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Ecological Resilience in Lakes and the Conjunction Fallacy[2]

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39 Abstract

40 There is a pressing need to apply stability and resilience theory to environmental management in such
41 a way as to restore degraded ecosystems effectively and to mitigate the effects of impending
42 environmental change. Lakes represent excellent model case studies in this respect and have been
43 used widely to demonstrate theories of ecological stability and resilience that are needed to underpin
44 preventative management approaches. However, we argue that this approach is not yet fully developed
45 because the pursuit of empirical evidence to underpin such theoretically-grounded management
46 continues in the absence of an objective probability framework. This has blurred the lines between
47 intuitive logic (based on the elementary principles of probability) and extensional logic (based on
48 assumption and belief) in this field.

49

50 Introduction[1]

51 A systematic bias in reasoning exists within ecological resilience research resulting from the conditional
52 selection of ecosystems for study that exhibit desirable responses[1]. This issue extends to the
53 application of resilience approaches in general and must be addressed to avoid the separation of
54 theoretical application from mechanistic understanding of the system of interest. Here we explore this
55 issue using lakes as a model system. The issue can be conceptualised generally using a probability
56 framework that is commonly applied in social psychology: *the conjunction rule*². This rule states that the
57 probability of two events occurring together cannot exceed the probability of either of the respective
58 single events. A *conjunction fallacy* occurs when it is stated that the co-occurrence of two events is
59 more likely than either event alone. This can happen when basic laws of probability have been ignored,
60 with conclusions being reached via simple heuristics that are derived from beliefs rather than robust
61 probabilistic assessment.

62 In lakes, indicators have been developed to provide evidence of the occurrence of sudden ecological
63 reorganisations, or *regime shifts*, and have been used to underpin assessments of changes in
64 ecological stability (e.g. Carpenter et al., 2011)[3]. However, in many cases this approach relies on
65 assumptions about the form of the regime shift (i.e. an underlying “model”) and faith in this underlying
66 model may be misplaced in the absence of systematic quantitative approaches[4]. [10] Specifically,
67 evidence of the occurrence of these phenomena is limited by the existence of multiple underlying
68 models representing possible real-world pressure-response relationships operating in lakes; be they
69 linear, non-linear or hysteretic in nature[5] [11].

70 A fallacy occurs when an assumption is made that sudden ecosystem-scale change has occurred in
71 response to changes in an environmental stressor. Such an assumption is commonly presented to
72 support reports that statistical signatures of reduced stability have been detected prior to a profound
73 ecological change. In the context of applying the conjunction rule to these systems, the probability of
74 each of these responses occurring individually, and the overall probability of the conjunction of those
75 responses occurring together can be calculated to provide a level of statistical certainty with which
76 preventative management approaches[6] could be underpinned. In reality, there is a degree of uncertainty
77 about whether either of these phenomena can be detected and this has led to contentious
78 methodological debates (e.g., Wang et al., 2015)[7].

79 We argue that overconfidence in the reporting of these phenomena limits our ability to perform
80 preventative, ‘resilience-based’ management. We draw on the experiences of the research community
81 working in this field to demonstrate these underlying issues and propose an alternative approach to
82 evaluating available evidence. We propose that the next phase of research in this potentially
83 transformative field should be grounded in robust assessments of probability coupled with an *a priori*
84 understanding of ecological processes.

85 Ecological stability and resilience in lakes

86 *Ecological stability theory* is a major contemporary theme in ecology and environmental management,
87 and has stimulated much debate. Two key aspects of the theory, referred to by Grimm et al. (1992)[8] as
88 resistance and resilience, describe the tendency of species, communities, meta-communities or
89 ecosystems to depart from established relationships with their biological and physical environments,
90 and their capacity to return to pre-defined baseline conditions in response to perturbations. These
91 departures can be profound, resulting in the reorganisation of communities in response to the
92 breakdown of internal feedback mechanisms at the ecosystem scale. Within *ecological resilience*
93 theory, this latter phenomenon is described as a *regime shift*. Regime shifts can be either smooth

94 (linear), non-linear (threshold) or discontinuous (hysteresis, critical) transitions^{8,9}. Lees et al. (2007)⁹
95 proposed that, to confirm the occurrence of a regime shift, a reorganisation that produces a novel and
96 stable ecosystem must be detectable across multiple physical and biological components. Quantifiable
97 terms relating to regime shifts include the *critical threshold*: the point on the pressure axis at which the
98 system shifts, and the *transition*: the period over which the switch between stable states occurs¹⁰.

99 Ecological resilience theory suggests that discontinuous regime shifts may be preceded by subtle
100 changes in ecological behaviour that can be detected using quantifiable indicators, thus providing useful
101 early warning of impending transitions. For example, an increase in the variance or autocorrelation of
102 phytoplankton biomass, due to phenomena known as *critical slowing down (CSD)* or *flickering*, may be
103 expected to precede the well documented transition between phytoplankton dominated conditions and
104 macrophyte dominated conditions in shallow lakes. Put simply, CSD is characterised by a reduction in
105 the speed of ecological recovery after a disturbance as an ecosystem approaches a critical threshold,
106 and flickering results from the alternation between stable ecological states following perturbations^{6,11,12}.
107 Frameworks for detecting changes in ecological stability⁵ and for the use of statistically derived early
108 warning indicators¹³⁻¹⁵ (EWIs) have been developed for predicting regime shifts. Currently, the
109 performance of these frameworks has been evaluated, mainly using simulated or experimental data^{15,16}.

110 Lakes are particularly important model ecosystems with which to examine the aforementioned
111 phenomena given that they represent 'aquatic islands' that are relatively contained, easily quantified
112 and manipulated, and exhibit a vast array of ecological responses to well-defined gradients of multiple
113 and interacting pressures. These pressures include eutrophication, acidification, and climate change.
114 Recent tests using long-term lake monitoring data have indicated low levels of agreement between
115 EWIs and statistically defined sudden ecological change. Burthe et al. 2015¹⁷ highlight that this lack of
116 coherence may arise due to insufficient knowledge of the causes of sudden changes in ecological
117 indicators that occur in long-term monitoring data and their relation to regime shifts. One significant
118 weakness in this approach is that the form and rate of regime shifts are very difficult to quantify, even
119 though they may dictate whether or not CSD or flickering may be expected to occur. Using the
120 terminology of the conjunction rule, this underlying model is flawed. Capon et al. (2015)¹⁸ reviewed the
121 evidence available for regime shifts in freshwater ecosystems and concluded that many of the studies
122 purporting to demonstrate this phenomenon fail to do so. Of the 135 studies analysed, few met all of
123 the criteria proposed by Lees et al. (2006)¹ to confirm a regime shift. This suggests that regime shifts
124 are less common in nature than the abundant literature would suggest. Ultimately, these reports of
125 regime shifts based on unwarranted extensional reasoning about the consequences of observed EWIs
126 support the widespread occurrence of conjunction fallacies in this field, with the occurrence of regime
127 shifts having been widely reported despite a lack of robust probabilistic evidence.

128 **Predicting regime shifts in real world systems**

129 If we are to improve our capacity to estimate the probability of regime shifts and changes in ecosystem
130 stability preceding them, we must first examine our underlying model and our capacity to quantify its
131 individual components. We can demonstrate this approach by considering lake ecosystems, which have
132 been widely used as model systems for the development and application of ecological resilience
133 theory^{17,20} and EWIs^{21,22}.

134 [FIGURE 1]

135 While EWIs have been applied with apparent success in small-scale and whole-lake experimental
136 settings, significant caveats have been identified regarding their use in real-world systems. Authors
137 have stated that EWIs may occur before specific types of regime shifts only^{23,24}, potentially including
138 both critical and non-critical transition types²⁵, and they may not be exclusive signals of critical
139 transitions²⁶. So, failure to observe an EWI may arise if the drivers of a regime shift are, themselves,
140 inherently unpredictable (e.g. noise-induced transitions¹²), or as a result of methodological issues such
141 as the resolution of monitoring data and/or the selection of (rolling) time windows within which EWIs are
142 calculated (Fig 1). When applied to monitoring data from lakes with reported regime shifts, the predictive
143 success of EWIs has been reported to be only at best about 50%²⁷. To achieve acceptable levels of
144 confidence in their application, any reliable use of EWIs needs to be embedded within a *priori*
145 knowledge of system-specific ecological mechanisms that underlie change²⁶; this limits wide scale
146 practical applications considerably¹⁷. Litzow and Husnicker (2016)¹ propose that uncertainty is a result
147 of applying the theory incorrectly through flawed logic in the underlying model and introduced a
148 systematic approach to assess pressure-response forms to address this. Specifically, they

149 demonstrated that success rates for EWIs could be significantly improved when assessments are made
150 using only case studies which exhibited hysteresis in the pressure-response model. [11]

151 By considering the underlying processes that drive change in EWIs more generally, we can begin to
152 understand important limitations in their current application. All EWIs are likely to be inherently variable
153 within a given ecosystem state, even one that is a long way from an impending transition, due to
154 transient ecological dynamics. For example, the widely ranging variance in phytoplankton biomass and
155 submerged macrophytes²⁸ exhibited over the long-term by apparently stable lakes makes it difficult to
156 identify changes that are indicative of a regime shift (Fig 1). Changes in EWIs can only be judged to be
157 “significant” if they vary outside of the range that is found under typical baseline conditions or in a
158 parallel and statistically well-defined control system¹³. Such assessments require time series data of
159 sufficient frequency and duration with which any departure from baseline conditions can be adequately
160 quantified.

161 Decisions must be made regarding ecologically relevant timescales over which loss of stability can be
162 assessed²⁹. Our definition of “sudden” change, which underlies the definition of discontinuous regime
163 shifts, is perhaps better judged on a scale of organismal and community turnover times, rather than
164 calendar dates or funding timelines. For example, Pace et al. (2016)⁵ consider the onset of a
165 phytoplankton bloom to be a short-term (i.e. days to months) ecological event that was preceded by a
166 change in EWIs from baseline. In shallow lakes, palaeolimnological records³⁰ and long-term monitoring
167 data³¹ show that a regime shift, characterised by the complete loss of submerged plants, can be
168 preceded by decades to centuries of change in community composition that culminates in the
169 dominance of a few nutrient tolerant species (i.e. *Potamogeton crispus*, *P. pusillus*, *P. pectinatus* and
170 *Zanichellia palustris*) before they disappear completely. In contrast to the duration of a typical
171 experiment (months to years), the plant loss regime shift described above demonstrates a mean
172 transition time from a non-eutrophic macrophyte flora to the penultimate community state of about 100
173 years, and from the penultimate state to plant loss of about 20 years. Similarly, studies of contemporary
174 monitoring data that quantify the responses in fish and macrophyte communities to catchment
175 phosphorus loading abatement in shallow lakes often report gradual time scales of response of the
176 order of decades^{32,33}. In this context, it is difficult to distinguish between categories of regime shifts or
177 to establish clear timelines across which EWIs would be expected to respond. To address this, there is
178 a need to develop more systematic definitions of regime shifts that occur in nature and to use these as
179 a framework within which changes in indicators of ecological stability can be assessed.

180 Despite the fact that regime shifts are ecosystem-scale phenomena, ecological indicators used for
181 calculating EWIs are often simple state variables that may not reflect ecosystem scale processes³⁴. The
182 selection of suitable indicators is not trivial, considering that complex ecosystem dynamics can amplify
183 or dampen EWIs in specific variables³⁵. The components of an ecosystem that are most likely to exhibit
184 the behaviours that underpin EWIs will depend upon the type of regime shift and on the underpinning
185 ecological mechanisms. Retrospective analyses of long-term monitoring data from lakes in which
186 regime shifts have been observed and defined can be used to test the sensitivity of EWIs²⁷. For the
187 development of monitoring programmes designed to predict unforeseen regime shifts, however, the
188 identification of suitable EWIs from the suite available is challenging. This selection must be combined
189 with *a priori* mechanistic understanding of the relevant ecological processes, feedback mechanisms
190 and regime shifts that occur across a wide range of pressure scenarios, lake types and timescales. That
191 is, we must develop more detailed underlying models, based on comprehensive understanding of the
192 ecosystem and its responses to defined environmental stressors. These models can then be used to
193 support diagnosis of time-varying ecosystem-scale changes in indicators of stability needed to quantify
194 the probability of regime shifts based on departure from baseline conditions using EWIs^{36,37}.

195 Learning from Experiments

196 The probabilities of observing both detectable changes in EWIs and subsequent regime shifts can best
197 be estimated by the statistical analysis of data from controlled experiments. Such estimates or
198 probabilities could be used to infer the likelihood of observing these phenomena in real world monitoring
199 data. Most experimental studies focusing on resilience and EWI development have assessed relatively
200 short-term responses to perturbations (i.e. weekly to monthly resolution) using high frequency data. The
201 advent of high-frequency monitoring systems (at hourly to daily level resolution) in lakes provides lake
202 ecologists with an impressive capacity to detect subtle and rapid changes in ecological indicators in
203 response to perturbations. As next generation monitoring systems are developed and/or improved (e.g.
204 remote sensing approaches including multi-parameter monitoring buoys), our detection power will also

205 improve. In contrast to this, we draw attention to the vast legacy of experimental studies that have
206 collected lower frequency monitoring data. These low-frequency experiments represent an untapped
207 resource with which non-stationary behaviour in ecosystems can be examined using the statistical tools
208 developed as EWIs in response to a controlled perturbation or otherwise.

209 One criticism of short-term experiments is that it is difficult to conclude that a persistent regime shift has
210 occurred, although they do provide important evidence of short-term dynamics in ecological responses
211 at high temporal frequency. With a few exceptions, mesocosm experiments span periods of only 3-12
212 months³⁸ (Fig 2). So, longer term changes including potential regime shifts, and changes in ecological
213 behaviour preceding (and following) them, are often difficult to assess. Nevertheless, they offer
214 invaluable insights into short-term effect, return, and recovery rates following perturbations. Tightly
215 controlled experiments in which regime shifts are achieved maintain a powerful approach to examining
216 and quantifying the performance of EWIs and responses in ecological stability, more generally.
217 Unfortunately, although an impressive legacy dataset exists documenting ecological responses
218 following manipulation of nutrient cycling or food-web structure, this evidence has been poorly utilised
219 in the context of ecological resilience in lakes.

220 [FIGURE 2]

221 Here we provide an example of the use of a short-term mesocosm experiment³⁹ to examine ecological
222 resilience in lakes and some misgivings in the context of the conjunction rule. Mesocosms were
223 subjected to contrasting nitrogen (N) loading during a 9 month shallow lake experiment that led to the
224 complete loss of submerged macrophytes at high N loading (Fig 2), a well-established regime shift
225 known to occur in shallow lakes. There were no apparent EWI signals or trends when the macrophytes
226 started to decline in the high N loaded mesocosms. EWI values from the treatment mesocosms were
227 found to be both higher and lower than the control mesocosms. When one considers the general
228 treatment effects, it is apparent that EWIs were significantly different across the treatments and that an
229 interaction between treatment and time was reported. However, the results provide no conclusive
230 evidence of an increase in EWIs prior to the regime shift in the high nutrient loading treatment. In
231 general, we observed more stable conditions under the highest N loading treatment, which appears to
232 contradict the increase in variance expected when CSD occurs prior to a regime shift. In this example
233 it is impossible to determine the form of the regime shift and so our underlying model, which
234 hypothesises the occurrence of CSD preceding the demise of the macrophytes, may be unfounded, as
235 in other similar experimental studies.

236 Few ecosystem scale experiments have been conducted to test the hypothesis that CSD can be
237 detected before a regime shift. The most comprehensive study to date involved the detection of
238 responses across a range of indicators in a treatment lake relative to a control lake, following
239 manipulation of the fish community from planktivore- to piscivore dominance^{3,14,35,30,41}. Thresholds in
240 some of these indicator variables were reported more than a year before the transition to piscivore
241 dominance was complete, providing evidence to support CSD. However, evidence also existed for
242 similar fluctuations in EWIs following the regime shift, suggesting on-going longer-term processes that
243 are not easily explained. While this experiment provided a rich and detailed dataset with at least daily
244 sampling resolution for a range of variables, there are three potentially important caveats that are
245 relevant to interpretation of the data. Firstly, the results indicated that ecosystem 'state variables' (e.g.
246 dissolved oxygen) were more sensitive indicators of the reported transition than estimates of rates (e.g.
247 gross primary production³⁴). This potentially indicates insufficiencies in available methods for
248 quantifying key system changes. Secondly, even in this very comprehensive study, response patterns
249 of different indicators and EWIs varied quite substantially. Thirdly, the methods used in whole lake
250 experiments require that the manipulated and reference lake(s) are in synchrony over the sampling
251 period and frequency of interest, which may be unlikely at such high monitoring frequency.

252 Lower temporal frequency data from many other whole lake experiments are available for the
253 determination of longer term effects of environmental change on ecological stability indicators. Such
254 studies are important because they have been conducted in systems for which there is adequate causal
255 understanding of the relevant ecological mechanisms driving change. Although few of these studies
256 have been framed using ecological resilience or stability terminology, we demonstrate the potential to
257 retrospectively explore the effects of perturbations on ecological stability more generally, irrespective of
258 whether a regime shift was reported or planned in the original design (Fig. 3). There are many whole
259 lake experiments lasting from years to decades, the longest of which are those aiming to restore lakes
260 from external pressures⁴². While some of these have focused solely on reducing external pressures,
261 others have been conducted to control some of the intrinsic processes, or feedback mechanisms,

262 known to determine ecological conditions after changes in external pressures have occurred. These
263 include measures to reduce internal phosphorus cycling in lakes⁴³, or to alter food-web structure and
264 macrophyte community by manipulating fish stocks and/or transplanting submerged macrophytes⁴⁴.
265 Whilst the data frequency may not be appropriate for assessing EWIs of regime shifts when potentially
266 expected, these experiments can be used to characterise the timelines of changes in the stability of
267 lake variables, for example, following commonly used management approaches (Fig. 3). In addition,
268 they may be used to explore non-stationary behaviour with and without management interventions.
269 When considered in the context of simple indicators of ecological stability, it becomes apparent that
270 responses to management can take decades to manifest and do not necessarily result in a more stable
271 ecosystem.

272 [FIGURE 3]

273 To maximise their applicability, we recommend these novel insights from single site experimental
274 studies be used to inform the re-analysis of the vast quantities of data from other experimental studies
275 so as to develop testable hypotheses of whole system responses to specific and controlled pressure
276 scenarios. The results of this work should inform the development of novel management approaches
277 designed to manipulate ecological stability at the ecosystem scale, which could, in turn, facilitate a more
278 valid conjunction of EWIs and subsequent regime shifts.

279 **Capitalising on Natural Events**

280 Given the recent focus on developing EWIs, we stress the need to continue to build and refine our best
281 conceptual models of ecosystem scale responses to pressures, in general. Multi-decadal to century-
282 long lake monitoring data⁴⁵⁻⁵³ are becoming increasingly available for use in this endeavour. Although
283 such data are useful for the identification of regime shifts, their relatively coarse temporal resolution,
284 may provide only limited opportunities to assess EWIs¹². Long time series provide more context to
285 ecosystem change than can be achieved by short term experiments however, and are more realistic in
286 terms of noise and stochasticity. We advocate the use of these long-term data which have, at their core,
287 the sound *a priori* knowledge of the mechanisms underlying ecosystem scale responses to past or
288 current environmental change needed to provide credible alternative approaches to early warning of
289 regime shifts across large populations of lakes.

290 Most studies purporting to show discontinuous regime shifts report that shallow lakes may switch from
291 a turbid to clear water state¹⁹. The most commonly reported regime shift is the response of shallow
292 lakes to increasing and decreasing phosphorus loading, which can cause a critical transition between
293 clear water, macrophyte dominated and turbid water phytoplankton dominated states, respectively⁵³.
294 While such shifts have been observed, numerous studies of shallow lakes in recovery after external
295 nutrient loading reduction have not exhibited this response, even when theory suggests they should
296 have³². These results suggest that either pressure reductions may have been insufficient to reach a
297 critical threshold, thresholds were not reached because of the impacts of other interacting processes
298 (warming, food web structure changes), not all shallow lakes exhibit regime shifts, or that reorganisation
299 at the ecosystem scale takes much longer than expected and follows the path of gradual adjustment of
300 the system as the pressures change. Process based modelling (i.e. PCLake) has been used in this
301 context to construct testable hypotheses with which the effects of lake typology (e.g. fetch, depth, fishery
302 practices, etc.) and pressure intensity interact to shape a continuum of ecosystem responses⁵⁴.
303 Additionally, evidence of multiple and varied ecosystem responses to alternative pressure scenarios
304 have been confirmed using multi-lake observations. For example, Bayley et al. (2007)⁵⁵ showed that
305 the 'clear water' to 'turbid water' regime shifts occurred across Canadian Prairie shallow lakes in
306 response to extreme weather.

307 [Figure 4]

308 The pursuit of evidence to support the classical shallow lake regime shift described above in single site
309 studies has dominated efforts in recent years. We call on the community to further develop ecological
310 understanding and encapsulate this within conceptual and process based models to help predict the
311 likelihood of novel regime shifts that threaten many lakes globally. For example, based on evidence
312 from long-term lake monitoring data and remote sensing archives coupled with process-based
313 modelling, we hypothesise that the widespread increase in dissolved organic carbon (DOC)
314 concentrations in temperate lakes associated with recovery from acidification⁵⁶ and a changing climate
315 will result in an increased occurrence of regime shifts across many lakes in the⁵⁷ coming decades. The
316 form of the regime shift is apparent from a critical transition observed in Lake Hårsvatten (Fig. 4) and

317 confirmed by other studies that have reported an increase in surface water DOC concentrations
318 resulting in a decrease in transparency, an increase in warming of epilimnetic waters, and longer and
319 stronger thermal stratification⁴⁸, potentially inducing a regime shift as lakes switch from di- to mono-
320 mixis. This, in turn, has the potential to cause more intense periods of anoxia in hypolimnetic waters⁵⁸,
321 resulting in increased internal loading of phosphorus (Fig. 4), stabilising the novel state. Couture et al.
322 (2015)⁵⁹ present a process based model for this form of regime shift that could be used to simulate the
323 effects of lake type on the probability of occurrence in response to changes in DOC concentrations.
324 Thus, while the principle response variable in this context (DOC) displays a linear response over time,
325 it can induce thresholds and a regime shift in secondary response variables. This DOC-response regime
326 shift represents a hitherto unforeseen effect of post-acidification recovery.

327 While the shifts in hypolimnetic water chemistry for Lake Hjärsvatten would not, necessarily, have been
328 detected using statistical EWIs, they could have been predicted based on *a priori* mechanistic
329 knowledge of lake function combined with process-based modelling. This well-established approach
330 should be developed to provide estimates of the probability of occurrence of regime shifts at the lake-
331 district scale to provide a test bed on which to address the current uncertainty associated with EWIs.
332 We propose that existing theory frameworks (e.g. alternative stable-state theory) be combined with the
333 requirements of EWI analysis to support future monitoring of lakes for which there is a high probability
334 of an impending regime shift, for example, following wide spread reduction in catchment phosphorus
335 loading or recovery from acidification, in response to increasing frequency of extreme weather events
336 or in line with the DOC example provided above.

337 **Quantifying Ecological Resilience: A New Perspective**

338 One primary focus of the discipline of ecology is the quantification of patterns of change in organism
339 productivity and biomass accumulation in response to changes in their biological and physical
340 environment. Clearly, the early detection of deviations from desirable, stable conditions promises
341 practical benefits in terms of motivating rapid management responses to mitigate potential, undesirable
342 regime shifts. However, recent assessments of regime shift EWIs using commonly collected monitoring
343 data have confirmed that confidence in their application to support management decisions is too low
344 for wide-scale practical application. This is due, at least in part, to a lack of consideration of temporal,
345 spatial and ecological scales, a failure to embed EWIs in an *a priori* mechanistic understanding of
346 ecosystem function and the lack of a clear probabilistic framework with which the co-occurrence of
347 regime shifts and loss of ecological stability preceding them have been confirmed.

348 Given the need for evidence based management underpinned by robust estimates of uncertainty, we
349 return to the framework of the conjunction rule. We have demonstrated that the research field is at an
350 early stage of development. Specifically, statistical tools are needed to credibly evaluate the probability
351 that regime shifts will occur in combination with responses in EWIs. To address this, we urge the
352 community to use the well-established statistical tools that are available to examine ecological resilience
353 theory by using objective criteria⁶ within a robust probabilistic framework. To address issues of detection
354 of EWIs and regime shifts outlined herein, we argue for future studies to adopt a formal probabilistic
355 framework, based on the conjunction rule. Specifically, quantification of the probability of detecting both
356 EWIs and a regime shift ($P(EWI_{t,s} \& RS_{t,s})$) in monitoring data given the probability of detecting EWIs
357 ($P(EWI_{t,s})$) and the conditional probability that we will then observe a subsequent regime shift (RS),
358 given the previously-identified EWIs ($P(RS_{t,s} | EWI_{t,s})$):

$$359 \quad P(EWI_{t,s} \& RS_{t,s}) = P(EWI_{t,s}) \times P(RS_{t,s} | EWI_{t,s})$$

360 This statement applies across statistical “populations” of lakes. The subscripts *t* and *s* acknowledge that
361 we would expect the probabilities of observing EWIs and regime shifts to differ among lakes belonging
362 to different ecological typologies (*t*, e.g. shallow versus deep, or nutrient-rich versus nutrient-poor lakes)
363 and with respect to the specific stressor (*s*, e.g. increased phosphorus loading, rising water
364 temperature) acting on lakes of any given typology. In order to properly evaluate the widespread
365 applicability and efficacy of any specific EWI, to inform lake management, we need to correctly quantify
366 the conditional probability $P(RS_{t,s} | EWI_{t,s})$ using experimental and observational data; the probability
367 that we will actually observe a regime shift following the detection of an EWI, for a lake of type *t*
368 responding to stressor *s*. Of specific interest is the “false discovery rate”, $1 - P(RS_{t,s} | EWI_{t,s})$, which is
369 the probability that a regime shift will not follow detectable EWIs^{1,40,60}, a scenario that could result in
370 unnecessary and costly management interventions.

371 As a first step toward providing robust estimates of probability to support the prediction of ecological
372 responses to multiple pressures, co-ordinated analyses of empirical case studies and scenario-based
373 modelling should be used to estimate the likely numeric values of the probabilities of the terms above.
374 In this respect, ensemble-modelling would be a particularly powerful approach, allowing systematic
375 assessment of multiple ecological scenarios using a series of structurally-different process-based
376 models. This approach allows more objective assessment of uncertainties in mechanistic knowledge,
377 ecological responses and current and future stressor scenarios⁹¹.

378 We propose that, alongside efforts to evaluate the real-world generic applicability of statistical EWIs of
379 “sudden change”, we should also strive to improve our capacity to predict, observe and manipulate
380 ecosystem stability, more generally. Ecosystems respond to a multitude of perturbations operating over
381 a wide range of temporal and ecological scales. The wide range of EWIs developed offer a suite of
382 indicators designed to provide insight into a short, but nevertheless critical, window of change preceding
383 regime shifts. However, these indicators can also be used to examine general ecological responses to
384 environmental change or management, as demonstrated here. The relative merits of these indicators
385 for such applications should be founded on advanced *a priori* mechanistic knowledge of lake ecology,
386 encapsulated within conceptual, empirical and theoretical ecological models.

387 There is a need to confront our current “best” projections of ecological responses to environmental
388 change scenarios with newly collected monitoring data and identify where models need to be developed
389 or improved to increase predictive power. The move from single experimental studies to integration of
390 data and *a priori* mechanistic understanding over broad scales will allow an iterative process of model
391 development and revised projections. This evidence base is essential to underpin effective preventative
392 management grounded with intuitive logic.

393

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531

532 **Figure Legends**

533 **Figure 1.** Standard deviation (SD) as an early warning indicator (EWI) for three lake ecosystems, over
534 different time scales. Left panel: 30-year time series of phytoplankton biomass (measured directly, or
535 using chlorophyll *a* as a proxy). Right panel: corresponding long-term changes in SD after seasonally-
536 detrending these data. For each lake, the SD is calculated using all 30 years of data, and when
537 truncating the time series to 20- and 10-year periods. Also, the SD is calculated within sliding windows
538 encapsulating 10, 25 and 50% of the available data (visualised using bars at the top right of each panel),
539 for each whole and truncated time series. The range of variation in the EWI increases when sliding time
540 windows are shorter (compare rows). Variable data availability (time series length) can have similar
541 effects; holding the percentage sliding window size constant, SD is more variable when calculated from
542 shorter time series than when calculated from longer ones (compare columns). This demonstrates the
543 impact 'catch-all' solutions can have on findings and the importance of 'informed' analytical decisions.

544 **Figure 2.** An assessment of early warning indicators during a transition from macrophyte to
545 phytoplankton dominance in a 9 month mesocosm experiment³⁹, 24th September 2012 to 2nd August
546 2013, Wuhan Botanical Gardens, China (upper left photograph). Eleven mesocosms (1.2 m internal
547 diameter and depth; upper right photograph) were placed in the pond covering stands of the
548 macrophytes *Potamogeton lucens* and *Cabomba caroliniana*. The figure shows three replicated
549 treatments of increasing nitrogen (N) loading via the addition of ammonium nitrate (NH₄NO₃) on every
550 tenth day for the duration of the experiment. Mesocosms were inoculated with *c.* 10 cm bighead carp
551 (*Aristichthys nobilis*; stocking density 100g m⁻² per mesocosm). Samples for chlorophyll *a* analysis and
552 observations of macrophyte PVI were collected every ten days and analysed as outlined by Olsen et
553 al. (2015)³⁹. This experiment achieved a transition from macrophyte to phytoplankton dominated state,
554 only under the highest N loading treatment. In the low N loading treatment, macrophytes declined
555 initially but recovered towards the end of the experiment. To demonstrate variation in ecological stability
556 throughout the experimental period, standard deviation, kurtosis and autocorrelation values were
557 calculated across a rolling window covering 25% of each time series using phytoplankton chlorophyll *a*
558 concentrations for each treatment mesocosm during the experiment. The display is relative to the mean
559 and +/- 1 standard deviation of the control mesocosms for each sample date and as ranges for each
560 treatment for the duration of the experiment. The effects of treatment and time, and interactions between
561 them were quantified using 2-way repeated measures analysis of variance with adjusted p-values using
562 the statistical programme R, using a data set constrained to May 2012 allowing examination of changes
563 preceding and during the transition. These tests show significantly higher standard deviation in the
564 control treatment ($f = 12.73$, $p = 4.10e-05$) compared to the low and high treatments and a significant
565 treatment:time interaction ($f = 12.95$, $p = 3.41e-05$). Significantly higher skewness and kurtosis was
566 reported in the high treatments compared to low and control (skewness: $f = 8.062$, $p = 0.002415$,
567 kurtosis: $f = 9.333$, $p = 0.00078$).

568
569 **Figure 3.** Examples of changes in variability following management intervention. Variability in
570 chlorophyll *a* concentrations (Standard Deviation, SD, calculated on log (X+1) data across a rolling
571 window covering 10% of the time series length). The arrows represent the timing of the disturbances,
572 as described. Lake Engelsholm was biomanipulated in 1992-1993 to support its recovery after nutrient
573 loading reduction^{44,45}. Nineteen tonnes of cyprinids were removed, decreasing the estimated biomass
574 from 675 to 150-300 kg ha⁻¹. This led to a substantial decrease in chlorophyll *a* concentrations, total
575 phosphorus (TP) and total nitrogen (TN) as well as an increase in Secchi depth, and marked changes
576 in SD; initially SD increased substantially, but then it declined markedly reaching the pre-manipulation
577 level in 2000 before increasing to a relatively consistent level 10 years after the manipulation; by then
578 SD was 30-50% higher than before manipulation. Aluminium (Al) was added to Lake Calhoun in 2001
579 (42 g m⁻²; see arrow) to reduce the release of excess, legacy P accumulated in the sediment (internal
580 loading). The Al inactivated 10.9 metric tonnes of mobile sediment P (by converting it the more stable
581 Al-bound P), thereby reducing sediment release by 953 kg P/y (>90%)^{46,47}. This decrease in internal P
582 release led to a substantial reduction of epilimnetic chlorophyll *a* concentration (70%) and TP (58%)
583 and an increase in Secchi depth (74%) compared to pre-treatment (1991-2000). After Al treatment, SD
584 decreased substantially until 2005, stabilized over the following 5 years (2006-2010), and then returned
585 to near pre-manipulation levels from 2011 onwards. The data for Lake Calhoun features late spring/
586 summer data only due to ice cover, therefore EWIs were calculated for each year individually. This
587 resulted in less data being contained within the rolling window but a consistent amount for each year
588 across the dataset.

589 **Figure 4.** Long term water quality measurements from Härsvatten, a lake experiencing a regime shift
590 in hypolimnetic dissolved oxygen levels (DO) associated with increasing epilimnetic total organic carbon
591 (TOC) concentrations (upper panel) and cumulative distribution of long-term (1988-2012) TOC trends
592 for lakes in the Swedish national monitoring programme. Water chemistry measurements (dots), long
593 term means (lines) and standard deviations (shaded boxes) before and after the 2004 DO regime shift
594 are shown in the upper panel. At Härsvatten, there has been a continuous increase in epilimnetic TOC
595 concentrations (blue dots), which is likely to have lengthened the duration and intensity of thermal
596 stratification, leading to declining summer hypolimnetic DO concentrations (red dots). Repeated
597 measurements of DO concentrations below 2 mg L⁻¹ are a potential early warning indicator for a regime
598 shift where internal P loading associated with suboxic and anoxic hypolimnetic waters induces a positive
599 feedback in which greater P availability facilitates higher rates of DO consumption, thereby maintaining
600 suboxic hypolimnetic conditions and on-going internal P release. There was a step change in the mean
601 and standard deviation of annual average hypolimnetic DO concentrations at the end of 2004 (Pettit's
602 test; p<0.001 for mean and p<0.02 for variance) followed by an approximately 250% increase in
603 hypolimnetic total phosphorus (TP) concentrations, most likely due to a sharp increase in internal P
604 loading. The lower panel puts the observations at Härsvatten into context by showing the cumulative
605 distribution of TOC trends for 233 Swedish lakes where long-term monitoring data are available.
606 Concentrations increased in 88% of monitored lakes (orange lines) and Härsvatten is at the 42nd
607 percentile of the cumulative distribution of trends (purple lines). While there is limited long term
608 monitoring of hypolimnetic water chemistry in Swedish lakes (n=14), the trends in TOC (n=233) are
609 suggestive of widespread regime shifts for dissolved oxygen in northern lakes. The 50th and 75th
610 percentiles of the trend distribution (grey lines) are at 0.13 and 0.23 mg TOC L⁻¹ yr⁻¹, respectively.