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Ecological resilience in lakes and the conjunction fallacy

Bryan M. Spears[1]*, Martyn N. Futter[2], Erik Jeppesen[3,4], Brian J. Huser[2], Stephen Ives[1,5], Thomas A. Davidson[3], Rita Adrian[6,7], David G. Angeler[2], Sarah J. Burthe[1], Laurence Carvalho[1], Francis Daunt[1], Alena S. Gsell[7], Dag O. Hessen[8], Annette B. G. Janssen[9,10], Eleanor B. Mackay[11], Linda May[1], Heather Moorhouse[12], Saara Olsen[3,4], Martin Søndergaard[3,4], Helen Woods[1] and Stephen J. Thackeray[11]

There is a pressing need to apply stability and resilience theory to environmental management 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.

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 conceptualized 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 reorganizations, or regime shifts, and have been used to underpin assessments of changes in ecological stability (for example, ref. [3]). However, in many cases this approach relies on assumptions about the form of the regime shift (that is, an underlying 'model') and faith in this underlying model may be misplaced in the absence of systematic quantitative approaches[2]. 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, nonlinear or hysteretic in nature[4].

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 (for example, ref. [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 a comprehensive 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

[1]Centre for Ecology and Hydrology, Penicuik, Midlothian EH26 0QB, UK. [2]Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Box 7050, 750 07 Uppsala, Sweden. [3]Department of Bioscience - Lake Ecology, Aarhus University, Vejlsøvej 25, 8600 Silkeborg, Denmark. [4]Sino-Danish Centre for Education and Research (SDC), University of Chinese Academy of Sciences, 100049 Beijing, China. [5]School of Geosciences, Crew Building, The King's Buildings, University of Edinburgh, Alexander Crum Brown Road, Edinburgh EH9 3FF, UK. [6]Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 301, D-12587 Berlin, Germany. [7]Department of Biology, Chemistry, Pharmacy, Free University of Berlin, 14195 Berlin, Germany. [8]Department of Biosciences, University of Oslo, Box 1066 Blindern, 0316 Oslo, Norway. [9]Department of Aquatic Ecology, NIOO-KNAW, Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands. [10]Department of Aquatic Ecology and Water Quality Management, Wageningen University & Research, PO Box 47, 6700 AA Wageningen, The Netherlands. [11]Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster LA1 4AP, UK. [12]Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, Oxfordshire OX10 8BB, UK. *e-mail: spear@ceh.ac.uk

debate. Two key aspects of the theory, referred to as resistance and resilience[7], describe the tendency of species, communities, metacommunities 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 reorganization of communities in response to the breakdown of internal feedback mechanisms on the ecosystem scale. Within ecological resilience theory, this latter phenomenon is described as a regime shift. Regime shifts can be either smooth (linear), nonlinear (threshold) or discontinuous (hysteresis, critical) transitions[8,9]. A previous study[9] proposed that, to confirm the occurrence of a regime shift, a reorganization that produces a new and stable ecosystem must be detectable across multiple physical and biological components. Quantifiable terms relating to regime shifts include the critical threshold, the point on the pressure axis at which the system shifts, and the transition, the period over which the switch between stable states occurs[10].

Ecological resilience theory suggests that discontinuous regime shifts may be preceded by subtle changes in ecological behaviour that can be detected using quantifiable indicators, thus providing useful early warning of impending transitions. For example, an increase in the variance or autocorrelation of phytoplankton biomass, due to phenomena known as critical slowing down (CSD) or flickering, may be expected to precede the well-documented transition between phytoplankton- and macrophyte-dominated conditions in shallow lakes. Put simply, CSD is characterized by a reduction in the speed of ecological recovery after a disturbance as an ecosystem approaches a critical threshold, and flickering results from the alternation between stable ecological states following perturbations[6,11,12]. Frameworks for detecting changes in ecological stability[5] and for the use of statistically derived early warning indicators[13–15] (EWIs) have been developed for predicting regime shifts. To date, the performance of these frameworks has been evaluated, mainly using simulated or experimental data[15,16].

Lakes are particularly important model ecosystems with which to examine the aforementioned phenomena given that they represent 'aquatic islands' that are relatively contained, easily quantified and manipulated, and exhibit a vast array of ecological responses to well-defined gradients of multiple and interacting pressures. These pressures include eutrophication, acidification and climate change. Recent tests using long-term lake monitoring data have indicated low levels of agreement between EWIs and statistically defined sudden ecological change. A previous study[17] highlighted that this lack of coherence may arise due to insufficient knowledge of the causes of sudden changes in ecological indicators that occur in long-term monitoring data and their relation to regime shifts. One significant weakness in this approach is that the form and rate of regime shifts are very difficult to quantify, even though they may dictate whether or not CSD or flickering may be expected to occur. Using the terminology of the conjunction rule, this underlying model is flawed. Another study[18] reviewed the evidence available for regime shifts in freshwater ecosystems and concluded that many of the studies purporting to demonstrate this phenomenon fail to do so. Of the 135 studies analysed, few met all of the criteria proposed in ref. [9] to confirm a regime shift. This suggests that regime shifts are less common in nature than the abundant literature would suggest. Ultimately, these reports of regime shifts based on unwarranted extensional reasoning about the consequences of observed EWIs support the widespread occurrence of conjunction fallacies in this field, with the occurrence of regime shifts having been widely reported despite a lack of robust probabilistic evidence.

Predicting regime shifts in real-world systems

If we are to improve our capacity to estimate the probability of regime shifts and changes in ecosystem stability preceding them, we must first examine our underlying model and our capacity to quantify its individual components. We can demonstrate this approach by considering lake ecosystems, which have been widely used as model systems for the development and application of ecological resilience theory[17,19] and EWIs[20,21].

Although EWIs have been applied with apparent success in small-scale and whole-lake experimental settings, significant caveats have been identified regarding their use in real-world systems. Authors have stated that EWIs may occur before only specific types of regime shift[22,23], potentially including both critical and non-critical transition types[24], and they may not be exclusive signals of critical transitions[25]. So, failure to observe an EWI may arise if the drivers of a regime shift are, themselves, inherently unpredictable (for example, noise-induced transitions[12]), or as a result of methodological issues such as the resolution of monitoring data and/or the selection of (rolling) time windows within which EWIs are calculated (Fig. 1). When applied to monitoring data from lakes with reported regime shifts, the predictive success of EWIs has been reported to be at best only about 50%[26]. To achieve acceptable levels of confidence in their application, any reliable use of EWIs needs to be embedded within a priori knowledge of system-specific ecological mechanisms that underlie change[25]; this limits wide-scale practical applications considerably[17]. One study[4] proposed that uncertainty is a result of applying the theory incorrectly through flawed logic in the underlying model and introduced a systematic approach to assess pressure–response forms to address this. Specifically, the authors demonstrated that success rates for EWIs could be significantly improved when assessments are made using only case studies that exhibited hysteresis in the pressure-response model.

By considering the underlying processes that drive change in EWIs more generally, we can begin to understand important limitations in their current application. All EWIs are likely to be inherently variable within a given ecosystem state, even one that is a long way from an impending transition, due to transient ecological dynamics. For example, the widely ranging variance in phytoplankton biomass and submerged macrophytes[27] exhibited over the long term by apparently stable lakes makes it difficult to identify changes that are indicative of a regime shift (Fig. 1). Changes in EWIs can be judged to be 'significant' only if they vary outside the range that is found under typical baseline conditions or in a parallel and statistically well-defined control system[13]. Such assessments require time series data of sufficient frequency and duration with which any departure from baseline conditions can be adequately quantified.

Decisions must be made regarding ecologically relevant timescales over which loss of stability can be assessed[28]. Our definition of 'sudden' change, which underlies the definition of discontinuous regime shifts, is perhaps better judged on a scale of organismal and community turnover times, rather than calendar dates or funding timelines. For example, one study[5] considered the onset of a phytoplankton bloom to be a short-term (that is, days to months) ecological event that was preceded by a change in EWIs from the baseline. In shallow lakes, palaeolimnological records[29] and long-term monitoring data[30] show that a regime shift, characterized by the complete loss of submerged plants, can be preceded by decades to centuries of change in community composition that culminates in the dominance of a few nutrient-tolerant species (that is, *Potamogeton crispus*, *P. pusillus*, *P. pectinatus* and *Zannichellia palustris*) before they disappear completely. In contrast to the duration of a typical experiment (months to years), the plant loss regime shift described above demonstrates a mean transition time from a non-eutrophic macrophyte flora to the penultimate community state of about 100 years, and from the penultimate state to plant loss of about 20 years. Similarly, studies of contemporary monitoring data that quantify the responses in fish and macrophyte communities to catchment phosphorus loading abatement in shallow lakes often report gradual timescales of response of the order of decades[31,32]. In this context, it is difficult to distinguish between categories of regime shift or to establish clear timelines across which EWIs would be expected to

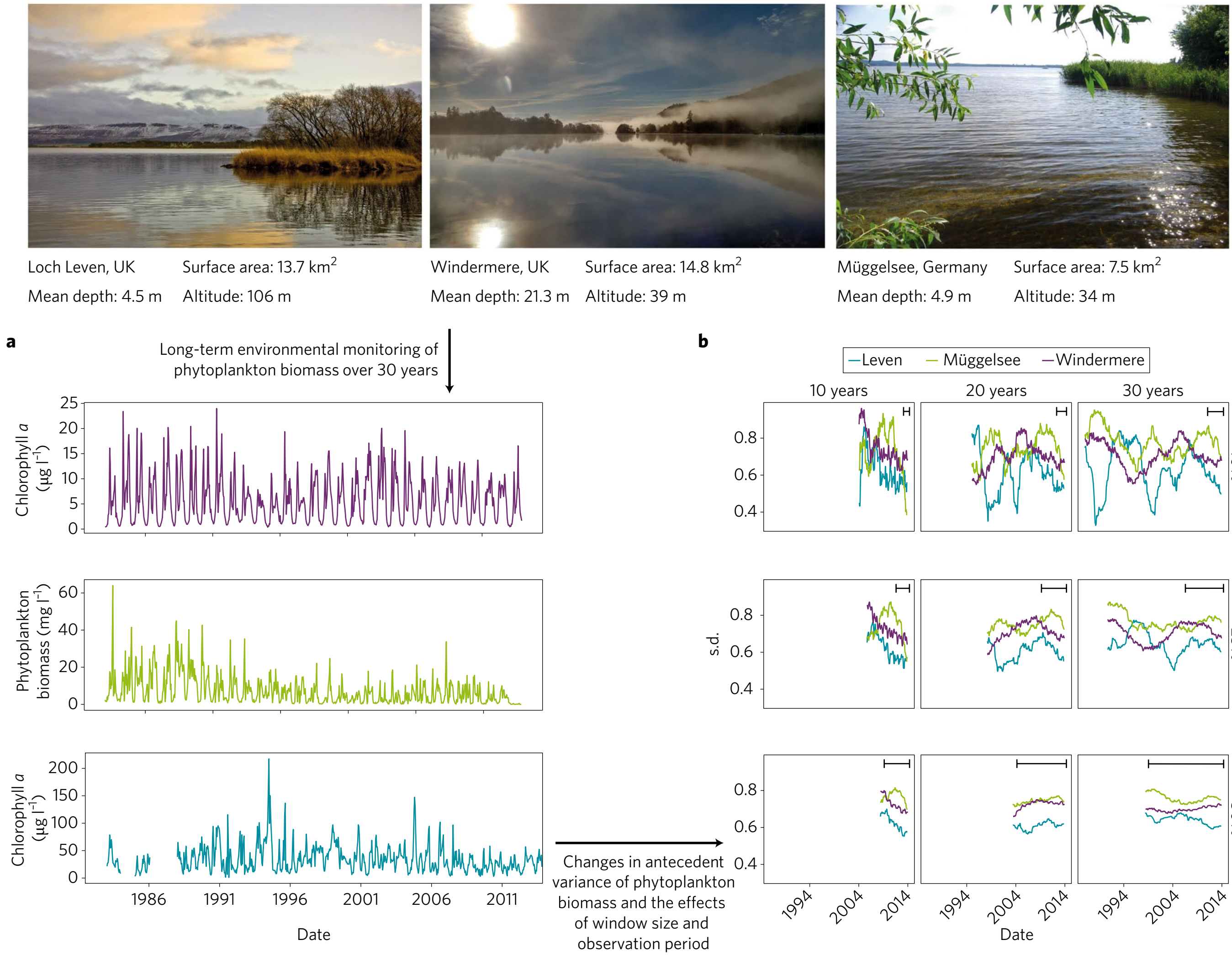

Fig. 1 | Standard deviation (s.d.) as an EWI for three lake ecosystems, over different timescales. a, Thirty-year time series of phytoplankton biomass (measured directly, or using chlorophyll *a* as a proxy). **b**, Corresponding long-term changes in s.d. after seasonally detrending these data. For each lake, the s.d. is calculated using all 30 years of data, and when truncating the time series to 20- and 10-year periods. Also, the s.d. is calculated within sliding windows encapsulating 10, 25 and 50% of the available data (visualized 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, s.d. is more variable when calculated from shorter time series than when calculated from longer ones (compare columns). This demonstrates the impact that 'catch-all' solutions can have on findings and the importance of 'informed' analytical decisions. Credits: Loch Leven photograph (left image), Jim Hampson/Scottish Natural Heritage; Windermere photograph (middle image), Mitzi M. De Ville; Müggelsee photograph (right image), T. Hintze.

respond. To address this, there is a need to develop more systematic definitions of regime shifts that occur in nature and to use these as a framework within which changes in indicators of ecological stability can be assessed.

Despite the fact that regime shifts are ecosystem-scale phenomena, ecological indicators used for calculating EWIs are often simple state variables that may not reflect ecosystem-scale processes[33]. The selection of suitable indicators is not trivial, considering that complex ecosystem dynamics can amplify or dampen EWIs in specific variables[34]. The components of an ecosystem that are most likely to exhibit the behaviours that underpin EWIs will depend on the type of regime shift and on the underpinning ecological mechanisms. Retrospective analyses of long-term monitoring data from lakes in which regime shifts have been observed and defined can be used to test the sensitivity of EWIs[26]. For the development of monitoring programmes designed to predict unforeseen regime shifts, however, the identification of suitable EWIs from the suite available is challenging. This selection must be combined with mechanistic understanding of the relevant ecological processes, feedback mechanisms and regime shifts that occur across a wide range of pressure scenarios, lake types and timescales. That is, we must develop more detailed underlying models, based on comprehensive understanding of the ecosystem and its responses to defined environmental stressors. These models can then be used to support diagnosis of time-varying ecosystem-scale changes in indicators of stability needed to quantify the probability of regime shifts based on departure from baseline conditions using EWIs[35,36].

Learning from experiments

The probabilities of observing both detectable changes in EWIs and subsequent regime shifts can best be estimated by the statistical analysis of data from controlled experiments. Such estimates or probabilities could be used to infer the likelihood of observing these phenomena in real-world monitoring data. Most experimental studies focusing on resilience and EWI development have assessed relatively short-term responses to perturbations (that is, weekly to monthly resolution) using high-frequency data. The advent of high-frequency monitoring systems (at hourly to daily level resolution) in lakes provides lake ecologists with an impressive capacity to detect subtle and rapid changes in ecological indicators in response to perturbations. As next-generation monitoring systems are developed and/or improved (for example, remote-sensing approaches including multi-parameter monitoring buoys), our detection power will also improve. In contrast to this, we draw attention to the vast legacy of experimental studies that have collected lower-frequency monitoring data. These low-frequency experiments represent an untapped resource with which non-stationary behaviour in ecosystems can be examined using the statistical tools developed as EWIs in response to a controlled perturbation or otherwise.

One criticism of short-term experiments is that it is difficult to conclude that a persistent regime shift has occurred, although they do provide important evidence of short-term dynamics in ecological responses at high temporal frequency. With a few exceptions, mesocosm experiments span periods of only 3–12 months[37] (Fig. 2). So, longer-term changes, including potential regime shifts, and changes in ecological behaviour preceding (and following) them, are often difficult to assess. Tightly controlled experiments in which regime shifts are achieved provide a powerful approach to examining and quantifying the performance of EWIs and responses in ecological stability, more generally. Unfortunately, although an impressive legacy dataset exists documenting ecological responses following manipulation of nutrient cycling or food-web structure, this evidence has been poorly utilized in the context of ecological resilience in lakes.

Here we provide an example of the use of a short-term mesocosm experiment[38] to examine ecological resilience in lakes and some misgivings in the context of the conjunction rule. Mesocosms were subjected to contrasting nitrogen (N) loading during a nine-month shallow lake experiment that led to the complete loss of submerged macrophytes at high N loading (Fig. 2), a well-established regime shift known to occur in shallow lakes. There were no apparent EWI signals or trends when the macrophytes started to decline in the high-N-loaded mesocosms. EWI values from the treatment mesocosms were found to be both higher and lower than the control mesocosms. When one considers the general treatment effects, it is apparent that EWIs were significantly different across the treatments and that an interaction between treatment and time was reported. However, the results provide no conclusive evidence of an increase in EWIs prior to the regime shift in the high-nutrient-loading treatment. In general, we observed more stable conditions under the highest-N-loading treatment, which seems to contradict the increase in variance expected when CSD occurs prior to a regime shift. In this example, it is impossible to determine the form of the regime shift and so our underlying model, which hypothesizes the occurrence of CSD preceding the demise of the macrophytes, may be unfounded, as in other similar experimental studies.

Few ecosystem-scale experiments have been conducted to test the hypothesis that CSD can be detected before a regime shift. The most comprehensive study to date involved the detection of responses across a range of indicators in a treatment lake relative to a control lake, following manipulation of the fish community from planktivore- to piscivore dominance[3,14,29,34,39]. Thresholds in some of these indicator variables were reported more than a year before the transition to piscivore dominance was complete, providing evidence to support CSD. However, evidence also existed for similar fluctuations in EWIs following the regime shift, suggesting ongoing longer-term processes that are not easily explained. Although this experiment provided a rich and detailed dataset with at least daily sampling resolution for a range of variables, there are three potentially important caveats that are relevant to interpretation of the data. First, the results indicated that ecosystem 'state variables' (for example, dissolved oxygen) were more sensitive indicators of the reported transition than estimates of rates (for example, gross primary production[33]). This potentially indicates insufficiencies in available methods for quantifying key system changes. Second, even in this very comprehensive study, response patterns of different indicators and EWIs varied quite substantially. Third, the methods used in whole-lake experiments require that the manipulated and reference lake(s) are in synchrony over the sampling period and frequency of interest, which may be unlikely at such high monitoring frequency.

Lower temporal frequency data from many other whole-lake experiments are available for the determination of longer-term effects of environmental change on ecological stability indicators. Such studies are important because they have been conducted in systems for which there is adequate causal understanding of the relevant ecological mechanisms driving change. Although few of these studies have been framed using ecological resilience or stability terminology, we demonstrate the potential to retrospectively explore the effects of perturbations on ecological stability more generally, irrespective of whether a regime shift was reported or planned in the original design (Fig. 3). There are many whole-lake experiments lasting from years to decades, the longest of which are those aiming to restore lakes from external pressures[40]. While some of these have focused solely on reducing external pressures, 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[41], or to alter food-web structure and macrophyte community by manipulating fish stocks and/or transplanting submerged macrophytes[42]. Although the data frequency may not be appropriate for assessing EWIs of regime shifts when potentially expected, these experiments can be used to characterize 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.

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

Capitalizing 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. Multidecadal to century-long lake monitoring data[43–51] 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 that 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.

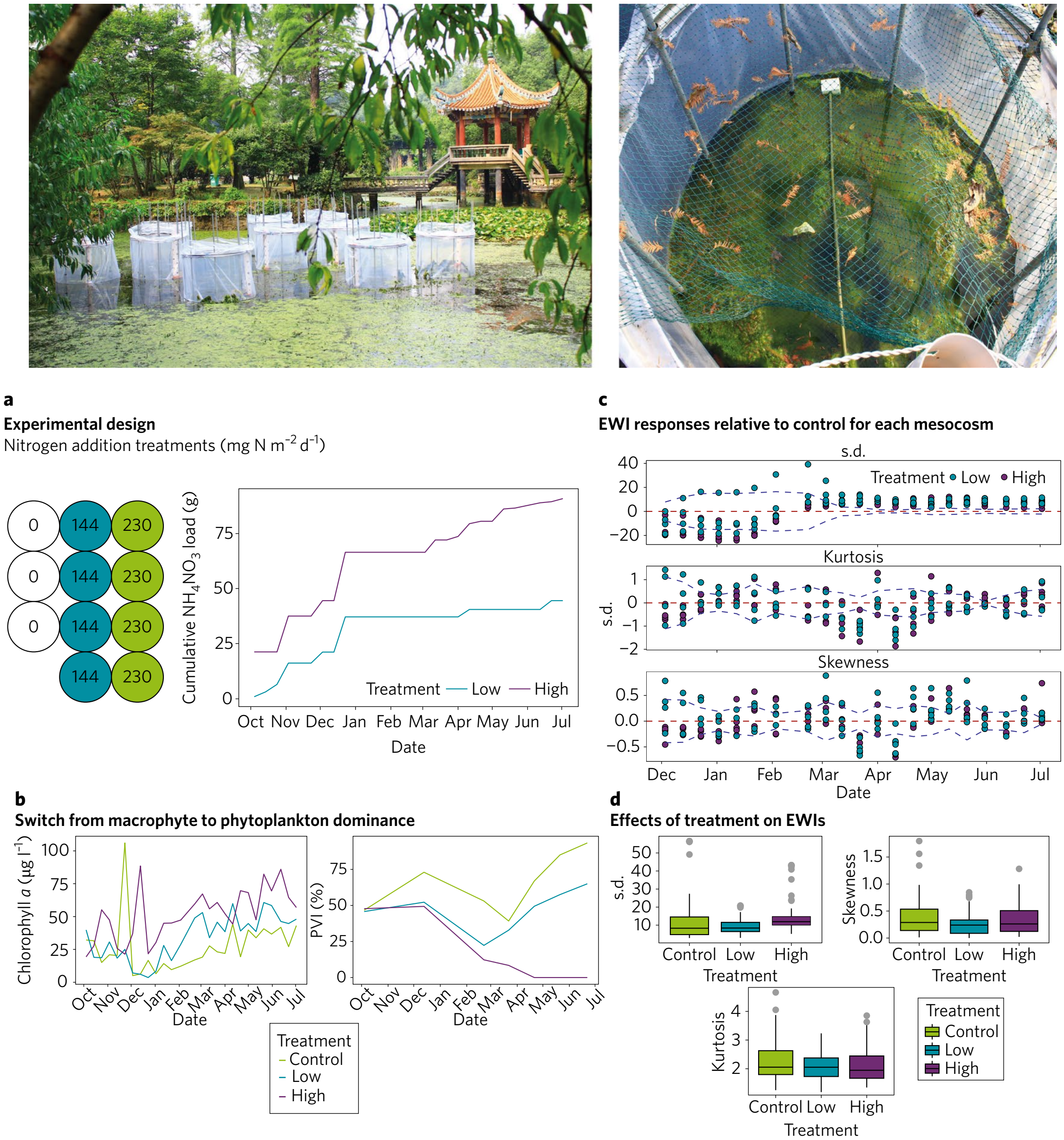

Fig. 2 | An assessment of EWIs during a transition from macrophyte to phytoplankton dominance in a nine-month mesocosm experiment[38], 24 September 2012 to 2 August 2013, Wuhan Botanical Gardens, China. Eleven mesocosms (1.2 m internal diameter and depth) were placed in the pond covering stands of the macrophytes *Potamogeton lucens* and *Cabomba caroliniana*. **a**, The treatment consisted of increasing nitrogen (N) loading via the addition of ammonium nitrate (NH_4NO_3) to three replicate mesocosms on every tenth day for the duration of the experiment. Mesocosms were inoculated with ~10 cm bighead carp (*Aristichthys nobilis*; stocking density 100g m^{-2} per mesocosm). Samples for chlorophyll *a* analysis and observations of macrophyte percent volume inhabited (PVI) were collected every ten days and analysed as outlined in ref. [38]. **b**, Transition from macrophyte- to phytoplankton-dominated state occurred only under the highest N-loading treatment. In the low-N-loading treatment, macrophytes declined initially but recovered towards the end of the experiment. **c**, To demonstrate variation in ecological stability throughout the experimental period, s.d., 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 ± 1 s.d. of the control mesocosms for each sample date and as ranges for each treatment for the duration of the experiment. **d**, The effects of treatment and time, and interactions between them, were quantified using two-way repeated measures analysis of variance with adjusted *P* values using the statistical program R, using a dataset constrained to May 2012 allowing examination of changes preceding and during the transition. These tests show significantly higher s.d. in the control treatment ($F = 12.73$, $P = 4.10\times10^{-5}$) compared with the low and high treatments and a significant treatment:time interaction ($F = 12.95$, $P = 3.41\times10^{-5}$). Significantly higher skewness and kurtosis was reported in the high treatments compared with low and control (skewness: $F = 8.062$, $P = 0.002415$; kurtosis: $F = 9.333$, $P = 0.00078$).

Most studies purporting to show discontinuous regime shifts report that shallow lakes may switch from a turbid to clear water state[52]. 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[51]. Although 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[31]. These results suggest that either pressure

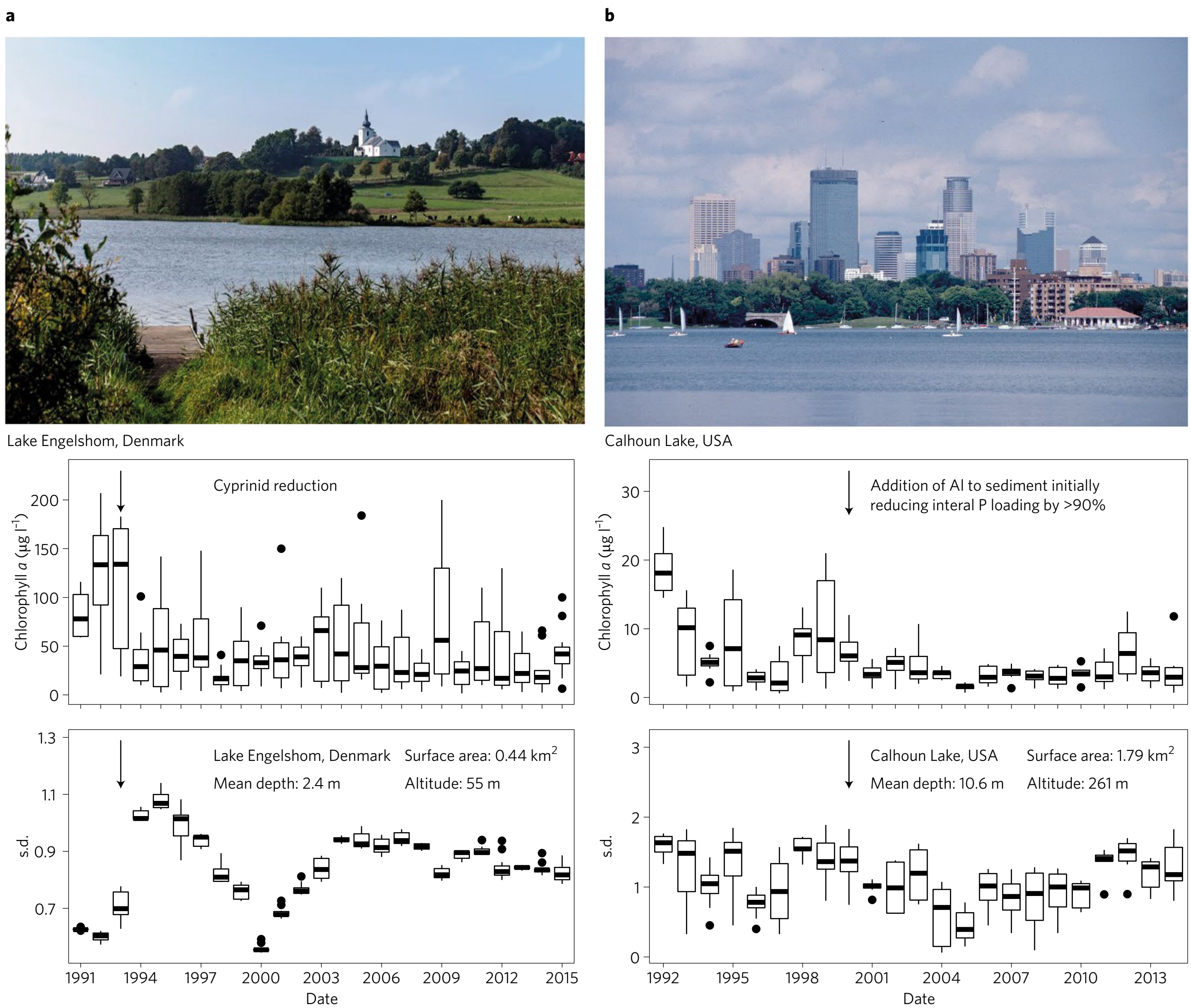

Fig. 3 | Examples of changes in variability following management intervention. Variability in chlorophyll *a* concentrations (s.d. calculated on $\log(X+1)$ data across a rolling window covering 10% of the time series length). The arrows represent the timing of the disturbances, as described. **a**, Lake Engelsholm was biomanipulated in 1992–1993 to support its recovery after nutrient loading reduction[42,43]. 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 and total nitrogen as well as an increase in Secchi depth, and marked changes in s.d. Initially, s.d. 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, s.d. was 30–50% higher than before manipulation. **b**, 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 yr^{-1} (>90%)[44,45]. This decrease in internal P release led to a substantial reduction of epilimnetic chlorophyll *a* concentration (70%) and total phosphorus (58%), and an increase in Secchi depth (74%) compared with pre-treatment (1991–2000). After Al treatment, s.d. decreased substantially until 2005, stabilized over the following five years (2006–2010), and then returned to near pre-manipulation levels from 2011 onwards. The data for Lake Calhoun feature 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. Credit: Calhoun Lake photograph (right image), Minneapolis Park and Recreation Board.

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 reorganization on 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 (that is, PCLake) has been used in this context to construct testable hypotheses with which the effects of lake typology (for example, fetch, depth, fishery practices and so on) and pressure intensity interact to shape a continuum of ecosystem responses[53]. Additionally, evidence of multiple and varied ecosystem responses to alternative pressure scenarios have been confirmed using multi-lake observations. For example, one study[54] showed that the 'clear water' to 'turbid water' regime shifts occurred across the Canadian Prairies shallow lakes in response to extreme weather.

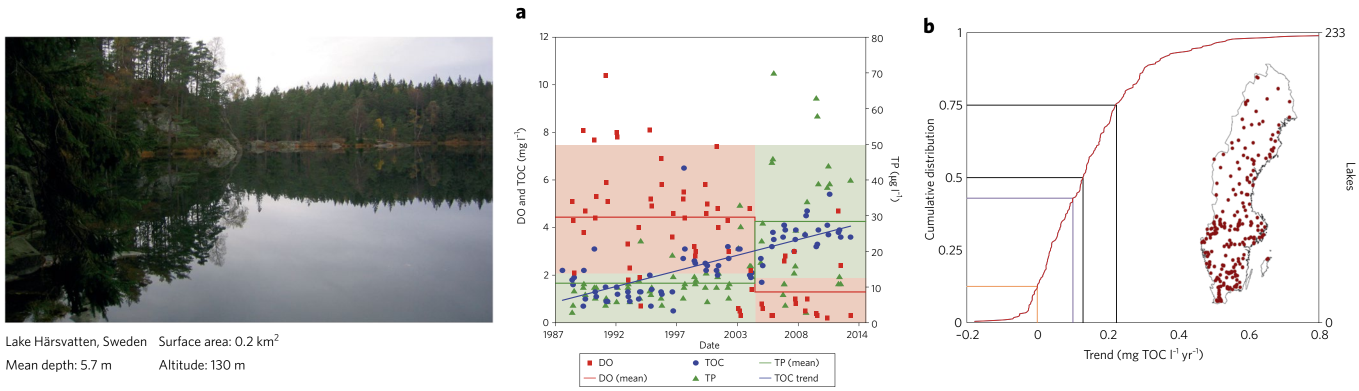

Fig. 4 | Developing a new underlying model for wide-scale regime shifts using Swedish lakes. a,**b**, Long-term water quality measurements from Härsvatten, a lake experiencing a regime shift in hypolimnetic dissolved oxygen levels (DO) associated with increasing epilimnetic total organic carbon (TOC) concentrations (**a**) and cumulative distribution of long-term (1988–2012) TOC trends for lakes in the Swedish national monitoring programme (**b**). Water chemistry measurements (symbols), long-term means (lines) and s.d. values (shaded boxes) before and after the 2004 DO regime shift are shown in **a**. At Härsvatten, there has been a continuous increase in epilimnetic TOC concentrations (blue circles), which is likely to have lengthened the duration and intensity of thermal stratification, leading to declining summer hypolimnetic DO concentrations (red squares). Repeated measurements of DO concentrations below 2 mg l^{-1} are a potential EWI 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 ongoing internal P release. There was a step change in the mean and s.d. 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 probably due to a sharp increase in internal P loading. Panel **b** 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). Although 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 DO 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.

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 new 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 hypothesize that the widespread increase in dissolved organic carbon (DOC) concentrations in temperate lakes associated with recovery from acidification[55] and a changing climate will result in an increased occurrence of regime shifts across many lakes in the coming decades[56]. 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[46], 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[57], resulting in increased internal loading of phosphorus (Fig. 4), stabilizing the new state. 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 is presented in ref. [58]. Thus, while the principal 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 on 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 (for example, alternative stable-state theory) should 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 widespread 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

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 a 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 ($P(\mathrm{EWI}_{t,s}$ & $\mathrm{RS}_{t,s}))$ in monitoring data given the probability of detecting EWIs ($P(\mathrm{EWI}_{t,s})$) and the conditional probability that we will then observe a subsequent regime shift (RS), given the previously identified EWIs ($P(\mathrm{RS}_{t,s} \mid \mathrm{EWI}_{t,s})$):

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

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, for example, shallow versus deep, or nutrient-rich versus nutrient-poor lakes) and with respect to the specific stressor (s, for example, increased phosphorus loading, increasing water temperature) acting on lakes of any given typology. To properly evaluate the widespread applicability and efficacy of any specific EWI, to inform lake management, we need to correctly quantify the conditional probability $P(\mathrm{RS}_{t,s} \mid \mathrm{EWI}_{t,s})$ 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', $1 - P(\mathrm{RS}_{t,s} \mid \mathrm{EWI}_{t,s})$, which is the probability that a regime shift will not follow detectable EWIs[1,59,60], a scenario that could result in unnecessary and costly management interventions.

As a first step towards providing robust estimates of probability to support the prediction of ecological responses to multiple pressures, co-ordinated analyses of empirical case studies and scenario-based modelling should be used to estimate the likely numeric values of the probabilities of the terms above. In this respect, ensemble modelling would be a particularly powerful approach, allowing systematic assessment of multiple ecological scenarios using a series of structurally different process-based models. This approach allows more objective assessment of uncertainties in mechanistic knowledge, ecological responses, and current and future stressor scenarios[61].

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

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

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Author contributions

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