

Responsiveness of Great Lakes Wetland Indicators to Human Disturbances at Multiple Spatial Scales: A Multi-Assemblage Assessment

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ABSTRACT. *Developing indicators of ecosystem condition is a priority in the Great Lakes, but little is known about appropriate spatial scales to characterize disturbance or response for most indicators. We surveyed birds, fish, amphibians, aquatic macroinvertebrates, wetland vegetation, and diatoms at 276 coastal wetland locations throughout the U.S. Great Lakes coastal region during 2002–2004. We assessed the responsiveness of 66 candidate indicators to human disturbance (agriculture, urban development, and point source contaminants) characterized at multiple spatial scales (100, 500, 1,000, and 5,000 m buffers and whole watersheds) using classification and regression tree analysis (CART). Non-stressor covariables (lake, ecosection, watershed, and wetland area) accounted for a greater proportion of variance than disturbance variables. Row-crop agriculture and urban development, especially at*

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larger spatial scales, were about equally influential and were more explanatory than a contaminant stress index (CSI). The CSI was an important predictor for diatom indicators only. Stephanodiscoid diatoms and nest-guarding fish were identified as two of the most promising indicators of row-crop agriculture, while *Ambloplites rupestris* (fish) and *Aeshna* (dragonflies) were two of the strongest indicators of urban development. Across all groups of taxa and spatial scales, fish indicators were most responsive to the combined influence of row-crop and urban development. Our results suggest it will be critical to account for the influence of potentially important non-stressor covariables before assessing the strength of indicator responses to disturbance. Moreover, identifying the appropriate scale to characterize disturbance will be necessary for many indicators, especially when urban development is the primary disturbance.

INDEX WORDS: Coastal wetlands, classification and regression trees, community, Great Lakes, multi-assemblage.

INTRODUCTION

One of the key steps in the development of ecological indicators is the assessment of their response to human disturbance. An important and difficult aspect of assessing indicator response is determining the spatial scale to characterize human disturbance. Disturbance must be measured at the appropriate spatial and temporal scales to achieve an accurate picture of the stressor-response relationship (e.g., Richards and Johnson 1998, Mensing *et al.* 1998, Wang *et al.* 2003a). While there have been exceptions (e.g., Roth *et al.* 1996, Strayer *et al.* 2003), assessment of indicator response has generally been conducted with disturbance characterized at a single spatial scale, usually driven by convenience of available data sources, logistic constraints, or particular interests of researchers or agencies (e.g., Steedman 1988, Reeves *et al.* 1993, O'Connor *et al.* 1996, Knutson *et al.* 1999, Walser and Bart 1999, Schleiger 2000, Sharma and Hilborn 2000).

Local habitat features and physical setting have been considered the template for organizing biological communities by some ecologists for many years (Southwood 1977) and much effort has been focused on how local habitat structure influences ecological dynamics and organizes biological communities (e.g., Gorman and Karr 1978, Eadie and Keast 1984, Minshall 1988, Benson and Magnuson 1992, Townsend and Hildrew 1994). There has also been considerable effort, particularly for stream and other aquatic ecosystems, to understand how processes functioning at watershed and broader scales influence ecosystem structure and function (Johnston *et al.* 1990, Schlosser 1991, Fisher 1994, Poff and Allan 1995, Stevenson 1997). These contrasting views have led to a dichotomy where disturbance characterization has often been at a site-specific scale when habitat alteration has been

of primary interest, or at a watershed scale when the focus has been on the influence of land use change. However, it is clear that aquatic ecosystems are hierarchically organized (Frissell *et al.* 1986, Maxwell *et al.* 1995, Poff 1997), that species respond to their environments at multiple spatial scales (e.g., Kotliar and Wiens 1990, Roland and Taylor 1997, Cushman and McGarigal 2002, Holland *et al.* 2004, Stoffels *et al.* 2005), and that the location and intensity of the stress in a species' environment plays a critical role in defining the observed response (Roland and Taylor 1997, Sponseller *et al.* 2001, Townsend *et al.* 2003, King *et al.* 2005).

Recognition of the hierarchical nature of organization and scale dependencies in streams and other aquatic ecosystems has led to attempts to assess the relative importance of disturbances characterized at different spatial scales to aquatic biota. Many of these studies examined the role of riparian buffer zones and the influence of disturbance in those zones relative to processes or disturbances characterized at the watershed scale (e.g., Barton *et al.* 1985, Jones *et al.* 1996, Lee *et al.* 2001). Others focused more specifically on determining the scale at which a particular disturbance seemed to be having its greatest impact on a few key components of the ecosystem, or on biological integrity (e.g., Sponseller *et al.* 2001, DeLuca *et al.* 2004). Depending on the types of organisms examined, results from these studies have varied from finding that local stresses were most important (e.g., Wang and Lyons 2003, King *et al.* in press), to finding that cumulative disturbance across a landscape appears to play a more important role (e.g., Allan *et al.* 1997).

The disturbance scale to which an indicator responds appears to depend on several factors, including the type of disturbance. Because land use disturbances are amenable to characterization

across a range of scales and have been a primary focus of efforts to understand the relative role of local and regional processes, these disturbance types are compared most often in multi-scale studies. Some of these studies have focused on the effects of forest fragmentation (e.g., Barton *et al.* 1985, Roland and Taylor 1997, Brazner *et al.* 2005, Holland *et al.* 2005b), but more have focused on agricultural practices and urbanization. The evidence is far from unequivocal (e.g., see Lammert and Allan 1999, Sponseller *et al.* 2001, Snyder *et al.* 2003, Townsend *et al.* 2003), but it appears that agricultural land uses, such as row-crops and pastures, often exert their primary influence at the whole watershed scale (Roth *et al.* 1996, Wang *et al.* 1997, Lyons *et al.* 2000, Wang and Lyons 2003a), while disturbance associated with urbanization may be more important immediately adjacent to a watercourse (Allen and O'Connor 2000, Wang *et al.* 2001, Wang *et al.* 2003b, DeLuca *et al.* 2004).

The relative importance of the disturbance scales to which indicators respond also seems to depend on the type of indicator (e.g., Mensing *et al.* 1998, Lammert and Allan 1999, Strayer *et al.* 2003). There is considerable evidence that nutrient and water quality related variables are most influenced by disturbance characterized at the watershed or regional scales (e.g., Richards *et al.* 1996, Allan *et al.* 1997, Herlihy *et al.* 1998), although the relative importance of these scales can vary with the particular water quality variable being measured (e.g., Johnson *et al.* 1997, King *et al.* 2005). Among biota, birds and fish seem more likely to respond to broad-scale disturbance (Allen *et al.* 1999, Strayer *et al.* 2003), while diatoms, wetland vegetation, and invertebrates often respond to more local features (Richards *et al.* 1997, Allen *et al.* 1999, Fitzpatrick *et al.* 2001, Johnson *et al.* 2004, King *et al.* 2004, Galatowitsch *et al.* 1999b) and amphibians to multiple scales (Lehtinen *et al.* 1999). Differences in the way species respond to their environments are likely controlled by relationships between mobility and body size (Roland and Taylor 1997, Townsend *et al.* 2003, Holland *et al.* 2005a). Larger organisms tend to have larger home ranges and therefore may experience the environment across larger spatial scales (Wiens and Milne 1989, Holling 1992, O'Neill *et al.* 1997).

Most evidence about scale-dependent responses to disturbance in aquatic ecosystems comes from stream and lake studies, but there has been some relevant work in wetlands. For example, several studies have examined the importance of riparian

buffers adjacent to wetlands (e.g., Castelle *et al.* 1994, Burke and Gibbons 1995, Haig *et al.* 1998, Detenbeck *et al.* 2002, Semlitsch and Bodie 2003) and the relative roles of riparian and landscape features (Fairbairn and Dinsmore 2001, Riffel *et al.* 2003). Studies suggest that both local and larger scale disturbances can influence a variety of wetland biota in important ways (Findlay and Houlihan 1997, Lehtinen *et al.* 1999, Findlay and Bourdages 2000, Pope *et al.* 2000), but little is known about the importance of particular scales of influence other than to say that land use disturbances as far as 5 km away from a wetland can be significant and that response varies by intensity and type of disturbance, as well as by ecosystem and organism type (Galatowitsch *et al.* 1999a, Whited *et al.* 2000). Systematic comparisons among watershed and local disturbance influences have rarely been completed for wetlands (Mensing *et al.* 1998, DeLuca *et al.* 2004), and better understanding of their relative roles awaits further study.

Developing indicators of ecosystem condition has only recently been made a priority in the Great Lakes (Environment Canada and U.S. EPA 2003) and for most indicators little is known about appropriate spatial scales for either disturbances or responses (Niemi *et al.* 2004, Niemi and McDonald 2004). However, there has been a concerted effort recently to develop and test indicators for Great Lakes coastal wetlands (Wilcox *et al.* 2002, Albert and Minc 2004, Uzarski *et al.* 2004, Lawson 2004). Earlier (Brazner *et al.* 2007), as part of a larger project to develop indicators of ecological condition for coastal ecosystems in the Great Lakes (Niemi *et al.* 2004, Danz *et al.* 2005), we examined the relative importance of geographic, geomorphic, and human disturbance on indicators from a wide range of wetland taxa (diatoms, wetland vegetation, macroinvertebrates, amphibians, fish, birds). As a follow-up to that study, we examine the scales of disturbance to which ecological indicators for coastal wetlands respond. Here, spatial scale refers to the geographic area or extent within which disturbance was characterized rather than grain, which is a separate aspect of spatial scale characterization (Holland *et al.* 2005a). Our overall objective was to assess the responsiveness of candidate indicators to three of the primary land use disturbances (agriculture, urbanization, and point source contaminants) across the Great Lakes basin. Specifically, our goals were to; 1) determine which disturbance type had the most influence on indicators and assemblages after accounting for variability associated with

other non-stressor covariables, 2) provide an approach for determining the spatial scale where the disturbance-response relationship was maximized for particular indicators, biotic assemblages, and disturbance types, and 3) identify the candidate indicators with the best potential as indicators of particular types of human disturbance in coastal wetlands across the Great Lakes.

Although we expected considerable variation among indicators and assemblages (Strayer *et al.* 2003) based on studies conducted in streams, we hypothesized that most indicators would be more responsive to agricultural land use at the watershed scale, and urbanization at more local scales (e.g., Roth *et al.* 1996, Wang *et al.* 2003b, Wang and Lyons 2003, Townsend *et al.* 2003). There is little precedence (see Strayer *et al.* 2003) for developing hypotheses related to scales for contaminant indicators, but the point-source nature of this disturbance type suggests that local effects might be most important. We also expected there would be similarities in the scale of response related to body size and mobility, with larger-bodied, mobile taxa most responsive to disturbance characterized at broader scales (e.g., Roland and Taylor 1997, Allen *et al.* 1999, Johnson *et al.* 2004, Holland *et al.* 2005a). However, diatoms may be an exception to the mobility-body size relationship because, although small, they respond directly to water chemistry which is generally determined by large-scale upland characteristics such as soil type and agriculture. Therefore, diatom indicators may be most responsive to disturbance characterized within the larger rather than smaller buffers. Finally, we expected that in some cases factors such as watershed area or geographic region would have at least as great an influence on indicator response as land use disturbance (Strayer *et al.* 2003, King *et al.* 2005, Brazner *et al.* 2007).

METHODS

Data Sources, Survey Methods, and Indicator Selection Criteria

The data sources, survey methods, and indicator selection criteria used for this paper were described by Brazner *et al.* 2007. Briefly, the data were collected as part of a basin-wide study to develop indicators using a single integrated conceptual framework (Niemi *et al.* 2004, Danz *et al.* 2005, Johnston *et al.* in press). Abundance information was collected on bird, fish, amphibian, aquatic

macroinvertebrate, wetland vegetation, and diatom assemblages using standard methodologies at 276 coastal wetland locations along U.S. shorelines throughout each of the Great Lakes.

Benthic and sedimented diatoms were sampled from 65 wetlands on natural substrates from 0.5 to 3 m depth and processed as described by Reavie *et al.* (2006). Surface sediments were sampled using a push corer and core tube or with a Ponar sampler in unconsolidated bottom substrates. In rocky areas, algal material was scraped from the surface of rocks and pebbles and collected in vials as epilithic samples. Vegetation was sampled in 90 wetlands from 1 m² quadrats distributed along randomly placed transects within emergent and wet meadow areas (Bourdagh *et al.* in press). Transect length and target number of sample plots were determined in proportion to the size of the wetland to be sampled (20 plots/60 ha, minimum transect length = 40 m, minimum plots/site = 8, average plots/site = 21) and plants were identified to the lowest taxonomic division possible. Cover was estimated visually for each taxon using modified Braun-Blanquet cover classes. Macroinvertebrates were sampled in 75 wetlands from the three dominant habitats as determined from shoreline and nearshore substrate type, extent and composition of riparian and aquatic vegetation, and anthropogenic impacts. Samples were collected along two to six transects set perpendicular to depth contours, depending on the size of the wetland. Samples were collected with D-framed nets (250 μ m mesh) at the midpoint of two depth zones along each transect, the emergent zone (defined as depths less than 50 cm) and the submergent zone (depths 50–100 cm). Bird surveys were conducted by trained observers (Hanowski and Niemi 1995) at 223 wetlands during June and early July in 2000, 2001, and 2002 using the Marsh Monitoring Workshop wetland breeding bird survey protocol (Ribic *et al.* 1999, and see www.bsc-eoc.org/mmp-main.html). We conducted amphibian calling surveys at most of the same points (n = 211) sampled for birds, following guidelines outlined by the Marsh Monitoring Program (Weeber and Valianatos 2000, and see www.bsc-eoc.org/mmp-main.html). Fish were sampled with both boat-mounted electrofishing gear (electro-fish) and fyke-nets (fyke-fish) (Trebitz *et al.* 2007). The two methods were used by separate field crews that overlapped at 35 sites. Fyke-nets were fished at the same wetlands where macroinvertebrates were sampled and a few additional sites (n = 80), while electrofishing was completed at 58 sites. Although six

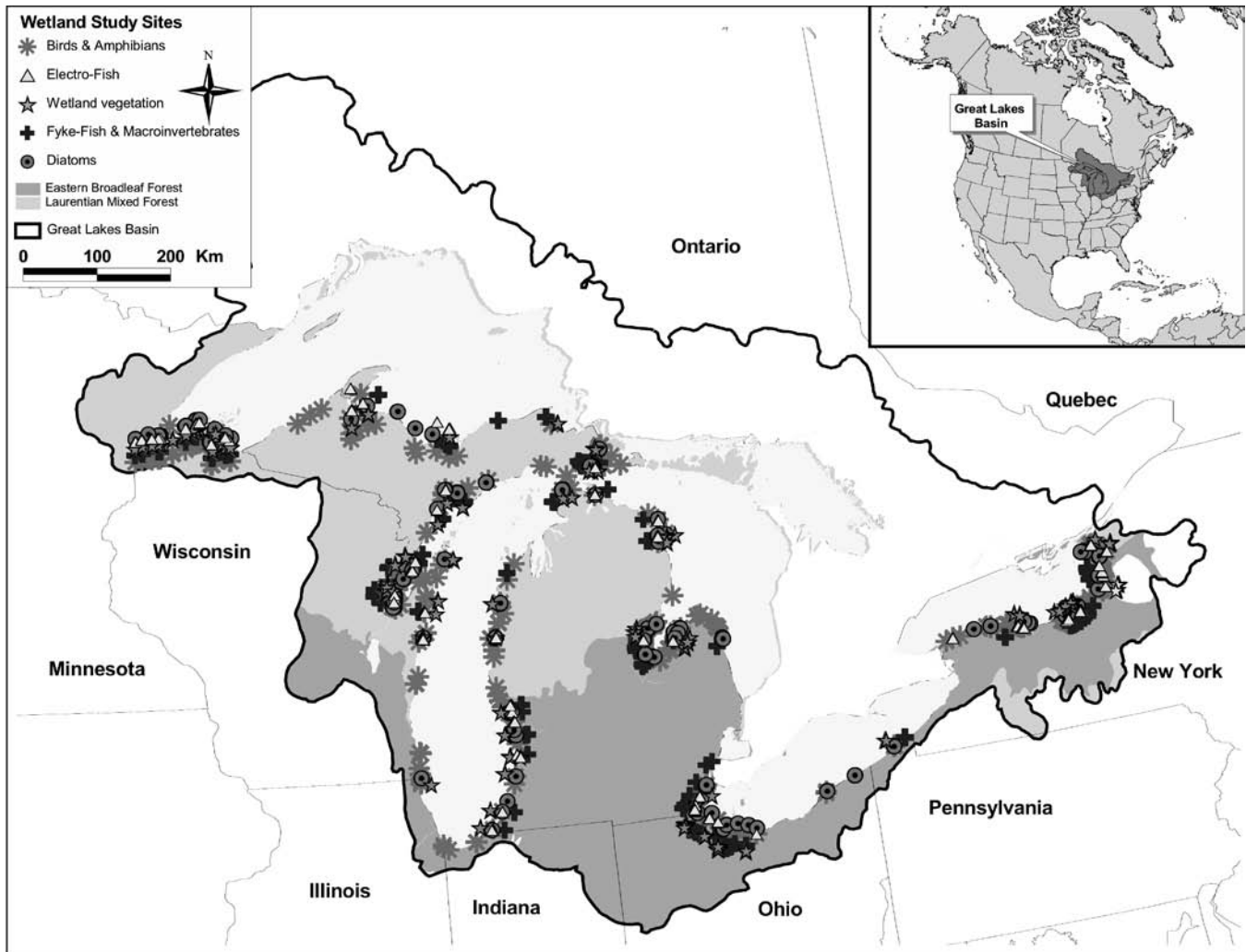


FIG. 1. Map of sampling locations in the Great Lakes for each of the assemblages (some sampling points have been moved slightly to reduce overlap and improve clarity).

ecosystem types were sampled as part of the larger project (Danz *et al.* 2005, Johnston *et al.* in press), for this paper we focus on responses within three wetland types (river-influenced, protected, and open-coastal). Sites were spread across the Great Lakes and approximately evenly distributed among the Laurentian Mixed Forest Ecoprovince in the northern lakes and the Eastern Broadleaf Forest Ecoprovince in the southern lakes (Fig. 1, Keys *et al.* 1995). Sites were selected using a stratified random design to span multiple human disturbance gradients (Danz *et al.* 2005).

Eight to ten candidate indicators for each assemblage were selected by appropriate lead co-authors (Table 1) based on an initial examination three to four times that number for most assemblages. The

initial list was reduced to the final candidates that we examine here by using criteria recommended in Hughes *et al.* (1998) and O'Connor *et al.* (2000). These included that indicators 1) were known or thought to be responsive to human disturbance, 2) represented ecologically important species or functions, 3) were sampled effectively (low intra-site variance), and 4) were of limited redundancy with other indicators. Similar measures of structural complexity (e.g., richness, abundance) and functional character (e.g., mobility, reproductive strategies) were included whenever possible. Data sets for fish captured with fyke-nets (fyke-fish) and fish captured from an electrofishing boat (electro-fish) were obtained by different field teams and kept separate for these analyses because previous analyses

TABLE 1. Classification and regression tree results for all indicators, including overall variance explained by the model (R^2) and the proportional reduction in error (partial r^2 equivalents - in parentheses) associated with each of the predictor variables. Predictor variables ordered by entry position in the tree and represent the most predictive variable at each node. Because the first four amphibian indicators were based on presence-absence data, results were derived from classification rather than regression trees. RC = proportion row-crop agriculture, DEV = proportion developed land, CSI = contaminant-stress index, subscripts indicate the spatial scale over which stressor variables were characterized, arrows indicate direction of relationship between indicator and predictor variables. Cases where predictor variables are repeated indicate that the variable was used at more than one split point in the tree. For lake subscripts, E = Erie, H = Huron, M = Michigan, O = Ontario, and S = Superior; for wetland type subscripts P = protected, R = riverine, C = open coastal; see text in methods for explanation of ecoregion subscripts).

Indicator	Overall R^2	Predictor Variables (partial r^2)
Diatoms (n = 65 wetlands)		
Shannon-Wiener Diversity (ln)	0.46	Lake _(O,H) (.14)↓; RC_5000(.19)↓; Lake _(E,M) (.06)↓; RC_100(.07)↑
% Motile	0.31	CSI_5000(.18)↑; RC_Watshed(.08)↑; DEV_Watshed(.05)↑
% Planktonic	0.21	RC_Watshed(.14)↑; Wet_Area(.07)↑
Lange-Bertalot Index	0.58	Ecoregion _(SCG,WSU,NGL,WUA,SLC,CTP) (.19)↑; CSI_5000(.12)↓; Wat_Area(.08)↓; DEV_5000(.09)↓; RC_5000(.10)↓
Trophic Diatom Index	0.53	Lake _(S,H,M,O) (.29)↓; Wat_Area(.16)↑; DEV_100(.08)↑
% Stephanodiscoids	0.50	RC_Watshed(.50)↑
% <i>Achnanthydium minutissimum</i> complex	0.40	DEV_Watshed(.13)↓; Lake _(E,M,S,O) (.13)↓; DEV_1000(.14)↑
% <i>Staurosira/Staurosirella/Pseudostaurosira</i>	0.40	DEV_500(.11)↓; Ecoregion _(EOL,CTP,SGL,SLC,WUA) (.11)↓; DEV_5000(.18)↑
% <i>Cocconeis</i>	0.23	Lake _(O) (.23)↑
% <i>Planothidium</i>	0.24	DEV_5000(.13)↑; Wet_Area(.11)↑
Wetland Vegetation (n = 90 wetlands)		
Species richness (number of taxa)	0.39	Ecoregion _(SCG,WSU,CTP,SGL,EOL,SLC) (.14)↓; DEV_5000(.10)↓; Wet_Area(.09)↑; DEV_100(.06)↑
% Invasive taxa	0.75	Lake _(O,E) (.44)↑; RC_Watshed(.17)↑; DEV_5000(.06)↑; Wat_Area(.08)↑
% Native taxa	0.51	RC_Watshed(.36)↓; Wat_Area(.09)↓; Wet_Area(.06)↓
% Wetland obligate taxa	0.29	Lake _(S,O) (.29)↑
% cover <i>Carex stricta</i>	0.62	DEV_Watshed(.20)↓; Dev_1000(.32)↑; Dev_100(.10)↓
% cover <i>Carex lasiocarpa</i>	0.49	RC_5000(.24)↓; Wet_Area(.15)↑; Dev_100(.11)↑
% cover <i>Sparganium eurycarpum</i>	0.47	Ecoregion _(SCG,WSU,NGL,SGL,CTP,EOL,SLC) (.20)↓; Wet_Area(.13)↓; Wet_Area(.09)↓; Wet_Area(.05)↑
% cover <i>Phragmites australis</i>	0.33	RC_5000(.33)↑
% cover <i>Typha angustifolia</i> and <i>Typha x glauca</i>	0.58	Lake _(O) (.24)↑; Wet_Area(.15)↑; Dev_5000(.10)↑; RC_1000(.10)↑

(Continued)

TABLE 1. Continued.

Indicator	Overall R ²	Predictor Variables (partial r ²)
Macroinvertebrates (n = 75 wetlands)		
% Burrowers	0.57	RC_Watshed(.15)↑; DEV_1000(.17)↓; Ecosession(SCG_NGL_THP_SLC)(.09)↑; Wat_Area(.10)↓; DEV_Watshed(.06)↑
% Clingers	0.44	Lake(s,o)(.16)↑; DEV_1000(.07)↑; DEV_500(.07)↑; Wat_Area(.05)↑; DEV_1000(.09)↓
% Predators	0.21	Wat_Area(.15)↑; RC_500(.06)↓
% Insect filter-gatherers	0.61	DEV_Watshed(.11)↓; Wat_Area(.08)↓; DEV_100(.07)↓; DEV_500(.06)↑; DEV_Watshed(.08)↓; Wat_Area(.08)↓; Ecosession(NGL_SSU_SLC)(.13)↑
Lowest taxonomic unit richness	0.43	Wet_Type(C)(.21)↓; Lake(E,M,H,S)(.13)↓; Wet_Area(.09)↑
% <i>Caenis</i> spp.	0.49	Wat_Area(.24)↓; Wet_Area(.13)↑; Ecosession(NGL_SSC_SSU)(.05)↓; Wat_Area(.07)↓
% <i>Coenagrion/Enallagma</i> spp.	0.28	Lake(M,H,O,E)(.14)↓; Wet_Area(.14)↓
% <i>Oecetis</i> spp.	0.39	Wet_Type(C)(.14)↑; RC_500(.08)↓; Lake(O,M,E)(.06)↑; Wet_Area(.11)↓
% <i>Proclleon/Callibaetis</i> spp.	0.16	DEV_100(.10)↓; Ecosession(THP_NGL_SSU_SLC_WSU)(.06)↑
% <i>Aeshna</i> spp.	0.49	DEV_Watshed(.16)↓; DEV_1000(.33)↑
Amphibians (n = 211 wetlands)		
Species richness	0.19	DEV_5000(.13)↓; Lake(M,H,O)(.06)↑
Species richness of tree frogs	0.43	Ecosession(EOL_CTP_SCG_SGL_NSU)(.29)↓; Lake(S,E,M)(.14)↓
Species richness of Ranids	0.35	Lake(O)(.22)↑; DEV_5000(.06)↓; Wet_Area(.07)↑
Species richness of early spring breeders	0.19	Ecosession(SSU_WSU_NSU_SGL_EOL)(.07)↓; Wet_Area(.07)↑; RC_1000(.05)↓
Presence-absence of <i>Bufo americanus</i>	0.13	Ecosession(SSU_SGL_THP_EOL_NSU_SLC)(.13)↓
Presence-absence of <i>Rana clamitans</i>	0.14	DEV_5000(.09)↓; Lake(O)(.05)↑
Presence-absence of <i>Hyla versicolor</i>	0.25	Lake(S,H,M,O)(.15)↑; Ecosession(SSU_WSU_NGL_THP_SLC_EOL)(.10)↑
Presence-absence of <i>Pseudacris crucifer</i>	0.42	Ecosession(EOL_CTP_SCG_SGL_NSU)(.18)↓; DEV_100(.06)↓; RC_1000(.09)↓; DEV_Watshed(.09)↓
Fish - electrofishing (n = 57 wetlands)		
Native species richness	0.43	Wat_Area(.14)↑; RC_500(.10)↓; DEV_500(.10)↑; DEV_100(.09)↓
% Large fish (> 200 mm average adult size)	0.70	Lake(S,H,M,O)(.52)↓; DEV_5000(.18)↑
% Nest-guarding spawners	0.58	RC_5000(.38)↓; DEV_Watshed(.12)↓; RC_1000(.08)↑
% Intolerant of turbidity	0.57	RC_Watshed(.15)↓; Wet_Area(.13)↑; Ecosession(THP_WSU_SLC_EOL)(.11)↓; Wet_Area(.18)↓
% Top carnivores as adults	0.55	RC_Watshed(.18)↓; RC_100(.15)↑; DEV_100(.17)↓; RC_Watshed(.05)↓
% <i>Lepomis macrochirus</i>	0.27	Wet_Area(.14)↓; Lake(H,O,M)(.07)↑; DEV_5000(.06)↓
% <i>Ameiurus nebulosus</i>	0.34	Ecosession(SCG_WSU_NGL_SLC_EOL_THP)(.18)↓; DEV_1000(.16)↑
% <i>Cyprinus carpio</i> and <i>Carassius auratus</i>	0.49	Lake(S,H,M,O)(.39)↓; RC_5000(.10)↑
% <i>Notemigonus crysoleucas</i>	0.58	Ecosession(SSU_SLC)(.42)↑; DEV_Watshed(.16)↑
% <i>Ambloplites rupestris</i>	0.58	RC_Watshed(.15)↓; DEV_5000(.10)↓; DEV_1000(.33)↑

Fish - fyke-nets (n = 80 wetlands)		
Native species richness	0.44	Wet_Area(.08)↓; RC_500(.07)↑; DEV_500(.05)↓; Wat_Area(.06)↑; Wat_Area(.06)↓; DEV_5000(.11)↑
% Large fish (> 200 mm average adult size)	0.42	Wat_Area(.16)↑; Wet_Area(.09)↑; Wat_Area(.10)↓; Lake(s,M,E)(.07)↑
% Nest-guarding spawners	0.46	Wet_Area(.09)↑; Wet_Type(C)(.09)↓; Wet_Area(.16)↓; Wat_Area(.07)↑; Lake(s,H,E,M)(.05)↓
% Intolerant of turbidity	0.54	Wat_Area(.18)↓; DEV_500(.29)↓; RC_Watshed(.07)↓
% Top carnivores as adults	0.38	RC_Watshed(.09)↓; DEV_500(.08)↑; DEV_1000(.09)↓; Wat_Area(.07)↑; CSI_5000(.05)↑
% <i>Lepomis macrochirus</i>	0.51	Ecosection(ssu,wsu,ngl,scg,slc)(.13)↓; DEV_500(.07)↑; RC_Watshed(.14)↓; DEV_100(.07)↑; DEV_5000(.10)↓
% <i>Ameiurus nebulosus</i>	0.19	Wet_Type(p,c)(.06)↓; Wat_Area(.13)↓
% <i>Cyprinus carpio</i> and <i>Carassius auratus</i>	0.35	RC_500(.19)↑; RC_5000(.16)↓
% <i>Notemigonus chrysoleucus</i>	0.15	DEV_1000(.15)↓
% <i>Ambloplites rupestris</i>	0.44	DEV_Watshed(.24)↓; Lake(s,H,O)(.07)↓; Wet_Area(.13)↓
Birds (n = 223 wetlands)		
# Short-distance migrants	0.17	RC_1000(.11)↑; DEV_Watshed(.06)↓
# Long-distance migrants	0.11	Lake(o)(.06)↓; RC_100(.05)↑
# Individuals	0.23	RC_1000(.12)↑; Wat_Area(.06)↓; DEV_Watshed(.05)↓
# Wetland obligates	0.19	RC_Watshed(.13)↑; DEV_Watshed(.06)↓
# Aerial foragers	0.15	RC_Watshed(.08)↑; Ecosection(eol,scg,ctp,slc)(.07)↓
# Insectivores	0.27	RC_1000(.11)↑; Wat_Area(.05)↓; DEV_1000(.05)↓; DEV_500(.06)↑
# <i>Geothlypis trichas</i>	0.12	Ecosection(ssu,wsu,ngl,thp,scg,nsu,ctp)(.12)↑
# <i>Dendroica petechia</i>	0.25	DEV_5000(.05)↑; DEV_500(.06)↓; RC_1000(.06)↑; RC_5000(.08)↓
# <i>Cistothorus platensis</i>	0.62	Wet_Area(.09)↑; Ecosection(eol,scg,thp,slc,sgl)(.12)↓; RC_100(.11)↑; RC_5000(.18)↓; DEV_500(.12)↓

(Brazner *et al.* 2007) suggested that indicators derived from these two data sets responded differently.

Characterizing Human Disturbance and Nonstressor Covariables

Human disturbance was characterized using a variety of publicly available geographic information system (GIS) data sources, quantified with ArcGIS and ArcView software (Danz *et al.* 2005, Wolter *et al.* 2006). Most GIS data sources and primary methodologies have already been described in detail (Danz *et al.* 2007, Johnston *et al.* in press), so we only cover them briefly here. We used the proportion of row-crop agriculture from the National Land Cover Database (NLCD, 30-m raster coverage; Wolter *et al.* 2006) to represent agricultural stress (RC); the proportional sum of low and high intensity urban, commercial/industrial, and road surface land covers in the NLCD (Wolter *et al.* 2006) to represent urban development stress (DEV); and a CSI based on point source and contaminant release information from the U.S. EPA National Pollution Discharge Elimination System (NPDES) and Toxic Release Inventory (TRI).

We developed the CSI using a simple weighting system for point-source inputs based on the type of input. Our intent was to create a semi-quantitative index of severity, potentially providing stronger predictive power than an area-weighted count of point sources. For example, each stressor tabulated in the NPDES database (sewage, metals, particulates, etc.) was given a weighting from 1 to 3—with sewage and pathogens given weights of 1; nutrients, particulates and salts a weight of 2; and more persistent or toxic stressors such as metals, solvents, PAHs, and hydrocarbons a weight of 3. Weights were summed across stressors to come up with a score scaled from 1 to 20 indicating severity (sewage systems and petroleum refineries were the worst, life insurance companies and commercial banks were among the least). We also applied weights based on whether the facilities were “major” or “minor” (major = weight*2, minor = weight*1) and active vs. inactive (active = weight * 1.3, inactive = 0.7). TRI data were included in the CSI as a density of land- and water-based TRI point sources in the landscape TRI data were given a weighting of 5, which was the median score for NPDES data, before being added to NPDES score to provide the combined CSI.

Each of the three disturbances was characterized

at five scales; within 100 m, 500 m, 1,000 m, and 5,000 m buffers, and at the whole watershed scale for each wetland sampled. The buffers were based on flow distance rather than Euclidean distance because this provides a more accurate representation of disturbance levels affecting biota (King *et al.* 2005). Flow distance was calculated in Arc Grid using elevation data and the “FLOWLENGTH” command. Flow distance buffers were calculated from the wetland complex perimeter, and buffers larger than the whole watershed were clipped to the watershed boundary.

In addition to characterizing disturbance in the landscape, we also characterized several macro-scale covariables that were unrelated to environmental stress (ecosection, ecoprovince, lake, wetland type, watershed area, and wetland area) that were likely to have an important influence on indicator response based on our previous analyses (Brazner *et al.* 2007, Hanowski *et al.* 2007, Host *et al.* 2005, Reavie *et al.* 2006) or other studies (Strayer *et al.* 2003, King *et al.* 2005). We knew it was important to account for the variance explained by these nonstressor covariables before attempting to assess differences in the relative importance of the various disturbance types or buffers on indicator responses (O’Connor *et al.* 2000, Kincaid *et al.* 2004).

Ecosection designations from Keys *et al.* (1995) (Erie and Ontario Lake Plain [EOL], Northern Great Lakes [NGL], Northern Superior Uplands [NSU], South Central Great Lakes [SCG], Southwestern Great Lakes Morainal [SGL], St. Lawrence and Champlain Valley [SLC], Southern Superior Uplands [SSU], Central Till Plains [CTP], Tug Hill Plateau [THP], Western Superior Uplands [WSU], Western Unglaciaded Allegheny Plateau [WUA]) were assigned based on which ecosection encompassed the majority of a wetland’s associated watershed. Watershed areas were calculated from digital elevation maps (<http://gisdata.usgs.net/ned/>) and wetland areas were delineated using National Wetland Inventory digital data (<http://wetlandsfws.er.usgs.gov/>), digital raster graphic files (<http://topomaps.usgs.gov/drg/>) and digital orthophoto quadrangles (<http://erg.usgs.gov/isb/pubs/factsheets/fs05701.html>). Median watershed area was 12.1 km² (range 0.02-16,489 km²), and median wetland area was 0.19 km² (range 0.004-23.4 km²). Ecoprovince, wetland type, and the Great Lake in which each wetland occurred were designated as described in the sampling design (Danz *et al.* 2005).

Data Analysis

Although we ultimately decided to use CART to characterize the relationships among candidate indicators and predictor variables related to land use disturbance and other potentially important ecological nonstressor covariables, we initially employed both multiple regression and a general linear modelling (GLM) approach to these data as part of our preliminary analyses. Both of these approaches provided results similar to those obtained with CART for most indicators, but have shortcomings that CART does not. CART is a nonparametric approach (Breiman *et al.* 1984) well-suited for characterizing nonlinear relationships common to ecological response data, and effectively accounts for higher-order interactions and indirect effects that are difficult or impossible to model with traditional multiple regression or other linear methods, particularly when many predictor variables are being examined (De'Ath and Fabricius 2000).

CART is best used to quantify the variation in single response variables explained by one or more predictor variables. Classification tree models require a categorical response variable, while regression tree models require a continuous response variable; both types of tree models can use either categorical or continuous predictor variables. We used classification trees for the four species-based amphibian indicators derived from presence-absence data and regression trees for all other indicators. For both classification and regression trees, the basic idea is to find predictor variables that split the data into groups that maximize within group homogeneity (Breiman *et al.* 1984, De'Ath and Fabricius 2000). Each group is characterized by an average value of the response variable, the number of samples in the group, and the value of the predictor that provides the best split.

We used SYSTAT's TREE program (Wilkinson 1998) to build all of our models. An automatic interaction detection (AID) algorithm (Morgan and Sonquist 1963) was used to find the best fit for regression trees. AID takes the initial single cluster of observations and performs a stepwise splitting procedure by searching all possible predictor variables for values that minimize the within-group sum of squares. Interactions among predictor variables are represented by branches from the same node (split points) of the tree that is associated with different predictors lower in the tree. Each tree was constructed by repeatedly splitting each group until the proportional reduction in error (PRE, Breiman *et al.*

1984) based on a least squares loss function fell below 5% for all predictors. In addition, all terminal nodes were required to include at least five wetlands. PRE values for a particular splitting variable can be interpreted as the increases in the proportion of variance explained, or a partial r^2 equivalent for that predictor. The overall PRE value for a particular model is the equivalent of a multiple R^2 (Wilkinson 1998). Classification trees used the same stopping rules as regression trees and used the Gini index as a loss function. This index is based on variance estimates from comparisons of all possible pairs of values in a subgroup, and uses the case distributions at each node to determine the best split points (Breiman *et al.* 1984, Wilkinson 1998).

CART models are based on the predictors at each node that provide the greatest explanatory power (i.e., highest reduction in PRE), but other correlated predictors may have provided similar explanatory power. This seemed especially likely for the land use stressors characterized at different buffer distances. Due to the large number of indicators ($n = 66$) we examined here, it was not feasible to characterize all possible alternative predictors at each node for each indicator. However, we did calculate a Pearson correlation matrix among all buffers for each disturbance type to provide an estimate of the similarity among these predictors.

We present the best CART model for each biological indicator and summarize indicator patterns by disturbance type, buffer scale, and assemblage.

RESULTS

Relationships among Disturbance Types and Buffers

Within each disturbance type, correlations among the spatial scales were all positive; correlations were highest for buffers most similar in size and declined with increasing disparity in scale (Table 2). For both RC and DEV, correlations ranged from 0.50 to 0.95. For the CSI, correlations among buffers were the lowest overall.

Correlations among disturbance types were generally low, sometimes negative, and highest between the CSI and DEV. The highest correlations among land use disturbance types were at similar spatial scales and at larger spatial scales. All correlations between RC and DEV were negative and small (largest was -0.17 , at the 5000 m scale). Correlations between RC and the CSI were also small (largest was $+0.17$ at watershed scale) but of vary-

TABLE 2. Mean land use disturbance levels across all sites and Pearson correlations among disturbance types characterized at different buffer distances (bold-faced, above and including the diagonal) and correlations between buffers within each disturbance type (below the diagonal). Sample size was 339–344 for all disturbance-buffer combinations.

Disturbance type	Mean	Std.Dev.	Range	Correlations				
				100 m	500 m	1,000 m	5,000 m	Watershed
<i>Development</i>								
<i>Row-crop Agriculture</i>								
RC _{100 m}	6.26	11.6	0.0–73.1	-0.08	-0.07	-0.09	-0.12	-0.07
RC _{500 m}	8.47	14.72	0.0–81.6	0.85	-0.08	-0.1	-0.12	-0.08
RC _{1000 m}	10.16	17.44	0.0–81.5	0.75	0.95	-0.11	-0.13	-0.09
RC _{5000 m}	14.05	20.59	0.0–83.9	0.62	0.79	0.87	-0.17	-0.12
RC _{watershed}	15.27	20.75	0.0–85.5	0.55	0.68	0.75	0.90	-0.12
<i>Contaminant Stress Index</i>								
<i>Urban Development</i>								
DEV _{100 m}	21.95	21.91	0.0–100.0	0.02	0.13	0.2	0.23	0.12
DEV _{500 m}	20.15	21.20	0.0–100.0	0.89	0.21	0.29	0.32	0.19
DEV _{1000 m}	19.19	20.78	0.0–100.0	0.79	0.95	0.32	0.4	0.26
DEV _{5000 m}	17.51	20.03	0.0–100.0	0.65	0.81	0.90	0.46	0.31
DEV _{watershed}	13.1	15.89	0.0–100.0	0.59	0.69	0.73	0.8	0.01
<i>Row-crop</i>								
<i>Contaminant Stress Index</i>								
CSI _{100 m}	0.18	1.39	0.0–19.5	0.03	0.02	0.03	0.02	0.04
CSI _{500 m}	0.52	2.38	0.0–19.5	0.69	-0.01	-0.01	-0.03	0.05
CSI _{1000 m}	0.78	2.82	0.0–19.5	0.57	0.85	-0.02	-0.03	0.12
CSI _{5000 m}	3.57	13.89	0.0–149.5	0.14	0.35	0.58	-0.07	0.11
CSI _{watershed}	54.74	291.7	0.0–2110.0	0.01	0.21	0.54	0.67	0.17

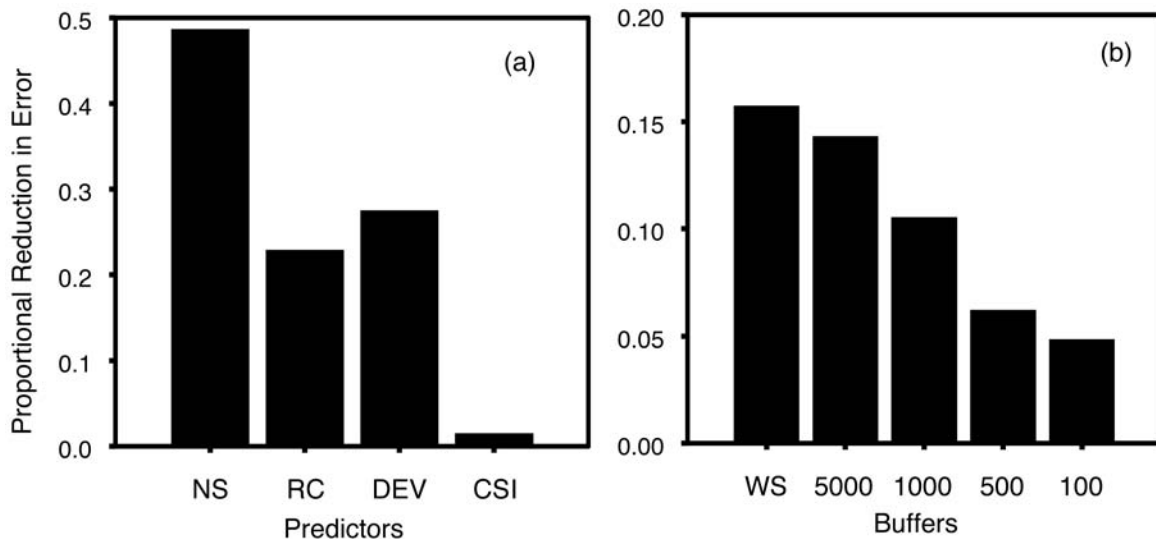


FIG. 2. Proportional reduction in error summarized across all indicators associated with each disturbance type and all non-stressor predictors as a group (a), and associated with each buffer irrespective of disturbance type (b) based on CART analyses (NS = all non-stressor predictors, RC = row crop, DEV = development and CSI = contaminant stress index).

ing direction (Table 2). Correlations between DEV and the CSI were somewhat larger (largest was 0.46, at 5000 m scale) and mostly positive.

CART Results across all Variables and Buffers

Across the 66 separate CART analyses conducted, nonstressor variables (e.g., lake and ecosection) accounted for a greater proportion of the total variance explained than any of the individual disturbance types and larger-scale characterizations of disturbance (watershed and 5,000 m) were most explanatory. RC and DEV each accounted for about a quarter of the total proportional reduction in error, whereas CSI accounted for much less (Fig. 2a). The 1,000 m and larger buffers explained the majority of variance across all disturbance types, and the watershed scale was the single most explanatory (Fig. 2b). Among the nonstressor predictors, lake and ecosection were the most explanatory variables, each accounting for more than 10% of the total explained variance (Fig. 3a), each being included in at least 20 of the 66 tree models (Fig. 3b), and each being the most explanatory variable in at least nine of the trees (Fig. 3c). Watershed and wetland area were also prominent in these models, but were less frequently the most explanatory variable for any particular indicator (Fig. 3c, Table 1). Among the stressor variables, RC_{watershed} was the most explanatory predictor, followed by DEV at spatial scales of 1,000 m or greater. The explanatory ability of the RC predictors clearly declined with declining buffer size, while the explanatory ability of the DEV predictors was distributed more evenly across buffer sizes (Figs. 3a-c). The influence of the CSI was minimal and apparent at the 5,000 m scale only (Fig. 3).

CART Results by Assemblage

There were no statistically significant differences in the mean number of predictors incorporated into trees for any assemblage (ANOVA $p > 0.26$). Trees typically included two or three predictors, although trees for fyke-net fish indicators tended to be the most complex (Table 1). There were also no significant differences among assemblages in the mean proportional reduction in error associated with the disturbance predictors (ANOVA $p = 0.79$). The mean amount of variance explained by all disturbances was typically between 15 and 25% (Fig. 4a). The total variance explained by all predictors was significantly different among assemblages, being

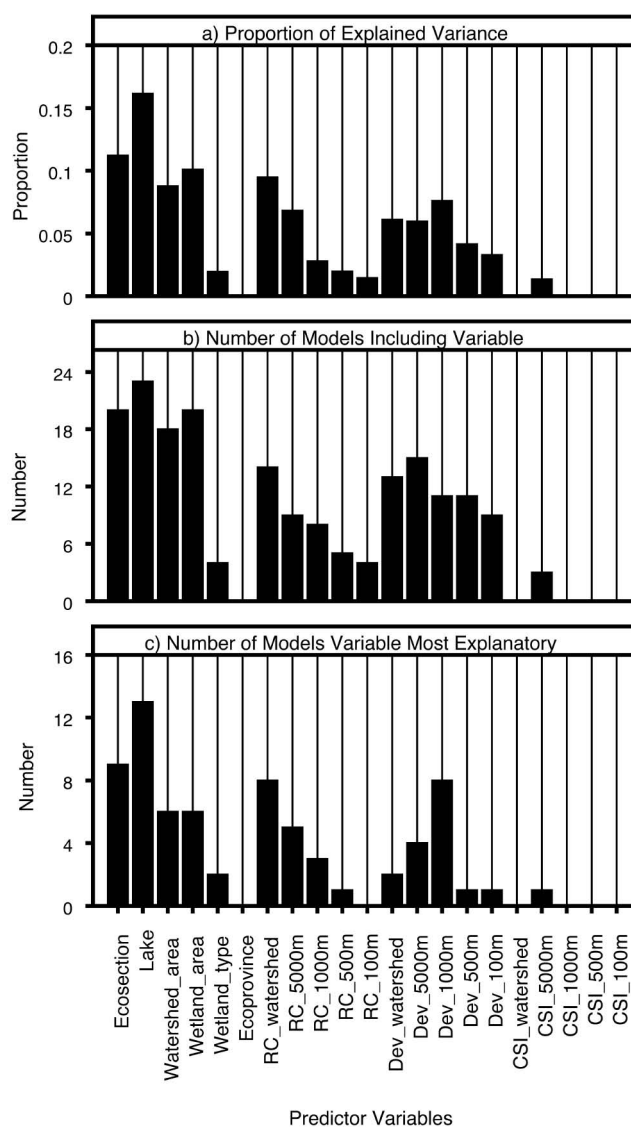


FIG. 3. Proportion of explained variance (a), number of models that included a particular predictor (b), and number of models in which a particular predictor was the most explanatory (c) in CART analyses summarized across all indicators.

higher for electro-fish and wetland vegetation than for birds and amphibians (ANOVA, $p = 0.01$, Fig. 4b).

The specific predictors with the strongest influence varied considerably among assemblages (Fig. 5). The majority of explained variance in amphibian indicators was accounted for by ecosection and lake, although many amphibian indicators did respond relatively strongly to development at the 5,000 m buffer (e.g., species richness, presence of

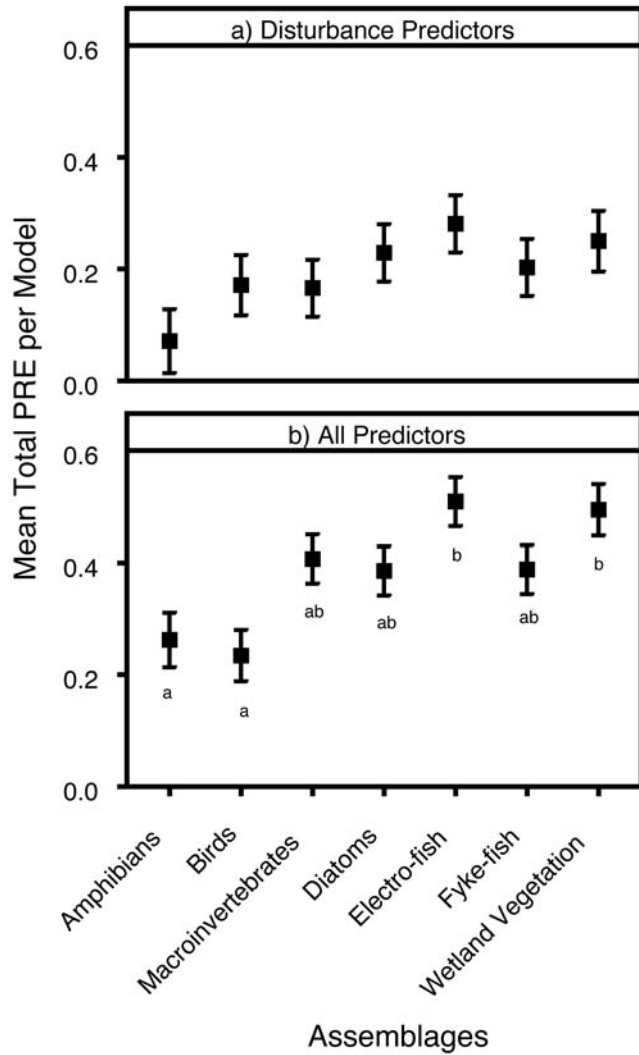


FIG. 4. Mean (± 1 s.e.) proportional reduction in error (PRE) associated with land use disturbances across all indicators for each assemblage (a), and mean (± 1 s.e.) PRE per model summarized across all indicators for each assemblage (b; means letters in common were not significantly different based on ANOVA with Tukey corrections for multiple comparisons, $p < 0.05$).

Rana clamitans; Table 1). Ecosession also explained much of the variance in bird indicators, but response to RC_{1000} was even more important (Fig. 5) and was the most explanatory predictor for short distance migrants, total number of individuals, and insectivorous birds (Table 1). Watershed area and DEV_{1000} accounted for the largest amount of explained variance in macroinvertebrate indicators (Fig. 5, Table 1). Both lake and $RC_{watershed}$

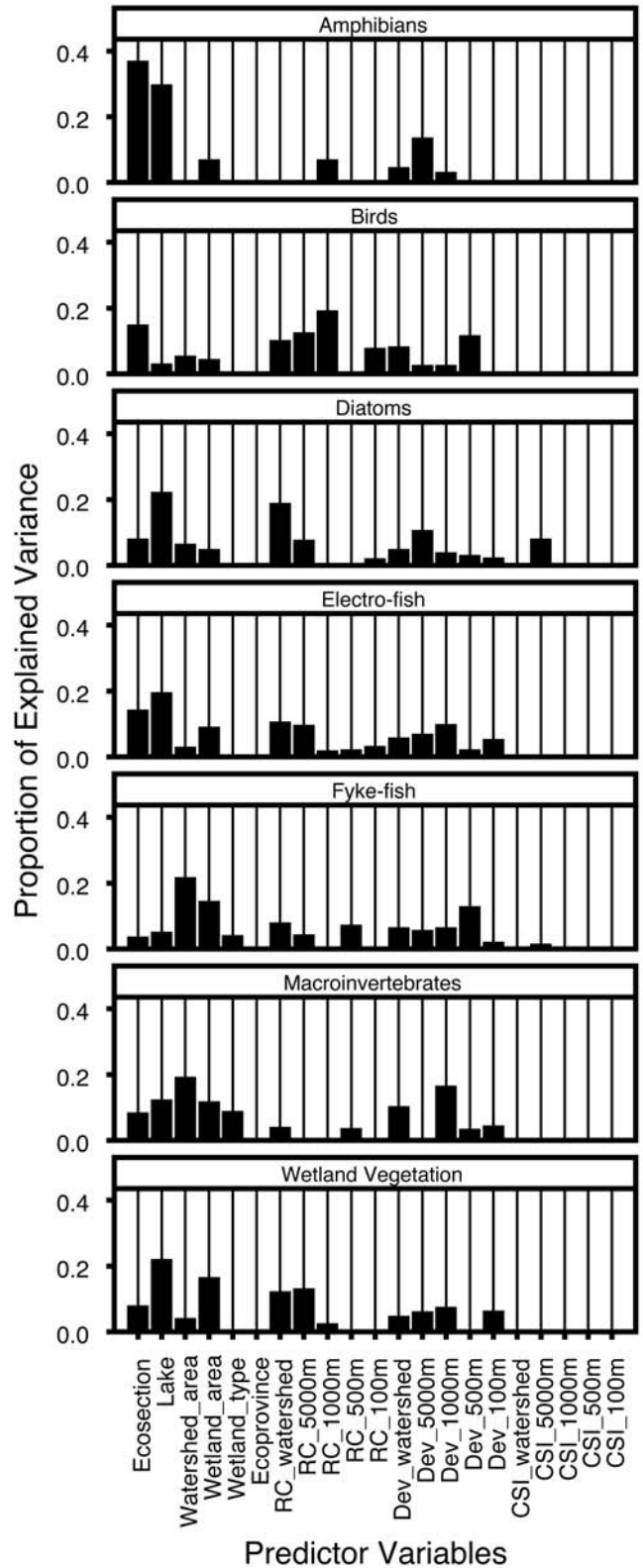


FIG. 5. Proportion of explained variance accounted for by each predictor across all indicators for each assemblage.

accounted for much of the explained variance in diatom indicators (Fig. 5). Stephanodiscoid diatoms responded only to $RC_{\text{watershed}}$, which explained 50% of the total variance in this indicator (Table 1). CSI_{5000} was a key predictor for the proportion of motile diatoms and the Lange-Bertalot index for diatoms (Table 1), but CSI at any scale was not an important predictor for any other indicators. Three electro-fish indicators were most responsive to multiple land use disturbances, responding to both RC and DEV. For example, the proportion of nest-guarding spawners was explained mainly by RC_{5000} (38% of total variance), but $DEV_{\text{watershed}}$ accounted for another 12% of total variance (Table 1). In contrast, fyke-fish responses were driven primarily by watershed and wetland area and were the only assemblage besides macroinvertebrates where wetland type played an important splitting role in any trees (e.g., % *Ameiurus nebulosus* [rock bass], % nest-guarding spawners; Table 1). Wetland vegetation indicators were similar to diatoms and birds in that the largest RC buffers were the main disturbances to which they were responding (Fig. 5). $RC_{\text{watershed}}$ and RC_{5000} accounted for the largest proportion of total variance for the proportion of native plant taxa, *Carex lasiocarpa* (slender sedge), and *Phragmites australis* cover, and explained 17% of the variance in the proportion of invasive taxa (Table 1). DEV predictors were also significant for wetland vegetation, being present in five of nine vegetation trees, albeit at a lower proportion of variance explained than RC predictors.

Patterns in the spatial scale to which indicators were responding were more consistent among assemblages, than patterns in the types of disturbance and geographic covariables to which the indicators were responding. Most assemblages responded most strongly to disturbance characterized at the larger scales (watershed, 5,000 m, or 1,000 m); watershed or 5,000 m buffers were the most explanatory for four assemblages (amphibians, diatoms, electro-fish, and wetland vegetation; Fig. 6). Bird and macroinvertebrate indicators responded most strongly to disturbance in the 1,000 m buffer, and fyke-fish were unique in responding most strongly to the 500 m buffer. The 100 m buffer was relatively uninfluential (Fig. 6), but did account for > 10% of the variance in several variables (e.g., the proportion of *Procladius* and *Callibaetis* mayflies, the percent cover of *Carex stricta* and *C. lasiocarpa* [Table 1]).

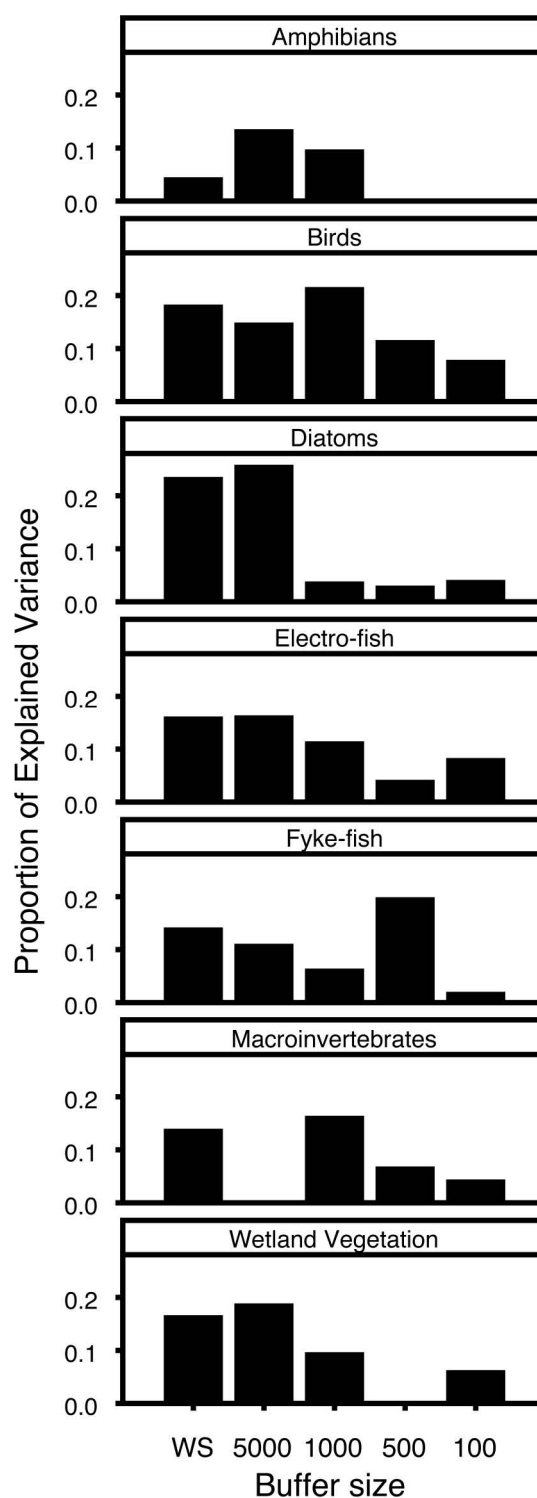


FIG. 6. Proportion of explained variance accounted for by each buffer across all disturbance types and indicators for each assemblage.

TABLE 3. Indicator responses with a total $R^2 \geq 0.40$ associated with all land use disturbances combined or total $R^2 \geq 0.35$ associated with a single land use disturbance type in classification and regression tree analyses; Response to disturbance summed across buffers, non-stressor covariables included when present in a particular tree; RC, DEV and CSI as defined in Table 1.

Indicator (Total disturbance R^2)	Assemblage	Disturbance type (r^2)	Non-stressor Covariable (r^2)
% <i>Carex stricta</i> (0.62)	Wetland Vegetation	DEV(0.62)	
% Nest-guarding fish (0.58)	Fish (electro)	RC(0.46), DEV(0.12)	
% <i>Ambloplites rupestris</i> (0.58)	Fish (electro)	DEV(0.43), RC(0.15)	
% Top carnivore (0.55)	Fish (electro)	RC(0.38), DEV(0.17)	
% Stephanodiscoids (0.50)	Diatoms	RC(0.50)	
% <i>Aeshna</i> (0.49)	Macroinvertebrates	DEV(0.49)	
# <i>Cistothorus platensis</i> (0.41)	Birds	RC(0.29), DEV(0.12)	Ecosection(0.12), Wetland Area (0.09)
% Native taxa (0.36)	Wetland Vegetation	RC(0.36)	Watershed Area (.09), Wetland Area (.06)
% <i>C. carpio</i> and <i>C. auratus</i> (fyke) (0.35)	Fish (fyke)	RC(0.35)	

Indicators with the Strongest Response to Land Use Disturbances

The indicator most responsive to land use disturbances was % *Carex stricta* (tussock sedge) ($R^2 = 0.62$, Table 1, Table 3). After % *C. stricta*, the next three indicators most responsive to land use disturbances were all based on fish captured by electrofishing (Table 3). Each of the electro-fish indicators responded to both RC and DEV. Responses of % *C. stricta* and electro-fish top carnivores were somewhat difficult to interpret due to apparently contradictory directional responses to disturbance characterized at different scales (Table 1). This sort of trend reversal arose whenever a disturbance entered a model for the second time regardless of buffer, and is a byproduct of the CART splitting methodology (the significance of this model behavior is discussed in more detail later). Responses of nest-guarding spawners and *Ambloplites rupestris* were relatively straightforward (Table 1). Nest-guarding spawners were less abundant when RC_{5000} was high ($> 32.8\%$) and when $DEV_{watershed}$ was higher ($> 6.5\%$), and *Ambloplites rupestris* were less prevalent when $RC_{watershed} > 3.5\%$ and DEV_{5000} was $> 9.2\%$. However, at the lowest end of the development gradient ($DEV_{1000} < 6.4\%$) *Ambloplites* was slightly less prevalent than when development was between 6.4 and 9.2%. Stephanodiscoid diatoms had the strongest response to any single land use disturbance, increasing when $RC_{watershed}$ was high ($> 46.2\%$; Table 1). Although the amount of variance explained by disturbance was high ($\geq 35\%$) for *Aeshna* (darner dragonflies), *Cistothorus platensis* (sedge wren), and *C.*

carpio/*C. auratus* (carp/goldfish), responses were complex and more difficult to interpret (Table 1). Responses of native vegetation taxa and turbidity intolerant fish captured by fyke-netting were more straightforward. Native vegetation taxa were sensitive to virtually any amount of row-crop in the watershed, decreasing when $RC_{watershed}$ was $> 0.10\%$, particularly in larger wetlands ($> 71,000$ m²) from medium- and larger-sized watersheds (> 3.1 km²). Turbidity intolerant fyke-fish were also reduced in medium- and larger-sized watersheds (> 2.1 km²) at low levels of row-crop land use ($RC_{watershed} > 1.8\%$), and when DEV_{5000} was high ($> 8.0\%$) in smaller watersheds (< 2.1 km²; Table 1). Two other diatom indicators with straightforward and fairly strong responses to disturbance were the Lange-Bertalot index (LBI; a species-based indicator of limnological quality where lower scores reflect poorer conditions; Lange-Bertalot 1979) and proportion motile. These were also the only two indicators that reflected the influence of the CSI in any important way (Table 1). The LBI responded negatively to CSI_{5000} (≥ 2) in five ecosections (EOL, NSU, SGL, SSU, THP), and to higher DEV and RC at the 5,000 m scale in the other ecosections (CTP, NGL, SCG, SLC, WSU, WUA). The proportion of motile diatoms increased when CSI, row-crop, and development were all higher ($CSI_{5000} > 15.5$, $RC_{watershed} > 45.3\%$, and $DEV_{watershed} > 21.5\%$) suggesting a generalized positive response to land use disturbance. Although the large number of indicators examined in this study precluded the inclusion of separate tree diagrams for each indicator, the full tree diagrams do aid considerably in the in-

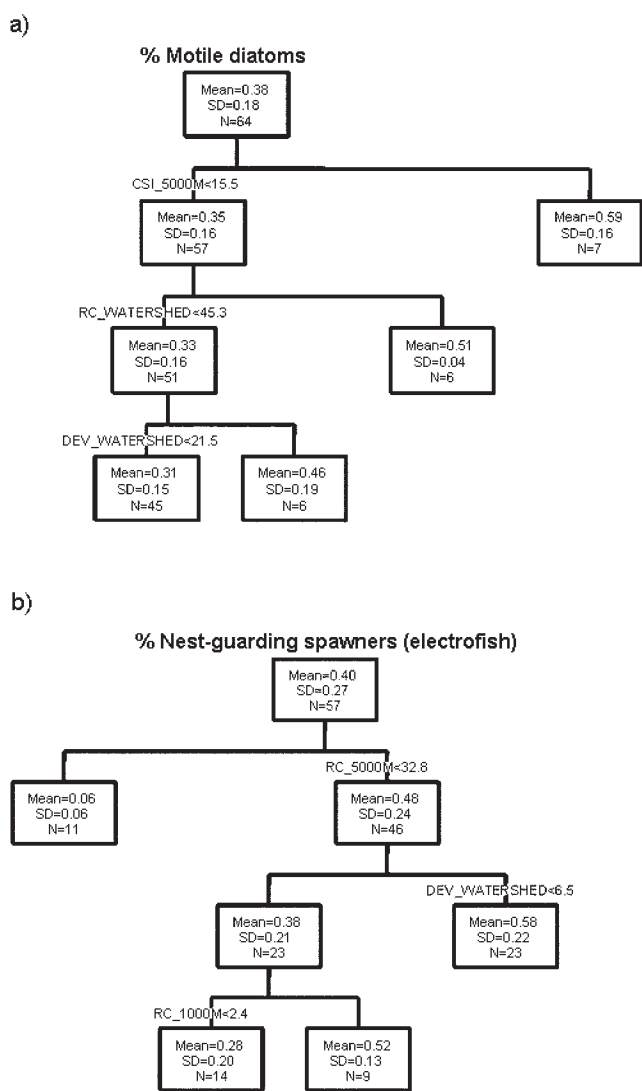


FIG. 7. Regression tree diagrams for proportion of motile diatoms (a) and proportion of nest-guarding fish captured by electrofishing (b). Threshold values of predictor variables, and mean, standard deviation, and sample size of response variables shown at each node.

interpretation of indicator responses for the complex cases and so we have included representative examples for two of the indicators with strong potential (Fig. 7), and the remaining trees have been made available in electronic format (<<http://glei.nrri.umn.edu/default>>).

DISCUSSION

Similar to what we found in earlier variance partitioning analyses (Brazner *et al.* 2007), geographic

features such as lake and ecosection were among the most important predictor variables in our CART analyses. Although some instances where the geographic variables were significant predictors may have been due to a geographical variable acting as a surrogate for a particular disturbance type with a skewed geographic distribution (e.g., agriculture was heavily skewed to the southern lakes), our results nevertheless support the hypothesis that certain nonstressor, macro-scale factors would have at least as great an influence on indicator response as the land use disturbances we examined. While they were not important for all of the candidate indicators, accounting for variance associated with these factors will be critical for developing many indicators of ecological condition for Great Lakes wetlands (Hanowski *et al.* 2007, Reavie *et al.* 2006). As we have suggested elsewhere (Brazner *et al.* 2007), indicators could either be developed for geographical subsets of the Great Lakes (e.g., within a lake or ecoregion) or by working with residual variance in assessing indicator responses after partitioning variance associated with key geographic factors (e.g., O'Connor *et al.* 2000, Fore 2003a). Developing indicators in this manner will be particularly important if there are nested scales of influence operating, as suggested by Uzarski *et al.* (2005), that result in the masking of more local influences, unless the influence of broader scale factors such as geography have been partitioned. Our results suggest that large-scale geographic factors such as lake and ecosection are driving many of the big differences among biota that we observed among wetlands and that smaller-scale factors may be driving many of the differences nested within these geographic units.

The fact that both watershed area and wetland area explained a significant portion of the variance in nearly a third of the CART models indicates that assessing the relative influence of different disturbance types without accounting for watershed and water body size differences would also provide misleading results in many instances. We expected that our ability to detect responses to different scales of stress might be more limited in smaller watersheds based on the results of Strayer *et al.* (2003) and King *et al.* (2005), where idiosyncrasies in land use patterns in small watersheds were thought to obscure patterns apparent in larger watersheds. However, we typically found responses of indicators to be more apparent in smaller watersheds in models where watershed size was a splitting variable (e.g., response of native fish species richness to develop-

ment was clearer in smaller watersheds). The apparent difference in response sensitivity in small watersheds between our study and Strayer *et al.* (2003) and King *et al.* (2005) may be due to differences in the way land use stressors were calculated (e.g., King *et al.* used an inverse distance weighting method) or a result of the way wetland indicators respond in Great Lakes watersheds compared to stream indicators in Mid-Atlantic watersheds. It suggests that effects of land use disturbance may actually be more easily detected in smaller Great Lakes watersheds. Since the relationship between species richness and ecosystem area has been known for many years (e.g., MacArthur and Wilson 1967), the fact that many indicator responses were modified by wetland area was not particularly surprising. The importance of ecosystem size in structuring wetland ecosystems has received some attention in inland wetlands (e.g., Pastor *et al.* 1996, Findlay and Houlihan 1997), but we believe this is the first time this relationship has been noted for Great Lakes coastal wetlands.

Spatial autocorrelation among different land-use disturbance types and between different spatial characterizations for the same disturbance type create analytical difficulties when trying to assess relative influence among these sorts of factors (Van Sickle *et al.* 2004, King *et al.* 2005). Correlations among disturbance types in our data set were typically low, but were relatively high ($r > 0.80$) among adjacent buffer sizes within the row-crop and urban development disturbance types. It is likely that substitution of an adjacent buffer size in models where particular row-crop or development buffers were selected as splitting variables would result in similar proportional reductions in error. The closer correlations between CSI and DEV compared to RC and DEV or RC and CSI, irrespective of buffer distance, suggests that in cases where CART models selected row-crop as a splitting variable it was likely due to a clear difference in predictive power. However, the choices between CSI and development were less clear cut, potentially underestimating the importance of CSI and overestimating the importance of development. The large number of indicators we examined prevented us from exploring these interrelationships in greater detail. However, the CART approach that we utilized to model indicator response did allow us to account for spatial autocorrelation effects among *selected* predictors as well as many interactions that would have been difficult to model using more traditional linear approaches (De'Ath and Fabricius 2000).

Our CART analyses suggested that row-crop and development land uses played more important roles in shaping our candidate indicator responses than contaminant stress. Although point-source contaminants have been found to be an important stress in numerous site-specific studies in aquatic ecosystems, their influence at the landscape scale has not been well studied due to difficulties in summarizing available digital coverages for point sources in a meaningful way. Our CSI was an attempt to index the relatively coarse resolution NPDES and TRI data in a way that would be more relevant to assessing their influence on the kinds of ecological responses we examined. It is unclear whether the limited response of most indicators to the CSI reflects a failing of our index or if contaminant sources really do have a relatively small influence compared to agriculture and development across the Great Lakes basin. Strayer *et al.* (2003) also suspected that inadequacies of the point-source data were at least partially responsible for their inability to detect contaminant influences on a range of ecological responses of stream biota from the Chesapeake Bay watershed. In our study, the paucity of data available to calculate the CSI at buffers less than 5,000 m made it difficult to draw any firm conclusions about contaminant effects at those scales.

Our results indicated clearly that row-crop agriculture characterized at the watershed scale was the single most important land use predictor-buffer combination. That row-crop at any scale was important should not have been a surprise given the prevalence of row-crop agriculture throughout much of the Great Lakes basin. However, the fact that it was at the watershed scale has both ecological and practical importance. It provides support for our hypothesis that agricultural influences would be strongest at broader scales and, along with the general importance of buffers $\geq 5,000$ m we observed across all disturbance types, suggests that the typical approach of characterizing land use disturbance at the watershed scale only may be adequate for many studies. However, the clarity of response to disturbance may be considerably better at other scales (e.g., Mensing *et al.* 1998, Lammert and Allan 1999) for certain indicators (e.g., RC₁₀₀₀ was the most important scale for one-third of our bird models). From a management perspective, the observation that relatively distant agricultural activities have a strong influence on wetland biota basin-wide implies that measures meant to minimize row-crop agricultural impacts (e.g., buffer strips, reduced rates or altering timing of nutrient

applications) are either insufficiently implemented or not working as effectively as desired. Our observation that development was important across a wider range of scales than row-crop refutes our hypothesis that the effects of development would be primarily at smaller, near-wetland scales. This was not altogether surprising given the contradictory nature of other results on scale effects of urban development (Snyder *et al.* 2003, Wang *et al.* 2003b, DeLuca *et al.* 2004). It suggests that in places where development is a primary disturbance, it would be wise to characterize it at multiple scales, whenever feasible. Our results also suggest that watersheds are more likely a good summary scale for things that accumulate down the drainage unit (e.g., row-crop agricultural influences), and that the effects of development are more complex and will require more effort to understand and predict.

Our hypotheses about relationships between organism size and mobility and response to disturbance scale were not well supported, but bird and electro-fish indicators did tend to respond most strongly at the larger spatial scales as predicted. Fry-fish indicators did not follow the pattern observed for electro-fish but rather responded across a broader range of scales, particularly to development at the 500 m scale. This highlights the importance of understanding bias associated with different sampling techniques when developing indicators. As smaller and less mobile taxa, macroinvertebrates and wetland vegetation indicators were expected to respond primarily to more local characterizations of disturbance (Allen *et al.* 1999) but typically did just the opposite, with a few notable exceptions (e.g., % *Carex lasiocarpa* responded primarily to row-crop at 500 m buffer). Macroinvertebrate responses to disturbance were relatively weak across all indicators, so even though the larger buffers were more explanatory, none explained a very large portion of the total variance in any indicator except for *Aeshna*. As was observed by Richards *et al.* (1997), watershed features (watershed and wetland area) had an important influence on macroinvertebrate responses, lending support to the idea that factors operating at broader scales were important for these indicators whether or not they were related to disturbance. For diatoms, stephanodiscoid taxa responded strongest to row-crop disturbance at a relatively broad scale, but for many other diatom indicators, the biogeographic influence of lake was particularly important. This differs from the observation that diatoms have been more responsive to human disturbance than ecoregion or watershed

size in streams (Leland and Porter 2000, Fore 2003b). It may be that diatom indicator response patterns in Great Lakes coastal wetlands are driven by different factors than those for streams, or that the broader geographic scale encompassed by our study favored the detection of effects associated with natural gradients over those related to human disturbance. Similar reasoning may explain why wetland vegetation responded primarily to the broader scales of disturbance, in distinct contrast to the Minnesota wetlands studied by Mensing *et al.* (1998) where shrub-carr and wet meadow vegetation were influenced primarily by local land use.

We identified several indicators with excellent potential to reflect disturbance in coastal wetlands across the Great Lakes basin. We considered those indicators with a strong (high partial r^2 in the CART analyses) and unidirectional response to a particular disturbance-buffer combination with few or no mediating nonstressor covariables to have strong potential for interpretation and implementation by resource agencies (some of the best examples are plotted in Fig. 8). Since we evaluated a representative rather than exhaustive list of indicators from each taxonomic group here, there may be other indicators with better potential that we have overlooked. We are confident that the proportion of both stephanodiscoid diatoms and nest-guarding fish are excellent indicators of row-crop agriculture at the watershed scale; an abundance of stephanodiscoids reflected high levels of RC while a predominance of nest-guarding fish (electro) suggests RC land use is low. The proportion of stephanodiscoid diatoms was one of the indicators we identified previously (Brazner *et al.* 2007) as responding strongly to a general human disturbance gradient, but our results here suggest an even stronger response to row-crop agriculture. The proportion of native plant taxa also appears to be an excellent indicator of row-crop stress at the watershed scale, even though watershed area and wetland area explained additional variation. *Ambloplites* (electro) and *Aeshna* were the two best indicators of development at the 1,000 m scale and larger. CART results suggest a bidirectional response for *Ambloplites* and *Aeshna* to development at different scales, but when these disturbance-buffer combinations were plotted against *Ambloplites* and *Aeshna* individually the overall trend in indicator response was negative in all cases. The indicator % *Carex stricta* also had a bidirectional response to DEV predictor variables, and although this indicator had the greatest amount of variance explained by disturbance predictors

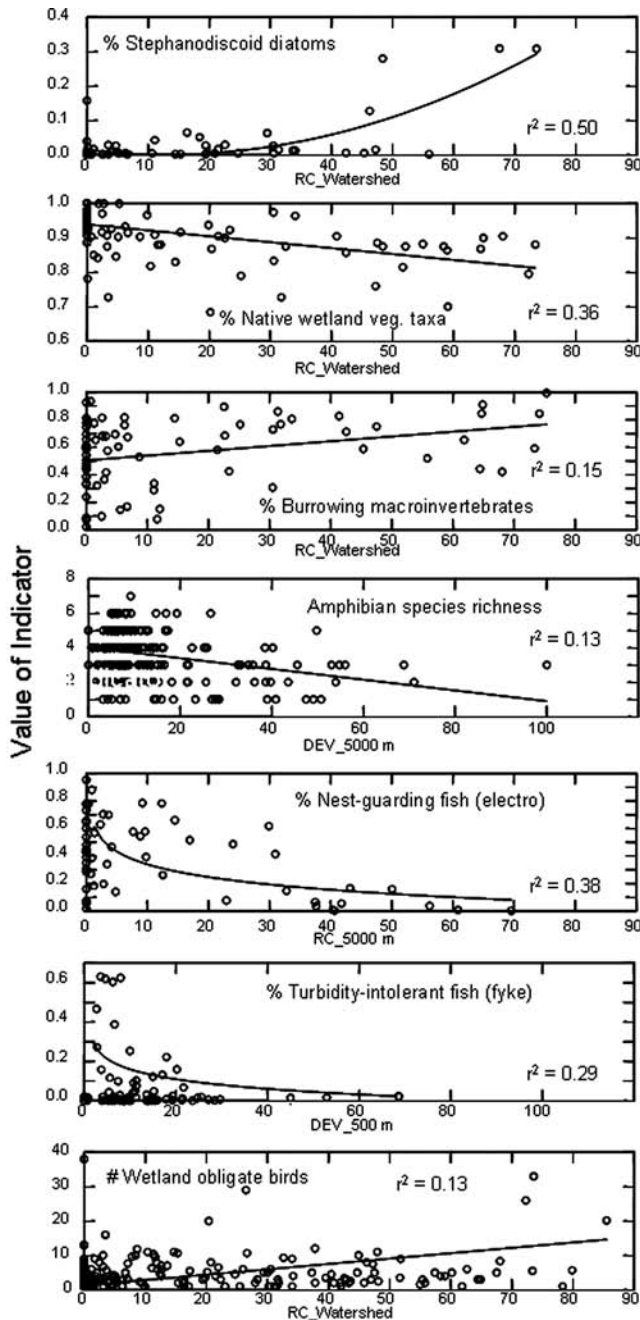


FIG. 8. Indicators from each assemblage with the strongest response (partial r^2) to a single disturbance-buffer combination (only the first disturbance-buffer combinations to enter CART models were considered; best-fit lines are linear fits except for stephanodiscoids [quadratic] and nest-guarding and turbidity tolerant fish [log]).

among all indicators ($R^2 = 0.62$), it was not considered a strong indicator because the bidirectional responses were less clear: while this indicator had uniformly 0% cover at the most developed sites and had its highest % cover at buffers with low development, it displayed a wide variety of responses in between.

The reason for the sort of bidirectional response we observed for % *Carex stricta*, *Ambloplites*, and *Aeshna* (and other indicators) in their full models was a function of the way the splitting algorithm works in CART. In all instances when a given disturbance predictor entered a model for a second time, regardless of whether it was at the same or a different buffer distance, its relationship to the indicator was opposite in direction to the first time it was included in the model. This bidirectional splitting happens when a regression type relationship is nonlinear, as with a wedge-shaped response (e.g., high disturbance led to uniformly low abundance, but low stress led to a lot of variance in the response, as in the case of % *C. stricta*; Mebane *et al.* 2003, Hughes *et al.* 2004), or when the indicators have higher or lower values towards the middle range of disturbance rather than when disturbance is high or low. What typically happened in our models was that an early split in the tree clipped off the most disturbed sites where indicator values were low. This split is interpreted as a negative relationship between abundance and disturbance. A subsequent split then cut off the least disturbed places where there also tended to be lower abundance (although with higher variance) resulting in a positive relationship with disturbance across a small range of these data (e.g., when disturbance is low, abundance is also low). In some cases (e.g., *Aeshna*), a final split segregated sites with high abundance but intermediate disturbance. CART seems particularly sensitive to teasing apart these sorts of nonlinear responses to disturbance. Despite the opposing trends some of the CART models identified for a particular disturbance, those effects did not cancel each other out. The total variance explained by the predictor is still important, but the relationship is more complicated than a simple split at one value of the predictor, and is based on residual variance after accounting for the effects at earlier nodes. A careful examination of the individual point scatter in two-way plots of the indicator values across a disturbance gradient, along with an inspection of the associated tree model, is the only way to obtain a

complete understanding of the splitting decisions made by CART for a particular indicator.

Turbidity-intolerant fyke-fish and amphibian species richness were also clear indicators of development (500 and 5,000 m scales respectively) with the turbidity-intolerant response being particularly strong. Even though the partial r^2 associated with amphibian species richness is fairly low, the response had a wedge-shaped distribution that clearly reflected decreasing richness as development increased. Wedge-shaped disturbance-response relationships are typical of situations where there are multiple limiting factors (Mebane *et al.* 2003, Hughes *et al.* 2004). We were not surprised by the lack of clear indicators of contaminant stress based on what Strayer *et al.* (2003) observed, but the proportion of motile diatoms and the LBI were both general indicators of disturbance because they responded relatively strongly to all three disturbance types, including the CSI; motile diatoms increasing with disturbance and the LBI decreasing.

The lack of strong indicators from the macroinvertebrate and bird assemblages was somewhat surprising. In an earlier analysis (Brazner *et al.* 2007), there were some bird indicators that had a relatively strong response to a general human disturbance gradient. However, we did not account for as many covariables in that analysis, and the response of both birds and macroinvertebrate indicators in *this* analysis were strongly influenced by several non-stressor covariables that were not included in the earlier study (ecosection, watershed area, wetland type and area). Amphibian indicator responses were also relatively weak in this study and primarily driven by geographic covariables rather than response to human disturbance. It was the wetland vegetation, diatom, and fish assemblages that were identified as having indicators with the most promise for reflecting the influence of row-crop agriculture and urban and commercial development. It is interesting that stephanodiscoid diatoms and *Ambloplites* were the only indicators we identified among the most promising here that were also identified as promising in our previous analyses (Brazner *et al.* 2007) although we worked with the same indicator set in both. It seems likely that this is due to the specific land use disturbances we examined compared to the general disturbance gradient (Danz *et al.* 2005) examined for the previous paper. This suggests that indicator responses are, at least in some cases, disturbance-specific and may be helpful for diagnosing causes of impairment (Fore 2003a, Yoder and DeShon 2003).

Some unexplained variability may be attributable to historic effects (Galatowitsch *et al.* 1999a, Findlay and Bourdages 2000), as well as other factors we did not examine here such as local habitat influences. In addition, conclusions about the relative importance of disturbances at different scales depend on the power to detect differences at a particular scale (Lammert and Allan 1999), our ability to accurately characterize certain disturbance types with remotely sensed data (Hollenhorst *et al.* 2006), sample size (Wiley *et al.* 1997), and a variety of other experimental design issues (Allan and Johnson 1997). Particular disturbance types may influence indicators at more than one spatial or temporal scale, sometimes for different reasons (Kotliar and Wiens 1990, Richards *et al.* 1996, Jonsen and Taylor 2000), so there may be multiple peaks of responsiveness at different scales of the disturbance each driven by a different controlling mechanism. Hollenhorst *et al.* (2006) demonstrated that it is easier to accurately measure and characterize agriculture than residential development, which often occurs in small linear blocks that are sometimes below the resolution of remotely sensed data and varies more through time than agriculture.

Despite the complexities associated with analyzing and interpreting indicator responses to disturbance, the results presented here will be useful for developing multi-metric, multi-assemblage indicators of coastal wetland condition in the Great Lakes. The CART approach is well-suited to analyzing the response of single variables to one or many predictor variables, and provides a tool for quantifying important interactions without examining all possible interactions as required by general linear models (De'Ath and Fabricius 2000). It also provides a method to account for the influence of potentially important covariables before attempting to assess an indicator's response to disturbance, a consideration that needs to be incorporated into any attempt at formal indicator development (O'Connor *et al.* 2000, Fore 2003a). Resource agencies currently have a keen interest in developing indicators of ecological condition for the Great Lakes (Keough and Griffin 1994, U.S. EPA 2002, Environment Canada and U.S. EPA 2003, Lawson 2004). We believe our results are an important step in this direction and one of the first attempts to identify how potential ecological indicators of Great Lakes coastal wetland condition vary in response to different types of human disturbance characterized across a range of spatial scales.

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