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Congruence of community thresholds in response to anthropogenic stress in Great Lakes coastal wetlands

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Abstract: Biological attributes of ecosystems often change nonlinearly as a function of anthropogenic and natural stress. Plant and animal communities may exhibit zones of change along a stressor gradient that are disproportionate relative to the incremental change in the stressor. The ability to predict such transitions is essential for effective management intervention because they may indicate irreversible changes in ecological processes. Despite the importance of recognizing transition zones along a stressor gradient, few, if any, investigators have examined these responses across multiple taxa, and no community threshold studies have been reported at large geographic scales. We surveyed benthic macroinvertebrate, fish, bird, diatom, and plant communities in coastal wetlands across a geospatially referenced gradient of anthropogenic stress in the Laurentian Great Lakes. We used Threshold Indicator Taxon Analysis (Baker and King 2010) to analyze each community's response to identify potential zones of disproportionate change in community structure along gradients of major watershed-scale stress: agriculture and urban/suburban development. Our results show surprising congruence in community thresholds among different taxonomic groups, particularly with respect to % developed land in the watershed. We also analyzed uncertainty associated with the community-specific thresholds to understand the ability of different assemblages to predict stress. The high and congruent sensitivity of assemblages to development demonstrates that watershed-scale stress has discernible effects on all biological communities, with increasing potential for ecosystem-scale functional changes. These findings have important implications for identifying reference-condition boundaries and for informing management and policy decisions, in particular, for selecting freshwater protected areas.

Key words: bioassessment, conservation, wetlands, Great Lakes, multi-assemblage, breakpoint, non-linear changes, land use

Threshold responses and catastrophic state changes have been recognized as critical features of biotic communities and ecosystems (Scheffer and Carpenter 2003, Folke et al. 2004). Feedback mechanisms and emergent behavior on the scale of ecosystems (e.g., Fauchald 2010), and nonlinearity in physiological mechanisms underlying stress responses imply that biological communities may often exhibit threshold changes to environmental factors. Characterization of threshold responses is important because community shifts, such as reduced biodiversity or changes in the dominance of an economically important species, are often undesirable

per se and because they may signal irreversible changes in underlying ecological processes (Scheffer 2009) and ecosystem function (e.g., Casini et al. 2009).

In general, biodiversity of different taxonomic groups is weakly correlated (Heino 2010). However, greater congruence of biodiversity could be expected at higher levels of stress as many species approach limits of environmental tolerance. Several researchers have examined the relative importance of environmental stressors in explaining variability of community composition of different taxonomic groups, primarily in lotic ecosystems (but see Brazner et al.

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2007a, Niemi et al. 2009, 2011 for lentic examples). Most studies showed discordance in the responses of different taxonomic groups (Hirst et al. 2002, Johnson et al. 2006, Brazner et al. 2007a, Lewis et al. 2007, Johnson and Hering 2009). Understanding the nature of these dissimilar responses is essential to predicting the impacts of anthropogenic stressors on local ecosystems.

An important question is whether large-scale anthropogenic stress results in synchronous thresholds across taxonomic assemblages or whether taxa respond differentially, leading to complex or chaotic community dynamics that defy prediction. Synchronous responses would provide critical evidence in support of regulatory and management frameworks, and lack of such data has been cited as one of the major issues in application of the ecological thresholds concept in biological conservation (Huggett 2005). Considering different mechanisms underlying assemblage-specific responses to anthropogenic stress, synchronous threshold responses across several assemblages would indicate sweeping changes in ecological communities as many species approach limits of environmental tolerance and an increasing potential for functional changes in the ecosystems. Despite rapid development in this area in the last few years (Dodds et al. 2010), few, if any, investigators have examined the concordance of community thresholds across different taxonomic groups and a common framework for addressing these changes, such as a well-defined stress gradient (e.g., Allan et al. 2013), is lacking. Predicting nonlinear responses of different assemblages is essential to forecast the impacts of anthropogenic stress, understand the trade-offs between biodiversity and development (Huggett 2005), inform management- and policy-relevant issues, and identify priority sites for management intervention.

The Laurentian Great Lakes coastal wetlands are a suitable and relevant ecological system for testing the concordance of community thresholds across taxonomic groups because they are critical habitats for many biological assemblages, they are functionally significant as zones of nutrient and contaminant processing at the aquatic–terrestrial interface, and most important, they are distributed across a wide gradient of anthropogenic impact ranging from severely degraded to nearly pristine (Danz et al. 2007). The responses of Great Lakes coastal wetland communities to environmental stress are both scientifically interesting and of crucial importance because of the enormous socioeconomic value of the health of the Great Lakes ecosystem, which contains 20% of the world's fresh water and provides countless ecosystem services ranging from commercial fisheries to recreation (Niemi and McDonald 2004, Niemi et al. 2007, Vaccaro and Reid 2011, Allan et al. 2013).

We used extensive multitaxon data sets from coastal wetlands representing the 762 watersheds bordering the 6044-km mainland shoreline of the US Laurentian Great Lakes (Danz et al. 2005, 2007, Reavie et al. 2006, Bhagat

et al. 2007, Howe et al. 2007). These data were collected as part of a multidisciplinary effort to identify community responses to anthropogenic stress in the Great Lakes coastal zone (the Great Lakes Environmental Indicators project; Niemi et al. 2007, Morrice et al. 2008). Here, we relate ecological stress to community changes observed in 5 different taxonomic groups using Threshold Indicator Taxa Analysis (TITAN; Baker and King 2010), a change-point and indicator-species analysis-based approach that integrates responses of many individual taxa to determine cumulative community response along an environmental stress gradient. Our study is the first attempt to examine the nonlinearity in responses of lentic assemblages and to integrate simultaneous responses of several assemblage types to anthropogenic stress. Our goal was to assess the degree of cross-taxon congruence in response to 2 watershed-scale anthropogenic stressors (agriculture and development). More specifically, our objective was to assess whether community changes in response to large-scale anthropogenic stressors were similar among the fish, benthic macroinvertebrate, bird, wetland plant, and diatom assemblages of coastal wetlands.

METHODS

Study sites

We sampled coastal wetlands across the US Great Lakes. We selected wetland sites ($n = 101$ – 172 , depending on assemblage; see below) via a stratified random procedure (Danz et al. 2005) to form clusters of coastal watersheds that spanned the full range of anthropogenic stress in the basin. Stressors represented 6 major classes of anthropogenic pressure: agriculture, atmospheric deposition, land cover, population density, point and nonpoint pollution, and shoreline modification. Our sampling scheme further accounted for the hydrogeomorphic type of coastal wetlands, ensuring that each of the 4 geomorphic types (riverine, palustrine, and lacustrine coastal wetlands, and embayments) was included in each stress cluster. Most wetlands were coastal lagoons connected to the main lake, with well-developed submerged and emergent macrophyte communities. We distributed sampling effort evenly across the geomorphic type–stress-gradient combinations and across the 5 Great Lakes (Fig. 1; Danz et al. 2005).

Stressor variables

The Great Lakes Basin has a long history of anthropogenic activities associated with ecosystem degradation (Evans 2005). Widespread clear-cutting across the landscape in the 1800s affected the entire basin, but later landscape disturbances were associated mainly with centers of population, which radiated from river mouths and estuaries and led to widespread habitat loss in tributaries and nutrient and industrial pollutant discharges in river mouths. The strong gradient of climate and landform (i.e., soil fer-

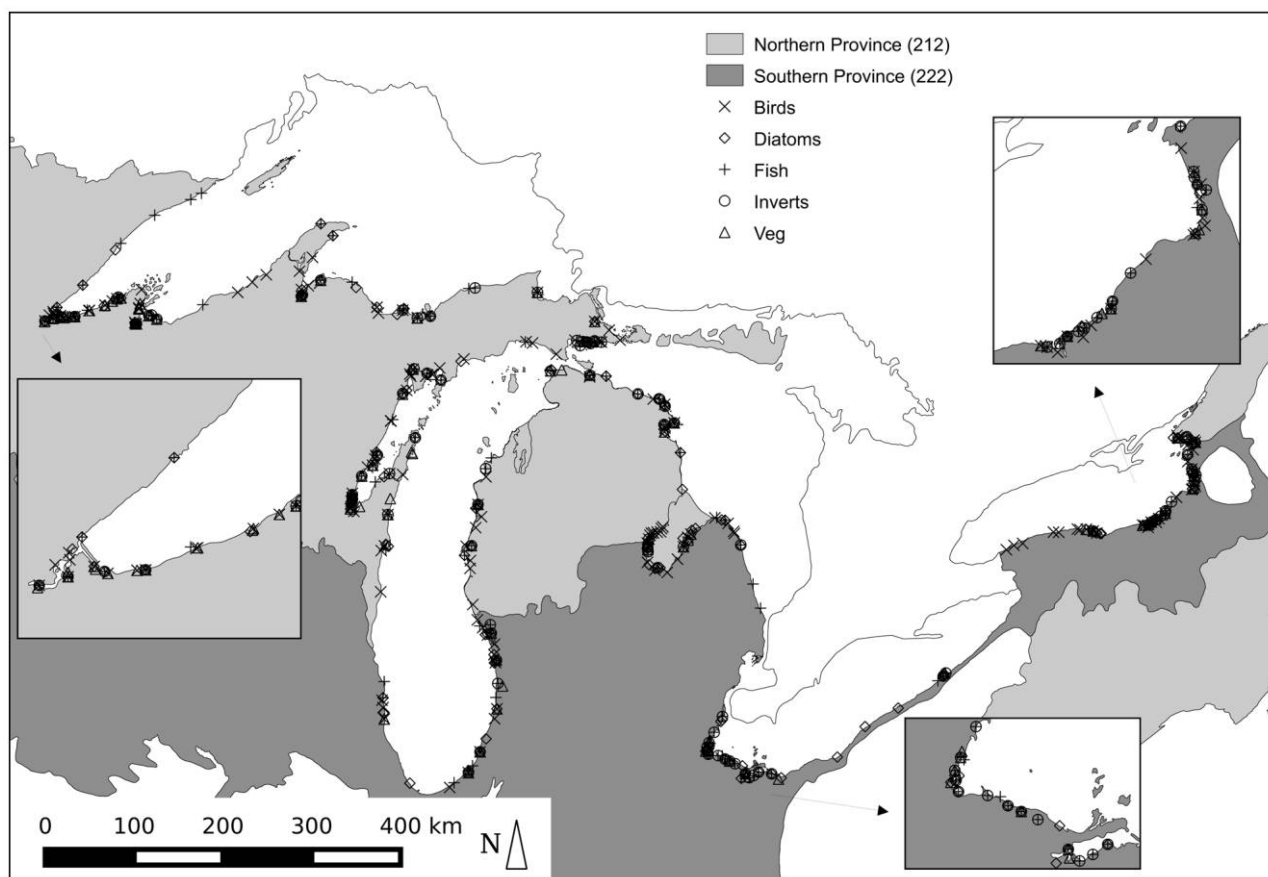


Figure 1. Distribution of 337 sampling sites in US Great Lakes coastal ecosystems in the Northern (Laurentian Mixed Forest) and Southern (Eastern Broadleaf Forest) ecological provinces.

tility) differences across the basin largely explain the land-use patterns that became established in the 20th century, continue today, and led to dominance of landscapes in the eastern portion of the basin by intensive agriculture.

We focused on 2 major watershed-scale stressors: % agriculture and % developed land in the watershed. These stressors serve as surrogates, or indicators, of the degree of potential human impact in a watershed, and their impact is mediated through a variety of mechanisms. The advantages of our approach include ability to relate biological responses to readily available, composite measures of stress, whereas disadvantages include lack of connection of these variables to the precise mechanisms responsible for potential effects. Previous investigators clearly demonstrated that biotic assemblages in Great Lakes coastal ecosystems are affected by these stressors (Brazner et al. 2007a, b, Niemi et al. 2009, 2011), but threshold relationships were not examined. A detailed description of the procedures used to characterize watershed-scale anthropogenic stress is available elsewhere (Hollenhorst et al. 2011). Briefly, ArcHydro[®] with 10-m Digital Elevation Models was used to delineate the boundaries of downstream catchments for

each representative watershed and proportions of agriculture and development in those watersheds were derived from the US Geological Survey National Land Cover Dataset (2001; <http://landcover.usgs.gov/usgslandcover.php>).

Stressor covariation

We addressed the confounding influence of geography caused by profound climatic and geomorphic differences across the Great Lakes basin (Bailey 1989, Brazner et al. 2007b, Hanowski et al. 2007) by conducting separate analyses for 2 ecological provinces (ecoprovince; described below). The Southern ecoprovince (Province 222, the Eastern Broadleaf Forest) encompasses all of Lake Erie, southern Lake Michigan, southern Lake Huron, and western Lake Ontario (Fig. 1). The dominant stressor in this ecoprovince is agriculture, but many areas are also heavily affected by urban development. The Northern ecoprovince (Province 212, the Laurentian Mixed Forest) is less developed overall, has less productive soils, and encompasses far less agricultural and urban land use. This ecoprovince includes Lake Superior, the northern parts of Lakes Huron and Michigan,

and far eastern Lake Ontario (Fig. 1). Our sampling sites covered similar gradients of agriculture (in terms of maximum range) in both ecoprovinces, but a shorter gradient of development in the Southern ecoprovince (Table 1).

Ecoprovince-specific analyses showed that % developed land was not correlated with latitude in either ecoprovince ($p > 0.05$). Percent agriculture was correlated with latitude in the Southern ecoprovince for sites sampled for fish and benthic macroinvertebrate assemblages and in the Northern ecoprovince for sites sampled for diatom assemblages (fish and macroinvertebrate sites: $p < 0.0001$, diatoms: $p = 0.0002$) but not for other assemblage/ecoprovince combinations ($p > 0.05$). As recommended by Payne et al. (2013) we ran separate TITAN analyses (Baker and King 2010) with latitude as the predictor for the specified assemblages and removed robust latitude indicators from the consequent stressor analyses. To examine robustness of the results to geographic correlation, we compared change-point estimates and bootstrapping intervals for models with and without the taxa influenced by latitude.

We also tested for correlation between the 2 types of stress with a subset of watersheds sampled for biotic assemblages. The 2 stressors were not correlated in the Northern ecoprovince ($p = 0.35$), but were negatively correlated in the Southern ecoprovince ($r = -0.64$ to -0.51 , depending on assemblage, $p < 0.001$ for all assemblages). The correlation is a natural consequence of high intensity of land use in the Southern ecoprovince, and the effects of the 2 stressors could not be partitioned. This correlation had only a marginal effect on the concordance of community thresholds across assemblages within the ecoprovince, but certainly affected the comparison of responses between the 2 ecoprovinces.

Biotic community variables

We sampled 5 biological assemblages (birds, fishes, benthic macroinvertebrates, diatom algae, vegetation; Fig. 1) in 2002 and 2003. We obtained bird data for each sampling unit from 10-min point-count listening surveys at 1

to 5 points within the wetland, each sampled twice during the June/early-July breeding season (see Howe et al. 1997, 2007 for details). We sampled fishes at each site with 2 sets of large and small fyke nets set overnight just offshore of the 2 dominant shoreline land uses (Brady et al. 2007). Upon net retrieval, we identified fishes to species and released them. We used D-frame nets to sample benthic macroinvertebrates and later identified them in the laboratory to the highest possible resolution (genus for most insects). We estimated vegetation cover for each taxon in randomly selected 1-m² quadrats (Johnston et al. 2010). We collected diatoms from natural substrates at 0.5- to 3-m depths with a push corer, Ponar sampler, or by rock scrubbing (see Reavie et al. 2006 for details). For each assemblage, we pooled within-site data to yield 1 data point per site. Sites sampled for fish and benthic macroinvertebrates overlapped almost completely, and sites sampled for other assemblages overlapped somewhat (Fig. 1). Sites sampled for each assemblage covered similar gradients of % agriculture but somewhat different gradients for % developed land (Table 1) related to issues of site accessibility and the need to satisfy conditions for site selection (e.g., minimum depth for fishing).

Community threshold analysis

We analyzed community responses to landscape stressors with TITAN (King and Baker 2010, Baker and King 2013), which finds values along the stressor gradient where the greatest community change occurs. This approach combines Indicator Species Analysis (Dufrêne and Legendre 1997) and a multivariate partitioning algorithm to determine the most reliable indicator values (maximum indicator values [IndVals]) for each taxon at each candidate change-point along the stress gradient and to retain change-points with maximum IndVals. As described by Dufrêne and Legendre (1997), a perfect indicator taxon will occur only at sites in the same stress category (i.e., it exhibits perfect *specificity* for that category, or stress level), and is observed in every site in this category (i.e., demonstrates com-

Table 1. Range of stressor values for the sites sampled for each of the 5 assemblages. Agriculture and development are expressed as a percentage of a watershed. Min = minimum, max = maximum.

Assemblage	% agriculture				% developed land			
	Northern		Southern		Northern		Southern	
	Min	Max	Min	Max	Min	Max	Min	Max
Bird	0	78.6	0.1	89.2	0	79.5	4.9	52.6
Fish	0	78.6	0	82.6	0	91.6	4.0	68.2
Invertebrate	0.1	78.6	0	82.6	1.5	69.1	4.0	66.0
Diatom	0.1	84.6	0	83.3	2.2	91.6	5.2	92.9
Vegetation	0.1	78.6	0	82.6	3.3	55.2	6.1	34.2

plete *fidelity* for that category, or stress level). Permutation of sites across the stress gradient is used to determine the significance of each IndVal. Objective partitioning of stress-category groups of taxa is achieved by accounting for uncertainty of taxon-specific change points with bootstrap replicates. Bootstrapping is further used to characterize *purity* of indicator taxa by the consistency with which they are assigned to a particular group and indicator *reliability* (consistency of significant IndVal scores across bootstrap replicates). The TITAN approach uses standardized IndVals (z scores) instead of raw IndVal scores to facilitate consideration of relatively infrequent taxa that exhibit strong responses to the stress gradient (Baker and King 2010).

A community threshold is identified at the point along a stress gradient at which one observes synchronous change in abundance of many taxa. The synchronous change is ascertained by summing all standardized individual taxa IndVals by response group for each candidate change point. The change points with maximum sums of standardized IndVals are then designated as community thresholds (see Baker and King 2010 for details). This method differentiates between taxa responding positively ($z+$) or negatively ($z-$) to the stress gradients. This approach was demonstrated to be more sensitive than methods that aggregate taxon responses prior to analysis (Baker and King 2010, King and Baker 2010, Kail et al. 2012).

For each assemblage, we removed taxa observed at <4 sites from the analysis. The resulting data sets contained 79 bird, 52 fish, 267 diatom, 192 wetland plant, and 99 benthic macroinvertebrate taxa in the Northern ecoprovince, and 54 bird, 39 fish, 192 diatom, 100 wetland plant, and 100 benthic macroinvertebrate taxa the Southern ecoprovince (Table S1). Stressor variables had skewed distributions, in particular in the Northern ecoprovince. However, recent simulations demonstrated relative insensitivity of TITAN to data with a much greater degree of skew (Bernhardt et al. 2012). We used raw stressor data in all analyses (as recommended by Baker and King 2013; but see below for sensitivity analyses), and we $\log(x)$ -transformed all taxon-abundance data prior to analysis. We ran all analyses in R (version 2.12.2; R Project for Statistical Computing, Vienna, Austria). We were most interested in responses of taxa sensitive to environmental disturbance. Therefore, only $z-$ (sensitive taxa) responses were compared across taxa. One of the strengths of this method is that sensitive (i.e., declining in response to stress) and degraded (increasing in response to stress) taxon responses are treated separately, not averaged for an overall community response. As recommended in Brenden et al. (2008) and Baker and King (2010), the stability of threshold solutions was evaluated by examining the shape of cumulative threshold frequencies, the width of quantile intervals around change-point locations, and response shapes of individual taxa.

Responses consistent with community threshold were expected to have synchronous changes in many taxa represented by sharp cumulative responses (cumulative threshold frequencies) for many species, with narrow quantile intervals (5–95% bootstrap quantile interval [QI]) around individual species change points (Baker and King 2010) and biologically meaningful taxon responses (Brenden et al. 2008).

Technical discussion of threshold approaches

The recent debate about threshold-identification approaches and TITAN, in particular, raised issues of inconsistent terminology, sensitivity of approaches to frequency of observations across the stressor gradients, and detection of false positives. Baker and King (2013) emphasized that TITAN was not designed for detecting single-species thresholds. Instead, synchrony in response of multiple taxa, regardless of individual taxon responses, is evaluated as evidence of a community threshold. TITAN successfully handled simulated data similar to species data (i.e., dominated by 0s), and presence of community thresholds was ascertained using additional, independent approaches (Baker and King 2013). However, the discussion of the strengths and limitations of this approach is still ongoing.

Most approaches for detection of ecological thresholds are dependent on sample size, magnitude of change, and frequency of observations across the stressor gradient (Daily et al. 2012). Most important, bootstrapping is essentially a smoothing operation, so all data-partitioning approaches that rely on it, such as nonparametric change-point analysis (nCPA) and TITAN display varying degrees of sensitivity to nonuniform distribution of samples across environmental gradients (Daily et al. 2012). We addressed this potential problem by examining consistency in change-point locations for transformed vs raw stressor data and potential threshold tracking of median stressor scores. $\log(x)$ -transforming the stressor data altered change-point locations by only 0.3 and 1.3% for agriculture and development, respectively, from estimates generated from raw stressor data. This result was expected because binary partitioning analyses are typically insensitive to monotonic transformations of the predictor because they operate on ranks rather than ratio values. Potential bias of this bootstrapping-based approach to distribution of sites across stressor gradient could result in threshold values that track median stressor scores. Therefore, we examined the correspondence between each assemblage's median value for each stressor and its community threshold. Across assemblages, lengths of gradients of % developed land differed more than lengths of gradients of % agriculture. Thus, if thresholds were confounded by distribution of sites across stressor gradient, we would expect greater

concordance among community thresholds in response to agriculture than to development.

RESULTS

Levels of anthropogenic stressors for the sampled coastal wetlands spanned a gradient from 0.0 to 89.2% agriculture and 0.0 to 92.9% developed land (Table 1). Synchronous thresholds were found for % developed land but not for % agriculture (Fig. 2A, B). Concordant thresholds in community composition in stress-sensitive (z^-) taxa for the 5 taxonomic groups occurred at 4 to 6% developed land in the watershed in the Northern ecoprovince and 7 to 10% in the Southern ecoprovince (Fig. 2A). Wider empirical confidence intervals (i.e., QIs) in community thresholds among the 5 assemblages were observed in response to % agriculture than to % developed land. Average thresh-

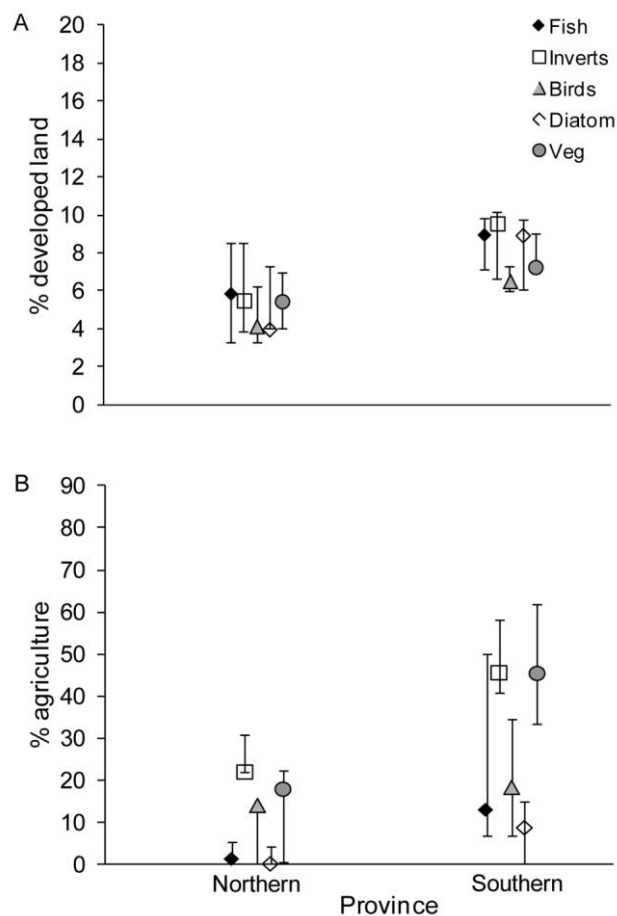


Figure 2. Thresholds (0.05–0.95 bootstrap quantile intervals [QIs]) for coastal fish, invertebrate, bird, diatom and wetland plant community thresholds in response to % developed land (A) and % agriculture (B) in the watershed for the Northern and Southern ecoprovinces of the Great Lakes. QIs can be asymmetrical because of skewed distribution of bootstrapped replicates. Veg = vegetation, Inverts = macroinvertebrates.

olds for % agriculture differed among the 5 assemblages, but the QIs overlapped (Fig. 2B). Thresholds for diatom and fish assemblages occurred at substantially lower % agriculture than those for bird and benthic macroinvertebrate assemblages (Fig. 2B). The community thresholds identified differed between ecoprovinces. For all assemblages, thresholds occurred at higher levels of % developed land and % agriculture in the Southern than in the Northern ecoprovince (Fig. 2A, B).

Threshold identification

Confidence in the existence of community breakpoints was greatest for the % developed land stressor. This confidence was supported by the steepness of cumulative threshold frequency curves (Fig. S1A, B); the number of significant (Fig. S2A), pure, and reliable (i.e., consistently assigned to a particular group and with consistently significant IndVals across bootstrap replicates) indicators; QIs associated with individual taxa (Fig. 3A–E); and individual taxa–stressor relationships (Fig. S3). However, birds in the Southern ecoprovince (Fig. 3I) and fishes in the Northern ecoprovince (Fig. 3A) were exceptions to this trend because the location of the change point was based on a very small number of reliable indicator taxa. In contrast to the sensitive-community responses, degraded communities exhibited more-gradual changes in response to stress (Fig. S1A, B).

Along the % agriculture stressor gradient in the Northern ecoprovince, 4 of the 5 assemblages exhibited threshold-consistent responses characterized by steep cumulative threshold frequency curves (Fig. S1C) and many reliable indicator taxa with narrow (0.05–0.95) QIs (Fig. 4A, C–E). The macroinvertebrate assemblage did not have a sufficient number of reliable indicator taxa and did not yield steep cumulative frequency curves characteristic of a typical threshold response (Fig. 4B, Fig. S1C). Along the % agriculture stressor gradient in the Southern ecoprovince, responses of all assemblages were inconsistent with the threshold model based on the criteria described above (Fig. 4F–J, Fig. S2B), possibly because the 2 stressors were confounded and because of the scarcity of relatively pristine watersheds (see Discussion).

No matches were found between stressor medians and community thresholds (Table S2), indicating that this method is relatively robust to the distribution of sites across the stress gradients. This situation is most obvious for % agriculture, where median values of the stressor were relatively consistent across assemblages, whereas thresholds were very different. This difference seemed a bit smaller for % developed land because of congruent thresholds, but large (e.g., 13 sites for diatoms) and inconsistent differences existed between sites with median % development and sites with % development at community threshold.

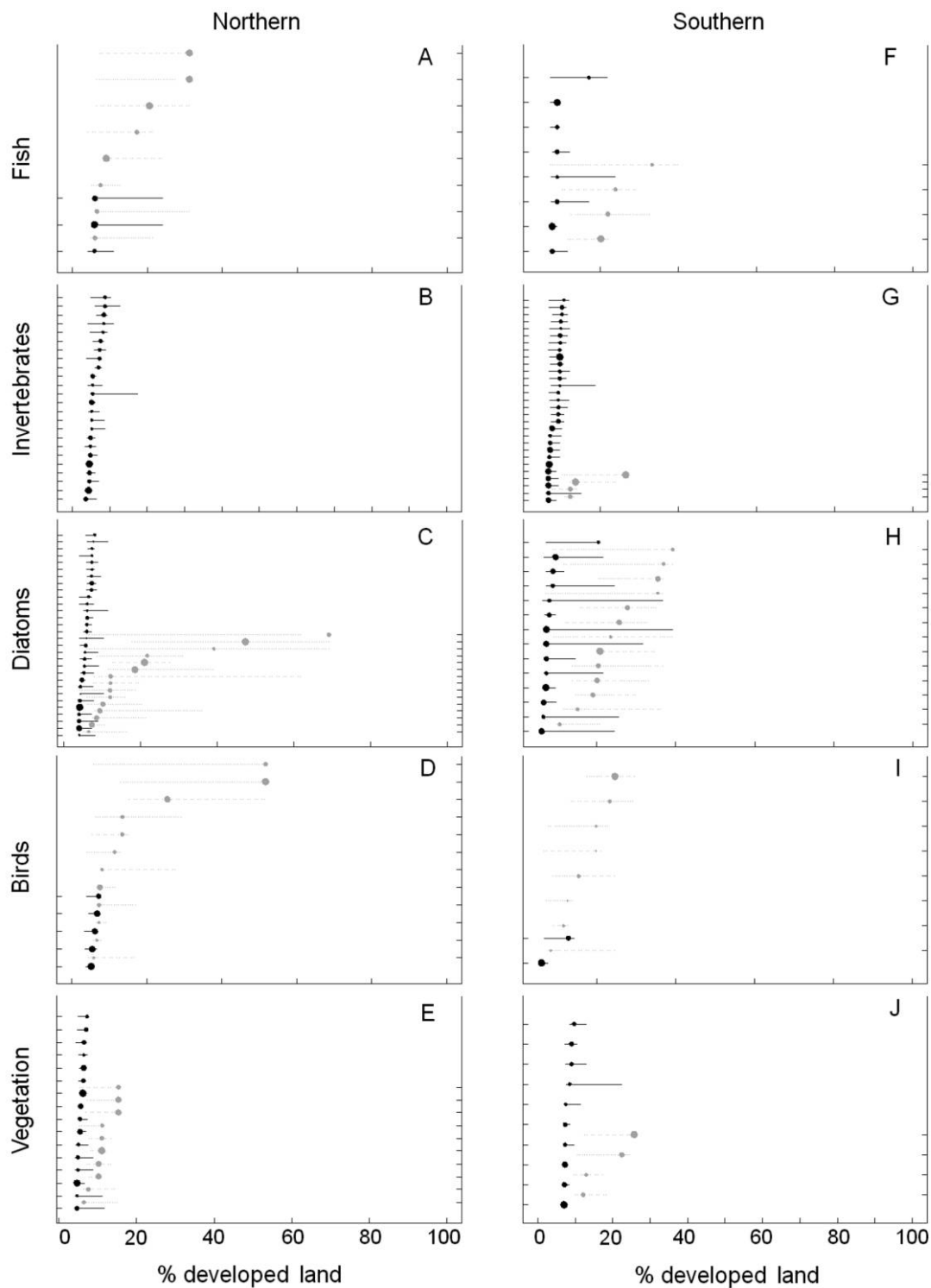


Figure 3. Change-points (0.05–0.95 bootstrap quantile intervals [QIs]) for significant sensitive indicator fish (A, F), invertebrate (B, G), diatom (C, H), bird (D, I), and vegetation (E, J) taxa along the stressor gradient % developed land in the Northern (A–E) and Southern (F–J) province that contribute to threshold determination. Responses consistent with the threshold model are characterized by a large number of individual indicators and narrow QIs around their change points. Indicator value p -value cut-off = 0.05; purity and reliability cut-offs = 0.8. Identity of indicator taxa is not discussed in this paper. Note that representation of $z+$ (tolerant) indicator responses (grey), although not discussed in the context of this paper, is important for comparison of results across methods and systems. The scale reflects the entire overall range of the stressor gradients.

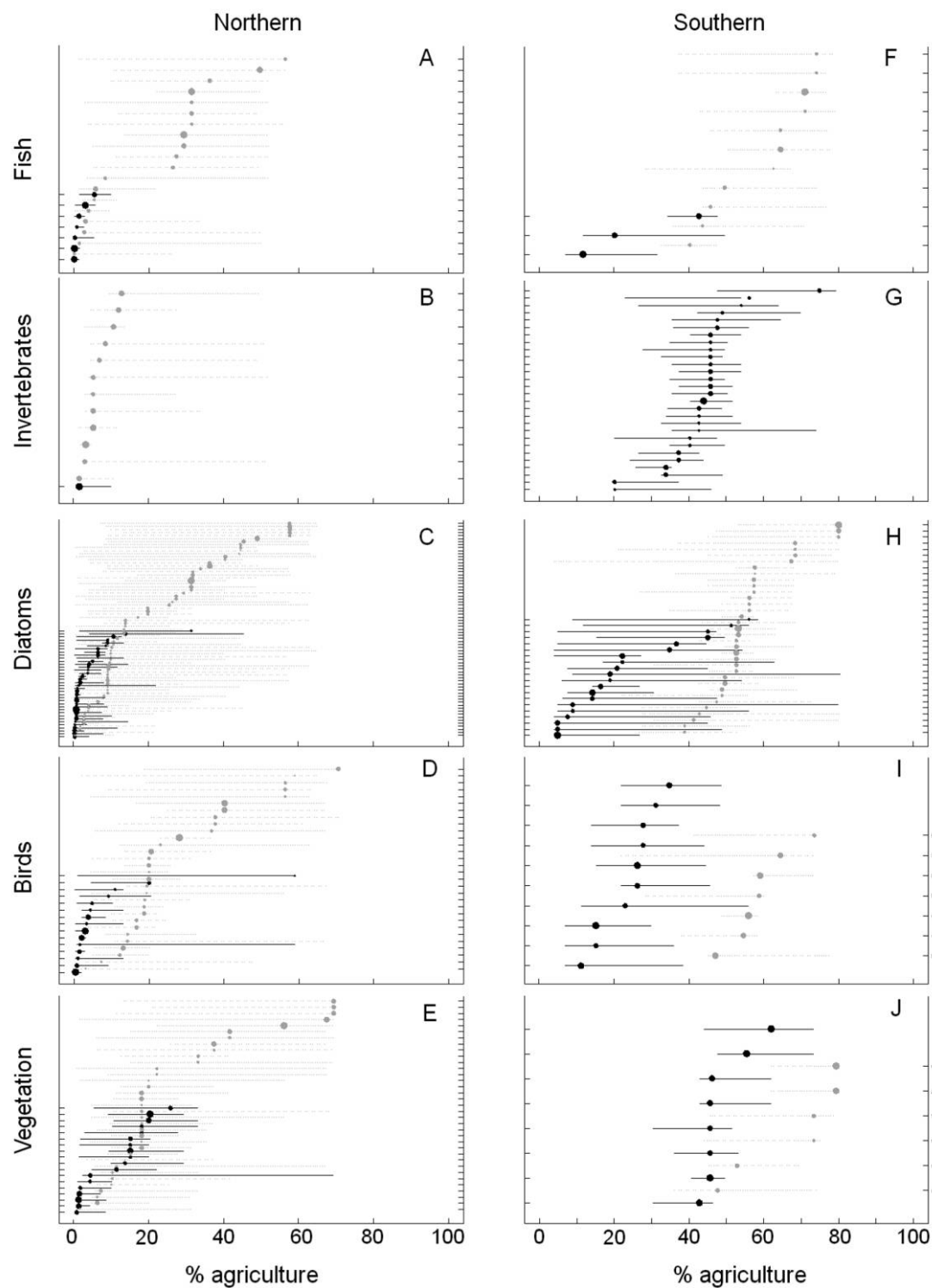


Figure 4. Change-points (0.05–0.95 bootstrap quantile intervals [QIs]) for significant sensitive indicator fish (A, F), invertebrate (B, G), diatom (C, H), bird (D, I), and vegetation (E, J) taxa along the stressor gradient % agriculture in the Northern (A–E) and Southern (F–J) province. See Fig. 3 for explanation of figure.

Community thresholds tended to be lower than the median % development.

Geographic covariation

For data sets with significant confounding between % agriculture and latitude, we repeated the analyses without the taxa responding to the latitudinal gradient. For diatoms in the Northern ecoprovince, when all species with significant responses to latitudinal gradient were excluded from the analysis (17 out of 40 robust indicators), no detectable difference was seen in the resulting community threshold, but the 5 to 95% QI decreased by 20%. For fish in the Southern ecoprovince, we removed 1 of 3 robust indicators and found no detectable change in the average change-point or the QI. For the benthic macroinvertebrate assemblage, we removed 14 of 27 robust indicators and found no change in the average change-point, but the QI decreased by 40%. These results indicate that observed community thresholds and their concordance across assemblages reported above are robust to the confounding effect of latitude on agriculture, where it existed.

DISCUSSION

The % developed land in a watershed at which community thresholds occurred was consistent across stress-sensitive taxa from 5 assemblage types: birds, fish, benthic macroinvertebrates, wetland vegetation, and diatoms. The approximate location of these thresholds along the stressor gradient agrees well with previous findings that changes in benthic macroinvertebrate and fish communities occur at low to very low (1–5%) levels of urbanization or impervious land cover associated with development (Wang et al. 2000, Stepenuck et al. 2002, Baker and King 2010, Hilderbrand et al. 2010, King et al. 2011, Utz and Hilderbrand 2011, Kail et al. 2012). Our threshold estimates for these 2 assemblages were slightly higher than 1 to 5% developed land, but still similar to published values given the length of the development gradient (0–92%).

Various approaches have been used to characterize community thresholds (e.g., Booth and Jackson 1997, Wang et al. 2000, Qian et al. 2004, Trebitz 2012). Utz et al. (2009) used cumulative frequency distributions to detect similar responses to development in stream macroinvertebrates. Gradient-boosted generalized linear models detected decreased macroinvertebrate richness in small streams draining watersheds with >3% impervious cover (Maloney et al. 2012). Threshold detection approaches have been a subject of recent controversy (Cuffney et al. 2011, Daily et al. 2012, but see Baker and King 2013), but the consistency of findings across methods, systems, and taxa is very encouraging and increases our confidence in the existence of a threshold response and its location along the stressor gradient. Documentation of such biological sensitivity to de-

velopment has been used to justify the importance of creating protected areas in streams (Hilderbrand et al. 2010), a scenario that may need to be considered for coastal and lacustrine systems as well. This sensitivity of assemblages also emphasizes the need for additional research on local habitat factors that could mitigate watershed-scale anthropogenic stress and on interactions between local- and watershed-scale factors in light of climate-change scenarios (e.g., Wiley et al. 2010).

Our findings support the conjecture that anthropogenic stress, particularly in the form of development, in watersheds exerts strong effects on ecological communities of coastal wetlands in the Laurentian Great Lakes (Brazner et al. 2007a, Niemi et al. 2011). In the Southern ecoprovince, strong responses to development were observed despite the negative correlation between development and agriculture, although absence of pristine habitats and their associated assemblages could have led to higher thresholds in the south than in the north. The mechanisms behind the effects of development on the resident communities may include pollutant and sediment discharge, increasing amount of impervious surfaces, and direct habitat destruction (reviewed in Allan 2004). A suite of factors acting on multiple scales (Brazner et al. 2007a) could have led to the observed congruence of thresholds across communities. Threshold congruence also could be caused by integration of the effects of watershed-scale stressors at the local scale. For example, watershed-scale degradation in water quality and disturbance of vegetation associated with increasing agriculture and development lead to consistent local-scale stressors on associated diatom (via water quality) and bird, fish, and macroinvertebrate communities (via habitat degradation). Aquatic and nearshore wetland vegetation is particularly important for persistence of wetland communities, and its destruction has cascading effects on wetland communities (Uzarski et al. 2009) by removing the structural matrix on which many assemblages rely (Diehl and Kornijów 1997, Kovalenko et al. 2012). King et al. (2011) argued that nonlinear responses are characteristic of assemblages facing novel stressors, such as those associated with changes in water quality or hydrology subsequent to development. Regardless of the mechanism, such congruence could indicate the presence of a true ecosystem threshold when changes in several biological assemblages occur around the same stressor value.

Communities could be less sensitive to % agriculture in the watershed than to the more-direct habitat disturbance associated with increasing development, especially if some mediating local factors, such as riparian buffers or other best-management practices, are in place. Many studies have demonstrated sensitivity of terrestrial birds and other taxa to habitat loss and fragmentation in developed landscapes. In some cases (Palomino and Carrascal 2007, Garaffa et al. 2009), species exhibited threshold responses

to landscape degradation. However, these studies illustrated changes associated with displacement of habitat by agriculture or urbanization. The effects of agricultural activities on coastal wetlands may be more indirect and, therefore, less likely to be manifested as threshold responses. For example, DeLuca et al. (2004) documented threshold changes in marsh bird assemblages of Chesapeake Bay in response to human land use, but the effects were seen at local scales, not at the watershed scale. Agricultural stressors act through a variety of mechanisms, including sediment and fertilizer run-off and nonpoint source pollution (reviewed in Allan 2004). Previous studies also showed a wide range of responses, absence of clear community thresholds, or changes that were noticeable only when most of the land was converted to agriculture (e.g., Wang et al. 2000, Allan 2004, Riseng et al. 2011). In the case of our data, the absence of truly pristine locations in the Southern ecoprovince, a consequence of a long history of agricultural land use, and covariation of the developmental and agricultural stress gradients may have contributed to absence of threshold responses to stress in associated communities.

The interprovince differences in stress thresholds in our study correspond with biogeographical differences in associated communities and their sensitivity to the stress gradient. For instance, diatom assemblages in the Southern ecoprovince are tolerant to the contemporary environmental stress in the region, such as higher nutrient concentrations, so a threshold was observed at a higher level of stress than for the Northern ecoprovince. Hanowski et al. (2007) noted that the composition of coastal wetland bird communities differs substantially between Northern and Southern ecoprovinces of the Great Lakes. Other investigators have found large differences in macroinvertebrate communities in rivers on and off the Precambrian shield (Neff and Jackson 2011) and in catchments across mountain, piedmont, and coastal physiogeographies in the Mid-Atlantic region (King et al. 2011). Human land use is often correlated with natural latitudinal gradients (reviewed in Allan 2004), but for the within-ecoprovince analyses, we demonstrated that land use had an overriding effect on community thresholds when agricultural land use and latitude were significantly correlated. In an analysis of communities along the US coast of Lake Superior, where latitudinal variation is minimal, Niemi et al. (2011) showed that at least some of the observed variation was associated with gradients of agricultural and urban development.

We are unaware of other analyses of congruence in community threshold responses, so we are unable to compare our results to patterns in other systems. However, the threshold congruence patterns observed in our study run contrary to previously reported diversity trends among different taxa. Most investigators have shown discordance in

the responses of different taxonomic groups (Hirst et al. 2002, Johnson et al. 2006, Brazner 2007a, Lewis et al. 2007, Johnson and Hering 2009). Fahrig (2001) simulated threshold responses of birds and other organisms to habitat loss, but she expected these thresholds to be asynchronous among species and species groups. Stralberg et al. (2009) predicted that varying responses of bird species to climate change would lead to novel community assemblages, and this lack of congruence would be expected to generate even greater differences in multitaxon assemblages. In a recent review, Heino (2010) reported low correspondence in diversity among various taxonomic groups across all freshwater systems and taxa, a result that limits application of cross-taxon congruence in conservation (i.e., use of certain assemblages as a proxy for others). Similarly low concordance in biodiversity was observed in a meta-analysis of biodiversity trends among terrestrial taxa (Flather et al. 1997). The difference between community thresholds and biodiversity trends might be explained by the fact that aggregate metrics, such as biodiversity, are confounded by synchronous changes in sensitive and tolerant taxa (King et al. 2011, Baker and King 2013).

Application of thresholds in management is complicated by uncertainties associated with their predicted location along the stressor gradient and, in most cases, limited understanding of the mechanisms underlying a system's response (Groffman et al. 2006, Dodds et al. 2010). The most promising warning signals of ecosystem thresholds are increasing autocorrelation (Scheffer et al. 2009) and variance (Carpenter and Brock 2006) in the system's pattern of fluctuations over time. Elucidating such patterns requires long-term data to distinguish proximity to a threshold from natural variability in system's response (Andersen et al. 2009). Thresholds associated with community shifts can be especially difficult to detect because of inherent variability in community composition and problems with detectability of less-common species. In our case, threshold similarity across different assemblages increases our confidence in its location. On the other hand, despite a relatively strong concordance in responses of different taxa, uncertainty associated with the response of each taxon (5–95% QIs) leads us to recommend a multitaxon approach rather than use of a particular assemblage as an indicator for all other groups to increase confidence in identifying environmental thresholds. This recommendation is consistent with those of many assessment programs (e.g., Barbour et al. 1999).

Changes in assemblage composition in response to development stress were more consistent with the threshold model than were changes in response to stress associated with agriculture. Nevertheless, with its limitations explicitly acknowledged, our approach can be used to infer the extent of environmental disturbance that is likely to cause significant changes in community composition. Therefore,

this approach can be used to inform watershed-restoration and land-use-planning decisions. Such information is especially valuable for identifying sites at greatest risk of significant change. Sites at risk that have not yet approached the threshold could be designated as priority sites for management intervention. Concordant changes in several communities emphasize the risk of functional changes in ecosystems and the need for management action. Furthermore, concerns regarding concurrent changes in several assemblages, some more charismatic than others, are easier to convey to stakeholders than concerns about a precipitous decline in a particular group for which public awareness may be nearly nonexistent.

Our analyses of Great Lakes coastal wetlands indicate that a relatively large number of sites are subject to levels of anthropogenic stress above that necessary to elicit a threshold response. This conclusion is not surprising, especially in the Southern ecoprovince, because of high population density, a long history of settlement and agriculture, and anthropogenic pressure on the Great Lakes coastal ecosystem. A combination of our results and the entire set of Great Lakes watershed-level stress scores (http://beaver.nrrri.umn.edu/gleidb/gleidb/gdb_main) can be used to identify areas that must be prioritized for management intervention to sustain biological communities associated with minimally degraded conditions. These results could be used to make long-term projections of watershed-scale changes on resident biological communities.

In summary, we detected congruent, marked changes in bird, fish, benthic macroinvertebrate, wetland plant, and diatom assemblage composition in response to watershed development across the Great Lakes coastal margin. Cross-taxon responses to agricultural stress were less congruent but still overlapped. Our results indicate that watershed-scale anthropogenic stress leads to pronounced simultaneous changes in many biotic assemblages, with potential for nonlinear functional changes in aquatic ecosystems.

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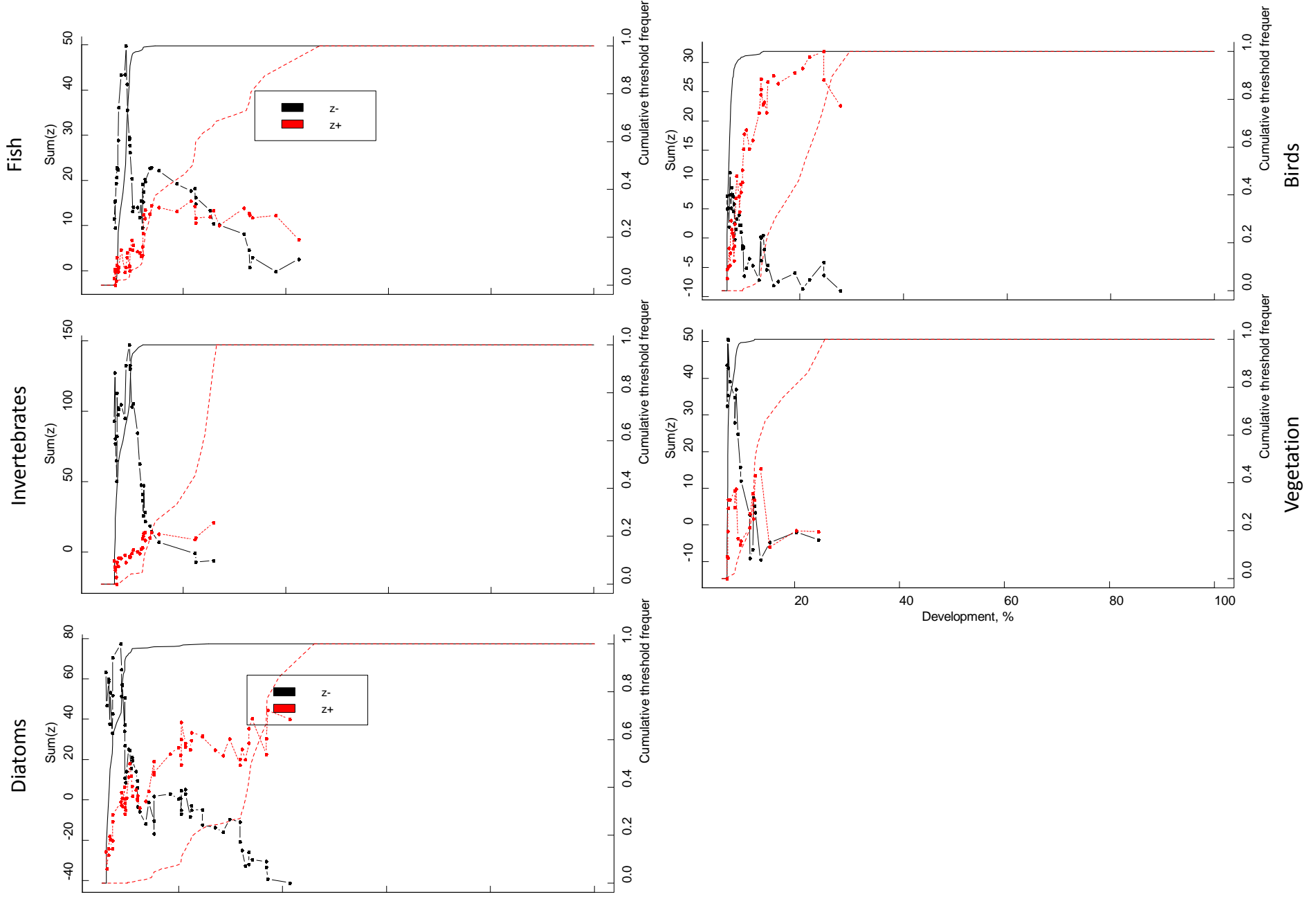
Table S1. Number of sites sampled, total number of taxa, and number of taxa used in the analyses (after removing taxa with frequency <4) for each assemblage in each of the 2 ecological provinces. *Original number of taxa in the merged-province data set was 2109. The number shown here is the number of taxa satisfying occurrence criteria as per Reavie et al. (2006).

Ecoprovince	Assemblage	Sites	Total taxa	Taxa used
Northern	Bird	99	139	79
	Fish	80	89	52
	Invert	57	193	99
	Diatom*	58	327	267
	Vegetation	96	227	192
Southern	Bird	53	98	54
	Fish	59	79	39
	Invert	44	182	100
	Diatom*	33	310	192
	Vegetation	74	183	100

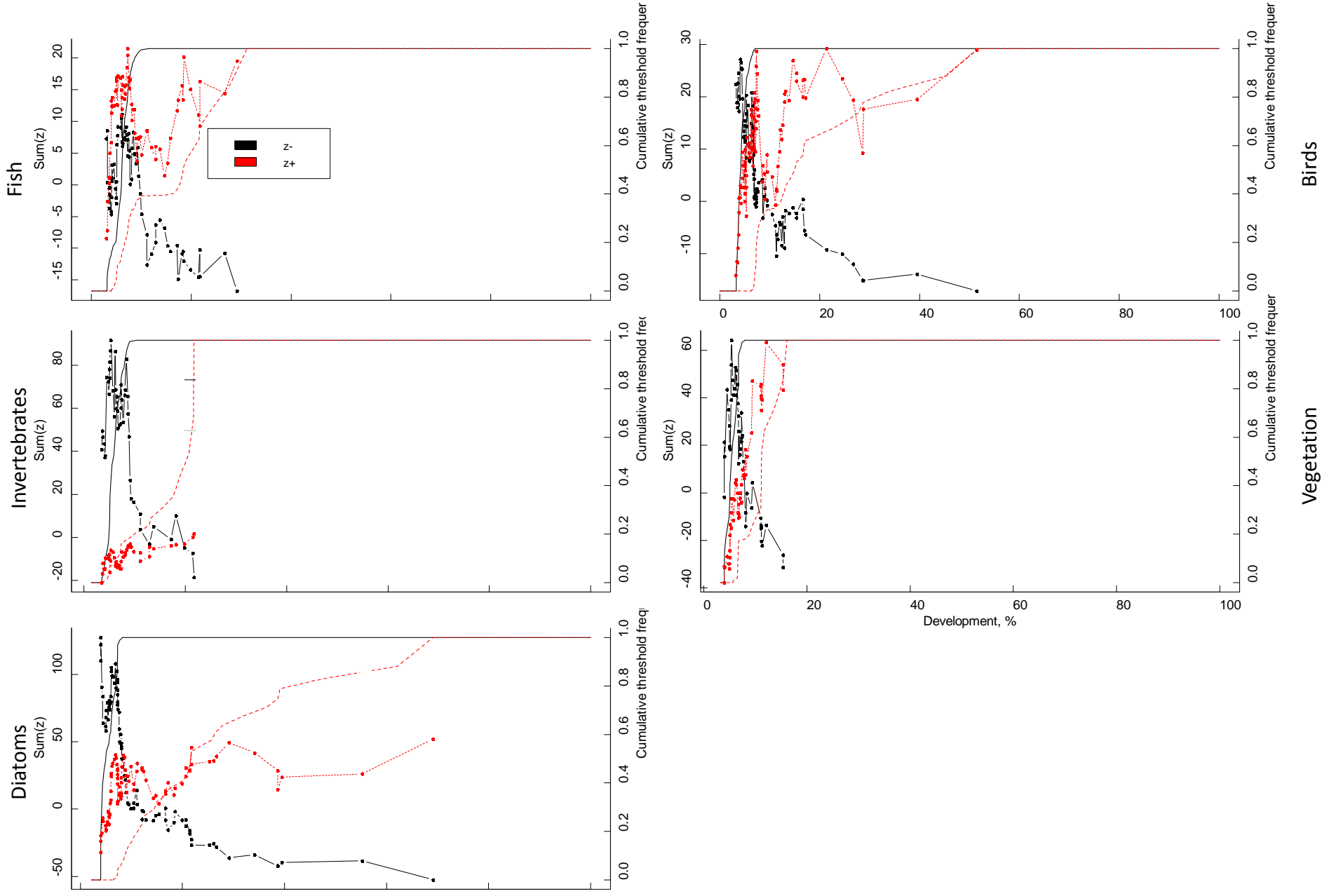
Table S2. Examination of effects of sample-to-environment distribution by comparing median stressor values and community thresholds (cp). Because median stress scores are similar, congruent threshold responses may seem to track those medians. However, the facts that change-points never coincide with the median and that a rather large absolute difference exists in the number of sites below the median vs the number of sites below the threshold indicate that sample-to-environment distribution is unlikely to have overriding effects on observed patterns.

Ecoprovince	Assemblage	Median % agriculture	cp	Median % developed land	cp
Northern	Fish	3.30	1.41	7.39	5.87
	Invertebrate	5.58	22.25	7.13	5.53
	Bird	8.85	14.29	6.91	4.18
	Diatom	4.22	0.41	8.05	4.02
	Vegetation	9.25	18.15	6.77	5.49
Southern	Fish	42.09	13.07	11.49	8.97
	Invertebrate	42.70	45.83	9.84	9.59
	Bird	45.21	18.59	8.94	6.55
	Diatom	44.49	8.99	13.08	8.97
	Vegetation	50.54	45.65	9.66	7.29

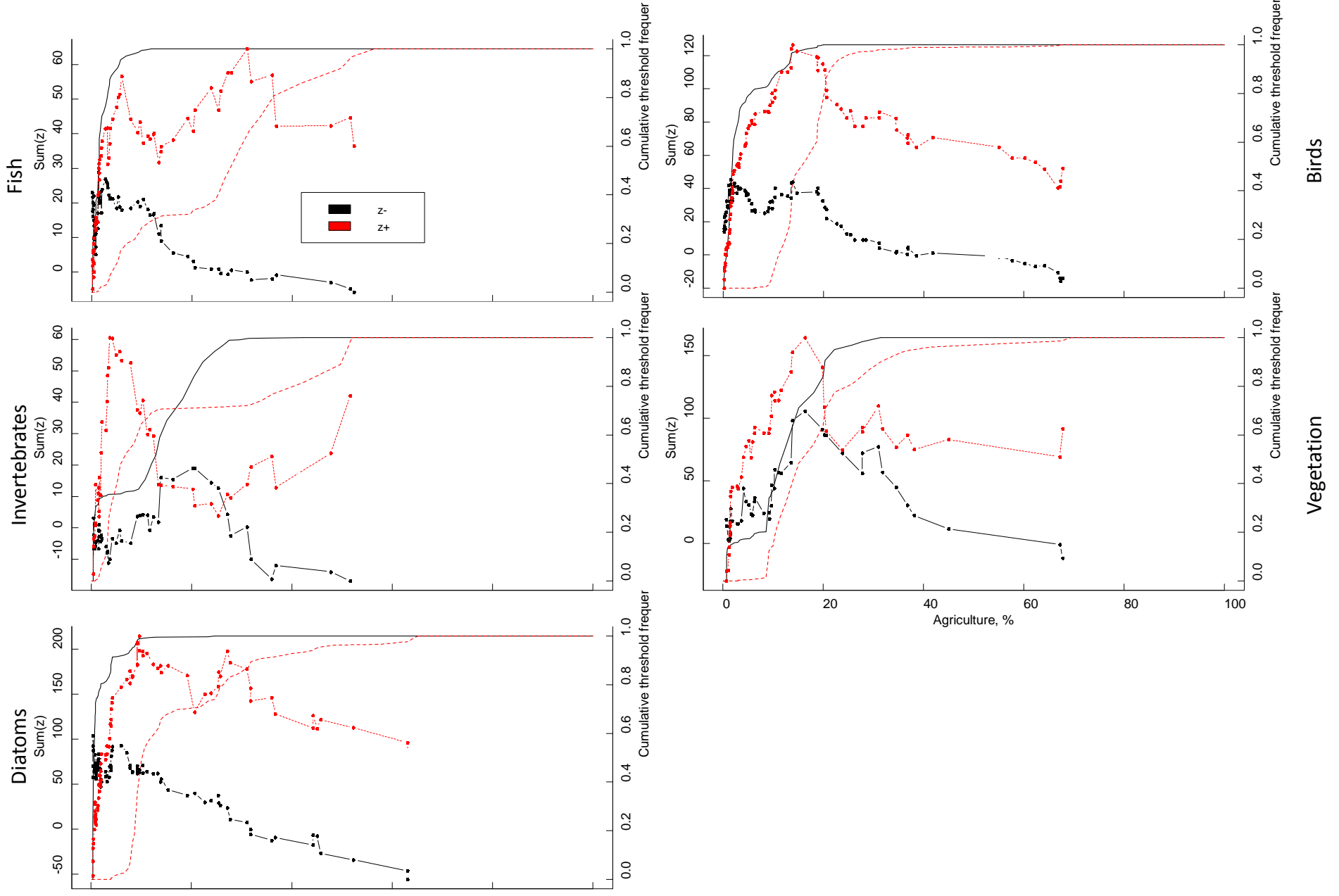
A) Northern province, % developed land



B) Southern province, % developed land



C) Northern province, % agriculture



D) Southern province, % agriculture

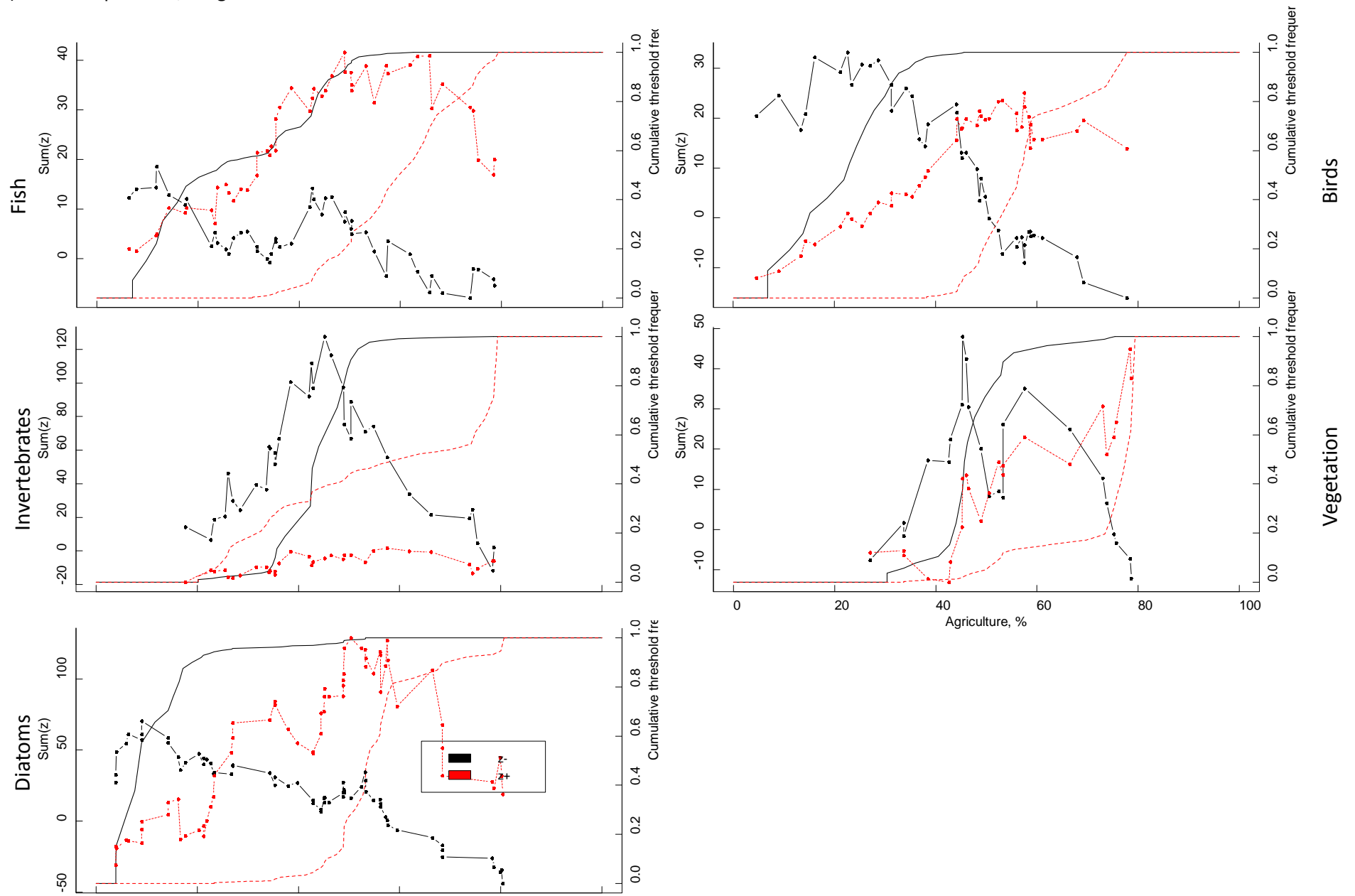


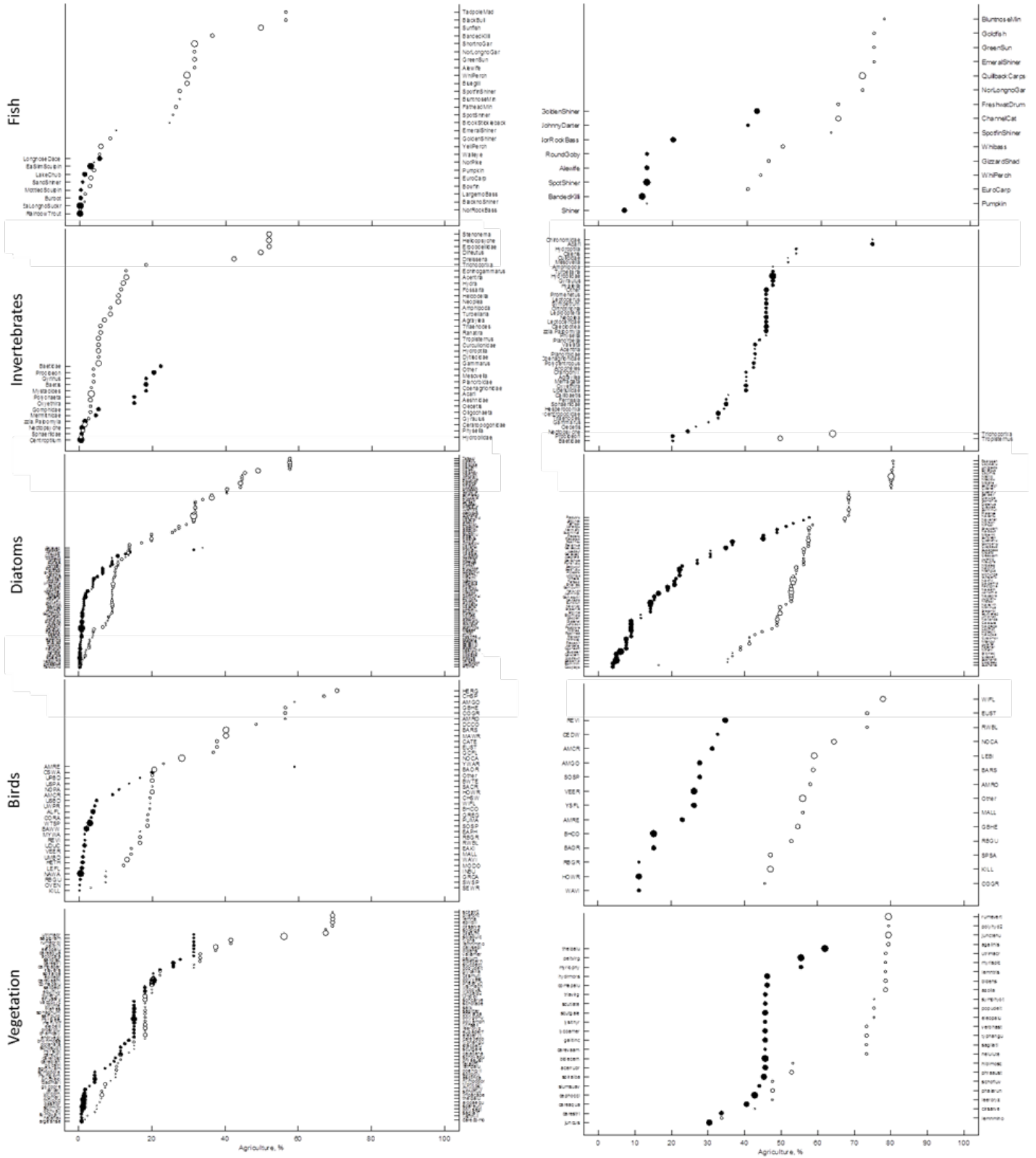
Fig. S1. All candidate change points for sensitive (black dots) and degraded (red) communities along the % urban land (A, B) and % agriculture (C, D) gradients in the Northern (A, C) and Southern (B, D) provinces. Lines (black solid for sensitive community and red dashed for degraded)

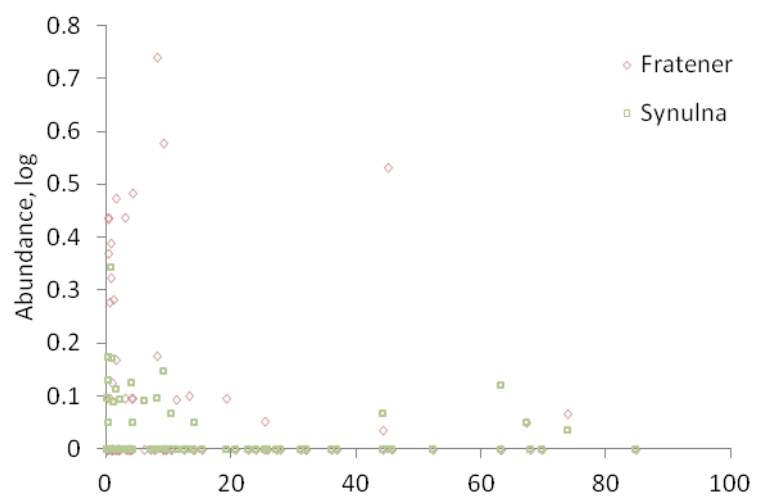
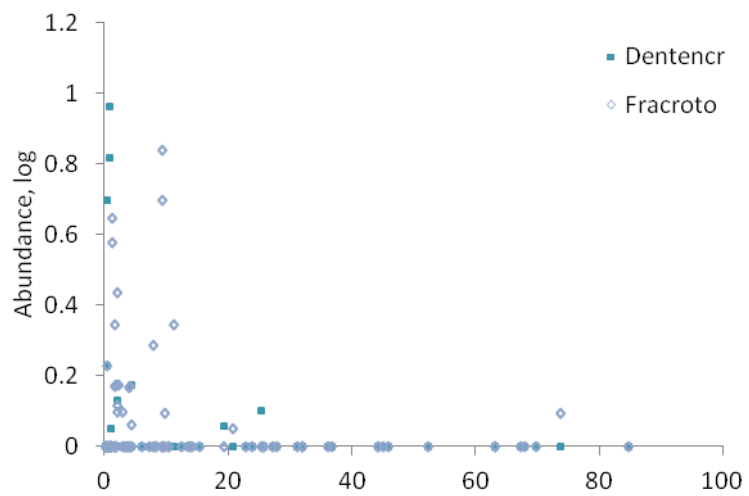
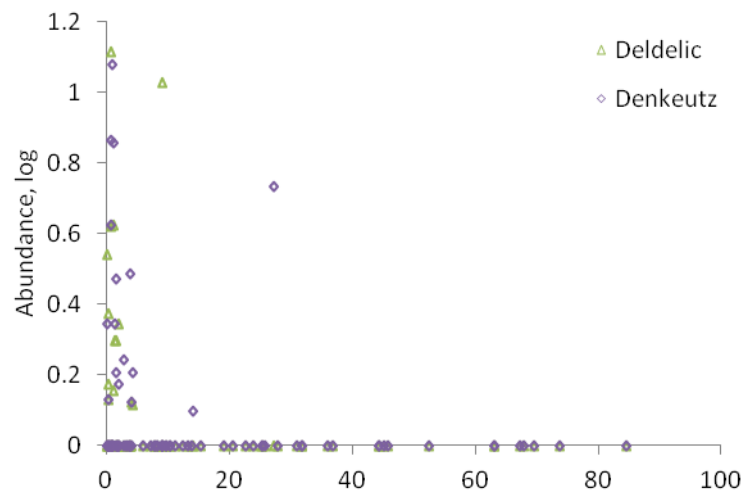
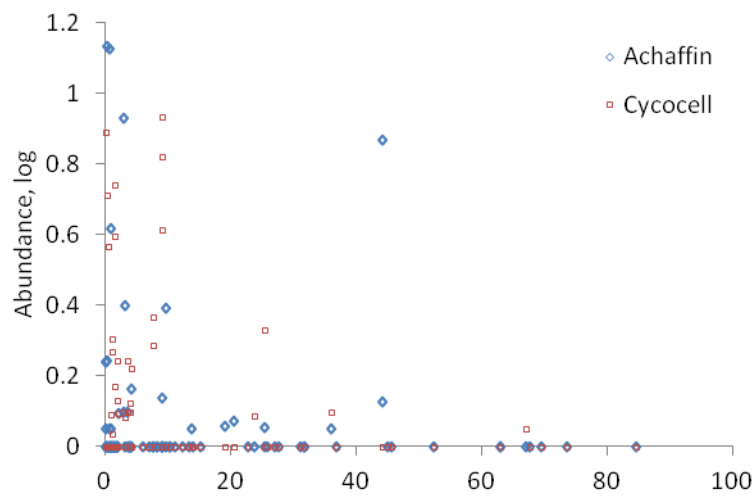
represent cumulative frequency distribution of change-points. Cumulative frequency curves are expected to be more steep (corresponding to synchronous changes in many taxa) in the case of true threshold response. The scale reflects the entire total range of the stressor gradients.

B) % agriculture

Northern Ecoprovince

Southern Ecoprovince





SI Fig. 3. An example showing declines in individual sensitive indicator taxa in response to stress. This example featuring several robust indicators, not confounded with latitude (see Results), from the diatom assemblage in the Northern province along the % agriculture stressor gradient.

Achaffin - *Achnanthydium affine*, Deldelic - *Delicata delicatula*, Denkuetz - *Denticula kuetzingii*, Dentencr - *Denticula tenuis* var. *crassula*,

Cycocell - *Cyclotella ocellata*, Fracroto - *Fragilaria crotonensis*, Fratener - *Fragilaria tenera*, Synulna - *Synedra ulna*.

Fig. S2. Community changes in the 5 assemblages as characterized by species with significant indicator values (sensitive species in black, tolerant in white) before applying reliability and purity constraints. This figure illustrates magnitude of change across the 5 assemblages. Identity of individual taxa is not discussed.