

# Limited Evidence For Indicator Species of High Floristic Quality Wetlands In The US Southern Plains

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## Research Article

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# Abstract

Floristic Quality Assessment requires compiling a full list of vascular plant species for the wetland. Practitioners may lack the time and taxonomic skills for full-community vegetation surveys, especially when wetlands are large and complex. In this paper we broadly ask whether floristic quality indicator species may exist for wetlands, specifically evaluating indicator species potential for high floristic quality wetlands in the US southern plains region. Indicators were identified for a broader context (wetlands in Oklahoma prairie ecoregions) and narrower context (depressional wetlands in the northern Central Great Plains ecoregion of Oklahoma) based on indicator value, indicator validity, hydrophytic status, and ecological conservatism. No candidate indicators satisfied all criteria for high floristic quality. Indicator values improved with increasing spatial-environmental context, but many candidates occurred too frequently in non-high quality sites or too infrequently in high quality sites, relative to predicted rates. The best performing indicator (*Eleocharis compressa*) lacked validity in the broader context and showed high false-positive rates in the narrower context. Combining *E. compressa* with select other candidates (*Amorpha fruticosa*, *Juncus torreyi*, *Leersia oryzoides*, *Schoenoplectus pungens*) may compensate for weaknesses but the combinations may rarely be found across the region. Overall, these results do not support relying on indicator species to rapidly identify or verify high floristic quality wetlands in the US southern plains. We recommend similar studies in other regions and testing other quality levels (low, moderate) before broadly concluding that floristic quality indicator species do not exist for wetlands.

## Introduction

Floristic Quality Assessment (FQA) is a widely used tool for conservation planning, ecological health assessments, and restoration monitoring. Floristic quality is commonly indexed as the product of species richness and mean ecological conservatism (Kutcher and Forrester 2018). Conservatism is estimated by expert opinion and ranges from nonnative and weedy native species at the low end to species of minimally human-disturbed areas at the high end (Taft et al. 1997). These subjective scores assigned to individual species can align with empirically derived scores (Bried et al. 2018) and with a variety of functional traits (Ficken and Rooney 2020). Wetlands feature prominently in FQA research and applications and the index ratings often correspond, to varying degrees, with ecological degradation and human footprint in and around wetlands (DeBerry et al. 2015).

The main requirement and challenge of FQA is compiling a complete species list for the wetland. Although mean conservatism may be robust to some level of misidentifications and failed detections (Spyreas 2016), all extant vascular plants should be detected and accurately identified to species level. The requisite field experience and taxonomic skills may be lacking (Noss 1996; Drew 2011) and many plant species are unidentifiable at certain times of the growing season. Furthermore, compiling a full list takes time, whether setting up plots and transects or meandering throughout the wetland. Wetland researchers have begun to propose shortcuts around full-community FQA, such as ignoring graminoids and non-dominant taxa (Chamberlain and Brooks 2016). Indicator species (Siddig et al. 2016) offer another possibility but have not, to our knowledge, appeared in FQA research or applications. Focusing on

a few target species linked to preset levels of floristic quality would ease the skill requirement and improve field work efficiency; in theory a well-supported indicator species could reduce the field visit to minutes or even seconds depending on how fast its detected.

High quality or minimally altered wetlands are sought for regulatory protection and used as baselines for assessing ecological disturbance and management actions (Brooks et al. 2016; Herlihy et al. 2019). Tools for rapid identification of potential reference wetlands are needed, especially when such conditions are rare over large areas containing abundant wetlands. An approach of indicator species, sufficiently calibrated (Bried et al. 2019), is one option worthy of consideration. Such species may be used for example to rapidly screen wetlands for potential regulatory protection and follow-up intensive assessments in the development permitting process (Stapanian et al. 2013).

In this paper we ask if certain species can represent high floristic quality as defined by relatively conservative, species-rich, native plant assemblages. We were specifically interested in finding these species for wetlands in the US southern plains, a region stretching from Texas through Nebraska between the Rockies and Xeric Plains to the west and the Temperate Plains and Southern Appalachians to the east (Kentula and Paulsen 2019). We focus on the prairie ecoregions of Oklahoma where establishing reference standards is a priority of the Wetland Program Plan ([www.ok.gov/wetlands](http://www.ok.gov/wetlands)) and where previous research has suggested floristic quality criteria for potential reference wetlands (Bried et al. 2014; Gallaway et al. 2019). Because Oklahoma's prairie ecoregions and dominant land use extend into neighboring states, developing efficient and reliable assessment tools in Oklahoma is a step towards rapid field identification (or verification) of potential reference-quality wetlands in the southern plains. Our broader question here, beyond the study region, is whether indicator species of wetland floristic quality may exist.

## Methods

### Study area

Oklahoma is centrally located in the US southern plains and intersected by a dozen Level III ecoregions (Omernik & Griffith 2014), two-thirds of which are largely non-forested and classified as "prairie" (Fig. 1). Historically the prairie ecoregions were dominated by short-grass, mixed-grass, or tall-grass vegetation communities but now they are dominated by pastures and rangeland (Hoagland 2000; Tyrl et al. 2007). The distribution of vegetation types is broadly divided among the ecoregions and follows a precipitation gradient from driest (< 50 cm annual rainfall) in the High Plains and Southwestern Tablelands to wettest (as much as 150 cm) in the South Central Plains (Hoagland 2000; Gallaway et al. 2019).

Table 1

Two sets of candidate indicators for high floristic quality ( $\geq 20.0$  or  $\geq 13.0$  index score) wetlands in Oklahoma prairie ecoregions; three additional sets are found in Table S1. Each set comes from a randomly drawn  $\sim 100$  sample (Main Samples #1 and #2 shown in Fig. 1) of 74 sites (37 high quality vs. 37 non-high quality). *C* value – Oklahoma ecological conservatism value; wetland status – regional obligate wetland (OBL), facultative wetland (FACW), facultative (FAC), facultative upland (FACU) status; LCL, UCL – lower and upper 95% confidence limits from 10,000 bootstrap iterations (lowest and highest bootstrap limits in six combinations of specificity and sensitivity thresholds); IV – Indicator Value (Specificity  $\times$  Sensitivity).

Sample	Indicator ( <i>C</i> value, wetland status)	Specificity (LCL, UCL)	Sensitivity (LCL, UCL)	IV
#1	<i>Ambrosia artemisiifolia</i> (3, FACU)	0.813 (0.529, 1.000)	0.212 (0.081, 0.361)	0.172
	<i>Echinochloa muricata</i> (0, FACW)	0.651 (0.413, 0.864)	0.273 (0.125, 0.433)	0.178
	<i>Eleocharis compressa</i> (6, FACW)	0.762 (0.618, 0.902)	0.545 (0.370, 0.719)	0.415
	<i>Juncus effusus</i> (5, OBL)	0.554 (0.329, 0.759)	0.273 (0.121, 0.436)	0.151
	<i>Phyla lanceolata</i> (3, FACW)	0.713 (0.541, 0.880)	0.424 (0.257, 0.594)	0.302
	<i>Pluchea odorata</i> (4, FACW)	0.691 (0.458, 0.908)	0.273 (0.125, 0.429)	0.189
	<i>Populus deltoides</i> (1, FAC)	0.583 (0.361, 0.789)	0.273 (0.125, 0.429)	0.159
	<i>Populus deltoides</i> (1, FAC) + <i>Salix nigra</i> (2, FACW) + <i>Typha angustifolia</i> (3, OBL)	0.713 (0.457, 0.932)	0.242 (0.107, 0.400)	0.173
	<i>Populus deltoides</i> (1, FAC) + <i>Typha angustifolia</i> (3, OBL)	0.691 (0.453, 0.903)	0.273 (0.125, 0.432)	0.189
	<i>Potamogeton diversifolius</i> (6, OBL)	1.000 (1.000, 1.000)	0.212 (0.077, 0.359)	0.212
	<i>Rhynchospora corniculata</i> (7, OBL)	0.861 (0.514, 1.000)	0.152 (0.034, 0.286)	0.131

Sample	Indicator (C value, wetland status)	Specificity (LCL, UCL)	Sensitivity (LCL, UCL)	IV
	<i>Typha angustifolia</i> (3, OBL)	0.541 (0.421, 0.657)	0.545 (0.375, 0.719)	0.295
#2	<i>Ambrosia artemisiifolia</i> (3, FACU)	0.882 (0.587, 1.000)	0.182 (0.059, 0.324)	0.161
	<i>Amorpha fruticosa</i> (6, FACW) + <i>Populus deltoides</i> (1, FAC)	0.788 (0.480, 1.000)	0.182 (0.061, 0.320)	0.143
	<i>Cephalanthus occidentalis</i> (4, OBL) + <i>Pluchea camphorata</i> (4, FACW)	0.624 (0.209, 1.000)	0.121 (0.028, 0.242)	0.076
	<i>Cephalanthus occidentalis</i> (4, OBL) + <i>Typha angustifolia</i> (3, OBL)	0.651 (0.415, 0.866)	0.273 (0.128, 0.432)	0.178
	<i>Cyperus acuminatus</i> (3, OBL)	0.832 (0.423, 1.000)	0.121 (0.028, 0.242)	0.101
	<i>Eleocharis compressa</i> (6, FACW)	0.724 (0.591, 0.860)	0.576 (0.400, 0.744)	0.417
	<i>Leersia oryzoides</i> (4, OBL)	0.640 (0.426, 0.835)	0.303 (0.152, 0.467)	0.194
	<i>Phyla lanceolata</i> (4, FACW)	0.729 (0.551, 0.899)	0.394 (0.229, 0.563)	0.287
	<i>Rhynchospora corniculata</i> (7, OBL)	1.000 (1.000, 1.000)	0.121 (0.027, 0.243)	0.121
	<i>Salix nigra</i> (2, FACW)	0.531 (0.433, 0.627)	0.636 (0.464, 0.794)	0.338
	<i>Salix nigra</i> (2, FACW) + <i>Typha angustifolia</i> (3, OBL)	0.629 (0.473, 0.782)	0.455 (0.281, 0.633)	0.286
	<i>Teucrium canadense</i> (3, FACW)	0.595 (0.425, 0.759)	0.394 (0.229, 0.568)	0.234

Table 2

Two sets of candidate indicators for high floristic quality ( $\geq 20.0$  or  $\geq 13.0$  index score) depressional wetlands in the northern Central Great Plains ecoregion of Oklahoma; three additional sets are found in Table S2. Each set comes from a randomly drawn  $\sim 8$  sample (Main Samples #1 and #2 shown in Fig. 1) of 48 sites (24 high quality vs. 24 non-high quality). Terms and acronyms same as defined in Table 1.

Sample	Indicator (C value, wetland status)	Specificity (LCL, UCL)	Sensitivity (LCL, UCL)	IV
#1	<i>Ammannia coccinea</i> (6, OBL)	0.867 (0.571, 1.000)	0.091 (0.450, 0.476)	0.079
	<i>Cyperus setigerus</i> (6, FAC)	0.867 (0.567, 1.000)	0.261 (0.087, 0.450)	0.226
	<i>Eleocharis compressa</i> (6, FACW)	0.685 (0.529, 0.851)	0.609 (0.400, 0.810)	0.417
	<i>Heteranthera limosa</i> (5, OBL)	1.000 (1.000, 1.000)	0.130 (0.000, 0.280)	0.130
	<i>Juncus torreyi</i> (6, FACW)	0.705 (0.514, 0.904)	0.478 (0.278, 0.688)	0.337
	<i>Leersia oryzoides</i> (4, OBL)	0.830 (0.604, 1.000)	0.391 (0.194, 0.591)	0.325
	<i>Persicaria lapathifolia</i> (4, FACW)	0.765 (0.534, 1.000)	0.391 (0.190, 0.600)	0.299
	<i>Phyla lanceolata</i> (3, FACW)	0.779 (0.608, 0.944)	0.565 (0.360, 0.765)	0.440
	<i>Typha angustifolia</i> (3, OBL)	0.583 (0.486, 0.696)	0.783 (0.600, 0.947)	0.456
#2	<i>Ambrosia artemisiifolia</i> (3, FACU)	1.000 (1.000, 1.000)	0.217 (0.050, 0.400)	0.217
	<i>Ammannia coccinea</i> (6, OBL)	0.743 (0.479, 1.000)	0.348 (0.158, 0.550)	0.259
	<i>Echinochloa muricata</i> (0, FACW)	0.559 (0.306, 0.805)	0.304 (0.125, 0.500)	0.170
	<i>Eleocharis compressa</i> (6, FACW)	0.671 (0.525, 0.827)	0.652 (0.444, 0.842)	0.437
	<i>Eleocharis compressa</i> (6, FACW) + <i>Rumex crispus</i> (0, FAC)	0.749 (0.553, 0.938)	0.478 (0.269, 0.684)	0.358
	<i>Juncus torreyi</i> (6, FACW)	0.705 (0.509, 0.909)	0.478 (0.273, 0.682)	0.337
	<i>Leersia oryzoides</i> (4, OBL)	0.743 (0.491, 1.000)	0.348 (0.158, 0.556)	0.259

Sample	Indicator ( <i>C</i> value, wetland status)	Specificity (LCL, UCL)	Sensitivity (LCL, UCL)	IV
	<i>Phyla lanceolata</i> (3, FACW)	0.731 (0.580, 0.894)	0.652 (0.448, 0.842)	0.477

Study sites (108 total) were located using National Wetlands Inventory data, the National Wetland Condition Assessment probability sample (Kentula and Paulsen 2019), and several Oklahoma-based sources (Bried et al. 2014; 2016). All sites exhibited seasonal to semi-permanent hydroperiods and dominance of scrub or herbaceous communities (i.e., non-forested wetlands). Most sites were geomorphically classified as depressionnal (84%) and the rest as lacustrine-fringe, riverine, or seep following Dvoretz et al. (2012).

## Vegetation surveys

Surveys occurred from mid-May to early August 2012–2018 across several Oklahoma prairie ecoregions, with intensified effort in the depression-rich northern Central Great Plains (Fig. 1). At 40 sites we used the plot-based methodology of the National Wetland Condition Assessment (USEPA 2011; Kentula and Paulson 2019). Vascular plant species were identified within and overhanging five square plots (100 m<sup>2</sup> each) arranged to representatively assess the wetland and conform with its size or shape (see USEPA 2011 for details). Additional species encountered outside the plots were recorded and used for analysis. At the remaining 68 sites we used meander surveys over the entire accessible area (smaller sites, < 0.5 ha) or in representative vegetation zones until no new species were recorded. The different methods (plot-based vs. meander) produced comparable plant checklists and apparently did not confound floristic quality estimates (Bried et al. 2016). We identified a grand total of 399 species belonging to 230 genera and 88 families.

## High floristic quality

We calculated site floristic quality using  $FQI = \bar{c} \times \sqrt{S}$  where  $\bar{c} = \sum_{i=1}^S c_i / S$ ,  $S$  is number of species, and  $c$  is the species conservatism value (integers 0 to 10) obtained from Ewing and Hoagland (2012) or B. Hoagland (pers. comm.). Sites with  $FQI \geq 20.0$  were designated as high quality wetlands; this criterion is empirically supported for Oklahoma wetlands (Bried et al. 2014; Gallaway et al. 2019) and has been used in wetland studies elsewhere (e.g. Matthews and Endress 2008). Additionally, west of the Interstate 35 corridor (Fig. 1) we lowered the benchmark ( $FQI \geq 13.0$  following Gallaway et al. 2019) to account for precipitation stress and naturally lower wetland quality compared to wetter eastern Oklahoma.

## Indicator value

Indicator species were extracted and valued based on their occurrence specificity and sensitivity for high quality sites ( $FQI \geq 20.0$ , or  $FQI \geq 13.0$  west of Interstate 35) compared to non-high quality sites. Indicator specificity measures exclusivity to the target group and indicator sensitivity measures frequency of occurrence in that group, such that strongest indicators occur exclusively (max Specificity = 1) and at all locations (max Sensitivity = 1) in the target group. In practice, an indicator's specificity may be viewed as

the chance it will correctly identify a target site (positive predictive value) and sensitivity as the chance of finding the indicator (Dufrêne and Legendre 1997; De Cáceres and Legendre 2009).

We evaluated species individually and in all possible pairs and triplet combinations assuming multispecies indicators cover more environmental space and heterogeneity than any single species (De Cáceres et al. 2012). We used the *indicspecies* package (De Cáceres and Legendre 2009) to generate the input matrix and calculate performance metrics (Specificity, Sensitivity). Candidate indicators were selected at each of three minimum thresholds of specificity (0.50, 0.60, 0.70) combined with two minimum thresholds of sensitivity (0.10, 0.25). We used 10,000 percentile bootstrap samples to establish 95% confidence intervals for the specificity and sensitivity of each indicator (De Cáceres et al. 2012). To reduce the candidate indicators, we removed indicators whose occurrence pattern was nested within that of other indicators or when subsets of indicators provided the same target group coverage as the full set (De Cáceres et al. 2012).

We repeated the analysis for wetlands of prairie ecoregions (i.e. all study sites, “prairie wetlands”) and for depressional wetlands of the northern Central Great Plains ecoregion (“CGP depressions”) in Oklahoma, expecting stronger indicators for CGP depressions due to increased spatial-environmental context (Bried et al. 2019). For both contexts we used randomly drawn ~100 Main Samples (e.g. Figure 1) to find indicator species, giving us 74 sites in the broader context and 48 sites in the narrower context. We constrained each draw to yield equal numbers of high quality and non-high quality sites, repeating the draws and analysis five times per context to help assess robustness of the indicators. Results from the first two samples (those shown in Fig. 1) are presented below and results from the remaining samples in the online Supplement.

## Indicator validity

Valid indicator species should occur with relatively high frequency in the target group (high floristic quality wetlands) and low frequency elsewhere. We tested discriminative ability in candidate indicators using 34 prairie wetlands and 22 CGP depressions (the remaining ~100 of samples) each split evenly into high and non-high quality as above. Indicator validity was measured by frequency of occurrence in high-quality sites (observed true positive rate) and non-high quality sites (observed false positive rate) relative to predicted rates. For predicted rates we focused on specificity and used the LCL (lower confidence limit) for true positives and  $1 - \text{UCL}$  (upper confidence limit) for false positives. In valid indicators observed true positives should equal or exceed the predicted rate (observed  $\geq$  Specificity LCL) and observed false positives should be at or below the predicted rate (observed  $\leq$  Specificity  $1 - \text{UCL}$ ). Clearly false positive rates should be zero or reasonably small (say  $< 0.2$ ) and true positive rates reasonably large (say  $\geq 0.5$ ) in any indicators chosen for practice.

## Final indicators

We judged indicators for practical use based on indicator value (Specificity  $\times$  Sensitivity), indicator validity, and two species characteristics: regional hydrophytic status (FACW or OBL according to USACE 2010) and Oklahoma *C* value (Ewing & Hoagland 2012; B. Hoagland pers. comm.). Hydrophytic status

ensures the indicator is more representative of wetlands than non-wetlands (Tiner 1999), and high to moderate  $C$  value ( $\geq 4$ ) helps prevent weedy species from being selected as indicators of intact wetland conditions.

## Results

Across the five samples we extracted 40 candidate indicators of high floristic quality wetlands of prairie ecoregions and 29 candidate indicators for northern Central Great Plains depressions (Tables 1, 2, S1, S2 and Figs. 2, 3, S1, S2). Depending on the sample, the broader context (prairie ecoregions) revealed 12 to 17 indicators and narrower context (CGP depressions) 8 to 12 indicators. The candidate pool for CGP depressions showed overall greater performance (higher indicator values, higher true positive rates, and lower false positive rates on average) than candidates for prairie wetlands. Most candidates were hydrophytes (79.4% OBL or FACW) and the majority had low to moderate  $C$  values (70.6%  $\leq 5$ ). High quality and non-high quality sites had similar conservatism distributions (Fig. 4).

The overall best indicator of high floristic quality was *Eleocharis compressa* based mainly on indicator value ( $> 0.3$  in prairie ecoregions,  $> 0.4$  in CGP depressions) and ecological conservatism (6) (Tables 1, 2, S1, S2). This was also a robust indicator being the only candidate selected across all five samples in both contexts. However, in prairie ecoregions *E. compressa* failed the validity test in all but one sample (Figs. 2, S1). Performance improved in the CGP depressions where it passed the true positive test (observed  $\geq$  Specificity LCL) in all samples and attained near 75% occupancy in four samples (Figs. 3, S2). However, it failed the false positive test (observed  $\leq$  Specificity  $1 - \text{UCL}$ ) in three samples (Fig. 3, S2).

Some candidates outperformed *E. compressa* in certain criteria, context, or samples but were lacking overall or in key respects. For example, all candidates showing higher indicator values (*Phyla lanceolata*, *Salix nigra*, *Typha angustifolia*) had lower  $C$  value than *E. compressa*, whereas all candidates with equal or higher  $C$  value (*Ammannia coccinea*, *Amorpha fruticosa*, *Boehmeria cylindrica*, *Ludwigia repens*, *Rhynchospora corniculata*) showed weaker indicator values ( $\leq 0.2$ ) than *E. compressa*. Many candidates appeared to trade off on performance (indicator value and validity) and species characteristics (hydrophytic status, ecological conservatism). For example, relatively conservative (6) and hydrophytic (FACW) *Amorpha fruticosa* showed evidence of false positive validity only, whereas *Rumex crispus* passed both validity tests but is introduced ( $C = 0$ ) and ambiguously hydrophytic (FAC status). Or similarly, wetland obligates *Leersia oryzoides* and *Schoenoplectus pungens* had higher indicator values but lower  $C$  value (4) than *A. fruticosa*. One of the best indicators after *E. compressa* may be *Juncus torreyi* ( $C = 6$ ) with its respectable indicator values (0.299 to 0.337) and evidence of false positive validity ( $\sim 0.1$  observed rates in two samples), but this applied only to the narrower spatial-environmental context (Table 2 and Figs. 3, S2).

## Discussion

By short-cutting full community Floristic Quality Assessment, indicator species (Dufrêne and Legendre 1997; Siddig et al. 2016) could drastically accelerate field identification of high floristic quality and help to screen or verify potential reference-quality wetlands, including verification of predictions made remotely (e.g., Host et al. 2005). Unfortunately, the present results do not support using indicator species to rapidly discriminate high floristic quality wetlands in the US southern plains. In the same study area Bried et al. (2014) reported plant indicator species of potential reference-quality wetlands defined by multimetric vegetation criteria, including the floristic quality benchmark ( $\geq 20.0$  FQI) used here. They reported some encouraging indicator values and false positive predictions but lacked a validation analysis (i.e. comparison with observed misclassification rates).

Several challenges may limit the performance of floristic quality indicator species. First and foremost, the species are being asked to indicate a level of quality derived from community data. We assumed species combinations (De Cáceres et al. 2012) would mitigate this disproportionality, but few species pairs and only one triplet combination met any specificity and sensitivity thresholds. Secondly, indicator species are always fixed to a target, but floristic quality is a “moving target” because theoretically many species compositions can result in the same level of quality. It seems indicator species would need strong associations or positive co-occurrence patterns with a large fraction of the assemblage to adequately represent floristic quality. Increased ecogeographic and environmental (e.g. hydrogeomorphic) stratification may reduce compositional variation and strengthen indicator performance (Brooks et al. 2006; Bried et al. 2019), but effective stratification may be difficult. In our study area wetlands are hard to geomorphically subclassify (Dvoretz et al. 2012) and subject to strong climatic gradients and other natural heterogeneity (Hoagland 2000; Gallaway et al. 2019), adding to the challenges.

One candidate (*Eleocharis compressa*) appeared in every scenario and consistently showed among the highest indicator values. This species also possesses a high  $C$  value (6) relative to the low-biased  $C$  distribution across the dataset (Fig. 4). In western Oklahoma *E. compressa* can dominate in small depressions (often interdunal swales) on clay soils (Hoagland 2002), suggesting it may occur commonly enough for practice. Some candidates selectively outperformed *E. compressa* but most of the final pool struggled on one or both sides of validity. We used the most conservative false positive prediction (1 – Specificity UCL) when measured against observed rates, in part to counterbalance the more relaxed true positive measure (Specificity LCL). Even if we relaxed the false positive prediction (to 1 – Specificity) many of these indicators still would not pass the test, or they would run an unacceptable 20–30% risk of erroneously indicating a site as high quality.

More sample stratification may alleviate misclassifications while strengthening indicator values (Dufrêne and Legendre 1997, Bried et al. 2019). Overall, indicator value and validity improved after filtering the samples to a specific prairie ecoregion and geomorphic setting. Deeper stratification by vegetation types and hydrogeomorphic subclasses (e.g. Dvoretz et al. 2012) could further strengthen indicators but requires adequate knowledge and acceptance of tradeoffs between accuracy and precision. Too much stratification may leave some strata poorly defined and lacking in indicator species or the data needed to extract and validate them.

Alternatives to traditional indicator value analysis (Dufrêne and Legendre 1997) might lead to improvements. Stapanian et al. (2013), for example, used classification and regression tree models to find indicator species of wetland vegetation quality in Ohio, USA. Their simplest model containing just two species predicted high-quality wetlands with 13% overall misclassification rate.

We tested species combinations (De Cáceres et al. 2012) but few combinations appeared in the candidate pool. Perhaps combining the single-species indicators post hoc would help mutually offset their deficiencies. For example, pairing *E. compressa* with *Juncus torreyi*, both relatively conservative ( $C=6$ ), may reduce misclassification error in the narrower spatial-environmental context (CGP depressions). Likewise joining *E. compressa* with *Amorpha fruticosa*, *Leersia oryzoides*, and/or *Schoenoplectus pungens* may strengthen performance in the broader context of prairie ecoregion wetlands. These latter species also have the advantage of being definitively recognizable throughout the growing season, unlike *E. compressa* which flowers early to mid-season and can look similar vegetatively to other *Eleocharis* species in the region (*E. albida*, *E. montevidensis*, *E. tenuis*). The potential drawback is whether such combinations will sufficiently occur in the target area, a problem mitigated ad hoc by preset sensitivity thresholds in the analysis of combinations (De Cáceres et al. 2012). Indeed, *E. compressa* and *J. torreyi* co-occurred in only 7.4% of our study sites, consistent with Hoagland (2002) who did not detect *J. torreyi* where *E. compressa* was most abundant. Similarly, *E. compressa* co-occurred with *A. fruticosa*, *L. oryzoides*, and *S. pungens* in 4.6%, 6.5%, and 7.4% of sites, respectively, and there was only one site where all four of these species co-occurred.

The present findings do not preclude the existence of high floristic quality indicators in other regions, especially where wetlands are well classified and training samples are given sufficient spatial-environmental context. Nor do our results negate potential for indicators in other ecosystems where Floristic Quality Assessment is commonly applied, namely forests and prairies. However, if wetlands tend to be less floristically diverse than forests and prairies (on average within climate zones) finding strong indicator species in those systems would seem even less likely for the reasons discussed above. Our study also cannot rule out potential for indicators at other levels of floristic quality. Indicators of low quality could be useful in avoiding a costly permitting process (Stapanian et al. 2013) or futile conservation investment, i.e. a site not worth protecting or restoring (a site “beyond repair”). Indicators of moderate quality could help direct protection and management effort to where there is both need and worth. Before broadly concluding that floristic quality indicator species do not exist for wetlands, we recommend exploring indicator potential in other regions and at other quality levels, and perhaps trying other statistical approaches (e.g. Stapanian et al. 2013).

## Declarations

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### **Compliance statement**

To the best of our knowledge this study was conducted in compliance with all relevant ethical and legal standards, and all necessary permissions (to access field sites, to collect and use data) were obtained.

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Consent to participate: Not applicable

Availability of data and material: Available from the corresponding author upon request

Code availability: Available from the corresponding author upon request

Authors' contributions: JTB and SKJ conceived the study idea. JTB designed the study. All authors collected the data. TSF and JTB performed the analysis. JTB wrote the manuscript with reading, input, and approval from TSF and SKJ.

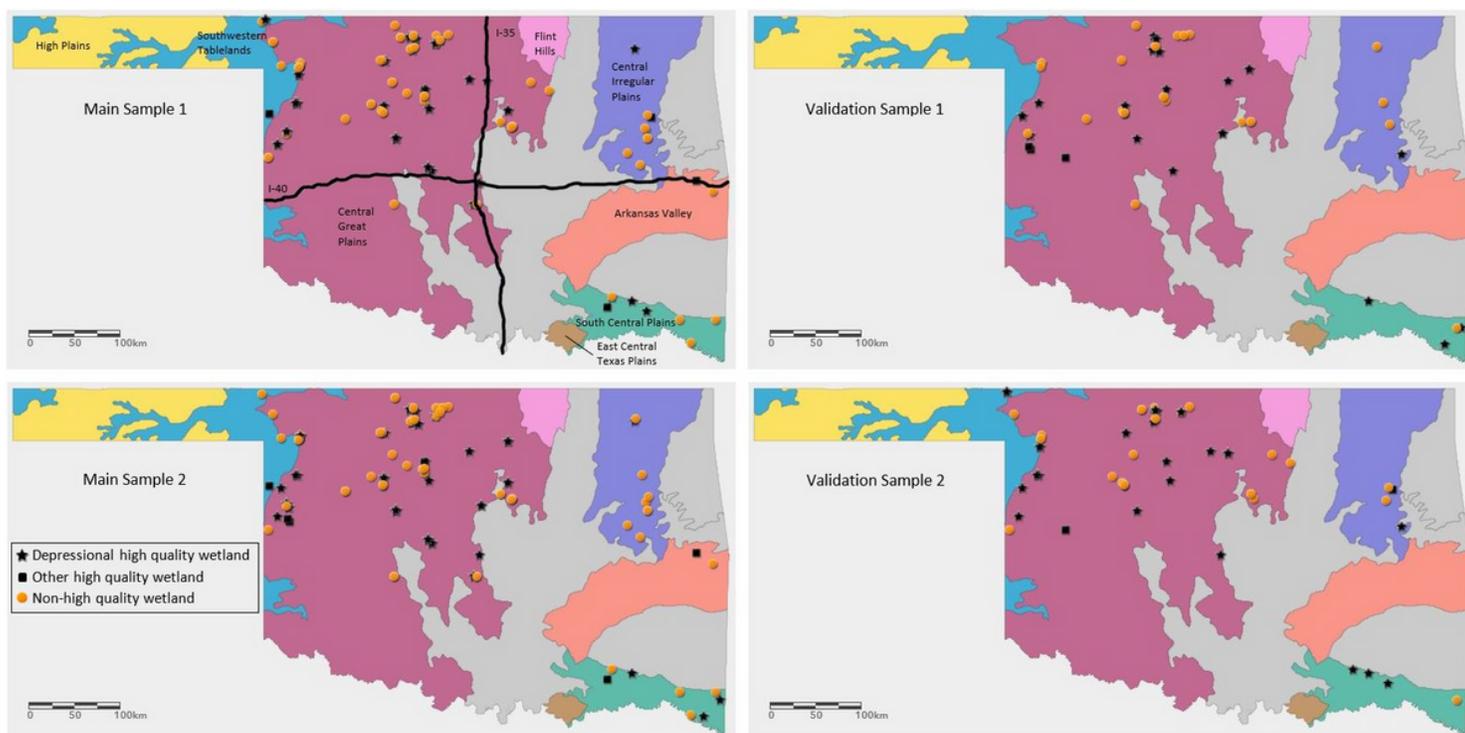
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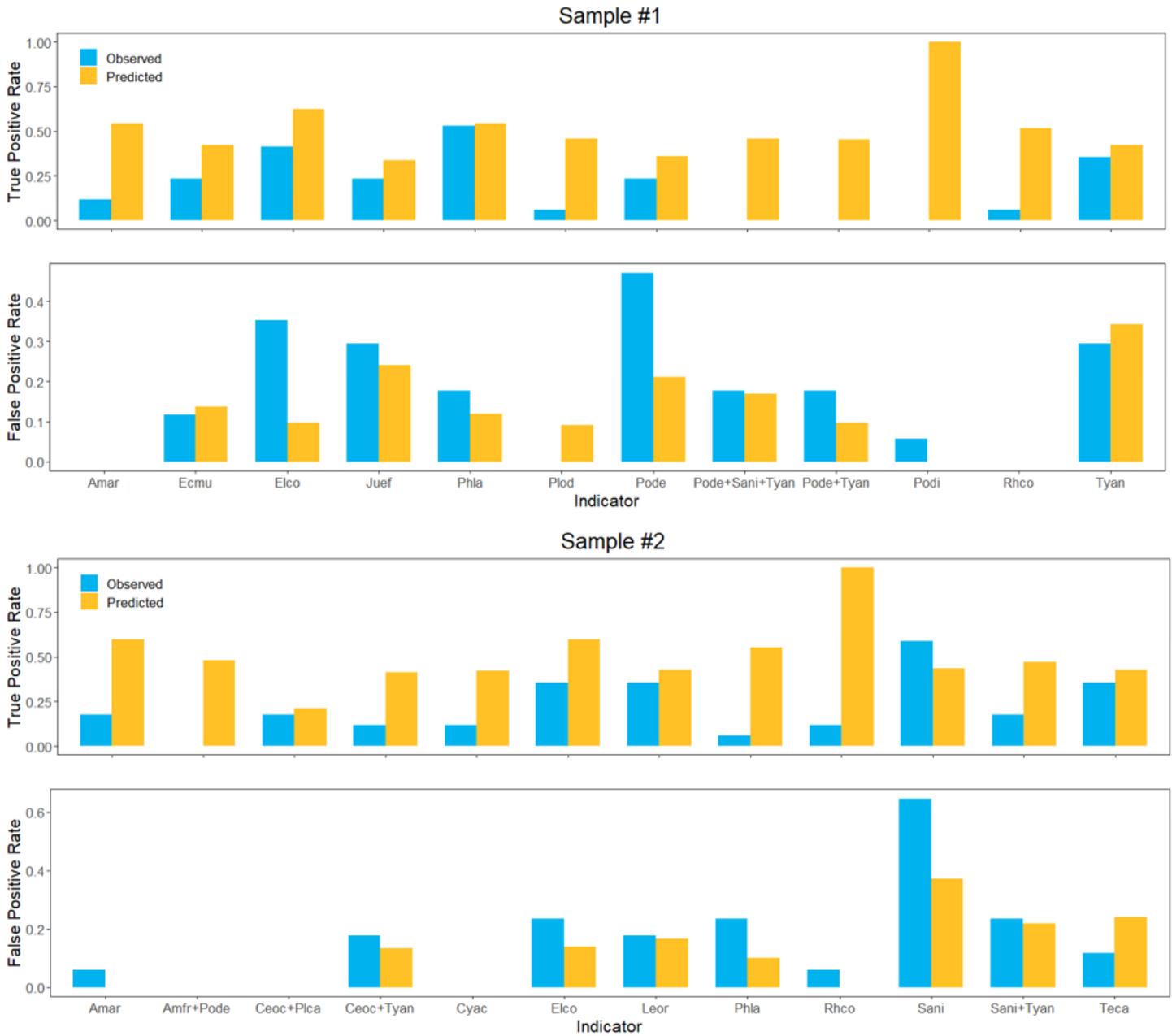
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## Figures



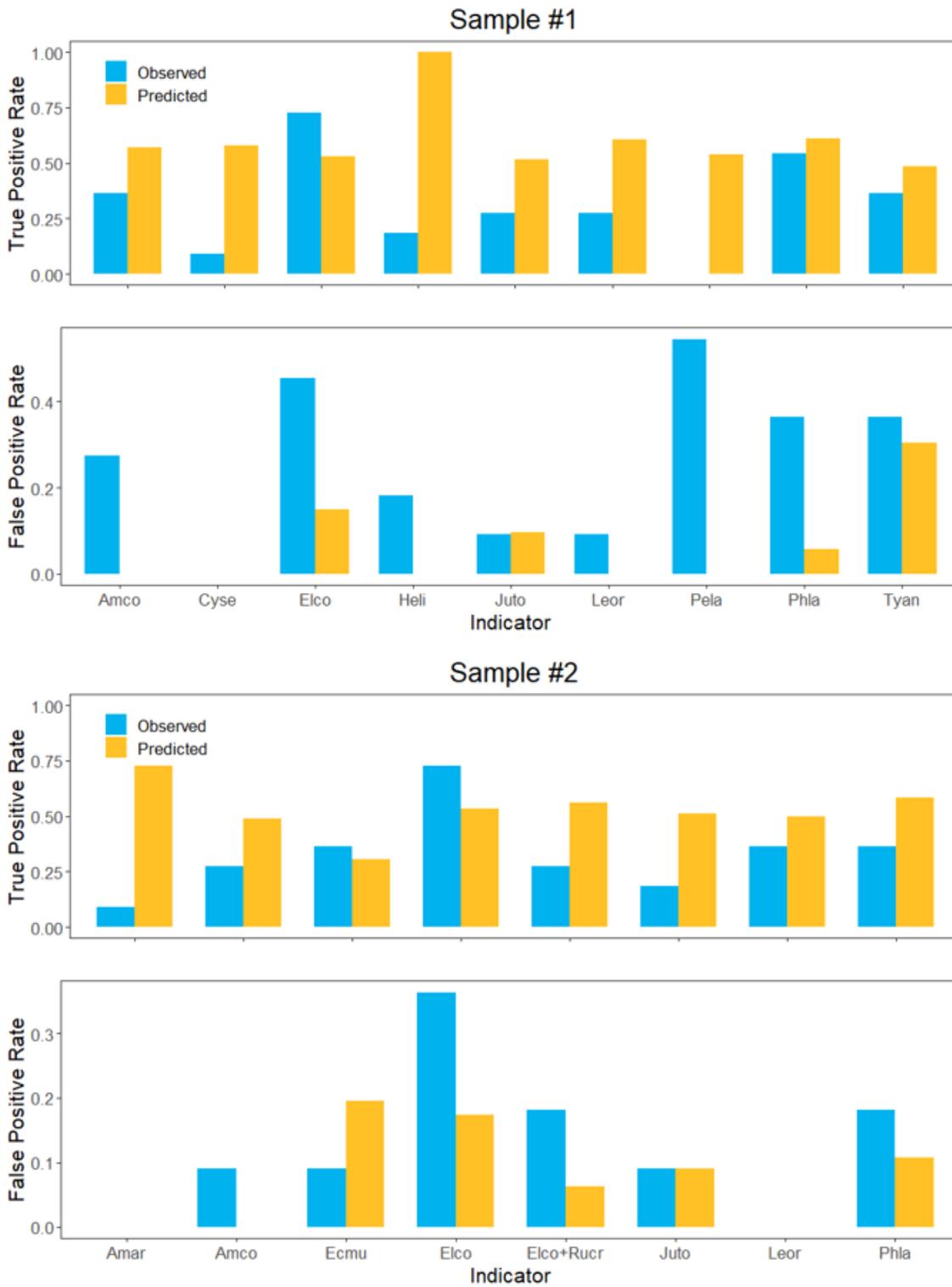
**Figure 1**

Samples for extraction and validation of indicator species (those reported in Tables 1, 2 and Figs. 2, 3) in Oklahoma, USA. Floristic quality scores of at least 20.0 (or  $\geq 13.0$  west of Interstate 35) separate 'high quality' from 'non-high quality' sites. 'Other' refers collectively to riverine, seep, and lacustrine-fringe wetlands. Prairie ecoregions are labelled and mapped in different colors; forest ecoregions are symbolized in grey.



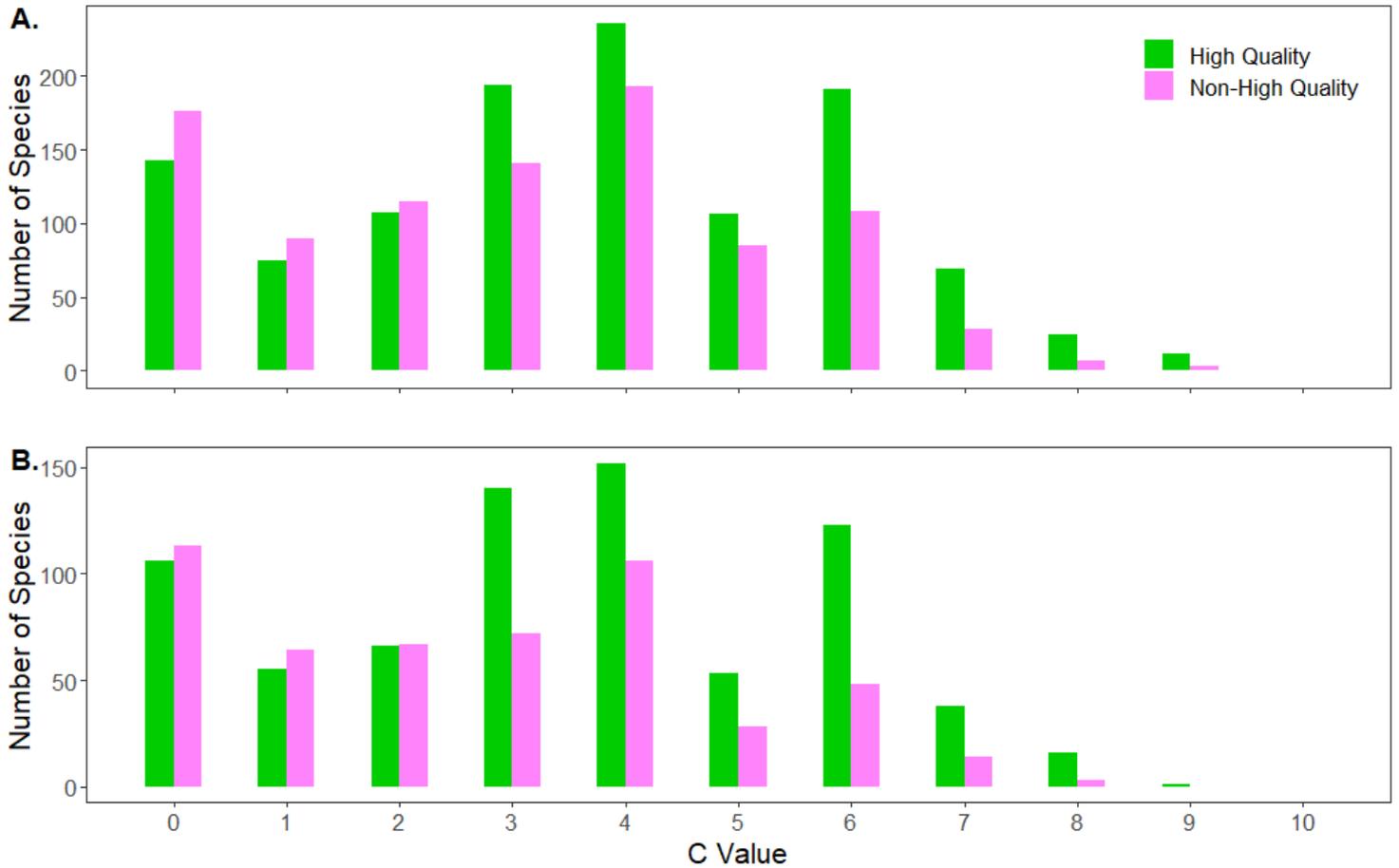
**Figure 2**

Indicator validity corresponding with Table 1. Predicted rates are derived from Specificity values in Table 1 and observed rates from the leftover sites (17 high quality, 17 non-high quality) not used in Table 1. Validation results from three additional samples are found in Fig. S1.



**Figure 3**

Indicator validity corresponding with Table 2. Predicted rates are derived from Specificity values in Table 2 and observed rates from the leftover sites (11 high quality, 11 non-high quality) not used in Table 2. Validation results from three additional samples are found in Fig. S2.



**Figure 4**

Conservatism (C) distributions of all 399 species as observed across (A) prairie ecoregion wetlands and (B) Central Great Plains depressional wetlands in Oklahoma, USA. Floristic quality scores of at least 20.0 (or  $\geq 13.0$  west of Interstate 35) separate 'high quality' from 'non-high quality' sites.

## Supplementary Files

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