Title: A probability-based indicator of ecological condition

Authors: Robert W. Howe, Ronald R. Regal, Gerald J. Niemi, Nicholas P. Danz, and JoAnn M. Hanowski

Abstract

We introduce a new method for quantifying the ecological condition (C) of sites based on documented species' responses to environmental stress. Preliminary research is needed to provide species-specific logistic functions, representing probabilities of finding individual species across an explicit reference gradient, ranging from maximally stressed (C = 0) to minimally stressed (C = 10) localities. Each function takes into account the species' tolerance to stress, the species' overall ubiquity, and the probability of detecting the species when it is present. Given a set of standardized species-specific functions, the ecological condition of any site can be derived by iteration, converging on the value of C that best "predicts" the species that are actually present. Species from multiple taxonomic groups can be included in the calculations, and results are not directly affected by species richness or sampling area. We demonstrate a successful application of this method for bird species assemblages in the U.S. portion of the Great Lakes coastal zone. Approximately 28% of the bird species observed in the Eastern Deciduous Forest Ecological Province and 35% of the species in the Laurentian Mixed Forest Ecological Province showed strong relationships with a reference gradient of land cover variables. Functional stress-response relationships of these species can be used effectively to estimate ecological condition at new sites. The estimated condition based on bird species generally mirrors the reference condition, but deviations from the expected 1:1 relationship provide meaningful insights about ecological condition of the target areas. Sensitivity analysis using different numbers of species shows that our method is robust and can be applied consistently with 25-30 species exhibiting strong stress-response functions.

Introduction

The use of biological assemblages as indicators of ecological condition has followed a long tradition (Niemi & McDonald 2004). In most applications, species or taxa are assigned weights reflecting their sensitivity to environmental degradation. Presence/absence or abundance of these species, alone or in some combination with other species, provides an indicator of a site's ecological condition. The saprobien system of Kolkwitz and Marsson (1908), for example, introduced the use of weighted abundances of benthic invertebrates as an index of water quality. Related measures such as the Hilsenhoff Index for stream invertebrates (Hilsenhoff 1982) and Floristic Quality Index (Wilhelm & Ladd 1988) are widely used today to characterize the condition of local ecosystems. Karr's Index of Biotic Integrity (IBI) addresses functional aspects of ecosystems and incorporates a range of ecological variables besides the presence/absence or abundance of indicator species (Karr 1981). This approach has been applied effectively to many environments and taxonomic groups during the past two decades (Karr *et al*. 1987, Miller *et al*. 1988, Lyons *et al*. 1995, O'Connell 1998, Harris & Silveira 1999 and others). An implicit feature of the IBI approach is the assignment of quantitative weightings (e.g., 1,3,5) that reflect ecologically meaningful deviations from a reference condition. These weightings are at least partly subjective because the variables and scores come largely from expert opinion and the scale of comparison for a given IBI may be complicated or inflated if the biological variables are correlated. Alternatively, multivariate approaches have been developed by Armitage *et al*. (1987), O'Connor *et al*. (2000), Marchant & Hehir (2002), Clarke *et al*. (2003), and others. These statistical methods tend to be data intensive but require fewer subjective decisions than in the IBI approach. RIVPACS (**R**iver **Inv**ertebrate **P**rediction **a**nd **C**lassification **S**ystem), one of the most successful multivariate approaches to indicator development (Wright *et al*. 2000), has influenced formulation of the European Union's Water Framework Directive (European Commission 2000).

Indicators of ecological condition are useful because they provide objective benchmarks for detecting environmental change, they create targets for management activities, and they can be used as standards for environmental regulations. Indicators based on biological communities have several important advantages over measurements of physical variables (Yoder & Rankin 1998, Karr & Chu 2001, Karr 2001). First, living organisms experience the entire range and variation of environmental conditions through time, whereas physical or chemical measures are often highly variable, and snapshot measurements can easily misrepresent the true nature of conditions. Second, species integrate the effects of multiple stressors, including those whose mechanisms or even existence might be poorly known. Finally, responses of animal species are directly relevant to humans because they reflect many of the same physiological and ecological needs that affect our health.

Although community metrics such as species richness and diversity are often used as biological indicators (Niemi & McDonald 2004), such measures can be misleading if species respond differently to stress. Some species may become more abundant with increased stress while other species may become less abundant. A more accurate and robust indicator of condition should account for these differences. Here we introduce a new, probabilistic approach to the development of ecological indicators that incorporates clearly documented information about species' sensitivities or tolerances to environmental stress. Condition is determined by the stress-response relationships of observed species; sites inhabited mainly by sensitive species yield high values of condition, whereas sites inhabited mainly by tolerant species will yield low values. Like the method of O'Connor *et al*. (2000), the indicator that we describe can include multiple taxonomic groups and, like the RIVPACS approach (Wright *et al*. 2000), it relates observed species presences to expected probabilities of presence. Our approach is unique in its probabilistic method of calculation and its ability to take into account both the ecological sensitivity of species as well as the detectability of species given a prescribed sampling method.

Our quantitative concept of "ecological condition" folds anthropogenic stressors into a single gradient. We define the optimal condition for a geographic region as having a value of 10 and the maximally degraded condition a value of 0. Field data of observed species presences are used to estimate ecological condition according to an iterative approach described by Hilborn & Mangel (1997).

A critical assumption of this approach is that species respond (in various ways) to a common gradient of ecological condition. Specifically, a reference gradient must be defined *a priori* in order to quantify parameters of the species-specific stress response relationships. Sites with ideal condition (e.g., C = 10) might not exist in nature, but the investigator nevertheless must be able to estimate the expected probabilities of presence under all conditions. Identification of the reference gradient is the primary level of subjectivity in our approach. Any application of environmental indicators requires some degree of subjectivity; in our case, the subjective element (definition of a reference gradient) is explicit. Alternative interpretations of optimal vs. degraded condition can be applied in the same way as we describe here, yielding alternative (but transparent) measures of a given site's ecological condition.

We apply the probability-based indicator to bird assemblages near coasts of the U.S. portion of the Great Lakes. An anthropogenic stress gradient was defined by remotely-sensed land cover, which we used to quantify stress/response relationships of individual species. Ecological condition (C) of novel sites was estimated by iteration, producing values of C that best reflect the stress/response profiles of targeted bird species. Our purpose is to illustrate the utility and flexibility of this method for biological assessment of local sites.

Methods

We start with a model describing how the probability of observing a particular species, $P_i(C)$, is related to ecological condition, C. The probability of observing the ith species at any given site is a function of the site's condition and quantitative attributes describing how the species responds to changes in ecological condition, its overall ubiquity or probability of presence in the study area, and how easily the species is detected when it is present. We will call this quantitative relationship a *species-specific sensitivity/dectability* (SSD) function.

Although there are many ways to describe a species' sensitivity to stress and its detectability, we use a four parameter logistic curve, similar to an equation used by Pinheiro & Bates (2000):

$$P_i(C) = \beta_{i,1} + \beta_{i,2} \frac{e^{\beta_{i,4}\left(C - \beta_{i,3}\right)}}{1 + e^{\beta_{i,4}\left(C - \beta_{i,3}\right)}} \qquad (1)$$

where

$\beta_{i,1}$ = the lowest probability of observing species i (across all values of C between - 4 and 4);

$\beta_{i,2}$ = the difference between highest and lowest probabilities of observing species i (across all values of C between - 4 and 4);

$\beta_{i,3}$ = the condition (C) where P = $\beta_{i,1}$ + ½ $\beta_{i,2}$; and

$\beta_{i,4}$ = a measure of the steepness of the function at $\beta_{i,3}$.

The parameters can be estimated from expert opinion or derived from field data. If expert opinion is used, the parameters can be approximated by specifying $\beta_{i,1}$. the minimum probability of observing the species, $\beta_{i,1}+\beta_{i,2}$. the maximum probability of observing the species, $\beta_{i,3}$. the condition (C) where the probability of observing the species is halfway between $P(C_0)$ and $P(C_{10})$, and $\beta_{i,4}$. an estimate of the function's steepness (with positive or negative sign) at $\beta_{i,3}$, where $\forall$ 5, for example, represents a steep increase or decrease and 0.5, for example, represents a gradual increase or decrease in probability. The simplest approach for eliciting expert opinion is to provide an Excel sheet that plots P(C) for given values of the β parameters and let the expert change the β parameters until the desired response function is generated. If field data are used, parameters for a species, $\boldsymbol{\beta}_\iota = (\beta_{i,1}, \ldots, \beta_{i,4})$, can be derived iteratively using a computer program such as Microsoft Excel's Solver. In this case, an explicit reference gradient must be specified, and probabilities (or frequencies) of observing the species at different points along the gradient need to be documented. Computer iteration can be employed to find the parameters that best "fit" the observed data. Once obtained, parameters from multiple species can be used to estimate the ecological condition of new areas or samples. The derived β parameters are fixed constants for an area or region of interest, much like fixed weights in traditional methods like the Hilsenhoff (1982) Index or Floristic Quality Index (Wilhelm & Ladd 1988).

Different forms of the SSD functions represent different species' responses to ecological condition (Fig. 1). Sensitive species typically show a strong positive response to condition (C), with a low probability of presence/detection at $P(C_0)$ and a much higher value at $P(C_{10})$ (Fig. 1a). Many (but not all) tolerant species show the opposite pattern, with highest probability of presence/detection at sites with a low value of condition, i.e., high $P(C_0)$ (Fig. 1b). The stress-response curves of inherently rare or cryptic species show relatively low probabilities of presence across the entire condition gradient (Fig. 1c). Widespread species that are relatively insensitive to environmental stress follow a rather flat distribution with little association between probability of presence/detection and condition; these species provide little information for estimating ecological condition.

Once the SSD functions have been derived or defined for individual species, C can be calculated iteratively for a new site (C_{obs}) by comparing expected probabilities of presence for all species (given the fixed values of β_ι) with observed probabilities of presence p at that site$_i$, assuming that the field sampling method is similar to the sampling method used to develop SSD functions. In other words, an approximation of C_{obs} can be achieved by changing C to minimize the sum of squared deviations $\Sigma(P_i(C) - p_i)^2$ or similar goodness-of-fit expression. The resulting value of C_{obs} is the iterated (trial and error) number between 0 and 10 that best reflects the SSD functions of all species simultaneously. The analysis can be restricted to species showing strong statistical responses to stress (SSD functions) or to species characteristic of the target habitat type.

Presence (or absence) of a species contributes to evidence of a site's ecological condition. Presence of a highly sensitive species and absence of a highly tolerant species, for example, both lead to a higher estimate of ecological condition. C_{obs} is the value that best "predicts" the observed presence/absence of species given the independently determined SSD functions. Any number of species can be included in the estimate of C_{obs}; in general, the more species included the better will be the estimate, although species that are insensitive to the reference gradient will contribute little or no improvement to the estimate. Data from multiple taxonomic groups can be used to estimate C_{obs}, and different sampling methods can be accommodated by adjusting the SSD functions or lists of potential species.

We built SSD functions and tested the logistic model using data from breeding bird assemblages in the coastal zone (approximately 1 km from shore) of the U.S. portion of the North American Great Lakes. Field samples were centered on coastal segments defined by watershed drainage areas (Danz *et al*. 2005). We collected data at 171 randomly selected coastal segments (from 762 total) stratified across a multi-gradient of environmental stressors (Danz *et al*. 2005). For each segment, we established a route of 15 roadside sampling points separated by at least 500 m. At each sampling point, trained field observers during 2002 and 2003 recorded all birds seen or heard during a standard 10 minute point count following the protocol described by Howe *et al*. (1997). Most stations were sampled only once during 2002 or 2003, but 23 routes were sampled during both years. Because we are simply interested in illustrating this method, we treated the 23 repeated samples as independent routes. The combined sample size consisted of 2544 point counts at 194 bird census routes.

A gradient of ecological condition for generating species-specific sensitivity/detectability (SSD) functions was developed through a multivariate analysis of land cover attributes. Digital pixels (30 m x 30 m) from Landsat 5 and Landsat 7 imagery, primarily from the year 2000, were assigned to one of 25 land cover classes (Table 1). These classes were subsequently combined into 6 general categories (Table 1). ArcGis 9.1 (ESRI 2005) was used to calculate proportional area of each general land cover category within 100 m, 500 m, 1 km, 3 km, and 5 km of the census routes. Proportions represented the combined land area associated with all 15 sampling points in a given route. Principal components analysis (PCA) was used to convert the large number of original land cover variables (6 general land cover categories x 5 buffer areas) into a smaller number of new orthogonal variables or principal components (McCune and Mefford 1999). The PCA scores were subsequently combined into a single index of environmental stress or observed land cover condition (= C_{ref}) by adding the scores for the most ecologically interpretable principal components. In our case the first 3 principal components accounted for 87% of the variation among the original land cover variables. The ordination was rotated so that the proportion of natural **vegetation** within 500 m was aligned with the first principal component axis (Fig. 2). The first principal component (53% of total variance) was strongly influenced by the proportions of natural vegetation and forest (high positive loadings) and proportions of residential and industrial land cover and roads (high negative loadings). The second principal component, accounting for 28% of the overall variation, was influenced largely by the proportions of cultivated land (high negative loadings) and proportions of industrial lands and roads (high positive loadings). The third principal component (not shown in Fig. 2) accounted for 5% of the overall variation and differentiated routes with a high proportion of residential land cover (high positive loadings) from routes with a high proportion of industrial/commercial land cover (high negative loadings). Scores for the 3 principal components, weighted according to the % variation associated with the principal component (53% for PC 1, 28% for PC2, and 5% for PC3) were summed to give a single value of reference condition (C_{ref}); the numeric scale of principal component 2 was reversed (i.e., if the score was -0.35, it was changed to 0.35) because we assumed that cultivated (rural) land cover reflects a less stressed ecological condition than industrial/commercial lands and roads. Values of C_{ref} (proportional to size of triangles in Fig. 2) are highest for routes with predominately natural vegetation and lowest for routes with a high proportion of industrial/commercial urban lands. Routes with intermediate proportion of natural vegetation yielded a higher value of C_{ref} if the proportion of agricultural lands was relatively higher than the proportion of urban lands and roads. The objective of this exercise was to identify a stress gradient separating sites (routes) that were highly impacted by human land uses from sites that were minimally impacted. To acknowledge that our samples might not represent the full range of possible conditions, we adjusted the observed values of C_{ref} to range between 0.5 - 9.5 instead of 0 – 10.

This stress gradient for C_{ref}, scaled between 0 and 10, was used as the x-axis for developing sensitivity/detectability (SSD) functions for bird species in the Great Lakes coastal zone. The observed probability of presence for each species in a sample route (p_i) was defined as the proportion of points (maximum = 15) where the species was recorded. Parameters of the SSD functions were estimated by iteration (Hilborn & Mangel 1997), minimizing the lack-of-fit (LOF) expression:

$$\sum_{n=1}^{N} (p_{i(n)} - P_i(C_{ref(n)}))^2/(P_i(C_{ref(n)}) * (1- P_i(C_{ref(n)}))) \qquad (2)$$

where N is the total number of samples (in this case, routes), $p_{i(n)}$ is the species' observed frequency of presence in the *n*th sample (route) and $P_i(C_{ref(n)})$ is the expected probability of presence from Equation 1, given the iterated set of parameter values and the reference condition of site *n* based on land cover (C_{ref}). Results were computed using the Solver Function of Microsoft Excel. Specifically, given the observed values of p_n and $C_{ref(n)}$, we minimized Expression 2 by changing values of $\beta_{i,1}$, $\beta_{i,2}$, $\beta_{i,3}$ and $\beta_{i,4}$ (yielding values of $P_i(C_{ref(n)})$ from Equation 1), subject to the constraints that $0 < \beta_{i,1} <1$, $0 < \beta_{i,2} < 1-\beta_{i,1}$, and $0 < P_i(C_{ref(n)}) < 1$. We also limited the steepness parameter to $-1 < \beta_{i,4} < 1$ in order to avoid unrealistically pronounced "tails" of the function near C = 0 and C = 10. Note that the values of $\beta_{i,1}$, $\beta_{i,2}$, $\beta_{i,3}$

and $\beta_{i,4}$ are constant across all sites (routes), although $P_i(C_{ref(n)})$ changes because C_{ref} differs among these sites.

If the observed proportions of presence are not monotonically increasing or decreasing across the condition (stress) gradient, the iterative process may yield two or more stable combinations of parameters. We selected the function with the lowest lack-of-fit (Equation 2) unless the result predicted a steep increase or decrease in expected probabilities at extremely (high or low) condition values, which were absent or poorly represented on our field samples.

Great Lakes Basin bird assemblages in the northern Laurentian Mixed Forest Ecological Province (Bailey 1995) are significantly different than assemblages in the southern Eastern Deciduous Forest Ecological Province due to biogeographic factors that are not necessarily related to differences in environmental stress (Venier *et al*. 2004). To account for these patterns we calculated separate SSD functions for birds in the two regions. We withheld 20 randomly selected sample routes (each with 15 census points) from the development of SSD functions, 9 from the Laurentian Mixed Forest Ecological Province and 11 from the Eastern Deciduous Forest Ecological Province. These “reserved” routes were later used to cross-validate the model. We used the SSD functions to calculate expected probabilities of presence for bird species in the 20 “reserved” samples. For a particular reserved route we estimated C_{obs} by comparing these probabilities for a potential value of C with observed proportions of presence in the 15 sample points. The values of C_{obs} were derived by iteration, minimizing the sum of squared deviations between expected and observed frequencies. Linear regression was used to compare estimates of C_{obs} with the corresponding measures of land cover condition (C_{ref}). If bird species are consistently associated with C_{ref}, then the slope of C_{obs} vs. C_{ref} should be close to 1 with a yintercept of x = 0. Deviations from this 1:1 relationship suggest that factors other than land cover are influencing bird occurrences.

The contributions of an individual species to estimates of condition (C_{obs}) depend largely on the sensitivity of the species to environmental stress, expressed as the absolute difference between $P_i(0)$ and $P_i(10)$. Additionally, species with a close fit to the derived SSD function will provide more reliable information about the condition of a target site. In order to differentiate species with strong stress-response relationships from species with weaker stress-response relationships, we arbitrarily defined strong responses as SSD functions with a difference between $P_i(0)$ and $P_i(10)$ of at least ∀ 0.1 and a lack-of-fit statistic (Equation 2) of less than 20.0. Initially, all species with strong SSD functions were included in the estimation of C. We examined the sensitivity of our probability-based indicator to different numbers of target species by selectively excluding species with weaker stress-response relationships, 5 at a time, beginning with species whose SSD functions exhibited the smallest absolute difference between $P_i(0)$ and $P_i(10)$.

Results

Species exhibiting the strongest functional relationship with reference condition in the Laurentian Mixed Forest Ecological Province (Table 2) included alien species like European Starling, Rock Pigeon, and House Sparrow, and area-sensitive bird species like Black-throated Green Warbler (Fig. 3), Ovenbird, and other Neotropical migrants (Whitcomb *et al*. 1981, Villard 1998). Species-specific sensitivity/detectability (SSD) functions were considered strong by our arbitrary standards ($*P_i(0) - P_i(10)* > 0.1$ and lack-of-fit (Equation 2) < 20.0) for 60 of the 170 species observed in this ecological province (n = 98 sample routes). Strong responses to reference condition ($*P_i(0) - P_i(10)* > 0.3$) also were exhibited by Herring Gull (*Larus argenatus*), Ring-billed Gull (*Larus delawarensis*), and White-throated Sparrow (*Zonotrichia albicollis*), but variation around the best-fit SSD function was high (lack-of-fit > 20.0) for these bird species compared with other species included in our list (Table 2).

Estimates of ecological condition for the 9 "reserved" routes in the Laurentian Mixed Forest Ecological Province (based on data from the 60 bird species in Table 2) were highly correlated with the ecological condition (C_{ref}) based on land cover variables ($r^2 = 0.68$, Fig. 4a). Two outliers or deviations from a 1:1 relationship were identified by this comparison: 1) the urban environment of Marquette, Michigan, which showed a higher quality bird fauna than expected according to land cover, and 2) a coastal segment in northern Sheboygan County, Wisconsin, which showed a lower quality bird fauna than expected. Notably, the Sheboygan County route was located near the southernmost part of the Laurentian Mixed Forest Ecological Province and was imbedded in a highly agricultural landscape.

Selective removal of species from the estimation of ecological condition showed a nonlinear relationship of deviations from the initial estimate (Fig. 5). For the 9 reserved sites in the Laurentian Mixed Forest Ecological Province, relatively little change ($< *0.5*$) in the estimate of C was observed until 25 or fewer species were kept in the estimate. In other words, addition of species beyond the 25-30 species with the strongest SSD functions ($*P_i(0) - P_i(10)*> 0.2$) contributed relatively little change in the estimate of C. In many cases (routes), consistent estimates were achieved by including as few as 10-20 species. In general, estimates of condition became less variable as more species were included in the analysis.

The Eastern Deciduous Forest Ecological Province is characterized by a narrower range of land cover conditions and a higher intensity of human influence. Of the 151 bird species identified in 76 sample routes, 43 yielded SSD functions that were considered strong by our standards ($*P_i(0) - P_i(10)* > 0.1$ and lack-of-fit (Equation 2) < 20.0). Species that showed a significant positive or negative association with land cover condition in the Laurentian Mixed Forest Ecological Province generally showed a similar pattern in this region, but in several cases the relationship was reversed (Tables 2 and 3). For example, Mourning Dove, Gray Catbird, and Song Sparrow exhibited a negative relationship with land cover condition (i.e., they tended to be more common at human-influenced sites) in the Laurentian Mixed Forest Province but exhibited an opposite relationship (i.e., they were more common at more natural sites) in the Eastern Deciduous Forest Province.

Estimates of ecological condition based on the 43 bird species with strong SSD models again produced a very good association with C_{ref} ($r^2 = 0.68$, Fig. 4b). Estimates of condition (C_{obs}) based on bird assemblages were higher than expected in sample routes near Lake Forest, Illinois, north of Chicago; near Indiana Dunes National Lakeshore in Michigan (Lake Michigan); and near Port Crescent State Park in eastern Michigan (Lake Huron). Bird-based condition was lower than expected in sample routes near Swan Creek in eastern Michigan (Lake Erie) and in several sites in New York state (Lake Ontario).

Discussion

The application of ecological indicators always implies an underlying gradient (univariate or multivariate) defining poor quality sites and high quality sites, although the nature of this gradient is often vague or unstated. The biotic indicator outlined in this paper reflects an explicit reference gradient of environmental stress associated with human land use. We have established clear relationships between the quality of land cover and the probabilities of finding certain bird species, leading to a rigorous and ecologically defensible framework for quantifying condition. Indicator values based on bird assemblages, however, do not simply mirror the reference gradient; otherwise we wouldn't need to use the biotic analysis at all. The explicit *a priori* gradient serves as a starting point and a basis for interpreting variations in ecological condition. Deviations from a 1:1 relationship between C_{ref} and C_{obs} illuminate places where land cover does not completely characterize ecological condition, at least with respect to bird assemblages. If a site supports more sensitive species than expected, for example, factors other than land cover likely contribute to their occurrence. These factors might include extensive native landscaping in urban areas, low levels of toxic chemicals, or other desirable features of the landscape. Sites with fewer sensitive species than expected (based on land cover) likely encompass undesirable features such as poor habitat quality, ecological imbalances, or unusually high levels of bird mortality. Identifying such sites can help guide preservation and remediation efforts. The extensive natural landscapes surrounding urban Marquette, Michigan, for example, might partly explain the unexpectedly rich bird assemblages there.

Unlike several widely used indices like the Floristic Quality Index (Wilhelm & Ladd 1988), our probability-based indicator is not directly correlated with species richness and it can be extended to include observations from multiple species groups. It also can be adjusted to different sampling schemes by modifying the species-specific sensitivity/detectability (SSD) functions or by including only species that can be easily detected. Recent studies of species detection probabilities (Tyre et al. 2003, Wintle et al. 2004, Pellet & Schmidt 2005), for example, might be extremely valuable for refining the application of SSD functions.

The development of species-specific sensitivity/detectability (SSD) functions is central to the use of our probability-based indicator. These functions, which can be defined by expert opinion or derived empirically, express a numeric relationship (Equation 1) between anthropogenic stress and probability of a species' presence. Such functions are standardized to facilitate comparisons of ecological condition among different sites or to compare condition at the same site over time. This approach is similar to the use of species-specific weights for calculation of other biotic indices (Lenat 1993, O'Connell *et al.* 1998), but in this case the calculations employ explicit functional relationships rather than single values or summary scores from multivariate analyses. Perhaps most importantly, the standardized relationships between reference conditions and species' probabilities of presence are not summed or combined in an arbitrary way; instead, computer iterations identify a single measure of ecological condition that best "fits" the observed multi-species data. Each species contributes to the estimate, but the magnitude of the result is not inflated by summing redundant or highly correlated variables.

Once the SSD functions have been established, ecological condition can be estimated iteratively for any observed assemblage of species. Caution is necessary to evaluate only species that can be expected to occur in the sample area and only those that can be detected with the sampling method, because absence of a species may contribute as much as presence of that species. This is particularly true for species that are highly sensitive to ecological condition (i.e., for species where $*P_i(0) - P_i(10)*$ is large).

We have used a least squares estimation of C, but alternative methods provide even broader applications of our method. For example, presence/absence data from the single point surveys at a site can be used to calculate C by maximizing the following expression:

$$\sum_{observed} \log\left(P_i(C)\right) + \sum_{unobserved} \log\left(1 - P_i(C)\right). \qquad (3)$$

The first sum represents all points and species observed at each point while the second sum represents all points and species unobserved at each point.

Again, an iterative process is used to derive the value of C that best “fits” the observed data. In other words, we seek a value of C that maximizes the product of the probabilities of having observed/not observed each species at a site. For computational reasons, the maximization is applied to the sum of the log-probabilities or equivalently the log of the product of the probabilities over the observed/unobserved species data. If the presences of species for a fixed condition C are independent, Equation 3 corresponds to the log likelihood function. To find a precise likelihood with dependent species, one would need to model dependencies between species. Certainly over all values of C, species will be dependent because locations of similar condition will tend to have similar species. For locations of a fixed condition, the dependence between observations of different species will be much less obvious. Maximization of Equation 3 rather than a full likelihood with dependencies will yield very similar optimal C values. If the observations of individual species are at least somewhat independent, then approximate confidence intervals for C can be computed using usual profile likelihood methods (Edwards 1992).

Our analysis of bird assemblages in the Great Lakes coastal zone demonstrates that this method can successfully characterize ecological condition, beginning with a reference gradient based on the degree of human-impacted land use. This gradient represents a meaningful framework for diagnosing problem areas and prescribing measures to improve condition. Bird assemblages from novel locations consistently reflected the reference gradient (Fig. 4), but deviations indicated additional information about local conditions. In general, deviations from the expected relationship between land cover condition (C_{ref}) and bird species condition (C_{obs})

reveal characteristics of the environment that cannot be measured by land cover variables alone. Of course, bird assemblages are of interest in their own right and this probability-based indicator also provides useful information about bird species composition for comparisons among geographic areas or among different time periods.

The most difficult element of our proposed approach is development of the SSD functions. We envision this to be accomplished by large scale studies like ours, which subsequently provide standardized species-specific parameters (e.g., Tables 2 and 3) for use by monitoring programs and local investigators. Several sets of parameters, adjusted to account for different sampling methods, might be developed for a specific geographic region. In the Great Lakes coastal zone, different functions also might be developed for different water level regimes, which have been shown to significantly affect coastal species assemblages (Wilcox et al. 2002).

Once the SSD parameters are established, all that is needed to apply this method is to document species assemblages at localities of interest. If the locality can be sampled multiple times or at multiple points, observed probabilities of presence can be calculated for each species; C_{obs} is derived using Equation 2 and the method outlined above. If the locality is sampled only once, then a modified approach using Equation 3 is appropriate.

As long as SSD functions are available, observations from multiple species groups (e.g., birds, flowering plants, dragonflies) can be combined to estimate ecological condition. In our analysis we included bird species representing a variety of habitat associations, but a more selective approach might be appropriate if the purpose is to evaluate condition in a specific habitat type or for a particular ecological guild (McGeoch & Chown 1998). In such cases, a systematic analysis such as the one described by Dufrene & Legendre (1997) might narrow the list of species used to calculate condition.

Because species are able to integrate many physical and biological characteristics of a locality, their abundance or their presence/absence often signals important information about the locality's ecological condition. Environmental scientists have proposed many methods for measuring or assessing this ecological condition, ranging from simple physical measurements to complex biotic indices. Our probability-based indicator offers a straightforward method for expressing the biological dimensions of environmental stress. Although one can argue that ecological condition is impossible to characterize by a single number, we often need such a number for assigning conservation priorities or for visualizing the combined effects of human activities. The probability-based indicator described here is attractive because it is objective, flexible, and grounded in an explicit gradient of environmental stress. We hope that our analysis will lead to future applications in different ecosystems and with different taxa, providing generalized templates and further insights into the development of probability-based ecological indicators.

Acknowledgements

This research was supported by a grant from the U.S. Environmental Protection Agency's Science to Achieve Results (STAR) Estuarine and Great Lakes (EaGLe) program through funding to the Great Lakes Environmental Indicators (GLEI) project, U.S. EPA Agreement EPA/R-8286750. This document has not been subjected to the Agency's required peer and policy review and therefore does not necessarily reflect the views of the Agency, and no official endorsement should be inferred. We are grateful for contributions by other scientists involved with the GLEI project, especially T. Hollenhorst, P. Wolter, C. Smith, V. Brady, T. Brown, J. Brazner, S. Price, D. Marks, and others, including more than 20 student field investigators. K. McKeefry assisted with data management. Important ideas underlying this analysis were communicated by J. Karr, D. Simberloff, P. Bertram, A. Tyre, H. Possingham, and an anonymous reviewer.

References

A.O.U. 1998. Check-list of North American Birds, 7th ed. American Ornithologists' Union, Washington, D.C.

Armitage, P.D., Gunn, R.J.M., Furse, M.J., Wright, J.F., & Moss, D. 1987. The use of prediction to assess macroinvertebrate response to river regulation. Hydrobiologia 144, 25-32.

Bailey, R.G. 1995. Description of the Ecoregions of the United States. 2nd edn. Misc. Publ. No. 1391, U.S. Forest Service, Washington, D.C.

Clarke R. T., Wright J. F. & Furse, M. T. 2003. RIVPACS models for predicting the expected macroinvertebrate fauna and assessing the ecological quality of rivers. Ecol. Model. 160, 219-233.

Danz, N., Regal, R., Niemi, G.J., Brady, V.J., Hollenhorst, T., Johnson, L.B., Host, G.E., Hanowski, J.M., Johnston, C.A., Brown, T., Kingston, J., & Kelly, J.R. 2005. Environmentally stratified sampling design for the development of Great Lakes environmental indicators. Environ. Monit. Assess. 102:41-65.

Danz, N.P., Niemi, G.J., Regal, R.R., Hollenorst, T., Johnson, L.B., Hanowski, J.M., Axler, R.J., Ciborowski, J.H., Hrabik, T., Brady, V.J., Kelly, J.R., Brazner, J.C., Howe, R.W., Johnston, C.A.

& Host, G.E. 2006. Integrated gradients of anthropogenic stress in the U.S. Great Lakes Basin. Environ. Manage. In press.

Dufrene, M., & Legendre, P. 1997 Species assemblages and indicator species: the need for flexible asymmetrical approach. Ecol. Monogr. 67, 345-366.

Edwards, A.W.F. 1992. Likelihood. Johns Hopkins University Press, Baltimore.

ESRI. 2005. ArcGIS 9.1. Environmental Systems Research Institute, Redlands, CA.

European Commission. 2000. Directive 2000/60/EC, Establishing a framework for community action in the field of water policy. European Commission PE-CONS 3639/1/100 Rev 1, Luxembourg.

Gergel, S.E. 2002. Cumulative impact of levees and dams on the duration of temporary floodplain ponds: a terrain model approach for assessing multiple disturbances at broad scales. Ecol. Appl. 12, 1740-1754.

Harris, J. H. & Silviera, R. 1999. Large-scale assessments of river health using an Index of Biotic Integrity with low-diversity fish communities. Freshw. Biol. 41, 235–252.

Hilborn, R. & Mangel, M. 1997. The Ecological Detective: Confronting Models with Data, Monogr. Pop. Biol. 28, Princeton University Press, New Jersey.

Hilsenhoff, W. L. 1982. Using a biotic index to evaluate water quality in streams. Techn. Bull. 132, WI Dept. Nat. Res., Madison WI.

Howe, R.W., Niemi, G.J., Lewis, S.J., & Welsh, D.A. 1997. A standard method for monitoring songbird populations in the Great Lakes Region. Pass. Pigeon 59, 183- 194.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6, 21-27.

Karr, J.R. & Chu, E.W. 1999. Restoring life in running waters: better biological monitoring. Island Press, Washington, DC.

Karr, J.R. & Rossano, E.M. 2001. Applying public health lessons to protect river health. Ecol. Civ. Eng. 4, 3–18.

Karr, J.R., Yant, P.R., Fausch, K.D. & Schlosser, I.J. 1987. Spatial and temporal variability of the index of biotic integrity in three midwestern streams. Trans. Am. Fish. Soc. 116, 1-11.

Kolkwitz, R., & Marsson, M. 1908. Okologie der pflanzlichen saprobien. Berichte der Deutschen botanischen Gesellschaft 26a:505-519. Translated 1967. Ecology of plant saprobia. In: Biology of water pollution ed. Kemp, L.E., Ingram, W.M. & Mackenthum, K.M.. Federal Water Pollution Control Administration, Washington, DC., pp. 47-52.

Lenat, D.R. 1993. A biotic index for the southeastern United States: derivation and list of tolerance values, with criteria for assigning water-quality ratings. J. N. Am. Benthol. Soc. 12, 279-290.

Lyons, J., S.Navarro-Perez, P.A. Cochran, E. Santana C., & Guzman-Arroyo, M. 1995. Index of biotic integrity based of fish assemblages for the conservation of streams and rivers in west-cental Mexico. Conserv. Biol. 9, 569-584.

Marchant, R. & Hehir, G. 2002. The use of AUSRIVAS predictive models to assess the response of lotic macroinvertebrates to dams in south east Australia. Freshw. Biol. 47, 1033-1050.

McCune, B., and M. J. Mefford. 1999. PC-ORD, Version 4.0. MjM Software, Gleneden Beach, OR.

McGeoch, M.A. & Chown, S.L. 1998. Scaling up the value of bioindicators. Trends Ecol. Evolut. 13, 46-47.

Miller, D.L., Leonard, P.M., Hughes, R.M., Karr, J.R., Moyle, P.B., Schrader, L.H., Thompson, B.A., Daniels, R.A., Fausch, K.D., Fitzhugh, G.A., Gammon, J.R., Halliwell, D.B., Angermeier, P.L., & Orth, D.J. 1988. Regional applications of an index of biotic integrity for use in water resource management. Fisheries 13, 12-20.

Niemi, G.J. & McDonald, M. Application of ecological indicators. Ann. Rev. Ecol. Syst. 35, 89-111.

O'Connell, T.J., Jackson, L.E., & Brooks, R.P. 1998. A bird community Index of Biotic Integrity for the mid-Atlantic highlands. Environ. Monit. Assess. 51, 145-56.

O'Connor, R.J., Walls, T.E., Hughes, R.M. 2000. Using multiple taxonomic groups to index the ecological condition of lakes. Environ. Monit. Assess. 61, 207-28.

Pinheiro, J.C. and Bates, D.M. 2000. Mixed-Effects Models in S and S-PLUS. Springer-Verlag, New York, NY.

Tyre, A.J., Tenhumberg, B., Field, S.A., Niejalke, D., Parris, K.,Possingham, H.P. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecol. Appl. 13, 1790–1801

Venier, L.A., Pearce, J., McKee, J.E., McKenney, D.W., & Niemi, G.J. 2004. Climate and satellite-derived land cover for predicting breeding bird distribution in the Great Lakes basin. J. Biogeogr. 31, 315-331

Villard, M.-A. 1998. On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. Auk 115, 801-805.

Whitcomb, R.E., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K., & Bystrak. D. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. In: Forest Island Dynamics in Man-dominated Landscapes ed. Burgess, R.L. & Sharpe, D.M.. Springer-Verlag, New York. pp. 125-205

Wilcox, D.A., Meeker, J.E., Hudson, P.L., Armitage, B.J., Black, M.G., and Uzarski, D.G. 2002. Hydrologic variability and the application of index of biotic integrity metrics to wetlands: a Great Lakes evaluation. Wetlands 22:588-615.

Wilhelm, G S. and Ladd, D. 1988. Natural area assessment in the Chicago region. Trans. N. Amer. Wildl. Nat. Res. Conf. 53:361-375.

Wintle, B.A., McCarthy, M.A., Parris, K.M., Burgman, M.A. 2004. Precision and bias of methods for estimating point survey detection probabilities. Ecol. Appl. 14, 703–712.

Wolter, P., Johnston, C. and Niemi, G.J. 2006. Land use change in the U.S. Great Lakes basin 1992-2001. J. Great Lakes Res. In press.

Wright, J.F. 2000. An introduction to RIVPACS. In: Assessing the Biological Quality of Fresh Waters: RIVPACS and Other Techniques eds. Wright, J. F., Sutcliffe, D.W. & Furse, M.T.. Freshwater Biological Association, Ambleside, UK. pp. 1-24.

Yoder, C.O. & Rankin, E.T. 1995. Biological response signatures and the area of degradation value: new tools for interpreting multimetric data. In: Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making eds. Davis, W.S. & Simon, T.P.. Lewis, Boca Raton, FL, pp. 236-286.

Yoder, C.O. & Rankin, E.T. 1998. The role of biological indicators in a state water quality management process. J. Environ. Mon. Assess. 51, 61-88.

Table 1. Land cover variables used to establish an environmental stress gradient associated with bird survey routes. Original land cover classes determined by Wolter et al. (2006) were combined into 6 general categories shown in the right column. Proportion of land cover in each general category was determined by GIS analysis for areas within 100 m, 500 m, 1 km, 3 km, and 5 km of the 15 bird census points in each route.

Number	Original Land Cover Class	General Category
1	open water	(not included)
2	low intensity residential	residential
3	high intensity residential	residential
4	roads	roads
5	commercial / industrial	industrial
6	bare	(not included)
7	quarry	industrial
8	transitional	(not included)
9	deciduous upland forest	natural
10	coniferous upland forest	natural
11	mixed upland forest	natural
12	shrub land	natural
13	orchard	cultivated
14	grassland	natural
15	pasture	cultivated
16	row crop	cultivated
17	grains	cultivated
18	urban grassland	cultivated
19	emergent wetland	natural
20	unconsolidated shoreline	natural
21	lowland grassland	natural
22	lowland shrub land	natural
23	lowland conifer forest	natural
24	lowland mixed forest	natural
25	lowland hardwood forest	natural

Table 2. Bird species used to estimate ecological condition in Great Lakes coastal segments in the Laurentian Mixed Forest Ecological Province. List includes top 25 species in decreasing order of sensitivity across a reference gradient (C_{ref}) based on land cover. Values of β_1, β_2, β_3, and β_4 correspond to estimates of the parameters in Equation 1. Species with negative β_4 are more likely to occur in sites with poor condition. LOF is the lack-of-fit statistic described in Equation 2. The quantity [P(10)-P(0)] describes the absolute difference in probabilities of a species' presence at poorest quality (C_{ref} = 0) vs. highest quality (C_{ref} = 10) sites. Scientific names of bird species are from A.O.U. (1998) and recent supplements.

Common Name	**Scientific Name**	β_1	β_2	β_3	β_4	**LOF**	[P(10)-P(0)]
European Starling	*Sturnus vulgaris*	0.00	0.79	6.02	-0.89	11.75	0.76
Rock Pigeon	*Columba livia*	0.00	1.00	1.65	-0.64	4.37	0.74
Black-throated Green Warbler	*Dendroica virens*	0.01	0.75	7.79	1.00	18.20	0.68
House Sparrow	*Passer domesticus*	0.00	0.67	4.82	-1.00	5.96	0.66
Ovenbird	*Seiurus aurocapillus*	0.01	0.66	7.04	1.00	14.78	0.63
Red-eyed Vireo	*Vireo olivaceus*	0.13	0.60	6.67	0.95	19.47	0.58
Common Grackle	*Quiscalus quiscula*	0.00	0.58	6.80	-1.00	14.99	0.56
American Redstart	*Setophaga ruticilla*	0.09	0.72	8.23	0.64	15.93	0.54
Hermit Thrush	*Catharus guttatus*	0.01	1.00	10.20	1.00	7.60	0.45
Nashville Warbler	*Vermivora ruficapilla*	0.01	0.53	8.29	1.00	13.80	0.45
Red-winged Blackbird	*Agelaius phoeniceus*	0.00	0.48	7.62	-1.00	17.91	0.44
Winter Wren	*Troglodytes troglodytes*	0.00	1.00	10.35	0.86	7.39	0.42
Song Sparrow	*Melospiza melodia*	0.00	0.59	9.21	-1.00	17.22	0.41
American Goldfinch	*Carduelis tristis*	0.00	0.51	9.00	-1.00	19.39	0.37
Yellow-rumped Warbler	*Dendroica coronata*	0.00	0.41	7.40	0.82	13.46	0.37
Mourning Dove	*Zenaida macroura*	0.00	0.42	8.22	-1.00	18.77	0.36
Veery	*Catharus fuscescens*	0.00	0.35	6.26	0.70	18.10	0.32
House Finch	*Carpodacus mexicanus*	0.00	0.33	6.77	-1.00	13.69	0.32
Northern Cardinal	*Cardinalis cardinalis*	0.00	0.34	7.55	-1.00	19.23	0.32
Northern Parula	*Parula americana*	0.00	1.00	11.00	0.79	5.97	0.31
Chimney Swift	*Chaetura pelagica*	0.01	0.31	4.87	-1.00	8.86	0.30
Black-throated Blue Warbler	*Dendroica caerulescens*	0.00	0.76	10.43	1.00	10.91	0.30
Common Yellowthroat	*Geothlypis trichas*	0.08	0.29	3.98	1.00	18.25	0.28
Cedar Waxwing	*Bombycilla cedrorum*	0.00	0.29	2.47	1.00	15.17	0.27
American Robin	*Turdus migratorius*	0.33	0.35	8.83	-1.00	16.61	0.27

Table 3. Bird species used to estimate ecological condition in Great Lakes coastal segments in the Eastern Deciduous Forest Ecological Province. List includes top 25 species in decreasing order of sensitivity across a reference gradient (C_{ref}) based on land cover. Values of β_1, β_2, β_3, and β_4 correspond to estimates of the parameters in Equation 1. Species with negative β_4 are more likely to occur in sites with poor condition. LOF is the lack-of-fit statistic described in Equation 2. The quantity [P(10)-P(0)] describes the absolute difference in probabilities of a species' presence at poorest quality (C_{ref} = 0) vs. highest quality (C_{ref} = 10) sites. Scientific names of bird species are from A.O.U. (1998) and recent supplements.

Common Name	**Scientific Name**	β_1	β_2	β_3	β_4	**LOF**	[P(10)-P(0)]
Ovenbird	*Seiurus aurocapillus*	0.00	1.00	8.78	1.00	4.04	0.77
Veery	*Catharus fuscescens*	0.00	1.00	8.84	1.00	3.58	0.76
House Sparrow	*Passer domesticus*	0.00	0.70	5.87	-0.83	11.17	0.68
Hooded Warbler	*Wilsonia citrina*	0.00	1.00	9.56	1.00	3.74	0.61
Red-eyed Vireo	*Vireo olivaceus*	0.10	0.60	7.01	1.00	12.10	0.57
European Starling	*Sturnus vulgaris*	0.25	0.57	5.35	-1.00	15.18	0.56
Chipping Sparrow	*Spizella passerina*	0.00	0.58	4.35	0.70	12.45	0.54
Common Grackle	*Quiscalus quiscula*	0.29	0.42	5.99	-1.00	16.88	0.41
Song Sparrow	*Melospiza melodia*	0.07	0.46	2.13	1.00	16.23	0.41
Chimney Swift	*Chaetura pelagica*	0.00	0.43	5.87	-0.67	14.67	0.39
Rock Pigeon	*Columba livia*	0.02	0.43	2.54	-0.91	4.41	0.39
Mourning Dove	*Zenaida macroura*	0.00	0.52	0.85	1.00	13.39	0.36
American Crow	*Corvus brachyrhynchos*	0.22	0.37	6.06	0.98	17.14	0.36
Black-capped Chickadee	*Poecile atricapilla*	0.09	0.38	7.30	1.00	7.55	0.36
Gray Catbird	*Dumetella carolinensis*	0.00	0.47	4.08	0.39	12.92	0.34
American Redstart	*Setophaga ruticilla*	0.07	0.32	6.61	1.00	11.05	0.31
Northern Cardinal	*Cardinalis cardinalis*	0.15	0.36	1.60	1.00	15.08	0.30
Canada Warbler	*Wilsonia canadensis*	0.00	1.00	10.91	1.00	0.79	0.29
Common Yellowthroat	*Geothlypis trichas*	0.09	0.27	3.88	1.00	17.85	0.26
Purple Finch	*Carpodacus purpureus*	0.01	1.00	11.11	1.00	2.14	0.25
American Robin	*Turdus migratorius*	0.45	0.30	1.55	1.00	11.67	0.25
American Goldfinch	*Carduelis tristis*	0.35	0.24	3.78	1.00	14.56	0.23
Northern Mockingbird	*Mimus polyglottos*	0.00	1.00	-2.95	-0.40	4.42	0.23
House Wren	*Troglodytes aedon*	0.00	0.49	5.01	0.19	12.52	0.22
Eastern Tufted Titmouse	*Baeolophus bicolor*	0.00	0.23	3.93	0.71	13.13	0.22

Legends for Figures

Figure 1. Theoretical forms of species-specific sensitivity/detectability (SSD) functions described by Equation 1: a) sensitive species that is restricted mainly to high quality sites, b) tolerant species that occurs mainly at low quality sites but is absent at high quality sites, and c) sensitive species that is relatively rare or difficult to observe even at high quality sites.

Figure 2. Principal components analysis (PCA) of bird survey routes (triangles) based on land cover variables within 100 m, 500 m, 1 km, 3 km, and 5 km of 15 bird survey points. Size of triangle is proportional to the index of environmental condition (0 = maximal stress, 10 = minimal stress) calculated by combining the first three principal components. Descriptive labels (e.g., natural, rural / agricultural) identify general attributes of routes in the corresponding area of the plot.

Figure 3. Species-specific sensitivity/detectability (SSD) functions for selected bird species from Laurentian Mixed Forest Ecological Province (left column) and Eastern Deciduous Forest Province (right column). Condition represents the gradient of land cover described in Figure 2. Y-axis gives the proportion of presence in 15 sample points (blue markers) or probability of presence (solid line) according to estimated SSD function. BTNW = Black-throated Green Warbler, REVI = Red-eyed Vireo, HOSP = House Sparrow.

Figure 4. Correlation (r) between index of environmental stress/condition based on land cover (x-axis) and condition based on bird species assemblages (y-axis) in a) Laurentian Mixed Forest

Ecological Province and b) Eastern Deciduous Forest Ecological Province. Sample routes shown here (n = 9 and n = 11) were not included in calculations of SSD functions.

Figure 5. Effect of removing species (5 at a time, left to right) from estimate of ecological condition based on bird species assemblages in 9 "reserved" survey routes in Laurentian Mixed Forest Ecological Province. Species with smallest absolute difference between predicted P(10) and P(0) were removed first. Best estimate is based on an iteration including 60 species. Ordinate represents absolute value of deviation from the best estimate. Points at the far right represent estimate based on only 5 species with greatest absolute difference between the predicted P(10) and P(0).

Figure 1.

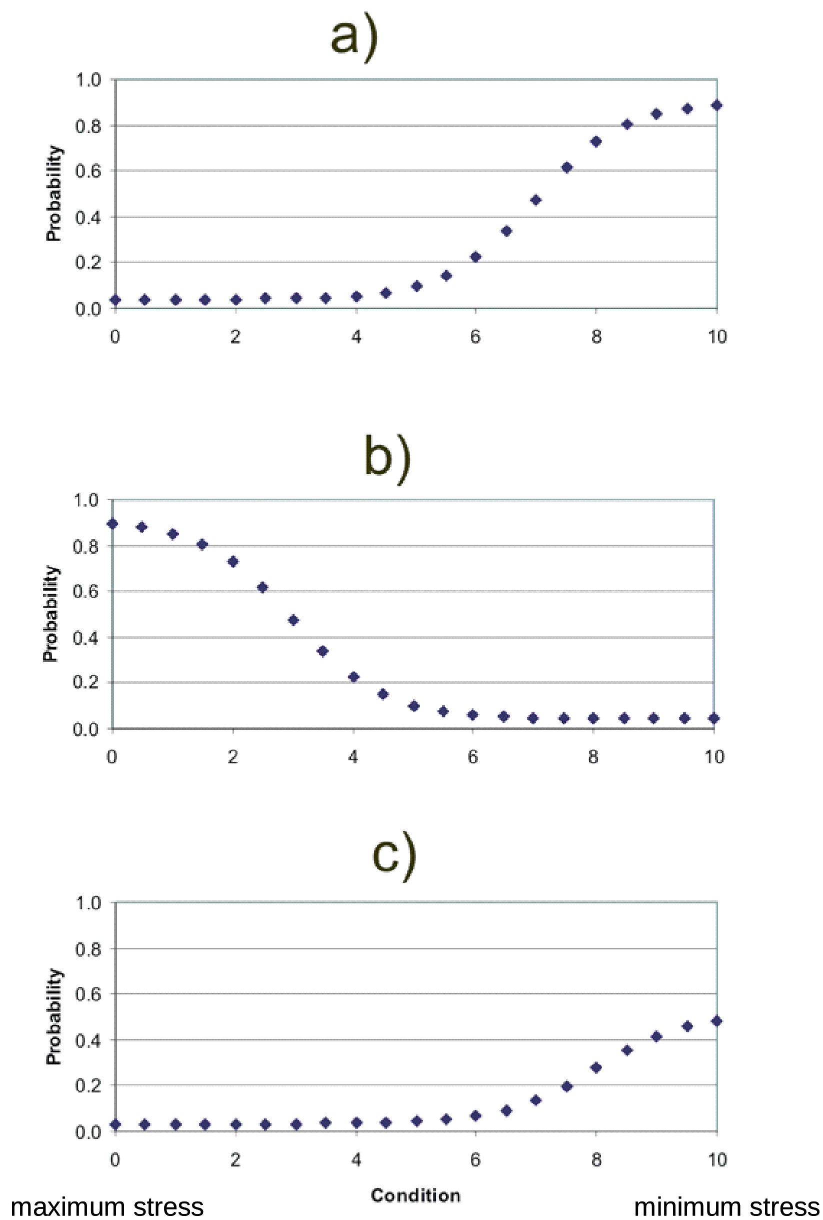

a)
Probability
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
b)
Probability
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
c)
Probability
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
maximum stress
Condition
minimum stress

Figure 2.

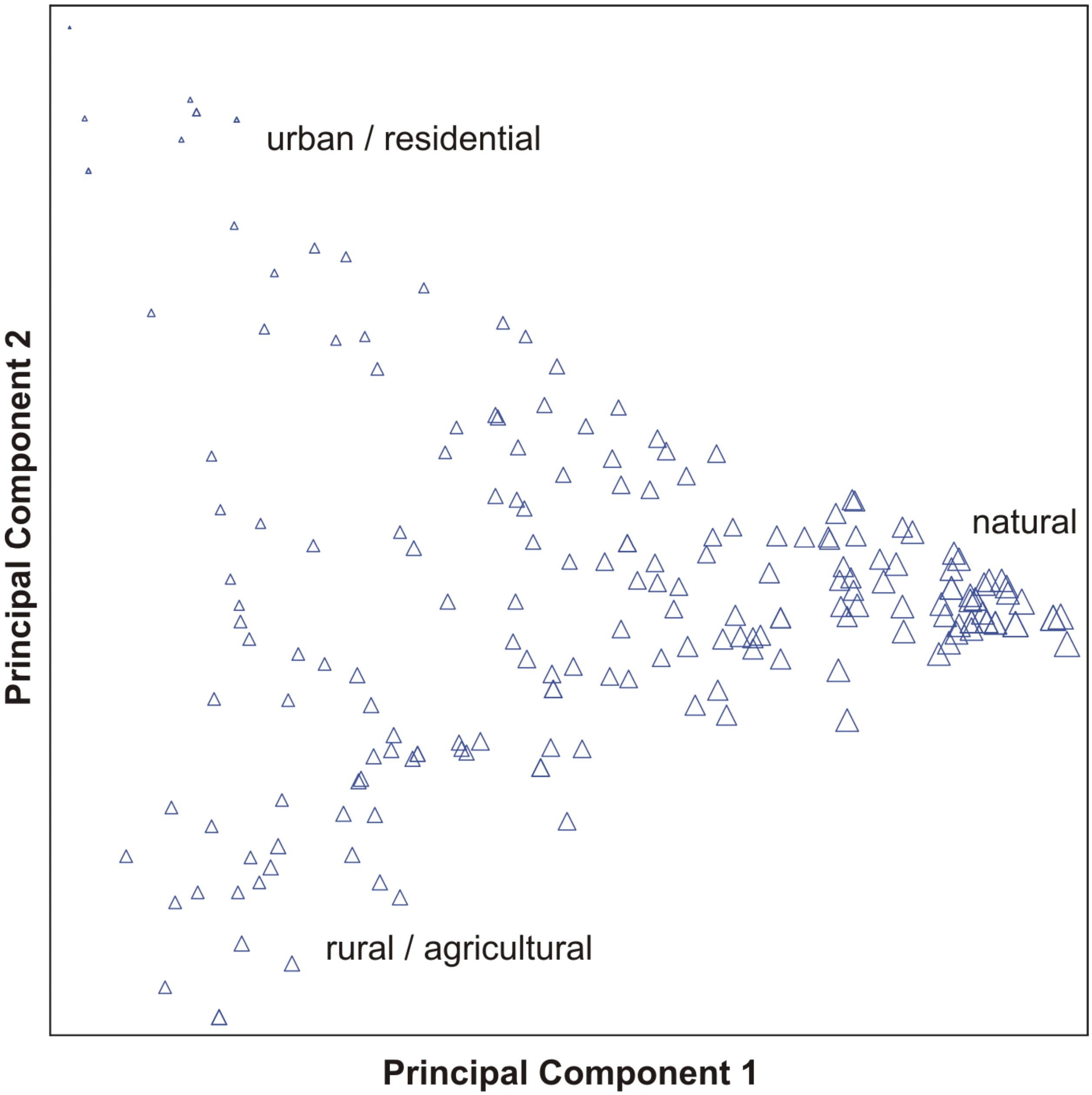

urban / residential
natural
rural / agricultural
Principal Component 2
Principal Component 1

Figure 3.

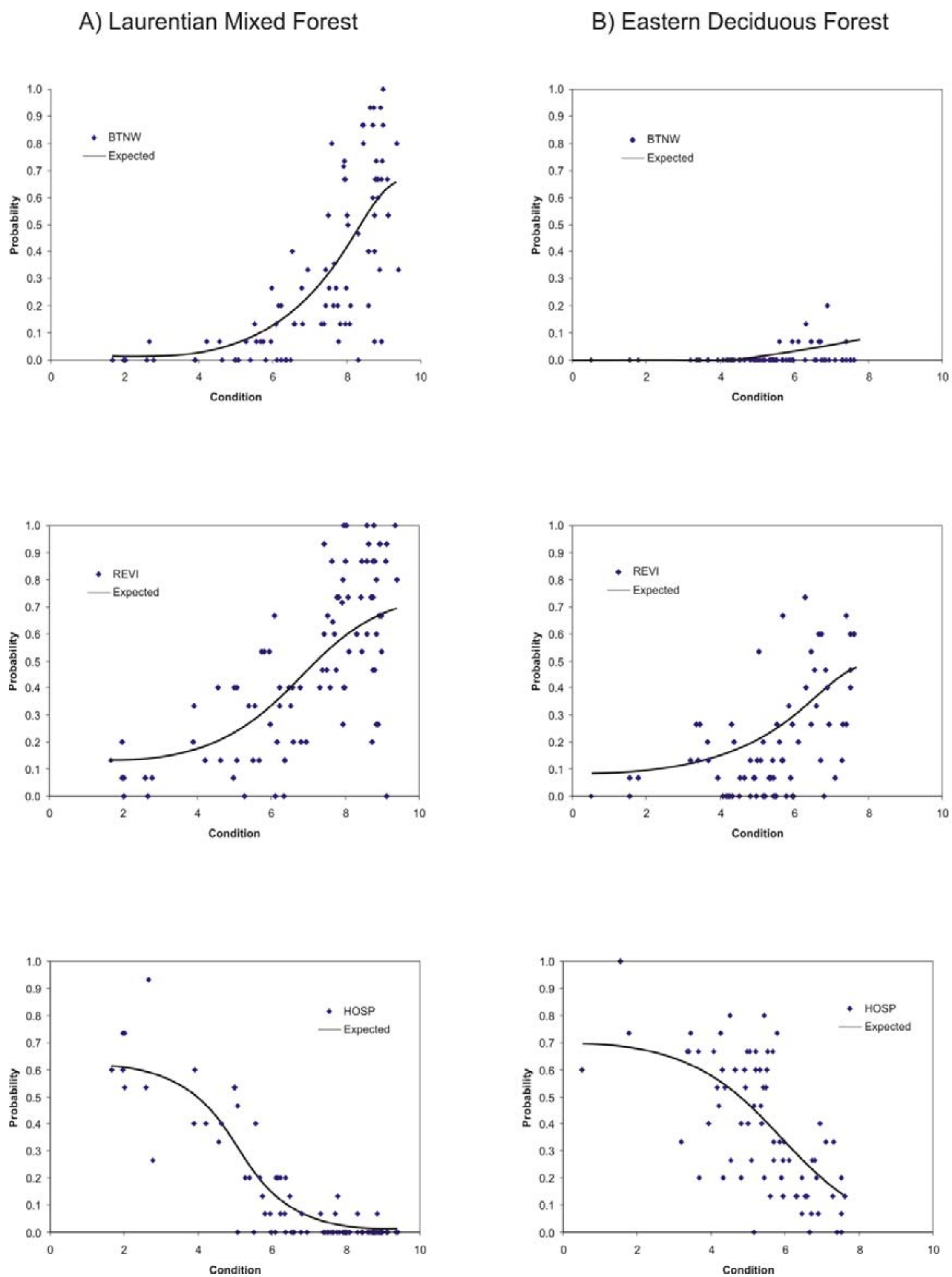
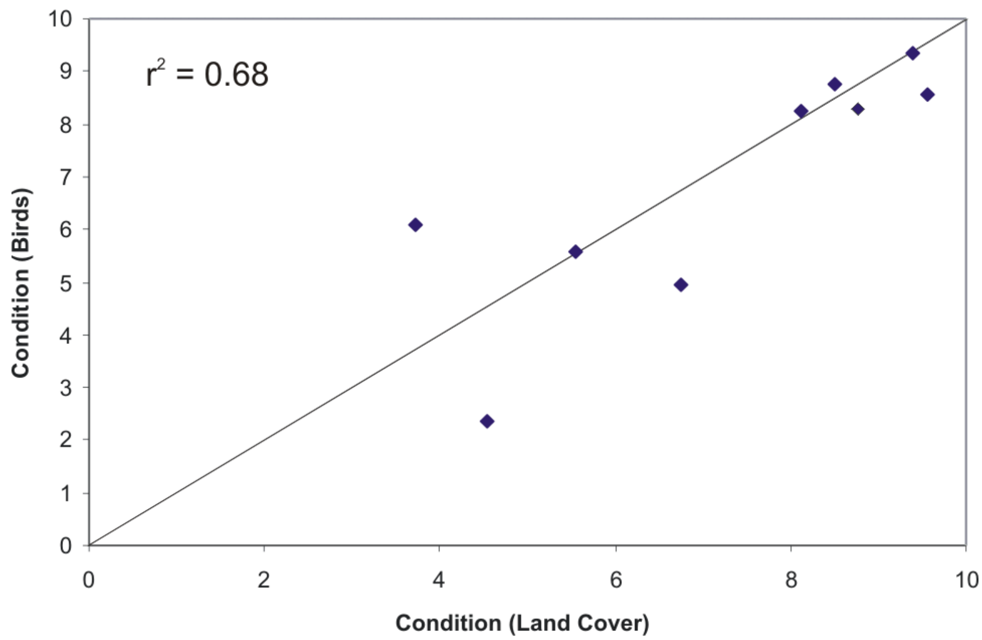

A) Laurentian Mixed Forest
B) Eastern Deciduous Forest
BTNW
Expected
REVI
HOSP
Probability
Condition

Figure 4.

a) Laurentian Mixed Forest



b) Eastern Deciduous Forest

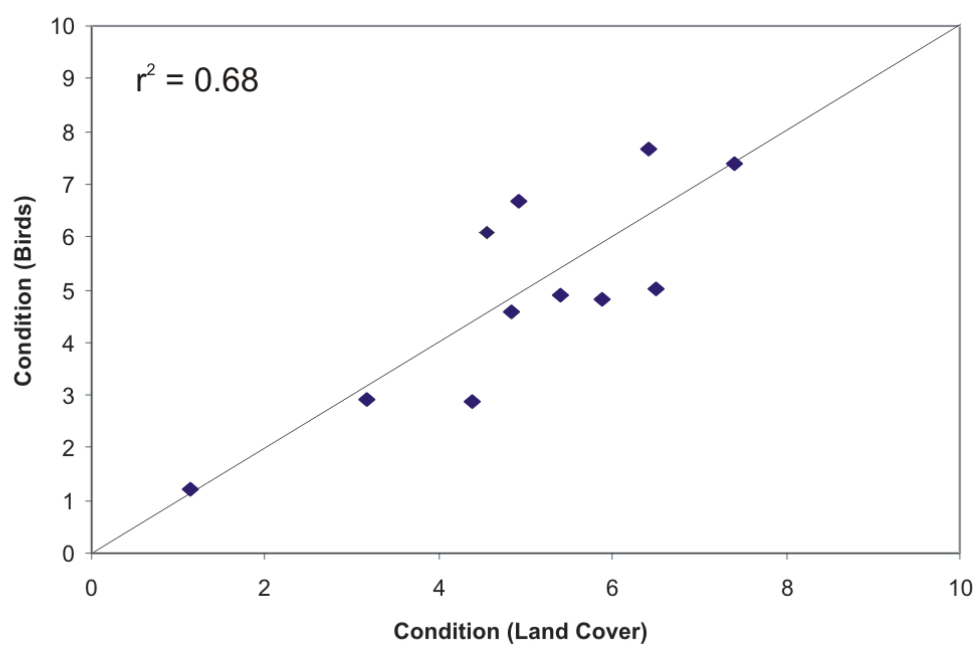
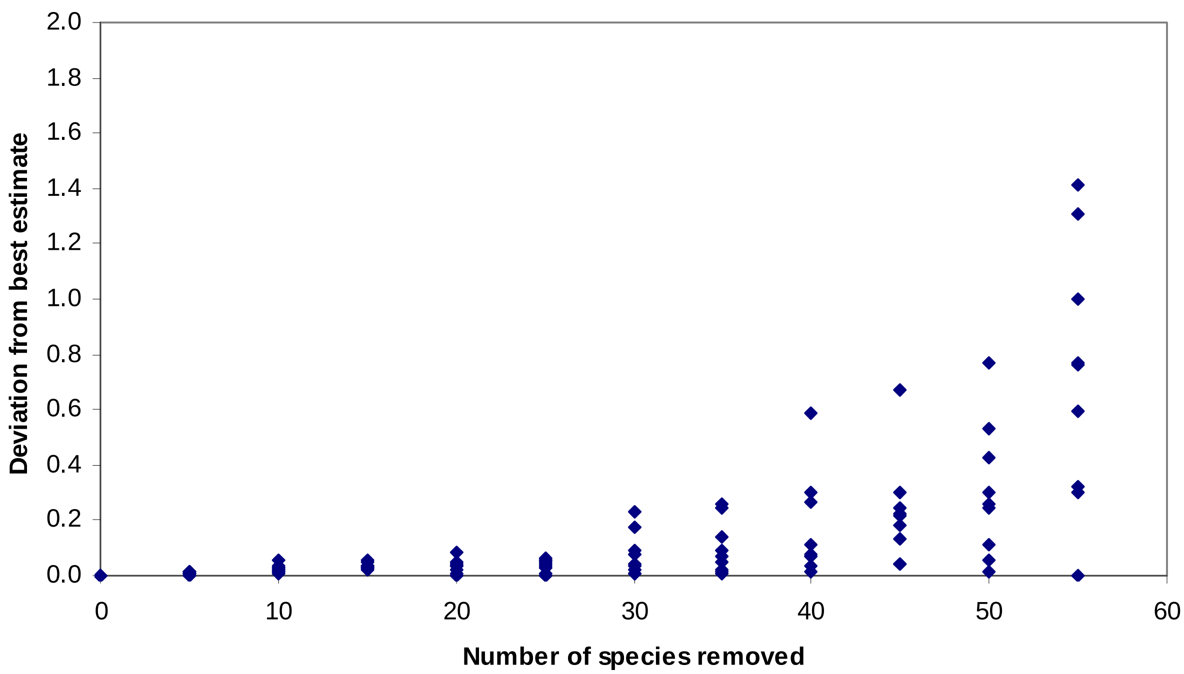


Figure 5.


2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Deviation from best estimate
0
10
20
30
40
50
60
Number of species removed