Enhanced indicator species performance with increasing contextualization

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Abstract
Indicator species need context to perform optimally for conservation purposes. If indicator potential is context-dependent, then indicators should improve with increasing spatial-environmental stratification. We tested this hypothesis by hierarchically stratifying a species combinations matrix (plants and wetlands) using regionalization and site typology and analyzing class specificity and occupancy rate for indicators shared across strata. Performance of indicators collectively improved with increased sample stratification providing greater spatial-environmental context. Carefully considered sample classification schemes could strengthen the value of indicator species for monitoring biodiversity loss, environmental change, and management progress. However, the better accuracy of context-specific indicators will have to be weighed against the practical need for fewer broad-based indicators.

Keywords: surrogates, vegetation, wetlands

1 | INTRODUCTION

Certain species hold potential to indicate the loss or status of other taxa and the quality (degraded, pristine, etc.) of their encompassing habitat, ecosystem, or environment (Carignan & Villard, 2002; Caro & O'Doherty, 1999; Fleishman & Murphy, 2009; Grantham, Pressey, Wells, & Beattie, 2013; Siddig, Ellison, Ochs, Villar-Leeman, & Lau, 2016). This surrogate potential is attractive in conservation planning and resource management because working with a few species is easier than entire assemblages (Tulloch, Possingham, & Wilson, 2011; Wiens, Hayward, Holthausen, & Wisdom, 2008). Other shortcuts around assemblages, such as ignoring hard-to-identify taxa or focusing on dominant taxa only (Chamberlain & Brooks, 2016; Gianopulos, 2018), may be more time consuming and prone to bias than searching for a few indicator species. And nonbiological assessment methods (e.g., Fennessy, Jacobs, & Kentula, 2007) may be disconnected from species' habitats and ecological disturbances (Bried, Jog, Davis, & Dzialowski, 2016; Herlihy et al., 2019b; Swartz, Stuart, Foster, & Lindquist, 2016). Indicator species by contrast offer the dual advantage of being biologically explicit and relatively efficient. However, as with any conservation surrogate (Kati et al., 2004; Lindenmayer et al., 2015), effective application of indicator species may require context.

Spatial-environmental heterogeneity can make it difficult to attribute changes in ecological responses to natural versus anthropogenic forces (Fratterigo & Rusack, 2008), or to apply taxonomic surrogates for biodiversity assessment (Stewart, Underwood, Rahel, & Walters, 2018). One way to reduce the effect of heterogeneity is to stratify samples geographically or into environmentally similar groups (Stoddard, 2005). Stratifying samples according to spatial-environmental similarity helps provide context and increases ability to detect patterns and changes not caused by natural variability (Mazor et al., 2016). As responses of indicator species improve with increasing stratification, it is necessary to determine how to best stratify samples to improve the value of indicator species.
species vary between regions and along environmental gradients (Zettler et al., 2013), optimal application may require geographic and environmental specification. As such, stratified sampling (or stratified analysis) may be needed to deal with spatial-environmental heterogeneity in the application of indicator species.

Performance of indicator species should improve with greater spatial-environmental contextualization. We tested this using a species combinations matrix of plants and wetlands hierarchically stratified by regionalization (ecoregion) and site typology (geomorphic setting). State and federal agencies of the United States have jurisdictional and statutory obligations for evaluating wetland ecological integrity in order to guide wetland conservation and management (Danielson, 1998; United States Army Corps of Engineers, 2002). Indicator species can offer these agencies and other practitioner organizations an efficient tool for helping track wetland health, prioritize protection and restoration efforts, and assess mitigation outcomes. Defining the context of proposed indicator species should not only improve their performance but also guide transferability to managing other taxa and conditions (Lindenmayer & Likens, 2011; Wiens et al., 2008).

2 | METHODS

2.1 | Study area

Oklahoma in the southcentral United States experiences about 200 frost-free days per year depending on latitude, with a gradient of 50–150 cm average annual precipitation from the northwest (“panhandle”) to southeast (Hoagland, 2000). The state is dominated by various forms of agriculture (e.g., pasture, wheat fields) and grasslands (short-grass, mixed-grass, tall-grass prairies) throughout the western plains, by transitional oak woodlands in the central region, and by highland oak-hickory forests to the east (Hoagland, 2000). Most wetlands of Oklahoma are present in riverine, depressional, or lacustrine-fringe geomorphic settings but large variation exists within each class (Dvoretz, Bidwell, Davis, & DuBois, 2013). Wetland assessment in Oklahoma is part of a broader Wetland Program Plan and Management Strategy led by the Oklahoma Conservation Commission in partnership with a multistakeholder group of agencies, tribes, academic institutions, and nongovernmental organizations (for details visit: ok.gov/wetlands/).

2.2 | Sample data

Plant checklists were accumulated from one-time surveys (during 2012–2016) of 117 nonforested wetlands (Figure 1). Sites were located from a variety of sources and spanned nine ecoregions, several major wetland classes, and a range of human disturbance (Bried et al., 2016; Jog et al., 2017). Many sites were targeted in the large depression-rich Central Great Plains ecoregion (Figure 1).

Vegetation surveys occurred from mid-May to early August using plot-based or census methods; the different methods appear to have negligible influence on wetland assessments in this study area (Bried et al., 2016). Plot-based sampling followed the federal wetland condition assessment protocol (United States Environmental Protection Agency [USEPA], 2011). The same botanist for all sites identified vascular plants within and overhanging five square plots (100 m² each) arranged to representatively assess the wetland and conform with its size or shape (see USEPA, 2011 for details). For consistency with census surveys, additional species encountered outside the plots were recorded and used for analysis. Census
involved searching the entire wetland at smaller sites (<0.5 ha) or the accessible portion of representative vegetation zones at larger sites until no new species were recorded. All vascular taxa were identified to the lowest possible taxonomic level, usually species but sometimes genus when important characteristics (e.g., flowers, mature fruits) were not available. We identified a cumulative total of 436 angiosperm species distributed among 250 genera and 90 families.

2.3 | Sample strata
Ecoregional and hydrogeomorphic stratification is commonly used in wetland assessment research to limit interference from natural heterogeneity (e.g., Herlihy et al., 2019a; Jog et al., 2017). We divided the sample between prairie ecoregions (85 sites) and forest ecoregions (32 sites) (Figure 1). We then subset the prairie sample into depressional wetlands (70 sites) and finally depressional wetlands in a single prairie ecoregion, the Central Great Plains (53 sites). This created a hierarchy of Central Great Plains depressional wetlands (hereafter “CGP depressions”) nested within prairie ecoregion depressional wetlands (hereafter “prairie depressions”) nested within all prairie ecoregion wetlands (hereafter “prairie wetlands”). Highest indicator values were expected for CGP depressions (most stratified), lowest values for prairie wetlands (least stratified), and intermediate values for prairie depressions.

2.4 | Analysis
Indicator species were extracted separately for prairie wetlands, prairie depressions, and CGP depressions (target groups or strata) against the 32 forest ecoregion wetlands (reference group) to standardize comparison of indicator performance across strata. To reduce computation time, candidate species were selected as those present within at least 10% of each target group, leaving 51 species for prairie wetlands, 58 species for prairie depressions, and 46 species for CGP depressions. We evaluated species individually and in pairs, triplet (3-species) combinations, and quadruplet (4-species) combinations following De Cáceres, Legendre, Wiser, and Brotons (2012), exploring a total of 272,051 potential indicators for prairie wetlands, 456,837 potential indicators for prairie depressions, and 179,446 potential indicators for CGP depressions.

Indicator performance was quantified based on occurrence specificity to a target group (relative to the reference group) and the frequency of occurrence, or sensitivity, within that group (De Cáceres et al., 2012). Specificity measures the indicator’s exclusivity to the target group and chance of correct attribution in future applications. Sensitivity measures the indicator’s ubiquity in the group as an estimate of how likely it will be found in practice. As such, strongest indicators occur exclusively in the target group (max specificity = 1) and at all locations within that group (max sensitivity = 1). The methodology follows Dufrêne and Legendre (1997) except the input matrix has species combinations in addition to individual species, on the theory that multispecies indicators cover more niche space and environmental heterogeneity than any single species and thus offer stronger indicator value (De Cáceres et al., 2012). We used the combinespecies and indicators functions of the “indicspecies” package (De Cáceres & Legendre, 2009) to generate the species combinations matrix and calculate performance (specificity, sensitivity) for each stratum.

We retained indicators having specificity ≥0.5 and sensitivity ≥0.2 for each stratum. These default thresholds capture the likely acceptable limits for practice (e.g., Bachand et al., 2014) and provided enough shared indicators among strata for analysis and inference. To evaluate the hypothesis, we averaged specificity and sensitivity across indicators and compared successive strata, that is, prairie wetlands versus prairie depressions and prairie depressions versus CGP depressions. Differences in mean specificity and mean sensitivity between successive strata were tested against 10,000 dataset iterations, shuffling the observations within each indicator to account for the repeated measures, that is, the same indicators over strata. The difference was recalculated with each iteration to determine p-value based on how many equaled or exceeded the observed differences between strata.

3 | RESULTS

Seventeen indicators, including nine pairs and eight single species, met the performance thresholds across all strata (Table 1). Half the singletons were nested within the two-species indicators and half stood alone. All triplet and quadruplet combinations failed to meet the thresholds.

Seven indicators were exclusive (1.0 specificity) to the broadest stratum (prairie wetlands) and therefore to the nested strata (Table 1). Of the remaining indicators, specificity improved in step with increasing stratification in all but three (Typha angustifolia, Xanthium strumarium, and Salix nigra + T. angustifolia). Sensitivity improved with each level of stratification for 11 indicators and was highest for the finest stratum (CGP depressions) in all but one indicator (X. strumarium).

Indicator performance improved overall (combining Table 1 indicators) with increasing sample stratification (Figure 2). Mean specificity of nonexclusive indicators (<1.0 specificity in Table 1) increased by 0.011 (randomization test p = .0061) after filtering the depressional wetlands, and then by 0.036 (p = .0024) filtering depressional wetlands to the Central Great Plains. Similarly, mean sensitivity increased by 0.014 (p = .0100) and 0.080 (p < .0001) over the same gradient. These statistics confirm (Figure 2, Table 1) that
improvement was more pronounced thinning prairie depressions to CGP depressions than splitting prairie wetlands into depressions and nondepressions.

4 | DISCUSSION

Performance of indicator species likely depends on geographic and environmental context. Strategically providing context through prudent sample/analysis stratification may therefore enhance indicator values. Results from our wetland vegetation system tested over spatially and environmentally nested strata supported this idea. On average the indicators became more specialized (higher specificity) and more frequent (higher sensitivity) with strategic thinning and refinement of the sample. Defining the context may select for a better autecological match (e.g., fitness advantage, habitat preference) and more successful indicator (Dufrêne & Legendre, 1997).

We showed overall improvement in the specificity and sensitivity of indicator plant species with hierarchical stratification.
of a wetland sample. Although filtering prairie wetlands to depressions strengthened indicator values, filtering depressions to a specific prairie ecoregion (CGP, or Central Great Plains) provided the greater boost. This suggests regionalization (ecoregion) is more important than site typology (geomorphic setting) for stratifying wetland samples and finding vegetation indicators. Ecoregions are well established throughout the United States and capture broadly consistent climate-soil-vegetation-landcover patterns over large areas (Stoddard, 2005). We previously found that splitting the CGP from other ecoregions helped to model wetland floristic quality and had more impact than separating depressional wetlands from riverine, seep, and lacustrine-fringe wetlands (Bried et al., 2016; Jog et al., 2017). Others have recommended ecoregional specification of depressional wetland floristic quality in Oklahoma (Gallaway, Davis, Dvorett, & Tramell, 2019). The state is intersected by many ecoregions, and with strong climatic gradients and a diversity of wetlands (Dvorett et al., 2013; Hoagland, 2000), we likewise recommend an ecoregion context for developing and applying wetland assessment indicator species in Oklahoma.

Our results imply that stratification may be important for using indicator species to assess degree of wetland disturbance. The state of Oklahoma is currently in the process of developing and testing its own wetland disturbance assessment methods (Gallaway et al., 2019). These involve either sampling entire assemblages (Floristic Quality Assessment), field work that does not explicitly assess biological conditions (Oklahoma Rapid Assessment Method), or geospatial data capture beyond the wetland boundary (Landscape Development Intensity Index). As vegetation indicator species are localized, biologically explicit, and efficiently applied, we recommend studies to test how well these species can represent the output (higher, lower, and moderate values) of non-localized, nonbiological, less efficient assessment tools.

Spatial-environmental contextualization could in theory optimize indicator species performance but will also limit the transferability and potential application (Lindenmayer & Likens, 2011), bringing practical significance into consideration. In our case honing the sample improved mean specificity from 0.731 for prairie wetlands (least context) to 0.779 for CGP depressions (most context) on a [0,1] scale. Inverting these predictive values (see De Cáceres et al., 2012), we have a 27% chance of misclassification working across Oklahoma prairie ecoregions and wetland types, and 20% chance of misclassification for depressional wetlands in the northern CGP. Users could debate whether the reduced (by 7%) false-positive rate is worth sacrificing indication over a broader spatial-environmental context. However, the degree varies by indicator (as in Table 1) and technically only one indicator is required for making determinations. Decisions to develop fewer broad-based indicators or many context-specific indicators will obviously depend on study system heterogeneity, ability to extract indicators (human capacity and data sufficiency), and how indicators perform across strata.

Contextualization helps optimize indicator species performance while defining the extent of indicator transferability for reliable interpretation and practice. Our results imply that spatial-environmental contextualization at least be carefully considered when extracting indicator species for conservation purposes, complementing other types of context study of indicator species (e.g., Tulloch et al., 2011). Sample classification schemes involving regionalization and typology (e.g., Herlihy et al., 2019a; Stoddard, 2005) could enhance species potential for indicating biodiversity loss/status, ecological disturbance, environmental change, and management progress (Stewart et al., 2018; Wiens et al., 2008; Zettler et al., 2013).

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

J.T.B. conceived the study; S.K.J., J.T.B. conducted field work; T.S.F., J.T.B. performed the analysis; J.T.B. wrote the manuscript with input from T.S.F., S.K.J.

ETHICS STATEMENT

Research was not conducted that would have required approval.

DATA AVAILABILITY STATEMENT

All raw data and code used in this study can be made available upon request.

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