Chapter 11
Use, Misuse, and Limitations of Threshold Indicator Taxa Analysis (TITAN) for Natural Resource Management

Ryan S. King and Matthew E. Baker

Abstract Detection of ecological thresholds has broad relevance to management of ecosystems. However, ecological community data present a distinct problem because current statistical methods used for identifying thresholds were not developed for analysis of multiple, individual species abundances. We developed a new method, Threshold Indicator Taxa ANalysis (TITAN), specifically to deal with some of the limitations of existing methods for estimating community thresholds. Our objectives in this chapter are to (1) summarize the theoretical basis for the method and related methods, (2) provide a brief overview of how it works, (3) use a real data set to illustrate an application of the method, and (4) conclude the chapter by addressing several issues related to the appropriate use of the method, misconceptions about how it works or what the results mean, and limitations that could lead to erroneous conclusions. We explain that step-function conceptualizations of community thresholds are not sufficiently inclusive of all the response forms that satisfy threshold criteria, how gradual responses of univariate community metrics do not rule out community thresholds, and that linear regression techniques do not provide an adequate test for the absence of thresholds, especially in the presence of long environmental gradients. We note substantial misunderstanding in the recent literature regarding appropriate use and interpretation of statistical change points identified by taxon-specific analysis in TITAN, that univariate community metrics are inappropriate response variables for such analyses, and that extreme variation in the density of the sample distribution can affect results of any method, including TITAN. We end by reminding users that despite the additional insight it brings to community analysis, TITAN is neither a causal analysis nor a black box for developing regulatory criteria. Instead, we intend TITAN to complement current analytical approaches, while highlighting assumptions and flaws in the broader paradigms in which they are often applied.

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Introduction

There is a growing interest in the application of ecological thresholds for natural-resource management (e.g., Huggett 2005; Suding and Hobbs 2009; Dodds et al. 2010). Indeed, threshold detection has broad relevance to management of aquatic ecosystems, such as conservation (DeLuca et al. 2008; Hilderbrand et al. 2010), biological invasions (King et al. 2007), ecosystem restoration (Walsh et al. 2005a; Martin et al. 2009; Clements et al. 2010), development of numerical water-quality criteria (King and Richardson 2003; Soranno et al. 2008), ecosystem management (Richardson et al. 2007), and forecasting effects of climate change (Smol et al. 2005).

Despite the recent interest in ecological thresholds, application of the threshold concept to aquatic-resource management remains tentative, if not contentious (e.g., Gaiser et al. 2008; Richardson et al. 2008). Threshold estimation depends upon the selection of a response variable, assumed shape of the response, and appropriateness of the corresponding statistical model, any of which may contribute to different interpretations regarding the location of a threshold or whether a threshold even exists (e.g., Walsh et al. 2005b; Moore and Palmer 2005; Dodds et al. 2010).

Ecological community data present a distinct problem because current statistical methods used for identifying thresholds were not developed for simultaneous analysis of multiple, individual species abundances (Brenden et al. 2008; Anderson et al. 2009). The vast majority of taxa in community data sets have low occurrence frequencies (i.e., do not occur in a large proportion of the sample units) and have highly variable abundances which make their individual response difficult to fit with various forms of regression analysis typically used for threshold detection (e.g., piecewise regression, Toms and Lesperance 2003, significant zero crossings, Sonderegger et al. 2009). Consequently, most investigators aggregate community data into univariate responses, selecting a priori attributes that presumably represent an important facet of community structure, such as the number of taxa, or deriving synthetic variables from multivariate analysis of taxa composition among sites (e.g., dissimilarity metrics, ordination axes; King and Richardson 2005; Walsh et al. 2005a). While aggregating taxa into one or more response variables may, in some instances, increase the community signal in response to anthropogenic gradients, it also likely obscures nonlinear changes in one or more taxa, potentially underestimating or misrepresenting the effect of an anthropogenic gradient on ecological communities. Thus, evaluating ecological community thresholds with existing approaches often involves undesirable generalities, loss of information, or assumptions regarding taxon-specific responses.

We developed a new method, Threshold Indicator Taxa ANalysis (TITAN), specifically to deal with some of the limitations of existing methods for estimating community thresholds (Baker and King 2010). Since the publication of the method,

we have published four additional papers describing applications of the method (King and Baker 2010; King and Baker 2011a; King et al. 2011; Bernhardt et al. 2012) and a detailed explanation of when to use it, how to interpret it, and what it does and does not do, largely in response to misunderstanding and misrepresentation of the approach by a few investigators (Baker and King 2013). Our objectives in this chapter are to (1) summarize the theoretical basis for the method and related methods, (2) provide a brief overview of how it works, (3) use a real data set to illustrate an application of the method, and (4) conclude the chapter by addressing several issues related to the appropriate use of the method, misconceptions about how it works or what the results mean, and limitations that could lead to erroneous conclusions.

Community Thresholds and Novel Gradients

We define an ecological community threshold to mean that the frequency and/or abundance of taxa will increase or decrease sharply at some level along an environmental gradient, such that an incremental change in a driver such as urban intensity, toxic compounds, or any number of anthropogenic variables results in a disproportionately large change in community structure relative to elsewhere along the gradient (Baker and King 2010). This definition does not necessarily imply a catastrophic, vertical increase or decrease in the response, preceded and followed by zones of minimal change (i.e., a step function), which is unrealistic for many ecological responses and corresponds more closely to a regime shift or alternative stable state (see reviews by Sheffer and Carpenter 2003 and Andersen et al. 2009). However, this interpretation is one that we have frequently encountered in discussions about ecological thresholds with other investigators. Moreover, our definition does not preclude the possibility that some taxa may decline prior to or following a synchronous decline in multiple taxa, but it is grounded in the fact that many interacting species may be influenced in similar ways by an environmental driver, either physiologically or through disruption of interspecific interactions (Økland et al. 2009).

Our definition of an ecological community threshold is particularly linked to and relevant in the context of anthropogenic changes to natural environments (Fig. 11.1). The physical and chemical conditions of many modern ecosystems increasingly diverge from environments known to have existed at any time in the history of Earth (Fox 2007). These "no-analog" or novel environments can lead to wholesale changes in community structure caused by a cascade of intra- and interspecific mechanisms ranging from extirpation of species due to physiological stress, decoupling of positive interactions such as facilitation, relaxation of resource limitations on some while imposing new ones on others, and altering competition or predation (Hobbs et al. 2006; Williams and Jackson 2007). Novel environmental gradients likely represent a strong selective pressure favoring native taxa that are less specialized, have greater physiological plasticity, or facilitate invasion of adaptive nonnative taxa (Stralberg et al. 2009). Species replacement results in novel biotic communities that may be difficult to manage, afford fewer ecosystem services, and may not respond to habitat
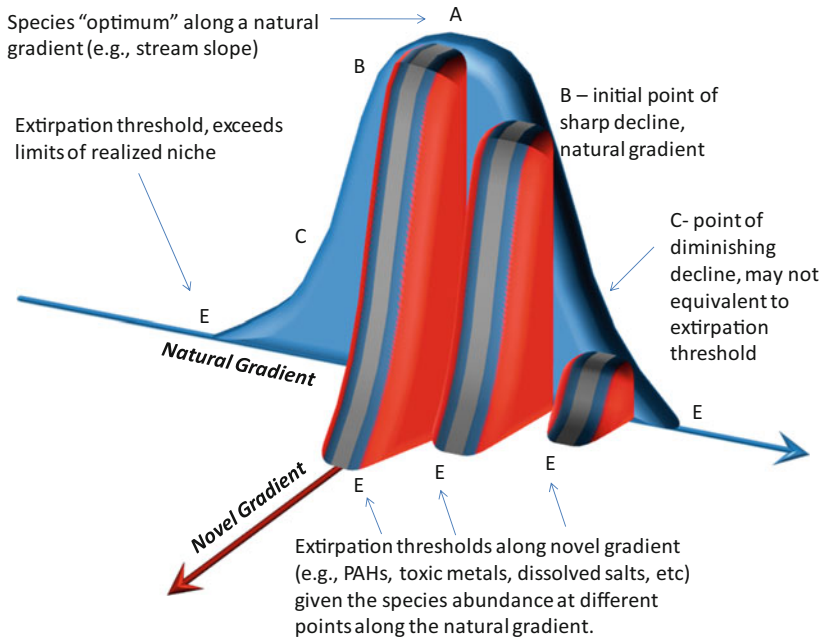
Species "optimum" along a natural gradient (e.g., stream slope)

A

B

B – initial point of sharp decline, natural gradient

Extirpation threshold, exceeds limits of realized niche

C

C- point of diminishing decline, may not equivalent to extirpation threshold

E

Natural Gradient

E

Novel Gradient

E

E

E

E

Extirpation thresholds along novel gradient (e.g., PAHs, toxic metals, dissolved salts, etc) given the species abundance at different points along the natural gradient.

Fig. 11.1 Conceptual diagram illustrating theoretical responses of a single taxon to a natural and novel environmental gradient. The *natural gradient* represents a long gradient such as latitude. The *solid curve* along this gradient represents the range of frequency and/or abundance expected with increasing values along the axis. The *novel gradient* represents a "new" dimension and is theoretically independent (or orthogonal) to the natural gradient. In this example, the *novel gradient* has a negative effect on the taxon, but depending upon the location along the *natural gradient*, the taxon may respond differently to the novel gradient

restoration efforts (Palmer et al. 2009; Clements et al. 2010). Thus, characterizing taxon-specific responses to novel anthropogenic gradients is important for detecting critical levels of alteration, understanding mechanisms of biodiversity loss, identifying adaptive traits that confer success, assessing changes to ecosystem function, and shaping restoration strategies.

A good illustration of a community response to novel gradients is the coincident decline of stream macroinvertebrate communities in response to anthropogenic changes. Although it is widely debated whether stream communities truly exhibit "threshold" responses, we suggest there is strong theoretical and empirical evidence that they do. Many streams, particularly in old landscapes such as the Appalachian Mountains, USA, exhibit high biodiversity as a result of subtle, yet critical differences in stream flow velocities and material transport through time and space (e.g., Poff 1997). Diverse microhabitats have resulted in extensive adaptive radiation of many stream-dwelling taxa (Vinson and Hawkins 1998), whereas moderate frequency and magnitude of hydrological disturbances have maintained high levels of species richness at a local scale (Connell 1978). Facilitation among taxa is also documented

in streams (Cardinale et al. 2002). Consequently, lotic species have coevolved to possess unique morphological, behavioral, and physiological adaptations that correspond to an often narrow range of environmental conditions. Small functional niches undoubtedly render many species intolerant of conditions that fall outside those experienced in evolutionary time (sensu Shelford 1913). Thus, taxa sensitive to the novel environment are selected against, sharply decline, and eventually disappear (Fig. 11.2a).

The theoretical sensitivity posed above appears borne out in some empirical responses to anthropogenic stressor gradients where marked synchrony occurs in the decline of sensitive taxa (e.g., King et al. 2011; Bernhardt et al. 2012). However, synchrony does not mean that all taxa exhibit exactly the same response function, but that their greatest declines (change in frequency and abundance) all occur within a narrow range of the environmental gradient. Many of the responding taxa may occupy distinct trophic positions and thus exhibit different responses, which is why their coincident declines are strong evidence of community organization.

In contrast to the synchronous declines of sensitive taxa, positive-responding taxa may or may not increase synchronously, and in our studies to date appear to increase gradually in frequency and abundance at various levels of increasing novel conditions (e.g., Baker and King 2010; King et al. 2011). The lack of synchronous change points, that is, locations along the novel gradient that result in the greatest amount of change in the response, and greater uncertainty in the location of individual taxa change points implies that positive responding taxa probably do not represent well-organized communities, but rather are composed of historically native taxa that either directly (resource subsidy) or indirectly (e.g., realized niche expansion, reduced competition or predation) benefited from it (Fig. 11.2b).

These theoretical and empirical responses represent the underlying basis for the development of TITAN. The following section details in brief how the method works and can be used to identify change points in individual taxa responses as well as provide an assessment of the degree of synchrony in multiple taxa responses as evidence for an ecological community threshold.

Threshold Indicator Taxa ANalysis (TITAN): What Is It and How Does It Work?

TITAN is an analytical approach for identifying and distinguishing threshold-type responses in ecological community data sets. Its basic premise is that community response to environmental gradients, particularly novel environmental gradients, is best detected empirically by aggregating the responses of individual taxa rather than seeking change in community summary metrics (King and Baker 2010). This is consistent with what Ferrier and Guisan (2006) identify as a "Predict first, assemble later" approach to modeling communities. Analyzing individual taxa in this way requires confronting the considerable variability in numerical abundance data and uncertainty typically associated with sparse community data matrices, where many
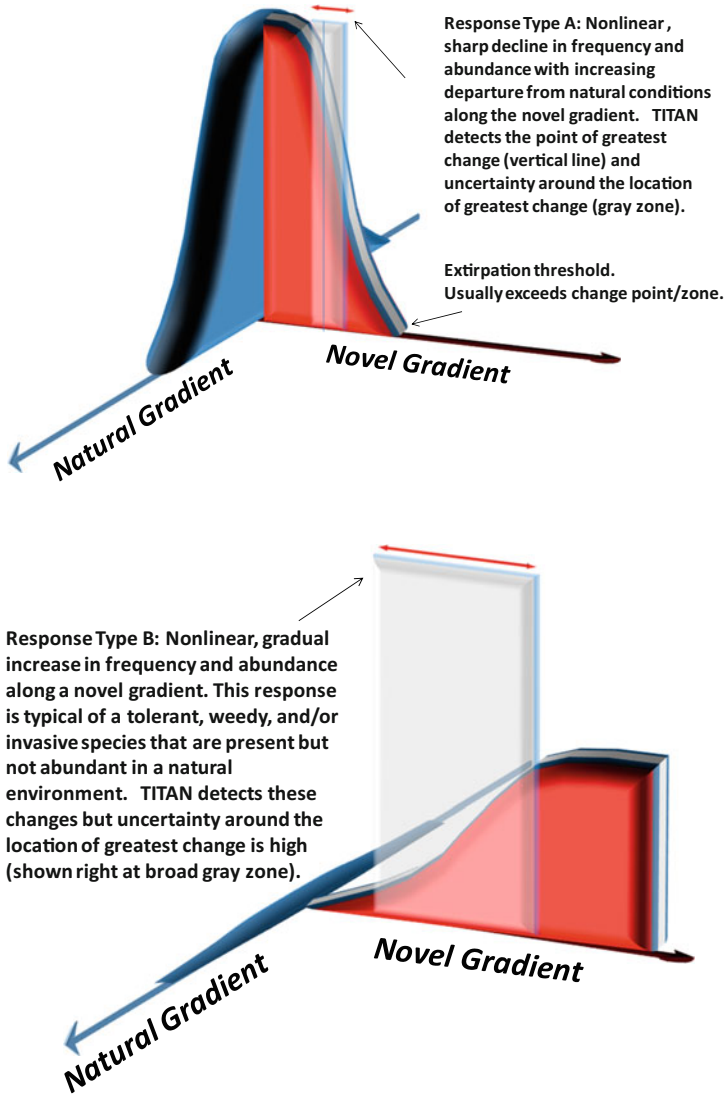
Response Type A: Nonlinear,
sharp decline in frequency and
abundance with increasing
departure from natural conditions
along the novel gradient. TITAN
detects the point of greatest
change (vertical line) and
uncertainty around the location
of greatest change (gray zone).

Extirpation threshold.
Usually exceeds change point/zone.

Novel Gradient

Natural Gradient

Response Type B: Nonlinear, gradual
increase in frequency and abundance
along a novel gradient. This response
is typical of a tolerant, weedy, and/or
invasive species that are present but
not abundant in a natural
environment. TITAN detects these
changes but uncertainty around the
location of greatest change is high
(shown right at broad gray zone).

Novel Gradient

Natural Gradient

Fig. 11.2 Conceptual diagram illustrating theoretical responses of different taxa to a novel environmental gradient. The x–y intercept represents absence of the anthropogenic stressor or a level that falls within the normal range of conditions experienced during evolutionary time. The response of Taxon A represents no change in its distribution along the gradient until a critical change point or zone is reached (*shaded region*), which leads to a nonlinear decline and eventual extirpation at a level beyond the initial change point. Taxon B represents a native taxon that is tolerant of the novel gradient and either directly (resource subsidy) or indirectly (e.g., realized niche expansion, reduced competition or predation) benefits, resulting in an indeterminate increase in its frequency and abundance among sites with increasing values of the gradient. Taxon B could also be an invasive taxon that is able to cross ecosystem boundaries and proliferate because of the altered and more favorable novel conditions that previously limited its distribution

taxa occur infrequently and irregularly in samples measured across time and space. Confounding detection efforts, taxon abundances are often observed to vary as a result of stochastic processes, sampling error, and strong correlation among unmeasured environmental factors (e.g., King et al. 2005, 2011). Fortunately, this autocorrelation means that the majority of variation in community structure can be explained with relatively few dimensions. It also means that some taxa (though which ones are not always clear) are likely to respond similarly to strong environmental drivers. This redundancy is the basis for multivariate ordination methods that presuppose a unimodal response model, but such methods are designed to detect species optima and do not necessarily describe change. At its core, TITAN is a filtering process that seeks to separate true and reliable response patterns of change from the high levels of unexplained variability, or noise, in community data.

TITAN works by integrating a relatively simple and elegant measure of association in taxon abundance with a nonparametric technique for detecting change. Indicator species analysis (Dufrene and Legendre 1997) uses abundance-weighted occurrence frequency to describe association between a particular taxon and groups of samples defined by their order along an environmental gradient. Baker and King (2010) provide explicit detail; however, for an intuitive understanding, it is perhaps useful to consider the patterns of abundance in Fig. 11.2. A taxon's indicator value (IndVal) at any position along the gradient is a function of the relative abundance on either side of a partition, weighted by its occurrence within each partition (i.e., the product of both). In TITAN, the larger IndVal on each side of a partition is retained and compared across partitions to find the value of the environmental gradient that results in the greatest change in taxon abundance and frequency within the observed sample. This value is a change point. However, a change point is not necessarily a "statistical threshold" per se. It is simply the value of x that best partitions the data so that difference in frequency and abundance is maximized. This analysis is repeated for each taxon to provide a set of observed change points and the direction of that change.

To facilitate comparison across taxa, TITAN compares each taxon's maximum IndVal score to those expected if the same sampled abundances were randomly distributed across the environmental gradient. A good indicator species is one that occurs frequently, so that changes in its abundance are easy to detect, but that is not the only kind of response worth noting. IndVal scores will always be small for rare, variable, or sensitive taxa, even though they can nonetheless represent important changes within a community. By comparison to the average IndVal scores derived by random permutation, TITAN standardizes measures of change for any given taxon to units of standard deviation (z scores; Baker and King 2010). Standardization emphasizes observed changes for each taxon relative to their own patterns of variability in abundance and occurrence.

To better understand uncertainty surrounding the observed change points, TITAN employs a bootstrap resampling technique (resampling with replacement; Manly 1997). However representative or large a sample may be, it remains only one estimate of true underlying population patterns, and given a taxon-specific pattern of abundance, another sample may yield an altogether different change point. Thus, for every taxon the entire analysis is repeated many times (we recommend a minimum

of 500), each with a slightly different collection of replicates drawn from the original sample set to obtain a distribution of potential change points.

Information provided by the bootstrap is critical for interpreting results in TITAN. In addition to the location and dispersion of the change-point distribution, TITAN evaluates consistency in the response direction as purity, and the frequency of a strong response magnitude as reliability (Baker and King 2010). Combined with a minimum occurrence frequency, these diagnostic indices are used as filters to help distinguish the signal produced by indicator taxa responses from stochastic noise along the gradient. This filtering is part of what distinguishes TITAN from many other multivariate techniques based on weighted averaging or dissimilarity.

Once indicator taxa have been identified, TITAN provides information that can be used to identify a potential community-level threshold. A plot of filtered indicator taxa showing change-point quantiles from bootstrap replicates provides evidence regarding the existence of synchronous changes in the community structure. Because the magnitude of all responses is standardized across taxa as z scores, their sum reflects the magnitude of community change at any point along the gradient. Distinct peaks in the sum(z) curve (maxima) plotted across the environmental gradient are another indication of coincident change in community structure. When bootstrap replicates used to compare the location of the sum(z) maxima across many sample replicates show a narrow band, this constitutes evidence for a threshold response (Baker and King 2010; King et al. 2011).

Case Study: Macroinvertebrate Community Response to a Phosphorus Gradient in the Everglades

The Everglades (Florida, USA) is a large subtropical wetland that has experienced significant anthropogenic changes in the past several decades. Modifications to hydrology, fire frequency and intensity, and other environmental factors all have played a role in the alteration structure and functioning of the Everglades ecosystem, but phosphorus (P)-enriched runoff from the Everglades Agricultural Area (EAA) is widely viewed as the primary stressor (SFWMD 1992). An extensive canal-and-levee system has compartmentalized most of the remaining Everglades ecosystem, a system that also serves as a conduit for P from the EAA. Water-control structures along the canals function as point sources of P to downstream portions of the wetland ecosystem. In areas near water-control structures, P has been found to be largely responsible for facilitating invasion of cattail, vines, willows, and other plants that are strongly limited by P (King et al. 2004; Richardson et al. 2007). Periphyton (floating and attached mats of algae and bacteria), macroinvertebrate, and fish communities have also changed dramatically in areas with even modest levels of P enrichment. Thus, P enrichment in the Everglades serves as an excellent example of a novel environmental gradient.

The data to be used for this example are from a previous study designed to identify a concentration of surface-water total P (TP) that corresponded to abrupt changes in

Fig. 11.3 Relationship between surface-water total phosphorus (TP) and distance from the canal in the northern Everglades
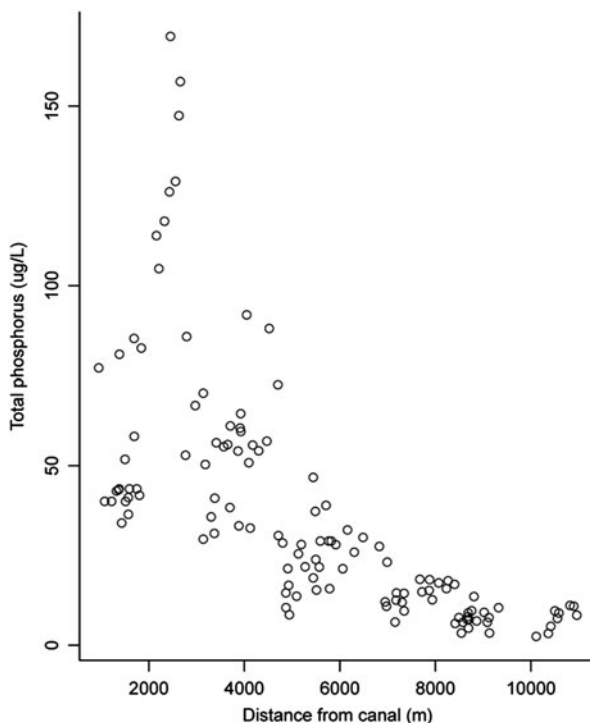
macroinvertebrate species composition in the Florida Everglades, USA (King and Richardson 2003). Macroinvertebrate species composition (no/m^2, 164 taxa, species or morphospecies-level taxonomy) was measured from 126 marsh sampling stations along a 10-km TP gradient. This gradient corresponds closely to proximity canal inflow structures, the point-sources of P to the interior marsh. Concentrations of TP in the data set ranged from < 10 to > 100 μg/L. The authors used several community variables and estimated TP change points using a univariate method called nonparametric change-point analysis (nCPA), a binary partitioning method that is computationally similar to regression tree analysis but incorporates bootstrapping for confidence interval (CI) estimation and allows specification of distribution families for response data (Qian et al. 2003). The resulting change points from their analysis ranged from approximately 10–25 μg/L TP, and authors concluded that TP > 12–15 μg/L was likely to correspond to ecologically significant changes in taxonomic composition.

In our example, we reanalyzed macroinvertebrate community response to TP as well as a second variable, distance from the canal inflow structures (canal, m), that was not analyzed by King and Richardson (2003). Because canal represents the source of TP, and TP responds in a nonlinear, negative manner to increasing distance from the canal (Fig. 11.3), taxa that respond in a strongly negative direction to increasing TP presumably should respond *positively* to increasing distance from

the canal. Thus, taxa that are classified as negative indicators (z−) for TP should be positive indicators (z+) for canal, assuming there is good correspondence in the explanatory power between the variables. To be clear, this is by no means a causal analysis but in this case substantial experimental work has been done to validate observational results implying TP as a driver of community thresholds (King and Richardson 2003). We will discuss the issue of confounded, intercorrelated variables in the concluding section of this chapter.

Prior to TITAN analysis, we $\log_{10}(x+1)$ transformed taxa abundances to reduce the influence of highly variable taxa on indicator score calculations, although it is certainly acceptable to use untransformed abundances in this nonparametric analysis. Taxa with < 5 occurrences were deleted (following previous analyses of these data). We ran TITAN using each variable separately to compare the relative strength of community response (sum(z)), number of threshold indicator taxa, and the correspondence between individual taxa responses to both variables. The minimum split size (minimum number of observations required on each side of a candidate change point) was set to 5, number of permutations was set to 250, and the number of bootstrap replicates was set to 100 (although we suggest using the default number of 500 in most cases for more precise confidence limits and purity/reliability estimates). Step-by-step instructions on how to load TITAN, import data, run the analysis, and graph results are provided online (http://onlinelibrary.wiley.com/doi/10.1111/j.2041-210X.2009.00007.x/suppinfo).

The first sets of results to examine are the individual threshold indicator taxa change points, confidence limits, and other diagnostic statistics. Table 11.1 reports a list of taxa that are deemed highly probable indicators of decline in response to a novel gradient, in this case, positive change with increasing distance from the canal (taxa classified as positive indicators, or z+) and negative change with increasing levels of surface-water TP. Recall that these predictors are negatively related so it is important to recognize that taxa that are negatively affected by a novel gradient can be either classified as negative (z−) or positive (z+) indicators depending upon the direction of the values of the gradient. The output from TITAN will not make value judgments about which direction is "good" or "bad" so it is imperative that the investigator be aware of this fact when sorting through output.

There are several columns of results included in Table 11.1. The first, Freq (Frequency of occurrence) merely summarizes how many times a taxon occurred in the data set. Note that a few taxa only occurred five times, the minimum requirement for inclusion in this analysis. The next column (Obs.cp) is the observed value of the predictor that resulted in the maximum indicator z score in the data set. The next two columns report the raw IndVal and its standardized z score (z). Note that some taxa have relatively low IndVal scores (recall that IndVal is scaled from 0–100) but relatively high z scores. The reason for this is that IndVal does not reflect the magnitude of difference in frequency and abundance between the groups of samples on either side of the change point, whereas the z score does. The z does this by subtracting the average IndVal score obtained by randomly reshuffling the data (250 permutations) from the observed IndVal and dividing this difference by the standard deviation of

Table 11.1 Indicator taxa identified by TITAN in response to distance from the canal and total phosphorus

Taxon code	FrEq	Distance from canal (m)						Total phosphorus (ug/L)					
		Obs. cp	IndVal	z	CI-90 %	Purity	Rel05	Obs. cp	IndVal	z	CI-90 %	Purity	Rel05
Ablarham	15	6,844	28.25	8.64	6,202	1.00	1.00	15.81	31.08	10.46	20.08	1.00	1.00
Acentria	7	6,327	11.82	4.29	5,094	1.00	0.95	14.56	14.65	5.00	28.80	1.00	0.95
Aphaopac	104	4,425	64.15	9.08	3,467	1.00	1.00	36.91	64.16	8.54	42.40	1.00	1.00
Beartrun	66	4,300	72.11	14.49	3,510	1.00	1.00	29.33	66.55	13.54	38.79	1.00	1.00
Bezzsp2	41	5,302	53.84	11.70	5,169	1.00	1.00	16.27	50.56	10.38	30.90	1.00	1.00
Bratunid	77	3,453	63.67	10.05	3,335	1.00	1.00	32.43	53.61	7.54	41.14	1.00	1.00
Caendimi	90	4,175	72.73	12.62	2,418	1.00	1.00	30.33	63.82	10.19	40.17	1.00	1.00
Calanoid	26	3,510	30.95	6.42	3,467	1.00	1.00	29.07	25.63	4.94	35.07	0.98	0.95
Callftor	**89**	**2,075**	**70.08**	**6.91**	**1,733**	**1.00**	**1.00**						
Celiepon	14	6,844	20.86	5.40	6,202	0.99	0.95	13.65	25.51	7.12	16.27	1.00	0.98
Ceriodap	**39**	**8,081**	**48.38**	**7.62**	**6,994**	**0.99**	**0.99**						
Cernotin	15	6,994	40.54	14.03	7,789	1.00	1.00	9.04	50.07	11.77	15.11	1.00	1.00
Cladopel	37	3,884	36.29	5.68	3,508	1.00	1.00	32.43	31.12	4.67	43.21	1.00	0.99
Cladotan	14	7,956	42.71	13.38	7,831	1.00	1.00	10.92	35.70	9.94	14.56	1.00	1.00
Coryspd	5	8,832	14.59	6.35	6,994	1.00	0.99	13.16	14.29	6.24	15.14	1.00	0.95
Cyprbrev	13	8,807	45.29	12.76	7,789	1.00	1.00	13.65	36.11	12.26	15.37	1.00	1.00
Dasyhele	**75**							**14.62**	**44.44**	**3.49**	**68.52**	**0.99**	**0.96**
Dicromod	21	5,277	23.06	4.76	3,506	0.98	0.96	33.70	22.63	5.04	40.17	0.99	0.99
Enalcivi	70	7,956	72.81	13.60	5,225	1.00	1.00	18.61	70.31	13.21	30.98	1.00	1.00
Ferrissi	59	4,175	48.31	6.29	3,403	1.00	1.00	30.33	44.05	5.44	37.01	0.99	0.99
Fittsert	18	4,300	23.68	6.15	3,861	1.00	1.00	9.64	23.02	3.98	35.24	0.99	0.95
Hyalazte	125	3,585	57.29	7.04	3,467	1.00	1.00	30.33	55.56	5.93	60.07	1.00	1.00
Hydbisp2	42	5,094	47.86	10.26	4,300	1.00	1.00	33.00	47.10	9.51	43.16	1.00	1.00
Ischnura	8	8,382	24.34	8.39	7,831	1.00	1.00	7.42	33.31	9.51	12.36	1.00	0.99
Labrneop	14	6,202	22.37	6.20	5,169	1.00	1.00	13.16	25.17	6.66	28.08	1.00	0.98
Laevpeni	**94**	**2,418**	**66.42**	**7.52**	**1,568**	**0.99**	**0.99**						
Micrdila	**58**	**4,175**	**54.94**	**9.07**	**3,467**	**1.00**	**1.00**						
Nanoalte	6	8,682	23.08	8.98	7,931	1.00	0.99	8.48	31.58	11.19	9.62	1.00	0.99
Nilothau	10	8,807	36.60	12.19	7,956	1.00	1.00	10.92	34.48	11.91	12.06	1.00	1.00

Table 11.1 (continued)

Taxon code	FrEq	Distance from canal (m)						Total phosphorus (ug/L)					
		Obs. cp	IndVal	z	CI-90 %	Purity	Rel05	Obs. cp	IndVal	z	CI-90 %	Purity	Rel05
Oecetspe	22	6,535	39.48	10.73	5,302	1.00	1.00	17.21	34.22	9.72	29.07	1.00	1.00
Oxyethir	22	7,956	62.88	18.84	7,413	1.00	1.00	14.62	45.63	13.34	14.77	1.00	1.00
Palapalu	83	4,175	84.18	16.04	3,585	1.00	1.00	28.08	71.97	13.34	36.91	1.00	1.00
Paracala	12	8,081	34.15	10.09	6,224	1.00	1.00	10.52	31.12	8.27	14.56	1.00	1.00
Parakspc	35	6,744	79.55	21.67	6,317	1.00	1.00	14.62	76.21	20.94	17.76	1.00	1.00
Parapony	11	7,956	35.48	12.69	7,931	1.00	1.00	12.06	34.38	11.92	12.66	1.00	1.00
Paraspb	21	8,382	73.54	18.72	7,953	1.00	1.00	10.92	59.88	17.32	14.62	1.00	1.00
Physcube	67	5,739	61.40	10.19	5,035	1.00	1.00	31.68	56.51	9.29	39.55	1.00	1.00
Plansp1	69	6,327	51.08	6.43	6,202	1.00	0.99	14.62	52.28	6.03	17.76	1.00	0.99
Polyhalt	14	6,844	32.56	11.86	6,327	1.00	1.00	16.87	30.43	12.11	16.87	1.00	1.00
Polypspa	21	6,844	46.10	14.86	6,202	1.00	1.00	14.62	43.71	13.67	21.61	1.00	1.00
Proclad	8	9,719	52.38	11.94	7,981	1.00	1.00	6.48	48.05	11.24	12.71	1.00	1.00
Spongill	13	6,077	24.53	8.09	5,277	1.00	1.00	8.22	34.80	7.93	21.92	1.00	1.00
Tanylimn	18	5,244	23.74	6.16	5,060	0.99	0.99	29.83	21.29	4.76	33.70	1.00	0.99
Tanyspg	**85**							**40.11**	**50.79**	**4.68**	**48.60**	**1.00**	**1.00**
Tanyspr	46	6,744	96.19	25.14	6,177	1.00	1.00	14.62	86.23	22.61	25.73	1.00	1.00
Tanyspt	5	7,413	13.89	5.87	6,869	0.99	0.95	7.64	25.87	7.74	9.43	1.00	0.95
Trichorx	11	6,844	22.20	8.02	5,706	1.00	1.00	21.38	20.75	7.45	24.71	1.00	1.00
Unionico	5	8,807	19.01	7.85	7,956	1.00	0.97	9.64	20.00	8.55	10.72	1.00	0.99

Taxa are listed in alphabetic order by code name. Frequency specifies the number of times each taxon occurred in the data set (out of 126 sample units). The observed change point (Obs.cp) is the value of the predictor that resulted in the maximum observed indicator score (IndVal) among all possible change point values. The IndVal score is scaled from 0–100, with 100 indicating a taxon that occurred in all of the samples above or below a change point value and in none of the samples on the other side of the change point, whereas the z score is scaled to reflect how different the IndVal was from values that were obtained by random reshuffling of the data (250 permutations). The CI-90 % is the value where 90 % of the change points estimated among all of the bootstrap replicates fell either below (for a declining, $z-$ taxon) or above (for an increasing, $z+$ taxon). Purity is proportion of the bootstrap replicates that correctly assigned the taxon as an increaser or decreaser, whereas reliability (rel05) is the proportion of the bootstrap replicates that resulted in a p-value of <0.05. Only indicator taxa that passed screening criteria ($p < 0.05$, purity > 0.95, reliability (rel05) > 0.95) for at least one variable are shown; taxa that passed criteria for only one variable are shown in bold

the random IndVals. The advantage of this standardization is that a taxon with relatively few occurrences but very strong fidelity to one end of the gradient can achieve a large z score despite having a relatively small IndVal. Nevertheless, both statistics are useful measures of taxa responses to the gradient.

The next column, CI-90 %, reports metrics of uncertainty about the change point location of individual taxa. The 90 % CI is the 90th quantile of the distribution of change points computed from 100 bootstrap replicates. In the case of an increasing taxon (z+, distance from the canal), this is the 90th quantile on the left end of the distribution, or the lowest level of the predictor where change points begin to be detected using bootstrapping. In the case of a decreasing taxon, the 90th quantile is near the highest level of the predictor where change points are detected using bootstrapping. These CIs serve as conservative estimates of change-point locations. Note that in some cases the 90 % CI is substantially higher (z−) or lower (z+) than the observed change point. In these instances, this suggests a broader range of change much like the taxon illustrated in Fig. 11.2b. We also acknowledge that CIs can be inaccurate for taxa with relatively few occurrences, which would be the case for any analysis, so strict interpretation of CIs for individual taxa is discouraged (Baker and King 2010). However, the CIs do provide an informative reflection of variability in IndVal scores among different samples of the data.

The final two columns report metrics of uncertainty about the repeatability of a taxon as a potential threshold indicator. Purity is the proportion of times that a taxon is given the same classification in each bootstrap replicate as in the observed data set. So, taxa that receive a purity score of 1.00 were assigned as a z+ taxon (distance from canal) or z− (TP) in every bootstrap replicate. The second metric is reliability. It counts the number of times out of the n number of bootstrap replicates that an individual taxon achieved a p–value < 0.05. The closer this value is to 1.00, the more likely the taxon is indeed responding in a predictable manner to the novel gradient. Note that we did not include a column for observed p-values; all of the p-values for these taxa were less than or equal to the lowest possible value for 250 permutations (< 0.004). The observed p-value is neither informative, nor is it an appropriate metric of statistical significance (Baker and King 2013). Taxa with purity > 0.95 and reliability > 0.95 always achieve $p < 0.05$ because the former two metrics are based on resampling of the data and thus much more robust indicators of taxa response. Thus, this list of taxa is of those that passed these two filtering criteria (purity > 0.95, reliability > 0.95). Note that for the sake of space, we did not include in Table 11.1 the taxa that increased along the variables representing the novel gradient (z− for distance from canal, z+ for TP), but did in the figures to follow.

Before we move on to a discussion of the graphical results, note in Table 11.1 the remarkable degree of overlap in the list of taxa that increase with distance from the canal and decrease with increasing TP. We expected substantial overlap given the correlation between variables but also some disagreement because of the moderate amount of variability in TP concentration as a function of distance from the canal (Fig. 11.3). The concordance between predictors provides at least some support for the idea that the effect of the canal is a function of TP, given that we already know
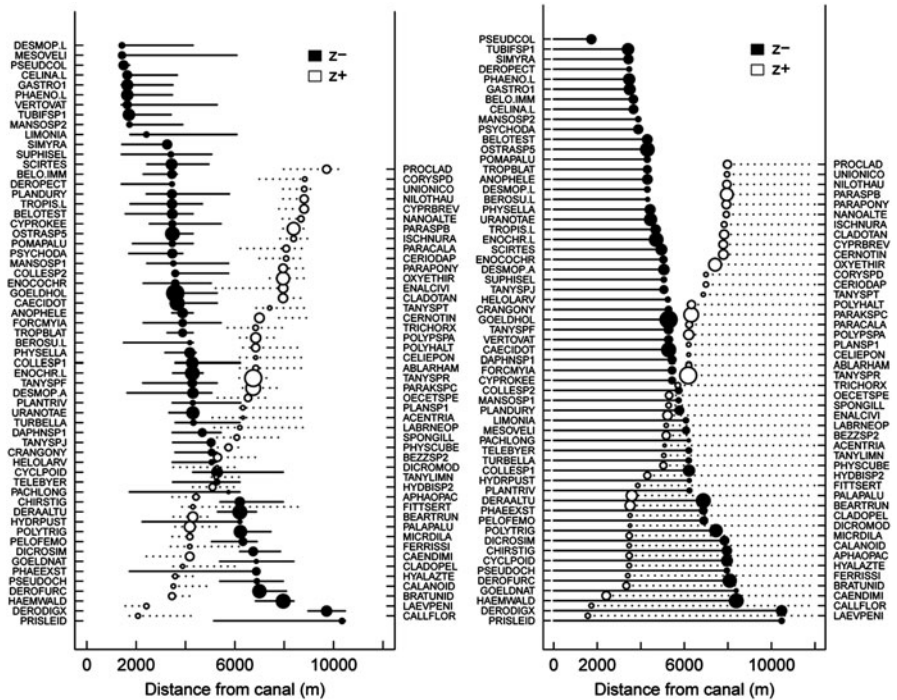
Fig. 11.4 Robust indicator taxa identified by TITAN in response to distance from the canal. In panel **a**, *horizontal lines* represent 90 % CIs of observed change points (*open or closed circles*) for each taxon. In panel **b**, taxa are ordered based on the 95th quantile of the bootstraps. *Horizontal lines* extend from the lowest (declining taxa) or the highest predictor value (increasing taxa) to the 95th quantile of the distribution of change points for each taxa ("diving board plot")

that the Everglades is very P limited and that experiments have validated strong community responses to TP in isolation.

Graphical evaluation of individual taxa results from TITAN provides a much cleaner depiction of most of the tabular output presented in Table 11.1. Figure 11.4 illustrates two types of graphs we developed for displaying indicator taxa results. In Fig. 11.4a, the open and filled circles are the observed change points for each indicator taxon that passed the screening criteria (as shown in Table 11.1). The horizontal lines intersecting each point are the 5th and 95th quantiles of the bootstrap distribution of change points for each taxon, i.e., confidence or variability bands such as those illustrated in Fig. 11.2a, b. The *y*-axes show the code names of the indicator taxon in rank order of the observed change point, starting with the lowest change point on the top left axis (negative indicator taxa, z−) and the highest change point on the top right (positive indicator taxa, z+). The size of the open or filled circles is proportional to the indicator z score, so larger circles are taxa with stronger relative responses to the gradient. Note that there actually were more taxa that favored conditions near the canal than the natural condition at the opposite end of the gradient, as shown by the longer list of taxa on the left *y*-axis.
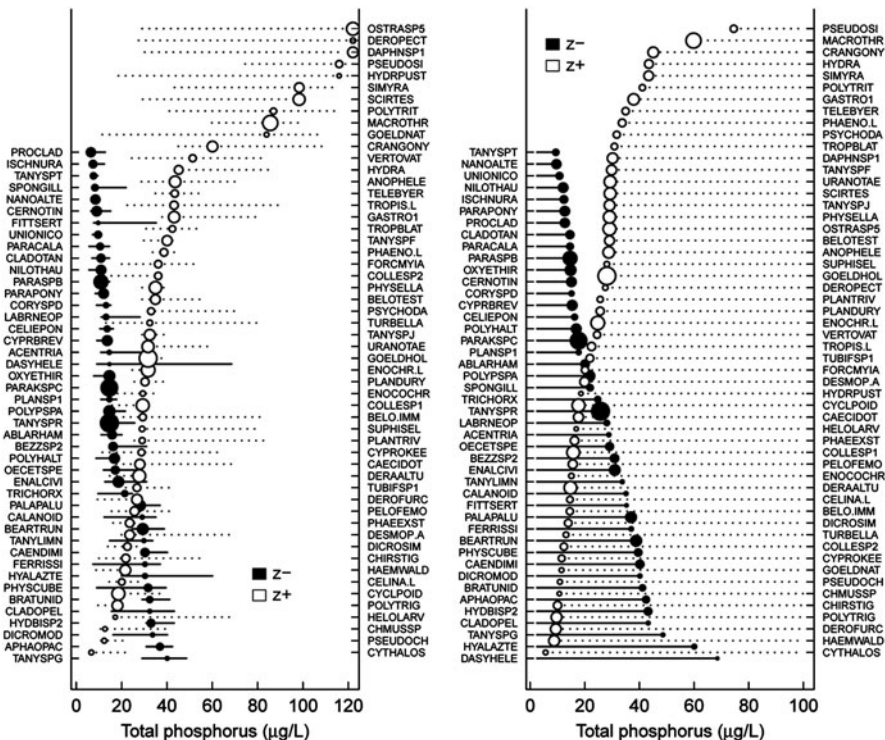
Fig. 11.5 Robust indicator taxa identified by TITAN in response to surface-water total phosphorus (TP). In panel **a**, *horizontal lines* represent 90 % CIs of observed change points (*open* or *closed circles*) for each taxon. In panel **b**, taxa are ordered based on the 95th quantile of the bootstraps. Horizontal lines extend from the lowest (declining taxa) or the highest predictor value (increasing taxa) to the 95th quantile of the distribution of change points for each taxa ("diving board plot")

The second figure (Fig. 11.4b) illustrates the same information but in a different way. In this figure, taxa are plotted in rank order of the CI-90 %. The open and filled symbols are placed at CI-90 % and sized in proportion to z scores. The horizontal lines are drawn from the 90 % CI to the *y*-axis to facilitate visualization of overlap of the increasing and decreasing indicators as well as the degree of synchrony in change point locations. We have termed this a "diving board plot" because the open or filled symbol at the end of the horizontal line represents the point where a taxon is likely to "dive."

In both subfigures of Fig. 11.4, the pattern of many taxa increasing and decreasing in a relatively narrow range of the novel gradient should be evident, particularly in the Fig. 11.4b. The zone of overlap nicely illustrates a region of substantial turnover in taxonomic composition. Despite relatively strong synchrony, there is evidence for some degree of a continuum of change in the middle of the gradient rather than a catastrophic "step function" type threshold.

However, Fig. 11.5 suggests that part of the reason for continuum of change with distance from the canal is the variability in TP at different distances from the canal,
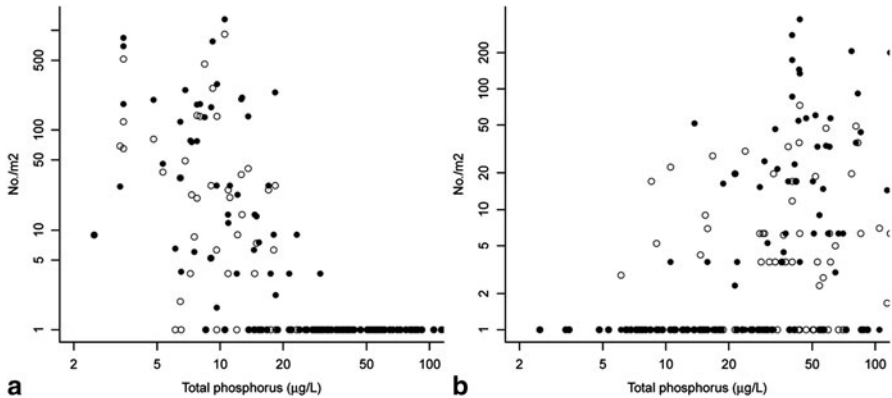
Fig. 11.6 Scatterplots of response of **a** two representative negative indicators (*Tanytarsus* sp. R, *filled symbols*, and *Parakiefferiella* sp. C, *open symbols*) and **b** two positive indicators (*Goeldichironomus holoprasinus*, *filled symbol*, and *Caecidotea*, *open symbol*) to the phosphorus gradient. Note that TP is expressed on a logarithmic scale

as shown in Fig. 11.3. The response of negative indicators to TP is much more abrupt and synchronous, ranging from about 10–40 ug/L TP. The strongest threshold indicators responded quite synchronously between 10 and 20 ug/L TP, evidenced by the clustering of larger filled symbols at low levels of TP. In some cases, taxa occurred in nearly every sample unit to the left of the threshold and none of the sample units to the right (Fig. 11.6a, b).

Recall that TITAN also provides a second set of results that attempts to synthesize individual taxa responses into an index of community-level change, sum(z). Table 11.2 reports several community-level results based on the aggregate response of negative and positive responding taxa, respectively. The raw sum(z) value is the sum of all z scores (not just ones that met screening criteria) at the value of the predictor where sum(z) is maximized. This value is computed for negative and positive responders separately. The sum(z) value is quite useful by itself because it provides a metric of the aggregate magnitude of change among negative and positive indicator taxa in the community. It is reasonable to compare the sum(z) value among multiple predictors as a metric of explanatory power, but it is not reasonable to compare sum(z) among different data sets because the absolute value is dependent upon the number of taxa in the data set. In this case, the sum(z) for positive responses to the canal gradient is slightly lower than sum(z) for the negative responses to the TP gradient, suggesting that TP did a slightly better job of capturing the effect of enrichment than the proximal "source" variable, canal. However, the opposite was true for the taxa that favored conditions near the canal, where sum(z) negative exceeded the TP sum(z) positive by a moderate value. This was also reflected in the larger number of taxa that were deemed negative indicators to canal than positive indicators of TP (59 vs. 54, respectively).

Table 11.2 Community-level results from TITAN using distance from canal and total phosphorus as predictors and macroinvertebrate taxa abundances as the response. (see Fig. 11.7)

	Distance from canal (m)		Total phosphorus (ug/L)	
	Negative	Positive	Negative	Positive
Sum(z)	304	311	327	283
No. of indicator taxa	59	46	44	54
Sum(z) change pt.	5,739	7,956	14.62	31.68
CI 5 %	3,485	5,169	12.36	20.08
CI 10 %	3,578	5,277	12.66	22.55
CI 50 %	5,048	6,794	15.11	29.83
CI 90 %	6,077	7,956	21.28	37.86
CI 95 %	6,202	8,382	28.31	40.11

Sum(z) is the sum of all taxa z scores at the level of the predictor that resulted in the greatest change in the aggregate response of negative (z−) or positive (z+) taxa. Sum(z) is a relative measure of response magnitude. The number of indicator taxa reflects only those taxa that passed all screening criteria ($p < 0.05$, purity > 0.95, reliability > 0.95; see Table 11.1). The sum(z) change point is the value of the predictor that resulted in the greatest aggregate change among negative and positive responding taxa, respectively. The CIs correspond to change point quantiles computed from the bootstrap replicates and are displayed visually as a cumulative frequency curve in Fig. 11.7

The next series of results are the observed and bootstrap quantiles of change points for the community-level response of negative and positive indicator taxa. The observed change points for both sum(z−) and sum(z+) are relatively similar for both predictors, reflecting the synchronous turnover in taxa in the zone of 6–8 km from the canal and 14–31 ug/L TP. The location of synchronous decline in response to TP was the tightest community-level response among the sum(z) change points, spanning a 90 % CI of 11–28 ug/L TP in comparison to the full range of values spanning ∼5 to 150 ug/L TP.

The last form of output from TITAN is the plot of all of the values of sum(z) along the novel gradient (Fig. 11.7). These plots are arguably less intuitive but quite informative once fully understood. The left *y*-axis is the sum of the z scores. As the value of the gradient increases, the sum of the z scores will climb as the community-level response increases in magnitude. The peak in the sum of the z scores represents the observed change point. Beyond the peak, values will decline but may show secondary peaks along the gradient where other groups of taxa change synchronously. If the peak is very sharp such that the sum of the z scores increases and decreases rapidly on either side of the peak, this is strong evidence for a sharp, synchronous change in the community. If the peak is broad, such that there are many values along the gradient that produce similar sum(z) scores, this is more indicative of a zone of change rather than an abrupt threshold. Contrasting the response of the sum(z) scores between canal and TP shows these two different responses. The response of both increasing and decreasing taxa to the canal gradient is more gradual, such that the peak in sum(z) bounces around in the middle of the gradient before declining sharply on either end. Conversely, the negative response to TP is quite sharp, with a clear peak evident at ∼15 ug/L. The positive response is less sharp but is still consistent with a rapid, synchronous increase in multiple taxa around 30–40 ug/L
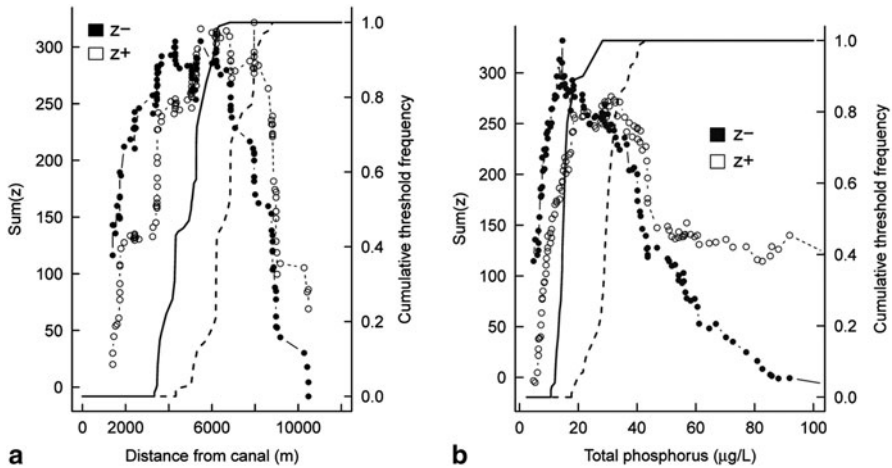
Fig. 11.7 TITAN sum(z−) and sum(z+) values for all possible change points in response to distance from canal (**a**) and total phosphorus (**b**). Peaks in sum(z−) correspond to locations along the *gradient* where synchronous declines of taxa occur. *Solid* and *dashed lines* represent the cumulative frequency distribution of change points among 100 bootstrap replicates for sum(z−) and sum(z+), respectively

TP. Finally, the right *y*-axis shows the cumulative frequency of sum(z) "peaks" among the bootstrap replicates. Steep cumulative frequency curves will span only a narrow range of *x* values and are further support for a community-level threshold. Broader curves imply more gradual change. Collectively, these results support the conclusion that macroinvertebrate communities respond strongly to TP, that the effect of TP on community structure is nonlinear, and that the source of TP, the canal, explains most of the same variability in community structure.

Misconceptions, Misuse, and Myths About Community Thresholds and TITAN

In this concluding section, we will address several ideas or issues that we consider important points of clarification for users of TITAN and anyone interested in analyzing ecological data in search of thresholds. We have attempted to group them but admit that these cover a wide range of topics and may not follow a logical progression.

Community thresholds are not necessarily "step functions." We have encountered numerous investigators who react to the idea of thresholds with much doubt if not disdain. Although reasons vary, one apparent reason for this reaction is the preconceived notion that a threshold necessarily implies a single point along a gradient where everything falls apart, and prior to and following that point essentially nothing happens. Perhaps the root of this confusion is the related but distinct theoretical ideas of "regime shifts" or "alternative stable states" where an entire ecosystem

undergoes a shift from one structural and functional identity to a very different one once the system is pushed beyond some theoretical limit (e.g., Sheffer and Carpenter 2003). The best (and one of the few) example of such a shift is lake eutrophication where a clear-water system with rooted macrophytes suddenly shifts to a turbid, phytoplankton system once nutrient loading exceeds its assimilative capacity (Sheffer et al. 2001). While such examples probably exist for ecological communities in response to novel gradients (and is actually approximated fairly well by the synchronous declines of taxa to TP in our Everglades example), this definition is by no means sufficiently inclusive of other responses that also may be deemed thresholds. Per our own definition, a community threshold need only demonstrate that a certain subset of taxa change in a relatively synchronous manner at a particular level of a novel environmental gradient, and that additional change prior to or beyond that point is entirely acceptable. Once investigators are willing to acknowledge this definition, we submit that the threshold concept will be less offensive to their sensibilities.

Linear responses of univariate community metrics to environmental gradients do not rule out community thresholds. It is of no surprise that different investigators can come to different conclusions about the response of communities to novel gradients using essentially identical data sets. One of the best examples of this has been the ongoing debate about stream community response to watershed urbanization (e.g., Walsh et al. 2005; Cuffney et al. 2010; King and Baker 2010, 2011). Some investigators claim no evidence in support of thresholds based on the result that variance in univariate community metrics is well explained by a linear regression. Others have claimed that a piecewise model with an immediate linear decline across a substantial fraction of the gradient followed by a second zone of essentially little or no change is the most probable response, whereas we have consistently detected a narrow zone of urban intensity where multiple taxa begin to decline, indicative of what we consider to be a community threshold (King and Baker 2010, 2011; King et al. 2011; Baker and King 2013). How can one reconcile these disparate results?

It is our opinion, one we base on multiple empirical lines of evidence, that the use of univariate community metrics as a response variable coupled with the very casual application of linear models has obscured nonlinear changes in community data. We have demonstrated this phenomenon using a simulation where we programmed taxa responses to sharply decline at a particular level of a novel gradient and combined these responses with more gradual increases (as in Fig. 11.2) and other taxa with no response. Once these responses were combined into a single value per sample unit, the response appeared roughly linear for most of the gradient whereas TITAN revealed very sharp synchronous declines in the taxa that we had programmed (King and Baker 2010). In sum, we caution the use of univariate metrics for community threshold analysis without careful consideration of the location, magnitude, and direction of individual taxa responses.

Linear regression does not provide a "test" for the absence of thresholds. We also caution the use of linear regression for "testing" for the presence or absence of thresholds (see King and Baker 2011). A significant *p*-value for a regression slope does not mean that response is necessarily linear. Only a graphical examination of the *x–y* relationship and the residuals from that relationship can yield the necessary

information about the appropriateness of the linear model. If investigators are set on analyzing univariate metrics, we suggest they read Zuur et al. (2010) and consider using loess regression (e.g., King and Baker 2011), or even better, generalized additive models (GAMs) in accordance with the assumptions of the analysis to determine whether the response has evidence of nonlinearity (e.g., Bernhardt et al. 2012). GAMs fit smoothing functions to the response but will only smooth the response if the addition of greater model complexity is deemed worthwhile based on cross validation. If the estimated degrees of freedom exceed 1 and the smoother p-values are < 0.001, it is highly likely that the response is nonlinear. GAMs also permit specification of appropriate distribution families to match the distribution of response data (e.g., negative binomial, Gaussian, etc).

Beware of long environmental gradients when dismissing thresholds. Another issue related to the use of univariate response variables for threshold identification is gradient length. The problem is that predictor variables that span a very wide range of conditions (long gradients; for example, urban intensity from none to downtown Chicago) can obscure sharp, nonlinear patterns at low levels of the gradient. If a variable does not respond immediately to a novel gradient, (generally, they do not) it may appear to do so if the response location is extreme relative to the complete gradient length. This was a major point of King and Baker (2011), who critiqued a different study that concluded responses to urbanization were linear but missed the lack of response at low levels of the gradient because the gradient was so long and difficult to visualize without looking more carefully at a narrower range of values. Once viewed at levels of urban intensity between 0 and 20, the responses were essentially flat until a critical level of urbanization was reached, which happened to be similar to the levels of urbanization identified as community thresholds by TITAN. Thus, we strongly recommend that users graph their data in such a way (log transformed or truncated axis) to reveal low-level responses to novel gradients (Zuur et al. 2010).

Do not use community metrics as response variables in TITAN. TITAN is designed for taxa abundance data sets (matrix of abundances of multiple taxa by sample units). Patterns of frequency of occurrence among sample units are the key component of the IndVal calculation. Data sets dominated by species that occur in all samples are poorly suited for TITAN because presence/absence of taxa no longer contributes any information to the analysis. This issue becomes particularly problematic when investigators attempt to use a matrix of community metrics (e.g., number of Ephemeroptera, Plecoptera, and Trichoptera taxa (EPT), percentage filterers, ratio of weevils to platypus, etc). TITAN is not intended for use in this way because most contain few if any nonzero values and do not approximate negative binomial distributed abundance data for which TITAN was designed. Such responses are better modeled with other approaches, such as GAM (Zuur et al. 2010), nonparametric multiplicative regression (NPMR; McCune 2006), or, in the rare case when data (residual variance) are normally distributed, piecewise regression.

Statistical change points are not necessarily "thresholds." Large data sets with numerous taxa will almost certainly yield at least a few taxa that are identified as having change points. In fact, even linear responses will yield a change point in

TITAN because the method is designed to find taxa that have greater frequency and abundance at one end of the gradient than another. A linear response will yield such a pattern. Thus, one or a few change points alone does not imply a community threshold using TITAN, although these responses are still potentially useful to managers. First, we strongly encourage users to evaluate the uncertainty around observed change point locations of individual taxa. If it is very broad, there is weak evidence for a sharp change in its distribution with respect to the novel gradient. Narrow confidence or variability bands provide greater support for a threshold-type response for a single taxon. However, more importantly, we recommend that users focus on the distribution of multiple taxa change points. Are the confidence limits narrow, and do they overlap (i.e., are they relatively synchronous)? Does the sum(z) peak sharply or is it poorly defined? If taxa change points are relatively widely distributed with broad confidence limits and poorly defined sum(z) peaks, the response is probably better characterized as a zone of gradual change. The main point here is that TITAN provides a lot of different types of information but it is up to the investigator or manager to interpret the output. See Baker and King (2013) for a thorough treatment of this issue.

Density of the distribution of sample units can affect results. The distribution of sample units along environmental gradients can be an important factor for any threshold analysis. If most of the data points are located near the low end of the gradient, it can lead to misleading change points because there may not be sufficient distribution of sample units at other levels of the gradient, particularly if there are large gaps. Using TITAN or most any other method under these circumstances will likely yield biased results and should be interpreted with caution, if at all (Daily et al. 2012).

TITAN is not a causal analysis. TITAN was designed primarily for use with observational data, particularly large biomonitoring data sets that span a wide range of novel environmental gradients. Such gradients are almost always confounded by multiple, correlated variables which make it very difficult to make strong inference about the cause of the observed response (e.g., King et al. 2005). We strongly caution users to think carefully about their data prior to using TITAN. All of the criteria used to define reference conditions and classify sites into comparable physiographic groupings should be applied to TITAN (e.g., Stoddard et al. 2006).

TITAN is not intended to be black box for developing regulatory criteria. TITAN has great potential to inform managers about critical levels of anthropogenic changes that are associated with rapid changes in ecological communities. However, the potential for confounded variables or study designs that lead to misleading results is certainly a distinct possibility. We strongly discourage using output from TITAN as the sole basis for supporting management decisions. We further suggest that multiple lines of evidence be used to further support or refute TITAN results. Manipulative field experiments and lab studies are certainly recommended when applicable. At a minimum, we recommend that investigators carefully examine the list of taxa identified as threshold indicators and apply knowledge of species sensitivities, evolutionary relationships, and life-history characteristics to support statistical conclusions.

Conclusion

TITAN is a tool. All tools have limitations and can be misused. However, TITAN has distinct advantages for detecting change in taxa distributions that may help identify levels of environmental change associated with disproportionate declines or increases in species abundances, which in turn may be indicative of community thresholds.

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