

## PARTITIONING VEGETATION RESPONSE TO ANTHROPOGENIC STRESS TO DEVELOP MULTI-TAXA WETLAND INDICATORS

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**Abstract.** Emergent plants can be suitable indicators of anthropogenic stress in coastal wetlands if their responses to natural environmental variation can be parsed from their responses to human activities in and around wetlands. We used hierarchical partitioning to evaluate the independent influence of geomorphology, geography, and anthropogenic stress on common wetland plants of the U.S. Great Lakes coast and developed multi-taxa models indicating wetland condition. A seven-taxon model predicted condition relative to watershed-derived anthropogenic stress, and a four-taxon model predicted condition relative to within-wetland anthropogenic stressors that modified hydrology. The Great Lake on which the wetlands occurred explained an average of about half the variation in species cover, and subdividing the data by lake allowed us to remove that source of variation. We developed lake-specific multi-taxa models for all of the Great Lakes except Lake Ontario, which had no plant species with significant independent effects of anthropogenic stress. Plant responses were both positive (increasing cover with stress) and negative (decreasing cover with stress), and plant taxa incorporated into the lake-specific models differed by Great Lake. The resulting models require information on only a few taxa, rather than all plant species within a wetland, making them easier to implement than existing indicators.

**Key words:** *Carex*; *dikes*; *emergent*; *fen*; *floristic quality*; *Great Lakes*; *hydrologic modification*; *invasive plants*; *land use*; *lemnids*; *marsh*; *Typha*.

### INTRODUCTION

Coastal wetlands are the focal point of much human activity, both direct and indirect, that threatens their condition and existence. Environmental managers in coastal regions and elsewhere seek indicators that can rank wetlands by their condition or provide early warning of environmental degradation. Plants are valued as potential indicator species because their responses to anthropogenic disturbance are less ephemeral than the chemical measurements that are typically used to characterize environmental quality. Plants also have the advantage over many faunal indicators in that they remain in place, simplifying sampling and increasing the likelihood that the biotic indicator is spatially coincident with in situ stressors. However, not all plants respond equally to human disturbance. Some plants

decrease in abundance with anthropogenic stress, some increase with anthropogenic stress, and some are insensitive to anthropogenic stress. The best (i.e., most parsimonious) vegetation-based indicator of coastal wetland condition would utilize information provided by the plants that are most responsive to anthropogenic stress, ignoring the rest. Unfortunately, such relationships are not known for all plants. We evaluated plant-environment relationships using a geographically extensive database for U.S. coastal wetlands of the Laurentian Great Lakes, and constructed indicator formulae that estimate coastal wetland condition based on the strength of those relationships.

A multi-taxa vegetation-based indicator that is commonly used to evaluate wetlands in the Great Lakes region is the floristic quality index (FQI), also known as the floristic quality assessment (FQA) or the floristic quality assessment index (FQAI) (National Research Council 2001, U.S. Environmental Protection Agency 2002). To compute the index, all plant species within a wetland are identified, and their average “coefficient of conservatism” (*C* value) is computed and multiplied by the square root of the total number of species within the area censused (Swink and Wilhelm 1994). *C* value is a number from 0 to 10 indicating a plant’s fidelity to “remnant natural plant communities,” a value of 10 signifying a plant that almost certainly comes from an

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undegraded natural plant community. The FQI has been tested and widely adopted as a biological indicator of human influence, and *C* values lists have been compiled by nine U.S. states and one Canadian province (Lopez and Fennessy 2002, Bourdaghs et al. 2006). The FQI requires that all plant species be tallied, even though some species may provide more information than others about anthropogenic stress, or the lack thereof. Additionally, the assignment of *C* values to plant species, typically done on a state-by-state basis by botanists knowledgeable of local flora, can be somewhat subjective (Bourdaghs et al. 2006). The main practical problem with using FQI, however, is the botanical expertise needed to identify to species all plants within a wetland. Thus, the availability of wetland indicators based on only a few taxa would greatly reduce the effort and cost of assessing wetland condition by environmental managers.

Initial development of coastal wetland indicators using field data requires characterization of sources of anthropogenic stress as well as identification of the vegetation present. Anthropogenic stressors may be activities that have occurred within the boundaries of the wetlands themselves, directly affecting wetland vegetation and function, or they may result from off-site activities in the landscape adjacent to the wetland, indirectly affecting coastal wetlands through fluxes of water, nutrients, and contaminants (Johnston 1994). An index of cumulative anthropogenic stress was developed for watersheds on the U.S. side of the Great Lakes basin by Danz and coworkers (2007) and was verified to be related to coastal wetland water quality (Morrice et al. 2007) and biotic characteristics (Reavie et al. 2006, Brazner et al. 2007). Other studies have also confirmed that wetland vegetation is affected by upslope agriculture and urbanization (Findlay and Houlihan 1997, Mensing et al. 1998, Galatowitsch et al. 2000, Lougheed et al. 2001). The mechanism by which these land uses affect wetland vegetation is often nutrient enrichment of runoff (Craft et al. 2007).

Structures such as roads, dikes, and ditches within wetlands have more direct effects on wetland vegetation than do other anthropogenic modifications. Dikes are intentionally constructed in Great Lakes coastal wetlands as a means of managing vegetation by controlling water levels, often with the purpose of maintaining waterfowl habitat (Sherman et al. 1996, Kroll et al. 1997, Sanzone and McElroy 1998, Thiet 2002). Diking of Great Lakes coastal wetlands modifies natural hydrologic regimes, leading to nutrient-rich aquatic environments that are vulnerable to plant invasion (Herrick and Wolf 2005). Dikes are also used to construct fly-ash disposal and cooling ponds in wetlands near power plants, which may raise water levels in adjacent undiked wetlands via seepage (Wilcox et al. 1985, Ellison and Bedford 1995). Roads have a variety of ecological effects on aquatic ecosystems, including disruption of the physical environment, alteration of the chemical envi-

ronment, and the spread of exotic species (Wilcox 1989, Forman and Alexander 1998, Trombulak and Frissell 2000). When roads bisect wetlands, they can interrupt the flow of water, changing the depth and duration of flooding on both the upslope and downslope sides, thereby altering wetland vegetation (Findlay and Bourdaghs 2000). Plant community alterations can also be caused by deicing road salts (Wilcox 1986). Ditches in highly impacted landscapes reduce native perennial importance (Galatowitsch et al. 2000).

Plants used as environmental indicators should be sensitive to human activities independent of their sensitivity to other environmental variables. However, identification of significant plant-environment relationships using field data is hampered by multiple co-occurring conditions that may obscure, amplify, or dampen the effects of each other. For example, climate directly influences plant distribution, but climate also affects the distribution of anthropogenic practices that can indirectly affect plant distribution, such as the presence of agriculture that releases excess nutrients to coastal wetlands. It is difficult to distinguish the effects of human activities from the effects of natural environmental variation when the two covary, particularly for such a large region as the 5900-km U.S. shoreline of the Great Lakes, which intercepts a range of climatic, geologic, hydrologic, and disturbance conditions.

We used hierarchical partitioning (HP) as a statistical tool to identify plant taxa with independent responses to anthropogenic stressors (Chevan and Sutherland 1991, Christensen 1992), implemented as a software module of the public domain statistical program, R (Mac Nally and Walsh 2004). HP employs goodness-of-fit measures (i.e.,  $R^2$  for multiple regression) for each of the  $2^K$  possible models for  $K$  predictor variables, partitioning the measures so that the total independent contribution of a given predictor variable is estimated (Mac Nally 2002). For each predictor variable, explanatory power is ultimately segregated into independent effects,  $I$ , and effects that cannot be unambiguously associated with that single variable but are due to joint effects with other variables,  $J$ . The utility of HP has been demonstrated in habitat studies for a variety of fauna, including butterflies (Luoto et al. 2006), birds (Bennett et al. 2004, Heikkinen et al. 2004, Betts et al. 2006), fish (Pont et al. 2005), amphipods (Walsh et al. 2004), diatoms (Newall and Walsh 2005), and rocky intertidal organisms (Lindgarth and Gamfeldt 2005, Arenas et al. 2006), but HP has been used less often for plant habitat studies (Kühn et al. 2004, Yao et al. 2006). HP was previously used for an analysis of Great Lakes fauna and flora by Brazner et al. (2007), which included five of the wetland plant taxa considered here.

The objective of this research was to develop vegetation-based indicators of coastal wetland condition utilizing only plants that respond (either positively or negatively) to anthropogenic stressors, distinct from naturally occurring environmental factors that influence

plant distribution and abundance. Specific goals of the research were to (1) identify Great Lakes coastal wetland plant taxa with a significant response to anthropogenic stress independent of other influences and (2) relate those responsive plant taxa to measures of anthropogenic stress to formulate vegetation-based environmental indicators for Great Lakes coastal wetlands based on those relationships.

## METHODS

### *Site selection and vegetation sampling*

Ninety wetlands along the U.S. Great Lakes coasts were selected using an objective, stratified random statistical design representing the entire range of existing anthropogenic stress (Danz et al. 2007). Wetlands were divided among two ecological provinces (Keys et al. 1995), the eastern broadleaf forest (EBF) ecoprovince ( $n = 35$  wetlands) and the more northerly Laurentian mixed forest (LMF) ecoprovince ( $n = 55$  wetlands). Wetlands were also selected to represent three hydrogeomorphic types based on wetland vulnerability to hydrologic forces (Keough et al. 1999): open-coast wetlands, river-influenced wetlands, and protected wetlands. Open-coast wetlands ( $n = 27$ ) contained emergent plants growing out of littoral lakebed that was relatively exposed to wave action. River-influenced wetlands ( $n = 35$ ) bordered a river at its confluence with one of the Great Lakes, receiving hydrologic inputs from upstream as well as from the lake. Protected wetlands ( $n = 28$ ) were hydrologically connected with the Great Lakes, but were protected from the full force of wave action by their location behind a sand spit, barrier beach, bayhead, or dike. Specific study wetlands and their assigned geomorphic types are listed in Johnston et al. (2007).

Plant sampling was conducted in  $1 \times 1$  m quadrats distributed along randomly placed transects within areas of emergent herbaceous wetland vegetation in the study wetlands selected. Transects were established with a geographic information system (GIS) prior to field campaigns, using a program called Sample (Quantitative Decisions, Rosemont, Pennsylvania, USA) to randomize transect placement (Johnston et al. 2007). Transects were placed in areas mapped by national and state wetland inventories as emergent wetland vegetation. Each transect intersected a randomly selected point generated by the Sample program, and was oriented along the water depth gradient extending from the deepwater edge of wetland emergents to the upland-wetland boundary, or to a shrub-dominated wetland zone, if present. Transect length and target number of sample quadrats were determined in proportion to the size of the wetland to be sampled (20 quadrats/60 ha, minimum transect length = 40 m, minimum quadrats/wetland = 8). Transect endpoint coordinates were uploaded into a handheld global positioning system (GPS) prior to field campaigns, but the location of

individual quadrats was determined and recorded in the field.

To establish quadrat locations in the field, each transect was first divided into 20-m segments, and then a  $1 \times 1$  m quadrat was randomly located within each segment using a random numbers table. Within each quadrat all vascular plant species were identified to the lowest taxonomic division possible by trained botanists who were tested to ensure consistency of visual observations. Although transects were terminated at the edges of zones dominated by tall shrubs or submergent aquatic vegetation (SAV), short-stature bog shrubs and isolated shrub or SAV patches occurring within a predominantly emergent plant matrix were included in the sampling. Large, identifiable nonvascular species such as *Chara vulgaris* and *Sphagnum* spp. were also given cover estimates. Plants were identified using published taxonomic manuals (e.g., Fassett 1957, Chadde 1998), but the Interagency Taxonomic Information System was used as the ultimate taxonomic authority (taxonomic information *available online*).<sup>9</sup> Percent cover was estimated visually for each taxon according to modified Braun-Blanquet cover class ranges (American Society for Testing and Materials 1997): <1%, 1% to <5%, 5% to <25%, 25% to <50%, 50% to <75%, and 75% to 100%. Quadrat cover classes for each taxon observed were converted to the midpoint percent cover of each class using the algebraic midpoints of the six cover class ranges (0.5%, 3.0%, 37.5%, 62.5%, 87.5%), and values for all quadrats at a wetland were averaged by taxon. Vegetation sampling was conducted from 2001 to 2003, and was restricted to the months of July and August to ensure that most of the vegetation could be identified and peak annual growth was observed.

### *Site environmental characterization*

All wetlands were categorized according to three non-anthropogenic environmental characteristics: hydrogeomorphic type, ecoprovince, and the Great Lake on which they occurred. The number of wetlands studied on each of the five Great Lakes varied due to differences in shoreline length and coastal wetland abundance (Table 1). Two indices of anthropogenic stress were also obtained for each wetland, the cumulative stress index (CSI) and the hydrologic modification index (HMI), of which the former is a watershed-scale stressor index and the latter is a within-wetland stressor index.

The CSI is a generalized stress gradient for watersheds draining to the U.S. Great Lakes coast developed by Danz and coworkers (2007), derived from a GIS database of 149 variables related to five types of anthropogenic stress: agriculture, atmospheric deposition, land cover, human population, and point source pollution. Principal components (PCs), normalized to

<sup>9</sup> (<http://itis.gov>)

TABLE 1. Summary of wetland site characteristics for each Great Lake and basin-wide.

Lake or basin	No. ecoprovince sites		No. geomorphology sites			CSI per site†	HMI per site†
	LMF	EBF	P	R	C		
Superior	26	0	8	14	4	1.39 <sup>a</sup> ± 0.06	14.9 <sup>a</sup> ± 3.5
Huron	8	6	2	1	11	1.86 <sup>a</sup> ± 0.21	12.9 <sup>a</sup> ± 3.3
Michigan	21	6	5	11	11	2.42 <sup>b</sup> ± 0.12	9.1 <sup>a</sup> ± 2.3
Erie	0	10	8	2	0	3.22 <sup>c</sup> ± 0.09	47.1 <sup>b</sup> ± 13.2
Ontario	0	13	4	7	2	2.84 <sup>bc</sup> ± 0.04	6.4 <sup>a</sup> ± 2.8
Basin	55	35	27	35	28	2.19 ± 0.08	15.2 ± 2.3

Notes: Abbreviations are: LMF, Laurentian mixed forest; EBF, eastern broadleaf forest; P, protected wetlands; R, river-influenced wetlands; C, open-coast wetlands; CSI, cumulative stress index; HMI, hydrologic modification index. Lake means within a column followed by the same lowercase letter are not significantly different ( $P > 0.05$ ).

† Values are the mean of the index ± SE.

range between zero and one, were used to integrate the information within each of the five categories of stress variables. The CSI is the sum of the normalized first principal component (PC) from each of the five stressor categories, with values ranging from 0.33 (least stress) to 4.03 (most stress) for the 762 watersheds of the U.S. Great Lakes coast. The CSI has been demonstrated to be strongly related to characteristics of diatom, bird, fish, amphibian, and coastal wetland vegetation communities (Reavie et al. 2006, Brazner et al. 2007, Danz et al. 2007). The constituent PCs of the CSI were also significantly related to coastal water chemistry (total P, total N, dissolved inorganic N, total suspended solids, and  $\text{Cl}^-$ ) measured in 98 Great Lakes coastal wetlands (Morrice et al. 2007). We adopted the CSI as an independent measure of watershed-scale anthropogenic stress based on its proven utility in prior studies, and did not attempt to evaluate or modify it.

The HMI was initially developed by Bourdaghs and coworkers (2006) to test the FQI and its variants. The HMI was computed by mapping linear features that likely disrupt the natural flow and fluctuation of water in wetlands (e.g., road beds, dikes, ditches), as interpreted from contemporary digital orthophotoquads displayed in an ArcView 3.3 GIS (ESRI, Redlands, California, USA). The summed length of these features (in meters) was then divided by the area (in hectares) of the wetland complex to calculate the HMI. Bourdaghs and coworkers (2006) tested the HMI in Great Lakes coastal wetlands of the LMF ecoprovince, and found that FQI significantly decreased with increasing HMI in open-coast wetlands; they did not test the HMI in the EBF ecoprovince. We employed the HMI in this study as a measure of within-wetland anthropogenic stress because of the demonstrated importance of dikes in altering Great Lakes coastal wetland vegetation (Sherman et al. 1996, Kroll et al. 1997, Thiet 2002, Herrick and Wolf 2005).

#### Plant-based indices of environmental condition

We used HP to evaluate the independent influence of geomorphology, geography (ecoprovince, Great Lake), and anthropogenic stress effects on percent cover of selected plant taxa. HP analyses were conducted for the

combined dataset from all 90 study wetlands (“basin-wide”), as well as the separate datasets for each of the five Great Lakes. Candidate plant taxa for hierarchical partitioning were restricted to those that could be identified to species, with the exception of the genus *Sphagnum*, several free-floating aquatic genera (*Wolffia*, *Azolla*, *Riccia*), and “invasive *Typha*” (TYinv), which included both *Typha angustifolia* and *Typha × glauca*. Candidate plant taxa were also required to be relatively common, occurring in at least 20% of all wetlands (i.e., 18 of the 90 study sites) to be considered for basin-wide indicators, and occurring in at least 30% of wetlands on an individual Great Lake to be considered for lake-specific indicators. A total of 119 plant taxa were evaluated (Appendix A). With the exception of TYinv and CHVU (*Chara vulgaris*), all taxa symbols follow the Plants Database (available online).<sup>10</sup>

We used the hier.part package (Walsh and Mac Nally 2004) in the statistical software R version 2.1.0 (R Development Core Team 2004) for each response, using three environmental variables and two anthropogenic stressors in the initial analysis: (1) wetland geomorphic type (three levels), (2) Great Lake (five levels), (3) ecoprovince (two levels), (4) the CSI (continuous variable), and (5) the HMI (continuous variable). We modeled the response of taxa percent cover as following a pseudo-binomial distribution of residuals and specified a generalized linear model in hier.part.  $R^2$  was used as the measure of fit. Taxa that independently explained a larger proportion of variance than would be expected by chance were identified by comparing their observed value of independent contribution to variance ( $I$ ) to a population of “ $I$ ” values from 1000 randomizations of the data matrix. Significance was accepted at the upper 90% confidence level ( $Z$  score  $\geq 1.28$ ) for lake-specific HP analyses, and at the 95% confidence limit for the basin-wide analysis ( $Z$  score  $\geq 1.65$ ; Mac Nally 2002). The HP results were evaluated using one-way analysis of variance (ANOVA) to determine statistically significant differences in mean  $I$  values associated with the variance components across environmental variables.

<sup>10</sup> (<http://plants.usda.gov>)

To develop the final multi-taxa indices, we generated predictive models of anthropogenic stress (CSI, HMI) using stepwise regression in SAS 9.1.3 (SAS Institute 2004), where the predictive variables entered in the modeling process were all taxa that had significant responses to the CSI or the HMI in HP analysis. Predictive models were developed for the basin-wide dataset (i.e., all 90 wetlands), as well as for individual Great Lakes.

## RESULTS

### *Measures of anthropogenic stress*

The CSI values for the wetlands studied ranged from 0.7 (least disturbed) for the Mismar Bay wetland on northern Lake Huron to 3.6 (most disturbed) for the Huron River wetland on the south shore of Lake Erie. Average CSI values were significantly greater in the EBF ecoprovince than in the LMF ecoprovince (Wilcoxon,  $W = 170$ ,  $P < 0.001$ ), and also varied significantly by Great Lake ( $F_{4,85} = 34.9$ ,  $P < 0.001$ ; Table 1). The large standard errors of the CSI averages for Lakes Huron and Michigan reflected large disturbance gradients from very disturbed in the south to relatively pristine in the north portions of those lakes. There was no significant effect of geomorphology on average CSI ( $F_{2,87} = 0.19$ ,  $P = 0.83$ ).

The HMI ranged from 0 to 111 m/ha, with the three highest values associated with diked wetlands of western Lake Erie. Twenty of the 90 wetlands contained no structures (HMI = 0). Mean HMI values were significantly greater on Lake Erie than on the other four Great Lakes ( $F_{4,85} = 8.6$ ,  $P < 0.001$ ; Table 1), but did not vary significantly by ecoprovince (Wilcoxon,  $W = 850$ ,  $P = 0.35$ ). There was no significant effect of geomorphology on average HMI ( $F_{2,87} = 2.74$ ,  $P = 0.07$ ), although the five wetlands with HMI values  $> 50$  m/ha were all of the "protected" geomorphic type.

### *Basin-wide analysis*

For the 49 taxa that occurred in 20% or more of the study wetlands basin-wide, the sum of  $I$  values for all five environmental characteristics ranged from 0.422 for TYinv to only 0.057 for the submergent *Ceratophyllum demersum* (CEDE4), the latter value indicating that CEDE4 abundance was poorly predicted by any of the five environmental variables (Fig. 1). "Lake" had the strongest influence among the five environmental variables (mean  $I = 51.6\%$ ), meaning that plants tended to be geographically aggregated within one of the five Great Lakes. For example, *Thelypteris palustris* (THPA) occurred primarily on Lake Ontario (lake  $I = 79.3\%$ ), and its cover was poorly predicted by any of the other environmental variables. "Lake" exhibited a significant independent contribution to variance for 25 of the 49 candidate taxa in the basin-wide analysis (Fig. 1).

Geomorphology had the next greatest influence on taxa abundance (mean  $I = 18.0\%$ ), but its independent effect was significant for only 10 species in the basin-

wide analysis (Fig. 1). Four species preferred open-coast wetlands (*Carex comosa* [CACO8], *Eleocharis erythropoda* [ELER], *Eupatorium perfoliatum* [EUPE3], *Juncus nodosus* [JUNO2]), four species preferred river-influenced wetlands (*Carex lacustris* [CALA16], *Comarum palustre* [COPA28], *Scutellaria galericulata* [SCGA], *Salix discolor* [SADI]), and two species preferred protected wetlands (*Carex lasiocarpa* [CALAA] and *Myrica gale* [MYGA]).

There was a small independent effect of ecoprovince when wetlands were analyzed basin-wide (mean  $I = 10.8\%$ ). The six taxa that preferred the southerly EBF ecoprovince were more invasive (*Phragmites australis* [PHAU7], TYinv) and weedy (e.g., *Boehmeria cylindrica* [BOCY], *Leersia oryzoides* [LEOR], *Urtica dioica* [URDI]) than those preferring the LMF ecoprovince (Table 2).

The independent effect of CSI was relatively small (mean  $I = 12.3\%$ ), and all but two of the 12 taxa with significant independent effects of CSI were also significantly affected by the "lake" or "ecoprovince" variables (Fig. 1). The independent effect of HMI was very small (mean  $I = 7.4\%$ ). The four species with significant independent effects of HMI included two invasives (*Phalaris arundinacea* [PHAR3] and PHAU7) and two free-floating plants (*Lemna minor* [LEMI3] and *Spirodela polyrrhiza* [SPPO]), which were very abundant in diked wetlands of western Lake Erie.

Life-form had a significant effect on plant responsiveness to watershed anthropogenic stress when species were separated into two groups: (1) submerged and floating aquatic plants (i.e., CEDE4, CHVU, *Elodea canadensis* [ELCA7], LEMI3, *Nymphaea odorata* [NYOD], SPPO, *Utricularia macrorhiza* [UTMA]) vs. (2) emergents and shrubs (i.e., the other taxa listed in Fig. 1). The average  $I$  value for the independent effect of CSI was significantly lower (Wilcoxon,  $W = 251$ ,  $P = 0.003$ ) for submerged and floating aquatic plant species ( $\bar{x} = 0.007$ ,  $SE = 0.005$ ) than it was for emergent and shrub species ( $\bar{x} = 0.032$ ,  $SE = 0.002$ ) and none of the submerged and floating aquatic plant species exhibited a significant independent response to CSI. The average  $I$  value for the independent effect of HMI was not significantly different between these two life-form groups (Wilcoxon,  $W = 103$ ,  $P = 0.21$ ).

### *Lake-specific analysis*

Separately analyzing the data for each of the five Great Lakes increased the average  $I$  values for the independent effect of CSI and HMI (Fig. 2). CSI mean  $I$  values for Lakes Huron and Erie were about four times greater than the CSI mean  $I$  value basin-wide (Fig. 2A). The HMI mean  $I$  value for Lake Erie (the lake with the greatest number of diked wetlands) was nine times greater than the HMI mean  $I$  value basin-wide, and HMI mean  $I$  values for Lakes Superior and Michigan were 4.4 times greater (Fig. 2B).

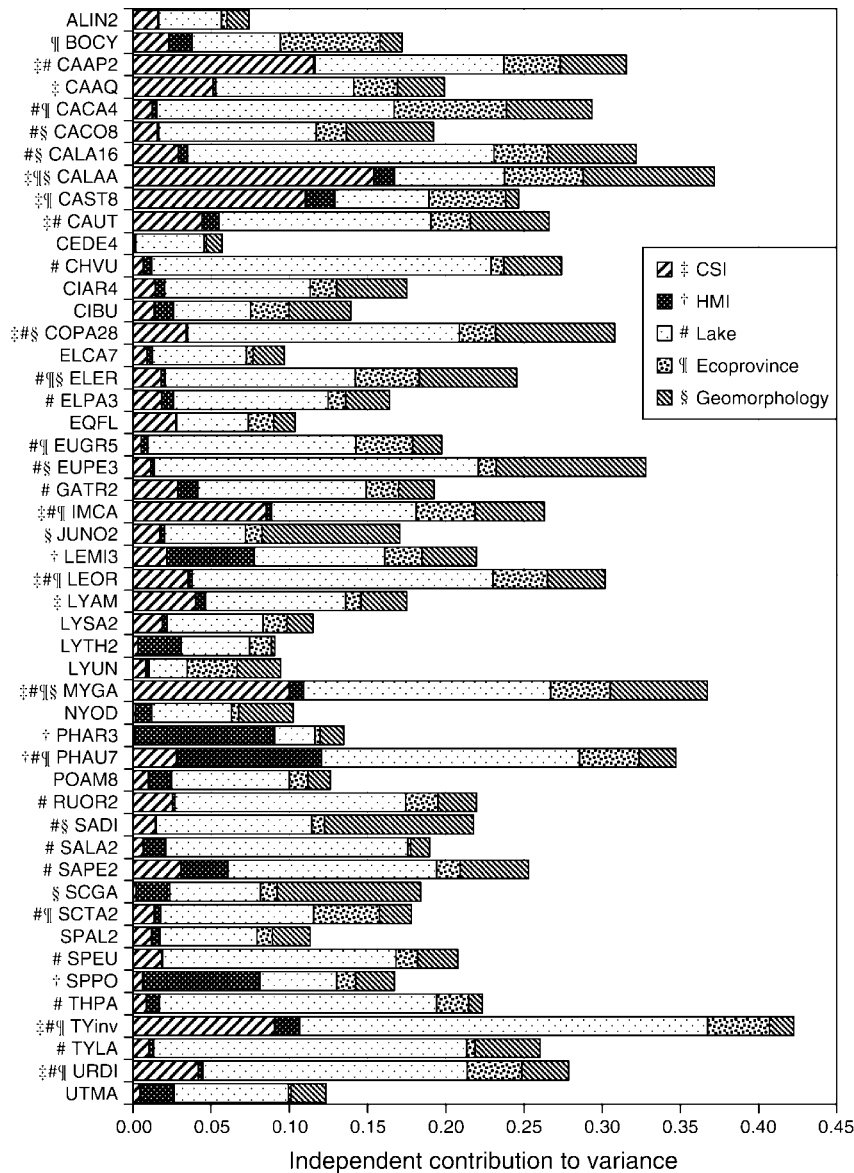


FIG. 1. Proportion of explained independent variance (relative  $T$ 's) associated with the five main variance components (lake, ecoprovince, geomorphology, cumulative stress index [CSI], and hydrologic modification index [HMI]) for each taxon occurring in 20% or more of wetlands. Indicators are ordered by the amount of variance attributed to CSI. Symbols to the left of each bar denote significant Z scores ( $P < 0.05$ ) from randomizations for each component. Taxa are listed in Appendix A.

Species response to stress generally differed among the Great Lakes. In some cases, this was the result of biogeography: 69 taxa were not sufficiently widespread to be considered for analysis on more than one of the Great Lakes (Appendix A). However, only five of the 50 taxa analyzed for multiple Great Lakes exhibited significant independent effects with CSI on more than one Great Lake (Table 3): *Campanula aparinoides* (CAAP2), *CALAA*, *Sagittaria latifolia* (SALA2), *Spartanium eurycarpum* (SPEU), and TYinv. Only *Scutellaria galericulata* (SCGA) exhibited independent effects with HMI on more than one Great Lake (Table 4).

None of the 37 taxa that were analyzed for Lake Ontario exhibited significant independent effects of geomorphology, CSI, or HMI. This is due in part to the relatively small variation in CSI and HMI values for Lake Ontario wetlands (i.e., low SE values in Table 1). Most Lake Ontario wetlands are highly stressed by watershed sources, and minimally stressed by within-wetland anthropogenic structures (i.e., low average HMI values).

In Lake Erie, only four and three taxa of the 30 taxa tested exhibited significant independent effects with CSI and HMI, respectively (Tables 3 and 4; see Plate 1).

TABLE 2. Taxa exhibiting significant independent effects of ecoprovince in the Great Lakes basin, Lake Huron, and Lake Michigan.

Taxon code	Basin	Lake Huron	Lake Michigan
BOCY	EBF*	‡	EBF*
CACA4	LMF*	ns	LMF*
CALAA	LMF*	ns	ns
CAST8	LMF*	LMF*	ns
ELER	LMF*	‡	ns
EUGR5	LMF*	ns	ns
EUMA6	‡	‡	EBF*
IMCA	EBF*	ns	ns
JUEF	‡	‡	EBF*
JUTE	‡	EBF*	‡
LEOR	EBF*	ns	EBF*
MYGA	LMF*	ns	‡
PHAU7	EBF*	ns	ns
PIFO	‡	‡	LMF*
PODE	‡	EBF*	‡
SAIN3	‡	EBF*	‡
SCPU10	‡	EBF*	ns
SCSU10	‡	LMF†	‡
SCTA2	LMF*	LMF†	ns
SPAL2	ns	LMF†	‡
STFI6	‡	EBF*	‡
TYinv	EBF*	ns	ns
URDI	EBF*	‡	EBF*

Notes: Taxon codes are explained in Appendix A. Key to abbreviations: EBF, eastern broadleaf forest; LMF, Laurentian mixed forest.

\*  $P < 0.05$ ; †  $P < 0.1$ ; ns, no significant independent effect of ecoprovince.

‡ Species insufficiently frequent to be considered in hierarchical partitioning (HP) analysis at this scale.

Notably absent from the Lake Erie taxa with independent effects of HMI was PHAU7, which covered extensive areas (16–64%) of five western Lake Erie wetlands and had significant independent effects with HMI in the basin-wide analysis (Fig. 1, Table 4).

Ecoprovince remained an environmental variable in the HP analyses for Lakes Huron and Michigan, whose north–south orientation spanned the two ecoprovinces. Ecoprovince was an important explanatory variable for Lake Huron (mean  $I = 0.11$ , 26.1% of explained variance), but was less so for Lake Michigan (mean  $I = 0.05$ , 18.9% of explained variance). Four of the seven species that exhibited significant independent effects of ecoprovince on Lake Michigan were similarly affected in the basin-wide analysis, but on Lake Huron only *Carex stricta* (CAST8) and *Schoenoplectus tabernaemontani* (SCTA2) exhibited significant independent effects of ecoprovince at both the basin and lake scales (Table 2). The ecoprovince boundary on Lake Huron split the six wetlands on Saginaw Bay from eight wetlands located on more northern shores of Lake Huron. Saginaw Bay wetlands are subject to more stress, particularly from agricultural sources, so that the average CSI value for the six Saginaw Bay wetlands ( $\bar{x} = 2.7$ ,  $SE = 0.08$ ) was more than twice that of the eight northern wetlands on Lake Huron ( $\bar{x} = 1.2$ ,  $SE = 0.10$ ). The cover of *Schoenoplectus pungens* (SCPU10), an icon of Saginaw Bay lakeplain marshes, ranged from 6% to 38% within

our six Saginaw Bay wetlands, but was absent from all but one of our other Lake Huron wetlands.

Of the 58 taxa that occurred in at least 30% of Lake Huron wetlands, 14 exhibited significant independent effects with CSI but only three were related to HMI (Tables 3 and 4). More than half of the species with significant independent effects of CSI were also significantly affected by ecoprovince, and all five species that were positively related to CSI occurred almost exclusively within Saginaw Bay on Lake Huron (EBF ecoprovince).

Eight of the 44 taxa tested for Lake Michigan exhibited significant independent effects of CSI (Table 3) and eight exhibited significant independent effects of HMI (Table 4). Six of the CSI-sensitive taxa (CAAP2, *Carex aquatilis* [CAAQ], CALAA, *Impatiens capensis*

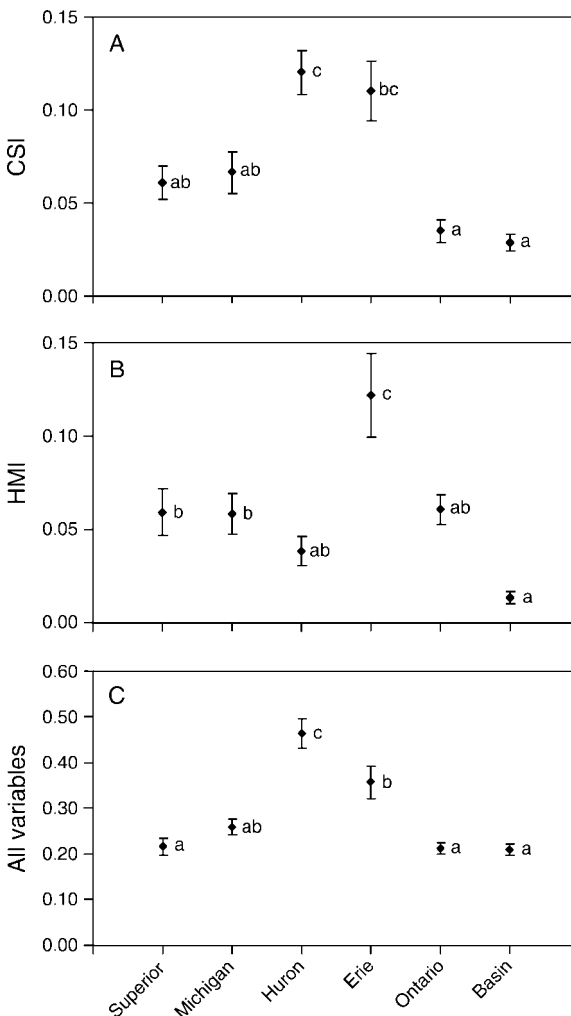


FIG. 2.  $I$  values (mean  $\pm$  SE) for wetland sites by each of the five Great Lakes and basin-wide (Basin) for: (A) cumulative stress index (CSI), (B) hydrologic modification index (HMI), and (C) all variables. Values with the same lowercase letter code within a graph are not significantly different ( $P > 0.05$ ).

TABLE 3. Independent contribution to variance ( $I$ ) values and trends for taxa exhibiting significant independent effects of CSI in basin-wide and lake-specific HP (hierarchical partitioning) analyses.

Taxon code	Lake					Basin
	Superior	Michigan	Huron	Erie	Ontario	
CAAP2	0.012	0.153*–	0.243*–	‡	0.002	0.115*–
CAAQ	0.004	0.094†–	0.095	‡	‡	0.051*–
CACA4	0.038	0.005	0.193†–	‡	0.010	0.012
CALA16	0.146*+	0.013	0.043	‡	0.022	0.029
CALAA	0.007	0.366*–	0.222*–	‡	‡	0.154*–
CAPA	0.162*+	‡	‡	‡	‡	‡
CAST8	0.077	0.066	0.384*–	‡	‡	0.110*–
CAUT	0.004	‡	‡	‡	‡	0.044*–
CIBU	0.108†+	0.054	0.019	‡	0.008	0.014
COPA28	0.026	‡	0.075	‡	0.005	0.034*–
ELPA3	0.107†+	‡	0.108	0.087	‡	0.018
HIMO	‡	‡	‡	0.261†–	‡	‡
IMCA	0.017	0.254*+	0.023	0.078	0.040	0.085*+
JUTE	‡	‡	0.214†+	‡	‡	‡
LEOR	‡	0.038	0.059	0.024	‡	0.035*+
LYAM	‡	‡	0.296*–	‡	0.032	0.040*–
MYGA	0.039	‡	0.071	‡	‡	0.100*–
PHAU7	‡	0.042	0.169†+	0.106	‡	0.028
PIFO	‡	0.194*+	‡	‡	‡	‡
PODE3	‡	‡	0.195†+	‡	‡	‡
POHY2	‡	‡	0.166	0.347*+	‡	‡
SALA2	0.195*+	0.158*+	0.031	0.098	‡	0.006
SAPU4	0.121†–	‡	‡	‡	‡	‡
SCPU10	‡	0.085	0.235*+	‡	‡	‡
SCSU10	‡	‡	0.319*–	‡	‡	‡
SCTA2	0.050	0.052	0.296*–	0.080	0.002	0.014
SPAL2	0.013	‡	0.301*–	‡	‡	0.012
SPEU	0.195*+	0.061	‡	0.272†–	0.000	0.018
SPHAG	0.181*–	‡	‡	‡	‡	‡
STFI6	‡	‡	0.258*+	‡	‡	‡
SYPUP	‡	‡	0.200†–	‡	‡	‡
TYinv	0.138*+	0.204*+	0.079	0.139	0.011	0.090*+
TYLA	0.166*+	0.004	‡	0.201	0.162	0.010
URDI	‡	0.101†+	‡	‡	‡	0.042*+
UTMA	0.171*+	‡	0.036	0.049	0.063	0.005
VEHA2	‡	0.024	‡	0.246†+	‡	‡

Notes: Trends are shown by + (species cover increases with increasing CSI) and – (species cover decreases with increasing CSI). Taxon codes (see footnote 10) are listed in Appendix A.

\*  $P < 0.05$ ; †  $P < 0.1$ .

‡ Species insufficiently frequent to be considered in HP analysis at this scale.

[IMCA], TYinv, URDI) were also significant CSI-sensitive taxa in the basin-wide analysis. In contrast to Lake Huron, only two species with significant independent effects of ecoprovince (*Pilea fontana* [PIFO] and URDI) also exhibited significant effects of CSI (Tables 2, 3).

On Lake Superior, eleven taxa exhibited significant independent effects of CSI, and with the exception of *Sphagnum* (SPHAG) moss and *Sarracenia purpurea* (SAPU4), all increased in cover with stress (Table 3). Despite their positive response to stress, most of those nine taxa were not particularly weedy species, reflecting the generally good condition of Lake Superior coastal wetlands. With the sole exception of TYinv, the CSI-sensitive taxa for Lake Superior did not exhibit significant independent effects with CSI in the basin-wide analysis. Five Lake Superior species exhibited significant independent effects with HMI, of which *Salix*

*pedicellaris* (SAPE2) was the only species that was negatively associated with HMI (Table 4).

#### Multi-taxa models

Stepwise multiple regressions using only those species with significant independent effects of CSI or HMI yielded highly significant multi-taxa models (Table 5). No models were attempted for Lake Ontario due to the lack of independent effects on any of the plant taxa there. The full basin-wide model for CSI incorporated two stress-promoted species (TYinv and URDI) and five stress-intolerant species (i.e., those with a negative coefficient in the model formula; CAST8, CALAA, CAAQ, *Carex utriculata* [CAUT], and MYGA). The cover of each taxon in the formula, expressed as a proportion, is multiplied by its model coefficient, and the results are summed to estimate the CSI value. The seven-taxon basin-wide model had an  $R^2$  of 0.534 with actual CSI values (Fig. 3A).



TABLE 4. *I* values and trends for taxa exhibiting significant independent effects of HMI in basin-wide and lake-specific HP analyses.

Taxon code	Lake					Basin
	Superior	Michigan	Huron	Erie	Ontario	
BOCY	‡	0.227*+	‡	0.011	0.149	0.015
CAAQ	0.000	0.224*+	0.010	‡	‡	0.002
CAST8	0.330*+	0.019	0.020	‡	‡	0.019
CAVU2	‡	0.240*+	‡	‡	‡	‡
CIBU	0.272*+	0.008	0.014	‡	0.186	0.012
JUEF	‡	0.162*+	‡	‡	‡	‡
LEOR	‡	0.119†+	0.058	0.048	‡	0.003
LEMI3	‡	0.048	0.017	0.524*+	0.012	0.056*+
MYGA	0.083	‡	0.264*+	‡	‡	0.010
PHAR3	‡	0.044	0.001	0.209	0.134	0.090*+
PHAU7	‡	0.004	0.115	0.038	‡	0.092*+
POAMS	‡	0.245*+	‡	‡	‡	‡
POCO14	‡	‡	‡	0.459*+	0.093	‡
PONA4	‡	‡	0.312*+	‡	‡	‡
SAPE2	0.132*-	‡	‡	‡	‡	0.030
SCGA	0.139†+	0.200*+	‡	‡	0.064	0.022
SCTA2	0.000	0.033	0.198†-	0.068	0.057	0.004
SISU2	0.414*+	‡	0.029	‡	‡	‡
SPEU	0.011	0.010	‡	0.260†+	0.061	0.000
SPPO	‡	‡	‡	0.101	0.056	0.075*+
TYLA	0.065	0.127†+	‡	0.026	0.037	0.003

Notes: Trends are shown by + (species cover increases with increasing HMI) and - (species cover decreases with increasing HMI). Taxon codes (see footnote 10) are listed in Appendix A.  
 \*  $P < 0.05$ ; †  $P < 0.1$ .  
 ‡ Species insufficiently frequent to be considered in HP analysis at this scale.

To develop an even more parsimonious model, we utilized the taxa selected for the first four steps of the stepwise regression (CALAA, CAST8, TYinv, and CAAQ), which yielded a basin-wide model with an  $R^2$  of 0.486 (Table 5). A separate analysis using SAS PROC GLM (SAS Institute 2004) and Akaike's Information Criterion confirmed that the model with those four species was the best of 13 possible four-taxon models.

Results from the seven-taxon model compare favorably with those obtained using the more established floristic quality index (FQI), which requires the user to identify all taxa present rather than just a few. A regression between computed FQI values for the 90 study wetlands vs. actual CSI values yielded a significant fit ( $R^2 = 0.560$ ,  $P < 0.001$ ) that was quite comparable to that obtained using the seven-taxon basin-wide model (Fig. 3B). In

TABLE 5. Plant taxa multiple regressions for anthropogenic stress.

Lake	Stressor	Model	$R^2$	Adj. $R^2$	<i>F</i>	df	<i>P</i>
All	CSI	2.38 - 2.93[CAST8] - 2.20[CALAA] - 10.07[CAAQ] + 1.21[TYinv] - 4.37[CAUT] + 2.95[URDI] - 1.98[MYGA]	0.534	0.494	13.4	7, 82	<0.001
	CSI	2.37 - 3.43[CAST8] - 3.10[CALAA] - 12.09[CAAQ] + 1.35[TYinv]	0.486	0.462	20.1	4, 85	<0.001
	HMI	7.94 + 98.7[PHAU7] + 55.0[PHAR3] + 427[SPPO] + 35.8[LEMI3]	0.412	0.385	14.9	4, 85	<0.001
Superior	CSI	1.16 + 2.96[UTMA] + 1.08[CALA16] + 27.3[CIBU]	0.518	0.452	7.9	3, 22	<0.001
	HMI	6.10 + 105[CAST8] + 2460[CIBU] - 392[SAPE2]	0.702	0.661	17.3	3, 22	<0.001
Huron	CSI	1.50 - 226[JUTE] + 2.63[PHAU7] + 250[PODE3] - 45.8[LYAM] + 3.14[SCPUP5] - 70.3[SYUPUP]	0.990	0.981	110.4	6, 7	<0.001
	HMI	15.5 + 553[PONA4] - 180[SCTA2]	0.465	0.367	4.8	2, 11	0.032
Michigan	CSI	2.43 + 1.25[TYinv] - 4.11[CALAA] - 21.1[CAAP2] + 2.71[URDI]	0.709	0.656	13.4	4, 22	<0.001
	HMI	4.08 + 7951[CAVU2] + 886[POAMS]	0.537	0.498	13.9	2, 24	<0.001
Erie	CSI	3.18 + 9.8[POHY2] + 72.5[VEHA2] - 3.9[HIMO]	0.754	0.631	6.13	3, 6	0.029
	HMI	32.9 + 2259[POCO14]	0.493	0.430	7.8	1, 8	0.024

Notes: For the models, [x] represents the average proportion of wetland area that is covered by species *x*, where CAAP2 = *Campanula aparinoides*, CAAQ = *Carex aquatilis*, CALA16 = *Carex lacustris*, CALAA = *Carex lasiocarpa* var. *americana*, CAST8 = *Carex stricta*, CAUT = *Carex utriculata*, CAVU2 = *Carex vulpinoidea*, CIBU = *Cicuta bulbifera*, HIMO = *Hibiscus moscheutos*, JUTE = *Juncus tenuis*, LEMI3 = *Lemma minor*, LYAM = *Lycopus americanus*, MYGA = *Myrica gale*, PHAR3 = *Phalaris arundinacea*, PHAU7 = *Phragmites australis*, POAMS = *Polygonum amphibium* var. *stipulaceum*, POCO14 = *Pontederia cordata*, PODE3 = *Populus deltoides*, POHY2 = *Polygonum hydropiperoides*, PONA4 = *Potamogeton natans*, SAPE2 = *Salix pedicellaris*, SCPUP5 = *Schoenoplectus pungens* var. *pungens*, SCTA2 = *Schoenoplectus tabernaemontani*, SYUPUP = *Symphotrichum puniceum*, SPPO = *Spirodela polyrrhiza*, TYinv = invasive *Typha*, URDI = *Urtica dioica*, UTMA = *Utricularia macrorrhiza*, and VEHA2 = *Verbena hastata*.

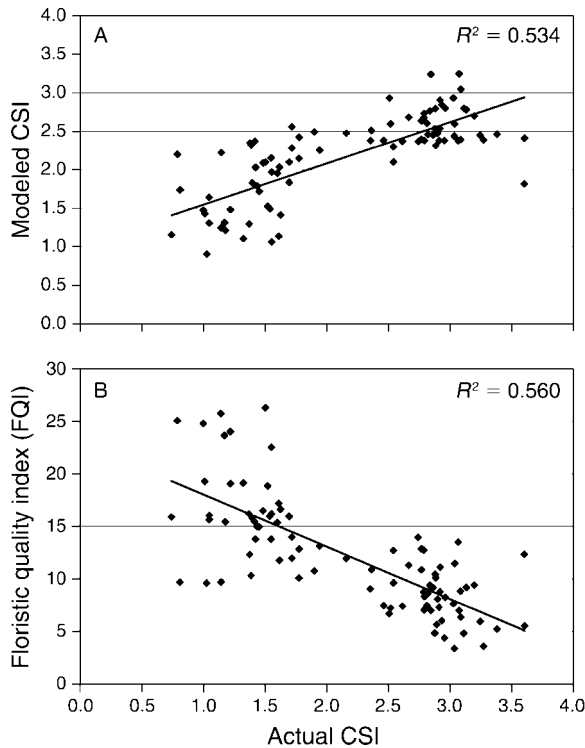


FIG. 3. Linear regression between CSI values and vegetation indices for (A) the seven-taxon basin-wide CSI model (Table 5) and (B) the floristic quality index.

addition, the regression between FQI and the output of the seven-taxon model was highly significant ( $R^2 = 0.470$ ,  $P < 0.001$ ).

Taxa incorporated into the lake-specific CSI models differed by Great Lake (Table 5). The Lake Michigan CSI model shared three taxa in common with the basin-wide model, TYinv, CALAA, and URDI, and also included CAAP2, which decreased with stress. The Lake Superior CSI model incorporated three species that increased with stress (UTMA, CALA16, and *Cicuta bulbifera* [CIBU]) and explained the least variance of any of the lake-specific models (adjusted- $R^2 = 0.45$ ).

The Lake Huron CSI model incorporated the greatest number of taxa (six), and was also the most predictive of the lake-specific models (adjusted  $R^2 = 0.98$ ). The cover of SCPU10, PHAU7, and *Populus deltoides* (PODE3) seedlings increased with increasing CSI (positive model coefficients); all three species occurred primarily in Saginaw Bay. *Symphotrichum puniceum* (SYPUP) and *Lycopus americanus* (LYAM), wet meadow species that were found primarily in four wetlands on Michigan's upper peninsula, were inversely related to CSI. *Juncus tenuis* (JUTE), a species that was significantly associated with the EBF ecoprovince (Table 2), had a negative coefficient in the CSI model because it was found in the four best wetlands within Saginaw Bay.

The Lake Erie CSI model utilized three of the four species identified as having significant independent

effects of CSI (Tables 3 and 5). Lake Erie had the fewest study wetlands ( $n = 10$ ), so its model was prone to influence by the two wetlands with the maximum CSI values for the Great Lakes, the westernmost sites on Lake Erie. These two wetlands contained no *Hibiscus moscheutos* (HIMO), which was found in five of the other eight Lake Erie wetlands, and had the greatest cover of *Verbena hastata* (VEHA2), which was found in only one other Lake Erie wetland, explaining the inclusion of these two variables in the Lake Erie CSI model. The third variable in the Lake Erie CSI model, *Polygonum hydropiperoides* (POHY2), occurred at these two wetlands as well as the Winous Point and Hickory Island wetlands. Due to our small sample size within Lake Erie and the apparent influence of a few wetlands on the results, we recommend that the multi-taxa CSI formula for Lake Erie be considered preliminary.

The basin-wide HMI model included all four species for which there was a significant independent effect of HMI: PHAU7, PHAR3, SPPO, and LEMI3 (Table 5). The Lake Superior HMI model incorporated a structure-intolerant species, SAPE2, and two species whose cover increased with increasing HMI, CAST8 and CIBU. The Lake Michigan model included *Carex vulpinoidea* (CAVU2) and *Polygonum amphibium* var. *stipulaceum* (POAMS), both of which increased in abundance with increasing HMI. The Lake Huron HMI model incorporated SCTA2 (negative association with HMI) and *Potamogeton natans* (PONA4; positive association with HMI). The Lake Erie HMI model utilized only *Pontederia cordata* (POCO14). The Lake Superior HMI model was the most predictive of the HMI models (adjusted  $R^2 = 0.66$ ), and the Lake Huron model was the least predictive (adjusted  $R^2 = 0.37$ ).

When the lake-specific CSI models were combined to calculate predicted CSI for the 77 wetlands on Lakes Superior, Huron, Michigan, and Erie, there was an excellent correlation ( $r = 0.96$ ) between predicted and actual CSI value (Fig. 4A). The fit of the models for Lakes Michigan and Huron was impressive given the very large ranges of CSI values spanned by those Great Lakes. CSI was overpredicted for two wetlands on northern Lake Michigan, Goose Bay and the Ford River Delta, but the calculated CSI values for other wetlands were quite close to the actual values.

Combining the lake-specific HMI models to calculate predicted HMI for the same 77 wetlands yielded a correlation that was lower ( $r = 0.82$ ) but still significant ( $P < 0.001$ ). The scatterplots for Lakes Erie, Huron, and Michigan showed that their HMI formulae were greatly affected by one or two sites within each of those Great Lakes (Fig. 4B), wetlands which had an unusually high cover of the taxa included in the HMI models. The Lake Huron HMI model was greatly affected by the Squaw Bay wetland (HMI = 38, the highest value for Lake Huron), which had 4.0% PONA4 cover. PONA4 covered only 0.2–0.3% of three other Lake Huron wetlands, and was absent from eight wetlands. On Lake

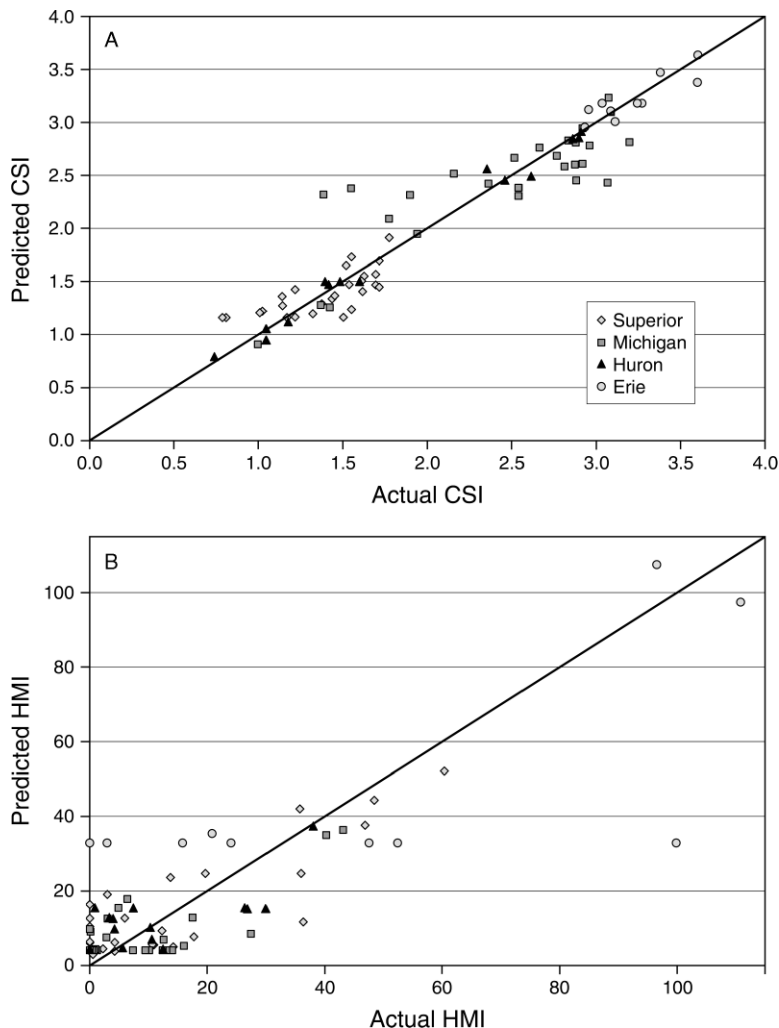


FIG. 4. Predicted vs. actual values based on output of lake-specific multi-taxa formulae (Table 5) for (A) cumulative stress index (CSI) and (B) hydrologic modification index (HMI).

Michigan, the two wetlands with the highest HMI values also had the greatest cover of the two species that were incorporated into the HMI model for Lake Michigan: CAVU2 cover was greatest on the Black River wetland (HMI = 40 m/ha) and POAMS cover was greatest on the Arcadia Lake wetland (HMI = 43 m/ha). On Lake Erie, the one-species HMI model distinguished the Hickory Island (HMI = 107 m/ha) and Winous Point (HMI = 97 m/ha) wetlands because they had the greatest POCO14 cover, but the other eight Lake Erie wetlands had predicted values at or close to the formula's intercept value of 33 because they were largely devoid of POCO14.

DISCUSSION

Using individual plant species to indicate environmental condition is a goal that ecologists have sought for decades. In 1950, Eville Gorham (1950) wrote, "The question of how far different organisms may 'indicate'

environmental conditions is one of great interest to ecologists, although the fact that so many of the organic and environmental factors concerned may vary independently suggests that close correlations of species to single habitat factors will be rather rare." More recently, environmental managers have promoted development of biotic indicators of anthropogenic disturbance, particularly for those anthropogenic disturbances over which they have some regulatory authority (National Research Council 2000, H. John Heinz III Center for Science, Economics and the Environment 2002, Niemi et al. 2004). Despite this long-standing and widespread interest, authoritative sources describing plant environmental responses are lacking. Horticultural plant species are categorized according to "hardiness zones," the coldest temperature zones in which they normally thrive (Cathey 1990), and the U.S. Department of Agriculture (see footnote 10) has begun to summarize "growth requirements" for some species in its Plants Database,



PLATE 1. Field assistant Randy Clark observes cover of American lotus (*Nelumbo lutea*), one of 30 Lake Erie taxa considered for effects of anthropogenic disturbance. Photo credit: L. Vaccaro.

but individual scientific studies are still the major source of information about plant responses to disturbance.

Evaluating species individually, rather than as plant community constituents, revealed the importance of taxa that are often overlooked in deference to more iconic wetland plants. Two examples are *Campanula aparinoides* (CAAP2) and *Cicuta bulbifera* (CIBU), which were incorporated into the Lake Michigan and Lake Superior CSI models, respectively. Both are subcanopy species that are often overlooked because they are so diminutive, yet they were two of the most frequently occurring species in our study, found in more than half of the 90 wetlands studied. Neither species was a dominant plant (Frieswyk et al. 2007) nor an indicator of soil type (Johnston et al. 2007), but both had utility as indicators of anthropogenic stress.

Evaluating individual species allows comparisons with experimental studies of species habitat preferences and competitive abilities. For example, two stress-promoted taxa, *Phalaris arundinacea* (PHAR3) and *Typha* × *glaucifera* (TYGL), had competitive effect values of 89% and 86% in an experimental study by Gaudet and Keddy (1995), whereas *Schoenoplectus tabernamontani* (SCTA2), a structure-intolerant species in the Lake Huron HMI

model, had a competitive effect value of only 59%. Such comparisons aid interpretation of field-observed relationships.

#### *Taxa incorporated into basin-wide CSI models*

We had few prior expectations of which taxa would be suitable indicators. We expected, and found, that the cover of invasive *Typha* (TYinv), *Phragmites australis* (PHAU7), and PHAR3 increased with increasing stress. Paradoxically, another common invasive, *Lythrum salicaria* (LYSA2), did not respond independently to CSI or HMI despite its dominance of the seed bank (Johnson 2003, Frieswyk and Zedler 2006) and reports that it increased with disturbance in Great Lakes coastal wetlands (Herrick and Wolf 2005, Stanley et al. 2005). We also expected that the cover of *Carex* species would decrease in response to land use intensification (Galatowitsch et al. 2000), grazing (Middleton 2002), sedimentation (Werner and Zedler 2002), nutrient inputs (Woo and Zedler 2002), and invasion by TYinv and PHAR3 (Wilcox et al. 1985, Kercher et al. 2004). Four of the five *Carex* species that were incorporated into the final models did decrease with increasing CSI, but *C. lacustris* (CALA16) unexpectedly increased with increas-

ing CSI on Lake Superior. Furthermore, *C. stricta* (CAST8) and *C. vulpinoidea* (CAVU2) increased with increasing HMI in lake-specific models, which was unexpected. In retrospect, the incorporation of lemnids (*Spirodela polyrrhiza* [SPPO], *Lemna minor* [LEMI3]) in the models made sense given other wetland studies (Galatowitsch et al. 2000, King et al. 2004, Lougheed et al. 2007), but we didn't anticipate this relationship because we thought that the rough waters commonly found in Great Lakes coastal wetlands would preclude free-floating plants. Many species incorporated into the final models were unanticipated because they were not dominants in wetland plant communities, and we had to search the literature to find corroboration for their inclusion.

*Carex lasiocarpa* (CALAA) was the species with the greatest independent effect of CSI basin-wide, and it also exhibited significant independent effects with CSI on Lakes Michigan and Huron (Fig. 1, Table 3). CALAA occurred in 46% of all wetlands and 18.5% of all quadrats sampled. CALAA is an indicator species for organic soils in the Great Lakes region (Johnston et al. 2007), and often forms floating mats (Flora of North America Editorial Committee 1993, van Diggelen et al. 1996). In our study, CALAA usually occurred in poor fens classified as protected wetlands (significant independent effect of geomorphology, Fig. 1), but it can grow in a variety of wetland types (Anderson et al. 1996, Thormann and Bayley 1997, Dwire et al. 2004). There is mixed evidence about the effect on CALAA productivity of nitrogen fertilization (Aerts et al. 1992, 1995) and water levels (Sala and Nowak 1997, Thormann et al. 1998, Steed et al. 2002). Galatowitsch and coworkers (2000) reported a decline in CALAA abundance with site impacts and landscape disturbance in a study of 40 wet meadows in southwest Minnesota, and CALAA was absent from restored wetlands in northern Iowa despite being frequently found in natural prairie wetlands within the region (Galatowitsch and van der Valk 1996).

*Carex stricta* (CAST8) was one of the most common sedges within the Great Lakes coastal wetlands sampled, occurring in 53% of all wetlands and 11.8% of all quadrats. CAST8 builds tussocks of roots, litter, and decomposed organic matter that support the growth of other species, thereby increasing plant diversity (Crain and Bertness 2005, Peach and Zedler 2006). Our previous analysis showed that tussock height, which averaged 18.8 cm for quadrats containing CAST8, was second only to water depth in explaining species-environment interactions in Great Lakes coastal wetlands (Johnston et al. 2007). CAST8 is impacted by cattle grazing (Costello 1936, Middleton 2002), sedimentation by stormwater runoff (Werner and Zedler 2002), and invasion by PHAR3 (Kercher et al. 2004).

Less is known about the effect of disturbance on the other two *Carex* species in the basin-wide CSI model, *C. aquatilis* (CAAQ) and *C. utriculata* (CAUT). In montane riparian meadows, the two species dominated

the wettest zone, which had the highest total biomass and lowest species richness along a gradient from wet to dry (Dwire et al. 2004). Both species have well-developed aerenchyma (Fagerstedt 1992), which allows them to grow in deeper water than many other sedge species (Appendix A). CAUT is an indicator of silt soils and riverine marshes, but CAAQ was not an indicator of any particular soil or geomorphic type (Bayley and Mewhort 2004; Johnston et al. 2007). CAAQ has been reported to be phosphorus limited (Pringle and Van Ryswyk 1965, Auclair et al. 1976).

*Myrica gale* (MYGA) occurred in 25 wetlands on all of the Great Lakes except Lake Erie. Although it frequently grows as a dominant species (Frieswyk et al. 2007), experimental removal of MYGA resulted in no evidence for competitive release of associated species (Keddy 1989). Grown experimentally at water table depths from 3 to 79 cm, MYGA produced maximum biomass at water table depths of 10–35 cm, and total biomass was substantially greater when grown on peat rather than sand (Schwintzer and Lancelle 1983). MYGA is an indicator species of organic soil in the Great Lakes (Johnston et al. 2007).

The increase in *Urtica dioica* (URDI) and TYinv with increasing stress in the basin-wide and Lake Michigan CSI models is consistent with their known responses to disturbance. URDI is a weed (Uva et al. 1997) with a *C* value of 1 (Andreas and Lichvar 1995, Bernthal 2003), and its growth is stimulated by nitrogen additions (Rosnitschek-Schimmel 1982). The invasive TYGL has displaced native *Typha* throughout the Great Lakes (Chow-Fraser et al. 1998, Frieswyk and Zedler 2007). TYGL has high growth and photosynthetic rates (Farnsworth and Meyerson 2003) and short rhizome lengths (Woo and Zedler 2002) that allow it to form dense, monotypic stands. TYGL is highly competitive under fluctuating water levels (Smith 1987, Waters and Shay 1992, Galatowitsch et al. 1999), in part due to its floating mat formation (Hogg and Wein 1988), but its expansion has been linked to water-level stabilization in several studies (Shay et al. 1999, Boers et al. 2007, Wilcox et al. 2007). *Typha* invasion is promoted by excess nutrients (Woo and Zedler 2002), and the relative cover of invasive *Typha* in Great Lakes coastal wetlands was positively related to watershed agricultural intensity (Vaccaro 2005; Brazner et al., *in press*).

#### *Taxa incorporated into the basin-wide HMI model*

PHAU7 was especially prevalent in diked wetlands at the western end of Lake Erie. PHAU7 has both native and nonnative genotypes that differ in their aggressiveness (Galatowitsch et al. 1999, Saltonstall 2002). Its recent expansion in Great Lakes coastal wetlands has been attributed to the spread of the invasive genotype and colonization of lake bottom sediments exposed by prolonged low lake levels that began in late 1999 (Pengra et al. 2007; Tulbure et al., *in press*). Linear anthropogenic habitats provide corridors that accelerate PHAU7

expansion (McNabb and Batterson 1991, Maheu-Giroux and de Blois 2007).

Like PHAU7, PHAR3 is an invasive with aggressive Eurasian strains (Lavergne and Molofsky 2007). PHAR3 appears to be the plant that is most responsible for loss in quality of southern Wisconsin wetlands (Zedler and Potter, *in press*). PHAR3 benefits from nutrients (Mason and Miltimore 1970, Dean and Clark 1972, Kline and Broersma 1983, Maurer and Zedler 2002), sedimentation (Werner and Zedler 2002), and hydrological disturbance (Kellogg et al. 2003, Maurer et al. 2003, Miller and Zedler 2003). Kercher and Zedler (2004) found that continuous flooding, high nutrient inputs and addition of nutrient-rich sediment interact to accelerate PHAR3 invasion. Using remote sensing, Bernthal and Willis (2004) found a correlation between the fraction of wetlands dominated by PHAR3 and the fraction of agricultural land use in the watershed.

Two free-floating species, LEMI3 and SPPO, increased in abundance with increasing HMI. LEMI3 was very common, occurring in 44% of all wetlands and 14.5% of all quadrats, but it achieved greatest cover when protected from wind by dikes and other linear features. Lemnids replace native vegetation in stormwater and nutrient-enriched wetlands (Galatowitsch et al. 2000, King et al. 2004, Lougheed et al. 2007), and dominance by free-floating plants has been suggested as an alternative stable state, in which reduction of aquatic ecosystem resilience causes abrupt and persistent changes in biological structure (Scheffer et al. 2003).

#### *Taxa incorporated into lake-specific models*

The three species that increased with increasing landscape stress in the Lake Superior CSI model, CALA16, *Utricularia macrorhiza* (UTMA), and CIBU, were not intuitive. None was weedy or invasive, and all had Wisconsin-assigned *C* values of 6 or greater (Bernthal 2003). UTMA is a carnivorous plant due to nutrient limitations in its environment, so it seems an unlikely candidate as a stress-promoted species. The inclusion of these three species in the CSI model makes sense, however, within the context of the disturbance regime (or lack thereof) on Lake Superior. Lake Superior has the least watershed development of any of the Great Lakes, and its maximum CSI value (1.8) was much lower than the minimum CSI values on Lakes Ontario (2.5) or Erie (2.9). Therefore, a stress-promoted species on Lake Superior would indicate high quality conditions in wetlands of the lower Great Lakes. Other studies have shown that the three species in the Lake Superior CSI model respond to stress: UTMA growth has been shown to respond to nutrient additions (Knight and Frost 1991, Ellison 2006, Kibriya and Jones 2007), and both CALA16 and CIBU were related to disturbance in a study of 40 Minnesota wet meadows (Galatowitsch et al. 2000).

Inclusion of CAST8 in the Lake Superior HMI model as a species promoted by within-wetland structures was

also initially counterintuitive because CAST8 is negatively impacted by stormwater runoff (Werner and Zedler 2002), but other studies corroborated an increase in CAST8 abundance associated with diked wetlands (Jorgensen and Nauman 1994, Ellison and Bedford 1995, Stanley et al. 2005). The tussock growth habit of CAST8 allows it to tolerate a broad range of seasonal drying and flooding conditions (Costello 1936, Sjöberg and Danell 1983, Wilcox et al. 1985), and water fluctuation at some time during the growing season benefits CAST8 growth (Budelsky and Galatowitsch 2004). Both CAST8 and CIBU increased in abundance when flooded by an adjacent power plant cooling pond (Ellison and Bedford 1995). The third species included in the Lake Superior HMI model, *Salix pedicellaris* (SAPE2), usually grows in bogs (Argus 1964) and is an indicator of organic soils (Johnston et al. 2007), where water levels would be expected to be relatively stable. In their study of commercial cranberry operations in northern Wisconsin, Jorgensen and Nauman (1994) found that CAST8 increased and SAPE2 decreased as a result of disturbance caused by roads or dikes.

Relatively little is known about the ecology of CAAP2, which was included in the Lake Michigan CSI model. CAAP2 is very common in fens and wet meadows (Auclair et al. 1976, Schwintzer 1978, Mensing et al. 1998, Nekola 2004). The importance value of CAAP2 was about twice as high in six reference wetlands as it was in six disturbed wet meadows in Saginaw Bay (Stanley et al. 2005).

The development of the CSI multi-taxa model for Lake Huron was complicated by below-normal lake levels that exposed lake bottom sediments to new colonization, an effect exacerbated by Saginaw Bay's shallow bathymetry (data available online).<sup>11</sup> For example, the presence of *Populus deltoides* (PODE3) seedlings in Saginaw Bay is probably due to germination by windblown seeds on the bare mineral substrate that was exposed during below-average lake levels prior to sampling in 2003. PODE3 is known to require bare, moist microsites for germination, but it can grow under a range of nutrient conditions (Braatne et al. 1996), so its presence in the Saginaw Bay wetlands is probably not due to landscape stress but rather to the germination opportunity afforded by exposure of Saginaw Bay sediments. Similarly, *Juncus tenuis* (JUTE) is a weed that grows in disturbed, moist soils (Flora of North America Editorial Committee 1993, Uva et al. 1997), and would not be expected to persist when lake levels return to normal or above-normal conditions. A modified CSI formula for Lake Huron that excluded PODE3 and JUTE remained highly significant (adjusted  $R^2 = 0.78$ ,  $F_{4,9} = 12.5$ ,  $P = 0.001$ ).

The increase in *Pontederia cordata* (POCO14) cover with increasing HMI on Lake Erie initially seemed

<sup>11</sup> <http://www.lre.usace.army.mil/greatlakes/hh/greatlakeswaterlevels/>

inconsistent with the ecology of the species, which has a *C* value of 7 (Andreas and Lichvar 1995), is intolerant of turbid, nutrient-rich conditions (Lougheed et al. 2001), and has been reported to decline in abundance with increasing anthropogenic stress on Lake Erie (Stuckey 1989). The three Lake Erie wetlands that contained POCO14 are all diked, and have historically had abundant POCO14 stands (Lowden 1969, Sherman et al. 1996). Thus, rather than causing stress, the dikes used to manage water levels in these three wetlands appear to be protecting the POCO14 from external stresses from Lake Erie, which is their intent (Sherman et al. 1996). POCO14 was absent, however, from the highly diked Little Lake Creek wetland (HMI = 100 m/ha) on the Michigan shore of Lake Erie.

#### *Biogeographical differences*

The set of plants that exhibited significant independent effects with CSI or HMI generally differed by Great Lake. In part, this was due to differences in the biogeography of the species, which were never uniformly distributed across the entire Great Lakes even prior to European settlement of the region. As a result, the set of plants sufficiently common to include in the analysis differed by Great Lake in taxa and total number (Appendix A).

In some cases, differences among the Great Lakes in the independent responses of plant taxa to stress may be due to the geographic distribution of stressors, rather than the geographic distribution of plants. For example, although CALAA occurred in 73% of Lake Superior wetlands and was a CSI-sensitive species on Lakes Michigan and Huron, it was not a CSI-sensitive species on Lake Superior, where anthropogenic stress in coastal wetland watersheds was minimal. Similarly, on Lake Ontario, invasive *Typha* was ubiquitous (occurring in 12 of 13 wetlands) and dominant (average cover of 30% where it occurred), yet it was not a CSI-sensitive species on that lake. In both cases, the abundance of these taxa may indicate a threshold effect, where the level of watershed stress was so uniformly high (Lake Ontario) or uniformly low (Lake Superior) that the taxa were unresponsive. Such non-linear responses have been previously documented in stream and wetland biota (King et al. 2005, Lougheed et al. 2007).

Recognition that individual species can behave differently as a function of biogeography is a concept that is built into commonly used ranking systems. For example, the states of Minnesota, Wisconsin, Illinois, Indiana, Michigan, and Ohio have all developed separate *C* value lists which assign similar but not identical *C* values to plant taxa. Our research on the FQI in the LMF ecoprovince showed that mean *C* values were higher when computed using Wisconsin *C* values than they were using Michigan *C* values, but we could not determine if this difference was biologically meaningful or due merely to subjective differences (Bourdaghs et al. 2006). Similarly, wetland affinity classes for

plant taxa in the *National List of Plant Species that Occur in Wetlands* differ slightly between the U.S. Fish and Wildlife Service's Region 1, which includes Lakes Ontario and Erie, and Region 3, which includes the other three Great Lakes (Reed 1988).

#### *Utility of models*

Ecological indicators should capture the complexities of the ecosystem yet remain simple enough to be easily and routinely monitored (Jackson et al. 2000, Dale and Beyeler 2001). We believe that the models presented here are scientifically rigorous, yet require less implementation effort than the currently used FQI, because users need only distinguish the few taxa that are in the models rather than all plants present in a wetland. Training could thus focus on species utilized in the models.

Despite their reliability as indicators of environmental condition, sedges are notoriously difficult to identify to species. The inflorescences utilized by taxonomic keys are often difficult to find, and may not be at a suitable stage of development when the wetland is visited by field monitoring personnel. However, several vegetative characters can be useful in distinguishing sedge species, especially when considered in concert: leaf color (blue-green, green, yellow-green), leaf width (sometimes shape), basal leaf sheath type (see Fassett 1976: Fig. 9), and whether the plants grow in dense tufts (i.e., are caespitose; Bernard 1990). Distinctive vegetative characters of the six *Carex* species incorporated in our models are listed in Appendix B.

Another desirable characteristic of environmental indicators is known temporal variability across years (Jackson et al. 2000). The models developed here are robust indicators based on conditions that occurred during the sampling period (2001–2003), but their temporal variability is not known. Given that lake levels in Lakes Michigan and Huron were near historic low levels during this time period (see footnote 11), the vegetation present in those lakes may reflect drier conditions than normal, and the inclusion of PODE3 and JUTE in the Lake Huron CSI model was likely influenced by the low lake levels. However, most of the taxa included in the models are perennials, and many have extensive rhizome systems and other growth forms (e.g., tussocks, floating mats) that would allow them to persist in an area despite water level fluctuations. This perennial duration may be a disadvantage if it imparts inertia (i.e., persistence of a plant population long after a change in stressor regime has occurred [Milchunas and Lauenroth 1995]).

The benefit of the models presented here is their discriminatory ability to separate extraneous variability from true signal of environmental degradation. By incorporating the technique of hierarchical partitioning into model development, we excluded taxa that are unresponsive to anthropogenic stress. We believe that this approach is worthwhile for any ecosystem in which

multiple environmental factors influence the biota present.

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#### APPENDIX A

Plant taxa analyzed, by Great Lake, and average water depth of plots occupied by each taxon (*Ecological Archives* A018-032-A1).

#### APPENDIX B

Distinctive characters of sedges incorporated into multi-taxa models (*Ecological Archives* A018-032-A2).