



Multi-species occurrence models to evaluate the effects of conservation and management actions

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ABSTRACT

Conservation and management actions often have direct and indirect effects on a wide range of species. As such, it is important to evaluate the impacts that such actions may have on both target and non-target species within a region. Understanding how species richness and composition differ as a result of management treatments can help determine potential ecological consequences. Yet it is difficult to estimate richness because traditional sampling approaches detect species at variable rates and some species are never observed. We present a framework for assessing management actions on biodiversity using a multi-species hierarchical model that estimates individual species occurrences, while accounting for imperfect detection of species. Our model incorporates species-specific responses to management treatments and local vegetation characteristics and a hierarchical component that links species at a community-level. This allows for comprehensive inferences on the whole community or on assemblages of interest. Compared to traditional species models, occurrence estimates are improved for all species, even for those that are rarely observed, resulting in more precise estimates of species richness (including species that were unobserved during sampling). We demonstrate the utility of this approach for conservation through an analysis comparing bird communities in two geographically similar study areas: one in which white-tailed deer (*Odocoileus virginianus*) densities have been regulated through hunting and one in which deer densities have gone unregulated. Although our results indicate that species and assemblage richness were similar in the two study areas, point-level richness was significantly influenced by local vegetation characteristics, a result that would have been underestimated had we not accounted for variability in species detection.

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1. Introduction

Conservation and management actions are generally designed to target a particular species of interest (e.g., Howe et al., 2007; Pauliny et al., 2008; Wang et al., 2009). However, actions focused on maintaining or improving habitat for a single species may also affect other species (e.g., Tikkanen et al., 2007). For example, management designed to improve conditions for the endangered red-cockaded woodpecker (*Picoides borealis*), such as forest burning and thinning, may have adverse impacts on neotropical migrant birds that nest in midstory and understory vegetation (Powell et al., 2000; Moore et al., 2005). Initial studies on wood thrush (*Hylocichla mustelina*) found that treatments had no effect on short term density and survival (Powell et al., 2000). However, further analyses have suggested that burning and thinning may be “incompatible” with wood thrush persistence (Moore et al.,

2005). Many conservation plans explicitly view management as influencing a variety of species, and balancing the losses and gains of species is an implicit part of managing biodiversity (e.g., Rich et al., 2004; Suarez-Rubio and Thomlinson, 2009). It is therefore important to consider the effects of management actions on not only the target species, but also on other species within a region.

One method for assessment is to compare local species richness (i.e., total number of species) in areas that are affected and unaffected by a specific action. Yet, determining species richness is complicated by variability in detection rates, which can vary across species or by landscape characteristics (Boulinier et al., 1998; Kéry and Schmidt, 2008) and may be affected by actions that create a change in habitat. As a result, estimates of species richness and composition would be biased if species-specific detection is not accounted for properly. This may feign a non-existing management effect or mask a genuine effect.

Rare species, many of which are of conservation concern, may show disproportionate responses to changes in habitat as compared to common species. Often there are inadequate data on rare species, which may be detected infrequently or not at all during

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sampling, resulting in limited inferences about occurrence (MacKenzie et al., 2005). However, management evaluations should include all species, not just those species that produce enough data. Recent advances in statistical methodology have improved the ability to account for imperfect detection and low occurrence of rare species through a community-level hierarchical modeling approach (Dorazio and Royle, 2005; Dorazio et al., 2006), a multi-species extension of the occurrence model described in MacKenzie et al. (2002). The fundamental idea behind the multi-species modeling approach is that collective community data can inform the occurrence probabilities for all observed species, even those that are rare or elusive, and allow for occurrence estimation of species that were never observed in the sample plots. This results in an improved composite analysis of the community and increased precision in species-specific estimates of occurrence (Kéry and Royle, 2009; Zipkin et al., 2009). Furthermore, the hierarchical model can be specified to incorporate habitat and sampling effects that influence occurrence and detection, respectively (Russell et al., 2009). Thus a multi-species approach can provide more precise estimates of species richness, while accounting for variation in occurrence and detection among species. Understanding how species richness and composition differ as a result of management treatments and habitat characteristics can aid in determining the ecological consequences of management.

In this paper, we explore the use of community hierarchical models in a conservation context by comparing bird species richness in two similar study areas in the Catoctin Mountains, Maryland (USA): one with an unharvested population of white-tailed deer (*Odocoileus virginianus*) and one in which deer densities have been regulated through hunting and are much lower as a result (Bates et al., 2005). White-tailed deer can severely alter vegetation structure and composition, reducing habitat availability and quality for some bird species (McShea and Rappole, 2000; Cote et al., 2004). Efforts to control deer densities have been implemented for a variety of reasons including to reduce wildlife/human conflicts (e.g., vehicle collisions, minimize human exposure to ticks) and to protect vegetation growth. Our interest lies in understanding how management decisions to control deer densities (in this case, by allowing hunting) affect total bird species richness as well as the richness of functional species groups, specifically assemblages of species that nest and forage on the ground or in the forest understory relative to the midstory and canopy. To this end, we built our model to include both a treatment effect (hunting vs. no hunting) as well as local vegetation characteristics to estimate species and assemblage richness at point-level to regional spatial scales.

2. Methods

The hierarchical community model is a multi-species approach to obtain composite information by estimating individual species occurrence probabilities (Dorazio and Royle, 2005; Dorazio et al., 2006). The basic idea is that: (1) non-detection can be distinguished from absence through repeated sampling and (2) species-specific estimates of occurrence can be improved using collective data on all species observed during sampling. This approach is especially useful for communities that include rare (or unobserved) species, which often yield too few detections to estimate occurrence. Because species are detected imperfectly, it is likely that some species do not appear in the sample. Inference about species richness, including the number of unobserved species, is a central objective in studies of species distributions (e.g., Cam et al., 2002; Husté et al., 2006) and can be a useful metric in assessing the impacts of management actions. The hierarchical multi-species model can produce estimates of richness that ac-

count for species unobserved during sampling (Dorazio et al., 2006). Before outlining the specific details of the model, we describe the study area and data.

2.1. Study area and data collection

High densities of white-tailed deer have led to increasing concern about the effects of intense browsing on biological resources and forest processes in the eastern United States and elsewhere. The United States National Park Service (NPS) implemented an assessment to determine whether deer in the Catoctin Mountain Park (CATO) should be managed to address declining forest regeneration to ensure that natural processes support native vegetation and wildlife in the region (Bates et al., 2005). As part of the assessment, bird surveys were conducted in CATO, where white-tailed deer abundance is unregulated, and in the nearby Frederick City Watershed Cooperative Wildlife Management Area (FCW), where deer are hunted. Estimates of white-tailed deer densities were more than seven times higher in CATO than in FCW (Bates et al., 2005). Sampling occurred at 35 random points in each study area in late May through early July 2002. During 12-min counts, all birds seen or heard were recorded. Bird species that were detected within 75 m of the point were considered present for the specified sampling occasion. All points were sampled on at least three separate days distributed throughout the breeding season and at different times in the morning. For each point, the percent cover by understory foliage (UFC) and the basal area of trees (BA) were also measured during a separate sampling effort carried out from mid-July to August. See Bates et al. (2005) and Royle et al. (2004) for further details on the data collection process.

2.2. Modeling framework

We define occurrence $z(i, j)$ as a binary variable in which $z(i, j) = 1$ if species i occurs within 75 m of point j (and zero otherwise). The occurrence state is assumed to be the outcome of a Bernoulli random variable, denoted by $z(i, j) \sim \text{Bern}(\psi_{ij})$, where ψ_{ij} is the probability that species i occurs at point j . True occurrence is imperfectly observed, which confounds the estimation of ψ_{ij} . However, sampling at a point j with $k > 1$ temporal replicates over a short period (such that the community remains closed for the duration of the survey) allows for a formal distinction between species absence and non-detection, which is specified through a detection model for the observed data $x(i, j, k)$ (MacKenzie et al., 2002). We define the detection model for species i at point j during replicate k as $x(i, j, k) \sim \text{Bern}(p_{ij,k}z(i, j))$ where $p_{ij,k}$ is the detection probability of species i for the k th replicate at point j , given that species i is in fact present at point j . Thus the detection model satisfies the condition that detection is a fixed zero when a species is not present because $z(i, j) = 0$.

We assumed that the occurrence (ψ_{ij}) and detection ($p_{ij,k}$) probabilities varied by species and were influenced by habitat and survey characteristics, respectively. These effects were incorporated into the model using the logit link function (Kéry and Royle, 2008; Kéry et al., 2008; Russell et al., 2009). We modeled the occurrence probabilities for species i at point j dependent on whether point j was in CATO ($Ind = 1$) or FCW ($Ind = 0$), thus allowing for species-level effects to differ between the two study areas. We also incorporated the point-specific habitat characteristics: UFC and BA. We included both linear and quadratic terms for UFC and BA so that species associations with these habitat characteristics could be maximized at any intermediate level (e.g., some understory foliage vs. 0% or 100%) and standardized the data to have mean zero. The occurrence model for species i at point j is specified:

$$\text{logit}(\psi_{ij}) = u\text{CATO}_i(\text{Ind}_j) + u\text{FCW}_i(1 - \text{Ind}_j) \\ + \alpha_1 i \text{UFC}_j + \alpha_2 i \text{UFC}_j^2 + \alpha_3 i \text{BA}_j + \alpha_4 i \text{BA}_j^2.$$

In this case, $u\text{CATO}_i$ and $u\text{FCW}_i$ are the occurrence probabilities (on the logit scale) for species i at points in the CATO and FCW study area, respectively, for average values of UFC and BA. The coefficients for the four α_i terms are the linear and squared effects of understory foliage and tree basal area on species i . The detection model was similarly constructed to accommodate species-specific detection probabilities separately in the two study areas. We included the survey date (linear and squared effects) and the time from sunrise (linear, since all surveys occurred in the morning) as possible species-specific detection covariates. The detection covariates were also standardized to have mean zero:

$$\text{logit}(p_{i,j,k}) = v\text{CATO}_i(\text{Ind}_j) + v\text{FCW}_i(1 - \text{Ind}_j) \\ + \beta_1 i \text{date}_j + \beta_2 i \text{date}_j^2 + \beta_3 i \text{sunrise}_j.$$

The species-specific occurrence and detection processes were related to one another through an additional component where it was assumed that each of the species parameters was drawn from a common (community-level) distribution. A major benefit of the multi-species approach is that it does not require *a priori* community or group designation; combining data from similar species will be an improvement over individual species models, provided that species occurrence responses can conceivably come from a common distribution (Sauer and Link, 2002). By linking the individual species occurrence probabilities through this community hierarchical component, precision of species-specific estimates is improved leading to enhanced composite analyses and a more efficient use of available data (Kéry and Royle, 2008; Zipkin et al., 2009).

The community-level hierarchical component of the model assumes that each of the species-level occurrence ($u\text{CATO}_i$, $u\text{FCW}_i$, α_i) and detection ($v\text{CATO}_i$, $v\text{FCW}_i$, β_i) parameters were random effects, governed by “hyper-parameters”. For example, we assumed that $u\text{CATO}_i \sim N(\mu_{u\text{CATO}}, \sigma_{u\text{CATO}})$ where $\mu_{u\text{CATO}}$ is mean occurrence across the community in CATO and $\sigma_{u\text{CATO}}$ is the standard deviation among species. We similarly specified the mean and standard deviations for each of the 12 community-level habitat parameters (mean and standard deviation parameter μ , σ for each species-specific random effect **uCATO**, **uFCW**, **α_1** , **α_2** , **α_3** , **α_4**) and the 10 detection parameters (mean and standard deviation for **vCATO**, **vFCW**, **β_1** , **β_2** , **β_3**).

Bayesian analysis of the model was carried out using the method of data augmentation described in Royle et al. (2007) and Kéry and Royle (2009), which allows for estimation of the number of species in the community that were unobserved (either locally or never detected) during the sampling process. Analysis by data augmentation assumes a uniform (0, M) prior for N , the “true” species richness, where M is a fixed constant chosen to be much greater than the number of observed species (n) and such that the resulting posterior distribution is not truncated. Implementation of the model with a uniform prior is done by augmenting the data set with $M-n$ all-zero encounter histories. Then the model for the augmented data set is a zero-inflated version of a model where the actual number of species in the community (N) is known (Royle et al., 2007; Kéry and Royle, 2009). The occurrence process is modified so that $z(i, j) \sim \text{Bern}(\psi_{ij} \cdot w_i)$ where $w_i \sim \text{Bern}(\Omega)$ for species $i = 1, 2, \dots, n, n+1, n+2, \dots, N, N+1, N+2, \dots, M$. The interpretation of this modified occurrence process is that if $w_i = 1$ (corresponding to species that were observed or that were unobserved but available for sampling), the probability of occurrence is simply ψ_{ij} . If $w_i = 0$ (indicating that a species was unavailable for sampling), then occurrence is zero by definition (i.e., a structural zero). The model is now modified to estimate the parameter Ω . The value

of M need only be large enough to not truncate the posterior distribution of N , which can be assessed by running short initial trials. Interpretation of the posterior of N must be done cautiously. It is not necessarily the number of species that occur in a particular landscape; rather, it is equivalent to the asymptote of a species accumulation curve (Kéry and Royle, 2009). In the context of our study, N is the intrinsic capacity of bird species in the study areas, suggesting the possible number of species that could occur in regions with similar vegetation characteristics and management actions.

We calculated species richness including unobserved species in the two study areas as well as at each point location by summing the number of estimated species in the occurrence matrix. We also estimated the degree of similarity in community composition between study areas by calculating the “coincidence index” (Dice, 1945; Dorazio and Royle, 2005, p. 387), a value between zero and one where zero indicates no overlap and one indicates complete overlap. Following McShea and Rappole (2000), we classified observed species into two assemblages that might respond differently to deer densities or vegetation characteristics: (1) low/ground nesting and foraging species and (2) midstory/canopy nesting species. We then estimated point-specific richness and the coincidence index between study areas for these assemblages, which we used for comparison. Recognizing the limitations of the design (confounding of study area and management regime), we compared the point-specific associations of richness with the habitat attributes that reflect understory openness (UFC) and forest maturity (BA). We note that the model does not build in explicit relationships between point-specific richness and covariates; instead we inferred these relationships from the point-specific richness results.

The model was analyzed using a Bayesian approach in the programs R and WinBUGS (Spiegelhalter et al., 2003). We used independent, diffuse proper prior distributions for the community-level hyper-parameters (see Appendix in Supplementary material for the complete R and WinBUGS model code). We ran three chains of length 10,000 after a burn-in of 20,000 and thinned the posterior chains by 10. Convergence was assessed using the R-hat statistic, which examines the variance ratio of the MCMC algorithm within and between chains across iterations (Gelman and Hill, 2007).

3. Results

A total of 58 bird species were observed during sampling: 52 species in CATO and 46 in FCW. The model estimated 60.3 species in the whole of the region (95% Posterior Interval, PI: 58–64) with 55.8 (52–60) and 51.2 (47–58) species in the CATO and FCW study areas, respectively. The species composition of the two study areas was similar with an estimated coincidence index of 0.89 (0.83–0.96). However, detection probabilities were low, with greater than 80% of observed species having mean detection probabilities of less than 0.5 per sampling occasion in both study areas (Fig. 1). There was a positive, but weak, relationship ($P < 0.02$, $R^2_{\text{CATO}} = 0.12$, $R^2_{\text{FCW}} = 0.10$) between estimates of occurrence and detection across species in both CATO and FCW, but no difference between study areas.

There was no difference between point-specific estimates of species richness in CATO and FCW (Fig. 2a) and most species had similar occurrence probabilities in the two study areas (Fig. 2b). The mean estimated point-specific richness was 29.3 (19–43) species in CATO and 27.4 (19–38) species in FCW. In contrast, the mean observed number of species was 17.2 (range: 9–33) in CATO and 14.0 (range: 4–24) in FCW. Species-specific detection probabilities were also similar between the two study areas, with varying

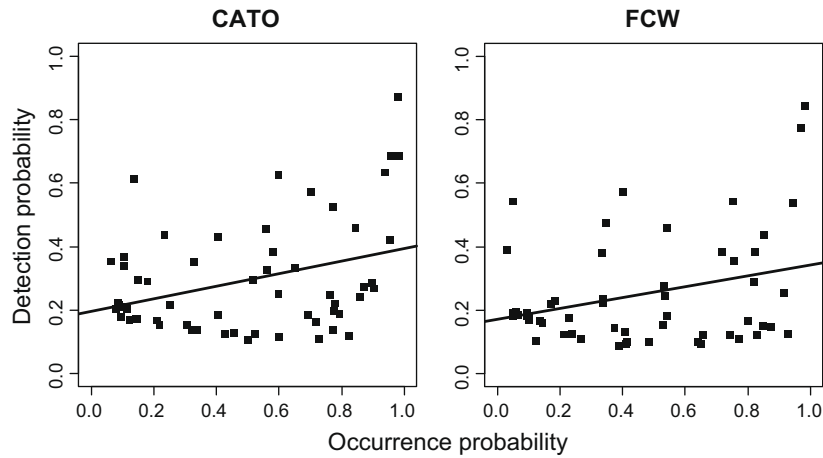


Fig. 1. Comparison of mean occurrence and detection probabilities for all bird species observed on surveys conducted during the nesting season of 2002 in the Catoctin Mountain Park (CATO) and the Frederick City Watershed (FCW), Maryland.

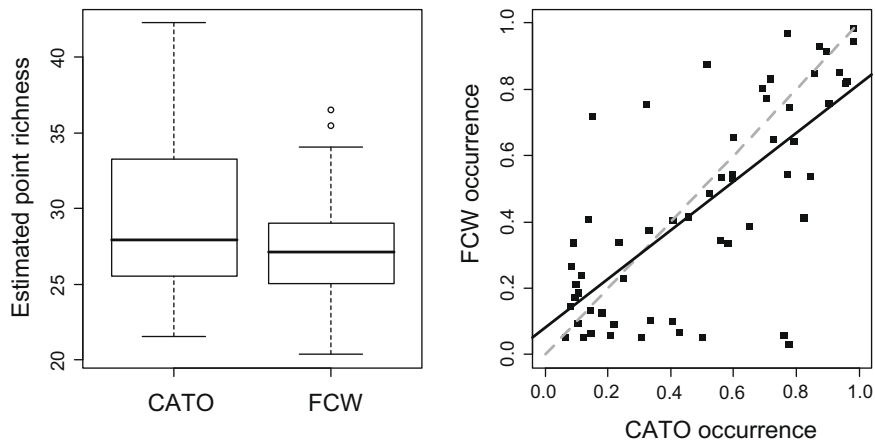


Fig. 2. Estimated point-specific bird species richness (including unobserved species) in the Catoctin Mountain Park (CATO) and the Frederick City Watershed (FCW; left panel) and mean estimated species-specific probabilities of occurrence in CATO vs. FCW (right panel; the solid black line shows the regression line and the dashed grey line is a 1-to-1 line).

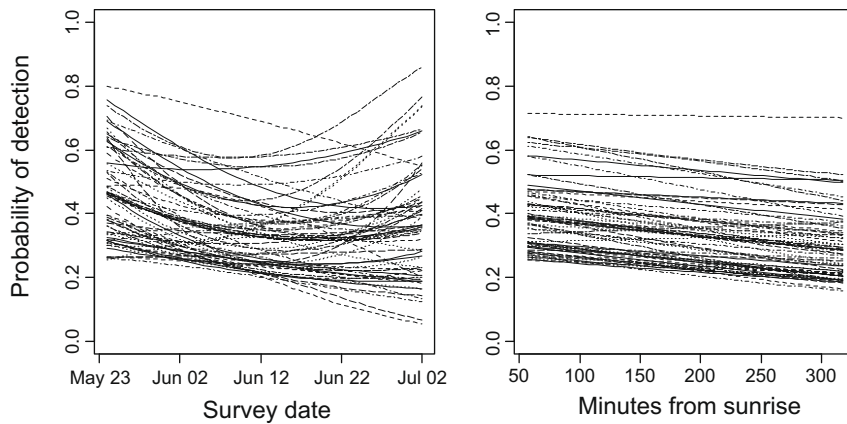


Fig. 3. Species-specific sampling effects on detection probabilities: survey date (left panel) and survey time (right panel).

effects of survey date on detection probability and a generally negative effect as time from sunrise increased (Fig. 3).

Estimated point richness for an assemblage of 14 observed understory species was 4.9 (1–10) in CATO and 7.2 (3–11) in FCW. The 29 observed midstory/canopy species had an estimated point richness of 16.3 (11–22) in CATO and 13.4 (9–18) in FCW.

The coincidence index suggested that the composition was similar in the two study areas for both understory species (0.96; 95% PI: 0.92–1.0) and midstory/canopy species (0.87; 95% PI: 0.79–0.96). Although posterior distributions for occurrence estimates in CATO and FCW overlapped for all bird species, a few notable species had visibly higher mean occurrence probabilities in one of the two

study areas. Several ground-nesting species had higher occurrence probabilities in FCW (and relatively little overlap in posterior distributions), including black-and-white warbler (*Mniotilta varia*, difference in mean occurrence between areas: 0.43), ovenbird (*Seiurus aurocapilla*, 0.20), and worm-eating warbler (*Helmitheros vermivorus*, 0.57), a species of continental and regional conservation concern (Rich et al., 2004; Rosenberg, 2003). Species with higher occurrence probabilities in CATO included others of high conservation priority (Rich et al., 2004; Rosenberg, 2003), such as cerulean warbler (*Dendroica cerulea*, 0.70) and yellow-throated vireo (*Vireo flavifrons*, 0.26).

Point-specific richness and individual species occurrence probabilities were significantly influenced by local vegetation characteristics (Fig. 4). The effect of vegetation characteristics on species richness was understated in an analysis that included only the locally observed number of species. There was a strong positive relationship between estimated point-specific species richness and understory foliage cover (UFC; $P < 0.001$ for estimated richness compared to $P = 0.017$ for observed richness) and a strong negative relationship between point-specific richness and tree basal area (BA; $P < 0.001$ for estimated richness compared to $P = 0.138$ for observed richness). As noted above, these relationships were deduced from species-specific responses to the covariates (i.e., Fig. 4 depicts the posterior means of the estimated richness for each sampled point plotted against the covariates used in the analysis). Additionally, there was a significant negative relationship between UFC and BA but no difference in the overall vegetation characteristics between the two study areas.

4. Discussion

Management actions can have significant impacts on the broader plant, animal, and bird communities. Our results demonstrate how multi-species models can be used in a conservation context to assess differences in the richness and composition of multi-species data based on: (1) whether an area is affected by a specific management action and (2) local habitat or landscape characteristics. The strength of the approach lies in the ability to estimate species-specific occurrence and detection separately, while linking members of the community. This leads to greater precision in species-specific parameter estimates, especially for rare or infrequently observed species (Zipkin et al., 2009) as well as an improved understanding of the overall community response to management actions.

Many species in our study had low detection probabilities. Inferences on occurrence distributions can be misleading without properly accounting for detectability (Nichols et al., 1998; Gu and Swihart, 2004; Kéry et al., 2008). Had the model not accounted for variability in detection probabilities among species, we would have underestimated point-level richness and the effects of local vegetation characteristics (Fig. 4). Additionally, several species had too few detections to yield occurrence estimates under individual species models. Yet for comprehensive assessments, it is important to examine the effects of management actions on all species, not just those species that produce enough data for standard analyses.

For conservation agencies interested in improving conditions for bird species, it may be more important to focus on the manipulation of local vegetation characteristics rather than on park-wide deer densities. In our study, we found no differences between the overall bird communities in CATO, where deer are unmanaged, and FCW, where deer density is regulated through hunting (Fig. 2). We found that point-specific richness estimates were most strongly associated with the local habitat characteristics, UFC and BA (Fig. 4), which is consistent with other studies that have examined the relationships between deer, vegetation, and birds (e.g., DeGraaf et al., 1991; McShea and Rappole, 1992, 2000; deCalesta, 1994). Since understory foliage and tree basal area are negatively correlated covariates, the response of species richness to these vegetation characteristics is necessarily opposing. To better understand the independent effects of UFC and BA on species richness, additional controlled studies should be conducted to sample a wider range of BA for prescribed levels of UFC (and vice versa). The vegetation in both study areas is heterogeneous, with species composition, stem density, and structure influenced not only by deer browsing, but by other factors, including soil type and depth, slope and aspect, and land use history. Despite the high deer densities in CATO, sections of the park still retain relatively high stem densities of woody understory plants such as spicebush (*Lindera benzoin*), which deer generally do not browse on, and points in these sections generally had higher richness than where understory was sparse (Bates et al., 2005). We did not detect a difference in the total percent of understory foliage between CATO and FCW. However, Bates et al. (2005) did find differences in understory foliage by height class, with significantly less foliage for heights between 0.1 and 1.5 m in CATO, which may account for lower occurrence estimates for some understory species in CATO as compared to FCW. Although the limited design of the study does not permit experimental evaluation of a wide array of habitat changes

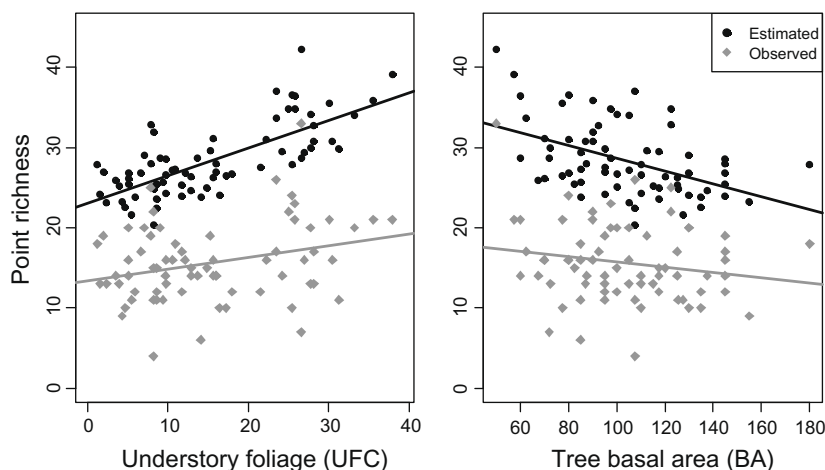


Fig. 4. Estimated (black circle) and observed (grey diamond) point-specific bird species richness compared to understory foliage (UFC; left panel) and tree basal area (BA; right panel), from the combined bird and vegetation data collected in the two study areas in the Catocin Mountains, Maryland.

associated with deer browsing, the associations of point-specific vegetation characteristics and estimated bird community attributes can provide park managers with initial models for manipulating habitats to improve bird occurrence and abundance. In addition, the modeling framework allows for explicit calculations of assemblage richness and composition, which should be helpful in further understanding trade-offs in species occurrences associated with management actions.

Multi-species hierarchical models can be used to advance understanding of how conservation and management actions affect birds and other taxa at the species and community-levels. The approach offers a unified framework for simultaneously estimating species and assemblage richness as well as occurrence and distribution of individual species at local and regional spatial scales. Covariates can be included in models to make spatial or temporal comparisons, or to assess the effects of factors that likely influence the occurrence or detection of species, thus refining parameter estimates. Recent advancements have extended the hierarchical multi-species model to account for colonization and extinction (Kéry et al., 2009), which should be useful for conservation agencies interested in studying the effects of management actions over time. Our approach can improve understanding of how species and communities respond to management actions, allows for explicit comparisons relevant to management (such as how deer influence understory vs. canopy birds), and provides enhanced information on manageable factors (i.e., density of understory shrubs) affecting species richness. Incorporating this approach into conservation should improve biodiversity assessments of species and community responses to management actions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.11.016.

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