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# Identifying spatially and temporally transferrable surrogate measures of species richness

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#### ABSTRACT

We developed a transferable method to identify indicator species and environmental variables that explain considerable variation in species richness. We applied this method to birds and butterflies and conducted novel, rigorous external evaluations of the spatial and temporal transferability of such indicator species. We collected data in the central Great Basin (Lander, Nye, and Eureka Counties, Nevada) and western Great Basin (Mono County, California and Mineral, Douglas, and Lyon Counties, Nevada), United States. We used Bayesian model selection to identify sets of five species that best explained observed variation in species richness of the same or the other taxonomic group in either subregion. We then built random forest models that included only the five identified indicator species and externally tested these models with new data from the other subregion (central or western Great Basin) or a later time in the same subregion. We compared the predictive accuracy of indicatorspecies only models to that of models based on environmental variables or on both indicator species and environmental variables. In external evaluations, models based on same-taxon indicator species predicted 34-52% of the variation in species richness of birds and 40-70% of the variation in species richness of butterflies. Comparable models based on environmental variables predicted 11-46% of the variation in species richness of birds and 12-67% of the variation in species richness of butterflies. Models based on same-taxon indicator species predicted more variation in species richness than those based on environmental variables in seven of eight cases. Our results suggested that the predictive accuracy and spatial and temporal transferability of models based on indicator species can exceed that of models based on environmental variables. If mechanistic responses to environmental change are consistent through time, tracking the occurrence of a subset of an assemblage during periods of environmental change may allow inference to species richness of the assemblage.

#### 1. Introduction

Interest in identifying standard and affordable ways to estimate species richness—the number of species in a given location and time period—has been maintained for decades (MacArthur and Wilson, 1967; Rosenzweig, 1995; Magurran and McGill, 2011). Gotelli and Colwell (2011) reviewed many robust methods for estimating species richness with incidence or abundance data, such as rarefaction (Sanders, 1968), the Chao 1 (Chao, 1984) and Chao 2 (Chao, 1987) estimators, and the jacknife (Burnham and Overton, 1978, 1979)

estimators. Several more-recent methods of estimating species richness capitalize on increases in computing power or the widespread use of occupancy models. For example, stacked and joint species distribution models (SDMs) (Dubuis et al., 2011; Pollock et al., 2014) make use of single-species SDMs, which project probability of occurrence on the basis of environmental variables that are measured in the field or derived from remotely sensed data (Elith and Leathwick, 2009). Stacked SDMs combine projections from multiple SDMs to estimate species richness (Dubuis et al., 2011), whereas joint SDMs use covariances among species to project occurrence of multiple species (Pollock et al.,

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2014). However, stacked SDMs generally overestimate species richness (Mateo et al., 2012; Calabrese et al., 2014), and the reliability of the projections of joint SDMs has not been tested rigorously, such as with independent, newly collected data (Harris, 2015).

Multiseason, multispecies hierarchical Bayesian models (Gelman and Hill, 2007; Dorazio et al., 2010) are another example of the many relatively new, computationally intensive methods that can be used to estimate species richness and to explain variation in occupancy as functions of environmental covariates, ideally predicting species' occupancy in space or time. The theory underlying these models is promising because the algorithms treat missing response-variable data as unknown quantities to be estimated from the data in the model (MacKenzie et al., 2006). Nevertheless, a relatively small number of species can disproportionately affect inferences about covariates' associations with species richness (Zipkin et al., 2009).

In contrast to these newer methods, many researchers have attempted to identify a small set of species with occurrence patterns that are related to species richness of a larger set of organisms—i.e., indicator species (Pearson, 1994; Morrison et al., 2012; Morelli, 2015). Others have defined indicator species as species that are characteristic of land-cover types or of environmental conditions (e.g., Niemi and McDonald, 2004; De Cáceres et al., 2010), but here we do not use the latter definition or associated methods (e.g., Dufrêne and Legendre, 1997).

If external evaluations-that is, tests with newly collected data--suggest that the indicator species-based models accurately predict species richness, then it may be possible to monitor the occurrence of a small number of indicator species rather than conducting comprehensive species inventories (Gustafsson, 2000; Tognelli, 2005; Heino, 2010). In many temperate ecosystems, the cost of sampling the occurrence of all species of certain taxonomic groups, such as passerines, is not appreciably greater than that of sampling a small subset of the group. For taxonomic groups that are more cryptic or that must be sampled with highly specialized methods, monitoring a subset of an assemblage may be much more feasible than monitoring the full assemblage. The identification of indicator species can be simpler computationally than innovative but largely unproven methods, such as the implementation of SDMs or hierarchical Bayesian models, and the relations between indicator species and species richness may be easier to interpret and to communicate to end-users.

We conducted previous work on indicator species in the Great Basin of the western United States, a large ( $> 425,000 \text{ km}^2$ ), topographically diverse desert with high climatic variability. Both average temperature and the annual number of days above 35° C have increased in the Great Basin since 1900. In that earlier work, we used objective statistical methods to identify butterflies and birds that could indicate species richness of the same taxonomic group or the other taxonomic group (Mac Nally and Fleishman, 2002, 2004; Thomson et al., 2005, 2007). For example, a model based on the occurrence patterns of five species of butterflies explained 88% of the deviance of species richness of 56 butterfly taxa; when predictions of this model were confronted with new data from a nearby set of locations, more than 90% of the observed values fell within the 95% credible intervals of the predictions (Mac Nally and Fleishman, 2004). We also built models with data on birds and butterflies that were collected from 1996 through 2003 in three mountain ranges in the central Great Basin (see Methods). We used bootstrapping to conduct internal evaluations of the models. We also used new data on birds, collected in 2004 in 25 previously unsampled locations in one of the mountain ranges, to conduct a preliminary external evaluation of the models (Thomson et al., 2007), but did not have sufficient data at that time to explicitly test the transferability of indicator species.

The extent to which particular indicator species are transferable is relevant to the management of extensive areas, including those in which there may be geographic differentiation in the responses of widely distributed organisms to their environment. For example, much current resource management in the Great Basin is intended to conserve Greater Sage-Grouse (*Centrocercus urophasianus*), with the hope that > 350 wildlife species associated with the sagebrush steppe also will benefit (BLM, 2015; USFS, 2015). However, little is known about whether co-occurrence patterns of these species are consistent, or whether different species have similar responses to environmental change (Knick et al., 2014). More generally, whether occurrence and species richness within one taxonomic group consistently explain species richness in other taxonomic groups is relevant to resource management actions and monitoring (Ekroos et al., 2013; Peters et al., 2016).

Here, we developed and tested a transferable model for identifying sets of indicator species that explained considerable variation in species richness. We compared predictions of species richness based on these indicator species to predictions based on a set of environmental variables. We conducted external evaluations of the spatial and temporal transferability of indicator species and environmental variables that were more rigorous than our previous (Thomson et al., 2007) evaluations. For example, we tested the extent to which indicator species identified from models built with data from the central Great Basin predicted variation in species richness of birds and butterflies in the zoogeographically distinct western Great Basin (Behle, 1963, 1978; Austin and Murphy, 1987), and vice versa. We tested whether models built from data collected over one to three years in a given subregion explained variation in species richness in that same subregion during one to three years of later sampling.

#### 2. Methods

#### 2.1. Bird surveys

In the central Great Basin, we collected data on breeding birds throughout the adjacent Shoshone Mountains and Toiyabe, Toquima, and Monitor Ranges (Lander, Nye, and Eureka Counties, Nevada) from 2001 through 2015 (Fig. 1). We sampled birds along the elevational gradients of a total of 27 canyons and one basin that drain the east and west slopes of the mountain ranges. We consistently sampled 313 points, and have  $\geq 9$  years of data for 254 (81%) of these points.

In the western Great Basin, we collected data on breeding birds on the east slope of the Sierra Nevada and in the adjacent Wassuk Range and Sweetwater Mountains (Mono County, California and Mineral, Douglas, and Lyon Counties, Nevada) (Fig. 1). We sampled the same set of 158 points, distributed among 13 canyons, from 2012 through 2014.

We conducted 100-m fixed-radius point counts during the peak of the breeding season (late May through June) (Ralph et al., 1993; Dobkin and Rich, 1998). The great majority of species on which we focused have breeding-season home ranges that seldom exceed 200 m in diameter (Leu et al., 2017). Also, most of the canyons in which we worked are relatively narrow, which complicates detection of birds at distances of greater than 100 m from the observer. During each visit, we recorded by sound or sight all birds using terrestrial habitat within the point. We restricted our analyses to adults of taxa that are sampled effectively by point counts, omitting taxa such as owls and raptors. We visited each point three times per year for 8 min per count (Buckland et al., 2001; Siegel et al., 2001; Dickson et al., 2009).

#### 2.2. Butterfly surveys

We located transects along the full elevational gradients of a total of 33 canyons in the Shoshone Mountains, Toiyabe Range, and Toquima Range. We sampled a total of 190 transects from 1995 through 2014; we have  $\geq 2$  years of data for 118 transects (62%) and  $\geq 3$  years of data for 98 transects (51%). In the western Great Basin, we sampled the same set of 100 transects, distributed among eight canyons in the Sierra Nevada, Wassuk Range, and Sweetwater Mountains, from 2012 through 2014. Given that most of these canyons are fairly narrow and resources

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