Ecological Resilience in Lakes and the Conjunction Fallacy[2]

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Abstract

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

Introduction[1]

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

In lakes, indicators have been developed to provide evidence of the occurrence of sudden ecological reorganisations, or *regime shifts*, and have been used to underpin assessments of changes in ecological stability (e.g. Carpenter et al., 2011)[3]. However, in many cases this approach relies on assumptions about the form of the regime shift (i.e. an underlying "model") and faith in this underlying model may be misplaced in the absence of systematic quantitative approaches[2]. [10] Specifically, evidence of the occurrence of these phenomena is limited by the existence of multiple underlying models representing possible real-world pressure-response relationships operating in lakes; be they linear, non-linear or hysteretic in nature[4] [11].

A fallacy occurs when an assumption is made that sudden ecosystem-scale change has occurred in response to changes in an environmental stressor. Such an assumption is commonly presented to support reports that statistical signatures of reduced stability have been detected prior to a profound ecological change. In the context of applying the conjunction rule to these systems, the probability of each of these responses occurring individually, and the overall probability of the conjunction of those responses occurring together can be calculated to provide a level of statistical certainty with which preventative management approaches[5] could be underpinned. In reality, there is a degree of uncertainty about whether either of these phenomena can be detected and this has led to contentious methodological debates (e.g., Wang et al., 2015)[6].

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

Ecological stability and resilience in lakes

Ecological stability theory is a major contemporary theme in ecology and environmental management, and has stimulated much debate. Two key aspects of the theory, referred to by Grimm et al. (1992)[7] as resistance and resilience, describe the tendency of species, communities, meta-communities or ecosystems to depart from established relationships with their biological and physical environments, and their capacity to return to pre-defined baseline conditions in response to perturbations. These departures can be profound, resulting in the reorganisation of communities in response to the breakdown of internal feedback mechanisms at the ecosystem scale. Within *ecological resilience* 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 occurs[10].

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 stability[5] and for the use of statistically derived early
108 warning indicators[13-15] (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. 2015[17] 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)[9] 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.

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 types[25], and they may not be exclusive signals of critical
139 transitions[26]. So, failure to observe an EWI may arise if the drivers of a regime shift are, themselves,
140 inherently unpredictable (e.g. noise-induced transitions[12]), 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 change[26]; this limits wide scale
146 practical applications considerably[17]. Litzow and Husnicker (2016)[4] 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

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 macrophytes[28] 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 system[13]. 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   assessed[29]. 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 records[30] and long-term monitoring
167   data[31] 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 processes[34]. The
182   selection of suitable indicators is not trivial, considering that complex ecosystem dynamics can amplify
183   or dampen EWIs in specific variables[35]. 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 EWIs[27]. 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].

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 months[38] (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 experiment[39] 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 production[34]). 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 pressures[42]. 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,

known to determine ecological conditions after changes in external pressures have occurred. These include measures to reduce internal phosphorus cycling in lakes[43], or to alter food-web structure and macrophyte community by manipulating fish stocks and/or transplanting submerged macrophytes[44]. Whilst the data frequency may not be appropriate for assessing EWIs of regime shifts when potentially expected, these experiments can be used to characterise the timelines of changes in the stability of lake variables, for example, following commonly used management approaches (Fig. 3). In addition, they may be used to explore non-stationary behaviour with and without management interventions. When considered in the context of simple indicators of ecological stability, it becomes apparent that responses to management can take decades to manifest and do not necessarily result in a more stable ecosystem.

[FIGURE 3]

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

Capitalising on Natural Events

Given the recent focus on developing EWIs, we stress the need to continue to build and refine our best conceptual models of ecosystem scale responses to pressures, in general. Multi-decadal to century-long lake monitoring data[45-53] are becoming increasingly available for use in this endeavour. Although such data are useful for the identification of regime shifts, their relatively coarse temporal resolution, may provide only limited opportunities to assess EWIs[12]. Long time series provide more context to ecosystem change than can be achieved by short term experiments however, and are more realistic in terms of noise and stochasticity. We advocate the use of these long-term data which have, at their core, the sound *a priori* knowledge of the mechanisms underlying ecosystem scale responses to past or current environmental change needed to provide credible alternative approaches to early warning of regime shifts across large populations of lakes.

Most studies purporting to show discontinuous regime shifts report that shallow lakes may switch from a turbid to clear water state[19]. The most commonly reported regime shift is the response of shallow lakes to increasing and decreasing phosphorus loading, which can cause a critical transition between clear water, macrophyte dominated and turbid water phytoplankton dominated states, respectively[53]. While such shifts have been observed, numerous studies of shallow lakes in recovery after external nutrient loading reduction have not exhibited this response, even when theory suggests they should have[32]. These results suggest that either pressure reductions may have been insufficient to reach a critical threshold, thresholds were not reached because of the impacts of other interacting processes (warming, food web structure changes), not all shallow lakes exhibit regime shifts, or that reorganisation at the ecosystem scale takes much longer than expected and follows the path of gradual adjustment of the system as the pressures change. Process based modelling (i.e. PCLake) has been used in this context to construct testable hypotheses with which the effects of lake typology (e.g. fetch, depth, fishery practices, etc.) and pressure intensity interact to shape a continuum of ecosystem responses[54]. Additionally, evidence of multiple and varied ecosystem responses to alternative pressure scenarios have been confirmed using multi-lake observations. For example, Bayley et al. (2007)[55] showed that the 'clear water' to 'turbid water' regime shifts occurred across Canadian Prairie shallow lakes in response to extreme weather.

[Figure 4]

The pursuit of evidence to support the classical shallow lake regime shift described above in single site studies has dominated efforts in recent years. We call on the community to further develop ecological understanding and encapsulate this within conceptual and process based models to help predict the likelihood of novel regime shifts that threaten many lakes globally. For example, based on evidence from long-term lake monitoring data and remote sensing archives coupled with process-based modelling, we hypothesise that the widespread increase in dissolved organic carbon (DOC) concentrations in temperate lakes associated with recovery from acidification[56] and a changing climate will result in an increased occurrence of regime shifts across many lakes in the[57] coming decades. The form of the regime shift is apparent from a critical transition observed in Lake Härsvatten (Fig. 4) and

confirmed by other studies that have reported an increase in surface water DOC concentrations resulting in a decrease in transparency, an increase in warming of epilimnetic waters, and longer and stronger thermal stratification[48], potentially inducing a regime shift as lakes switch from di- to mono-mixis. This, in turn, has the potential to cause more intense periods of anoxia in hypolimnetic waters[58], resulting in increased internal loading of phosphorus (Fig. 4), stabilising the novel state. Couture et al. (2015)[59] present a process based model for this form of regime shift that could be used to simulate the effects of lake type on the probability of occurrence in response to changes in DOC concentrations. Thus, while the principle response variable in this context (DOC) displays a linear response over time, it can induce thresholds and a regime shift in secondary response variables. This DOC-response regime shift represents a hitherto unforeseen effect of post-acidification recovery.

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

Quantifying Ecological Resilience: A New Perspective

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

Given the need for evidence based management underpinned by robust estimates of uncertainty, we return to the framework of the conjunction rule. We have demonstrated that the research field is at an early stage of development. Specifically, statistical tools are needed to credibly evaluate the probability that regime shifts will occur in combination with responses in EWIs. To address this, we urge the community to use the well-established statistical tools that are available to examine ecological resilience theory by using objective criteria[9] within a robust probabilistic framework. To address issues of detection of EWIs and regime shifts outlined herein, we argue for future studies to adopt a formal probabilistic framework, based on the conjunction rule. Specifically, quantification of the probability of detecting both EWIs and a regime shift (P($EWI_{t,s}$ & $RS_{t,s}$)) in monitoring data given the probability of detecting EWIs (P($EWI_{t,s}$)) and the conditional probability that we will then observe a subsequent regime shift (RS), given the previously-identified EWIs (P($RS_{t,s}$ | $EWI_{t,s}$)):

$$P(EWI_{t,s} \text{ \& } RS_{t,s}) = P(EWI_{t,s}) \times P(RS_{t,s} \mid EWI_{t,s})$$

This statement applies across statistical "populations" of lakes. The subscripts *t* and *s* acknowledge that we would expect the probabilities of observing EWIs and regime shifts to differ among lakes belonging to different ecological typologies (*t*, e.g. shallow versus deep, or nutrient-rich versus nutrient-poor lakes) and with respect to the specific stressor (*s*, e.g. increased phosphorus loading, rising water temperature) acting on lakes of any given typology. In order to properly evaluate the widespread applicability and efficacy of any specific EWI, to inform lake management, we need to correctly quantify the conditional probability P($RS_{t,s}$ | $EWI_{t,s}$) using experimental and observational data; the probability that we will actually observe a regime shift following the detection of an EWI, for a lake of type *t* responding to stressor *s*. Of specific interest is the "false discovery rate", 1- P($RS_{t,s}$ | $EWI_{t,s}$), which is the probability that a regime shift will not follow detectable EWIs[1,40,60], a scenario that could result in 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 scenarios[61].

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.

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Figure Legends

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

Figure 2. An assessment of early warning indicators during a transition from macrophyte to phytoplankton dominance in a 9 month mesocosm experiment[39], 24th September 2012 to 2nd August 2013, Wuhan Botanical Gardens, China (upper left photograph). Eleven mesocosms (1.2 m internal diameter and depth; upper right photograph) were placed in the pond covering stands of the macrophytes *Potamogeton lucens* and *Cabomba caroliniana*. The figure shows three replicated treatments of increasing nitrogen (N) loading via the addition of ammonium nitrate (NH_4NO_3) on every tenth day for the duration of the experiment. Mesocosms were inoculated with *c.* 10 cm bighead carp (*Aristichthys nobilis*; stocking density 100g m^{-2} per mesocosm). Samples for chlorophyll *a* analysis and observations of macrophyte PVI were collected every ten days and analysed as outlined by Olsen et al. (2015)[39]. This experiment achieved a transition from macrophyte to phytoplankton dominated state, only under the highest N loading treatment. In the low N loading treatment, macrophytes declined initially but recovered towards the end of the experiment. To demonstrate variation in ecological stability throughout the experimental period, standard deviation, kurtosis and autocorrelation values were calculated across a rolling window covering 25% of each time series using phytoplankton chlorophyll *a* concentrations for each treatment mesocosm during the experiment. The display is relative to the mean and +/- 1 standard deviation of the control mesocosms for each sample date and as ranges for each treatment for the duration of the experiment. The effects of treatment and time, and interactions between them were quantified using 2-way repeated measures analysis of variance with adjusted p-values using the statistical programme R, using a data set constrained to May 2012 allowing examination of changes preceding and during the transition. These tests show significantly higher standard deviation in the control treatment (f = 12.73, p = 4.10e-05) compared to the low and high treatments and a significant treatment:time interaction (f = 12.95, p = 3.41e-05). Significantly higher skewness and kurtosis was reported in the high treatments compared to low and control (skewness: f = 8.062, p = 0.002415, kurtosis: f = 9.333, p = 0.00078).

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

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