

Evaluating early-warning indicators of critical transitions in natural aquatic ecosystems

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Ecosystems can show sudden and persistent changes in state despite only incremental changes in drivers. Such critical transitions are difficult to predict, because the state of the system often shows little change before the transition. Early-warning indicators (EWIs) are hypothesized to signal the loss of system resilience and have been shown to precede critical transitions in theoretical models, paleo-climate time series, and in laboratory as well as whole lake experiments. The generalizability of EWIs for detecting critical transitions in empirical time series of natural aquatic ecosystems remains largely untested, however. Here we assessed four commonly used EWIs on long-term datasets of five freshwater ecosystems that have experienced sudden, persistent transitions and for which the relevant ecological mechanisms and drivers are well understood. These case studies were categorized by three mechanisms that can generate critical transitions between alternative states: competition, trophic cascade, and intraguild predation. Although EWIs could be detected in most of the case studies, agreement among the four indicators was low. In some cases, EWIs were detected considerably ahead of the transition. Nonetheless, our results show that at present, EWIs do not provide reliable and consistent signals of impending critical transitions despite using some of the best routinely monitored freshwater ecosystems. Our analysis strongly suggests that a priori knowledge of the underlying mechanisms driving ecosystem transitions is necessary to identify relevant state variables for successfully monitoring EWIs.

competition | intraguild predation | trophic cascade | time series | resilience indicators

Ecosystems can exhibit multistate stability and occasionally sudden transitions from one regime to another despite only incremental changes in drivers (1–5). These critical transitions are characterized by the occurrence of alternative regimes under the same environmental conditions and by abrupt, discontinuous transitions between regimes when a critical threshold is exceeded. As each regime is stabilized by feedback loops, the thresholds for the forward and backward shifts may differ, resulting in hysteresis (5). A well-known example of this phenomenon is the nutrient-driven shift between a clear, macrophyte-dominated regime and a turbid, phytoplankton-dominated regime in some shallow lakes (6).

At the ecosystem level, such fundamental reorganizations affect ecological processes and hence ecosystem services, potentially incurring large economic costs. Therefore, reliable tools for assessing ecosystem resilience are sought, ideally providing management with time to avert an impending critical transition (7). Stabilization through feedback loops often precludes a systematic response in state variables ahead of the shift, hindering the prediction of critical transitions (8). The development of early-warning indicators (EWIs)

derived from bifurcation theory has drawn considerable interest for their ability to detect critical transitions, particularly given their promise of generalizability. These EWIs have been shown to precede critical transitions in modeled time series (8–10), experimental time series (11–13), reconstructed paleo-climate records (14, 15) and whole-lake experiments (16). Until now, however, an assessment of the generality and the detection power of EWIs on long-term monitoring data in aquatic systems is lacking (17).

EWIs are statistical metrics that quantify the loss of temporal or spatial resilience and thereby provide advance warning of the potential proximity to a critical threshold (18). Several EWIs are related to critical slowing down, a characteristic property of dynamic systems close to catastrophic local bifurcations (19). A bifurcation marks a threshold at which the stabilizing properties of the state of the system change. As the system approaches such a threshold, the return rate to equilibrium after a small perturbation slows, so that the system tends to become more similar to its own past, resulting in an increase in autocorrelation at lag-1 (AR-1) (20). This lack of decay of the impact of past perturbations also leads to a buildup in variance, typically measured as an increasing

Significance

Early-warning indicators (EWIs), statistical metrics of system resilience, have been hypothesized to provide advance warning of sudden shifts in ecosystems, or so-called “regime shifts.” Here we tested this hypothesis for four commonly used EWIs. We used empirical time series from five freshwater ecosystems with documented sudden, persistent transitions hypothesized to represent critical transitions. EWIs were detected in several of these long-term records, and in some cases several years before the transition; however, these EWIs varied in reliability, and agreement between indicators was low. Moreover, their applicability was strongly limited by the requirement for ecosystem-specific knowledge of transition-generating mechanisms and their drivers to choose relevant state variables for analysis.

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trend in SD (21). Concurrent increases in SD and AR-1 in a time series also produces greater variability in low-frequency processes compared with high-frequency processes in the power spectrum of a time series, which can be quantified as an increasing density ratio (DR) of variance at low to high frequencies (7, 22). In addition to critical slowing down, the system tends to remain longer at the basin boundary between the two alternative attractors, resulting in a skewed distribution of the state variable (SK) (23). The expected trends in AR-1, SD, DR, and SK are not exclusive indicators of critical transitions as false positives and false negatives can occur (24). Thus, before the application of EWIs based on critical slowing down, careful analysis of whether a system is actually undergoing a critical transition is required (25).

Abrupt changes in the state of an ecosystem can develop from several mechanisms, including (i) linear tracking of large changes in environmental conditions, (ii) nonlinear but continuous (reversible) responses to gradual changes in environmental conditions, and (iii) nonlinear discontinuous (irreversible) responses to gradual changes in environmental conditions (26). Whereas the first mechanism is distinguished by concurrent large changes in environmental drivers (e.g., a sudden increase in temperature), the difference between the other two mechanisms becomes apparent only when the driver is reversed. Thus, single step changes in time series cannot provide direct evidence of a critical transition (27). Given the rarity of empirical time series covering forward and backward shifts, identification of critical transitions in natural systems is difficult; however, by linking observed step changes to a mechanistic understanding of the driving processes that can give rise to bistability, one can hypothesize (but not prove) the existence of a potential critical transition (5, 28).

Lakes have been proposed as particularly suitable ecosystems to test for EWIs associated with critical transitions. The modular nature of lakes also allows for comparisons across different lakes (29). In aquatic systems, various ecological mechanisms have been shown to generate critical transitions between alternative states; the most commonly identified mechanisms include (i) competition between two or more species (2, 28); (ii) trophic cascades through inclusion or exclusion of top predators (16) or parasites (30), resulting in overexploitation traps; and (iii) intraguild predation (IGP) through resource competitors that also prey on one another (31, 32). In the present work, we selected 14 state variables of five well-documented case studies of freshwater critical transitions to test whether four commonly used EWIs (AR1, SD, SK, and DR) can be detected reliably in advance of the transition. We assessed how often these EWIs showed the same trends (agreement), and whether their behavior depended on the mechanism, type of state variable, magnitude of the step, or sampling frequency. Finally, we also tested how many years ahead of the transition EWIs were detectable. We strive to provide a comprehensive assessment of EWIs in some of the best-documented aquatic time series collected following standard monitoring schemes.

Results

Selection of Case Study Ecosystems and State Variables. We selected five case study ecosystems based on expert knowledge of well-described regime shifts that can be qualified as critical transitions in aquatic ecosystems: Lake Müggelsee (Germany; LMS), Lake Veluwemeer (The Netherlands; LVM), Lake Zwemlust (The Netherlands; LZL), Lake Washington (United States; LW), and Lake Võrtsjärvi (Estonia; LV). Based on the literature on these case study ecosystems, we identified relevant critical transition-generating mechanisms, which guided our choice of 14 state variables for EWI analysis. The case studies, mechanisms, state variables, and drivers are summarized in Table 1. A more detailed description of each case study and rationale for choosing the 14 state variables is presented in *SI Appendix, section S1*.

Transition Detection and Seasonal Adjustment. We used three complementary methods—piecewise linear regression, Pettit, and STARS (*Methods*)—to robustly assess the timing of transitions (i.e., breakpoints, defined as large, persistent step changes) in the time series of each state variable. We found one breakpoint in 12 state variables and two breakpoints in two state variables (Table 2 and Fig. 1), resulting in 16 prebreakpoint time series (i.e., from start to step change) for further analysis. In all state variables, the timing of the breakpoints confirmed the timing of transitions reported in the literature. Information on the data structure, including time period, sampling interval, number of data points, and the percentage of missing values in the prebreakpoint time series, are summarized in *SI Appendix, Table S2*. Each state variable showed significant differences in the means before and after the breakpoint (Table 2), with step magnitudes ranging from 0.24–1.59*standard deviation (Table 2). Each prebreakpoint time series was detrended and seasonally adjusted using a Gaussian smoother with a bandwidth corresponding to 12 data points (for monthly datasets) or 26 data points (for fortnightly datasets). Testing of the residual time series for remaining linear trends and seasonality showed a persistent, but greatly reduced, seasonal signal in some time series (*SI Appendix, Table S2*).

EWI Analysis. In 14 of 16 analyzed time series, loss of resilience before the breakpoint was signaled by at least one of the four EWI metrics (coded “+” in Table 2; details provided in *SI Appendix, section S3*), based on the median of the trend distribution across yearly increments of rolling window sizes (*Methods*). We found trends towards increasing AR-1 and DR in 10 cases each (63%), toward increasing SD in nine cases (56%), and toward increasing or decreasing SK (according to the direction of the state change) in seven cases (44%) (Fig. 2 and Table 2). In some cases, AR-1 trends were increasing from negative values to positive values (*SI Appendix, section S3*). We recorded these trends as positive [coded “(+)” in Table 2]. In several cases, indicators showed trends opposite to the theoretical expectation (coded “-” in Table 2). Only the state variable phytoplankton biomass in LMS showed the theoretically expected trends in all EWIs, whereas in two state variables—nonalgal attenuation in LVM and cyanobacteria biomass in LW—all EWIs failed. The agreement was low between positive AR-1 and SD trends (five cases), but higher between positive AR-1 and DR trends (10 cases). Logistic regression revealed no significant relationships ($P < 0.05$) between EWI behavior and mechanism (competition, IGP, or trophic cascade), state variable level (species, group, or ecosystem), step change height, length of prebreakpoint time series, nor sampling interval (fortnightly or monthly).

Robustness to Rolling Window Size and Significance of EWI Trends.

We estimated the robustness of EWI trends to the size of the rolling window, shown as the distribution of trends around their median (boxplots in Fig. 2 for AR-1 and SD and in *SI Appendix, Fig. S4* for DR and SK). The large majority of trends were qualitatively robust to rolling window size, as demonstrated by the low number of trend distributions in which the boxplot crossed zero on the y axis.

We also tested for the significance of the trends by estimating the rate of false positives using simulated surrogate time series (*Methods*). Among all 64 EWI trends (16 time series by four EWIs), only three trends were significant in >50% of the comparisons between data-based and surrogate-based trends. An additional 29 EWIs were significant in <50% of comparisons, and 32 EWIs showed no significant differences between data-based and surrogate-based trends (gray bars in Fig. 2 and *SI Appendix, Fig. S4*).

Table 1. Summary of case study systems, state variables, and drivers by mechanism: Trophic cascade, intraguild predation, and competition

Mechanism	Case study	Shift in state variable	Driver	Process	References
Trophic cascade	LW	Increase in water transparency	Increase in grazing pressure	Trophic cascade from longfin smelt (<i>Spirinchus thaleichthys</i>) on secondary consumer <i>Neomysis</i> on primary consumer <i>Daphnia</i> and finally on producers (phytoplankton)	(53, 54)
	LMS	Increase in <i>Dreissena polymorpha</i> larvae Decrease in <i>Leptodora kindtii</i> (period 1) Increase in <i>Leptodora kindtii</i> (period 2)	Decrease in predation pressure Increase in predation pressure Decrease in predation pressure	Changes in dominant carnivorous zooplankton species coincided with increase in <i>Dreissena</i> larvae. <i>Leptodora</i> are a preferred prey for fish and likely indicate changes in overall fish predation pressure	(55, 56)
Competition	LMS	Decrease in phytoplankton biomass	Reoligotrophication	Reduction in nutrients decreases phytoplankton growth, improving light climate favoring macrophyte reestablishment	(57, 58)
		Decrease in <i>Aphanizomenon</i> (period 1)	Reoligotrophication counteracted by spring warming	Warmer springs promote cold-adapted cyanobacteria development	(59)
		Decrease in <i>Aphanizomenon</i> (period 2)	Reoligotrophication	Reduction in nutrients decreases phytoplankton growth, improving light climate favoring macrophyte reestablishment	(57)
	LW	Decrease in non- <i>Daphnia</i> cladocera	Reduction in predation pressure on <i>Daphnia</i>	Indirect effect of trophic cascade through increasing resource competition by <i>Daphnia</i>	(53, 54)
		Increase in cryptophytes Decrease in cyanophytes	Reoligotrophication Reoligotrophication	Reduction in nutrients decreases cyanobacteria competitive ability and releases other phytoplankton from competition	
	LZL	Decrease in water transparency	Eutrophication, epiphyte shading, and herbivory reduction in nutrients and benthivorous fish	Competition between submerged vegetation and phytoplankton under eutrophication and herbivory on macrophytes	(60, 61)
	LVM	Decrease in nonalgal attenuation		Recovery of submerged vegetation cover and subsequent stabilization of sediments	(62)
LV	Increase in functional group P, decrease in functional group U	Eutrophication	Competition between functional groups P (eutrophic epilimnion species) and U (summer epilimnion species)	(63, 64)	
	Increase in functional group H1	Reoligotrophication	Competition between nonnitrogen-fixing and dinitrogen-fixing species (functional group H1)		
Intraguild predation	LMS	<i>C. vicinus</i> – <i>C. kolensis</i> dominance switch	Reduction of shared food source	The inferior resource competitor <i>C. vicinus</i> preys on juveniles of the smaller <i>C. kolensis</i>	(32)

Case study systems are Lake Müggelsee (LMS), Lake Veluwemeer (LVM), Lake Zwemlust (LZL), Lake Washington (LW), and Lake Vörtsjärv (LV).

EWIs in Stepwise Shortened Time Series. To assess whether EWI trends could have been detected in incomplete time series that would have been available at 1 y or longer before the actual transition took place, we repeated the EWI analysis on stepwise shortened (i.e., yearly increments) time series of each state variable. In 14 of the 16 time series, at least one of the EWIs would have indicated a loss in ecosystem resilience between 1 and >10 y before the critical transition. In three instances, positive EWIs trends were seen in only the year before the shift (*SI Appendix, Table S5*), whereas in 17 instances, the median of the EWI trend distribution remained positive (i.e., showing the expected sign) up to the minimum time series period analyzed (3 y).

Discussion

In this study, we assessed the detectability of four commonly used EWIs (AR-1, SD, SK, and DR) in empirical time series of freshwater ecosystems. By combining high-quality empirical time series with ecological understanding and standardized methods, we have shown that EWIs preceded critical transitions in natural aquatic ecosystems, in some cases even several years ahead of the shift, despite the potential shortcomings of empirical datasets, such as observation error, sparse sampling, and low signal-to-noise ratio (9, 24, 33). However, in a large proportion of cases the EWIs failed, and the cases with positive EWIs generally showed low or no significance. In addition, we found little agreement among signals,

Table 2. Overview of all 14 state variables (16 time series) listing the direction of the shift, timing of the breakpoint (year-month), step height (scaled to SD), two-sample Welch test significance, and for each EWI the sign of the median of the trend distribution (across all rolling window sizes)

Case study	State variable	Direction of shift	Breakpoint (y-mo)	Step (scaled to SD)	t (Welch)	AR-1	SD	SK	DR
LMS	Phytoplankton, mg L ⁻¹	Decrease	1990-5	0.803	9.92	+	+	+	+
	<i>Aphanizomenon</i> , mg L ⁻¹ P1	Decrease	1990-11	0.413	4.47	+	+	-	+
	<i>Aphanizomenon</i> , mg L ⁻¹ P2	Decrease	2002-12	0.317	5.92	-	+	+	-
	<i>Cyclops vicinus</i> , ind L ⁻¹	Decrease	1992-6	0.629	7.86	+	-	+	+
	<i>Dreissena polymorpha</i> larvae, ind L ⁻¹	Increase	1993-9	0.388	-6.79	+	+	-	+
	<i>Leptodora kindtii</i> , ind L ⁻¹ P1	Decrease	1987-11	0.776	6.58	-	+	-	-
	<i>Leptodora kindtii</i> , ind L ⁻¹ P2	Increase	2005-7	0.239	-5.21	(+)	-	-	+
LW	Secchi depth, m	Increase	1976-10	1.29	-21.94	+	+	-	+
	Cryptophytes, 100 μm ³ L ⁻¹	Increase	1977-7	0.627	-13.16	(+)	-	-	+
	Cyanobacteria, 100 μm ³ L ⁻¹	Decrease	1973-4	1.587	9.33	-	-	-	-
	Non- <i>Daphnia</i> cladocerans, ind L ⁻¹	Decrease	1976-8	0.783	6.09	-	+	+	-
LV	H1, mg L ⁻¹	Increase	1992-8	0.569	-6.75	(+)	+	-	+
	P, mg L ⁻¹	Increase	1977-12	0.281	-4.61	(+)	-	+	+
	U, mg L ⁻¹	Decrease	1977-12	0.532	3.17	(+)	-	+	+
LVM	Nonalgal attenuation, m ⁻¹	Decrease	1995-9	1.058	9.05	-	-	-	-
LZL	Secchi depth, m	Decrease	1992-9	1.098	7.97	(-)	+	+	-
Proportion of EWI trend distribution medians corresponding to the theoretical trend expectation						10/16	9/16	7/16	10/16

The t (Welch) values in bold type are significant at the $\alpha = 0.05$ level. The tested EWIs are autocorrelation at lag-1 (AR-1), standard deviation (SD), skewness (SK), and density ratio (DR). Median trends that corresponded with the theoretical expectation are coded with "+"; trends that showed the opposite of expected with "-"; brackets denote AR-1 trends crossing 0 on the scale.

and observed no relationship between EWI trends and potential predictors, such as the ecological mechanism of the shift, state variable level, magnitude of the transition, or sampling interval.

Use of Ecological Understanding in the Choice of State Variables. The choice of case studies and state variables in this study was based on expert knowledge of ecosystems that likely experienced critical transitions. Although this choice was based on an understanding of the ecological mechanisms that can give rise to alternative states in aquatic ecosystems, it does not provide conclusive evidence that the regime shifts that we analyzed correspond to true critical transitions. Nonetheless, such a priori choices of state variables for EWI analysis implicitly excluded assumptions based on other transition types, such as responses to step changes in the driver (34), but offered clear expectations of the EWI behavior that should precede a transition (25). Because mechanisms generating critical transitions can operate at all ecosystem levels, relevant state variables range from discrete variables, such as species-specific biomass (e.g., ref. 32), to aggregated variables, such as Secchi depth, turbidity, or metabolism (e.g., ref. 12). In addition, the case studies were chosen based on the availability of long time series of monitoring data for relevant state variables at sufficiently high temporal resolution and with few missing values (35). Despite our conscientious choice of ecosystems and state variables, we still found contradicting patterns in EWIs.

Detection and Agreement Among Indicators. Not all EWIs were equally reliable in detecting impending transitions (Table 2). In 44% of the 64 cases, the EWI failed. Only in three cases where signals were positive were trends significant in >50% of data-based and surrogate-based trend comparisons. Our significance testing relied on estimating EWI trends in surrogate stationary data fitted to the original time series to determine the rate of false positives. Unfortunately, we lacked records to serve as controls when comparing trends from comparable aquatic systems in which no transition occurred to estimate the rate of true negatives (no alarm, or sensitivity) of the EWIs. Given the lack of such controls, one potential way to measure the no alarm rate is to derive trends from nonstationary models fitted to the data

(36). In future work, it would be valuable to compare trends in EWI in study systems that did not exhibit any changes or in which changes were brought about by large external shifts in drivers.

Agreement between AR-1 and SD trends has been postulated as a minimum requirement to signal the approach of a transition (8). In our dataset, these two indicators concurrently increased in only 5 of 16 time series. Critical transitions with increasing AR-1 and decreasing SD have been observed in other studies as well (36). Such inconsistent trends between indicators may occur in ecosystems that are subject to multiple concurrent regime shift-generating processes that may or may not interact via shared state variables and that may react differently to drivers and environmental noise (9). If such connected regime shift processes work toward muffling variance in the measured state variable, then the variance-based EWI signal could be suppressed (37). Transitions from cycles to stable points also can generate decreasing variation (38) and may explain decreasing SD trends like in the LMS *Cyclops vicinus* abundances or the LV functional group U biomass.

In many cases, autocorrelation (AR-1) was generally low, and in some cases it was even negative (e.g., LW non-*Daphnia* cladocerans). Low AR-1 values (far from the theoretical value of 1 at which critical transitions occur) reflect the fact that transitions in the real world are likely triggered well before the actual tipping point is reached (25, 39). Evaluation of the full power spectrum for changes in power in aggregated low vs. high frequencies over time indicated that higher-order AR processes did not provide more information than the AR-1. This finding suggests that the reported low or negative autocorrelation in our records likely originated from too long sampling intervals in cyclic variables (e.g., population cycles), resulting in undersampled cycles of fast-growing plankton and its related variables.

Successful detection of EWIs often has been related to the availability of high sampling frequency data (40), although it has been shown that EWIs still can be detected robustly in infrequently sampled data as long as the time series are sufficiently long (41). Our study was based on data sampled at (or averaged to) fortnightly and monthly intervals. Monthly intervals are rather long compared with the generation or reaction times of the state

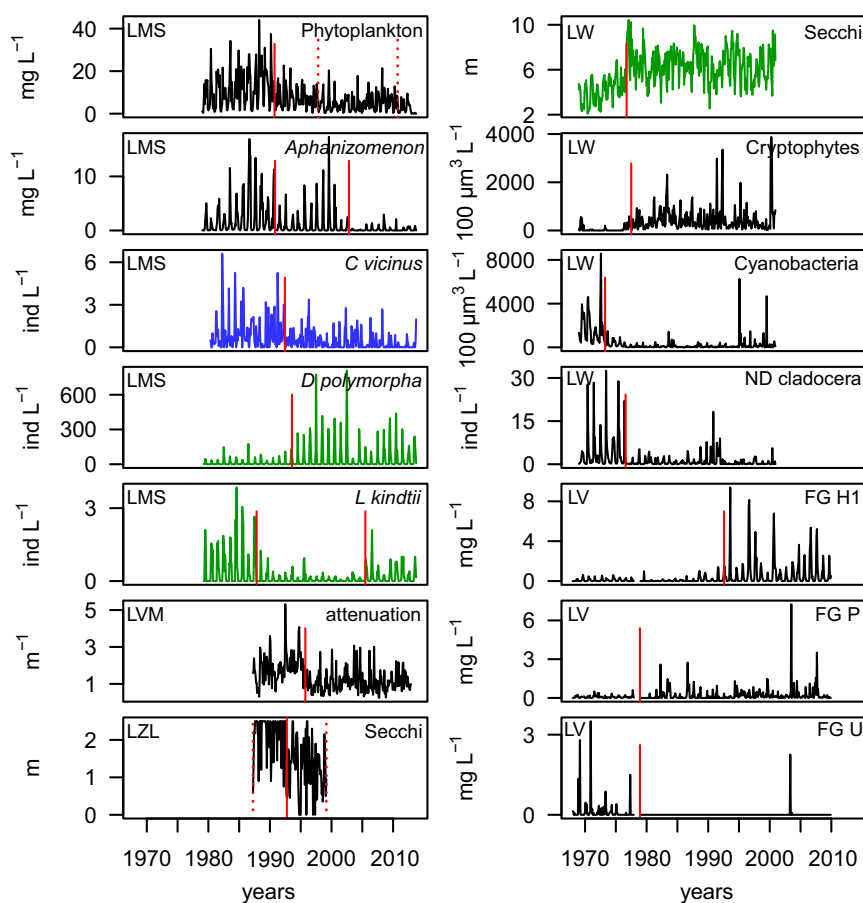


Fig. 1. Time series of 14 selected state variables (black lines, competition; green lines, trophic cascade; blue line, intraguild predation) of five lakes. The solid red lines indicate the timing of critical transitions (estimated by breakpoint analysis; *Methods*). The dashed red lines indicate additional data-based breakpoints that were not used in this study because they either were not described in the literature (LMS phytoplankton biomass) or resulted from biomanipulation (LZL Secchi depth).

variables tested in our study; for example, phytoplankton generation times are on the order of days, and thus monthly averages of biomass aggregate multiple generations of phytoplankton. Nevertheless, we could not detect a relationship between sampling interval and the proportion of failing EWIs in our dataset.

Finally, data preparation, particularly choices regarding detrending and seasonal adjustment methods, can affect the autocorrelation structure in time series and hence the outcome of EWI analyses. We used Gaussian filtering with a fixed bandwidth based on the sampling frequency to detrend and seasonally adjust the data before EWI analysis (*SI Appendix, section S6*); however, despite this data preparation, some time series still showed reduced traces of seasonality. Remaining seasonal signals may increase or decrease the intercept of the EWI trends, but not the sign of the trend.

Early Detection Based on Incomplete Time Series. Informative changes in some of the EWI metrics were already detectable several years before the actual transition, although large differences in detection windows between state variables were observed. These differences may be explained in part by the fact that the actual shift is usually triggered by external stochastic perturbations, which in turn are often independent of the drivers of ecosystem stability loss (42). However, in many cases EWIs indicated sustained instability over the period tested in our study, which may be attributed to either an insufficient time span available for testing (e.g., LZ) or unrecognized interacting processes that promoted prolonged instability in these ecosystems.

Conclusion

Despite our informed and conscientious choice of case study ecosystems and state variables, we found relatively low detectability of EWIs before the documented transitions, and when EWIs were detected, the agreement among them was low. Our findings are in line with results from an assessment of the detectability of EWIs before nonlinear transitions (43). Although it is encouraging that we could detect EWIs in some of our empirical aquatic time series using data derived from commonly used monitoring schemes that were not designed for this purpose, the lack of reliability and agreement among signals limits the potential application of EWIs only to well-understood ecosystems (35). In such well-understood ecosystems, harnessing EWIs as metrics of loss of resilience may aid planning for the unpredictable and could be part of strategic foresight programs for management and conservation (44); however, our analysis suggests that these metrics can be of added value only in combination with existing frameworks (e.g., alternative stable-state theory) and in-depth ecosystem knowledge. Furthermore, taking into account the underlying assumptions and requirements of EWI analysis can inform managers about adaptations in monitoring schemes by advising about relevant variables and temporal sampling resolution to adequately capture changes in the resilience of systems.

One way forward may be the advent of automated, continuous high-frequency monitoring, ideally monitoring multiple lakes with similar properties for comparison (35). To increase our

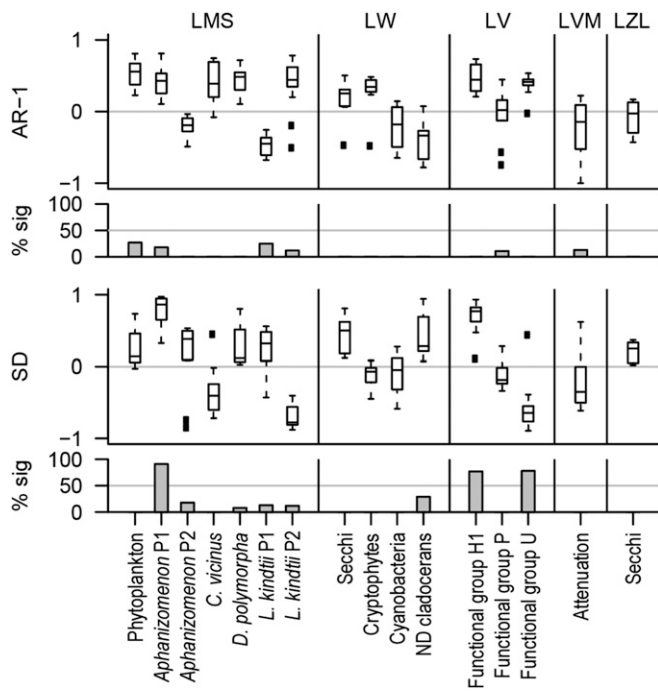


Fig. 2. Robustness and significance testing. Mann–Kendall trend distributions for EWIs AR-1 and SD (panel) and per analyzed time series (boxplots) and the proportion of significant differences in trends between data-based and surrogate time series across all rolling window sizes (significance, gray bar plots). Positive values of trends in the boxplots represent increasing EWI trends. Note that in almost all time series, the trends were robust to the choice of rolling window size. Significance testing was based on comparing indicator trends produced from stationary surrogate time series to the empirically reported for fixed rolling window size (Methods).

understanding of critical transition generating processes, ecosystem models, such as PCLake, can help bridge the gap between simple minimal models and the full complexity of natural systems and allow combined analysis of, e.g., food-web theory and alternative stable states theory and indicators of ecosystem resilience (45). Ideally, such insights can serve to broaden our search image in empirical EWI patterns instead of relying on a generic increase in variance without understanding the inherent variability in ecosystems. In the meantime, the reliability of EWIs for predicting abrupt shifts in ecosystem state should be viewed with caution.

Methods

Data Preparation and Breakpoint Detection. The data preparation and statistical analysis protocol was identical for all 16 state variable time series. Each time series was analyzed at the highest temporal resolution available or at a lower resolution that resulted in less missing data (SI Appendix, Table S2). LMS and LW were analyzed at fortnightly; all other case studies were analyzed at monthly intervals. Because our time series methodology requires continuous and equidistant data, we imputed missing values up to a maximum of four consecutive time steps using a Kalman filter (46). Time series with longer gaps were shortened to start or end at the gap (e.g., LV). Each time series was standardized by mean centering and SD scaling for convenient comparison of step change heights. The timing of the step was determined by breakpoint analysis, given that step changes in the respective state variables may differ from the timing of whole-system step changes reported in the literature. Robust estimates of the timing of step change were achieved using three complementary breakpoint estimation methods: (i) additive decomposition of time series in seasonal, trend, and residual components and subsequent iterative fitting of piecewise linear season and trend models (47) using the R package “bfast” (48); (ii) testing for step changes in the average using the Pettitt test (49); and (iii) STARS, a combination of a sequential partial CUSUM method and a *t* test (50). If at least two methods showed similar timing for a step change (± 12 mo), then the stan-

dardized original time series was split at that breakpoint. Differences between prebreakpoint and postbreakpoint means of the time series were tested with the Welch two-sample *t* test (51) (Table 2).

Because of a 1-y gap in the time series, breakpoint timing of two state variables—LV functional groups P (eutrophic epilimnion species) and U (summer epilimnion species)—was determined differently. Here we assessed whether large changes in the biomasses of the functional groups occurred during the gap, indicating a potential shift. The pre-1978 and post-1978 time series showed significantly different means for functional group U (Welch two-sample *t* test, $t = 3.52$; $df = 128$; $P < 0.001$; difference in means, $0.29 \times SD$) and functional group P (Welch two-sample *t* test, $t = -4.67$; $df = 439$; $P < 0.001$; difference in means, $0.55 \times SD$), suggesting that the shift in functional groups U and P occurred during the year 1978 (Table 2). Because both of these time series showed no further breakpoints in the years after 1978, we conservatively assumed 1977 to be the transition year.

EWI Analysis. The prebreakpoint time series was seasonally adjusted using a Gaussian smoother with a kernel bandwidth based on the number of data points per year (i.e., 12 for monthly datasets and 26 for fortnightly datasets; other methods are compared in SI Appendix, section S6). A bandwidth of 1 y was chosen to account for annually recurring patterns while retaining informative low- and high-frequency variability other than long-term trend and season (15). In three residual time series—LMS *Dreissena* (two outliers) and *Aphanizomenon* period 1 and LW Cyanobacteria (one outlier each)—local outliers were replaced by Kalman-imputed values. The residuals were then passed on to analysis of EWIs AR-1, SD, SK, and DR with testing for robustness to the size of rolling window and testing for significance (false positives) using the R package “earlywarnings” (9). In addition, the static choice of fixed compared frequencies in the EWI DR was confirmed to be sufficiently capturing changes of the full power spectrum of the prebreakpoint residuals time (based on its estimated smoothed fast Fourier periodogram).

Robustness and Significance Testing. The trends in the estimated temporal evolution of EWIs from the rolling window approach were quantified using the nonparametric Mann–Kendall trend test, which tests for monotonic trends based on the Kendall τ rank correlation coefficient (9). Because the size of the rolling window can affect EWI trends (36), a robustness analysis was performed to estimate the distribution of trends and proportion of trends that did not differ in sign from the median of the trend distribution. This was done using yearly increments of the residuals time series covered by the rolling time window [2 to $n - 2$ y, function “sensitivity_ews” (9), where n is the number of years in each prebreakpoint time series]. Significance testing was done by comparing the data-based EWI trend against a bootstrapped distribution of 200 surrogate time series-based EWI trends. The surrogate time series were generated based on an ARMA(p,q) model fitted on the residuals time series. The bootstrapped distribution of trends depicts the probability that a particular trend could occur by chance in time series of the same ARMA structure [function “surrogates_ews” in R package “earlywarnings” (9)]. The data-based EWI trend was deemed significant if it fell on one of the 5% tails of the surrogate-based trend distribution ($\alpha = 0.1$). This significance testing was repeated for all rolling window sizes, and the proportion (%) of significant trends over all rolling window sizes was reported.

Relationship of EWIs with State Variable Categories and Agreement Among Signals.

The relationships between the occurrence of each EWI and the predictor variables mechanism (competition, IGP, or trophic cascade), state variable category (species, group, ecosystem), step change height, length of prebreakpoint time series, and sampling interval (fortnightly or monthly) were analyzed by logistic regression [identity link for continuous predictors (step change height and time series length); logit link for categorical predictors] with Bonferroni-corrected post hoc testing. The median of the trend distribution across all time window sizes was used to assess agreement among EWIs.

Early Detection of EWIs. To assess the potential timeliness of EWIs in detecting the approaching transition, EWI trends were quantified on stepwise shortened prebreakpoint time series, starting with the full time period and continuing with stepwise reduction of the time series by cutting off the last year of data. The minimum time series length was set to 3 y to allow for meaningful Kendall τ estimation. The number of years before the shift that an EWI could have been detected was set by assessing the maximum number of stepwise reductions before the theoretically expected EWI trend disappeared (i.e., when the median of the Kendall τ trend distribution turned negative for AR-1, SD,

and DR or changed sign for SK). All data analyses and graphing were conducted using the R language environment for statistical computing (52) and associated library extensions.

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- Lewontin RC (1969) The meaning of stability. *Brookhaven Symp Biol* 22(22):13–24.
- May RM (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269:471–477.
- Holling CS (1973) Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4:1–23.
- Sutherland JP (1974) Multiple stable points in natural communities. *Am Nat* 108(964):859–873.
- Scheffer M, Carpenter SR, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413(6856):591–596.
- Scheffer M, Hosper SH, Meijer ML, Moss B, Jeppesen E (1993) Alternative equilibria in shallow lakes. *Trends Ecol Evol* 8(8):275–279.
- Biggs R, Carpenter SR, Brock WA (2009) Turning back from the brink: Detecting an impending regime shift in time to avert it. *Proc Natl Acad Sci USA* 106(3):826–831.
- Ditlevsen PD, Johnsen SJ (2010) Tipping points: Early warning and wishful thinking. *Geophys Res Lett* 37(19):L19703.
- Dakos V, et al. (2012) Methods for detecting early warnings of critical transitions in time series illustrated using simulated ecological data. *PLoS One* 7(7):e41010.
- Carpenter SR, Brock WA, Cole JJ, Kitchell JF, Pace ML (2008) Leading indicators of trophic cascades. *Ecol Lett* 11(2):128–138.
- Veraart AJ, et al. (2011) Recovery rates reflect distance to a tipping point in a living system. *Nature* 481(7381):357–359.
- Batt RD, Carpenter SR, Cole JJ, Pace ML, Johnson RA (2013) Changes in ecosystem resilience detected in automated measures of ecosystem metabolism during a whole-lake manipulation. *Proc Natl Acad Sci USA* 110(43):17398–17403.
- Dai L, Vorselen D, Korolev KS, Gore J (2012) Generic indicators for loss of resilience before a tipping point leading to population collapse. *Science* 336(6085):1175–1177.
- Lenton T, Livina V, Dakos V, Scheffer M (2012) Climate bifurcation during the last deglaciation. *Clim Past Discuss* 8(1):1127–1139.
- Dakos V, et al. (2008) Slowing down as an early warning signal for abrupt climate change. *Proc Natl Acad Sci USA* 105(38):14308–14312.
- Carpenter SR, et al. (2001) Trophic cascades, nutrients, and lake productivity: Whole-lake experiments. *Ecol Monogr* 71:163–186.
- Seekell D, Carpenter SR, Cline T, Pace M (2012) Conditional heteroskedasticity forecasts regime shift in a whole-ecosystem experiment. *Ecosystems* 15:741–747.
- Scheffer M, et al. (2009) Early-warning signals for critical transitions. *Nature* 461(7260):53–59.
- van Nes EH, Scheffer M (2007) Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. *Am Nat* 169(6):738–747.
- Ives AR (1995) Measuring resilience in stochastic systems. *Ecol Monogr* 65(2):217–233.
- Carpenter SR, Brock WA (2006) Rising variance: A leading indicator of ecological transition. *Ecol Lett* 9(3):311–318.
- Kleinen T, Held H, Petschel-Held G (2003) The potential role of spectral properties in detecting thresholds in the Earth system: Application to the thermohaline circulation. *Ocean Dyn* 53(2):53–63.
- Guttal V, Jayaprakash C (2008) Changing skewness: An early warning signal of regime shifts in ecosystems. *Ecol Lett* 11(5):450–460.
- Boettiger C, Ross N, Hastings A (2013) Early warning signals: The charted and uncharted territories. *Theor Ecol* 6(3):255–264.
- Dakos V, Carpenter SR, van Nes EH, Scheffer M (2015) Resilience indicators: Prospects and limitations for early warnings of regime shifts. *Philos Trans R Soc Lond B Biol Sci* 370(1659):20130263.
- Andersen T, Carstensen J, Hernández-García E, Duarte CM (2009) Ecological thresholds and regime shifts: Approaches to identification. *Trends Ecol Evol* 24(1):49–57.
- Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends Ecol Evol* 18(12):648–656.
- Collie JS, Richardson K, Steele JH (2004) Regime shifts: Can ecological theory illuminate the mechanisms? *Prog Oceanogr* 60(2–4):281–302.
- Carpenter SR (2003) *Regime Shifts in Lake Ecosystems: Pattern and Variation* (International Ecology Institute, Oldendorf/Luhe, Germany), Vol. 15.
- Gerla DJ, et al. (2013) Alternative states and population crashes in a resource-susceptible-infected model for planktonic parasites and hosts. *Freshw Biol* 58(3):538–551.
- Verdy A, Amarasekare P (2010) Alternative stable states in communities with intraguild predation. *J Theor Biol* 262(1):116–128.
- Scharfenberger U, Mahdy A, Adrian R (2013) Threshold-driven shifts in two copepod species: Testing ecological theory with observational data. *Limnol Oceanogr* 58(2):741–752.
- Perretti CT, Munch SB (2012) Regime shift indicators fail under noise levels commonly observed in ecological systems. *Ecol Appl* 22(6):1772–1779.
- Boettiger C, Hastings A (2012) Quantifying limits to detection of early warning for critical transitions. *J R Soc Interface* 9(75):2527–2539.
- Spears BM, et al. (2016) Ecological instability in lakes: A predictable condition? *Environ Sci Technol* 50(7):3285–3286.
- Livina VN, Ditlevsen PD, Lenton TM (2012) An independent test of methods of detecting system states and bifurcations in time series data. *Physica A* 391(3):485–496.
- Brock WA, Carpenter SR (2010) Interacting regime shifts in ecosystems: Implication for early warnings. *Ecol Monogr* 80(3):353–367.
- Batt RD, et al. (2013) Asymmetric response of early warning indicators of phytoplankton transition to and from cycles. *Theor Ecol* 6(3):285–293.
- Reid PC, et al. (2016) Global impacts of the 1980s regime shift. *Glob Change Biol* 22(2):682–703.
- Carpenter SR, et al. (2011) Early warnings of regime shifts: A whole-ecosystem experiment. *Science* 332(6033):1079–1082.
- Clements CF, Drake JM, Griffiths JJ, Ozgul A (2015) Factors influencing the detectability of early warning signals of population collapse. *Am Nat* 186(1):50–58.
- Scheffer M, et al. (2012) Anticipating critical transitions. *Science* 338(6105):344–348.
- Burthe SJ, et al. (2015) Do early warning indicators consistently predict nonlinear change in long-term ecological data? *J Appl Ecol* 53:666–676.
- Cook CN, Inayatullah S, Burgman MA, Sutherland WJ, Wintle BA (2014) Strategic foresight: How planning for the unpredictable can improve environmental decision-making. *Trends Ecol Evol* 29(9):531–541.
- Kuiper JJ, et al. (2015) Food-web stability signals critical transitions in temperate shallow lakes. *Nat Commun* 6(6):7727.
- Durbin J, Koopman SJ (2012) *Time Series Analysis by State Space Methods* (Oxford Univ Press, Oxford, UK).
- Verbesselt J, Hyndman R, Newnham G, Culvenor D (2010) Detecting trend and seasonal changes in satellite image time series. *Remote Sens Environ* 114(1):106–115.
- Verbesselt J, Hyndman R, Zeileis A, Culvenor D (2010) Phenological change detection while accounting for abrupt and gradual trends in satellite image time series. *Remote Sens Environ* 114(12):2970–2980.
- Pettitt A (1979) A non-parametric approach to the change-point problem. *Appl Stat* 28(2):126–135.
- Rodionov SN (2004) A sequential algorithm for testing climate regime shifts. *Geophys Res Lett* 31(9):L09204.
- Welch BL (1947) The generalisation of student's problems when several different population variances are involved. *Biometrika* 34(1–2):28–35.
- R Core Team (2012) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria), version 3.0.0.
- Hampton SE, Scheuerell MD, Schindler DE (2006) Coalescence in the Lake Washington story: Interaction strengths in a planktonic food web. *Limnol Oceanogr* 51(5):2042–2051.
- Edmondson W (1994) Sixty years of Lake Washington: A curriculum vitae. *Lake Reserv Manage* 10(2):75–84.
- Wilhelm S, Adrian R (2007) Long-term response of *Dreissena polymorpha* larvae to physical and biological forcing in a shallow lake. *Oecologia* 151(1):104–114.
- Gsell AS, Özkundakci D, Hébert M-P, Adrian R (2016) Quantifying change in pelagic plankton network stability and topology based on empirical long-term data. *Ecol Indic* 65:76–88.
- Köhler J, et al. (2005) Long-term response of a shallow, moderately flushed lake to reduced external phosphorus and nitrogen loading. *Freshw Biol* 50(10):1639–1650.
- Hilt S, Köhler J, Adrian R, Monaghan MT, Sayer CD (2013) Clear, crashing, turbid and back: Long-term changes in macrophyte assemblages in a shallow lake. *Freshw Biol* 58(10):2027–2036.
- Shatwell T, Koehler J, Nicklisch A (2008) Warming promotes cold-adapted phytoplankton in temperate lakes and opens a loophole for Oscillatoriales in spring. *Glob Change Biol* 14(9):2194–2200.
- Van De Bund WJ, Van Donk E (2002) Short-term and long-term effects of zooplanktivorous fish removal in a shallow lake: A synthesis of 15 years of data from Lake Zwemlust. *Freshw Biol* 47(12):2380–2387.
- Van Donk E, Gulati RD (1995) Transition of a lake to turbid state six years after bio-manipulation: Mechanisms and pathways. *Water Sci Technol* 32(4):197–206.
- Ibelings BW, et al. (2007) Resilience of alternative stable states during the recovery of shallow lakes from eutrophication: Lake Veluwe as a case study. *Ecosystems* (N Y) 10(1):4–16.
- Nöges T, et al. (2007) Reaction of large and shallow lakes Peipsi and Võrtsjärv to the changes of nutrient loading. *Shallow Lakes in a Changing World*, eds Gulati RD, Lammens E, DePauw N, Van Donk E (Springer, Dordrecht, The Netherlands), pp 253–264.
- Nöges P, Mischke U, Laugaste R, Solimini AG (2010) Analysis of changes over 44 years in the phytoplankton of Lake Võrtsjärv (Estonia): The effect of nutrients, climate and the investigator on phytoplankton-based water quality indices. *Hydrobiologia* 646(1):33–48.