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

3

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

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37

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

Introduction

71

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 the14 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   Võrtsjärv 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 Võrtsjärv). 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 (± 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*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*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 τ 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 (α=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 τ 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 τ 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**

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Figure captions

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

Figure 2: Robustness and Significance testing. Mann-Kendall trend distributions for EWIs AR-1 and SD (panel) and per analysed time series (boxplots) and the proportion of significant differences in trends between data-based and surrogate time series across all rolling window sizes (significance, grey bar plots). Positive values of trends in the boxplots represent increasing EWI trends. Note almost in 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 (see Methods).

Table captions

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

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

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643 **Table 1:** Summary of case-study systems, state variables and drivers by mechanism: trophic

644 cascade, intraguild predation and competition

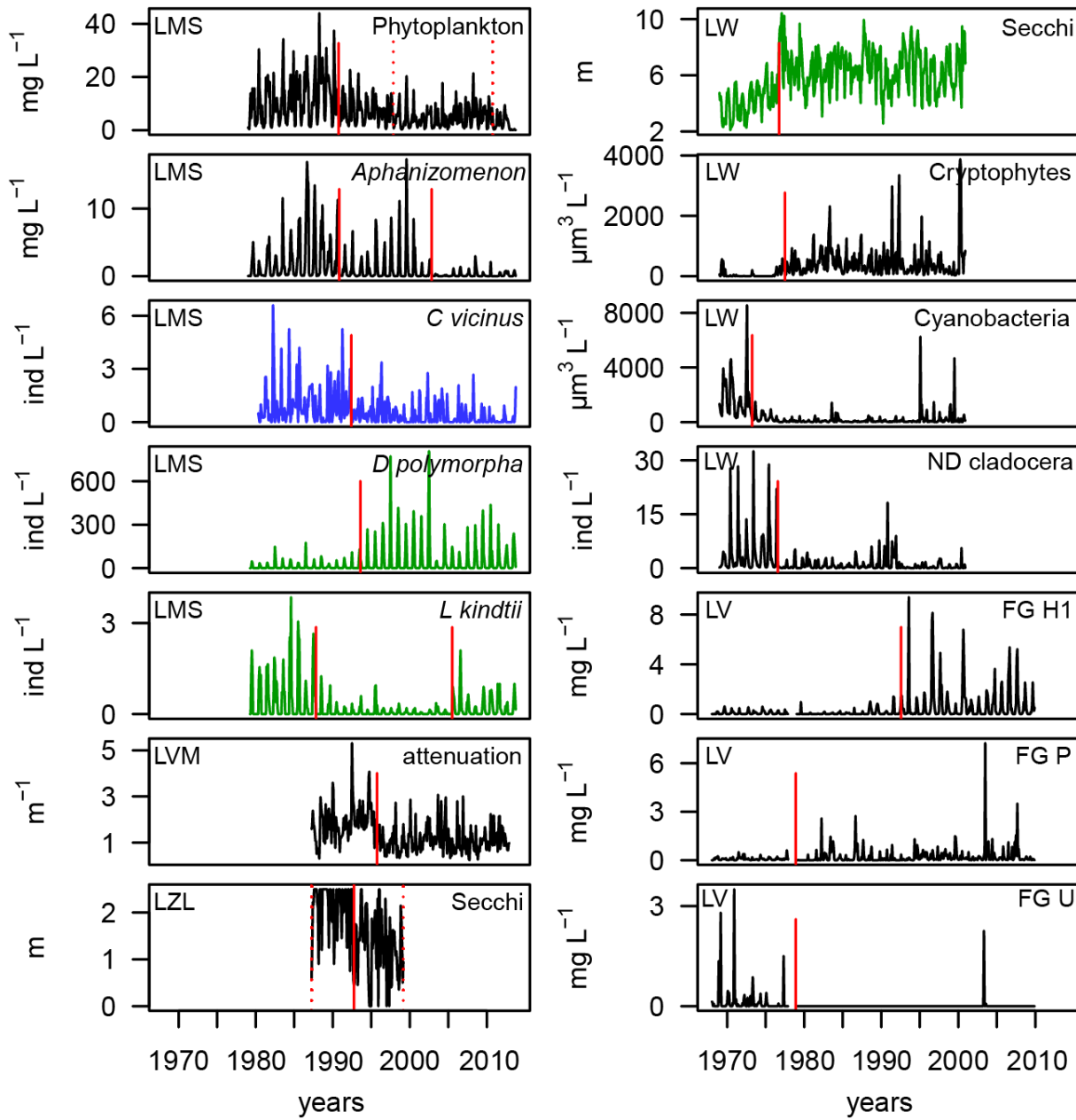| Mechanism	Case-Study	Shift in State Variable	Driver	Process	References
Trophic cascade	LW	Increase in water transparency	Increase in grazing pressure	Longfin smelt (*Spirinchus thaleichthys*) preys on secondary consumer *Neomysis* which releases primary consumer *Daphnia* who grazes on producers (phytoplankton)	(53, 54)
	LMS	Increase in *Dreissena polymorpha* larvae	Decrease in predation pressure	Changes in dominant carnivorous zooplankton species coincided with increase in *Dreissena* larvae.	(55, 56)
	LMS	Decrease (period 1) and increase (period 2) in *Leptodora kindtii*	Increase (period 1) and decrease (period 2) in predation pressure	*Leptodora* 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 *Aphanizomenon* (period 1)	Re-oligotrophication counteracted by spring warming	Warmer springs promote cold-adapted cyanobacteria development	(59)
	LMS	Decrease in *Aphanizomenon* (period 2)	Re-oligotrophication	Reduction in nutrients decreases phytoplankton growth, improving light climate favouring macrophyte reestablishment	(57)
	LW	Decrease in non-*Daphnia* cladocera	Reduction in predation pressure on *Daphnia*	Indirect effect of trophic cascade through increasing resource competition by *Daphnia*	(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	Decease 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	*C. vicinus - C. kolensis* dominance switch	Reduction of shared food source	The inferior resource competitor *C vicinus* preys on juveniles of the smaller *C kolensis*	(32)

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652 **Table 2:** Overview for all 14 state variables (16 time series) listing the direction of the shift,

653 timing of the transition (year-month), step height (scaled to standard deviation), the two-sample

654 Welch test significance, and for each EWI the sign of the median of the trend distribution (across

655 all rolling window-sizes). Bold t (Welch) values are significant at α= 0.05 level. The tested EWI

656 are autocorrelation at lag-1 (AR-1), standard deviation (SD), skewness (SK), and density ratio

657 (DR). Median trends that corresponded with the theoretical expectation were coded with '+',

658 trends that showed the opposite to expectation with '-'. Brackets denote AR-1 trends crossing zero

659 on the scale.

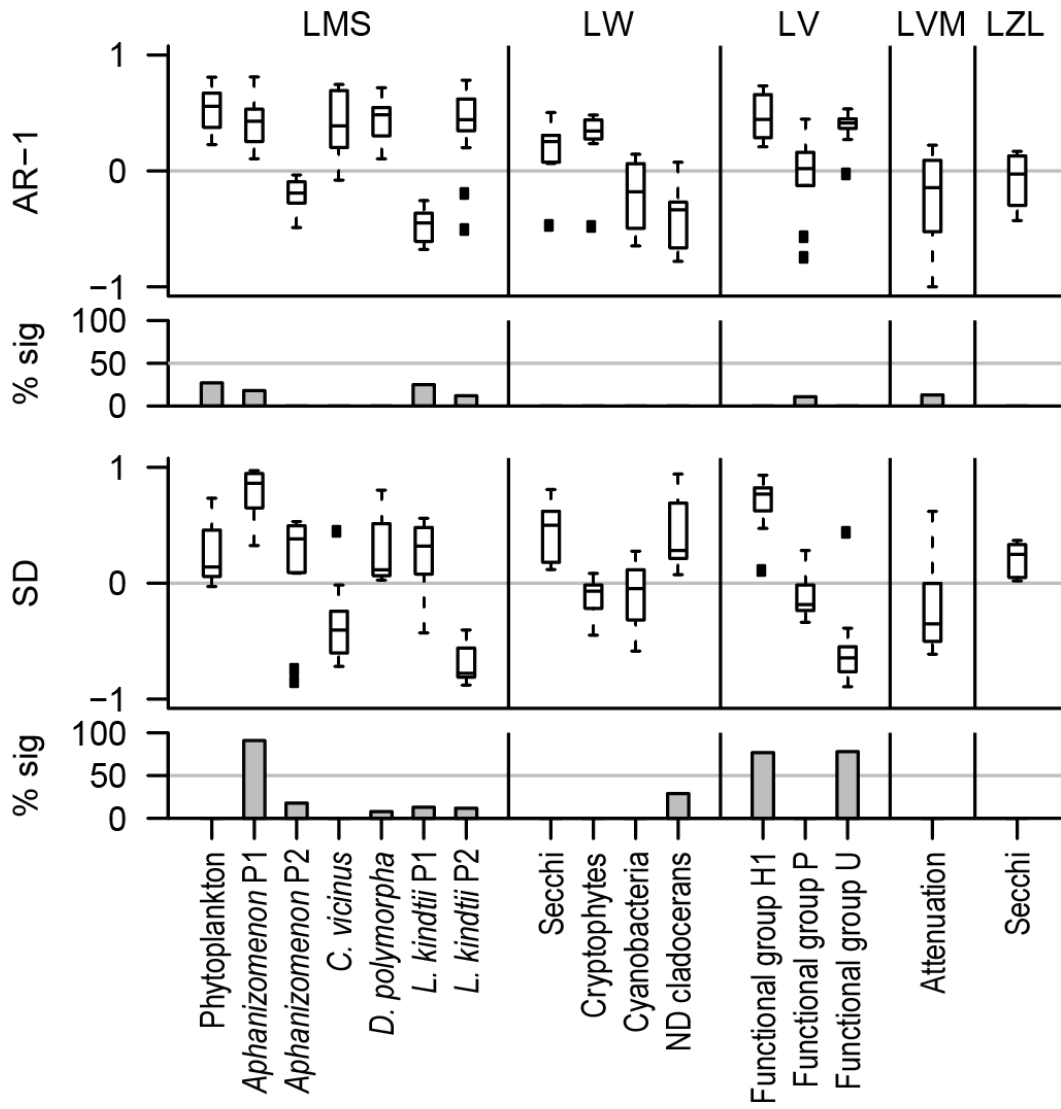| Case-Study	State Variable	Direction of Shift	Break-Point (Year-Month)	Step (scaled to SD)	t (Welch)	AR-1	SD	SK	DR
LMS	Phytoplankton mg L^{-1}	Decrease	1990-5	0.803	**9.92**	+	+	+	+
	Aphanizomenon mg L^{-1} P1	Decrease	1990-11	0.413	**4.47**	+	+	-	+
	Aphanizomenon mg L^{-1} P2	Decrease	2002-12	0.317	**5.92**	-	+	+	-
	Cyclops vicinus ind L^{-1}	Decrease	1992-6	0.629	**7.86**	+	-	+	+
	Dreissena polymorpha larvae ind L^{-1}	Increase	1993-9	0.388	**-6.79**	+	+	-	+
	Leptodora kindtii ind L^{-1} P1	Decrease	1987-11	0.776	**6.58**	-	+	-	-
	Leptodora kindtii ind L^{-1} P2	Increase	2005-7	0.239	**-5.21**	(+)	-	-	+
LW	Secchi depth m	Increase	1976-10	1.29	**-21.94**	+	+	-	+
	Cryptophyceae 100 µm^3 L^{-1}	Increase	1977-7	0.627	**-13.16**	(+)	-	-	+
	Cyanophyceae 100 µm^3 L^{-1}	Decrease	1973-4	1.587	**9.33**	-	-	-	-
	Non-*Daphnia* cladocerans ind L^{-1}	Decrease	1976-8	0.783	**6.09**	-	+	+	-
LV	H1 g/m^3	Increase	1992-8	0.569	**-6.75**	(+)	+	-	+
	P g/m^3	Increase	1977-12	0.281	**-4.61**	(+)	-	+	+
	U g/m^3	Decrease	1977-12	0.532	**3.17**	(+)	-	+	+
LVM	Non algal 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**

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671   **Figure 1**

Figure 2