

1 BIOLOGICAL SCIENCES: Ecology; Environmental Sciences

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

3

4 Short title: Early-warning indicators in empirical time series

5

6 Alena S. Gsell<sup>1,2\*</sup>, Ulrike Scharfenberger<sup>1,3</sup>, Deniz Özkundakci<sup>4</sup>, Annika Walters<sup>5</sup>, Lars-Anders  
7 Hansson<sup>6</sup>, Annette B. G. Janssen<sup>2,7</sup>, Peeter Nõges<sup>8</sup>, Philip C. Reid<sup>9,10,11</sup>, Daniel E. Schindler<sup>12</sup>,  
8 Ellen van Donk<sup>2</sup>, Vasilis Dakos<sup>13</sup> and Rita Adrian<sup>1,3</sup>

9

10 <sup>1</sup> Ecosystem Research, Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB),  
11 Müggelseedamm 310, 12587 Berlin, Germany

12 <sup>2</sup> Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10,  
13 6708 PB Wageningen, The Netherlands

14 <sup>3</sup> Freie Universität Berlin, Department of Biology, Chemistry, Pharmacy; Takustr. 3, 14195 Berlin,  
15 Germany

16 <sup>4</sup> Waikato Regional Council, 401 Grey St, 3216 Hamilton, New Zealand

17 <sup>5</sup> U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department  
18 3166, 1000 E. University Avenue, University of Wyoming, Laramie, Wyoming 82071 USA

19 <sup>6</sup> Institute of Ecology, Lund University, 223 62 Lund, Sweden

20 <sup>7</sup> Department of Aquatic Ecology and Water Quality Management, Wageningen University,  
21 Wageningen, The Netherlands

22 <sup>8</sup> Centre for Limnology, Institute of Agricultural and Environmental Sciences, Estonian University  
23 of Life Sciences, Rannu, 61117 Tartumaa, Estonia

24 <sup>9</sup> Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth PL1  
25 2PB, United Kingdom

26 <sup>10</sup> Marine Institute, Plymouth University, Drake Circus, Plymouth PL4 8AA, UK

27 <sup>11</sup> Marine Biological Association of the UK, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

28 <sup>12</sup> School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle,  
29 Washington 98195 USA

30 <sup>13</sup> Institute of Integrative Biology, Center for Adaptation to a Changing Environment, ETH Zürich,  
31 Universitätstrasse 16, 8092 Zürich Switzerland

32

33 \* Corresponding author:

34 Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW),  
35 Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands

36 Phone: +31 (0) 317 473 553, Email: a.gsell@nioo.knaw.nl

37

38 Keywords: alternative stable states, competition, intra-guild predation, resilience indicators, time  
39 series, trophic cascade

40 **Abstract**

41 Ecosystems can show sudden and persistent changes in state despite only incremental changes in  
42 drivers. Such critical transitions are difficult to predict as the state of the system often shows little  
43 change prior to the transition. Early-warning indicators are hypothesised to signal the loss of  
44 system resilience and have been shown to precede critical transitions in theoretical models, paleo-  
45 climate time series, and in laboratory as well as whole lake experiments. However, the generality  
46 of early-warning indicators for detection of critical transitions in empirical time series of natural  
47 aquatic ecosystems remains largely untested. Here, we assessed four commonly used early-  
48 warning indicators on long-term datasets of five freshwater ecosystems that have experienced  
49 sudden, persistent transitions and for which the relevant ecological mechanisms and drivers are  
50 well-understood. These case-studies were categorised by three mechanisms that can generate  
51 critical transitions between alternative states: competition, trophic cascade, and intra-guild  
52 predation. While early-warning indicators could be detected in most case-studies, agreement  
53 among the four indicators was low. In some cases, early-warning indicators were detected  
54 considerably ahead of the transition. Our results, however, show that, at present, early-warning  
55 indicators do not provide reliable and consistent signals of impending critical transitions despite  
56 using some of the best routinely monitored freshwater ecosystems. Our analysis strongly suggests  
57 that *a priori* knowledge of the underlying processes driving ecosystem transitions is necessary to  
58 identify relevant state variables to successfully monitor early-warning indicators.

59

60 **Significance Statement**

61 Early-warning indicators are statistical metrics of system resilience and have been hypothesized to  
62 provide advance warning of sudden shifts in ecosystems, so-called regime shifts. Here we test this  
63 hypothesis for four commonly used early-warning indicators. We used empirical time series from  
64 five freshwater ecosystems with documented sudden, persistent transitions hypothesised to  
65 represent critical transitions. Early-warning indicators were detected in several of these long-term  
66 records, and in some cases, indicators were detected several years before the transition. However,  
67 the indicators varied in their reliability, and agreement between indicators was low. Moreover,  
68 their applicability was strongly limited by the requirement of ecosystem-specific knowledge of  
69 transition generating mechanisms and their drivers to choose relevant state variables for analysis.

70

71 **Introduction**

72 Ecosystems can show multi-state stability and occasionally sudden transitions from one regime to  
73 another despite only incremental changes in drivers (1-5). These critical transitions are  
74 characterised by the occurrence of alternative regimes under the same environmental conditions  
75 and by abrupt, discontinuous transitions between regimes when a critical threshold is exceeded.  
76 As each regime is stabilised by feedback loops, the thresholds for the forward and backward shifts  
77 may differ, resulting in hysteresis (5). A well-known example is the nutrient-driven shift between  
78 the clear, macrophyte-dominated and the turbid, phytoplankton-dominated regime in some  
79 shallow lakes (6). At ecosystem level, such fundamental reorganisations affect ecological  
80 processes and hence ecosystem services potentially incurring large economic costs. Therefore,  
81 reliable tools to assess ecosystem resilience are sought, ideally providing management with time  
82 to avert an impending critical transition (7). Stabilisation through feedback loops, however, often  
83 precludes a systematic response in state variables ahead of the shift, rendering prediction of  
84 critical transitions difficult (8). The development of early-warning indicators (EWIs) derived from  
85 bifurcation theory has drawn considerable interest for detecting critical transitions, particularly for  
86 their promise of generality. These EWIs have been shown to precede critical transitions in  
87 modelled (8-10), experimental time series (11-13), reconstructed paleo-climate records (14, 15)  
88 and whole-lake experiments (16). Up to now, however, an assessment of the generality and the  
89 detection power of EWIs on long-term monitoring data in aquatic systems is lacking (17).

90  
91 Early-warning indicators are statistical metrics that quantify the loss of temporal or spatial  
92 resilience and thereby provide advance warning of the potential proximity to a critical threshold  
93 (18). Several of these EWIs are related to critical slowing down, a characteristic property of  
94 dynamic systems close to catastrophic local bifurcations (19). A bifurcation marks a threshold  
95 where the stability properties of the state of the system change. As the system approaches such a  
96 threshold, the return rate to equilibrium after a small perturbation slows down so that the system  
97 tends to become more similar to its own past, resulting in an increase in autocorrelation at lag-1  
98 (AR-1) (20). This lack of decay of the impact of past perturbations also leads to a build-up in  
99 variance, typically measured as an increasing trend in standard deviation (SD) (21). A concurrent  
100 increase in SD and AR-1 in a time series also produces higher variability in low frequency  
101 processes compared to high frequency processes in the power spectrum of a time series, which

102 can be quantified as an increasing density ratio (DR) of variance at low to high frequencies (7,22).  
103 In addition to critical slowing down, the system tends to remain for longer at the basin boundary  
104 between the two alternative attractors resulting in a skewed distribution of the state variable (SK)  
105 (23). However, the expected trends in AR-1, SD, DR, and SK are not exclusive indicators of  
106 critical transitions as false positives and false negatives can occur (24). Hence, prior to the  
107 application of EWIs based on critical slowing down a careful analysis is needed of whether a  
108 system is actually undergoing a critical transition (25).

109  
110 Abrupt changes in the state of an ecosystem can develop from several mechanisms, including: i)  
111 linear tracking of large changes in environmental conditions, ii) non-linear but continuous  
112 (reversible) responses to gradual changes in environmental conditions, or iii) non-linear  
113 discontinuous (irreversible) responses to gradual changes in environmental conditions (26). While  
114 the first mechanism is distinguished by concurrent large changes in environmental drivers (e.g. a  
115 sudden increase in temperature), the difference between the other two mechanisms only becomes  
116 apparent when the driver is reversed. Hence, single step changes in time series cannot provide  
117 direct evidence of a critical transition (27). As empirical time series covering forward and  
118 backward shifts are rare, identification of critical transition in natural systems is difficult.  
119 However, by linking observed step changes to a mechanistic understanding of the driving  
120 processes that can give rise to bi-stability, one can hypothesise (but not prove) the existence of a  
121 potential critical transition (5, 28).

122  
123 Lakes have been proposed as particularly suitable ecosystems to test for EWIs associated to  
124 critical transitions. The modular nature of lakes additionally allows comparison across different  
125 lakes (29). In aquatic systems, a number of ecological mechanisms have been shown to generate  
126 critical transitions between alternative states. The most commonly identified mechanisms include  
127 i) competition between two or more species (2, 28), ii) trophic cascades through inclusion or  
128 exclusion of top predators (16) or parasites (30) resulting in overexploitation traps, and iii) intra-  
129 guild predation through resource competitors that also prey on each other (31, 32). For the  
130 purpose of this paper, we selected 14 state variables of five well-documented freshwater case-  
131 studies of critical transitions to test whether four commonly used EWIs (AR1, SD, SK and DR)  
132 can be detected reliably in advance of the transition. We assessed how often these EWIs showed

133 the same trends (agreement) and whether their behaviour depended on the mechanism, the type of  
134 state variable, the magnitude of the step, and the sampling frequency. Lastly, we also tested how  
135 many years ahead of the transition EWIs were detectable. To our knowledge, this study provides  
136 the first comprehensive assessment of EWIs in some of the best-documented aquatic time series  
137 collected following standard monitoring schemes.

138

## 139 **Results**

### 140 *Selection of case-study ecosystems and state variables*

141 We selected five case-study ecosystems based on expert knowledge of well-described regime  
142 shifts that can be qualified as critical transitions in aquatic ecosystems: Lake Müggelsee  
143 (Germany, LMS), Lake Veluwemeer (The Netherlands, LVM) and Lake Zwemlust (The  
144 Netherlands, LZL), Lake Washington (United States, LW), and Lake Võrtsjärv (Estonia, LV).  
145 Based on the literature on these case-study ecosystems, we identified relevant critical-transition  
146 generating mechanisms, which guided our choice of 14 state variables for EWI analysis. A short  
147 summary of the case-studies, mechanisms, state variables and drivers is presented in Table 1. A  
148 more detailed description of each case-study and reasoning for the choice of the 14 state variables  
149 is presented in the Supplementary Information Appendix (SI Case-studies S1).

150

### 151 *Transition detection and seasonal adjustment*

152 We used three complementary methods (piece-wise linear regression, Pettit and STARs, see  
153 Methods) to robustly assess the timing of transitions (breakpoints; i.e. large, persistent step  
154 changes) in the time series of each state variable. In 12 state variables we found one breakpoint  
155 and in two state variables two breakpoints (Table 2 and Figure 1), resulting in 16 pre-breakpoint  
156 time series (i.e. from start to step change) for further analysis. In all state variables, the timing of  
157 the breakpoints confirmed the timing of transitions reported in the literature. Information on the  
158 data structure including time period, sampling interval, number of data points and the percentage  
159 of missing values in the pre-breakpoint time series are summarised in SI Table S2. Each state  
160 variable showed significant differences in the pre- to post-breakpoint means (Table 2), with step  
161 magnitudes ranging from 0.24\*standard deviation to 1.59\*standard deviation (Table 2). Each pre-  
162 breakpoint time series was detrended and seasonally adjusted using a Gaussian smoother with a  
163 bandwidth corresponding to 12 (for monthly data sets) or 26 (for fortnightly datasets) data points.

164 Testing the residual time series for remaining linear trends and seasonality showed in some time  
165 series a remaining, but much reduced seasonal signal (SI Table S2).

166

### 167 *Early-warning indicator analysis*

168 In 14 out of 16 analysed time series, a loss of resilience before the breakpoint was signalled by at  
169 least one of the four EWI metrics (coded '+' in Table 2, detailed figures in SI Figures S3) based on  
170 the median of the trend distribution across yearly increments of rolling window sizes (see  
171 Methods). We found rising AR-1 and DR trends in 10 cases each (63 %), rising SD trends in 9  
172 cases (56 %), and increasing or decreasing SK trends (according to the direction of the state  
173 change) in 7 cases (44 %) (Figure 2, Table 2). In some cases, AR-1 trends were increasing from  
174 negative values to positive ones (see SI Figures S3). We counted these trends as positive (coded  
175 '(+)') in Table 2). In several cases, indicators showed trends opposite to the theoretical expectation  
176 (coded '-' in Table 2). Only the state variable phytoplankton biomass in Lake Müggelsee (LMS)  
177 showed the theoretically expected trends in all EWIs, while in two state variables (non-algal  
178 attenuation in Lake Veluwemeer (LVM) and cyanobacteria biomass in Lake Washington (LW)) all  
179 EWIs failed. The agreement between positive AR-1 and SD trends was low (5 cases), but higher  
180 between positive AR-1 and DR trends (10 cases). Logistic regressions showed no significant  
181 relationship ( $p < 0.05$ ) between EWI behaviour and mechanism (competition, IGP, or trophic  
182 cascade), state variable level (species, group, or ecosystem), step change height, length of pre-  
183 breakpoint time series, nor sampling interval (fortnightly or monthly).

184

### 185 *Robustness to rolling window size and significance of EWI trends*

186 We estimated the robustness of EWI trends to the size of the rolling window, shown as the  
187 distribution of trends around their median (boxplots in Figure 2 for AR-1 and SD and SI Figure S4  
188 for DR and SK). A large majority of trends were robust to rolling window size, as shown in the  
189 low number of trend distributions in which the boxplot extended to negative values. We also  
190 tested for the significance of the trends by estimating the rate of false positives using simulated  
191 surrogate time series (see Methods). Out of all 64 EWI trends (16 time series by four EWIs) only  
192 three trends were significant in more than 50% of the comparisons between data-based and  
193 surrogate-based trends. Additional 29 EWI were significant in less than 50% of comparisons, and  
194 32 EWI showed no significant differences between data-based and surrogate-based trends (grey

195 bars in Figure 2 and SI Figure S4).

196

### 197 *Early warning indicators in stepwise shortened time series*

198 To assess whether EWI trends could have been detected in incomplete time series that would have  
199 been available one or several years before the actual transition took place, we repeated the EWI  
200 analysis on stepwise shortened (yearly increments) time series of each state variable. In 14 (out of  
201 16) time series, at least one of the EWIs would have indicated a loss in ecosystem resilience 1 to  
202 >10 years before the critical transition. In three instances positive EWIs trends occurred just the  
203 year before the shift (SI Table S5), while in 17 instances the median of the EWI trend distribution  
204 remained positive (i.e. showing the expected sign) up to the minimum time series period that was  
205 analysed (three years).

206

## 207 **Discussion**

208 In this study we assessed the detectability of four commonly used EWIs (AR-1, SD, SK, and DR)  
209 in empirical time series of freshwater ecosystems. By combining high quality empirical time  
210 series with ecological understanding and standardised methods we showed that EWIs preceded  
211 critical transitions in natural aquatic ecosystems, in some cases even several years ahead of the  
212 shift, despite potential shortcomings of empirical datasets such as observation error, sparse  
213 sampling or low signal to noise ratio (9, 24, 33). However, in a large proportion of cases the  
214 EWIs failed, and the cases with positive EWIs generally showed low or no significance. In  
215 addition, we found little agreement among signals and we observed no relationship between EWI  
216 trends and potential predictors, like ecological mechanism of shift, state variable level, magnitude  
217 of transition, or sampling interval.

218

### 219 *Use of ecological understanding in the choice of state variables*

220 The choice of case-studies and state variables in our study was based on expert knowledge of  
221 ecosystems that likely experienced critical transitions. Although this choice was based on  
222 ecological understanding of the mechanisms that can give rise to alternative states in aquatic  
223 ecosystems, it does not provide conclusive evidence that the regime shifts we analysed correspond  
224 to true critical transitions. Still, such *a priori* choices of state variables for EWI analysis implicitly  
225 excluded assumptions based on other transition types, such as responses to step changes in the

226 driver (34), but offered clear expectations of what EWI behaviour should precede a transition (25).  
227 As mechanisms generating critical transitions can operate at all ecosystem levels, relevant state  
228 variables range from discrete variables, such as species-specific biomass (e.g. (32)), to aggregated  
229 variables, such as Secchi depth, turbidity or metabolism (e.g. (12)). Additionally, the case-studies  
230 were chosen based on the availability of long time series of monitoring data of relevant state  
231 variables at sufficiently high temporal resolution and with few missing values (35). Despite our  
232 conscientious choice of ecosystems and state variables, we still found contradicting patterns in  
233 EWIs.

234

#### 235 *Detection and agreement among indicators*

236 Not all EWIs were equally reliable in detecting impending transitions (Table 2). In 44 % of the  
237 total 64 cases the EWI failed. Only in 3 cases where signals were positive, trends were significant  
238 in more than 50% of data-based and surrogate-based trend comparisons. Our significance testing  
239 relied on estimating EWI trends in surrogate stationary data fitted to the original time series to  
240 determine the rate of false positives. Unfortunately, we lack records to act as controls for  
241 comparing trends from comparable aquatic systems where no transition took place to estimate the  
242 rate of true negatives (no alarm, or sensitivity) of the EWIs. Given the lack of such controls, one  
243 potential way to measure the no alarm rate is to derive trends from non-stationary models fitted to  
244 the data (36). It would be valuable in future work to compare trends in EWI in study systems that  
245 either did not show any changes or in which changes were brought about by large external shifts  
246 in drivers.

247

248 Agreement between AR-1 and SD trends has been postulated as a minimum requirement to signal  
249 the approach of a transition (8). In our dataset, these two indicators concurrently increased in only  
250 5 out of 16 time series. Critical transitions with increasing AR-1 and decreasing SD have also  
251 been observed in other studies (36). Such inconsistent trends between indicators may occur in  
252 ecosystems that are subject to multiple concurrent regime-shift generating processes that may or  
253 may not interact via shared state variables and that may react differently to drivers and  
254 environmental noise (9). If such connected regime-shift processes work towards muffling variance  
255 in the measured state variable, the variance-based EWI signal may be suppressed (37). Transitions  
256 from cycles to stable points can also generate decreasing variation (38) and may explain



257 decreasing SD trends like in the Lake Müggelsee *Cyclops vicinus* abundances or the Lake  
258 Vörtsjärv functional group U biomass.

259  
260 In many cases autocorrelation (AR-1) was generally low and in some cases even negative (e.g.  
261 Lake Washington non-*Daphnia* cladocerans). Low AR-1 values (far from the theoretical value of  
262 1 where critical transitions occur) reflect that transitions in the real world are likely triggered well  
263 before the actual tipping point is reached (25, 39). Evaluating the full power spectrum for changes  
264 in power in aggregated low versus high frequencies over time indicated that higher order AR  
265 processes did not provide more information than the AR-1. This suggests that the reported low or  
266 negative autocorrelation in our records probably originated from the too long sampling intervals in  
267 cyclic variables (e.g. population cycles) resulting in under-sampled cycles of fast growing  
268 plankton and its related variables.

269  
270 Successfully detecting EWIs has often been related to the availability of high sampling frequency  
271 data (40), although it has been shown that EWIs could still be detected robustly in infrequently  
272 sampled data as long as the time series were sufficiently long (41). Our study was based on data  
273 sampled at (or averaged to) fortnightly and monthly intervals. Monthly intervals are rather long  
274 compared to the generation or reaction times of the state variables tested in our study (e.g.  
275 phytoplankton generation times are in the order of days, therefore monthly averages of biomass  
276 aggregate multiple generations of phytoplankton). Nevertheless, we could not detect a relationship  
277 between sampling interval and the proportion of failing EWIs in our dataset. Finally, data  
278 preparation, in particular choices on detrending and seasonal adjustment methods, can affect the  
279 autocorrelation structure in time series and hence the outcome of EWI analyses. We used Gaussian  
280 filtering with a fixed bandwidth based on the sampling frequency to detrend and seasonally adjust  
281 the data before EWI analysis (see SI S6 for a comparison of seasonal adjustment methods).  
282 Despite data preparation, some time series still showed reduced traces of seasonality. Remaining  
283 seasonal signals may increase or decrease the intercept of the EWI trends but not the sign of the  
284 trend.

285  
286 *Early detection based on incomplete time series*

287 Informative changes in some of the EWI metrics were already detectable several years preceding

288 the actual transition, although large differences in detection windows between state variables were  
289 observed. These differences may partly be explained by the fact that the actual shift is usually  
290 triggered by external stochastic perturbations which in turn are often independent of the drivers of  
291 ecosystem stability loss (42). However, in many cases EWIs indicated sustained instability over  
292 the period tested in our study which may be attributed to either a too short time span available for  
293 testing (e.g. Lake Zwemlust) or unrecognised interacting processes that promoted prolonged  
294 instability in these ecosystems.

295

### 296 *Conclusion*

297 Despite our informed and conscientious choice of case-study ecosystems and state variables, we  
298 found relatively low detectability of EWIs prior to the documented transitions, and when EWIs  
299 were detected, the agreement among EWIs was low. Our findings are in line with results from an  
300 assessment of the detectability of EWIs prior to non-linear transitions (43). Although it is  
301 encouraging that we could detect EWIs in some of our empirical aquatic time series using data  
302 derived from commonly used monitoring schemes that were not designed for this purpose, the  
303 lack of reliability and agreement between signals limits the potential application of EWIs to well-  
304 understood ecosystems only (35). In such well-understood ecosystems, harnessing EWIs as  
305 metrics of resilience loss may help in planning for the unpredictable and could be part of strategic  
306 foresight programs for management and conservation (44). However, our analysis suggests that  
307 these metrics could be of added value only in combination with existing frameworks (e.g.  
308 alternative stable state theory) and in-depth ecosystem knowledge. Furthermore, taking into  
309 account the underlying assumptions and requirements of EWI analysis can inform managers about  
310 adaptations in monitoring schemes by advising about relevant variables and temporal sampling  
311 resolution to adequately capture changes in the resilience of systems. One way forward may be  
312 the advent of automated, continuous high-frequency monitoring (35), ideally monitoring multiple  
313 lakes with similar properties for comparison (35). To increase our understanding of critical  
314 transition generating processes, ecosystem models, such as PCLake, can help to bridge the gap  
315 between simple minimal models and the full complexity of natural systems and allow combined  
316 analysis of e.g. food-web theory and alternative stable states theory and indicators of ecosystem  
317 resilience (45). Ideally, such insights can serve to broaden our search image in empirical EWI  
318 patterns instead of relying on a generic increase in variance without understanding the inherent

319 variability in ecosystems. In the meantime, the reliability of EWIs for predicting abrupt shifts in  
320 ecosystem state should be treated with caution.

321

## 322 **Methods**

### 323 *Data preparation and breakpoint detection*

324 The data preparation and statistical analysis protocol was identical for all 16 state variable time  
325 series. Each time series was analysed at the highest temporal resolution available or at a lower  
326 resolution that resulted in fewer missing data (see SI Table S2). Lakes Müggelsee and Washington  
327 were analysed at fortnightly, all other case-studies at monthly intervals. As our time series  
328 methods require continuous and equidistant data, we imputed missing values up to a maximum of  
329 four consecutive time steps using a Kalman filter (46). Time series with longer gaps were  
330 shortened to start or end at the gap (e.g. Lake Vörtsjärv). Each time series was standardized by  
331 mean centering and standard deviation scaling for convenient comparison of step change heights.  
332 The timing of the step was determined by breakpoint analysis as step changes in the respective  
333 state variables may differ from the timing of whole-system step changes reported in the literature.  
334 Robust estimates of the timing of step change were achieved by employing three complementary  
335 breakpoint estimation methods: a) additive decomposition of time series in seasonal, trend and  
336 residual components and subsequent iterative fitting of piecewise linear season and trend models  
337 (47) using the R package “bfast” (48), b) testing for step changes in the average using the Pettitt  
338 test (49) and c) STARS, a combination of a sequential partial CUSUM method and a t-test (50). If  
339 at least two methods showed similar timing for a step change ( $\pm 12$  months), the standardized  
340 original time series was split at that breakpoint. Differences between pre- and post-breakpoint  
341 means of the time series were tested with a Welch two sample t-test (51) (Table 2).

342

343 Due to a one-year gap in the time series, breakpoint timing of two state variables (LV functional  
344 groups P (eutrophic epilimnion species) and U (summer epilimnion species)) was determined  
345 differently: here we assessed whether large changes in the biomasses of the functional groups  
346 occurred during the gap indicating a potential shift. The pre-1978 and post-1978 time series  
347 showed significantly different means for functional group U (Welch two-sample t-test,  $t=3.52$ ,  
348  $df=128$ ,  $p<0.001$ , difference in means =  $0.29 \times \text{standard deviation}$ ) and functional group P (Welch  
349 two-sample t-test,  $t=-4.67$ ,  $df=439$ ,  $p<0.001$ , difference in means =  $0.55 \times \text{standard deviation}$ )

350 suggesting that the shift in functional groups U and P occurred during the year 1978 (Table 2). As  
351 both of these time series showed no further breakpoints in the years after 1978, we conservatively  
352 assumed 1977 to be the transition year.

353

#### 354 *Early-warning indicator analysis*

355 The pre-breakpoint time series was seasonally adjusted using a Gaussian smoother with a kernel  
356 bandwidth based on the number of data points per year (i.e. 12 for monthly and 26 for fortnightly  
357 datasets, see SI S6 for comparison of other methods). A bandwidth of one year was chosen to  
358 account for yearly recurring patterns while retaining informative low and high frequency  
359 variability other than long-term trend and season (15). In three residuals time series, local outliers  
360 were replaced by Kalman imputed values (LMS *Dreissena* (two outliers) and *Aphanizomenon*  
361 Period 1 and LW Cyanobacteria (one outlier each)). The residuals were then passed on to analysis  
362 of EWIs AR-1, SD, SK, and DR with testing for robustness to the size of rolling window and  
363 testing for significance (false positives) using the R package “earlywarnings”(9). Additionally, we  
364 confirmed that the static choice of fixed compared frequencies in the EWI density ratio (DR) was  
365 sufficiently capturing changes of the full power spectrum of the pre-breakpoint residuals time  
366 (based on its estimated smoothed Fast Fourier Periodogram).

367

#### 368 *Robustness and significance testing*

369 The trends in the estimated temporal evolution of EWIs from the rolling-window approach were  
370 quantified by the non-parametric Mann-Kendall trend test, which tests for monotonic trends based  
371 on the Kendall  $\tau$  rank correlation coefficient (9). As the size of the rolling window can affect the  
372 EWI trends (36), a robustness analysis was performed estimating the distribution of trends and  
373 proportion of trends that did not differ in sign from the median of the trend distribution. We did  
374 this by using yearly increments of the residuals time series covered by the rolling time-window  
375 (two to n-two years, function “sensitivity\_ews” (9), where n was the number of years in each pre-  
376 breakpoint time series). Significance testing was conducted by comparing the data-based EWI  
377 trend against a bootstrapped distribution of 200 surrogate time series-based EWI trends. The  
378 surrogate time series were generated based on an ARMA(p,q) model fitted on the residuals time  
379 series. The bootstrapped distribution of trends depicts the probability that a particular trend could  
380 occur by chance in time series of the same ARMA structure (function “surrogates\_ews” in R-

381 package “earlywarnings” (9)). The data-based EWI trend was deemed significant if it fell on one  
382 of the 5% tails of the surrogate-based trend distribution ( $\alpha=0.1$ ). This significance testing was  
383 repeated for all rolling window sizes and the proportion (%) of significant trends over all rolling  
384 window sizes was reported.

385

### 386 *Relationship of EWIs with state variable categories and agreement among signals*

387 The relationship between the occurrence of each EWI and predictor variables mechanism  
388 (competition, IGP or trophic cascade), state variable category (species, group, ecosystem), step  
389 change height, length of pre-breakpoint time series and sampling interval (fortnightly or monthly)  
390 was tested with logistic regressions (identity link for continuous predictors (step change height  
391 and time series length); logit link for categorical predictors) with Bonferroni corrected post hoc  
392 testing. The median of the trend distribution across all time-window sizes was used to assess  
393 agreement among EWIs.

394

### 395 *Early detection of early-warning indicators*

396 To assess how timely EWIs could have detected the approaching transition, we quantified EWI  
397 trends on stepwise shortened pre-breakpoint time series, starting with the full time period and  
398 continuing with stepwise reduction of the time series by cutting off the last year of data. The  
399 minimum time series length was set to three years to allow meaningful Kendall  $\tau$  estimation. How  
400 many years before the shift an EWI could already have been detected was set by assessing the  
401 maximum number of stepwise reductions before the theoretically expected EWI trend disappeared  
402 (i.e. when the median of the Kendall  $\tau$  trend distribution turned negative for AR-1, SD and DR or  
403 changed sign for SK). All data analyses and graphing were conducted using the R language  
404 environment for statistical computing (52) and associated library extensions.

405

### 406 **Acknowledgements**

407 ASG, RA and LAH were supported by the EU-project LIMNOTIP funded under the FP7 ERA-  
408 Net Scheme (Biodiversa, 01LC1207A) and LakeShift (DFG). ABGJ was funded by the  
409 Netherlands Organization for Scientific Research (NWO) project no. 842.00.009. VD  
410 acknowledges a Rubicon fellowship from the Netherlands Science Foundation (NWO), a EU  
411 Marie Curie grant, and an ACE fellowship by ETH Zurich. The authors would like to

412 acknowledge Rijkswaterstaat as source for the Lake Veluwemeer dataset. We thank Bryan Spears,  
413 Francis Daunt, Sarah Burthe, Silke Schmidt, Erik Jeppesen, Brian Moss and the members of  
414 LIMNOTIP for valuable discussions. The authors also thank the anonymous reviewers and the  
415 subject editor for their constructive and positive comments which helped to improve this  
416 manuscript considerably. We also thank the Federal Ministry of Education and Research (BMBF)  
417 for their administrative support. Any use of trade, firm, or product names is for descriptive  
418 purposes only and does not imply endorsement by the U.S. Government.

419  
420  
421  
422  
423  
424  
425  
426  
427  
428  
429  
430  
431  
432  
433  
434  
435  
436  
437  
438  
439  
440  
441  
442

443 **Figure captions**

444 **Figure 1:** Time series of 14 selected state variables (black lines: competition, green lines: trophic  
445 cascade, blue line: intra-guild predation) of five lakes. Solid red lines indicate the timing of  
446 critical transitions (estimated by breakpoint analysis, see Methods). Dashed red lines indicate  
447 additional data-based breakpoints that were not used in this study as they were either not  
448 described in the literature (LMS phytoplankton biomass) or resulted from bio-manipulation (LZL  
449 Secchi depth).

450  
451 **Figure 2:** Robustness and Significance testing. Mann-Kendall trend distributions for EWIs AR-1  
452 and SD (panel) and per analysed time series (boxplots) and the proportion of significant differences in  
453 trends between data-based and surrogate time series across all rolling window sizes (significance, grey  
454 bar plots). Positive values of trends in the boxplots represent increasing EWI trends. Note almost  
455 in all time series the trends were robust to the choice of rolling window size. Significance testing  
456 was based on comparing indicator trends produced from stationary surrogate time series to the  
457 empirically reported for fixed rolling window size (see Methods).

458  
459 **Table captions**

460 **Table 1:** Summary of case-study systems, state variables and drivers by mechanism: trophic  
461 cascade, intra-guild predation and competition

462  
463 **Table 2:** Overview for all 14 state variables (16 time series) listing the direction of the shift,  
464 timing of the break-point (year-month), step height (scaled to standard deviation), the two-sample  
465 Welch test significance, and for each EWI the sign of the median of the trend distribution (across  
466 all rolling window-sizes). Bold t (Welch) values are significant at  $\alpha=0.05$  level. The tested EWI  
467 are autocorrelation at lag-1 (AR-1), standard deviation (SD), skewness (SK), and density ratio  
468 (DR). Median trends that corresponded with the theoretical expectation were coded with '+',  
469 trends that showed the opposite to expectation with '-'. Brackets denote AR-1 trends crossing zero  
470 on the scale.

471  
472  
473

474 **References**

- 475 1. Lewontin RC (1969) The meaning of stability. *Brookhaven Symposia in Biology* (22) 13-  
476 24.
- 477 2. May RM (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable  
478 states. *Nature* (269) 471-477.
- 479 3. Holling CS (1973) Resilience and stability of ecological systems. *Annual Review of*  
480 *Ecology and Systematics* (4) 1-23.
- 481 4. Sutherland JP (1974) Multiple Stable Points in Natural Communities. *The American*  
482 *Naturalist* (108) 859-873.
- 483 5. Scheffer M, Carpenter SR, Foley JA, Folke C & Walker B (2001) Catastrophic shifts in  
484 ecosystems. *Nature* (413) 591-596.
- 485 6. Scheffer M, Hosper S, Meijer M, Moss B & Jeppesen E (1993) Alternative equilibria in  
486 shallow lakes. *Trends in Ecology & Evolution* (8) 275-279.
- 487 7. Biggs R, Carpenter SR & Brock WA (2009) Turning back from the brink: Detecting an  
488 impending regime shift in time to avert it. *Proceedings of the National Academy of*  
489 *Sciences* (106) 826-831.
- 490 8. Ditlevsen PD & Johnsen SJ (2010) Tipping points: early warning and wishful thinking.  
491 *Geophysical Research Letters* (37) L19703.
- 492 9. Dakos V, *et al.* (2012) Methods for detecting early warnings of critical transitions in time  
493 series illustrated using simulated ecological data. *Plos One* (7) e41010.
- 494 10. Carpenter SR, Brock W, Cole J, Kitchell J & Pace M (2008) Leading indicators of trophic  
495 cascades. *Ecology Letters* (11) 128-138.
- 496 11. Veraart AJ, *et al.* (2012) Recovery rates reflect distance to a tipping point in a living  
497 system. *Nature* (481) 357-359.
- 498 12. Batt RD, Carpenter SR, Cole JJ, Pace ML, & Johnson RA (2013) Changes in ecosystem  
499 resilience detected in automated measures of ecosystem metabolism during a whole-lake  
500 manipulation. *Proceedings of the National Academy of Sciences* (110) 17398-17403.
- 501 13. Dai L, Vorselen D, Korolev KS & Gore J (2012) Generic indicators for loss of resilience  
502 before a tipping point leading to population collapse. *Science* (336) 1175-1177.
- 503 14. Lenton T, Livina V, Dakos V & Scheffer M (2012) Climate bifurcation during the last  
504 deglaciation. *Climate of the Past Discussions* (8) 1127-1139.
- 505 15. Dakos V, *et al.* (2008) Slowing down as an early warning signal for abrupt climate change.  
506 *Proceedings of the National Academy of Sciences* (105) 14308-14312.
- 507 16. Carpenter SR, *et al.* (2001) Trophic cascades, nutrients, and lake productivity: whole-lake  
508 experiments. *Ecological Monographs* (71) 163-186.
- 509 17. Seekell D, Carpenter SR, Cline T & Pace M (2012) Conditional Heteroskedasticity  
510 Forecasts Regime Shift in a Whole-Ecosystem Experiment. *Ecosystems* (15) 741-747.
- 511 18. Scheffer M, *et al.* (2009) Early-warning signals for critical transitions. *Nature* (461) 53-59.
- 512 19. Van Nes EH & Scheffer M (2007) Slow recovery from perturbations as a generic indicator  
513 of a nearby catastrophic shift. *The American Naturalist* (169) 738-747.
- 514 20. Ives AR (1995) Measuring Resilience in Stochastic Systems. *Ecological Monographs* (65)  
515 217-233.
- 516 21. Carpenter SR & Brock WA (2006) Rising variance: a leading indicator of ecological  
517 transition. *Ecology Letters* (9) 311-318.



- 518 22. Kleinen T, Held H & Petschel-Held G (2003) The potential role of spectral properties in  
519 detecting thresholds in the Earth system: application to the thermohaline  
520 circulation. *Ocean Dynamics* (53) 53-63.
- 521 23. Guttal V & Jayaprakash C (2008) Changing skewness: an early warning signal of regime  
522 shifts in ecosystems. *Ecology Letters* (11) 450-460.
- 523 24. Boettiger C, Ross N & Hastings A (2013) Early warning signals: the charted and uncharted  
524 territories. *Theoretical Ecology* (6) 255-264.
- 525 25. Dakos V, Carpenter SR, van Nes EH, & Scheffer M (2015) Resilience indicators: prospects  
526 and limitations for early warnings of regime shifts. *Philosophical Transactions of the  
527 Royal Society of London B: Biological Sciences* (370) 20130263.
- 528 26. Andersen T, Carstensen J, Hernández-García E & Duarte CM (2009) Ecological thresholds  
529 and regime shifts: approaches to identification. *Trends in Ecology & Evolution* (24) 49-57.
- 530 27. Scheffer M & Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking  
531 theory to observation. *Trends in Ecology and Evolution* (18) 648-656.
- 532 28. Collie JS, Richardson K & Steele JH (2004) Regime shifts: can ecological theory  
533 illuminate the mechanisms? *Progress in Oceanography* (60) 281-302.
- 534 29. Carpenter SR (2003) Regime Shifts in Lake Ecosystems: Pattern and Variation (Vol. 15).  
535 Oldendorf/Luhe: International Ecology Institute.
- 536 30. Gerla DJ, *et al.* (2013) Alternative states and population crashes in a resource-susceptible-  
537 infected model for planktonic parasites and hosts. *Freshwater Biology* (58) 538-551.
- 538 31. Verdy A & Amarasekare P (2010) Alternative stable states in communities with intraguild  
539 predation. *Journal of Theoretical Biology* (262) 116-128.
- 540 32. Scharfenberger U, Mahdy A, & Adrian R (2013) Threshold-driven shifts in two copepod  
541 species: Testing ecological theory with observational data. *Limnology and Oceanography*  
542 (58) 741-752.
- 543 33. Perretti CT & Munch SB (2012) Regime shift indicators fail under noise levels commonly  
544 observed in ecological systems. *Ecological Applications* (22) 1772-1779.
- 545 34. Boettiger C & Hastings A (2012) Quantifying limits to detection of early warning for  
546 critical transitions. *Journal of the Royal Society Interface* (9) 2527-2539.
- 547 35. Spears BM, *et al.* (2016) Ecological Instability in Lakes: A Predictable Condition?  
548 *Environmental Science & Technology* (50) 3285-3286.
- 549 36. Livina VN, Ditlevsen PD & Lenton TM (2012) An independent test of methods of  
550 detecting system states and bifurcations in time series data. *Physica A: Statistical  
551 Mechanics and its Applications* (391) 485-496.
- 552 37. Brock WA & Carpenter SR (2010) Interacting regime shifts in ecosystems: implication for  
553 early warnings. *Ecological Monographs* (80) 353-367.
- 554 38. Batt RD, *et al.* (2013) Asymmetric response of early warning indicators of phytoplankton  
555 transition to and from cycles. *Theoretical Ecology* (6) 285-293.
- 556 39. Reid PC, *et al.* (2015) Global impacts of the 1980s regime shift. *Global Change Biology*  
557 (22) 682-703.
- 558 40. Carpenter SR, *et al.* (2011) Early Warnings of Regime Shifts: A Whole-Ecosystem  
559 Experiment. *Science* (332) 1079-1082.
- 560 41. Clements CF, Drake JM, Griffiths JI & Ozgul A (2015) Factors Influencing the  
561 Detectability of Early Warning Signals of Population Collapse. *The American Naturalist*  
562 (186) 50-58.
- 563 42. Scheffer M, *et al.* (2012) Anticipating critical transitions. *Science* (338) 344-348.

- 564 43. Burthe SJ, *et al.* (2015) Do early warning indicators consistently predict nonlinear change  
565 in long-term ecological data? *Journal of Applied Ecology* (53) 666-676.
- 566 44. Cook CN, Inayatullah S, Burgman MA, Sutherland WJ & Wintle BA (2014) Strategic  
567 foresight: how planning for the unpredictable can improve environmental decision-  
568 making. *Trends in Ecology & Evolution* (29) 531-541.
- 569 45. Kuiper JJ, *et al.* (2015) Food-web stability signals critical transitions in temperate shallow  
570 lakes. *Nature Communications* (6) 7727.
- 571 46. Durbin J & Koopman SJ (2012) *Time Series Analysis by State Space Methods* Oxford  
572 University Press.
- 573 47. Verbesselt J, Hyndman R, Newnham G, & Culvenor D (2010) Detecting trend and  
574 seasonal changes in satellite image time series. *Remote Sensing of Environment* (114) 106-  
575 115.
- 576 48. Verbesselt J, Hyndman R, Zeileis A, & Culvenor D (2010) Phenological change detection  
577 while accounting for abrupt and gradual trends in satellite image time series. *Remote*  
578 *Sensing of Environment* (114) 2970-2980.
- 579 49. Pettitt A (1979) A non-parametric approach to the change-point problem. *Applied Statistics*  
580 (28) 126-135.
- 581 50. Rodionov SN (2004) A sequential algorithm for testing climate regime shifts. *Geophysical*  
582 *Research Letters* (31) L09204.
- 583 51. Welch BL (1947) The generalization of student's problem when several different  
584 population variances are involved. *Biometrika* (34) 28-35.
- 585 52. R-Core-Team (2012) R: A Language and Environment for Statistical Computing (R  
586 Foundation for Statistical Computing, Vienna, Austria), 3.0.0.
- 587 53. Hampton SE, Scheuerell MD, & Schindler DE (2006) Coalescence in the Lake  
588 Washington story: Interaction strengths in a planktonic food web. *Limnology and*  
589 *Oceanography* (51) 2042-2051.
- 590 54. Edmondson W (1994) Sixty years of Lake Washington: a curriculum vitae. *Lake and*  
591 *Reservoir Management* (10) 75-84.
- 592 55. Wilhelm S & Adrian R (2007) Long-term response of *Dreissena polymorpha* larvae to  
593 physical and biological forcing in a shallow lake. *Oecologia* (151) 104-114.
- 594 56. Gsell AS, Özkundakci D, Hébert M-P, & Adrian R (2016) Quantifying change in pelagic  
595 plankton network stability and topology based on empirical long-term data. *Ecological*  
596 *Indicators* (65) 76-88.
- 597 57. Köhler J, *et al.* (2005) Long-term response of a shallow, moderately flushed lake to  
598 reduced external phosphorus and nitrogen loading. *Freshwater Biology* (50) 1639-1650.
- 599 58. Hilt S, Köhler J, Adrian R, Monaghan MT & Sayer CD (2013) Clear, crashing, turbid and  
600 back–long-term changes in macrophyte assemblages in a shallow lake. *Freshwater*  
601 *Biology* (58) 2027-2036.
- 602 59. Shatwell T, Koehler J & Nicklisch A (2008) Warming promotes cold-adapted  
603 phytoplankton in temperate lakes and opens a loophole for Oscillatoriales in spring.  
604 *Global Change Biology* (14) 2194-2200.
- 605 60. Van De Bund WJ & Van Donk E (2002) Short-term and long-term effects of  
606 zooplanktivorous fish removal in a shallow lake: a synthesis of 15 years of data from Lake  
607 Zwemlust. *Freshwater Biology* (47) 2380-2387.
- 608 61. Van Donk E & Gulati RD (1995) Transition of a lake to turbid state six years after  
609 biomanipulation: Mechanisms and pathways. *Water Science and Technology* (32) 197-206.

- 610 62. Ibelings BW, *et al.* (2007) Resilience of alternative stable states during the recovery of  
611 shallow lakes from eutrophication: Lake Veluwe as a case study. *Ecosystems* (10) 4-16.  
612 63. Nõges T, *et al.* (2007) Reaction of large and shallow lakes Peipsi and Võrtsjärv to the  
613 changes of nutrient loading. *Shallow Lakes in a Changing World*, (Springer), pp 253-264.  
614 64. Nõges P, Mischke U, Laugaste R, & Solimini AG (2010) Analysis of changes over 44  
615 years in the phytoplankton of Lake Võrtsjärv (Estonia): the effect of nutrients, climate and  
616 the investigator on phytoplankton-based water quality indices. *Hydrobiologia* (646) 33-48.

617  
618  
619  
620  
621  
622  
623  
624  
625  
626  
627  
628  
629  
630  
631  
632  
633  
634  
635  
636  
637  
638  
639  
640  
641  
642

643 **Table 1:** Summary of case-study systems, state variables and drivers by mechanism: trophic  
 644 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	Longfin smelt ( <i>Spirinchus thaleichthys</i> ) preys on secondary consumer <i>Neomysis</i> which releases primary consumer <i>Daphnia</i> who grazes on producers (phytoplankton)	(53, 54)
	LMS	Increase in <i>Dreissena polymorpha</i> larvae	Decrease in predation pressure	Changes in dominant carnivorous zooplankton species coincided with increase in <i>Dreissena</i> larvae.	(55, 56)
	LMS	Decrease (period 1) and increase (period 2) in <i>Leptodora kindtii</i>	Increase (period 1) and decrease (period 2) in predation pressure	<i>Leptodora</i> are a preferred prey for fish and likely indicate changes in overall fish predation pressure	(56)
Competition	LMS	Decrease phytoplankton biomass	Re-oligotrophication	Reduction in nutrients decreases phytoplankton growth, improving light climate favouring macrophyte reestablishment	(57, 58)
	LMS	Decrease in <i>Aphanizomenon</i> (period 1)	Re-oligotrophication counteracted by spring warming	Warmer springs promote cold-adapted cyanobacteria development	(59)
	LMS	Decrease in <i>Aphanizomenon</i> (period 2)	Re-oligotrophication	Reduction in nutrients decreases phytoplankton growth, improving light climate favouring 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)
	LW	Increase in cryptophytes and decrease in cyanobacteria	Re-oligotrophication	Reduction in nutrients decreases cyanobacteria competitive ability and releases other phytoplankton from competition	(53, 54)
	LZL	Decrease in water transparency	Eutrophication, epiphyte shading and herbivory	Competition between submerged vegetation and phytoplankton under eutrophication and herbivory on macrophytes	(60, 61)
	LVM	Decrease in non-algal attenuation	reduction in nutrients and benthivorous fish	Recovery of submerged vegetation cover and subsequent stabilisation 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)
	LV	Increase in functional group H1	Re-oligotrophication	Competition between non-nitrogen fixing and di-nitrogen fixing species (functional group H1)	(63, 64)
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)

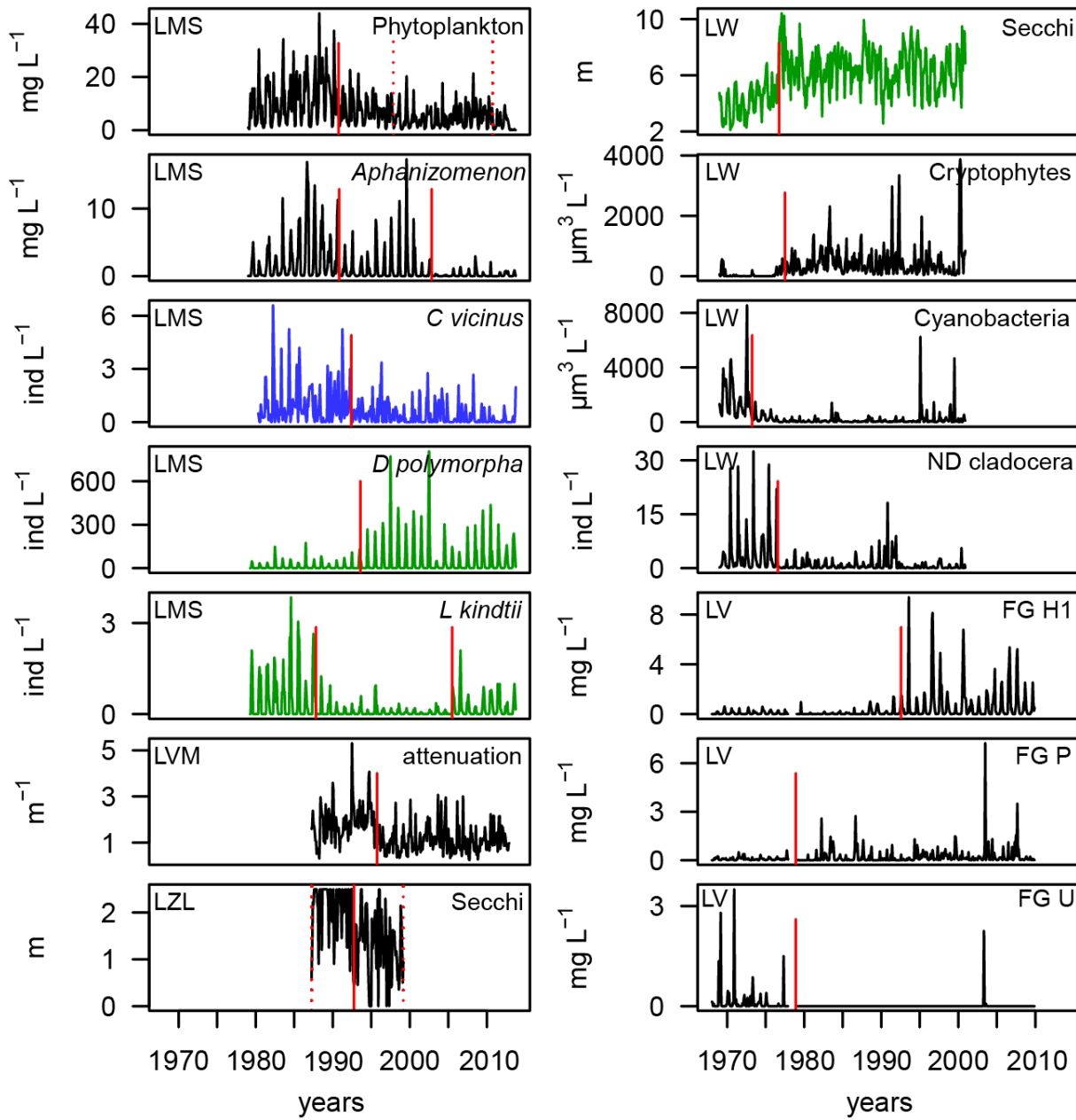
645  
 646  
 647  
 648  
 649  
 650

651 **Table 2:** Overview for all 14 state variables (16 time series) listing the direction of the shift,  
652 timing of the transition (year-month), step height (scaled to standard deviation), the two-sample  
653 Welch test significance, and for each EWI the sign of the median of the trend distribution (across  
654 all rolling window-sizes). Bold t (Welch) values are significant at  $\alpha=0.05$  level. The tested EWI  
655 are autocorrelation at lag-1 (AR-1), standard deviation (SD), skewness (SK), and density ratio  
656 (DR). Median trends that corresponded with the theoretical expectation were coded with '+',  
657 trends that showed the opposite to expectation with '-'. Brackets denote AR-1 trends crossing zero  
658 on the scale.

Case-Study	State Variable	Direction of Shift	Break-Point (Year-Month)	Step (scaled to SD)	t (Welch)	AR-1	SD	SK	DR
LMS	Phytoplankton mg L <sup>-1</sup>	Decrease	1990-5	0.803	<b>9.92</b>	+	+	+	+
	<i>Aphanizomenon</i> mg L <sup>-1</sup> P1	Decrease	1990-11	0.413	<b>4.47</b>	+	+	-	+
	<i>Aphanizomenon</i> mg L <sup>-1</sup> P2	Decrease	2002-12	0.317	<b>5.92</b>	-	+	+	-
	<i>Cyclops vicinus</i> ind L <sup>-1</sup>	Decrease	1992-6	0.629	<b>7.86</b>	+	-	+	+
	<i>Dreissena polymorpha</i> larvae ind L <sup>-1</sup>	Increase	1993-9	0.388	<b>-6.79</b>	+	+	-	+
	<i>Leptodora kindtii</i> ind L <sup>-1</sup> P1	Decrease	1987-11	0.776	<b>6.58</b>	-	+	-	-
	<i>Leptodora kindtii</i> ind L <sup>-1</sup> P2	Increase	2005-7	0.239	<b>-5.21</b>	(+)	-	-	+
LW	Secchi depth m	Increase	1976-10	1.29	<b>-21.94</b>	+	+	-	+
	Cryptophyceae 100 $\mu\text{m}^3$ L <sup>-1</sup>	Increase	1977-7	0.627	<b>-13.16</b>	(+)	-	-	+
	Cyanophyceae 100 $\mu\text{m}^3$ L <sup>-1</sup>	Decrease	1973-4	1.587	<b>9.33</b>	-	-	-	-
	Non- <i>Daphnia</i> cladocerans ind L <sup>-1</sup>	Decrease	1976-8	0.783	<b>6.09</b>	-	+	+	-
LV	H1 g/m <sup>3</sup>	Increase	1992-8	0.569	<b>-6.75</b>	(+)	+	-	+
	P g/m <sup>3</sup>	Increase	1977-12	0.281	<b>-4.61</b>	(+)	-	+	+
	U g/m <sup>3</sup>	Decrease	1977-12	0.532	<b>3.17</b>	(+)	-	+	+
LVM	Non algal attenuation m <sup>-1</sup>	Decrease	1995-9	1.058	<b>9.05</b>	-	-	-	-
LZL	Secchi depth m	Decrease	1992-9	1.098	<b>7.97</b>	(-)	+	+	-
<b>Proportion of EWI trend distribution medians corresponding to the theoretical trend expectation</b>						<b>10/16</b>	<b>9/16</b>	<b>7/16</b>	<b>10/16</b>

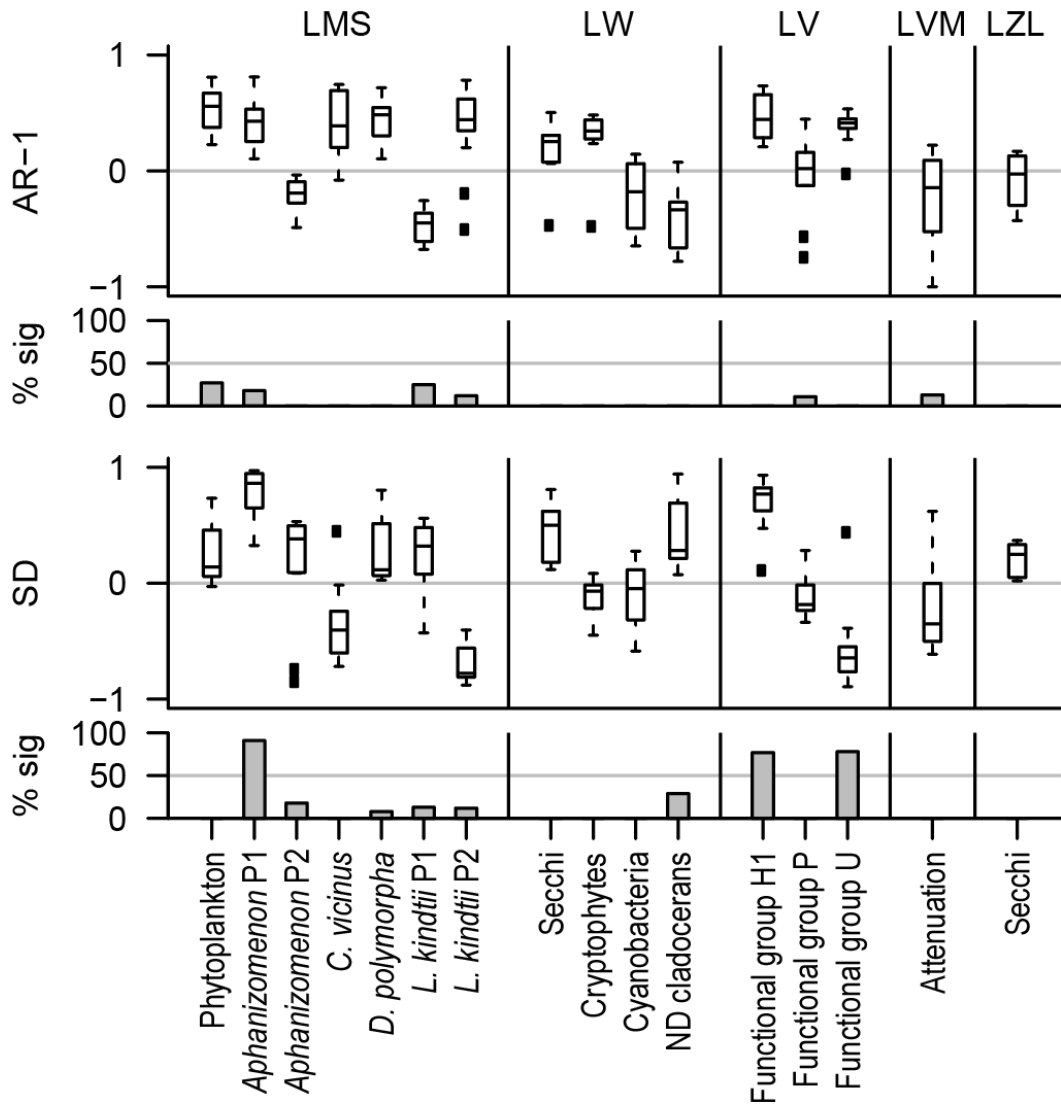
659  
660  
661  
662  
663  
664  
665  
666  
667  
668  
669

670 **Figure 1**



671  
672  
673  
674  
675  
676  
677  
678

679 **Figure 2**



680