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Major limnology paradigm questioned by new study

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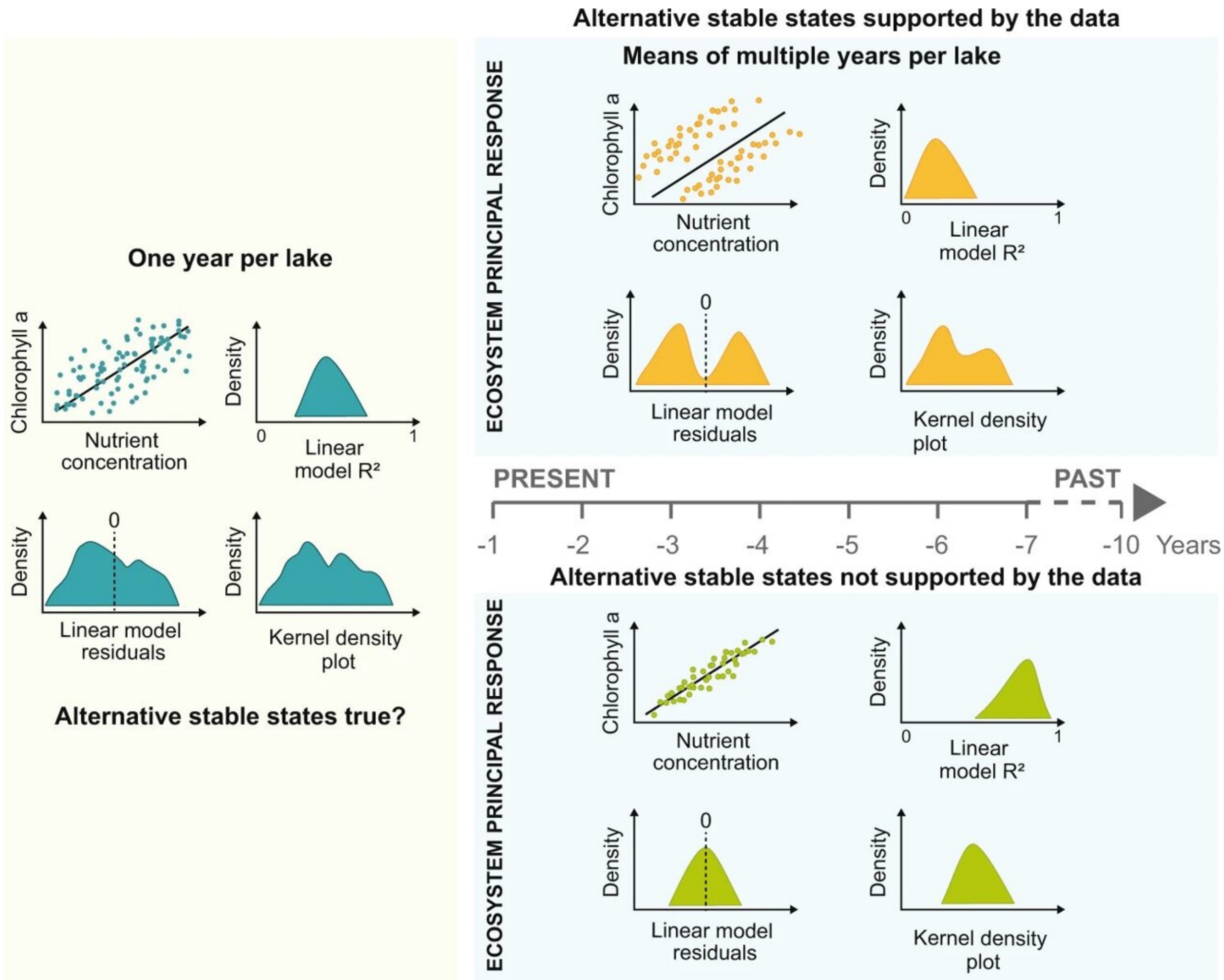

Detecting alternative equilibria in spatial data at different temporal scales. The temporal scale increases from a single year on the left to the decadal scale on the right. The data shows typical patterns of nutrient and chlorophyll-a found in shallow lakes for a single year, with results of the three diagnostic tests (see methods) applied to detect the presence or absence of alternative stable states (ASS). Single-year data does not provide strong evidence for or against the existence of ASS. In addition to examining the patterns in the scatter plots of nutrients vs chlorophyll-a, the tests are (i) the R^2 of the model, (ii) the residuals of a linear model of nutrients vs chlorophyll-a, (iii) Kernel density plots of chlorophyll-a data. We present expected patterns (derived from simulations) that would suggest the presence (above the line) or absence (below the line) of ASS in shallow lakes. As the temporal scale of the observations increases from single-year data to multiple-year means the expectation is that inter-annual variability should even out and the presence or absence of ASS should become apparent in the proxies (above the horizontal line). The scatter plot of chlorophyll-a versus the nutrients will show two clouds of data (turbid or clear), hence, (i) the R^2 of the model will decrease, as a single linear model cannot predict two alternatives, (ii) the residuals of a linear model correlating nutrients to chlorophyll-a will show multimodality and (iii) the kernel density plot of chlorophyll-a will deviate from unimodality. Conversely, in the absence of ASS (below the horizontal line), the link between nutrient concentration and chlorophyll-a becomes increasingly well predicted by a linear model, resulting in a larger R^2 with an increasing number of averaged year, unimodality of the model residuals and of the kernel density function. Credit: *Nature Communications* (2023). DOI: 10.1038/s41467-023-36043-9

Shallow lakes can take on two alternative stable states, according to a theory on ecological equilibrium in the study of inland waters (limnology). This paradigm has now been called into question by a study conducted by the Helmholtz Centre for Environmental Research (UFZ) and Aarhus University (Denmark) and published in the journal *Nature Communications*.

In a data analysis of 902 shallow lakes, the research team found no evidence for the existence of two alternative stable states. The authors are critical of lake management measures based on this theory. They recommend that greater emphasis be placed on the reduction of nutrient inputs in the future to ensure the ecological equilibrium of shallow lakes.

Roughly 42 percent of lakes worldwide are so-called shallow lakes with an average depth of up to three meters. "Shallow lakes are highly important bodies of water for us humans: They provide us with water for drinking, for fishing and for recreational activities. A good ecological state is crucial for this," says last author Dr. Daniel Graeber from the UFZ Department of Aquatic Ecosystem Analysis and Management.

"Because shallow lakes are usually fed from surface waters, they often receive increased inputs of nutrients. This can easily throw off their ecological equilibrium."

According to a theory developed in the 1990s and broadly accepted in limnology, shallow lakes should be able to independently oscillate between two alternative stable states with the same nutrient availability: One condition is characterized by turbid water dominated by phytoplankton and the other by clear water and abundant aquatic plants.

"The theory also says that these two states each exhibit long-term stability following a change," explains Dr. Thomas A. Davidson, limnologist at Aarhus University and lead author of the study. "Biomanipulative measures based on this explanatory model have already been implemented several hundred times in Europe and the U.S. to improve the ecological condition of lakes."

The goal of such intervention: to counteract the effects of a high nutrient supply—increased growth of phytoplankton, oxygen deficiency, toxic blooms of blue-green algae and fish kills. The addition of piscivorous fish, for example, is intended to regulate the increased phytoplankton production via ecological feedback effects: Piscivorous fish eat prey fish, fewer prey fish eat fewer small crustaceans, and more small crustaceans eat more phytoplankton.

In this way, a turbid shallow lake characterized by high phytoplankton growth, is to be moved to its second stable state—clear water with aquatic plants and spawning grounds for fish—with long-term stability despite a high availability of nutrients. "That somehow sounds too good to be true," says Graeber.

"Over the past years, a few studies have already yielded initial indications that, in reality, this theory might only play a minor role. We wanted to investigate this in further detail and to give a reality check to this explanatory model of alternative stable states of shallow lakes that is widely accepted in limnology."

To do this, the research team analyzed long-term monitoring data from 902 shallow lakes. The lakes were located in Denmark and the U.S. and were less than three meters deep. The researchers investigated the relationship between nutrient concentration and chlorophyll a concentration (as a measure of phytoplankton biomass) in the lakes and its variation over time.

They developed a special statistical method to test whether alternative states occurred in the lakes and whether, as the theory predicted, they were also stable and self-sustaining over several years. "We first used simulations to test whether our statistical method also actually works and whether it is even able to detect any alternative stable states. These simulations included scenarios with and without alternative stable states, and our method reliably detected the presence or absence of alternative stable states," says the UFZ limnologist.

The results of the data analysis of the 902 lakes can therefore also be considered reliable: In the lakes studied, the research team found no indications whatsoever of the presence of two alternative stable states. "What we were able to clearly establish is a pronounced linear relationship between nutrient concentration and phytoplankton concentration," says Graeber. "So more nutrients inevitably lead to more phytoplankton. None of the lakes exhibited a different response to high nutrient concentrations. The explanatory model of two alternative stable states therefore does not appear to occur in reality—at least for lakes in the temperate zones."

But what do these results mean in practice? How can we maintain the ecological equilibrium of shallow lakes? "Biomanipulative measures such as adding piscivorous fish cannot stabilize the shallow lake ecosystem in the long term, because there is no alternative stable state," says Graeber. "There is only one way to maintain the equilibrium of shallow lakes in a continuous stable state, and there's no alternative: Nutrient inputs have to be consistently reduced."

More information: Thomas A. Davidson et al, Bimodality and alternative equilibria do not help explain long-term patterns in shallow lake chlorophyll-a, *Nature Communications* (2023). DOI: 10.1038/s41467-023-36043-9

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