

Influence of the temporal resolution of data on the success of indicator species models of species richness across multiple taxonomic groups

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Abstract

Indicator species models may be a cost-effective approach to estimating species richness across large areas. Obtaining reliable distributional data for indicator species (and therefore reliable estimates of species richness) often requires longitudinal data, that is, surveys for indicator species repeated for several years or time steps. Maximum information must be extracted from such data. We used genetic algorithms and a Bayesian approach to compare the influence of presence/absence data and reporting rate data (the proportion of survey years in which a species was present) on models of species richness based on indicator species. Using data on birds and butterflies from the Great Basin (Nevada, USA), we evaluated models of species richness for one taxonomic group based on indicator species drawn from the same taxonomic group and from a different group. We also evaluated models of combined species richness of both taxonomic groups based on indicator species drawn from either group. We identified suites of species whose occurrence patterns explained as much as 70% of deviance in species richness of a different taxonomic group. Validation tests revealed strong correlations between observed and predicted species richness, with 83–100% of the observed values falling within the 95% credible intervals of the predictions. Whether reporting rate data improved the explanatory and predictive ability of cross-taxonomic models depended on the taxonomic group of the indicator species. The discrepancy in predictive ability was smaller for same-taxon models. Our methods provide a manager with the means to maximize the information obtained from longitudinal survey data.

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1. Introduction

Protection of locations with a relatively large number of native species is thought to be an efficient way to maintain overall biodiversity, and species richness is used extensively as a criterion for development of conservation and management strategies (Scott et al., 1987; Myers et al., 2000; Gladstone, 2002). The potential

contribution of estimates of species richness to prioritizing locations for conservation and other land uses, of course, increases with consideration of additional measures such as species composition, endemism, functional significance, and the severity of threats. Given that survey data for many regions are sparse and acquisition of new data is costly, surrogate-based approaches to estimate species richness from data on land cover, land use, climate, and topography have become common (e.g., Mayer and Laudenslayer, 1988; Boyce and McDonald, 1999; Scott et al., 2002). Workers also have

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attempted to build functional relationships between species richness and the occurrence of “indicator” species (Pearson, 1994; Scott, 1998; Mac Nally and Fleishman, 2004), which we define as a small set of species with occurrence patterns that functionally are related to species richness of a larger set of organisms. If validation data sets demonstrate that the functional models are effective (i.e., make accurate predictions), then, depending on the target system and the experience level of the individuals charged with conducting surveys, it may be far more feasible to measure occurrence of a small number of indicator species than to conduct comprehensive species inventories (Gustafsson, 2000; Cardoso et al., 2004; Tognelli, 2005).

Statistically based methods are likely to be the most effective way to select potential indicator species, especially when compared with selection based on ad hoc criteria such as a species’ charisma or its protection status (Landres et al., 1988; Andelman and Fagan, 2000; Mac Nally et al., 2000). Our recent work suggested that species from one taxonomic group might serve as indicators of the species richness of other taxonomic groups (Fleishman et al., in press). We used genetic algorithms to model individual and combined species richness of birds and butterflies as functions of occurrence patterns of indicator species drawn from either one or both of those groups. Our best-fitting models of bird species richness, butterfly species richness, and combined species richness explained $\geq 80\%$ of deviances (Fleishman et al., in press), suggesting indicator species models may be a realistic approach to derive estimates of species richness. These models in turn can be used to inform strategies for allocation of multiple land uses and prioritization of management actions.

Surrogate-based approaches involve a trade-off between the quality of information provided by the surrogate measure and the cost of obtaining that information. For indicator species models, as for all statistical and modeling approaches, both the quality of species richness predictions and the cost of obtaining those predictions will depend on the type and quality of data used to build and apply models, including the extent to which workers have accounted for potential sources of error. These sources include, but are not limited to, grain and extent of sampling (Wilson and Shmida, 1984; Ricklefs and Schluter, 1993), unequal and imperfect probabilities of detection (Nichols et al., 1998; MacKenzie et al., 2002, 2003; Tyre et al., 2003; Wintle et al., 2004), and spatial autocorrelation (Legendre, 1993; Dale et al., 2002). On the whole, we agree with Hutto and Young, 2003, 903 that in many cases, credibility “[u]ltimately... comes down to common-sense evaluation of the possible sources of bias in the process of science.”

Not only do species have imperfect probabilities of detection when present, even with rigorous sampling, but species are not always present at sites they some-

times occupy. Therefore, “snapshots” (single surveys) of species distributions in principle may be inadequate to build and apply models of species richness. Throughout this manuscript, we use the term “single surveys” to mean sites have been visited only within a single year or meaningful time step (e.g., breeding season), even if, as in our data, the sites have been visited multiple times within a time step. We define “species richness” as the total number of species that occupy a site across multiple years or time steps. Thus, in this paper, we primarily are concerned with potential failure to account for temporal turnover in species composition, although our methods also apply to data that are subject to other sources of detection error. In arid landscapes, species composition of a site may differ considerably among years even when species richness is relatively consistent (Johnson, 1995; Brown et al., 2001; Gutzwiller and Barrow, 2001). Snapshot data increase the risk of obtaining false negatives, or recording species as being absent from sites they sometimes do occupy, which potentially limits their usefulness in species richness models. False negatives in model building data reduce the quality of models because estimates of species richness (the response variable) are inaccurate and the distribution of potential indicator species (the predictor variables) is poorly characterized.

False negatives also may cause prediction errors when models built from reliable distributional data are applied to predict species richness of new sites. Concluding that indicator species are absent from sites that they sometimes do occupy will produce inaccurate predictions of species richness. The risk of obtaining one or more false negatives increases as the number of indicator species that occupy a site increases. For example, assume four indicator species are required to estimate species richness (four is the minimum number that Fleishman et al. (in press) found to be effective), and each of those species is present at suitable sites, on average, only two out of every three surveys (i.e., the site-level probability of a false-negative in one survey is 0.33). In a single survey, the probability of observing all four indicator species at a site that they all sometimes occupy would be just 0.2, on average, assuming that species’ occurrence probabilities are independent of each other. Because the false-negative risk will be greatest at sites that support the greatest number of indicator species, erroneous estimates of species richness may be more likely at sites for which such errors could have the most serious ecological or economic consequences.

The risk of false negatives is greatly reduced by the use of longitudinal data, that is, data collected by surveying sites repeatedly (i.e., multiple visits in each of two or more years or time steps). In the example above, the probability of observing all four indicator species would increase from 0.2 to 0.63, 0.86, and 0.95 if one were to use two, three, or four surveys, respectively. Gi-

ven that distributions of many species are temporally variable, and that detection rates in one-off surveys rarely are perfect even when species are present, longitudinal data generally will be preferable, and often essential, for predicting species richness from indicator species models. In our study system, for example, despite implementation of methods that reliably detect species in years that they are present, more than half of both bird species and butterfly species have false-negative rates >0.5 (i.e., most species occupy suitable sites in fewer than half of all years). Unfortunately, the few taxa with low false-negative rates are widespread species that have limited value as indicators of species richness,

Collection of longitudinal data to build and apply models of species richness on the basis of indicator species will be cost effective provided repeated surveys for a few indicator species are less costly than comprehensive surveys of all species. The ability of observers to identify simultaneously all species (often >60) compared to searching for just a small subset of species, of course, will vary geographically and by taxon. Longitudinal indicator species data are likely to be more cost-effective when species richness of multiple taxonomic groups needs to be estimated. It generally will be less costly to conduct multiple surveys for a small number of indicator species from a single taxonomic group (e.g., birds) than to survey comprehensively all species from many taxonomic groups (e.g., birds, mammals, and beetles) even once. Situations also may arise in which one taxonomic group is surveyed intensively over multiple years, but managers also wish to estimate species richness of other taxonomic groups. In those cases, the distributions of some species from the intensively surveyed taxon may provide useful information about species richness of other taxonomic groups, even if species richness itself of those groups is not correlated (Fleishman et al., in press).

Longitudinal data can be used to calculate either a binary occurrence value (present in any year[s] or absent) or a “reporting rate” value. We define reporting rate as the proportion of years that a species was found to be present at a given site (number of present years/number of survey years). Reporting rate provides different information to a measure of species presence based on multiple years of data and, potentially, offers greater resolution in model building. We asked whether reporting rates of indicator species provide useful information about site-level species richness. That is, are models of species richness improved by the use of reporting rate data instead of presence/absence data for indicator species? If multiple surveys are required to obtain reliable presence/absence data, then collecting reporting rate data incurs no additional expense, so any improvement in species richness models warrants use of reporting rate data. It is possible that the improvement in model performance using reporting rate data may be sufficient to justify their use even if reliable presence/absence data

can be obtained more cheaply. This will be the case when reporting rates of indicator species provide good estimates of species richness of multiple taxonomic groups, but presence/absence data on the indicator species, or other surrogate measures of species richness, do not.

Accordingly, we examined whether the fit of models of species richness based on indicator species was affected by the use of occurrence data compared with reporting rate data to build the models. We evaluated models of species richness for one taxonomic group based on indicator species drawn from the same taxonomic group and on indicator species drawn from a different taxonomic group. We also evaluated models of combined species richness of both taxonomic groups based on indicator species drawn from either one of the groups. Where possible, we validated the predictive ability of our models using independent data collected from locations not used to build the models. Last, we consider the ecological characteristics of selected indicator species to gain insight into why the selected species might convey information about species richness.

2. Methods

2.1. Field methods

Data for our analyses were collected in three adjacent mountain ranges in the central Great Basin that have similar biogeographic and human land-use histories, the Shoshone Mountains (1850 km², approximate north-south boundaries 39°14' to 38°57'), Toiyabe Range (3100 km², 39°54' to 38°30'), and Toquima Range (1750 km², 39°17' to 38°29') (Lander and Nye counties, NV, USA). Our data collection incorporated established techniques that detect species presence reliably and permit assessment of distributional trends (Pollard and Yates, 1993; Pullin, 1995; Bibby et al., 2000; Buckland et al., 2001; Siegel et al., 2001). These methods have been described in detail and tested for sampling adequacy (e.g., Dobkin and Wilcox, 1986; Dobkin and Rich, 1998; Fleishman et al., 1998, 2000, 2001; Mac Nally et al., 2004). Based on those tests, we assume that detection error was relatively low, although not zero. Thus, a substantial proportion of the false-negatives in our data arise primarily from temporal variations in site occupancy rather than from failure to detect species when present. From 1996 to 2003, inventories for butterflies were conducted in a total of 195 sites, and inventories for birds were conducted in 84 of those sites. We recorded 74 species of breeding birds and 65 species of resident butterflies (a complete list is available from E.F.). Site-level species richness was calculated as the total number of species recorded in the site across all years. Site-level species richness ranged from 5 to 34

for birds (mean 17.3) and from 3 to 51 for butterflies (mean 24.9). Site areas ranged from 1.5 to 44.4 ha. At the site level, area explained little variance in species richness (<3%) of either taxonomic group (Mac Nally et al., 2003).

2.2. Model building

We modelled the site-level species richness of birds (henceforth, bird species richness) and butterflies (butterfly species richness) as functions of the occurrences (i.e., presence or absence based on multiple years of data) or the reporting rates (proportion of years that a given site was surveyed in which a certain species was present) of small subsets of “indicator” species. We modelled species richness of each taxon as a function of indicator species from either the same taxon (same-taxon models) or a different taxon (cross-taxon models). We also modelled the combined species richness of both taxonomic groups as functions of indicator species drawn from each taxon. For each response–predictor (species richness–indicator group) combination, we examined three types of models: models using presence/absence data for all indicator species (presence/absence models), models using reporting rate data for all indicator species (reporting rate models), and models using presence/absence data for some indicator species and reporting rate data for others (mixed models).

All models with butterflies as indicator species were built with data from the Shoshone and Toiyabe ranges because we do not presently have reporting rate data for butterflies in the Toiyabe Range; each Toiyabe site was surveyed for butterflies in only one year. Although we previously used data from all three mountain ranges to build butterfly presence/absence models (Fleishman et al., in press), in order to compare presence/absence and reporting rate models directly, those models must be based on the same data. All models with bird indicator species were built using data collected with equal survey effort from all three mountain ranges; models using presence/absence data for bird indicator species are the same as those presented in Fleishman et al. (in press).

To find practically useful models, we limited the number of indicator species for each model to six, which is <10% of the total number of species in each taxonomic group. We used Poisson regression to model species richness because Poisson error structures are likely to be most appropriate for non-negative “counts” data, such as number of species (McCullagh and Nelder, 1989).

2.2.1. Selection of indicator species

With large sets of predictor variables, many of the screening approaches used to identify the “best” subset of variables are suspect statistically (Mac Nally, 2000). Information criteria, such as Bayes information crite-

riion (BIC, Schwarz, 1978), have been recommended to identify the most efficient model(s) (Kass and Raftery, 1995; Mac Nally, 2000). BIC represents a compromise between model fit (ability to explain observed deviance in the response variable) and model complexity (number of predictor variables). BIC is calculated as $-2 \times \log(\text{likelihood}) + \log(N) \times Q$, where N is the number of observations and Q is the number of model parameters. BIC imposes a larger penalty on additional terms than other common criteria (e.g., Akaike's Information Criterion; Rawlings et al., 1998) and is, therefore, more likely to find practical, simpler indicator species models. Each additional indicator species increases the risk of false-negatives, and potentially increases the effort or expertise needed to conduct surveys. Therefore, only indicator species that substantially improve model predictions should be included. Usually, all possible models are fitted and the model with the lowest BIC value is retained (i.e., an exhaustive search of model space). However, because we had such a large number of potential predictor variables (potential indicator species), we could not undertake exhaustive searches, even though we considered only models with ≤ 6 predictors. Instead, we used a genetic algorithm to search for very good, but not demonstrably the most efficient, models (Fleishman et al., in press).

Genetic algorithms are iterative search procedures that emulate the process of natural selection. They are useful for large combinatoric problems and have been used successfully to select input variables in neural networks (Jefferson et al., 1997) and logistic regression models (Vinterbo and Ohno-Machado, 1999). Genetic algorithms iteratively refine an initial “population” of potential solutions, usually generated randomly. The value of the function to be optimized – in our case, BIC for each model – is used as a measure of individual “fitness,” with fitter individuals (models) given a greater probability of “reproducing.” Genetic operations such as crossover and mutation are emulated and applied to a proportion of individuals in each generation. Characteristics of individuals with high fitness (viz., low BIC) are retained and recombined until very good solutions are found.

We used a genetic algorithm, implemented with the *R* statistical programming software (Sekhon and Mebane, 1998; R Development Core Team, 2003), to search for Poisson models with low BIC values for each combination of response and predictor variables. First, an initial population of 1000 random models (individual “genomes”) was generated. Each model in the population was represented by a vector of k digits, where k is the number of candidate species (in our case, $k = 74$ bird species, 65 butterfly species, or 139 species total), which indicated the species included in the model. For presence/absence and reporting rate models, we used a binary code in which species were either included in the

model (1) or excluded from the model (0). For mixed models, we used a ternary code in which species were included as reporting rate data (1), included as presence/absence data (2), or excluded (0).

In each generation, the BIC was calculated for every model in the population, and fitness ranks were assigned accordingly (fitness increases as BIC decreases). The model in each generation with the lowest BIC was propagated into the next generation. All other models were replaced with the results of genetic operators (cloning, crossover, mutation) applied to parents selected, with replacement, from the entire population. The probability that a model was to be selected to be a parent increased as its fitness increased (i.e., as BIC decreased). After 25 generations with no improvement in fitness (i.e., no reduction in the minimum BIC value for all models), the genetic algorithm was terminated and the model with the lowest BIC (the solution) was reported. For each response–predictor combination, we obtained solutions from ten random starts of the genetic algorithm, and selected the solution with the lowest BIC value as the final model. For each model, ten runs of the genetic algorithm produced four or fewer unique solutions. Those solutions invariably shared several indicator species, and the best solution occurred at least four times, and often ten times, in the ten runs. We are therefore confident that the selected final models included the most effective indicator species.

2.2.2. Model fitting

We computed model parameters for the best genetic algorithm solutions with the WinBUGS software for Bayesian inference (version 1.4, Spiegelhalter et al., 2003). The model used was

$$\log(\mu_i) = \alpha_0 + \sum_{k=1}^Q \alpha_k X_{ik}, \quad (1)$$

$$Y_i \sim \text{Poisson}(\mu_i),$$

where the α s are the regression coefficients to be estimated (an intercept [α_0] and coefficients for each of the Q indicator species); μ_i is the estimated mean species richness at site i given the state (X_i) of each of the Q indicator species; and Y_i is the observed species richness at site i , which is assumed to be distributed (\sim) as a Poisson variable with mean μ_i .

Bayesian methods incorporate prior knowledge about parameter values and produce posterior probability distributions for each parameter. If one has virtually no prior knowledge about a parameter's value, then it is appropriate to use a "non-informative" prior distribution for that parameter – a normal distribution with high variance is typical for regression coefficients – which means that the posterior probability distributions are dictated by the newly collected data (Lee, 1989).

(For a general overview of Bayesian statistical methods and associated terminology, see Bergerud and Reed, 1998 and references therein.) We initially gave the α s non-informative normal priors [$\alpha_i \sim \text{normal}(\mu_i = 0, \sigma_i^2 = 1000)$]. WinBUGS uses Markov chain Monte Carlo methods to estimate model parameters iteratively by repeatedly "sampling" from distributions specified in the model (Gilks et al., 1996). Initial parameter values for Markov chain Monte Carlo were generated randomly. Probability distributions for parameters were allowed to settle ("burn in") over 1000 iterations before posterior parameter distributions were built for another 10000 iterations.

We used the posterior probability distributions of estimated model coefficients to evaluate whether selected indicator species made an important contribution to the prediction of species richness. If $\geq 90\%$ of the posterior probability distribution of a species' coefficient was either greater than zero (positive effect) or less than zero (negative effect), we deemed that species to have an important effect and retained it in the model. All species selected in final genetic algorithm solutions met this criterion and were therefore retained in fitted models.

2.3. Model validation

2.3.1. Internal validation

We used bootstrapping to estimate the expected predictive performance of models. Bootstrapping is a method of internal validation that provides near-unbiased estimates of predictive accuracy with relatively low variance (Efron and Tibshirani, 1993, 1997; Harrell et al., 1996; Wintle et al., in press). Importantly, bootstrapping does not involve data splitting, so the entire dataset is used for model development. For each model, we calculated a "naïve" estimate of apparent predictive performance (R_{apparent}) by correlating predicted and observed species richness for the model building data. We then generated 100 bootstrap samples by randomly sampling n sites with replacement from the model building data, where n is the number of sites in the model building data. The model building process, including variable selection, was repeated for each bootstrap sample to produce 100 "bootstrap models."

We computed the apparent predictive performance (R_{boot}) of each bootstrap model by correlating (Spearman coefficient) predicted and observed species richness for the corresponding model building data (bootstrap sample). We then tested the predictive performance of each bootstrap model against the original data, denoting the correlation between observed and predicted data as R_{original} . The average difference between R_{boot} and R_{original} for all bootstrap models is an estimate of the average optimism (O) in the apparent (naïve) performance statistic. The original model's performance statistic (R_{apparent}) therefore was adjusted by subtracting the

average optimism ($R_{\text{expected}} = R_{\text{apparent}} - O$). R_{expected} is a near-unbiased estimate of the expected external predictive performance (i.e., the expected correlation between observed and predicted species richness) of the original model (Harrell et al., 1996).

2.3.2. External validation

The most stringent test of any model is external validation. Predictions of species richness based on any functional relationship, including occurrence of indicator species, should be confronted with independent data that were not used to build the models (Landres et al., 1988; Mac Nally et al., 2000; Fleishman et al., 2003; Mac Nally and Fleishman, 2004). Because multiple-year surveys are required to calculate reporting rate, and are preferable for estimating presence/absence, a full evaluation of the models developed here is not yet possible. However, by combining recently collected data with data collected in the 1980s (Dobkin and Wilcox, 1986) we were able to perform a preliminary examination of the bird indicator species models. Twenty-three sites in the Toiyabe Range were surveyed for birds in 1983 and/or 1984 (Dobkin and Wilcox, 1986). These sites also were surveyed for butterflies in 1995 or 1996, and were re-surveyed for birds in 2004. Combining these data produced a validation data set comprising multiple-year presence/absence and reporting rate data for all bird species, measures of bird species richness, and measures of butterfly species richness. We used these validation data to assess the performance of bird indicator species models. The validations necessarily assume that the site-level species richness of birds and butterflies was relatively constant throughout the period 1983–2004 (Fleishman and Mac Nally, 2003). We could not conduct external validation for butterfly indicator species models because we do not yet have new multiple-year survey data for butterflies (surveys anticipated during the next few years will rectify this deficiency).

We used WinBUGS to produce a posterior distribution of predicted species richness at each validation site given the state (presence/absence or reporting rate as appropriate) of the indicator species at that site and the posterior distributions of the model parameters. We then examined the correlation between observed and predicted (median of the posterior distribution) species richness, and determined the number of sites for which the observed species richness fell within the 95% credible intervals of predicted species richness. For models of bird species richness, we also examined potential bias in model predictions (systematic overestimation or underestimation of species richness) by calculating the mean difference between predicted and observed values for each model. We denote this value as mean bias, B . We estimated bootstrap confidence intervals (CI) for B by calculating the 2.5 and 97.5 percentiles of the distribution of mean bias values, which in turn were calcu-

lated from 1000 bootstrap samples of the validation data and corresponding model predictions.

Our measures of butterfly species richness for the validation sites were based on a single year of data for each site. Therefore, we almost certainly underestimated the multiple-year species richness of those sites. However, because there is a strong linear relationship between single-year species richness of butterflies and multiple-year species richness of butterflies (average Spearman correlation for 1996–2003 across all mountain ranges = 0.80), the rank correlations between predicted and observed species richness of butterflies should provide a reasonable indication of model performance. We did not attempt to infer multiple-year species richness of butterflies based on the single-year data because the functional form of the relationship differs between years and mountain ranges, and data were insufficient to parameterize the relationship for validation sites in the Toiyabe Range. Accordingly, we were unable to quantify bias for models of butterfly species richness or combined species richness.

2.3.3. Use of single-year survey data

We investigated whether single-year (presence/absence) data for indicator species, when entered into “good” models parameterized with multiple-year data, might generate reliable predictions of multiple-year species richness. We entered single-year presence/absence data for bird indicator species at the validation sites into the appropriate presence/absence models for bird species richness, butterfly species richness, and combined species richness. We therefore produced three separate sets of predictions from each model based on the occurrence of the bird indicator species in 1983, 1984 and 2004. We then compared each set of predictions with observed species richness as described in Section 2.3.2.

3. Results

3.1. Birds as indicator species

3.1.1. Cross-taxon models

Models of butterfly species richness with bird indicator species were improved by using reporting rate data rather than presence/absence data for at least some indicator species. The best reporting rate model (64% deviance explained) and mixed model (65%) explained substantially more deviance in butterfly species richness than the best presence/absence model (55%) (Fig. 1). Bootstrapped estimates of expected predictive performance (R_{expected}) also were higher for the reporting rate model (0.64) and mixed model (0.65) than the presence/absence model (0.58). The best reporting rate, presence/absence, and mixed models included six indicator species, the maximum number we allowed (Table 1).

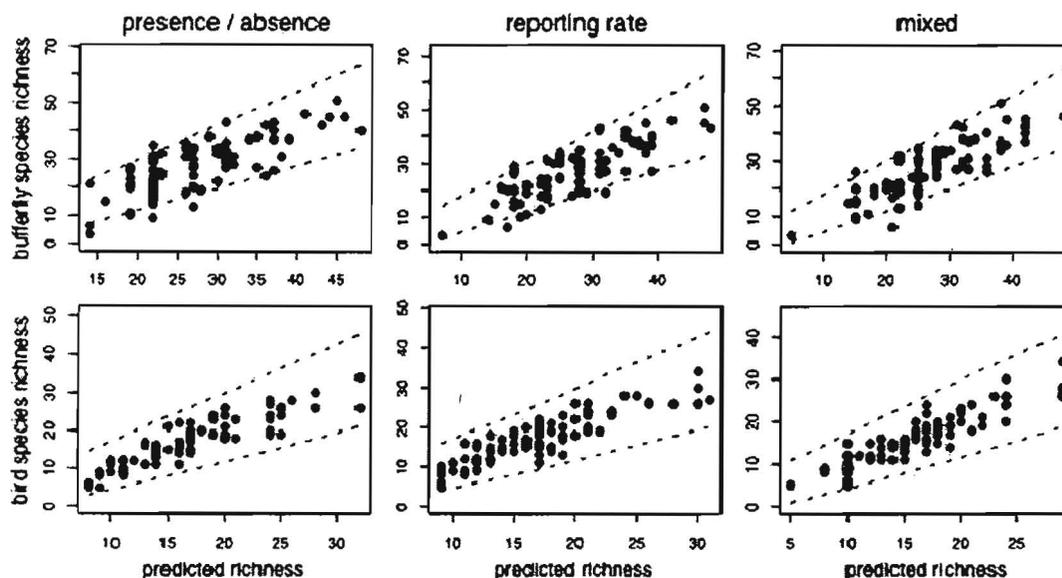


Fig. 1. Fitted versus observed species richness for models with bird indicator species. Top row (left to right): models of butterfly species richness based on presence/absence data, reporting rate data, or both presence/absence and reporting rate data, for bird indicator species. Bottom row (left to right): models of bird species richness based on presence/absence data, reporting rate data, or both presence/absence and reporting rate data, for bird indicator species. Dashed lines show 95% credible intervals for fitted species richness.

3.1.2. Same-taxon models

Reporting rates of some bird species also provided information about bird species richness (Fig. 1). The best models of bird species richness with presence/absence data and mixed data each included six bird indicator species and explained 82% of the deviance in bird species richness (Table 1). The best reporting rate model of bird species richness similarly included six indicator species and explained 78% of deviance (Table 1). Expected predictive performance was high for all models, but was greatest for the presence/absence model ($R_{\text{expected}} = 0.86$), followed by the mixed model ($R_{\text{expected}} = 0.83$) and the reporting rate model ($R_{\text{expected}} = 0.81$).

3.1.3. Combined-richness models

The best presence/absence, reporting rate, and mixed models of combined species richness of birds and butterflies with bird indicators explained 72%, 71%, and 76% of deviance, respectively (for brevity, figures and tables are not presented here; complete information is available from E.F.). Expected predictive performance was higher for the presence/absence model ($R_{\text{expected}} = 0.81$) than the reporting rate and mixed models ($R_{\text{expected}} = 0.76$ for both).

3.1.4. Identity of bird indicator species

Across all models, eleven bird species were selected as indicators of butterfly species richness. Five bird indicators were selected as presence/absence terms only, four

as reporting rate terms only, and two as either presence/absence and reporting rate terms in different models. Eleven bird species were selected as indicators of bird species richness, three as presence/absence terms only, four as reporting rate terms only, and four as both presence/absence and reporting rate terms. Two bird indicator species, Western Tanager (*Piranga ludoviciana*) and Lark Sparrow (*Chondestes grammacus*), were included in models of both butterfly species richness and bird species richness. Western Tanager was included as a presence/absence term only, whereas Lark Sparrow was included as a reporting rate term only.

3.2. Birds as indicator species: external validation

3.2.1. Cross-taxon models

For models of butterfly species richness with bird indicator species, observed species richness was more strongly correlated with predicted species richness values from the reporting rate and mixed models ($R_{\text{Spearman}} = 0.49$ and 0.42 , respectively) than with predictions from the presence/absence model ($R_{\text{Spearman}} = 0.35$). Note, however, that the low correlation coefficient for the presence/absence model was largely caused by one site for which butterfly species richness was greatly over-estimated (predicted = 35, actual = 10). Omitting that site resulted in a correlation coefficient of 0.59 for the presence/absence model. Observed values of species richness fell within predicted 95% credible intervals for 19 of the 23 validation sites (83%) for all three models (Fig. 2).

Table 1

Parameter values (mean and standard deviation) for Poisson-regression models of species richness of butterflies (butterfly S) and birds (bird S) based on presence/absence patterns and reporting rates of bird indicator species

Variable (indicator species)	Mean	e^{mean^a}	SD
<i>Butterfly S with bird indicators: presencelabsence data</i>			
55% deviance explained, BIC ^b = 599			
Intercept	2.943	18.97	0.046
Rock Wren <i>Salpinctes obsoletus</i>	0.158	1.17	0.045
Western Tanager <i>Piranga ludoviciana</i>	0.204	1.23	0.044
Yellow Warbler <i>Dendroica petechia</i>	0.316	1.37	0.044
Black-headed Grosbeak <i>Pheucticus melanocephalus</i>	0.154	1.17	0.046
Chukar <i>Alectoris chukar</i>	0.255	1.29	0.062
Western Meadowlark <i>Sturnella neglecta</i>	-0.312	0.73	0.079
<i>Butterfly S with bird indicators: reporting rate data</i>			
64% deviance explained, BIC = 569			
Intercept	3.350	28.50	0.036
Blue-gray Gnatcatcher <i>Poliophtila caerulea</i>	-0.370	0.88–0.69	0.086
Yellow Warbler	0.293	1.10–1.34	0.058
Black-headed Grosbeak	0.324	1.11–1.38	0.086
Black-throated Sparrow <i>Amphispiza bilineata</i>	-0.679	0.80–0.51	0.159
Plumbeous Vireo <i>Vireo plumbeus</i>	-0.425	0.87–0.65	0.113
Lark Sparrow <i>Chondestes grammacus</i>	-1.348	0.64–0.26	0.222
<i>Butterfly S with bird indicators: mixed model (presencelabsence and reporting rate data)</i>			
65% deviance explained, BIC = 567			
Intercept	3.224	25.13	0.039
Western Tanager (presence/absence)	0.226	1.25	0.043
Blue-gray Gnatcatcher (reporting rate)	-0.370	0.89–0.69	0.083
Yellow Warbler (reporting rate)	0.424	1.15–1.53	0.056
Plumbeous Vireo (reporting rate)	-0.354	0.89–0.70	0.114
Lark Sparrow (reporting rate)	-1.479	0.61–0.23	0.261
Northern Harrier <i>Circus cyaneus</i> (presence/absence)	0.588	1.80	0.155
<i>Bird S with bird indicators: presencelabsence data</i>			
82% deviance explained, BIC = 453			
Intercept	2.158	8.65	0.075
Black-throated gray Warbler <i>Dendroica nigrescens</i>	0.218	1.24	0.067
MacGillivray's Warbler <i>Oporornis philadelphia</i>	0.230	1.26	0.072
Western Scrub-jay <i>Aphelocoma californica</i>	0.252	1.29	0.061
Red-shafted Flicker <i>Colaptes auratus</i>	0.187	1.21	0.064
Western Tanager	0.141	1.15	0.056
Fox Sparrow <i>Passerella iliaca</i>	0.290	1.34	0.077
<i>Bird S with bird indicators: reporting rate data</i>			
78% deviance explained, BIC = 461			
Intercept	2.248	9.47	0.067
Black-throated Gray Warbler	0.322	1.11–1.38	0.073
American Robin <i>Turdus migratorius</i>	0.251	1.09–1.29	0.091
Western Scrub-jay	0.251	1.09–1.29	0.094
Red-shafted Flicker	0.225	1.08–1.25	0.093
Warbling Vireo <i>Vireo gilvus</i>	0.266	1.09–1.30	0.089
Fox Sparrow	0.430	1.15–1.54	0.183
<i>Bird S with bird indicators: mixed model (presencelabsence and reporting rate data)</i>			
82% deviance explained, BIC = 452			
Intercept	2.308	10.05	0.075
Spotted Towhee <i>Pipilo maculatus</i> (reporting rate)	0.211	1.07–1.23	0.089
MacGillivray's Warbler (presence/absence)	0.280	1.32	0.057
Western Scrub-jay (presence/absence)	0.172	1.19	0.059
Red-shafted Flicker (presence/absence)	0.219	1.24	0.060
Hermit Thrush <i>Catharus guttatus</i> (presence/absence)	0.172	1.19	0.069
Lark Sparrow (reporting rate)	-0.755	0.78–0.47	0.304

^a The exponentiated mean (e^{mean}) of the intercept term is the expected species richness in the absence of all indicator species. For indicator species, e^{mean} is a multiplicative factor by which the presence of that species affects the predicted species richness. For presence/absence data, the presence of a species always result in factor of $e^{\text{mean} \times 1}$. For reporting rate data, the presence of a species results in a factor of $e^{\text{mean} \times \text{reporting rate}}$. We calculated the minimum ($e^{\text{mean} \times 0.33}$) and maximum ($e^{\text{mean} \times 1}$) factor values for an indicator species present at a site surveyed for three years.

^b Bayesian information criterion.

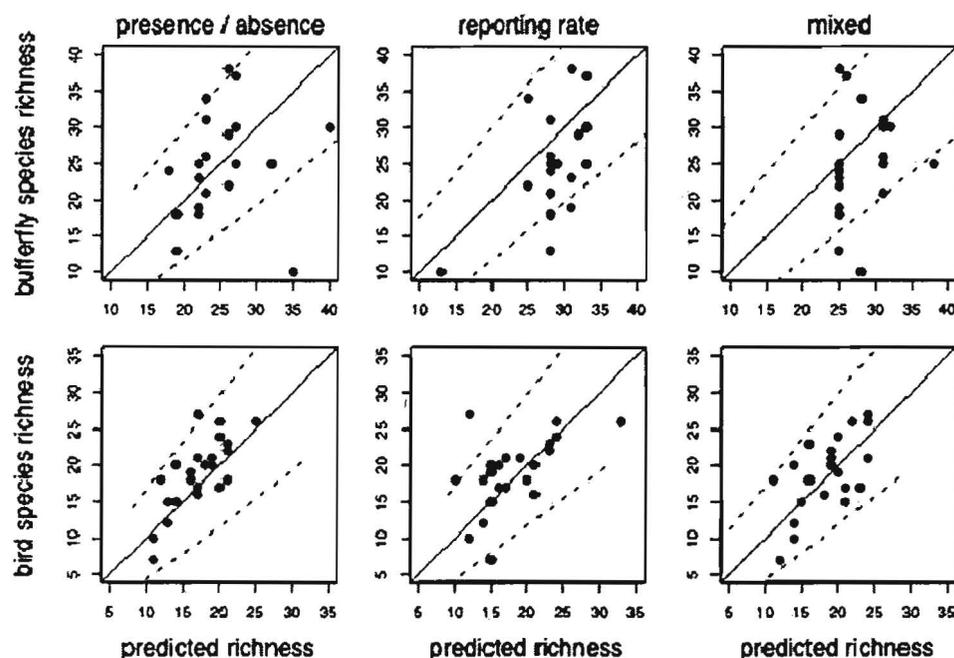


Fig. 2. Predicted versus observed species richness at external validation sites for models with bird indicator species. Top row (left to right): models of butterfly species richness based on presence/absence data, reporting rate data, or both presence/absence and reporting rate data, for bird indicator species. Bottom row (left to right): models of bird species richness based on presence/absence data, reporting rate data, or both presence/absence and reporting rate data, for bird indicator species. Dashed lines show 95% credible intervals for predicted species richness.

3.2.2. Same-taxon models

For models of bird species richness with bird indicators, observed species richness was more strongly correlated with predicted values of species richness from the presence/absence model ($R_{\text{Spearman}} = 0.75$) than with predictions from the reporting rate model ($R_{\text{Spearman}} = 0.57$) or mixed model ($R_{\text{Spearman}} = 0.61$). Observed values of species richness fell within the predicted 95% credible intervals for 22 (96%), 21 (91%), and 23 (100%) of the 23 validation sites for the presence/absence, reporting rate, and mixed models, respectively (Fig. 2). The presence/absence model slightly underestimated bird species richness ($B = -1.7$, $CI = -3.4$ to 0.4), but the reporting rate model ($B = -1.0$, $CI = -2.7$ to 1.0) and mixed model ($B = -0.5$, $CI = -2.1$ to 1.1) showed no consistent bias (Fig. 2).

3.2.3. Combined-richness models

For models of combined species richness based on bird indicators, correlations between observed and predicted values of species richness for validation sites were highest for the presence/absence model ($R_{\text{Spearman}} = 0.67$), followed by the mixed model ($R_{\text{Spearman}} = 0.57$) and reporting rate model ($R_{\text{Spearman}} = 0.33$). Observed values of species richness fell within predicted 95% credible intervals for 20 (87%), 19 (83%) and 18 (78%) of the 23 validation sites for the presence/absence, reporting rate, and mixed models, respectively.

3.2.4. Use of single-year data

The predictions of presence/absence models with bird indicator species proved unreliable when based on single-year presence/absence data for the indicator species. Predictions were moderately successful when based on 2004 data (Table 2), but not as successful as predictions that were based on multiple-year presence/absence data (see Sections 3.2.1, 3.2.2, 3.2.3). Predictions of multiple-year species richness based on single-year data from 1983 or 1984 were poor, especially compared with predictions based on multiple-year presence/absence data (Table 2). Of the potential reasons for the discrepancy in success among individual years, differences in short-term to moderate-term trends in precipitation are among the most likely. Annual precipitation in 1983 and 1984 was well above the mean for the 117-year period of record (70% and 30%, respectively), and approximately double the annual precipitation during the period of drought that extended from 1999 to 2004 (Western Regional Climate Center, 2005). Predictions made on the basis of single-year data consistently underestimated bird species richness (Table 2), demonstrating the effect of false-negatives on species richness estimates.

3.2.5. External versus internal validation

The bootstrapping method of internal validation appeared to be useful for ranking models in terms of likely predictive accuracy. For each model type (presence/

Table 2

Parameter values (mean and standard deviation) for Poisson-regression models of species richness of birds (bird S) and butterflies (butterfly S) based on presence/absence patterns and reporting rates of butterfly indicator species

Variable (indicator species)	Mean	e^{mean^a}	SD
<i>Bird S with butterfly indicators: presence/absence data</i>			
70% deviance explained, BIC ^b = 294			
Intercept	1.511	4.53	0.467
<i>Hesperia comma</i>	1.082	2.95	0.470
<i>Papilio rutulus</i>	0.191	1.21	0.074
<i>Papilio multicaudatus</i>	0.415	1.51	0.070
<i>Papilio zelicaon</i>	-0.884	0.41	0.355
<i>Bird S with butterfly indicators: reporting rate data</i>			
55% deviance explained, BIC = 298			
Intercept	2.504	12.23	0.070
<i>Incisalia eryphon</i>	0.256	1.09–1.29	0.102
<i>Papilio multicaudatus</i>	0.465	1.17–1.59	0.088
<i>Bird S with butterfly indicators: mixed model (presence/absence and reporting rate data)^c</i>			
56% deviance explained, BIC = 296			
Intercept	1.537	4.65	0.416
<i>Hesperia comma</i> (presence/absence)	1.125	3.08	0.418
<i>Papilio multicaudatus</i> (reporting rate)	0.524	1.19–1.69	0.083
<i>Butterfly S with butterfly indicators: presence/absence data</i>			
83% deviance explained, BIC = 542			
Intercept	1.937	6.94	0.125
<i>Hesperia juba</i>	0.547	1.73	0.124
<i>Coenonympha tullia</i>	0.194	1.21	0.069
<i>Speyeria zerene</i>	0.162	1.18	0.053
<i>Icaricia lupini</i>	0.357	1.43	0.053
<i>Chlosyne acastus</i>	0.204	1.23	0.046
<i>Phyciodes pulchella</i>	0.235	1.27	0.050
<i>Butterfly S with butterfly indicators: reporting rate data</i>			
79% deviance explained, BIC = 557			
Intercept	2.316	10.14	0.096
<i>Lycaeides melissa</i>	0.336	1.12–1.40	0.104
<i>Papilio rutulus</i>	0.257	1.09–1.29	0.073
<i>Euchloe ausonides</i>	0.589	1.21–1.80	0.082
<i>Chlosyne acastus</i>	0.302	1.10–1.35	0.050
<i>Lycaena heteronea</i>	0.381	1.13–1.46	0.048
<i>Phyciodes pulchella</i>	0.408	1.14–1.50	0.084
<i>Butterfly S with butterfly indicators: mixed model (presence/absence and reporting rate data)</i>			
81% deviance explained, BIC = 548			
Intercept	2.501	12.19	0.054
<i>Limnitis weidemeyerii</i> (presence/absence)	0.190	1.21	0.051
<i>Ochlodes sylvanoides</i> (presence/absence)	0.169	1.18	0.056
<i>Euchloe ausonides</i> (reporting rate)	0.367	1.13–1.44	0.077
<i>Chlosyne acastus</i> (reporting rate)	0.237	1.08–1.27	0.054
<i>Lycaena heteronea</i> (reporting rate)	0.344	1.12–1.41	0.050
<i>Phyciodes pulchella</i> (presence/absence)	0.272	1.31	0.049

^a The exponentiated mean (e^{mean}) of the intercept term is the expected species richness in the absence of all indicator species. For indicator species, e^{mean} is a multiplicative factor by which the presence of that species affects the predicted species richness.

^b Bayesian information criterion.

^c For presence/absence data, the presence of a species always results in factor of $e^{\text{mean} \times 1}$. For reporting rate data, the presence of a species results in a factor of $e^{\text{mean} \times \text{reporting rate}}$. We calculated the minimum ($e^{\text{mean} \times 0.33}$) and maximum ($e^{\text{mean} \times 1}$) factor values for an indicator species present at a site surveyed for three years.

absence, reporting rate, or mixed), the model with the highest R_{expected} value had the highest actual correlation between observed and expected species richness at validation sites. Actual correlations consistently were lower than expected values, but this partly may reflect a small sample size for the validation data. With only 23 valida-

tion sites, correlation coefficients may be much influenced by a few outliers. R_{expected} values assume that sample size is equal to the original data (i.e., 84 sites for same-taxon bird models), for which outliers (e.g., points outside of the 95% credible intervals) would have little influence. For most models, correlations of pre-

dicted and observed richness excluding observed points outside of the predicted 95% credible intervals were within 10% of the R_{expected} values.

3.3. Butterflies as indicator species

3.3.1. Cross-taxon models

The best presence/absence model explained 70% of the deviance in bird species richness (Fig. 3) and included four indicator species (Table 3). The best reporting rate and mixed models explained 55% and 56% of deviance in bird species richness, respectively, but each included only two indicator species (Table 3). R_{expected} values were higher for the presence/absence model (0.68) than the reporting rate model (0.65) and mixed model (0.61).

It is difficult to compare directly the usefulness of reporting rate and presence/absence data for butterfly indicator species from the above models because the reporting rate and mixed models included two indicator

species, whereas the presence/absence model included four indicator species. BIC represents a compromise between model fit (ability to explain observed deviance in the response variable) and model complexity (number of predictor variables). However, in general, we would expect models with a greater number of variables to explain a greater percentage of deviance. Therefore, to ensure that our comparison of presence/absence data versus reporting rate data was “fair,” we examined whether models with an equal number of variables have equivalent explanatory power.

To compare the use of presence/absence and reporting rate data in models with the same number of butterfly indicator species, we ran the genetic algorithm so that residual deviance (rather than BIC) was minimized, with a maximum of six indicator species. The solutions to these searches were extensions of the lowest BIC models: they included all indicator species from the lowest-BIC models. The presence/absence, reporting rate, and mixed models with six indicator species explained 73%, 66%,

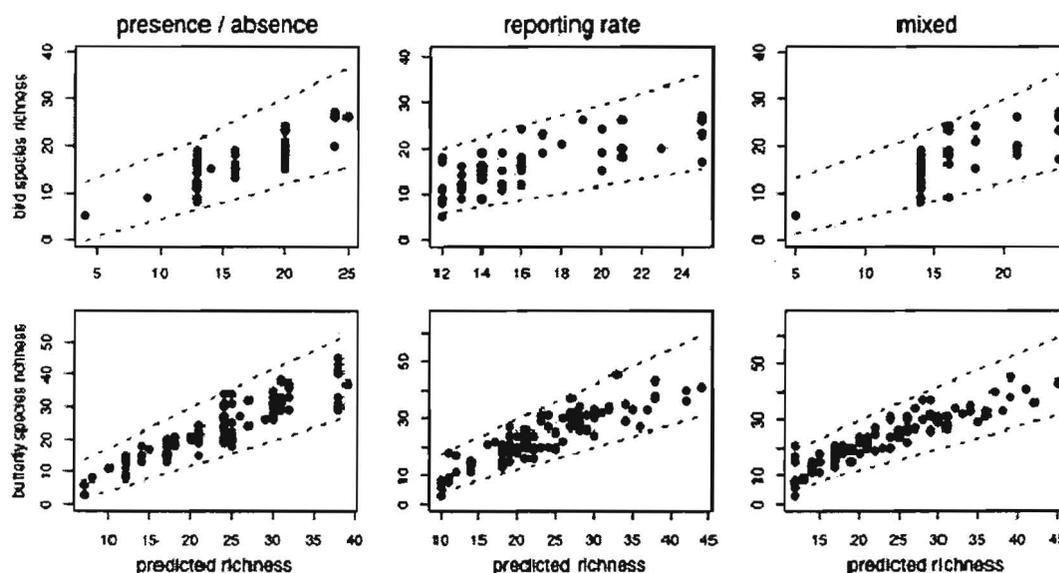


Fig. 3. Fitted versus observed species richness for models with butterfly indicator species. Top row (left to right): models of butterfly species richness based on presence/absence data, reporting rate data, or both presence/absence and reporting rate data, for butterfly indicator species. Bottom row (left to right): models of bird species richness based on presence/absence data, reporting rate data, or both presence/absence and reporting rate data, for butterfly indicator species. Dashed lines show 95% credible intervals for fitted species richness.

Table 3

Success of models of species richness of birds (bird S), butterflies (butterfly S), and combined species richness (combined S) for the combined years 1983, 1984, and 2004 based on single-year presence/absence data from 1983, 1984, or 2004 for bird indicator species

Response variable	1983		1984		2004	
	<i>R</i>	<i>B</i>	<i>R</i>	<i>B</i>	<i>R</i>	<i>B</i>
Bird S	0.2	-6.8 (-9.2, -4.5)	0.33	-5.9 (-8.1, -3.6)	0.65	-6.6 (-8.1, -5.0)
Butterfly S	0.43	NC	0.02	NC	0.35	NC
Combined S	0.42	NC	0.37	NC	0.55	NC

S, species richness; *R*, Spearman correlation coefficient between predicted and observed species richness; *B*, mean bias. Lower and upper bounds of 95% bootstrap confidence intervals for *B* values are in parentheses. NC, not calculated, see Section 2.3.2.

and 74% of deviance in bird species richness, respectively. R_{expected} values were 0.69, 0.62, and 0.69 for the presence/absence, reporting rate, and mixed models, respectively. Thus, we found that our application of BIC appeared to have selected the best models of each type (presence/absence or reporting rate) in terms of predictive capacity; our original comparison of reporting rate models (two indicator species) and presence/absence models (four indicator species) probably was fair.

3.3.2. Same-taxon models

The best presence/absence, reporting rate, and mixed models of butterfly species richness with butterfly indicators explained 83%, 79%, and 81% of deviance, respectively (Fig. 3). R_{expected} values were highest for the presence/absence and mixed models (both 0.86), but still high for the reporting rate model (0.82). Each model included six indicator species (Table 2).

3.3.3. Combined-richness models

The best presence/absence, reporting rate, and mixed models of combined species richness of birds and butterflies with butterfly indicators explained 82%, 78%, and 83% of deviance, respectively (figures and tables not presented; complete information is available from E.F.). R_{expected} values were marginally higher for the mixed model (0.79) than the presence/absence model (0.78) and reporting rate model (0.76). The presence/absence and reporting rate models each included six indicator species. The mixed model included five indicator species.

3.3.4. Identity of butterfly indicator species

Considering lowest BIC models only, five butterfly species were selected as indicators of bird species richness. Three butterfly indicator species were selected as presence/absence terms only, one as a reporting rate term only, and one as both presence/absence and reporting rate terms. The six-species (lowest residual deviance) models of bird species richness included an additional three butterfly species as presence/absence terms only and one species as a reporting rate term only. Twelve butterfly species were selected as indicators of butterfly species richness, five as presence/absence terms only, four as reporting rate terms only, and two as both presence/absence and reporting rate terms. Only one butterfly species, *Papilio rutulus*, was included in models of both bird species richness (as a presence/absence term) and butterfly species richness (as a reporting rate term).

4. Discussion

Evaluation of the comparative usefulness of different types of data, including but not limited to data on presence/absence and reporting rate, stimulates research in ecology and its application (e.g., Loiselle et al., 2003;

Tyre et al., 2003) and is highly relevant for managers concerned with either balancing the cost of data collection with the information content of those data or determining how to obtain the greatest value from data with a fixed acquisition cost. Our work suggests that it is possible to identify small suites of species whose occurrence patterns can be used to predict species richness of either the same taxonomic group, a different taxonomic group, or combined species richness of two taxonomic groups. Importantly, preliminary external validation tests revealed strong correlations between observed species richness and predicted species richness based on occurrence patterns of indicator species, with 83% (all cross-taxon models) to 100% (the best same-taxon model) of the observed values falling within the 95% credible intervals of the predictions.

Our framework for model building and validation is applicable to any ecosystem and may be a useful tool for estimating cross-taxonomic species richness at scales pertinent to conservation and land management. In other circumstances (e.g., different locations, different taxonomic groups, different ecological and socioeconomic considerations) there inevitably will be a different answer to the question of whether a given threshold of explanatory or predictive accuracy (e.g., 70%) is sufficient. Each real-world situation must be considered to determine the optimum or acceptable tradeoff between the ability and need to make predictions and the accuracy of those predictions.

4.1. Temporal variation in species occurrence

Whether reporting rate data improved the explanatory ability of cross-taxonomic models depended on the taxonomic group from which indicator species were drawn. Models of butterfly species richness with bird indicators based on reporting rate data for some or all indicator species explained approximately 10% more of the total deviance in species richness than models based on presence/absence data. The outcome of external validation tests was consistent with these results; observed species richness of butterflies was more strongly correlated with predicted species richness values from the reporting rate and mixed models with birds as indicators than with predictions from the presence/absence model. In contrast, models of bird species richness with butterfly indicators were not improved, in terms of model fit or expected predictive accuracy, by incorporation of reporting rate data.

Why might reporting rate data for birds contain information not conveyed by presence/absence data? One possible explanation is that for birds, which appear to have relatively specialized resource requirements in our study system (Mac Nally et al., 2004), reporting rates are correlated with local habitat quality for both birds and butterflies. For species of birds that are limited

by nesting sites, prey, or other environmental conditions, intermediate reporting rates may be associated with temporal variability in resource availability. Integrated over several years, variation in resource availability for birds might be related to species richness of terrestrial invertebrates either directly (e.g., relatively low abundance or density of invertebrates could lead to fluctuation in occurrence of birds that are obligate or facultative insectivores) or indirectly (e.g., both birds and butterflies may be responding to the mean or variance in magnitude and duration of primary productivity (McLaughlin et al., 2002)). Alternatively, at least in some situations, intermediate reporting rates of birds might be associated with sites with constant but intermediate habitat quality for birds that cannot support certain species of butterflies, such as sites with trees and shrubs suitable for nesting but with few grasses and forbs (i.e., few larval hostplants and adult nectar sources for butterflies) in the understory.

The discrepancy in predictive ability of reporting rate data and presence/absence data was smaller for same-taxon models than for cross-taxon models, but presence/absence data were more effective. For models of both bird species richness and butterfly species richness with same-taxon indicators, presence/absence-only models explained more deviance and had higher expected predictive accuracy than reporting rate-only models. The results of external validation tests similarly suggested that models of bird species richness based on same-taxon presence/absence data have greater predictive ability than models based on reporting rate data.

For models of combined species richness, models that included a combination of presence/absence and reporting rate terms explained more deviance than either presence/absence-only or reporting rate-only models, regardless of whether birds or butterflies were used as indicator species. In validation tests, however, the presence/absence model with bird indicators had better expected and actual predictive ability than the mixed model. Similarly, internal validation results suggested that the presence/absence model with bird indicators would have predictive accuracy similar to the mixed model.

4.2. Characteristics of indicator species

As we noted previously (Fleishman et al., in press), the best models of species richness appeared to be those in which indicator species collectively represented the variety of land-cover associations in the taxonomic group(s) for which they conveyed information about species richness. Vegetation structure and the distribution of particular species of trees are believed to be major influences on occurrence patterns of birds in general (MacArthur et al., 1966; Anderson and Shugart, 1974; Rotenberry and Wiens, 1980) and in our study system

(Mac Nally et al., 2004). Occurrence patterns of most butterflies, by contrast, are influenced by the distribution of certain larval hostplants and by the availability of nectar, which often is correlated with the availability of running or standing water (Wilcox et al., 1986; Pullin, 1995; Mac Nally et al., 2004). For example, in the reporting rate model of butterfly species richness with birds as indicators, species with positive model coefficients were associated with riparian vegetation (Yellow Warbler [*Dendroica petechia*]) and mixed riparian and upland trees and shrubs (Black-headed Grosbeak [*Pheucticus melanocephalus*]), whereas species with negative model coefficients were associated with relatively arid shrublands (Blue-gray Gnatcatcher [*Polioptila caerulea*], Lark sparrow [*C. grammacus*]), arid, rocky areas (Black-throated Sparrow [*Amphispiza bilineata*]), and arid woodlands with limited understory (Plumbeous Vireo [*Vireo plumbeus*]).

Similarly, the presence/absence model of species richness of birds with butterflies as indicators included species whose larvae feed on a full range of vegetation growth forms (Fleishman et al., 1997). Species whose larval host plants typically are found in land cover types that are used by both birds and butterflies, such as grasses (fed on by *Hesperia comma*) and riparian trees (*Papilio rutulus*, *P. multicaudatus*), had positive model coefficients, whereas a species that feeds on forbs on open slopes (*Papilio zelicaon*) had a negative model coefficient.

For same-taxon models, it may appear superficially that any (sufficiently large) subset of species could serve as indicator species because any given species is more likely to be present at species-rich sites than at species-poor sites. But this assumes that species are distributed randomly across landscapes, which is not the case. Suites of indicator species selected with the genetic algorithm explained, on average, twice as much deviance in species richness as randomly selected suites of the same number of species, and had far superior predictive accuracy (many arbitrary subsets had no predictive capacity, J.T., unpublished data). Thus, the selected indicator species are not mere random “sub-samples” of the distributions of all species from that taxonomic group. Rather, the distribution of indicator species appeared to reflect the distribution of resources and other underlying factors that influence species richness. We believe that this is an important result ecologically and warrants the use of methods such as those we have described in this paper.

4.3. Applications

Any practical tool for ecological assessment must be both scientifically reliable and cost-effective. We found that the explanatory ability of species-richness models differed when indicator species were selected using

reporting rate data or presence/absence data. Presence/absence data were more effective than reporting rate or mixed data for same-taxon models, and appeared to be at least as effective as reporting rate or mixed data for combined richness models. For the cross-taxonomic models, however, the comparative value of the two types of data depended on the taxonomic group from which indicator species were drawn. Preliminary external validation tests were consistent with these observations, suggesting that in a given situation, the success rate of species-richness predictions is likely to differ when indicator species are selected using reporting rate data or occurrence data.

Because it is difficult to characterize the “true” distributions of most species in one-off surveys, and poor predictions frequently result from false-negatives in indicator species data, longitudinal data often will be essential for indicator species models. False negatives that result from imperfect detections rather than true variation in species occurrence will have similar effects. Our methods provide a manager with the means to evaluate how to maximize the accuracy of models using that longitudinal data. Our work also potentially provides the means to evaluate the degree to which additional accuracy of models gained by greater survey effort is warranted against the added cost for situations in which reliable presence/absence data can be obtained with single surveys. This tradeoff should always be the driving agent in such circumstances: is an extra 10% accuracy derived from reporting rate-based models, for example, worth the added expense of conducting three years’ of surveys compared with one year? These questions cannot be answered without conducting the type of analyses that we present here. For example, our results suggest that reporting rate data are not needed for same-taxon or combined-richness models of bird and butterfly species richness in this system. So if reliable occurrence data could be obtained with single surveys (or with survey methods that did not require revisiting sites after all indicator species had been observed), there would be little justification for repeat surveys to estimate species richness using those models.

Efforts to identify surrogate-based approaches to estimate species richness and other measures of ecological status are popular because inventory data for many regions are insufficient to inform conservation and land-use planning decisions directly. Accordingly, a method for selecting indicator species that requires relatively complete species data might appear to be anything but a shortcut. However, our methods select indicator species potentially applicable across an extensive landscape on the basis of data that, while representative of the larger system, are collected from a small fraction of the total land area. Across planning landscapes of tens to hundreds of thousands of square kilometers, we believe the method is a viable approach to deriving estimates of

species richness that can inform strategies for allocation of multiple land uses, including conservation. The Great Basin, for example, covers more than 400,000 km² and includes approximately 350 major mountain ranges. If indicator species identified on the basis of data collected from sections of three mountain ranges can be used to predict species richness at any location even within the 30,000 km² biogeographic subregion in which our work was centered (Austin and Murphy, 1987), we believe the method can serve as an effective and practical tool for prioritizing management activities.

We reiterate that our approach is designed to deal with species richness and we note that specific efforts probably will be needed to deal with the presence or number of rare species (Lawler et al., 2003). Rare species need not occur in locations with greatest species richness, prevalence of individual species often varies across a landscape, and low prevalence rates may not equate to extinction risk (Fleishman et al., 2003). In our system, no species of bird or butterfly is listed as threatened or endangered, and there are no species-level endemics. Moreover, the relatively uncommon resources (such as plants with patchy distributions) used by some species of birds and butterflies with erratic occurrences in space and time are not threatened directly by current land uses.

Survey data for many regions are insufficient to inform preservation and management decisions directly. When applied to planning landscapes of tens or hundreds of thousands of square kilometers, we believe our methods represent a realistic approach to deriving estimates of species richness that can inform strategies for allocation of multiple land uses, including conservation. It appears that the data required to build models potentially applicable across those extensive landscapes, while representative of the larger system, may be collected from a small fraction of the total land area. In addition, by exploring why particular species convey information about a larger biota, we may gain insight into underlying mechanisms that influence species richness and the structure and composition of ecological assemblages.

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