

Methods in Ecology and Evolution

Integrated community occupancy models: A framework to assess occurrence and biodiversity dynamics using multiple data sources

Jeffrey W. Doser^{1, 2}, Wendy Leuenberger^{2, 3}, T. Scott Sillett⁴, Michael T. Hallworth⁵,
Elise F. Zipkin^{2, 3}

¹Department of Forestry, Michigan State University, East Lansing, MI, USA

²Ecology, Evolution, and Behavior Program, Michigan State University, East Lansing, MI, USA

³Department of Integrative Biology, Michigan State University, East Lansing, MI, USA

⁴Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC, USA

⁵Vermont Center for Ecostudies, Norwich, VT, USA

Corresponding Author: Jeffrey W. Doser, email: doserjef@msu.edu; ORCID ID: 0000-0002-8950-9895

Running Title: Integrated community occupancy models

Abstract

1. The occurrence and distributions of wildlife populations and communities are shifting as a result of global changes. To evaluate whether these shifts are negatively impacting biodiversity processes, it is critical to monitor the status, trends, and effects of environmental variables on entire communities. However, modeling the dynamics of multiple species simultaneously can require large amounts of diverse data, and few modeling approaches exist to simultaneously provide species and community level inferences.
2. We present an “integrated community occupancy model” (ICOM) that unites principles of data integration and hierarchical community modeling in a single framework to provide inferences on species-specific and community occurrence dynamics using multiple

data sources. The ICOM combines replicated and nonreplicated detection-nondetection data sources using a hierarchical framework that explicitly accounts for different detection and sampling processes across data sources. We use simulations to compare the ICOM to previously developed hierarchical community occupancy models and single species integrated distribution models. We then apply our model to assess the occurrence and biodiversity dynamics of foliage-gleaning birds in the White Mountain National Forest in the northeastern USA from 2010-2018 using three independent data sources.

3. Simulations reveal that integrating multiple data sources in the ICOM increased precision and accuracy of species and community level inferences compared to single data source models, although benefits of integration were dependent on the information content of individual data sources (e.g., amount of replication). Compared to single species models, the ICOM yielded more precise species-level estimates. Within our case study, the ICOM had the highest out-of-sample predictive performance compared to single species models and models that used only a subset of the three data sources.
4. The ICOM provides more precise estimates of occurrence dynamics compared to multi-species models using single data sources or integrated single-species models. We further found that the ICOM had improved predictive performance across a broad region of interest with an empirical case study of forest birds. The ICOM offers an attractive approach to estimate species and biodiversity dynamics, which is additionally valuable to inform management objectives of both individual species and their broader communities.

Keywords: avian, Bayesian, data fusion, data integration, hierarchical modeling, imperfect detection, joint likelihood

Introduction

Populations and communities of a wide range of organisms, including birds (Rosenberg et al., 2019), bats (Rodhouse et al., 2019), and insects (Wagner et al., 2021), have experienced severe declines in their distributions and abundances across large geographical regions as a result of habitat loss, climate change, and other anthropogenic stressors. As a result, there is growing interest in developing enhanced monitoring techniques to estimate species' trends and distributions. While species-level assessments can be valuable, it is critical to quantify the status and dynamics of entire communities to understand global change effects on biodiversity. However, multi-species approaches require large numbers of observations for each species or make assumptions about equal detectability of species during sampling, precluding robust assessments of rare species and overall community dynamics (Sor et al., 2017).

Despite these limitations, many sampling approaches (e.g., autonomous recording units for birds and bats, camera traps for mammals) naturally provide data on the occurrence patterns of multiple species in a community. However, occurrence data for each species are confounded by imperfect detection during sampling. An observer may record a species as absent if it is indeed absent, or the observer may fail to detect the species during sampling, and thus we refer to such data as detection-nondetection data. Replicated sampling can provide additional information on species' detection rates, allowing for the separation of the occurrence process from the detection process to enable ecologically relevant inferences. Most commonly, this information is obtained by collecting multi-species detection-nondetection data on several occasions over short time periods when closure—no permanent extinction or colonization—can be reasonably assumed (MacKenzie and Royle, 2005). By accounting for imperfect detection of species during sampling, these data (hereafter “replicated data”) allow for estimation of species distributions and occurrence patterns within an occupancy modeling framework (MacKenzie et al., 2002). This additional information required to separate detection from occurrence is often more costly and time consuming to collect, which motivates the desire to use nonreplicated detection-nondetection data to model species distribution patterns. Accordingly, there is widespread interest in determining statistically robust ways to incorporate nonreplicated data sources into species and community level analyses to inform effective biodiversity conservation.

Two recent statistical modeling developments, data integration and hierarchical community occupancy models, have led to improved inference on individual species and community

dynamics, respectively, to help inform biodiversity assessments. Data integration is a model-based approach to combining multiple data types (Zipkin and Saunders, 2018; Miller et al., 2019). This approach yields many key benefits compared to single data source models, such as higher accuracy and precision of parameter estimates (Dorazio, 2014), inference across broader spatio-temporal extents (Zipkin et al., 2021), and the opportunity to accommodate sampling biases and imperfect detection for the various data sources (Miller et al., 2019). Data integration is particularly useful for combining large-scale nonreplicated data with replicated data, as the replicated data allow for the explicit modeling of imperfect detection while still using the information contained in the nonreplicated data. The combination of these data types can thus greatly expand the spatial scope of analysis.

Hierarchical community occupancy models provide combined inference on the occurrence of multiple species using a single replicated detection-nondetection data source (Dorazio and Royle, 2005; Gelfand et al., 2005). Species-specific parameters are viewed as random effects arising from a common, community-level distribution with a mean and variance parameter representing the average effect across species in the community and the variation of species-specific effects within the community, respectively (Dorazio and Royle, 2005). In addition to providing more precise estimates of species-specific effects (Zipkin et al., 2009), these models can estimate community-level parameters, as well as biodiversity metrics (Guillera-Arroita et al., 2019), all with associated uncertainty. Community occupancy models have led to improved insights into understanding species occurrence patterns for insects (Mata et al., 2017), birds (Frishkoff et al., 2016), mammals (Gallo et al., 2017), and a variety of other taxa (Devarajan et al., 2020).

While substantial development of both data integration and hierarchical community models has occurred over the last decade (reviewed in Zipkin and Saunders 2018; Guillera-Arroita et al. 2019; Miller et al. 2019), there has been comparatively less research focused on modeling multiple species using more than one data source. Multi-species integrated population models have been used to assess competition (Péron and Koons, 2012), synchrony (Lahoz-Monfort et al., 2017), and predator-prey dynamics (Barraquand and Gimenez, 2019; Clark, 2021), but these approaches are not designed for assessment of larger communities. Clark et al. (2017) introduced generalized joint attribute modeling (GJAM), a broad framework for using multiple data sets to estimate the distribution and abundance of multiple species, but their approach does

not model the observation process hierarchically, making it difficult to account for differences in sampling protocols and species detections among data sources. Thus, a new modeling approach that combines the benefits of data integration and hierarchical community modeling in a single framework has the potential to yield detailed inferences on individual species occurrence patterns while simultaneously providing inference on community dynamics.

Here we develop an “integrated community occupancy model” to simultaneously estimate occurrence patterns of multiple species within a community as well as community metrics by incorporating multiple available data sources into a single analysis. Our modeling framework combines one or more “replicated” detection-nondetection data sources with one or more “non-replicated” data sources. The integrated model consists of a single, ecological process model and multiple observation models that explicitly account for different detection processes in each data source. The detection models are linked to the process model using a joint-likelihood framework (Miller et al., 2019). Our ecological process model is a dynamic community occupancy model in which we explicitly model the latent occurrence process as a function of space and/or time varying covariates and a temporal autologistic parameter (Royle and Dorazio, 2008). We validate our model using simulations and assess its ability to estimate species-specific and community level dynamics using different amounts of data sources. We then compare inferences from our integrated community occupancy model to those generated by single species integrated models to evaluate the marginal benefits of the approach. We apply our model to an empirical case study of a community of twelve foliage-gleaning insectivorous birds in the White Mountain National Forest in the northeastern USA to assess patterns and trends in species occurrence and community metrics (i.e., richness, composition) from 2010-2018. Our integrated community occupancy model provides a rigorous approach to elucidate both species specific and community level dynamics that can provide crucial insights on the specific mechanisms driving biodiversity shifts and population declines.

Materials and Methods

Integrated community occupancy model

We develop an “integrated community occupancy model” (ICOM) that leverages one or more replicated detection-nondetection data sources with one or more nonreplicated detection-nondetection

data sources to provide inferences on species-specific and community occurrence dynamics. We present the model using one replicated and one nonreplicated data source, but our framework can be extended to incorporate additional data sources (if available) in an analogous manner. The ICOM consists of a single ecological process model for individual species, which is shared across the various data sets. Here, we demonstrate the model with a dynamic ecological process that describes species occurrences as a function of spatio-temporally varying covariates and an autologistic parameter that accounts for temporal correlation (Royle and Dorazio, 2008). This process model is then linked to individual likelihoods for each data set via a hierarchical framework that assumes independence among the detection processes and which is conditional on the true latent occurrence state (i.e., whether a species is truly present or absent at sampling locations; Miller et al. 2019). To link the individual species models, we assume species-level occurrence and detection parameters are random effects coming from common, community level distributions (Dorazio and Royle, 2005; Gelfand et al., 2005), enabling information sharing across the community to increase precision of species effects and estimation of biodiversity attributes.

Ecological Process Model

Our goal is to model the occurrence dynamics of multiple species at sites $j = 1, \dots, J$ within a specified region of interest A . Let $z_{i,j,t}$ denote the true presence (1) or absence (0) of species i at site j during year t , where $i = 1, \dots, I$ and $t = 1, \dots, T$. We assume $z_{i,j,t}$ arises from a Bernoulli process following

$$z_{i,j,t} \sim \text{Bernoulli}(\psi_{i,j,t}), \quad (1)$$

where $\psi_{i,j,t}$ is the probability species i occurs at site j in year t . For the first year, we model $\psi_{i,j,t}$ according to

$$\text{logit}(\psi_{i,j,1}) = \beta_{0i,1} + \beta_i \cdot \mathbf{x}_{j,1}, \quad (2)$$

where $\beta_{0i,1}$ is the species-specific occurrence probability (on the logit scale) in the first year (at average covariate values) and β_i is a vector of species-specific regression coefficients that describe the effect of standardized covariates (i.e., mean 0 and standard deviation 1) $\mathbf{x}_{j,1}$

on the occurrence probability of species i . In subsequent years, the occurrence probability for species i in year t at site j depends on whether or not the species was present at the site j in the previous year $t - 1$ in addition to covariates (which can vary spatially and/or temporally). We accommodate the temporal dependence by incorporating a species-specific autologistic parameter ϕ_i into the occurrence model, such that for $t > 1$

$$\text{logit}(\psi_{i,j,t}) = \beta_{0i,t} + \beta_i \cdot \mathbf{x}_{j,t} + \phi_i \cdot z_{i,j,t-1}, \quad (3)$$

where $\beta_{0i,t} + \phi_i$ is the species-specific intercept in year t when species i occurred at site j in the previous year $t - 1$ and $\beta_{0i,t}$ is the intercept in year t when species i did not occur at site j in the previous year $t - 1$. We use the autologistic parameterization of the dynamic community occupancy model as it allows us to assess covariate effects directly on species occurrence probabilities (i.e., the covariate effects remain the same regardless of the value of $z_{i,j,t-1}$) and derive species-specific trends post-hoc from the occurrence probabilities ($\psi_{i,j,t}$). However, the ecological process model can be readily modified to incorporate relevant biological processes of interest (provided sufficient data are available; Royle and Dorazio 2008). For example, the ecological process model can be modified to explicitly include a trend effect (covariate on year), assess covariate effects on colonization and persistence (Dorazio et al., 2010), or the autologistic component can be removed if that is not relevant to the target community.

Observation Model: replicated detection-nondetection data

For the replicated data type, we assume $K > 1$ “sampling replicates” within each year t are available at a subset of sites $r = 1, \dots, R$. The sampling replicates can be observations from multiple independent surveys, multiple independent observers, spatial subsamples, or sampling intervals from a removal design, which enable separate estimation of occurrence and detection probabilities (MacKenzie et al., 2002). We assume the R sites are a subset of the total J sites (i.e., $R \leq J$), which may cover the entire region of interest A or, more commonly, only a portion of it. Let $y_{i,r,k,t}$ denote the detection (1) or nondetection (0) of species i during replicate k at site r during year t . We model $y_{i,r,k,t}$ as

$$y_{i,r,k,t} \sim \text{Bernoulli}(p_{i,r,k,t} \cdot z_{i,j[r],t}), \quad (4)$$

where $p_{i,r,k,t}$ is the probability of detecting species i during visit k at site r in year t and $z_{i,j[r],t}$ is the true occurrence status of species i in year t at site j corresponding to the r th replicated data site.

Species detection probabilities can vary by site and/or sampling covariates following

$$\text{logit}(p_{i,r,k,t}) = \alpha_{0i,t} + \boldsymbol{\alpha}_i \cdot \boldsymbol{w}_{r,k,t} \quad (5)$$

where $\alpha_{0i,t}$ is the species-specific detection probability (on the logit scale) in year t at average covariate values and $\boldsymbol{\alpha}_i$ is a vector of parameters that describe the effect of standardized covariates $\boldsymbol{w}_{r,k,t}$ on the detection probability of species i .

Observation Model: nonreplicated detection-nondetection data

Let $v_{i,m,t}$ be the detection (1) or non-detection (0) of species i at site m in year t for the nonreplicated data source, where $m = 1, \dots, M$. We assume the M sites are a subset of all J sites of interest (i.e., $M \leq J$) within the area of interest A . The replicated data may be available at different sites than the nonreplicated data in the same region A , the same sites, or a subset of the same sites in A .

We model the detection-nondetection data $v_{i,m,t}$ according to

$$v_{i,m,t} \sim \text{Bernoulli}(\pi_{i,m,t} \cdot z_{i,j[m],t}), \quad (6)$$

where $\pi_{i,m,t}$ is the probability of detecting species i in site m in year t for the nonreplicated data set and $z_{i,j[m],t}$ is the true occurrence status of species i in year t at the site j corresponding to the m th nonreplicated data site. Detection probability $\pi_{i,m,t}$ can vary by species, site, and time following

$$\text{logit}(\pi_{i,m,t}) = \gamma_{0i,t} + \boldsymbol{\gamma}_i \cdot \boldsymbol{s}_{m,t}, \quad (7)$$

where $\gamma_{0i,t}$ is a species and year specific intercept and γ_i is a vector of parameters that describe the effect of standardized covariates $\mathbf{s}_{m,t}$ on the detection probability of species i .

Nonreplicated data alone are unable to separate occurrence probabilities from detection probabilities as the model structure is generally unidentifiable (Dorazio, 2014). While detection and occurrence parameters can be weakly identifiable under certain circumstances (e.g., detection varies with covariates, large number of sites and years; Lele et al. 2012; Kéry and Royle 2021), estimates often do not converge or have unreasonably large credible intervals, such that inferences are not ecologically useful.

Linking species models across the community

Following the structure of the hierarchical community occupancy model (Dorazio and Royle, 2005; Gelfand et al., 2005), species-specific parameters in both the ecological process model and observation models are treated as random effects arising from community level normal distributions with associated community level mean and variance parameters. For example, $\beta_{0i,t}$, the intercept on occurrence probabilities for species i in year t , is modeled as

$$\beta_{0i,t} \sim \text{Normal}(\mu_{\beta_{0t}}, \sigma_{\beta_{0t}}^2), \quad (8)$$

where $\mu_{\beta_{0t}}$ is the hyper-mean for occurrence probability (on the logit scale) of all species in the community in year t (at average covariate values) and $\sigma_{\beta_{0t}}^2$ is the hyper-variance for occurrence probability across all species in the community in year t . Models for all other species-specific effects in the ecological and observation models are defined analogously. By treating species-specific effects as random, we improve estimates for both rare and abundant species (Zipkin et al., 2009) while simultaneously estimating community level effects.

A further benefit of the hierarchical community modeling approach is the ability to easily calculate biodiversity metrics (e.g., species richness (Dorazio and Royle, 2005), beta diversity (Dorazio et al., 2010), Hill numbers (Broms et al., 2015)) from the latent occurrence state ($z_{i,j,t}$) that account for imperfect detection of species. Under a Bayesian framework, we can calculate any biodiversity metric as a derived parameter at each iteration of the MCMC to obtain a full posterior distribution from which we can obtain estimates with fully propagated uncertainty. For example, we can estimate species richness at each site j and year t at each iteration of the MCMC by summing the latent occurrence state ($z_{i,j,t}$) for all species. As a metric of beta

diversity, we can calculate the Jaccard index (Magurran, 2013), which describes the similarity between two sites in terms of the number of species that occur at both sites. More specifically, we calculate the Jaccard index between site j and j' in year t as

$$\text{JACCARD}_{j,j',t} = \frac{\sum_{i=1}^I z_{i,j,t} \cdot z_{i,j',t}}{\sum_{i=1}^I z_{i,j,t} + \sum_{i=1}^I z_{i,j',t} - \sum_{i=1}^I z_{i,j,t} \cdot z_{i,j',t}}, \quad (9)$$

which takes value 0 if the two sites have no species in common and value 1 if the same species occur at the two sites.

Data integration via joint likelihood

We use a joint likelihood framework to integrate the replicated and nonreplicated detection-nondetection data sources into a single model (the ICOM; Miller et al. 2019). To do this, we assume the likelihoods for the individual data sets are independent, conditional on the shared latent ecological process. This assumption can be interpreted as the detection of a species in one data set (conditional on the species being present) is independent of the detection of the species in any other data set (Schaub and Abadi, 2011; Kéry and Royle, 2021). Thus, our full joint likelihood, conditional on the true, shared ecological process, is the product of the individual conditional likelihoods for each data set:

$$L_{\text{ICOM}}(\alpha\mathbf{0}, \alpha, \gamma\mathbf{0}, \gamma \mid \mathbf{z}, \beta\mathbf{0}, \beta, \mathbf{y}, \mathbf{v}) = L_{\text{REP}}(\alpha\mathbf{0}, \alpha \mid \mathbf{z}, \beta\mathbf{0}, \beta, \mathbf{y}) \cdot L_{\text{NREP}}(\gamma\mathbf{0}, \gamma \mid \mathbf{z}, \beta\mathbf{0}, \beta, \mathbf{v}). \quad (10)$$

Simulation study 1: Assessing benefits of integration

We performed a simulation study to assess whether integration of multiple data sources in an ICOM framework could provide improved accuracy and precision for species and community level parameters compared to individual analyses under a range of realistic parameter values (Supplemental Information S1.1). We simulated data from one replicated data source with $K = 3$ replicates and two nonreplicated data sources, with the replicated data source having medium community-level detection probability (mean hyper-parameter = 0.5), one nonreplicated data source having low community-level detection probability (mean = 0.22), and the other having high community-level detection probability (mean = 0.78), which allowed us to

compare the benefits of integration across varying qualities of nonreplicated data. We generated 100 replicates of each data source under the ICOM framework using a range of community-level ecological parameter values and subsequently drew simulated species data for $I = 25$ species for $T = 6$ years. We generated species' occurrence probabilities according to Equations 2 and 3 with a single spatially-varying covariate. We generated detection processes for each data source as a function of a species and year specific intercept, and a species-specific effect of a spatio-temporally varying covariate unique to each data set. We simulated all covariates as normally distributed random variables with mean zero and standard deviation one. We generated each data source at 50 distinct sites that were randomly distributed across the range of covariates, resulting in a total of $J = 150$ sites. We compared model performance by fitting models individually for each of the seven unique combinations of the three data sources and subsequently computing the average bias (i.e., true simulated value minus estimated value) of the species-specific occurrence parameters across all 25 species and 100 simulations, as well as the average bias of the community level parameters.

Simulation study 2: Assessing benefits of community modeling

To evaluate the benefits of the hierarchical community model approach used in the ICOM, we assessed how species-level estimates from the ICOM compared to estimates from single species integrated distribution models (IDMs). The IDM took the same form as the ICOM except species-specific parameters were no longer random effects from a community level distribution; rather, species-specific parameters were estimated individually in a model for each species. We simulated data from one replicated data source with $K = 3$ replicates and one nonreplicated data source, both with medium community-level detection probabilities (mean = 0.5). We simulated a community of $I = 25$ species, where each of the two data sources consisted of 50 unique locations sampled over $T = 6$ years, where the locations were randomly distributed across the range of a spatially varying covariate influencing occurrence. We assumed detection for both data sets was a function of a species and year specific intercept, and a species-specific spatio-temporally varying covariate unique to each survey replicate at each site. We generated species-specific occurrence and detection intercepts and covariate effects from uniform distributions (Supplemental Information S1.1), which allowed us to compare the ICOM to individual IDMs under the scenario when species level effects may not follow a normal distribution. We simulated

100 data sets from the community under realistic parameter values (Supplemental Information S1.1). We assessed model performance across the 100 simulated data sets by comparing the accuracy and precision of estimates from the ICOM to the IDMs.

Case study: foliage-gleaning birds in the White Mountains

We applied the ICOM to characterize temporal trends and spatial variability in individual species occurrence, species richness, and species composition of a community of twelve foliage-gleaning birds from 2010-2018 across the White Mountain National Forest using two replicated data sets and one nonreplicated data set (Figure 1). Our two replicated data sets come from the Hubbard Brook Experimental Forest (HBEF) and the National Ecological Observatory Network (NEON) at Bartlett Experimental Forest (Barnett et al., 2019; National Ecological Observatory Network (NEON), 2021), while our nonreplicated data set comes from the North American Breeding Bird Survey (BBS; Pardieck et al. 2020). At HBEF, observers performed three replicate surveys at each of 373 sites in each survey year to account for imperfect detection, while observers at NEON used a removal design at 81 sites to separate detection from occurrence. BBS observers performed point counts at 50 point count locations (called stops) along four routes (i.e., roads) that at least partially fell within the White Mountain National Forest, resulting in a total of 200 nonreplicated point count locations during each survey year. Integration of these three data sets is particularly valuable as each data source has clear advantages and disadvantages (Table 1) and covers disparate areas within the study region. Thus, data integration may yield parameter estimates more indicative of the entire White Mountains rather than analyses of the data sources independently. See Supplemental Information S1.2 for additional details on the three data sets.

We modeled occurrence dynamics for the following twelve foliage-gleaning bird species: American Redstart (*Setophaga ruticilla*), Black-and-white Warbler (*Mniotilta varia*), Blue-headed Vireo (*Vireo solitarius*), Blackburnian Warbler (*Setophaga fusca*), Blackpoll Warbler (*Setophaga striata*), Black-throated Blue Warbler (*Setophaga caerulescens*), Black-throated Green Warbler (*Setophaga virens*), Canada Warbler (*Cardellina canadensis*), Magnolia Warbler (*Setophaga magnolia*), Nashville Warbler (*Leiothlypis ruficapilla*), Ovenbird (*Seiurus aurocapilla*), and Red-eyed Vireo (*Vireo olivaceus*). We specified species occurrence following Equation 1, with occurrence probability in the first year, $\psi_{i,j,1}$, modeled according to

Table 1: Characteristics of the three data sources used to model occurrence dynamics of twelve foliage-gleaning birds in the White Mountain National Forest from 2010-2018. Forest Cover corresponds to the amount of forest within a 250m radius of a point count site. Values for elevation and forest cover are mean (minimum, maximum).

	HBEF	NEON	BBS
Data type	Replicated	Replicated	Nonreplicated
Years	2010-2018	2015-2018	2010-2018
Number of sites	373	81	200
Elevation (m)	607 (240, 932)	432 (268, 766)	352 (134, 917)
Forest Cover (%)	97.7 (71, 100)	94.2 (75, 100)	70.6 (0, 92)
Survey Location	Experimental forest	Experimental forest	Roadside

$$\text{logit}(\psi_{i,j,1}) = \beta_{0i,1} + \beta_{1i} \cdot \text{ELEV}_j + \beta_{2i} \cdot \text{ELEV}_j^2 + \beta_{3i} \cdot \text{FOR}_j, \quad (11)$$

where $\beta_{0i,1}$ is the species-specific intercept in year 1, and β_{1i} , β_{2i} , and β_{3i} are species-specific effects of elevation (ELEV, linear and quadratic) and local forest cover within a 250m radius (FOR), respectively. Occurrence in subsequent years is modeled analogously with a year-specific intercept and an autologistic parameter following Equation 3. We extracted elevation data at a 30×30 m resolution from the National Elevation Dataset (Gesch et al., 2002) and associated each point count site with the elevation at the center of the point count. We used the National Land Cover Database (Homer et al., 2015) to determine the amount of local forest cover in 2016 within a 250m radius of each point count location. To compute species-specific temporal trend estimates, we performed a post-hoc linear regression using the average occurrence probability of each species during each year as a response variable and year as a covariate. Under a Bayesian framework, we obtain full uncertainty propagation by calculating the trend for each posterior sample of the average occurrence probabilities (Supplemental Information S1.3). All species-specific occurrence intercepts and regression coefficients were modeled hierarchically following Equation 8.

We incorporated multiple covariates in the conditional likelihoods of each data type to account for variation in detection probabilities following the species' detection models described in the "Integrated community occupancy model" section. For the HBEF and NEON data, we included species and year-specific intercepts, a species-specific linear effect of the time of the survey, and species-specific linear and quadratic effects of the day of the survey. For the BBS

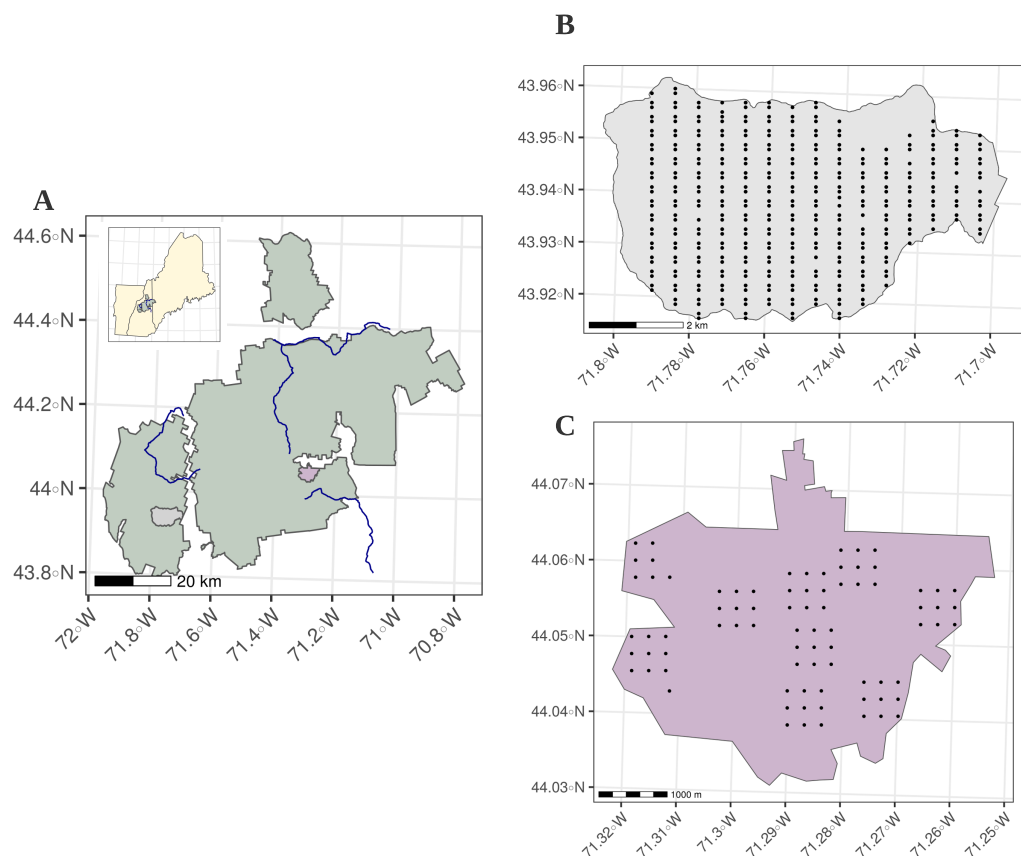


Figure 1: Study location for the case study. Panel (A) shows the White Mountain National Forest (shaded dark grey region) and the location of the Hubbard Brook Experimental Forest (HBEF; light grey region), the BBS routes (dark blue lines), and the NEON data from Bartlett Forest (purple region). Panel (B) shows the distribution of point count locations in HBEF, and Panel (C) shows the distribution of points in the NEON data set. Note different axis spacings across the three plots.

data, we modeled detection as a function of a species and year specific intercept, species-specific linear and quadratic effects of day of survey, and a random observer effect to account for variation in detection among observers. All detection covariates were modeled hierarchically following Equation 8. Species and year specific intercepts were also modeled hierarchically, but were drawn from a single distribution for all species and years within each data set (Supplemental Information S1.3).

Goodness of fit and model validation

Model assessment and validation for integrated models is an active area of research (Fletcher et al., 2019). We assessed model fit for the case study using a Bayesian p-value approach with a Chi-square fit statistic. We calculate a separate Bayesian p-value for each data source

(Supplemental Information S1.4). We used two-fold cross validation with the log predictive density (Vehtari et al., 2017) as a predictive performance metric to assess the out-of-sample predictive performance of the full ICOM compared to six models using subsets of the three data sets for the case study. Assessing out-of-sample predictive performance with occupancy models presents additional complexities since the ecological state of interest is not directly observed (Zipkin et al., 2012). We split each data set into two parts, such that each half consisted of the data from half of the spatial locations for all years those locations were sampled. For a given data set, we compared the occurrence predictions at each hold out location during each year it was sampled to the occurrence values generated from models that were fit using the data at the hold out locations. To account for model uncertainty, we compared the yearly occurrence predictions individually to latent occurrence values generated from the subset of the seven models that used the data set in the model fitting process (see Supplemental Information S1.5 for details). We summarize predictive performance for each species and the entire community individually at each data set location, as well as across the entire study region (i.e., White Mountains). We used a similar approach to compare the performance of the ICOM to individual species IDMs (Supplemental Information S1.5).

Model implementation

We estimated the parameters in all model versions (simulations and case study) with a Bayesian framework using Markov Chain Monte Carlo (MCMC). We fit the models in NIMBLE (de Valpine et al., 2017, 2021) within the R statistical environment (R Core Team, 2020) using vague priors for all hyper-parameters (Supplemental Information S1.3). For all simulations, we ran three chains, each with 20,000 iterations with a burn-in period of 10,000 iterations and a thinning rate of four. For the case study, we ran models for three chains of 450,000 iterations with a burn-in period of 200,000 iterations and a thinning rate of 20, resulting in a total of 52,000 samples from the posterior distribution. We assessed model convergence using the Gelman-Rubin R-hat diagnostic (Brooks and Gelman, 1998) and visual assessment of trace plots using the coda package (Plummer et al., 2006).

Results

Simulations

The ICOM using one replicated data set, one nonreplicated data set with low average detection probability across the community, and one nonreplicated data set with high detection probability yielded unbiased estimates and was generally more precise in community and species-level occurrence parameter estimates than models using smaller combinations of the three data sets or data sets individually (Figure 2, Supplemental Figure S1). Patterns were similar across community effects and species-specific effects, with increases in precision more prominent in species-level effects. Despite the general improvement in estimates found when integrating all three data sources, models using only two data sources, particularly the replicated data source and the nonreplicated data source with high detection probability, also yielded estimates with low bias and high precision. Models using only the nonreplicated data source with low detection probability often failed to converge, while models using only the nonreplicated data source with high detection probability mostly converged but were less precise than models using replicated data (and with essentially unidentifiable intercept values; Figure 2A).

The ICOM also led to substantial improvements in precision of parameter estimates compared to single species IDMs (Table 2, Supplemental Figure S2). Species-level IDMs provided slightly more accurate estimates of species-specific occurrence parameters for some species as compared to the ICOM, which is a result of Bayesian shrinkage (i.e., borrowing strength) driving species-level parameters closer to the community average for those species with extreme parameter values in the ICOM. However, the true species-level parameters were contained within the 95% Bayesian credible interval of the estimated parameter values across 94.9% of all simulations, indicating that this loss in accuracy is negligible. Further, we simulated species-level effects from a uniform distribution rather than a normal distribution, which led to more extreme species values. Losses in accuracy would be much lower for communities of species where the normal assumption is adequate. Thus, in addition to providing community-level parameter effects, the ICOM provides more precise estimates of species-specific effects compared to IDMs with only minor losses in accuracy for species with extreme intercepts and/or covariate effects.

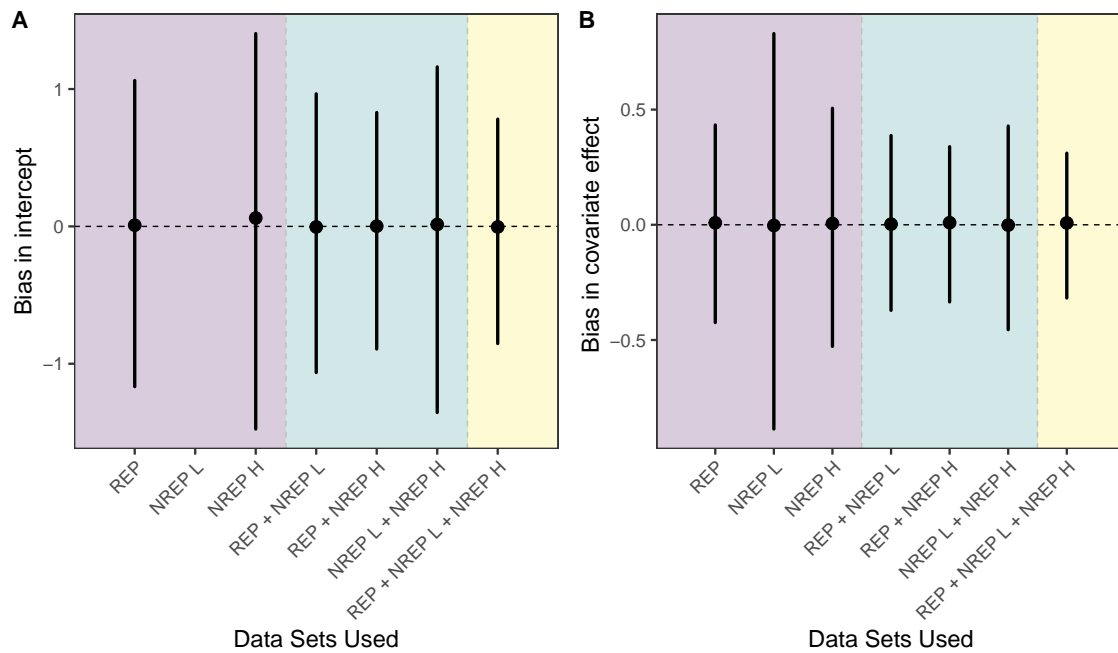


Figure 2: Sampling distribution of estimated bias in simulated species level occurrence intercepts (A) and covariate effects (B) under models using different combinations of a replicated (REP) data set and nonreplicated data sets with low (NREP L) and high (NREP H) detection probability. Points represent the median bias (posterior mean - true simulated value) in a species-level effect across 100 simulations for a community of 25 species. Lines represent the 95% quantiles of the bias values. The intercept parameter using only NREP L is not shown as it failed to converge.

Case Study

The ICOM estimated variable trends in occurrence for the twelve foliage-gleaning bird species across the White Mountain National Forest, with five species having >75% probability of increasing occurrence rates and three species having >75% probability of decreasing (Supplemental Figure S3) from 2010-2018. Community level parameters revealed that average occurrence probability peaked at mid-level elevations and higher amounts of local forest cover across foliage-gleaning species, although species-specific parameters were highly variable (Supplemental Table S3). Occurrence probabilities peaked at a variety of elevations across the twelve species (Supplemental Figure S4), which resulted in species richness being maximized at mid-level elevations (600-800m; Figure 3A). Species composition of the community, as measured by the Jaccard index, largely followed similar patterns (Figure 3B). Estimated trends in species-specific occurrence probabilities were highly dependent on the data sets included in the model (Figure 4), suggesting important spatial variability across the White Mountains. For example, while Red-eyed Vireo occurrence showed consistent trends across models from all data source com-

Table 2: Precision and accuracy of species-specific parameter estimates when using the integrated community occupancy model (ICOM) compared to a single species integrated distribution model (IDM) for a simulated community of 25 species over six years across 100 simulations with one replicated (REP) data set and one nonreplicated (NREP) data set. Precision improvement is the percentage improvement in precision when using the ICOM compared to the IDM, where precision is defined as the difference between the 2.5% and 97.5% quantiles of the posterior means. Bias is the average magnitude of the posterior means minus the true simulated value. Values are averaged across all 25 species and six years.

Parameter	Precision Improvement (%)	ICOM Bias	IDM Bias	Parameter
$\gamma 0_i$	41.9	0.235	0.101	NREP detection intercept
$\gamma 1_i$	33.4	0.070	0.027	NREP detection covariate
ϕ_i	30.0	0.173	0.121	Auto-logistic
$\beta 0_i$	29.2	0.173	0.108	Occurrence intercept
$\beta 1_i$	22.5	0.042	0.017	Occurrence covariate
$\alpha 0_i$	18.8	0.104	0.044	REP detection intercept
$\alpha 1_i$	9.63	0.023	0.012	REP detection covariate

binations, trends for the Black-throated Blue Warbler and Black-throated Green Warbler were stable in estimates from most data combinations, but occurrence probabilities were estimated to have declined over this time period based on the model that used only BBS data.

Integration of all data sources in the ICOM yielded better predictive performance for the community of birds across the three data set locations than models using only a subset of the available data (Table 3). This is likely a result of both a larger number of detections and a wider range of the covariate space when using all three data sources. The model using only HBEF and BBS data had the highest predictive performance for data at HBEF, while the model using NEON data only had the highest predictive performance for data at NEON. The ICOM had higher predictive performance compared to single species IDMs across all 12 species for the three data sets, and outperformed single species IDMs individually for each species for 64%, 91%, and 100% of the species at HBEF, BBS, and NEON, respectively (Supplemental Table S6).

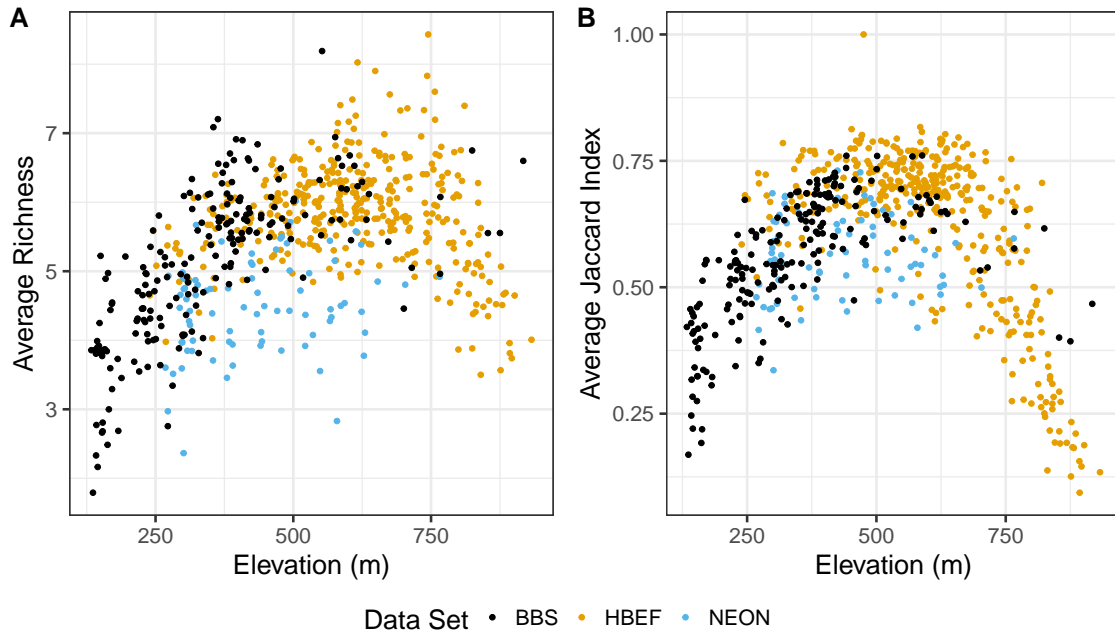


Figure 3: Estimated average site-level species richness (A) and Jaccard index (B) of a community of twelve foliage-gleaning bird species in the White Mountain National Forest. Points are posterior means. Jaccard index values are relative to a single site in the Hubbard Brook Experimental Forest with value 1, with 0 indicating no species in common to the reference site, and 1 indicating identical community composition to the reference site.

Discussion

Assessing species distributions and occurrence dynamics of multiple species in a community is an important task for biodiversity conservation (Guillera-Arroita et al., 2019). Monitoring programs collect different types of data that vary in amount, spatial extent, quality, and information content, and incorporating these varied data into a unified analysis can yield improved estimates on quantities of interest (Zipkin and Saunders, 2018). We developed an “integrated community occupancy model” (ICOM) that uses replicated and nonreplicated detection-nondetection data to simultaneously provide inferences on species-specific and community-level dynamics. Using simulations and empirical bird data, we showed that the ICOM can provide more accurate and precise estimates of occurrence dynamics than analyses using single data sources (Figure 2) or single species models (Table 2) as well as improved predictive performance across a study region (Table 3, Supplemental Table S6).

In our simulation study, the ICOM using one replicated data set, one nonreplicated data set with low detection probability, and one replicated data set with high detection probability provided unbiased and generally more precise parameter estimates than models using a subset of

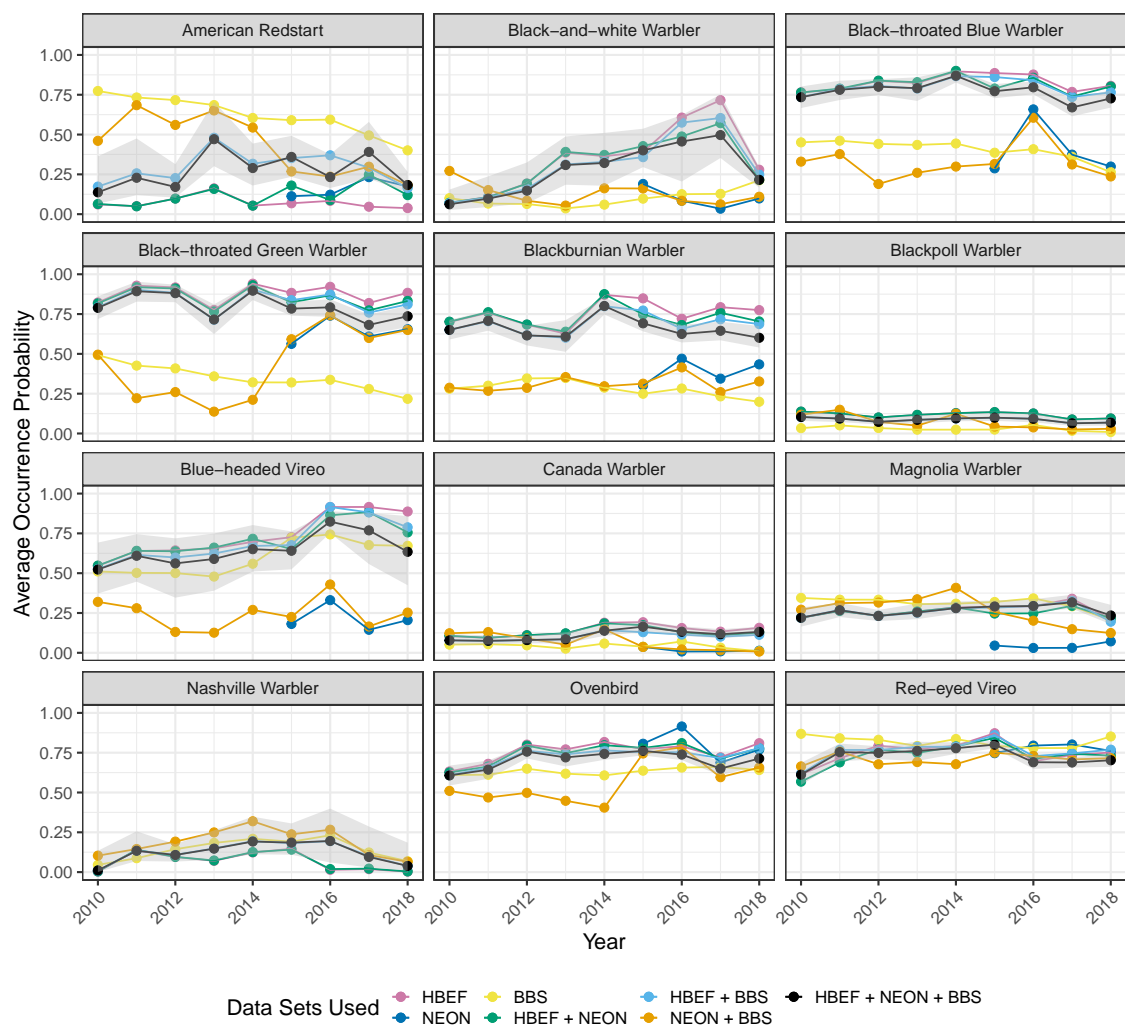


Figure 4: Average occurrence probabilities of twelve foliage-gleaning bird species in the White Mountain National Forest from 2010 to 2018 from models using different subsets of the three data sources. Points show posterior mean occurrence probabilities averaged across all sites in a given year. Gray shaded region indicates the 95% credible interval of estimates derived from the model that incorporated all three data sources.

Table 3: Two-fold cross validation results comparing predictive performance across models using different combinations of the three data sets. The fitted model is shown in the first column and log predictive density measures are shown for the entire community with each data set and across all data sets. Values in parentheses show the average rank of the model for an individual species across all models, with 1 indicating the model is the best for all species and 7 indicating the the model is worst for all species. Bold values indicate the best performing model for each individual data set. Predictive performance of the model using only NEON data is only assessed at NEON locations because NEON data are only available for four of the nine study years.

Model	HBEF	BBS	NEON	All
HBEF	-10174 (3.75)	-6200 (4.67)	-947 (4.75)	-17321 (4.5)
NEON	-	-	-792 (2.83)	-
BBS	-13876 (3.75)	-5702 (3.5)	-1148 (5.08)	-20726 (3.83)
HBEF+NEON	-10097 (3.58)	-5878 (3.33)	-852 (3.67)	-16829 (3.33)
HBEF+BBS	-9732 (2.67)	-5717 (3.67)	-934 (4.42)	-16383 (2.67)
NEON+BBS	-12560 (4.5)	-5759 (3.25)	-801 (3.83)	-19121 (4.33)
HBEF+NEON+BBS	-9767 (2.75)	-5691 (2.58)	-836 (3.42)	-16294 (2.33)

the three data sources (Figure 2), which aligns with previous single species data integration work (Fletcher et al., 2019). Despite this general improvement in the simulation study, integrating the single replicated data source with the high detection nonreplicated data source yielded comparable accuracy and precision to the model using one replicated and two nonreplicated data sources. This suggests that integrating a data source of particularly low quality (e.g., nonreplicated, potentially large detection variability) with higher quality data sources may not yield any practical benefits (Simmonds et al., 2020). We generated each data source at random locations across the range of the covariate with no systematic bias in sampling locations. In reality, many sources of detection-nondetection data are spatially biased (e.g., collected along road transects or near locations with high human density), which can lead to a narrow range of habitat variables (e.g., forest cover) that drive species and community occurrence dynamics. Such biases can result in different species being observed across data sets or estimated parameters that are either biased, only span a portion of the covariate range of interest, or are not indicative of the larger spatial areas of interest (Conn et al., 2017). By integrating disparate data sources from multiple locations in the ICOM, we can increase the likelihood that the sampled sites vary along important ecological and environmental gradients, which in turn enables more precise and accurate inference on the environmental conditions driving species occurrence (Zipkin et al., 2017).

In the foliage-gleaning bird case study, we used a two-fold cross validation approach to show that integration of all three data sets yielded the best overall predictive performance across the White Mountain National Forest compared to models using smaller subsets of the three data sources (Table 3). Further, the ICOM generally yielded improved predictive performance for individual species and the overall community compared to single species integrated distribution models (Supplemental Table S5). In contrast to the simulation study, parameter precision was not always highest when integrating all three data sets in the case study (Supplemental Tables S4, S5). Additionally, models with smaller subsets of the three data sources outperformed the ICOM with all three data sets individually for the HBEF and NEON data sets, although the improvements in predictive performance were not large (Table 3). This is likely a result of different covariate ranges among the three data sources and only having NEON data for a subset of the time period of interest. For example, precision of species-specific effects of local forest cover was highest for the model using HBEF and NEON data. Sites at HBEF and NEON have low variability in forest cover, with average forest cover of sites being 94.2% and 97.7%, respectively. However, variability in forest cover is comparatively higher at BBS sites, which likely explains why precision is lower when incorporating BBS data. For most intercept parameters at the community and species-specific level, models using either NEON data alone or NEON and BBS were the most precise. In the model using NEON and BBS data, information for separating detection probability from true occurrence comes solely from the NEON data, which are only available for four of the nine years of the study period. This shorter time period likely results in less unexplained variability in occurrence probability and detection across years, which in turn leads to more precise intercept estimates. However, the ICOM using all three data sets enables inference across the entire temporal period of interest as well as a broader range of covariates, generating more informative estimates on trends and spatial patterns across the White Mountains.

The large variation in temporal trends when using different combinations of the three data sources suggests spatially-varying occurrence trends for the community of twelve foliage-gleaning birds. NEON data were only available from 2015-2018, which may account for differences in estimated trends from the model using only NEON data compared to other models. BBS data were sampled along road transects and thus have less forest cover than both the NEON and HBEF sites, suggesting that occurrence trends could vary as a result of differences in amount

of local forest cover and/or proximity to roads (Furnas, 2020). Estimates from the full ICOM are a weighted average across heterogeneity in trends across the region, where the weights are determined by the amount of available data from each data source (Fletcher et al., 2019). In our case study, the HBEF data source comprised a majority of observations (77%; Supplemental Table S2) and thus contributed the most to estimates of model parameters, which we deemed acceptable because the HBEF data are a high-quality replicated data source. Alternatively, a profiling approach could be used within the MCMC sampler to change the weights for each data set similar to the maximum likelihood approach of Fletcher et al. 2019. By including information from multiple data sources within a region, the ICOM yields area-wide averaged species-specific trends. If an area-wide averaged trend is not desired, trends from different spatial locations could be estimated hierarchically in a multi-region framework (Doser et al., 2021b) or treated as spatially varying coefficients to explicitly model spatial heterogeneity (Finley, 2011).

BBS data are a nonreplicated data source and so there is little information to separate the occurrence and detection processes when using only BBS data in a community model (Kéry and Royle, 2021). In our model using only BBS data, this resulted in large uncertainty in the autologistic parameter and subsequent occurrence estimates (Supplemental Table S5). This weak identifiability of the occurrence and detection intercepts contributed to substantial differences in average occurrence probabilities estimated using only BBS data compared to models using multiple data sources in our ICOM (Figure 4). When the BBS data were integrated with NEON or HBEF, the information used to separately estimate detection from occurrence came from only the replicated data source(s). This may explain why yearly occurrence probabilities from the NEON + BBS and BBS models for the Black-throated Blue Warbler, Black-throated Green Warbler, and Blue-headed Vireo were nearly identical in the years NEON data were available (2015-2018; Figure 4). The limited temporal span of the NEON data sometimes resulted in the BBS data effectively “pulling down” estimates of occurrence from 2010-2014 in the NEON + BBS model for certain species (e.g., Black-throated Green Warbler), while for other species (e.g., Blue-headed Vireo) estimates in 2010-2014 from the NEON + BBS model appeared to be less influenced by the BBS data (Figure 4). These varying species-level patterns highlight the complexities that can arise when integrating data sets of different qualities, types, and size, which should be carefully considered by end-users of integrated modeling approaches such as the ICOM.

The benefits of data integration for multi-species detection-nondetection data sets will depend on the characteristics and goals of each specific study. Our simulations and foliage-gleaning bird case study demonstrate that the ICOM can yield more accurate and precise estimates of occurrence dynamics than alternative approaches. However, it is impossible to explore the full range of data integration complexities within a single study. Future analyses motivated by specific data sets, sample sizes, and ecological questions are necessary to provide further guidance on the practical benefits and potential drawbacks of integrating multiple data sources within an ICOM framework. While the ICOM generally leads to improved inference for species and community level effects, integrating multiple data sets leads to increased computation times and potential complications in achieving model convergence. For example, in our simulation study, the ICOM with three data sets took approximately twice as long to run as a community model using only one replicated data source (i.e., 27 minutes vs. 13 minutes for 20,000 iterations). The added computational costs will depend on numerous analysis-specific factors, such as the number of data sets, and the number of species, sites, and years available within each data set.

When determining what data sources to use in an ICOM, we recommend considering the following factors: (1) the amount of the different data sources within the area of interest and how they are distributed across the range of ecological and environmental gradients; (2) the precision of estimates required for the analysis objectives; (3) amount of time and computational power available to run the models; (4) the spatial resolution of each data source; and (5) the quality and information content of each data source (e.g., replicated vs. nonreplicated, large detection variability vs. standardized protocol). For example, suppose multiple data sources are available for a study seeking to reveal the effect of a spatially-varying covariate (e.g., amount of urbanization) on species-specific and community-level occurrence dynamics. If one of the data sources is a high quality, replicated data set that spans the entire environmental gradient of the covariate, a community model using only this single data source would likely suffice. Alternatively, if each individual data source only spans a portion of the environmental gradient, integration of the data sets in an ICOM would be necessary to fully understand the covariate effect on species and community occurrence dynamics. We encourage the use of model validation techniques, such as the cross-validation approach we presented in the foliage-gleaning bird case study to evaluate the benefits of the ICOM for specific study objectives.

We envision numerous possible methodological extensions to the ICOM framework. While

we used three data sources arising from the same method in our case study (i.e., point count surveys), the ICOM can incorporate detection-nondetection data from different data collection approaches, such as autonomous recording units (Doser et al., 2021a) and citizen science checklists (Kéry et al., 2010) in an analogous manner. The ICOM assumes the detection processes of each data source are independent, conditional on the true occurrence process. This conditional independence could be violated for certain data sources where trained observers performing structured surveys also submit observations to citizen science repositories (e.g., eBird). The consequences of violating such conditional independence should be explored before combining data types, although results for integrated population models suggest this violation likely has negligible impacts on the accuracy of inferences (Abadi et al., 2010).

The ICOM can help address a variety of questions in applied population and community ecology. As in the single data source hierarchical community model (Dorazio and Royle, 2005), data augmentation (Royle et al., 2007) could be incorporated into the ICOM to account for missing species and to estimate richness of the community. If regional species pools differ between data source locations, the ICOM could be adapted to a multiregion framework (Sutherland et al., 2016) or extended to explore variation of species traits among disparate communities (Garrard et al., 2013; Tenan et al., 2017). Given our model’s ability to estimate species and community level effects, the ICOM can be applied to help elucidate individual species sensitivities to various global change drivers, determine factors causing shifts in taxonomic or functional diversity, or forecast future species and community shifts under varying climate and land use change scenarios to help prioritize conservation strategies. In particular, the ICOM will assist multi-species conservation planning by providing estimates for rare species that lack adequate data for common analysis approaches, while simultaneously obtaining inference on an entire community that may elucidate specific species traits linked to occurrence trends.

As changes in environmental and climate conditions continue globally, continued development of monitoring and analysis techniques that can effectively produce accurate and precise estimates of biodiversity metrics are needed to understand global change impacts and develop appropriate mitigation plans. Our integrated community occupancy models provide a new approach to simultaneously analyze multi-species data from numerous available sources. This framework can be used to elucidate both species specific and community level dynamics, improving understanding of the mechanisms driving biodiversity distributions and informing ap-

propriate management and conservation actions to address ongoing global change.

Acknowledgements

This manuscript is a contribution of the Hubbard Brook Ecosystem Study. Hubbard Brook is part of the Long- Term Ecological Research network, which is supported by the U.S. National Science Foundation. The Hubbard Brook Experimental Forest is operated and maintained by the USDA Forest Service, Northern Research Station, Newtown Square, PA. Development of the ICOM framework was supported by the National Science Foundation through grant DBI-1954406.

Conflict of Interest

We declare no conflicts of interest.

Authors' Contributions

JWD and EFZ developed the modeling framework with critical insight provided by WL. TSS and MTH assisted in data management and preparation. JWD performed all analyses and led writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability

All data and code associated with this manuscript are available at <https://doi.org/10.5281/zenodo.5883950> (Doser et al., 2022).

References

Abadi, F., Gimenez, O., Arlettaz, R., and Schaub, M. (2010). An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology*, 91(1):7–14.

- Barnett, D. T., Duffy, P. A., Schimel, D. S., Krauss, R. E., Irvine, K. M., Davis, F. W., Gross, J. E., Azuaje, E. I., Thorpe, A. S., Gudex-Cross, D., et al. (2019). The terrestrial organism and biogeochemistry spatial sampling design for the National Ecological Observatory Network. *Ecosphere*, 10(2):e02540.
- Barraquand, F. and Gimenez, O. (2019). Integrating multiple data sources to fit matrix population models for interacting species. *Ecological Modelling*, 411:108713.
- Broms, K. M., Hooten, M. B., and Fitzpatrick, R. M. (2015). Accounting for imperfect detection in Hill numbers for biodiversity studies. *Methods in Ecology and Evolution*, 6(1):99–108.
- Brooks, S. P. and Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, 7(4):434–455.
- Clark, J. S., Nemergut, D., Seyednasrollah, B., Turner, P. J., and Zhang, S. (2017). Generalized joint attribute modeling for biodiversity analysis: Median-zero, multivariate, multifarious data. *Ecological Monographs*, 87(1):34–56.
- Clark, T. J. (2021). *Large carnivore recolonization reshapes population and community dynamics in the Rocky Mountains: Implications for harvest management*. PhD thesis, University of Montana.
- Conn, P. B., Thorson, J. T., and Johnson, D. S. (2017). Confronting preferential sampling when analysing population distributions: Diagnosis and model-based triage. *Methods in Ecology and Evolution*, 8(11):1535–1546.
- de Valpine, P., Paciorek, C., Turek, D., Michaud, N., Anderson-Bergman, C., Obermeyer, F., Wehrhahn Cortes, C., Rodriguez, A., Temple Lang, D., and Paganin, S. (2021). *NIMBLE: MCMC, Particle Filtering, and Programmable Hierarchical Modeling*. R package version 0.11.1.
- de Valpine, P., Turek, D., Paciorek, C., Anderson-Bergman, C., Temple Lang, D., and Bodik, R. (2017). Programming with models: writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics*, 26:403–413.
- Devarajan, K., Morelli, T. L., and Tenan, S. (2020). Multi-species occupancy models: review, roadmap, and recommendations. *Ecography*, 43(11):1612–1624.

- Dorazio, R. M. (2014). Accounting for imperfect detection and survey bias in statistical analysis of presence-only data. *Global Ecology and Biogeography*, 23(12):1472–1484.
- Dorazio, R. M., Kery, M., Royle, J. A., and Plattner, M. (2010). Models for inference in dynamic metacommunity systems. *Ecology*, 91(8):2466–2475.
- Dorazio, R. M. and Royle, J. A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, 100(470):389–398.
- Doser, J. W., Finley, A. O., Weed, A. S., and Zipkin, E. F. (2021a). Integrating automated acoustic vocalization data and point count surveys for estimation of bird abundance. *Methods in Ecology and Evolution*, 12(6):1040–1049.
- Doser, J. W., Leuenberger, W., Sillett, T. S., Hallworth, M. T., and Zipkin, E. F. (2022). Code and data for Integrated community occupancy models: A framework to assess occurrence and biodiversity dynamics using multiple data sources. *Zenodo*, <https://doi.org/10.5281/zenodo.5883950>.
- Doser, J. W., Weed, A. S., Zipkin, E. F., Miller, K. M., and Finley, A. O. (2021b). Trends in bird abundance differ among protected forests but not bird guilds. *Ecological Applications*, 31(6):e2377.
- Finley, A. O. (2011). Comparing spatially-varying coefficients models for analysis of ecological data with non-stationary and anisotropic residual dependence. *Methods in Ecology and Evolution*, 2(2):143–154.
- Fletcher, R. J., Hefley, T. J., Robertson, E. P., Zuckerberg, B., McCleery, R. A., and Dorazio, R. M. (2019). A practical guide for combining data to model species distributions. *Ecology*, 100(6):e02710.
- Frishkoff, L. O., Karp, D. S., Flanders, J. R., Zook, J., Hadly, E. A., Daily, G. C., and M’Gonigle, L. K. (2016). Climate change and habitat conversion favour the same species. *Ecology Letters*, 19(9):1081–1090.
- Furnas, B. J. (2020). Rapid and varied responses of songbirds to climate change in california coniferous forests. *Biological Conservation*, 241:108347.

- Gallo, T., Fidino, M., Lehrer, E. W., and Magle, S. B. (2017). Mammal diversity and meta-community dynamics in urban green spaces: implications for urban wildlife conservation. *Ecological Applications*, 27(8):2330–2341.
- Garrard, G. E., McCarthy, M. A., Williams, N. S., Bekessy, S. A., and Wintle, B. A. (2013). A general model of detectability using species traits. *Methods in Ecology and Evolution*, 4(1):45–52.
- Gelfand, A. E., Schmidt, A. M., Wu, S., Silander Jr, J. A., Latimer, A., and Rebelo, A. G. (2005). Modelling species diversity through species level hierarchical modelling. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, 54(1):1–20.
- Gesch, D., Oimoen, M., Greenlee, S., Nelson, C., Steuck, M., and Tyler, D. (2002). The national elevation dataset. *Photogrammetric Engineering and Remote Sensing*, 68(1):5–32.
- Guillera-Arroita, G., Kéry, M., and Lahoz-Monfort, J. J. (2019). Inferring species richness using multispecies occupancy modeling: Estimation performance and interpretation. *Ecology and Evolution*, 9(2):780–792.
- Homer, C., Dewitz, J., Yang, L., Jin, S., Danielson, P., Xian, G., Coulston, J., Herold, N., Wickham, J., and Megown, K. (2015). Completion of the 2011 national land cover database for the conterminous united states—representing a decade of land cover change information. *Photogrammetric Engineering & Remote Sensing*, 81(5):345–354.
- Kéry, M. and Royle, J. A. (2021). *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance, and Species Richness in R and BUGS: Volume 2: Dynamic and Advanced Models*. Academic Press.
- Kéry, M., Royle, J. A., Schmid, H., Schaub, M., Volet, B., Haeffliger, G., and Zbinden, N. (2010). Site-occupancy distribution modeling to correct population-trend estimates derived from opportunistic observations. *Conservation Biology*, 24(5):1388–1397.
- Lahoz-Monfort, J. J., Harris, M. P., Wanless, S., Freeman, S. N., and Morgan, B. J. (2017). Bringing it all together: multi-species integrated population modelling of a breeding community. *Journal of Agricultural, Biological and Environmental Statistics*, 22(2):140–160.

- Lele, S. R., Moreno, M., and Bayne, E. (2012). Dealing with detection error in site occupancy surveys: what can we do with a single survey? *Journal of Plant Ecology*, 5(1):22–31.
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., and Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8):2248–2255.
- MacKenzie, D. I. and Royle, J. A. (2005). Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology*, 42(6):1105–1114.
- Magurran, A. E. (2013). *Measuring Biological Diversity*. John Wiley & Sons.
- Mata, L., Threlfall, C. G., Williams, N. S., Hahs, A. K., Malipatil, M., Stork, N. E., and Livesley, S. J. (2017). Conserving herbivorous and predatory insects in urban green spaces. *Scientific Reports*, 7(1):1–12.
- Miller, D. A., Pacifici, K., Sanderlin, J. S., and Reich, B. J. (2019). The recent past and promising future for data integration methods to estimate species’ distributions. *Methods in Ecology and Evolution*, 10(1):22–37.
- National Ecological Observatory Network (NEON) (2021). Breeding landbird point counts (dp1.10003.001).
- Pardieck, K., Ziolkowski Jr, D., Lutmerding, M., Aponte, V., and Hudson, M.-A. (2020). North American Breeding Bird Survey Dataset 1966–2019. *U.S. Geological Survey data release*, <https://doi.org/10.5066/P9J6QUF6>.
- Péron, G. and Koons, D. N. (2012). Integrated modeling of communities: parasitism, competition, and demographic synchrony in sympatric ducks. *Ecology*, 93(11):2456–2464.
- Plummer, M., Best, N., Cowles, K., and Vines, K. (2006). CODA: Convergence Diagnosis and Output Analysis for MCMC. *R News*, 6(1):7–11.
- R Core Team (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rodhouse, T. J., Rodriguez, R. M., Banner, K. M., Ormsbee, P. C., Barnett, J., and Irvine, K. M. (2019). Evidence of region-wide bat population decline from long-term monitoring

and Bayesian occupancy models with empirically informed priors. *Ecology and Evolution*,
9(19):11078–11088.

Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A.,
Stanton, J. C., Panjabi, A., Helft, L., Parr, M., et al. (2019). Decline of the North American
avifauna. *Science*, 366(6461):120–124.

Royle, J. A. and Dorazio, R. M. (2008). *Hierarchical Modeling and Inference in Ecology: The
Analysis of Data from Populations, Metapopulations and Communities*. Elsevier.

Royle, J. A., Dorazio, R. M., and Link, W. A. (2007). Analysis of multinomial models with
unknown index using data augmentation. *Journal of Computational and Graphical Statistics*,
16(1):67–85.

Schaub, M. and Abadi, F. (2011). Integrated population models: a novel analysis framework
for deeper insights into population dynamics. *Journal of Ornithology*, 152(1):227–237.

Simmonds, E. G., Jarvis, S. G., Henrys, P. A., Isaac, N. J., and O’Hara, R. B. (2020). Is more
data always better? A simulation study of benefits and limitations of integrated distribution
models. *Ecography*, 43(10):1413–1422.

Sor, R., Park, Y.-S., Boets, P., Goethals, P. L., and Lek, S. (2017). Effects of species prevalence
on the performance of predictive models. *Ecological Modelling*, 354:11–19.

Sutherland, C., Brambilla, M., Pedrini, P., and Tenan, S. (2016). A multiregion community
model for inference about geographic variation in species richness. *Methods in Ecology and
Evolution*, 7(7):783–791.

Tenan, S., Brambilla, M., Pedrini, P., and Sutherland, C. (2017). Quantifying spatial variation
in the size and structure of ecologically stratified communities. *Methods in Ecology and
Evolution*, 8(8):976–984.

Vehtari, A., Gelman, A., and Gabry, J. (2017). Practical Bayesian model evaluation using
leave-one-out cross-validation and WAIC. *Statistics and Computing*, 27(5):1413–1432.

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., and Stopak, D. (2021).
Insect decline in the anthropocene: Death by a thousand cuts. *Proceedings of the National
Academy of Sciences*, 118(2).

- Zipkin, E. F., DeWan, A., and Andrew Royle, J. (2009). Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. *Journal of Applied Ecology*, 46(4):815–822.
- Zipkin, E. F., Grant, E. H. C., and Fagan, W. F. (2012). Evaluating the predictive abilities of community occupancy models using AUC while accounting for imperfect detection. *Ecological Applications*, 22(7):1962–1972.
- Zipkin, E. F., Rossman, S., Yackulic, C. B., Wiens, J. D., Thorson, J. T., Davis, R. J., and Grant, E. H. C. (2017). Integrating count and detection–nondetection data to model population dynamics. *Ecology*, 98(6):1640–1650.
- Zipkin, E. F. and Saunders, S. P. (2018). Synthesizing multiple data types for biological conservation using integrated population models. *Biological Conservation*, 217:240–250.
- Zipkin, E. F., Zylstra, E. R., Wright, A. D., Saunders, S. P., Finley, A. O., Dietze, M. C., Itter, M. S., and Tingley, M. W. (2021). Addressing data integration challenges to link ecological processes across scales. *Frontiers in Ecology and the Environment*, 19(1):30–38.