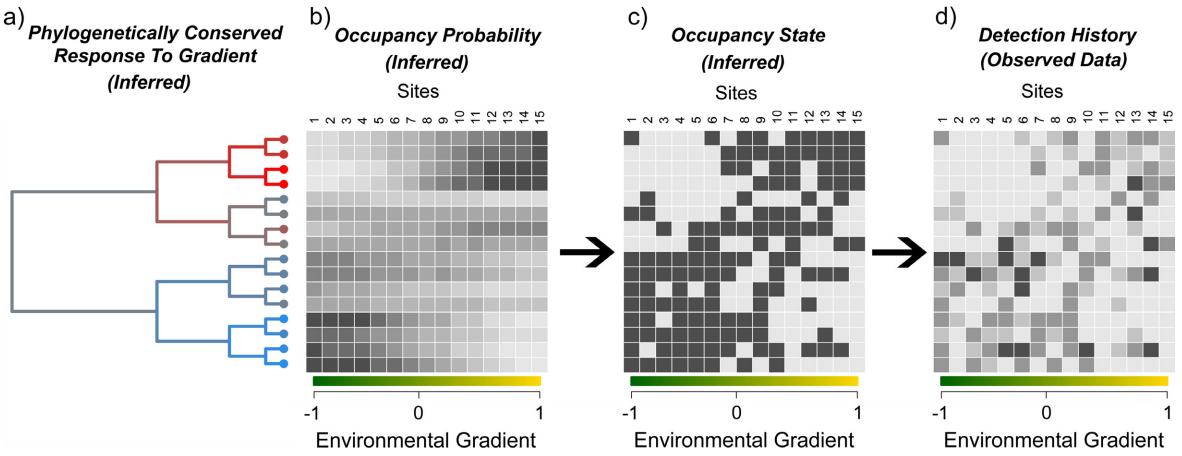

FIG. 1. Example community responding to an environmental gradient. (a) Here 16 species' responses to an environmental gradient are phylogenetically conserved (simulated $\lambda = 1$). Some species (branches colored more strongly red) maximize their occurrence probability as values of the environmental gradient increase. Others (branches colored more strongly blue) maximize occurrence probability in sites with low values of the gradient. Generalists with no strong response to the gradient have branches colored grey. (b) Darker squares in the species by site matrix indicate greater probability that a species will occupy a site. (c) In any given season whether a species actually occurs at a site or not depends on its site-specific occupancy probability. Species are either present (dark grey) or absent (light grey). (d) Whether a species is observed when a researcher visits a sight depends on a species being present at the site, and on the species' specific detectability. Here we illustrate a situation in which each site is visited four times, with colors indicating whether a species was observed all four times (darkest grey), not at all (lightest grey), or an intermediate number of times (intermediate shades). The phylogenetic occupancy model is designed to take a set of observed detection histories (in d) and a phylogeny, and use them to infer the true occupancy state in each season (c), the overall occupancy probability (b), and the phylogenetic signal in response to the environmental gradient across sites (shading in a). [Colour figure can be viewed at wileyonlinelibrary.com]

explicitly incorporate phylogenetic information accomplishes two major goals. First, it allows the estimation of phylogenetic signal in response to environmental gradients while incorporating sampling and detection uncertainty. Second, it allows investigators to test the effects of species-specific covariates (e.g., life history traits) on occupancy, or response to environmental gradients, while correcting for phylogenetic non-independence (Felsenstein 1985). As a result, it disentangles the effect of specific traits from variation in occupancy that comes from shared ancestry between organisms (presumably in the form of other unmeasured traits). We test the performance of the POM using simulated data to determine how well the model can detect phylogenetically conserved responses to an environmental gradient, with and without incorporating species trait values that mediate this response.

Methods

Structure of the phylogenetic occupancy model

Estimating occupancy probability—.The POM estimates the true occupancy state of N species across M sites over S seasons from raw detection data, using information about the sites (i.e., environmental conditions) and species (i.e., traits and phylogenetic relatedness). Using the POM, one can ask whether species respond to an environmental gradient in a phylogenetically conserved manner because the strength of the phylogenetic signal is directly included as a parameter. For example, if sites are sampled along a moisture gradient, do closely related species share similar preferences for wet vs. dry sites? We can also ask whether traits mediate this response. For example, after accounting for phylogenetic correlation between species, does body size predict habitat preferences? We focus on phylogenetic correlations in this response-to-environment slope term, because it is biologically meaningful as a way to assess habitat affiliation. In practice one could also assess phylogenetic correlation in site-specific species intercepts as a means of quantifying whether closely related species tend to co-occur in the absence of specific hypotheses regarding environmental gradients.

Within a season, we make the standard assumption that sites are closed to immigration/emigration during sampling (i.e., a species may not colonize new sites or go extinct from already colonized sites between the beginning and the end of the sample period within a season). Between sample periods, however, it is possible that species may change occupancy state at some sites. For our model, we assume that occupancy in each season is independent of occupancy in other seasons. Alternatively one can model the extinction and colonization processes directly (MacKenzie et al. 2006). However, these dynamic models (or "multi-season") tend to be more computationally intensive and parameter rich, so for simplicity we use a "single-season" model generalized to include multiple seasons. In practice, the most suitable model will depend on the study system and the time-scale over which sampling occurs (e.g., when occupancy in one year is highly dependent on occupancy in the previous year, one should favor a dynamic model over a single-season model).

We let $X[i,j,t,k]$ denote the observation data for the ith species at the jth site during the kth visit of the tth season. If a species was detected, then $X[i,j,t,k] = 1$, if it was not detected $X[i,j,t,k] = 0$. To account for imperfect detection, we denote the true occupancy state of species i at site j and season t as $Z[i,j,t]$ and model $X[i,j,t,k]$ as an imperfect observation of $Z[i,j,t]$. We assume that the true occupancy state can be described as a Bernoulli random variable: $Z[i,j,t] \sim \text{Bern}(\psi[i,j,t])$. Occupancy probability, $\psi[i,j,t]$, is assumed to be the outcome of species-specific traits interacting with a site-specific environmental value. In the framework of a generalized linear mixed effect model, $\psi[i,j,t]$ is assumed to be described by:

$$\text{logit}(\psi[i,j,t]) = \psi_0[i] + \psi_{\text{Env}}[i] \times \text{Env}[j] + \psi_{\text{site}}[j] + \psi_{\text{season}}[t] \quad (1)$$

where $\psi_0[i]$ is species occupancy probability at the midpoint of the environmental gradient (intercept), $\psi_{\text{Env}}[i]$ is the species-specific response to the environmental gradient (slope), $\text{Env}[j]$ is a site's value along a (scaled and centered) environmental gradient, and $\psi_{\text{site}}[j]$ and $\psi_{\text{season}}[t]$ are random intercepts to account for consistent differences in mean rates of occupancy across sites and seasons, respectively. Specifically:

$$\psi_{\text{site}}[j] \sim \text{Normal}(0, \sigma^2_{\psi_{\text{site}}})$$

$$\psi_{\text{season}}[t] \sim \text{Normal}(0, \sigma^2_{\psi_{\text{season}}})$$

The species-specific intercept, $\psi_0[i]$, is modeled here as a fixed effect. This parameter determines overall occupancy levels across a landscape—large values of $\psi_0[i]$ indicate that a species is more common across all environments, whereas small values indicate that it is rare. This could, alternatively, be parameterized as a random intercept. We chose to use a fixed effect because it speeds MCMC mixing by allowing each species' intercept term to vary freely and conforms more closely to past parameterization of PGLMMs (Ives and Helmus 2011). Note that because there is a fixed intercept for each species we do not include a "main" effect of the species' trait (i.e., on the intercept). Including trait effects on the intercept (which are indexed by species) would be redundant, and, therefore, non-identifiable. If main effects of species traits wish to be tested, a random species intercept parameterization would be necessary.

We incorporate phylogenetic covariance between closely related species in their responses to an environmental gradient ($\psi_{\text{Env}}[i]$). This is accomplished by parameterizing $\psi_{\text{Env}}[i]$ as:

$$\psi_{\text{Env}}[i] = \beta_0 + \beta_{\text{trait}} \times \text{Trait}[i] + \varepsilon_{\text{Env}}[i], \quad (2)$$

where β_0 describes the expected response to the gradient when the (scaled and centered) trait value is 0 and β_{trait} describes how strongly the trait influences this response. By substituting equation 2 into equation 1, β_{trait} is effectively a trait-by-environment interaction coefficient. The residual $\varepsilon_{Env}[i]$ incorporates variation in species responses not accounted for by the trait. In a traditional MSOM, these residual error terms are assumed to be independent of each other. However if they are correlated with one another due to phylogenetic non-independence, other parameter estimates can be biased (Revell 2010). To address this we replace the standard random effect with a phylogenetic random effect where we allow for phylogenetic signal among these residuals. Specifically, we assume:

$$\varepsilon_{Env}[i] \sim \text{MultivariateNormal}(\mathbf{0}, \sigma^2_{\psi_{Env}} \times \mathbf{C}_{phylo}), \quad (3)$$

where $\mathbf{0}$ is a vector of zeros with length N, $\sigma^2_{\psi_{Env}}$ is the variance in responses to the environmental gradient, and $\mathbf{C}_{phylo}$ is the $N \times N$ correlation matrix resulting from the phylogeny.

Pagel's λ parameter (Pagel 1999, Revell 2010) is estimated from the data and modulates the strength of phylogenetic effects according to:

$$\mathbf{C}_{phylo} = \lambda \times \mathbf{D} + (1 - \lambda) \times \mathbf{I}, \quad (4)$$

where $\mathbf{D}$ is the expected correlation matrix from the phylogeny for a trait undergoing Brownian motion evolution and $\mathbf{I}$ is the $N \times N$ identity matrix. The expected correlation between any two taxa corresponds to the proportion of their evolutionary history that they share. When $\lambda = 1$, species responses to an environmental gradient follow the Brownian motion expectation, whereas when $\lambda = 0$, $\mathbf{C}_{phylo}$ becomes an identity matrix and values of ψ_{Env} have no systematic phylogenetic correlation (identical to a traditional random effects model). Note that the phylogenetic signal estimated here through parameter λ represents residual variation in the response to the environmental gradient, after accounting for the effect of the species' trait. The trait values themselves may or may not also be phylogenetically correlated, and our simulation scenarios below include both cases. Finally, if no trait effect were included in Eq. 2, λ would represent the total amount of phylogenetic signal in the responses to the environmental gradient.

So far, our formulation of the POM is mathematically similar to the PGLMM (model II) of Ives and Helmus' (2011), with some added generality and an alternative parameterization of phylogenetic variance component. Specifically, the traditional PGLMM uses data from a single sampling instance within a single season, does not include traits as covariates, and uses separate terms for the non-phylogenetic and phylogenetic components of variation in species' responses, rather than a single overall variance term and a parameter (λ) to scale the partitioning of this overall variance (though, these two parameterizations of the phylogenetic component are mathematically equivalent). Our models diverge more substantially when we incorporate imperfect species detection.

Incorporating imperfect detection—.Whether a species was actually observed at a site during visit k ($X[i,j,t,k]$) is assumed to be a Bernoulli random variable such that $X[i,j,t,k] \sim \text{Bern}(p[i,j,t,k] \times Z[i,j,t])$, where $p[i,j,t,k]$ is the probability that species i was detected at the jth site in the kth visit of the tth season, given that it was actually present. If species i was absent ($Z[i,j,t] = 0$), then it was not possible to detect it ($X[i,j,t,k] = 0$). We allow detection probabilities to vary by species and environment such that the detection probability of species i at site j in the kth replicate of the tth season is given by:

$$\text{logit}(p[i,j,t,k]) = p_0[i] + p_{Env}[i] \times \text{Env}[j], \quad (5)$$

where $p_0[i]$ is species detection probability at the midpoint of the environmental gradient (intercept), and $p_{Env}[i]$ describes how detection probability of the species changes along the environmental gradient. Both $p_0[i]$ and $p_{Env}[i]$ are considered to be random effects:

$$p_0[i] \sim \text{Normal}(\mu_{p0}, \sigma^2_{p0}).$$

$$p_{Env}[i] \sim \text{Normal}(\mu_{pEnv}, \sigma^2_{pEnv}).$$

Additionally, some species traits might correlate with detectability (e.g., coloration or volume of call), or detectability might vary between seasons, either randomly or systematically (e.g., it might be easier to observe woodland mammals in winter due to a lack of leaves on trees). In such cases additional terms could be introduced into the detection component (Eq. 5) analogous to those described in the occupancy component (Eqs 1 and 2).

Model implementation—.We implement these models using JAGS called from the R programming environment. JAGS provides a Bayesian framework for parameter estimation (Plummer 2003, Su and Yajima 2014). In all cases we used vague priors. JAGS code for the POM is provided in the supplement, and a tutorial and code are provided at https://github.com/lofrishkoff/pom. Some questions might be more appropriate in a frequentist framework, but it is not straightforward to implement maximum likelihood estimation for the POM due to its large number of random effects (Bolker et al. 2009, de Valpine 2012). Methods such as data cloning (Lele et al. 2007) are too computationally intense for the simulation exercises here. Therefore, we focus on Bayesian parameter estimates and model comparison methods, taking a calibrated Bayes perspective (Rubin 1984, Little 2006) by evaluating frequentist performance of these Bayesian procedures.

Estimation and inference of phylogenetic signal—.We evaluate the ability of the POM to estimate λ by comparing the posterior mode (highest posterior probability: HPP) to the true value of λ for simulated datasets. To assess whether the POM supports the existence of phy-

logenetic signal in response to the environment, we examine whether the 95% highest posterior density (HPD) includes $\lambda = 0$. Because values of λ are bounded by 0 and 1, we estimated the density using a truncated kernel and evaluated a 95% credible interval using the 95% HPD interval rather than the 95% equal-tailed interval. This allowed a value of 0 (or 1) to be included in the 95% credible interval. Our R function to accomplish this is provided as supplementary material.

To complement this approach we additionally explored using Bayes factors between nested models to test the importance of including phylogenetic signal. Bayes factors results broadly conform to 95% HPD results, and are presented in the Appendix S1.

Evaluating the performance of the POM

We ask two major questions regarding the performance of the Phylogenetic Occupancy Model:

1. What are the consequences of ignoring imperfect detection in phylogenetic community analyses?
2. How well does the POM estimate the effect of a trait on species' responses to an environmental gradient?

We addressed these questions using simulated datasets. We first outline the general protocol used for data simulation, then discuss how we evaluated each of the core questions. When data simulation deviates from the general case, we detail these differences in the relevant section.

General data simulation

To generate data, we simulated detection histories for 15 sites with three site visits per season across three seasons (nine total visits to each site). Preliminary analyses (presented in Appendix S1) indicated that statistical power to detect phylogenetic signal was primarily dictated by the number of species in the community, and relatively invariant to number of sites surveyed. We, therefore, focused on contrasting community sizes, and simulated 16, 32, or 64 species, under the assumption that most community-level data sets will have a total number of observed species in this range. To standardize comparisons, we used a fully balanced phylogenetic tree. To simulate a continuous environmental gradient (Env) we spaced sites evenly along a continuum, and then scaled and centered their values. Species-specific responses to the gradient were simulated with $\sigma_{\psi Env} = 3$ and $\beta_0 = 0$. This resulted in a roughly equal number of species responding positively and negatively to increasing values of Env. We varied the strength of phylogenetic signal in response to the gradient (λ: 0, 0.5, and 1). Detection probabilities were drawn with μ_{p0} set to -1, which is equivalent to detection probabilities of 0.25 on the probability scale. Variation in detectability was set to $\sigma_{p0} = 1$ (for $\mu_{p0} = -1$, this results in species detectabilities with an interquartile range extending from 0.15 to 0.42 on the probability scale). We drew values of ψ_0 (species occupancy intercept, i.e., occupancy probability at Env = 0) from a normal distribution with a mean equal to 0 and a standard deviation equal to 1. Other parameter values included $\sigma_{\psi site} = 1$, $\sigma_{\psi season} = 1$. See Table 1 for a complete summary of parameters in the POM, their description, and simulation values.

1. What are the consequences of incorporating imperfect detection in phylogenetic community analyses? (POM vs. PGLMM or post-hoc testing)—.Previous methods for evaluating phylogenetic signal in communities do not take into account imperfect species detection. What improvements in estimation and inference are then gained by incorporating imperfect detection into models (i.e., POM) vs. methods that ignore detection probability (e.g., phylogenetic generalized linear mixed model, PGLMM; Ives and Helmus 2011))? Does failure to account for detection lead to systematic biases in estimates of phylogenetic signal?

To address these questions, we analyzed simulated datasets with the POM in three ways biologists might treat data if they are avoiding quantifying detection probability hierarchically: two alternative Bayesian implementation of PGLMMs, and by calculating phylogenetic signal post-hoc from a series of species-specific regressions against the environmental gradient. For the first PGLMM ($PGLMM_{naïve}$) we collapsed detection histories across visits: Instead of modeling the true (but latent) occupancy states as $Z[i,j,t] \sim \text{Bern}(\psi[i,j,t])$ and detection histories (the observed data) as $X[i,j,t,k] \sim \text{Bern}(p[i,j,t,k] \times Z[i,j,t])$, this PGLMM models apparent occupancy directly as $Y[i,j,t] \sim \text{Bern}(\psi[i,j,t])$, where $\psi[i,j,t]$ is as defined previously for the POM (Eq. 1). Here, the observed data $Y[i,j,t]$ is the naïve occupancy history of species i at site j in season t. To create $Y[i,j,t]$ from the full detection history, $X[i,j,t,k]$, we collapsed over the k site visits such that $Y[i,j,t] = 1$ if a species was observed at site j in season t during any visit, and $Y[i,j,t] = 0$ if the species was never observed at site j during season t. This method throws away information, but attempts to correct for imperfect detection (this correction is only faulty in those cases when a species was actually present but never observed). We additionally evaluated a PGLMM ($PGLMM_{visit}$) that preserved the visit data. In this case $X[i,j,t,k]$ is modeled directly as $\text{Bern}(\psi[i,j,t])$, bypassing the detection hierarchy. Here $\psi[i,j,t]$ represents the probability that a species is observed. Finally we used single species generalized linear mixed models, implemented in *lme4* (Bates et al. 2012), to obtain MLEs for each species' responses to the environmental gradient. To do so, we modeled detection during a visit as a function of a fixed intercept and environment effects and random site and season effects) under binomial error. We extracted each species' MLE associated with the environment effect (along with its standard error) and did a post-hoc analysis of phylogenetic signal of these terms by estimating λ using the fitContinuous function

TABLE 1. Summary of parameters in POM.

Hierarchy	Parameter Family	Name	Indexed by	Description	Simulation Value
Occupancy	Intercept	ψ_0	*Species*	Occ. prob. at Env midpoint	From normal dist. (mu = 0, sigma = 1)
	Response to Environment	β_0	*None*	Expected ψEnv for species with *Trait* = 0	0
		β_{Trait}	*None*	Effect of trait on ψEnv*	0 [Q1] or 1 [Q2]
		$\sigma^2_{\psi_{\text{Env}}}$	*None*	Variation among species in ψEnv	9 (=3^2)
		λ	*None*	Phylogenetic signal in ψEnv	0, 0.5, 1
		ε_{Env}	*Species*	Residual of ψEnv after accounting for trait effects	NA
		ψ_{Env}	*Species*	Effect of Env on species occupancy probability (slope)	NA
	Site Effect	$\sigma^2_{\psi_{\text{site}}}$	*None*	Variation among sites in occupancy	1
		ψ_{site}	*Site*	Site effect on occupancy	NA
	Season Effect	$\sigma^2_{\psi_{\text{season}}}$	*None*	Variation among seasons in occupancy	1
		ψ_{season}	*Season*	Season effect on occupancy	NA
Detection	Intercept	μ_{p0}	*None*	Mean across species of *p0*	−1
		σ^2_{p0}	*None*	Variation among species in *p0*	1
		p_0	*Species*	Detection prob. at Env midpoint.	NA
	Response to Environment†	μ_{pEnv}	*None*	Mean across species of *p*Env	0
		σ^2_{pEnv}	*None*	Variation among species in *p*Env	0 [Q2] or 0, 1, 9 (=3^2) [Q1]
		p_{Env}	Species	Effect of Env on species detection probability (slope)	NA

* In question 1, the effect of traits were not evaluated, so β_{Trait} was not estimated in the model.
† In questions 2, variation in the effect of the environment on species' detection was not evaluated, so this family of parameters (μ_{pEnv}, σ^2_{pEnv}, p_{Env}) was not estimated in the model.

in *geiger* (Harmon et al. 2008), incorporating uncertainty of the MLE estimates by including each estimates' standard error.

Methods that ignore detection probability might be particularly biased when the probability of detecting a species depends on the environment (because changes in detectability along a gradient are confounded with changes in species' occupancy probabilities). We, therefore, explicitly simulated datasets in which species detection probabilities depended on values of the environmental gradient. All simulation parameters adhered to the general values described previously, except those related to species detection. For the first case, detection probability for all species did not depend on the environment ($\mu_{p\text{Env}} = 0$, $\sigma_{p\text{Env}} = 0$). We next considered systematic covariation between the environment and species detectabilities, such that all species were easier to detect at higher values of Env ($\mu_{p\text{Env}} = 1$, $\sigma_{p\text{Env}} = 0$). We then added variation in how individual species' dectectabilites changed along the environmental gradient, simulating a low variation scenario ($\mu_{p\text{Env}} = 1$, $\sigma_{p\text{Env}} = 1$), and a high variation scenario ($\mu_{p\text{Env}} = 1$, $\sigma_{p\text{Env}} = 3$). These latter two cases result in some species getting easier to detect at high values of the environmental gradient, while other species become more difficult. Note that in the high variation scenario, the amount of variation in the environment's effect on species' detection probabilities was of the same magnitude as the variation in occupancy along the gradient (because $\sigma_{\psi\text{Env}} = \sigma_{p\text{Env}} = 3$). We simulated data for 16, 32, and 64 species and with phylogenetic signals of either $\lambda = 0$, 0.5 or 1.0. We ran 100 simulations for each set of parameters, and compared the performance of the POM, PGLMMs, and post-hoc analysis of serial regressions by contrasting the estimates of λ with its true value, and using 95% HPD (for Bayesian methods) or CI (for ML methods) to quantify type I and type II error rates across simulations. In many cases the *fitContinuous* function was unable to calculate a CI around λ resulting from singular Hessian matrices when estimates of λ were near either 0 or 1. When the CI was undefined, we considered that the null hypothesis that λ was greater than 0 could not be rejected. Development of analytical methods that would enable us to construct ML confidence intervals for boundary scenarios is beyond the scope of this work. Thus, we chose this conservative approach to mirror what would occur in practice; empiricists whose data-sets prohibit construction of confidence intervals using currently implemented methods will be unable to reject their null hypothesis.

For question 1, we were not interested in how traits influenced response to the environmental gradient. We, therefore, neither simulated traits nor included their effects in the POM model. Specifically Eq. 2 was replaced by the simpler:

$$\psi_{Env}[i] = \beta_0 + \varepsilon_{\text{Env}}[i],$$

Question 2: How well does the POM estimate the effect of a trait on species' responses to an environmental gradient?—.Community ecologists often seek to understand why certain species are found at some sites but not others. Therefore, we tested how well the POM quantified the magnitude of species' responses to an environmental gradient when those responses were mediated by their trait values. Here a key issue is whether the trait values are themselves phylogenetically correlated and, if they are, how that impacts our ability to isolate the influence of the trait itself from the residual phylogenetic signal in response to the gradient. Following Revell (2010), we simulated four scenarios in which phylogenetic signal was present in either the trait (independent variable) and/or in the residuals of species' responses to the gradient (estimated within the POM). For clarity, we designate the phylogenetic signal in the trait as λ_{Trait} to differentiate it from the phylogenetic signal in the residuals (denoted λ, defined above). Note that the POM, as in PGLS, is used to estimate the phylogenetic signal in the residual, λ (see Eqs 3 and 4). λ_{Trait}, on the other hand, is used for data generation purposes, as the species trait values are simulated using the phylogeny and then these values are entered into the model as data.

First, we simulated cases in which there is neither phylogenetic signal in trait values ($\lambda_{Trait} = 0$) or in the residual variation around ψ_{Env} ($\lambda = 0$). This is the scenario that MSOMs with species level covariates are designed to address. Second, we simulated phylogenetic signal in the trait ($\lambda_{Trait} = 1$), but not in the residual variation ($\lambda = 0$). Third we simulated a trait with no phylogenetic signal ($\lambda_{Trait} = 0$) but signal in the residual variation ($\lambda = 1$). Finally, we simulated data with phylogenetic signals in both the trait and the residual variation ($\lambda_{Trait} = 1$ and $\lambda = 1$). Prior to analysis, we standardized trait values by subtracting the mean and dividing by the standard deviation. Across all of these simulations, other parameter values were the same as described previously, except that β_{Trait}, the effect of the trait, was set to 1 (i.e., species with large values of the trait will, all else equal, be more likely to occupy sites with large values of Env).

For each scenario, we simulated data using 16, 32, or 64 species. In each case we simulated 100 datasets and compared the performance of the POM to a simple MSOM. We first assessed the quality of β_{Trait} estimates across both models using Root Mean Square Error. We assessed the quality of inference by both quantifying the proportion of the 100 analyses for which the true value of β_{Trait} were contained in the 95% BCI derived from the POM and MSOM (indicative of type I error), and by examining the proportion of analyses for which the BCI around β_{Trait} excluded 0 (power).

Results

What are the consequences of ignoring imperfect detection in phylogenetic community analyses?

Phylogenetic signal, or correlation between closely related species in their response to the environment, is governed by the parameter λ. Statistical power to detect phylogenetic signal was maximized when number of species was large but was relatively unaffected by the number of sites surveyed (Appendix S1: Fig. S1). To assess whether accounting for imperfect detection improved the estimates of λ in the data, we compared the POM with two PGLMMs that do not explicitly account for the detection process, and with post-hoc analysis of single species regressions against the environment. Ignoring imperfect detection can bias estimates of phylogenetic signal (Fig. 2). Estimates of λ using PGLMMs tend to be lower than those using the POM. The PGLMM deviates most strongly from the true value of λ when detection probabilities vary along the environmental gradient in a species-specific manner (when $\sigma p_{Env} > 0$). In these cases the PGLMM estimates phylogenetic signal with a strong downward bias. For example, when σp_{Env} is approximately of the same magnitude as $\sigma_{\psi Env}$ (e.g., when both equal 3) estimates of phylogenetic signal by the PGLMMs are, on average, cut by more than half compared to both the true value and the value estimated by the POM. Post-hoc testing for phylogenetic signal generates even more downward-biased estimates than the PGLMMs for most parameter combinations tested.

With only 16 species, variance in λ estimates are high (interquartile ranges of posterior modes across model runs can span most of λ parameter space, Fig. 2). But as additional species are included in the dataset, estimation improves. Further, POM estimates are most accurate when there is strong phylogenetic signal in response to the environmental gradient.

The PGLMMs generally have lower statistical power than the POM when inferring the magnitude of the phylogenetic signal in response to environmental gradients (Fig. 3). This behavior was most severe when species' detection probabilities vary along the environmental gradient. When the true value of λ was 0, and the number of species in the dataset was large, the POM generally displayed a type I error rate approximating 0.05 when using the 95% HPD. However when only 16 species were included type I error was often inflated above 0.05 for both the POM and the PGLMMs. In these cases 0 was not included in the 95% HPD in up to 20% of simulations. Power when conducting post-hoc tests of phylogenetic signal from serial regressions typically followed that of the PGLMMs, with the exception that when phylogenetic signal was strong, post-hoc testing had quite low power, even in cases when PGLMMs perform well (i.e., when all species' detectabilities change identically across the gradient; $\sigma_{pEnv} = 0$).

How well does the POM estimate the effect of a trait on species' responses to an environmental gradient?

How a species' trait governs its response to the environment is determined by the parameter β_{Trait}, such that high values of β_{Trait} lead to increasing occupancy probabilities with high values of Env. To ask whether the POM can

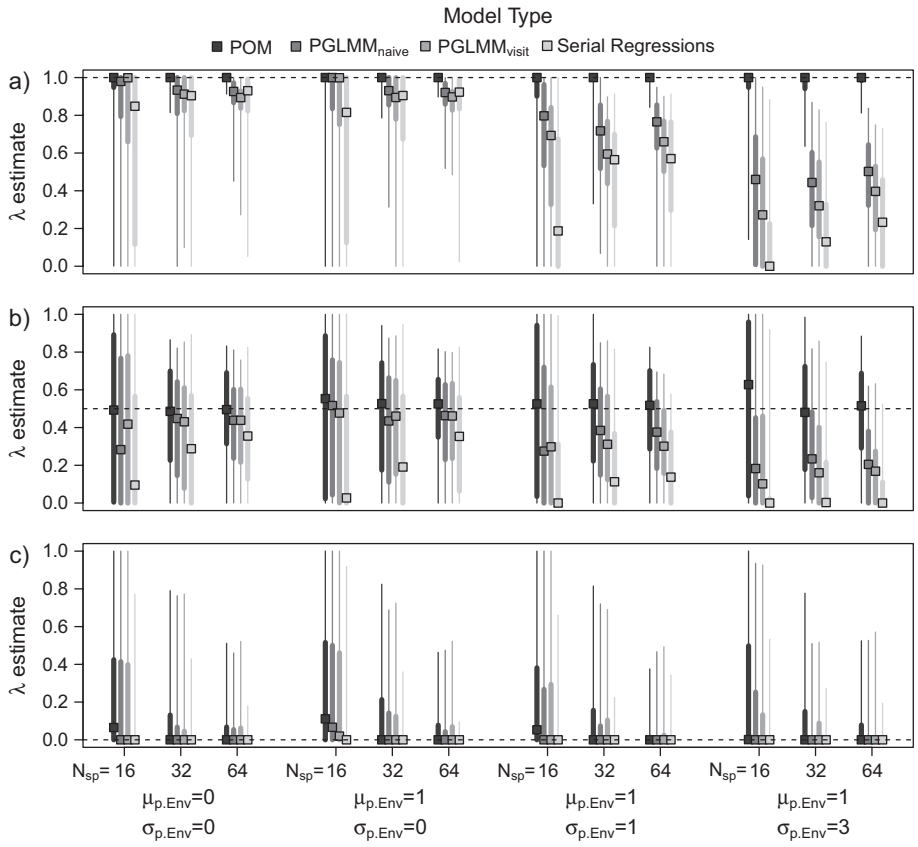

FIG. 2. Modeling the detection process improves estimation of phylogenetic signal. Estimates of λ are depicted from POM, both varieties of PGLMMs, and testing for phylogenetic signal from single species regressions parameters (serial regressions), under alternative simulation scenarios. We varied the species mean change in detectability across the environmental gradient ($\mu_{p.Env}$), species-specific variation around this mean response ($\sigma^2_{p.Env}$), and the true value of λ (panel a: λ = 1.0, panel b: λ = 0.5, panel c: λ = 0.0). Central points in distributions represent medians of the posterior HPP for λ across 100 data simulations and model runs (thick bars represent interquartile ranges, and thin bars indicate 95% quantiles. In each panel the dashed line indicates the true value of λ.

estimate how strongly species respond to an environmental gradient when response is mediated by species' trait values, we examined model performance with and without a phylogenetic signal in the species' trait values (λ_{Trait} = 1 or 0) and with and without a phylogenetically conserved residual response to the gradient ($\varepsilon_{Env}[i]$ derived from λ = 0 or 1, see Eqs 3 and 4). When there is no phylogenetic signal in either the trait of interest or in $\varepsilon_{Env}[i]$, the MSOM and the POM perform equivalently (Fig. 4a, b, c). However, when there is a phylogenetic signal in the trait only, the MSOM outperforms the POM. In this case POM estimates of β_{Trait} have slightly greater root mean square error, and the POM has less power than the MSOM (Fig. 4a, b). This is not surprising, because the entire phylogenetic signal is encapsulated in the species' trait values, which are already accounted for in the fixed effect β_{Trait}. Therefore the POM is over-parameterized relative to the MSOM, as both β_{Trait} and $\varepsilon_{Env}[i]$ are competing to explain the same variance.

When there is phylogenetic signal in response beyond the trait itself (i.e., in $\varepsilon_{Env}[i]$), the POM outperforms the MSOM. If there is no phylogenetic signal in the trait, then the POM provides the benefit of reduced RMSE in the estimation of β_{Trait}, and increased statistical power (Fig. 4a, c). If there is signal in both the trait and $\varepsilon_{Env}[i]$, the benefit of the POM comes from avoiding a perception of accuracy when it does not, in fact, exist. In this case the MSOM has high RMSE and inflated type I error (Fig. 4a, b). For example, with 32 species the estimated credible interval for the effect of the trait (β_{Trait}) did not include the true value for roughly half of all models runs using a MSOM. Apparent increases in power in these cases (Fig. 4c) are pyrrhic, generated from high rates of type I error. While the MSOM often makes the correct inference that β_{Trait} does not equal 0, its actual estimates of β_{Trait} are widely off the mark, often with the wrong overall direction of the effect (i.e., negative instead of positive). Further, because uncertainty in parameter estimates decreases with increasing sample size, this pathological behavior becomes more problematic as more species are included in the dataset.

DISCUSSION

Here we have developed and tested a framework for incorporating phylogenetic information into a hierarchical species occupancy model. Specifically, we have

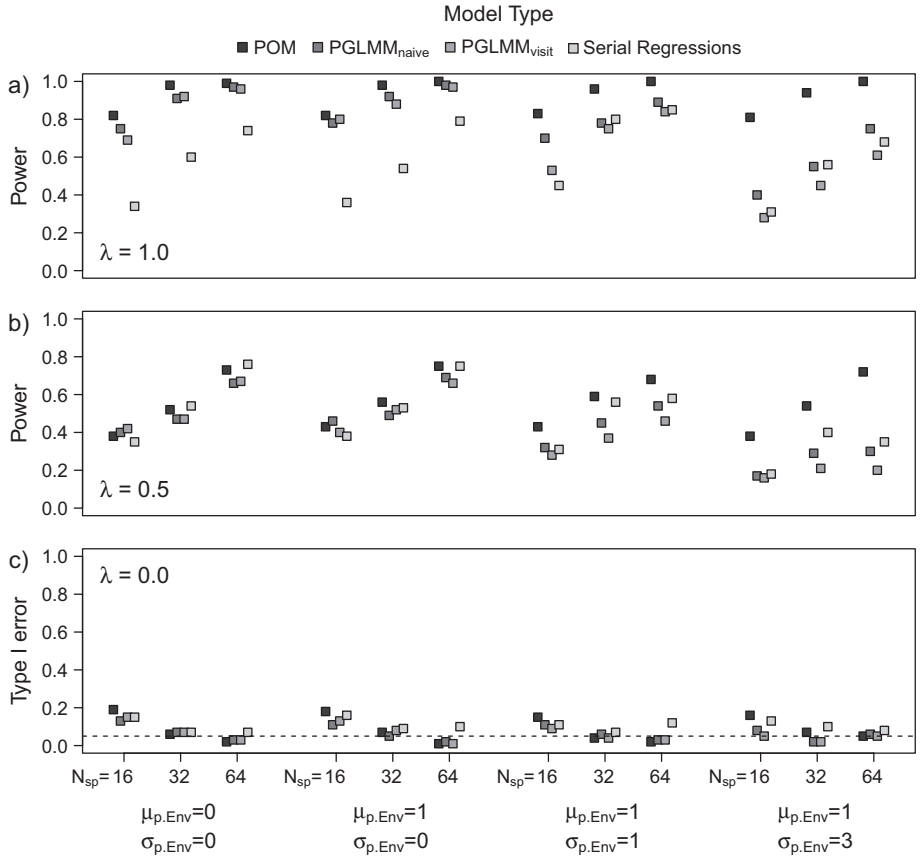

FIG. 3. Modeling the detection process improves inference of phylogenetic signal. Points represent the proportion of data simulations and model runs (out of 100) for which the 95% HPD (for POM and PGLMMs), or the 95% CI (for phylogenetic signal test from serial regressions) did not include λ = 0. Panels show power for different simulated values of λ: a) λ = 1.0, b) λ = 0.5, c) λ = 0. *X*-axis labels, and shading equivalent to Fig. 2.

extended standard multi-species occupancy models so that species can respond to an environmental gradient in a way that is phylogenetically conserved and, potentially, modulated by a phenotypic trait. Our framework incorporates imperfect species detection, a topic that has gained significant attention in the ecological statistics literature in recent years (Royle and Dorazio 2008). We show that when the number of species analyzed is sufficiently large (>16 in our tests), the POM can effectively distinguish between scenarios in which species respond to an environmental gradient in a phylogenetically conserved manner from scenarios in which they do not. Furthermore, we find that incorporating species detection and phylogenetic signal often results in improved parameter estimates.

Accounting for imperfect detection can improve estimates of phylogenetic signal

Species are seldom detected perfectly in natural communities. Incorporating this imperfect detection can have dramatic effects on ecological studies, occasionally even leading to complete flips in the directions of inferred patterns and overall conclusions (Tingley and Beissinger 2013). While effects of imperfect detection have not been investigated in phylogenetic community analyses, in some cases they could also be significant.

Here we have shown that, by explicitly accounting for imperfect detection, we can improve estimates of the strength of phylogenetic signal in how species respond to an environmental gradient. Furthermore, accounting for imperfect detection is most crucial when the number of species is large, when phylogenetic signal is strong, and when detection probability is affected by the same environmental gradient that affects species occupancy. However, when phylogenetic signal is not strong and species detection probabilities do not vary with environment, a simple PGLMM that does not account for detection returns estimates of phylogenetic signal that are only slightly downward biased. Further, in small analyses, such as when there are only 16 species, type I error rates on phylogenetic signal for both POMs and PGLMMs can be inflated. Analysis of such small datasets should therefore be conducted with caution. Increasing the number of sites surveyed had relatively modest effects on statistical power to detect phylogenetic signal (see Appendix S1). This suggests that when phylogenetically

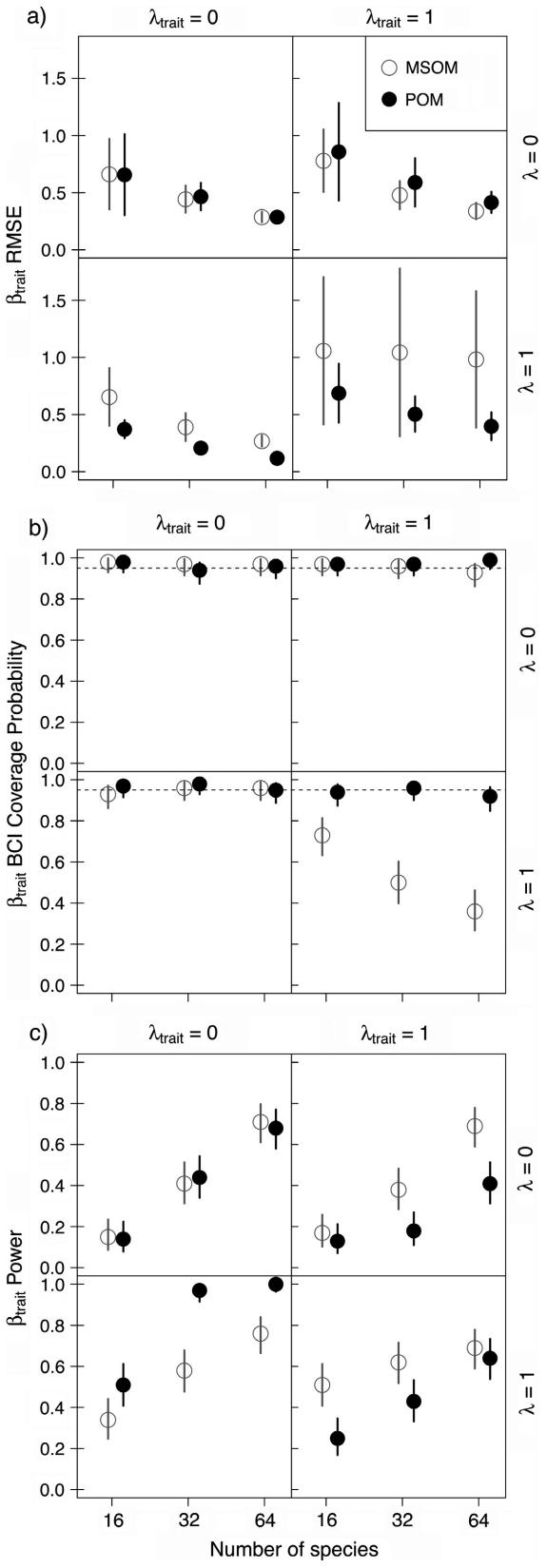

FIG. 4. When phylogenetic signal exists, incorporating phylogeny improves estimates of trait effects on how species respond to an environmental gradient. (a) Points represent average root mean square error of β_{Trait} across 100 simulated datasets (±variance). Lower values indicate better model performance. (b) Points represent the proportion of 100 simulated datasets for which the 95% BCI of β_{Trait} included the true value (±95% CIs). Values below 0.95 are indicative of high rates of type I error. (c) Points represent proportion of 100 simulated datasets for which the 95% BCI did not include 0, indicating a significant effect of the trait in determining how species respond to the gradient. In all cases, data were simulated with $\beta_{Trait} = 1$. Note that in the case of $\lambda = 1$, $\lambda_{Trait} = 1$, the apparent high degree of power for the MSOM (in c) is attributable to the highly inaccurate β_{Trait} estimates (in a and b).

conserved responses to an environmental gradient do exist, such effects can be detected even with a relatively small number of surveyed sites, so long as they sufficiently span the gradient in question.

Empiricists may wonder whether choosing to use the simpler PGLMM instead of the more complex POM might suffice for a specific set of data. In many cases the PGLMM has only slightly downward biased estimates of λ and, thus, if assessing the degree of phylogenetic signal is the primary goal, neglecting to account for the detection process will not significantly change conclusions. Unfortunately, in other scenarios, the PGLMM can be strongly biased. Because the only way to differentiate between these two scenarios is to run and compare both the POM and the PGLMM, we advocate doing so.

When accounting for the detection process, there is always a risk that the detection component will be misspecified. In such cases, the POM might return biased or overly uncertain credible intervals. Problems with misspecification can be addressed through various model selection procedures (see Hooten and Hobbs 2015). Importantly, ignoring the detection component altogether almost certainly ensures that this part of the model is misspecified.

When specifying a model, careful attention must be given to ensuring that appropriate fixed and random effects are included. These decisions should be based on the nature of available information and on the biological properties of the system (e.g., how the covariates are expected to influence the response variables). We suggest empirical biologists without prior experience using occupancy models consult Kéry and Schaub (2011) for background in how to set up a basic occupancy models. From that point, they can use the methods we provide here to add phylogenetic components. Hooten and Hobbs (2015) provide guidelines that can be used for model selection and determining whether various occupancy and detection components improve model fit.

Phylogeny improves estimates of multispecies occupancy models

We find that incorporating phylogenetic information into occupancy models can improve estimates of the role

species traits play in determining community structure. When there is phylogenetic signal in species' responses to an environmental gradient above and beyond that which is explained by the measured trait(s), failure to account for this will lead to imprecise and/or inaccurate inferences. In this respect, the behavior of the POM closely follows the behavior of simple linear models such as phylogenetic generalized least squares (Revell 2010). When there is not phylogenetic signal in the residuals, using the POM can result in a slight loss of power, and slightly greater error in estimating the effect of the trait. Testing whether the 95% HPD of λ overlaps with 0 (or using Bayes factors) provides a means of conducting model selection when deciding whether to use the POM or a MSOM, such that an inferior model can be avoided.

As long as a phylogeny already exists for a group of species, there is no significant cost to testing for the effects of phylogeny (beyond implementation). Situations where inclusion of a phylogenetic effect would lead to a less appropriate model can be avoided by using model selection criteria (e.g., removing phylogenetic effect if the 95% HPD includes $\lambda = 0$, or if associated Bayes factor is below some specified threshold). The biggest potential cost, in our opinion, is computation time. Even relatively small communities can lead to inherently large data matrices, because the number of potential detections is equal to the number of species × number of sites × number of seasons × number of visits per season (in the case of the 32 spp × 15 sites × 3 seasons × 3 visits, this equals 4320 data points). Further, the size of the $\mathbf{C}_{\text{phylo}}$ matrix is on the order of number-of-species^2 and thus, when there are many (> 64), running a POM until convergence is reached can take several CPU hours.

Extensions

The phylogenetic occupancy models we have developed here are relatively simple parameterizations that can be used to address commonly asked questions in community ecology. In addition, such models are flexible and can easily be expanded to test other questions of interest beyond whether phylogenetic signal exists in species' slope terms (see PGLMM I-V of Ives and Helmus 2011). Such possibilities might include assessing whether there are phylogenetic patterns in species co-occurrence within sites or whether species exhibit phylogenetic repulsion (an indicator that there might be competition between closely related species).

Similarly, the type of correlation structure used to estimate phylogenetic signal could be expanded to allow for heterogeneity in phylogenetic signal or rates of evolution across the tree or to potentially incorporate stabilizing selection with multiple trait optima (Butler and King 2004). Such approaches could then be used to ask whether clades behave differently from one another (e.g., does one clade have very high phylogenetic signal in response to environmental gradient compared to another clade). While we restrict our analyses of phylogenetic signal to species-specific responses to the environment, it is also reasonable to ask whether other attributes of species might be phylogenetically conserved. For example, it is conceivable that detection probabilities might possess phylogenetic signal because apparency (e.g., colorfulness, loudness) may be phylogenetically conserved. Additionally, closely related species may modulate each others' detectability when both are present in communities, either because competition decreases abundances, or because species undergo behavioral changes when in the presence of competitors (Yackulic et al. 2014). Allowing detection probabilities to be phylogenetically correlated offers an alternative (or complementary) strategy to categorically grouping species based on their microhabitat preferences or dietary guilds in hierarchical community models (Pacifici et al. 2014).

Additionally, minor reparameterizations of the POM can be instituted. For example, in some systems, responses to environmental gradients may not be monotonic—instead some species might specialize on the midpoint of a gradient. In such cases, non-linear environmental terms could be introduced to the model. Likewise, assumptions regarding species' intercepts (i.e., occupancy probability halfway along the environmental gradient; $\psi_0[i]$) could also be altered. In the POM described above, we treat each species' intercept as a fixed effect, such that it is freely estimated from the data. This could, alternatively, be parameterized as a random occupancy intercept of species so that species inform one another, optionally with phylogenetic signal. This alternative parameterization would be preferred if investigators suspected that species' trait values influence overall occupancy probability.

Finally, occupancy models are part of a more general class of zero-inflated models, which includes N-mixture and mark-recapture analyses. Incorporating phylogenetic information into these related classes of hierarchical models will improve estimates of abundance, population extinction, or individual survival rates through time (e.g., Abadi et al. 2014).

When testing for a phylogenetic signal in real datasets, it is advisable to evaluate the type I error around λ estimates. Inference of phylogenetic signal is challenging even using well-established frequentist methods and relatively simple models, as likelihood ratios between models with different parameterizations of phylogenetic signal rarely follow expected distributions. This has led some (e.g., Boettiger et al. 2012) to propose parametric bootstrapping using simulated data to generate null distributions of likelihood ratios between nested models. Similar methods could be instituted to compare the POM and an MSOM, using Bayes factors in place of likelihood ratios. This procedure would ensure that increased type I error using 95% HPD on λ does not lead to acceptance of the importance of phylogeny when it is not in fact warranted.

Conclusion

We have designed and tested a Phylogenetic Occupancy Model that explores how species' traits and site

characteristics shape community structure and composition, while explicitly accounting for imperfect detection and phylogenetic correlations. We found that accounting for imperfect detection decreases biases in estimates of phylogenetic signal. Similarly, occupancy models that do not account for phylogenetic non-independence can make incorrect inferences about how strongly a trait might predispose a particular species to respond to an environmental gradient. If one seeks to estimate how individual species will respond to an environmental gradient, accounting for detection is necessary in order to ensure that occupancy estimates are not biased by correlates with detectability, while accounting for phylogeny can increase both precision and accuracy of model parameters. Using available phylogenetic information, therefore, provides a powerful means to improve model estimates. Integration of phylogenetic structure with real world community data will lead to better inferences about how species react to environmental gradients.

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Literature Cited

Abadi, F., et al. 2014. Importance of accounting for phylogenetic dependence in multi-species mark-recapture studies. Ecological Modelling 273:236–241.

Bates, D., M. Maechler, and B. Bolker. 2012. lme4: Linear mixed-effects models using S4 classes.

Bennett, J. A., E. G. Lamb, J. C. Hall, W. M. Cardinal-McTeague, and J. F. Cahill. 2013. Increased competition does not lead to increased phylogenetic overdispersion in a native grassland. Ecology Letters 16:1168–1176.

Boettiger, C., G. Coop, and P. Ralph. 2012. Is your phylogeny informative? Measuring the power of comparative methods. Evolution 66:2240–2251.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127–135.

Butler, M. A., and A. A. King. 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. American Naturalist 164:683–695.

Cadotte, M. W., and S. Y. Strauss. 2011. Phylogenetic patterns of colonization and extinction in experimentally assembled plant communities. PLoS ONE 6:e19363.

Cavender-Bares, J., K. H. Kozak, P. V. A. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12:693–715.

de Valpine, P. 2012. Frequentist analysis of hierarchical models for population dynamics and demographic data. Journal of Ornithology 152:393–408.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1–15.

Frishkoff, L. O., D. S. Karp, L. K. M'Gonigle, C. D. Mendenhall, J. Zook, C. Kremen, E. A. Hadly, and G. C. Daily. 2014. Loss of avian phylogenetic diversity in neotropical agricultural systems. Science 345:1343–1346.

Harmon, L., J. T. Weir, C. D. Brock, R. E. Glor, and C. Wendell. 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24:129–131.

Helmus, M. R., K. Savage, M. W. Diebel, J. T. Maxted, and A. R. Ives. 2007. Separating the determinants of phylogenetic community structure. Ecology Letters 10:917–925.

Helmus, M. R., W. B. Keller, M. J. Paterson, N. D. Yan, C. H. Cannon, and J. A. Rusak. 2010. Communities contain closely related species during ecosystem disturbance. Ecology Letters 13:162–174.

Hooten, M. B., and N. T. Hobbs. 2015. A guide to bayesian model selection. Ecological Monographs 85:3–28.

Iknayan, K. J., M. W. Tingley, B. J. Furnas, and S. R. Beissinger. 2013. Detecting diversity: emerging methods to estimate species diversity. Trends in Ecology & Evolution 29:97–106.

Ives, A., and M. Helmus. 2011. Generalized linear mixed models for phylogenetic analyses of community structure. Ecological Monographs 81:511–525.

Kéry, M., and M. Schaub. 2011. Bayesian Population Analysis using WinBUGS: A hierarchical perspective:1–554.

Lele, S. R., B. Dennis, and F. Lutscher. 2007. Data cloning: easy maximum likelihood estimation for complex ecological models using Bayesian Markov chain Monte Carlo methods. Ecology Letters 10:551–563.

Little, R. J. 2006. Calibrated Bayes: a Bayes/frequentist roadmap. American Statistician 60:213–223.

MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101:377–385.

MacKenzie, D., J. Nichols, J. Royle, K. Pollock, L. Bailey, and J. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, Burlington, Massachusetts, USA.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13:1085–1093.

Narwani, A., M. A. Alexandrou, T. H. Oakley, I. T. Carroll, and B. J. Cardinale. 2013. Experimental evidence that evolutionary relatedness does not affect the ecological mechanisms of coexistence in freshwater green algae. Ecology Letters 16:1373–1381.

Pacifici, K., E. F. Zipkin, J. A. Collazo, J. I. Irizarry, and A. Dewan. 2014. Guidelines for a priori grouping of species in hierarchical community models. Ecology and Evolution 4:877–888.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature 401:877–884.

Peay, K. G., M. Belisle, and T. Fukami. 2012. Phylogenetic relatedness predicts priority effects in nectar yeast communities. Proceedings of the Royal Society B: Biological Sciences 279:749–758.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing, March:20–30.

Revell, L. J. 2010. Phylogenetic signal and linear regression on species data. Methods in Ecology and Evolution 1:319–329.

Rota, C. T., C. K. Wikle, R. W. Kays, T. D. Forrester, W. J. McShea, A. W. Parsons, and J. J. Millspaugh. 2016. A two-species occupancy model accommodating simultaneous spatial and interspecific dependence. Ecology 97:48–53.

Royle, J., and R. Dorazio. 2008. Hierarchical modeling and inference in ecology. The analysis of data from populations, metapopulations and communities. Academic Press, London, UK.

Rubin, D. B. 1984. Bayesianly justifiable and relevant frequency calculations for the applied statistician. Annals of Statistics 12:1151–1172.

Su, Y.-S., and M. Yajima 2014. R2jags: A Package for Running jags from R.

Tingley, M. W., and S. R. Beissinger. 2013. Cryptic loss of montane avian richness and high community turnover over 100 years. Ecology 94:598–609.

Vamosi, S. M., S. B. Heard, J. C. Vamosi, and C. O. Webb. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. Molecular Ecology 18:572–592.

Webb, C. O. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. American Naturalist 156:145–155.

Yackulic, C. B., J. Reid, J. D. Nichols, J. E. Hines, R. Davis, and E. Forsman. 2014. The roles of competition and habitat in the dynamics of populations and species distributions. Ecology 95:265–279.

Supporting Information

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