Network-based metrics of community resilience and dynamics in lake ecosystems

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Abstract

Some ecosystems can undergo abrupt critical transitions to a new regime after passing a tipping point, such as a lake shifting from a clear to turbid state as a result of eutrophication. Metrics-based resilience indicators acting as early warning signals of these shifts have been developed but have not always been reliable in all systems. An alternative approach is to focus on changes in the structure and composition of an ecosystem, but this can require long-term food-web observations that are typically unavailable. Here we present a network-based algorithm for estimating community resilience, which reconstructs past ecological networks from palaeoecological data using metagenomic network inference. Resilience is estimated using local stability analysis and eco-net energy (a neural network-based proxy for "ecological memory"). The algorithm is tested on model (PCLake+) and empirical (lake Erhai) data. We find evidence of increasing diatom community instability during eutrophication in both cases, with changes in eco-net energy revealing complex eco-memory dynamics. The concept of ecological memory opens a new dimension for understanding ecosystem resilience and regime shifts, and further work is required to fully explore its drivers and implications.

Keywords: Lake Eutrophication; Early Warning Signals; Resilience; Palaeoecology; Neural Networks

1. Introduction

The potential for pressurised ecosystems to abruptly shift to a new regime once tipping points are reached has led to a proliferation of metrics attempting to quantify ecosystem resilience [1–10]. Lake eutrophication is a well-studied example of an ecological tipping point, with evidence of alternative stable states, regime shifts, and strong hysteresis [11–13]. Eutrophication occurs when increasing nutrient loading triggers positive feedbacks driving a rapid shift from clear to turbid conditions [14,15], with recovery requiring nutrient levels to be reduced far below the original threshold [13]. This should be reflected by declining ecosystem resilience, defined here as a relative weakening of negative feedbacks resulting in greater sensitivity to small shocks [16]. However, current metrics for evaluating resilience loss (e.g. time-series metrics of critical slowing down) have mixed reliability when applied as early warning signals (EWS) in freshwater [17] and other ecosystems [18–21]. Methodological issues include the choice of system variable for analysis, false or missed alarms, and subjective parameter choices, while palaeorecord applications presents an additional challenge of variable temporal resolution due to compaction or changing accumulation rates [7,22–25].

An alternative approach to metric-based "classical" EWS is to analyse ecosystem structure in order to detect the changing dynamics of the whole ecosystem without having to understand the full trophic ecology of any one species. To this end Doncaster et al. [26] assessed the compositional disorder of diatoms and chironomids from sediment cores in three Chinese lakes (Erhai, Taibai, and Longgan). The correlation of nestedness and biodiversity in these lakes becomes negative prior to the critical transition before reverting to positive values, which was hypothesised to result from eutrophication shifting the competitive balance between 'keystone' and 'weedy' species. However, the link between this and ecosystem resilience is indirect and the competition dynamics remain theoretical. Another recent network-based method is nodal degree skewness, with increasing human pressure inducing

more negative skewness in Chinese lake ecosystems [27].

An alternative approach is to reconstruct the lake's food web and monitor for signs of dynamical instability. Kuiper et al. [28] showed that food-web data can be used to reconstruct the interactions between different species, which correspond to the interaction matrix of a Lotka-Volterra ecosystem model. Given food-web observations, the food web's local stability can be estimated from the intraspecific interaction strengths or the maximum loop weight of the ecosystem's longest trophic loop, both of which are closely related to the system's dominant eigenvalue (λ_d) [29,30]. This approach enabled destabilising food web reorganisations prior to eutrophication to be tracked in the PCLake model [28]. However, this requires detailed food-web data to be generated at regular intervals during eutrophication, a laborious task which is often unavailable for real-world lakes.

Many lakes nevertheless have palaeoecological records of species abundances from sediment cores. If past ecosystem structure can be reconstructed from abundance data, it would be possible to estimate changes in ecosystem resilience over time. Here we develop and apply an algorithm for reconstructing ecological networks (eco-nets) from palaeoecological data using metagenomic network inference [31–34]. We then estimate ecosystem resilience using local stability analysis and novel neural network methods.

2. Methods

2.1. Eco-Network Inference

All analysis was conducted in R [35]. Abundance data was first transformed by isometric log ratio to account for compositionality in relative data and imputed to counter data sparseness [36] to form abundance matrix $\boldsymbol{X}$. To find the structure of the eco-net, we followed the methods of metagenomics network inference [33,34]. We first assumed that ecological interactions follow a generalised Lotka-Volterra model:

$$\frac{dx_i(t)}{dt} = x_i(t)\left[\beta_i - \sum_j \alpha_{ij} x_j(t)\right]$$

Equation 1

where x is the abundance of species *i* or *j*, α_{ij} is the interaction coefficient between species *i* and *j* ($<-1 < \alpha_{ij} < 1$), and β_i is the constant unitary net growth rate of species *i*. Taking the logarithm of a discrete-time Lotka-Volterra model based on Equation 1 and assuming constant time-steps [33] gives:

$$ln\, x_i\,(t+1) - ln\, x_i\,(t) = \zeta_i(t) + \beta_i - \sum_j \alpha_{ij}(x_j(t) - \langle x_j \rangle)$$

Equation 2

where ζ is the noise term and $\langle x_j \rangle$ is the median abundance (approximating to equilibrium abundance and carrying capacity for normalising against; assumes sufficient data to capture equilibrium population dynamics and ephemeral species). Given abundance time-series, the interaction coefficients α_{ij} can be found by performing multiple linear regression (lasso regularised due to data sparseness and limited observations relative to variables, and k-Fold cross-validated to improve prediction performance) of $[ln\, x_i\,(t+1) - ln\, x_i\,(t)]$ against $[x_j(t) - \langle x_j \rangle]$. The regression coefficients populate the elements of interaction matrix $\boldsymbol{A}$, which represents the eco-net's structure at time *t*.

We use only non-interpolated data to avoid well-known biases interpolation introduces to time-series analysis [24], although this results in slightly varying time-steps. Network inference and linear regression are less sensitive to non-equidistant time points than time-series analysis [32], but the discrete-time Lotka-Volterra model still assumes constant time-steps. To minimise this limitation, input data should be scrutinised prior to analysis and sections with substantial shifts in time resolution excluded.

2.2. Local Stability

The eco-net's stability was estimated using local stability analysis, by taking the

absolute of the interaction matrix $\boldsymbol{A}$ (which is equivalent to the Jacobian of the Lotka-Volterra system [28,37,38]; the system is considered stable at its equilibrium point if the real part of the Jacobian's eigenvalues remain negative, indicating net negative feedbacks), setting α_{ii} to 0 (to satisfy the Perron-Frobenius Theorem [29]), and calculating the dominant eigenvalue λ_d (which is tightly related to other ecosystem stability metrics [28–30]). This was calculated on a 50% rolling window to estimate changes in stability over time.

2.3. Ecological Memory

Recent theory suggests that ecosystems may have a distributed 'memory' of past states as a result of a process akin to unsupervised Hebbian learning in a neural network [39,40]. In Hopfield Networks frequent correlations between neurones (nodes) lead to an increase in their synaptic connection strength (edges) – a process described colloquially as "*neurons that fire together, wire together*" [41–44]. Over time this allows the emergence of distributive associative memory of training data that can be recovered when given degraded input. Power et al. [39,40] proposed that eco-nets experience similar dynamics, with frequently co-occurring species (nodes) developing stronger interactions (edges), allowing a distributed associative "ecological memory" (eco-memory) of past environmental forcing (training data) to emerge (Figure 1). We have no direct metric of Hopfield Network memory strength, but we can calculate its energy, which is minimised at stable points. By assuming the eco-net's interaction matrix $\boldsymbol{A}$ is equivalent to a neural network's weight matrix $\boldsymbol{W}$ [39] and treating it as a continuous Hopfield Network, we posit that the eco-net energy, E_n, can be calculated by:

$$\mathrm{E}_n = -\frac{1}{2}\mathbf{X}(\mathbf{t})^{\boldsymbol{T}}\mathbf{A}\mathbf{X}(\mathbf{t})$$

Equation 3

where $\boldsymbol{X}(\boldsymbol{t})$ is a vector of species abundances at time *t* [41–44]. We hypothesise that stable eco-nets 'learning' from long-term environmental conditions leads to lower E_n, and that destabilisation would conversely result in higher E_n. However, asymmetric matrices with non-

zero diagonals, such as community matrices, can lead to chaotic behaviour and the network converging to alternative less-stable points, meaning eco-nets may not always completely minimise their energy.

2.4. Comparison Metrics

For comparison we also calculated time-series metrics (Z-scores of AR1, standard deviation (SD), skewness, and kurtosis) on keystone abundance (Cyclostephanos Dubius; Erhai) or surface chlorophyll concentration (PCLake+) with variance-stabilising square-root transformation and Gaussian detrending (bandwidth: PCLake+ 1%; Erhai 5%) (R: *generic_ews*, "*earlywarnings*"[6]). However, due to methodological limitations [7,22–25] time-series metrics are shown for comparison only and are not useful results by themselves. We also calculate compositional disorder metrics [26] (nestedness, biodiversity (inverse Simpson index), and their correlation; R: *nestedtemp* & *diversity*, "*vegan*"[45]) where possible.

3. Test-Case 1: PCLake+

We first apply the algorithm to output from PCLake+ [46], an extension of the widely used PCLake model of lake eutrophication, as a test-bed with well-known dynamics and drivers. PCLake+ is initialised in default clear state with monthly time-steps, run for 200 years to ensure stability, and nutrient input increased (0.0001 to 0.005 $gPm^{-2}d^{-1}$) over 50 years to induce eutrophication. Dry-weight ecosystem outputs (binned to represent sedimentary preservation with variable accumulation rates) are used as abundance inputs for the algorithm. We cannot compute nestedness for PCLake+ as only functional groups rather than individual species are available.

The impact of nutrient input is clearly visible (Fig. 2a) in both local stability (λ_d) and eco-net energy (E_n), with λ_d increasing shortly after input begins in conjunction with a peak in

E_n at ~50 cm (along with increases in time-series metrics and biodiversity). However, after a second λ_d peak (~35 cm) both λ_d and especially E_n decrease unexpectedly (whilst apart from standard deviation the time-series and biodiversity metrics plateau or decline). This is contrary to our hypothesis that destabilisation should lead to higher E_n, indicating more complex resilience and eco-memory dynamics than anticipated. It may result from initial destabilisation away from memorised conditions being followed by a "relearning" process as the eco-net adapts to the emergence of a new structure (reflected by higher biodiversity) and conditions, leading to the latter decrease in E_n. We also simulate the impact of increasing accumulation rates, compaction, or variable temporal resolution with a non-linear age-depth model, as these effects are common in palaeorecords. This does not alter the overall signal, but significantly reduces the resolution of deeper features (Supplementary Figure S1).

4. Test-Case 2: Lake Erhai

Data from lake Erhai – a lake in south-western China which has undergone eutrophication after decades of nutrient-enrichment – consists of relative diatom abundances sampled at regular radioisotope-dated depth intervals down sediment cores [26,47]. We focus on diatoms as they are well-preserved and all belong to the same trophic level, but this also means significant parts of the wider ecosystem are not captured. However, we posit that diatom λ_d indirectly reflects the wider ecosystem, as diatoms play a key role in the trophic loops involved in eutrophication [28] and are ecologically sensitive to water quality [48,49].

As expected, real-world data exhibits more complexity than model results, but some phases of activity can be observed (Fig. 2b). Phase 1 corresponds to elevated λ_d and E_n (along with increasing SD), before both λ_d and E_n decline in phase 2 (along with elevated AR1 and biodiversity, and negative compositional disorder) prior to the transition, after which E_n rises sharply (while biodiversity sharply drops and compositional disorder recovers). These patterns are similar to the PCLake+ results, with initially elevated λ_d and E_n suggesting a shift

away from the memorised state during early destabilisation, followed by a decline in λ_d and E_n, suggesting the eco-net relearning a new state during pre-transition reorganisation.

5. Further Development

There are several key methodological limitations that can be improved with future development. To work best, the algorithm requires long datasets with minimal sparseness that sufficiently resolve equilibrium population dynamics. Many palaeorecords do not meet these requirements though, rendering them unsuitable for this analysis. Further development will attempt to improve the algorithms capacity to analyse limited or sparse data using innovative techniques from metagenomic network inference [32]. We also assume these ecosystems fit a generalised Lotka-Volterra model, in which all of the changes in abundance are caused either by interspecific interactions or by a broad noise term encompassing all other influences. But interspecific interactions may not fit a simplified model of linear pairwise interaction, and other important processes are simplified into the noise term [50–53]. Nonlinear interaction terms are expected in some ecosystems [54] and potentially allow a better representation of multiple alternative stable states [55], but are harder to parameterise. Future work will assess the feasibility of allowing nonlinear functional responses.

The assumed model only includes biotic elements with life-environment interactions implicit, but in reality the environment dynamically interacts with life. Incorporating life-environment feedbacks explicitly would allow more realistic feedback loops critical to resilience to emerge, but the eco-net cannot simply be extended to include abiotic elements as the environment is currently assumed to be its training data. One solution might be using a neural network that allows training data that is dynamic (e.g. continuous-time recurrent neural networks) and affected by the eco-net itself (e.g. multi-layer or adversarial networks).

6. Conclusions

In this paper we develop a novel algorithm to reconstruct eco-networks from palaeoecological abundance data and estimate their changing resilience. With further refinement, this method might allow the past resilience of ecosystems over time to be inferred from palaeoecological data. We also introduce eco-net energy as a proxy of "ecological memory", by treating the eco-network as a neural network that has undergone unsupervised Hebbian learning of past environmental forcing. This concept has only been applied to a simplified ecosystem model before now [39,40], but the development of eco-net energy has allowed us to explore eco-memory in more realistic models and empirical data for the first time. The concept of ecological memory opens a new dimension for understanding ecosystem resilience and regime shifts, with the formation of eco-memory potentially helping to improve ecosystem resilience by allowing past eco-network stable states to be recovered after disruptions. Further work is required to fully understand the drivers and implications of eco-memory dynamics, and to disentangle the effects of eco-memory from other drivers of changing ecosystem resilience.

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Figures

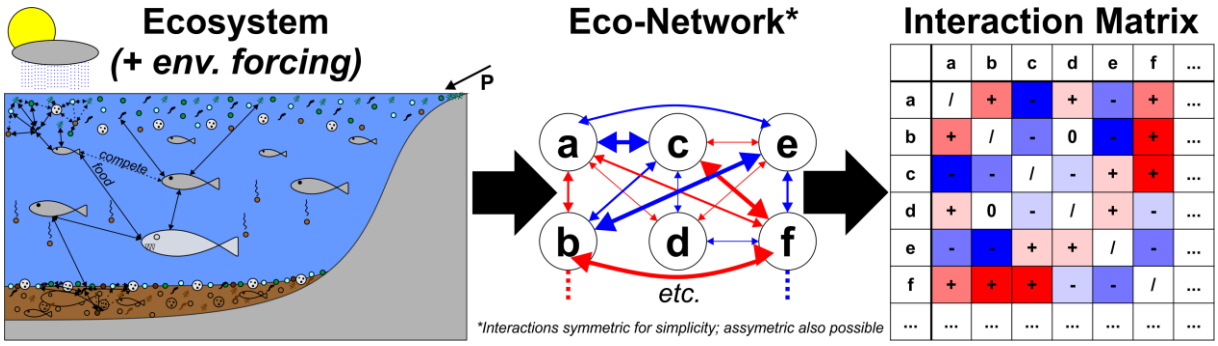

Figure 1: Diagram showing how ecosystem interactions (left) can be represented as an eco-network (middle), the structure of which forms an interaction matrix (right) suitable for resilience analysis. Only symmetric interactions are shown here for simplicity; asymmetric interactions are also likely.

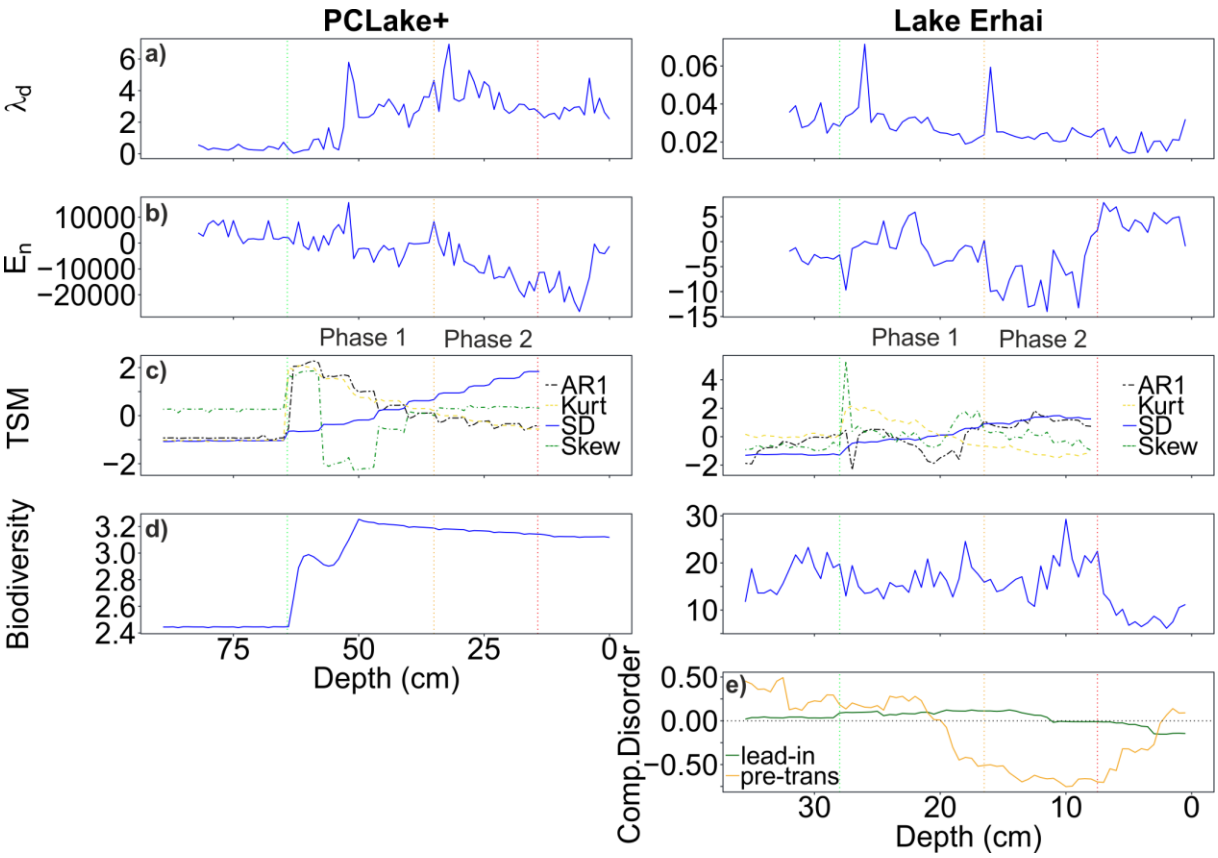

Figure 2: Results for PCLake+ (left) and lake Erhai (right) plotted against depth (time running left-to-right), showing output for (a) linear instability λ_d and (b) eco-net energy E_n. Also shown are (c) normalised time-series metrics (TSM; shown for comparison only), (d) biodiversity (inverse Simpson index), and (e, Erhai only) compositional disorder (see [26] for details). Vertical dotted lines (green: phase 1, orange: phase 2, red: transition) mark suggested transition phases.

References

1. Scheffer M *et al.* 2009 Early-warning signals for critical transitions. *Nature* **461**, 53–9. (doi:10.1038/nature08227)

2. Dakos V, Carpenter SR, van Nes EH, Scheffer M. 2015 Resilience indicators: prospects and limitations for early warnings of regime shifts. *Philos. Trans. R. Soc. B Biol. Sci.* **370**, 20130263–20130263. (doi:10.1098/rstb.2013.0263)

3. Lenton TM. 2013 Environmental Tipping Points. *Annu. Rev. Environ. Resour.* **38**, 1–29. (doi:10.1146/annurev-environ-102511-084654)

4. Kéfi S, Dakos V, Scheffer M, Van Nes EH, Rietkerk M. 2013 Early warning signals also precede non-catastrophic transitions. *Oikos* **122**, 641–648. (doi:10.1111/j.1600-0706.2012.20838.x)

5. Scheffer M *et al.* 2012 Anticipating critical transitions. *Science* **338**, 344–8. (doi:10.1126/science.1225244)

6. Dakos V *et al.* 2012 Methods for Detecting Early Warnings of Critical Transitions in Time Series Illustrated Using Simulated Ecological Data. *PLoS One* **7**, e41010. (doi:10.1371/journal.pone.0041010)

7. Lenton TM. 2011 Early warning of climate tipping points. *Nat. Clim. Chang.* **1**, 201–209. (doi:10.1038/nclimate1143)

8. Dakos V, Scheffer M, van Nes EH, Brovkin V, Petoukhov V, Held H. 2008 Slowing down as an early warning signal for abrupt climate change. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 14308–12. (doi:10.1073/pnas.0802430105)

9. Carpenter SR, Brock WA. 2006 Rising variance: a leading indicator of ecological transition. *Ecol. Lett.* **9**, 311–318. (doi:10.1111/j.1461-0248.2005.00877.x)

10. Lenton TM, Livina VN, Dakos V, Scheffer M. 2012 Climate bifurcation during the last deglaciation? *Clim. Past* **8**, 1127–1139. (doi:10.5194/cp-8-1127-2012)

11. Scheffer M, Van Nes EH. 2007 Shallow lakes theory revisited: Various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia* **584**, 455–466. (doi:10.1007/s10750-007-0616-7)

12. Scheffer M, Hosper S, Meijer M, Moss B, Jeppesen E. 1993 Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* **8**, 275–279.

13. Scheffer M, Carpenter SR. 2003 Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends Ecol. Evol.* **18**, 648–656. (doi:10.1016/j.tree.2003.09.002)

14. Carpenter SR, Ludwig D, Brock WA. 1999 Management of Eutrophication for Lakes Subject To Potentially Irreversible Change. *Ecol. Appl.* **9**, 751–771. (doi:10.1890/1051-0761(1999)009[0751:MOEFLS]2.0.CO;2)

15. Carpenter SR. 2005 Eutrophication of aquatic ecosystems: Bistability and soil phosphorus. *Proc. Natl. Acad. Sci.* **102**, 10002–10005. (doi:10.1073/pnas.0503959102)

16. Armstrong McKay DI, Lenton TM. 2018 Reduced carbon cycle resilience across the Palaeocene–Eocene Thermal Maximum. *Clim. Past* **14**, 1515–1527. (doi:10.5194/cp-14-1515-2018)

17. Gsell AS *et al.* 2016 Evaluating early-warning indicators of critical transitions in natural aquatic ecosystems. *Proc. Natl. Acad. Sci.* **113**, E8089–E8095. (doi:10.1073/pnas.1608242113)

18. Bestelmeyer BT *et al.* 2011 Analysis of abrupt transitions in ecological systems. *Ecosphere* **2**, art129. (doi:10.1890/ES11-00216.1)

19. Burthe SJ *et al.* 2016 Do early warning indicators consistently predict nonlinear change in long-term ecological data? *J. Appl. Ecol.* **53**, 666–676. (doi:10.1111/1365-2664.12519)

20. Hastings A, Wysham DB. 2010 Regime shifts in ecological systems can occur with no warning. *Ecol. Lett.* **13**, 464–472. (doi:10.1111/j.1461-0248.2010.01439.x)

21. Litzow MA, Hunsicker ME. 2016 Early warning signals, nonlinearity, and signs of hysteresis in real ecosystems. *Ecosphere* **7**. (doi:10.1002/ecs2.1614)

22. Boettiger C, Ross N, Hastings A. 2013 Early warning signals: The charted and uncharted territories. *Theor. Ecol.* **6**, 255–264. (doi:10.1007/s12080-013-0192-6)

23. Boettiger C, Hastings A. 2012 Early warning signals and the prosecutor's fallacy. *Proc. Biol. Sci.* **279**, 4734–9. (doi:10.1098/rspb.2012.2085)

24. Carstensen J, Telford RJ, Birks HJB. 2013 Diatom flickering prior to regime shift. *Nature* **498**, E11-2. (doi:10.1038/nature12272)

25. Taranu ZE, Carpenter SR, Frossard V, Jenny J-P, Thomas Z, Vermaire JC, Perga M-E. 2018 Can we detect ecosystem critical transitions and signals of changing resilience from paleo-ecological records? *Ecosphere* **9**, e02438. (doi:10.1002/ecs2.2438)

26. Doncaster CP, Chávez VA, Viguier C, Wang R, Zhang E, Dong X, Dearing JA, Langdon PG, Dyke JG. 2016 Early warning of critical transitions in biodiversity from compositional disorder. *Ecology* **97**, n/a-n/a. (doi:10.1002/ecy.1558)

27. Wang R *et al.* 2019 Network parameters quantify loss of assemblage structure in human-impacted lake ecosystems. *Glob. Chang. Biol.* , 1–12. (doi:10.1111/gcb.14776)

28. Kuiper JJ, van Altena C, de Ruiter PC, van Gerven LPA, Janse JH, Mooij WM. 2015 Food-web stability signals critical transitions in temperate shallow lakes. *Nat. Commun.* **6**, 7727. (doi:10.1038/ncomms8727)

29. Neutel A-M, Heesterbeek JAP, Ruiter PC de. 2002 Stability in Real Food Webs: Weak Links in Long Loops. *Science (80-.).* **296**, 1120–1123. (doi:10.1126/science.1068326)

30. Neutel A-M, Heesterbeek JAP, van de Koppel J, Hoenderboom G, Vos A, Kaldeway C, Berendse F, de Ruiter PC. 2007 Reconciling complexity with stability in naturally assembling food webs. *Nature* **449**, 599–602. (doi:10.1038/nature06154)

31. Faust K, Raes J. 2012 Microbial interactions: From networks to models. *Nat. Rev. Microbiol.* **10**, 538–550. (doi:10.1038/nrmicro2832)

32. Faust K, Lahti L, Gonze D, de Vos WM, Raes J. 2015 Metagenomics meets time series analysis: Unraveling microbial community dynamics. *Curr. Opin. Microbiol.* **25**, 56–66. (doi:10.1016/j.mib.2015.04.004)

33. Fisher CK, Mehta P. 2014 Identifying Keystone Species in the Human Gut Microbiome from Metagenomic Timeseries Using Sparse Linear Regression. *PLoS One* **9**, 1–10. (doi:10.1371/journal.pone.0102451)

34. Mounier J, Monnet C, Vallaeys T, Arditi R, Sarthou A-S, Helias A, Irlinger F. 2008 Microbial Interactions within a Cheese Microbial Community. *Appl. Environ. Microbiol.* **74**, 172–181. (doi:10.1128/AEM.01338-07)

35. R Foundation for Statistical Computing. 2016 R: A language and environment for statistical computing.

36. Aitchison J. 1982 The Statistical Analysis of Compositional Data. *J. R. Stat. Soc. Ser. B. Methodol.* **44**, 139–177. (doi:10.2307/2345821)

37. de Ruiter PC, Neutel A-M, Moore JC. 1995 Energetics, Patterns of Interaction Strengths, and Stability in Real Ecosystems. *Science (80-.).* **269**, 1257–1260. (doi:10.1126/science.269.5228.1257)

38. Lade SJ, Gross T. 2012 Early Warning Signals for Critical Transitions: A Generalized Modeling Approach. *PLoS Comput. Biol.* **8**, e1002360. (doi:10.1371/journal.pcbi.1002360)

39. Power DA, Watson RA, Szathmary E, Mills R, Powers ST, Doncaster CP, Czapp B. 2015 What can ecosystems learn? Expanding evolutionary ecology with learning theory. *Biol. Direct* **10**, 69. (doi:10.1186/s13062-015-0094-1)

40. Watson RA, Szathmáry E. 2016 How Can Evolution Learn? *Trends Ecol. Evol.* **31**, 147–157. (doi:10.1016/j.tree.2015.11.009)

41. Hopfield JJ. 1982 Neural networks and physical systems with emergent collective computational abilities. *Proc. Natl. Acad. Sci.* **79**, 2554–2558. (doi:10.1073/pnas.79.8.2554)

42. MacKay DJC. 2005 *Information Theory, Inference, and Learning Algorithms*. Cambridge University Press. (doi:10.1198/jasa.2005.s54)

43. Rojas R. 1996 *Neural Networks: a Systematic Introduction*. (doi:10.1016/0893-6080(94)90051-5)

44. Kröse B, Smagt P van der. 1996 *An Introduction To Neural Networks*.

45. Oksanen J *et al.* 2017 vegan: Community Ecology Package.

46. Janssen ABG, Teurlincx S, Beusen AHW, Huijbregts MAJ, Rost J, Schipper AM, Seelen LMS, Mooij WM, Janse JH. 2019 PCLake+: A process-based ecological model to assess the trophic state of stratified and non-stratified freshwater lakes worldwide. *Ecol. Modell.* **396**, 23–32. (doi:10.1016/j.ecolmodel.2019.01.006)

47. Wang R, Dearing JA, Langdon PG, Zhang E, Yang X, Dakos V, Scheffer M. 2012 Flickering gives early warning signals of a critical transition to a eutrophic lake state.

Nature **492**, 419–22. (doi:10.1038/nature11655)

48. Hall R, Smol J. 1999 Diatoms as indicators of lake eutrophication. In *The Diatoms: Applications for the Environmental and Earth Sciences* (eds EF Stoermer, JP Smol), pp. 128–168. Cambridge, UK: Cambridge University Press.

49. Dixit SS, Smol JP, Kingston JC, Charles DF. 1992 Diatoms: Powerful Indicators of Environmental Change. *Environ. Sci. Technol.* **26**, 22–33. (doi:10.1021/es00025a002)

50. Suzuki K, Yoshida K, Nakanishi Y, Fukuda S. 2017 An equation-free method reveals the ecological interaction networks within complex microbial ecosystems. *Methods Ecol. Evol.* **8**, 1774–1785. (doi:10.1111/2041-210X.12814)

51. Xiao Y, Angulo MT, Friedman J, Waldor MK, Weiss ST, Liu Y-Y. 2017 Mapping the ecological networks of microbial communities. *Nat. Commun.* **8**, 2042. (doi:10.1038/s41467-017-02090-2)

52. Levine JM, Bascompte J, Adler PB, Allesina S. 2017 Beyond pairwise mechanisms of species coexistence in complex communities. *Nature* **546**, 56–64. (doi:10.1038/nature22898)

53. Cao H-T, Gibson TE, Bashan A, Liu Y-Y. 2016 Inferring human microbial dynamics from temporal metagenomics data: Pitfalls and lessons. *BioEssays* **39**, 1600188. (doi:10.1002/bies.201600188)

54. Neutel A-M, Thorne MAS. 2016 Linking saturation, stability and sustainability in food webs with observed equilibrium structure. *Theor. Ecol.* **9**, 73–81. (doi:10.1007/s12080-015-0270-z)

55. Gunderson LH. 2000 Ecological Resilience—In Theory and Application. *Annu. Rev. Ecol. Syst.* **31**, 425–439. (doi:10.1146/annurev.ecolsys.31.1.425)