Network-based metrics of ecological memory and resilience in lake ecosystems

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Abstract

Some ecosystems undergo abrupt transitions to a new regime after passing a tipping point in an exogenous stressor, for example lakes shifting from a clear to turbid 'eutrophic' state in response to nutrient-enrichment. Metrics-based resilience indicators have been developed as early warning signals of these shifts but have not always been reliable. Alternative approaches focus on changes in the structure and composition of an ecosystem, which can require long-term food-web observations that are typically beyond the scope of monitoring. Here we prototype a network-based algorithm for estimating ecosystem resilience, which reconstructs past ecological networks solely from palaeoecological abundance data. Resilience is estimated using local stability analysis, and eco-net energy: a neural network-based proxy for 'ecological memory'. We test the algorithm on modelled (PCLake+) and empirical (lake Erhai) data. The metrics identify increasing diatom community instability during eutrophication in both cases, with eco-net energy revealing complex eco-memory dynamics. The concept of ecological memory opens a new dimension for understanding ecosystem resilience and regime shifts; further work is required to fully explore its drivers and implications.

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

1. Background

The potential for stressed ecosystems to tip abruptly into a new regime has led to a proliferation of metrics attempting to quantify ecosystem resilience [1–10]. Lake eutrophication is a well-studied example of a regime shift, often with evidence of alternative stable states and 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 to clear conditions often requiring nutrient levels reduced far below the original threshold [13]. Prior to tipping, the ecosystem experiences declining resilience, defined here as the weakening of negative relative to positive feedbacks resulting in greater sensitivity to small shocks [16]. Attempts to develop resilience indicators broadly fall into three approaches: time-series metrics, compositional analysis, and network-based.

Many resilience indicators test for ‘critical slowing down’: a slowing recovery rate from perturbations and increasing variability, which can be detected in various environmental time-series [4–10]. These time-series metrics have had inconsistent success, however, as early-warning signals (EWS) of tipping points in freshwater [17] and other ecosystems [18–21]. A key methodological issue is the need for prior knowledge of one response variable that captures the dynamics of the whole system. Other limitations include possible false positives or negatives (where EWS indicate an impending transition which never occurs, or is absent prior to a known transition), and sensitivity to subjective time-series analysis parameter choices [7,22,23]. These limitations are partially rectified by using multiple sensitivity-tested metrics as generic resilience indicators rather than as EWS of specific critical transitions [16,24]. Palaeorecords present additional problems, with variable temporal resolution from changing accumulation rates or compaction making robust time-series analysis challenging [25,26].

As an alternative to metric-based EWS, analysis of ecosystem composition seeks to detect changes in community functional dynamics without having to select or understand the full trophic ecology of any one species. To this end Doncaster et al. [27] quantified the compositional disorder of diatoms and chironomids from sediment cores in three Chinese lakes, where low disorder signifies highly-nested sequential compositions. Several decades prior to a critical transition, the correlation of disorder with biodiversity becomes negative and strengthens towards the tipping point. Theory and simulations suggested that nutrient loading shifted competitive balance from 'weedy' (weakly competitive, fast-replicating) towards 'keystone' (strongly competitive, slow-replicating) species. This correlative approach avoids issues of variable temporal resolution, but the link with ecosystem resilience is indirect and the competition dynamics remain hypothetical. Another recent composition-based method identified negative skewness in nodal degree of diatoms as a response to increasing nutrient input into Chinese lake ecosystems [28], which is compatible with rising keystone dominance with exogenous stress.

Network-based approaches perform local stability analysis on reconstructions of the lake food-webs. Kuiper et al. [29] showed that food-web data in the form of material flux descriptions can be used to reconstruct the interaction strengths between different species, which correspond to the interaction coefficients of a Lotka-Volterra ecosystem model (Figure 1a). This is equivalent to a dynamical system's Jacobian matrix, which is considered stable if the real part of the Jacobian's eigenvalues remain negative (representing net-negative feedbacks) [29–31]. Given food-web measurements, the food-web's local stability can be estimated from the intraspecific interaction strengths, and is closely related to the Jacobian's dominant eigenvalue (λ_d) [29,32–34]. λ_d increases with post-perturbation recovery times from weakened net-negative feedbacks, and so tracks ecosystem resilience. This approach enabled destabilising food-web reorganisations prior to eutrophication to be tracked in the PCLake model [29].

Although network-based methods depends less on temporal resolution than time-series analysis [29] and avoids reliance on a single variable, it requires gathering detailed food-web data at regular intervals during eutrophication, a laborious [35] and often unmanageable task for real-world lakes. Nevertheless, many lakes have palaeoecological records of species abundances obtained from sediment cores. If past ecosystem interactions can be reconstructed from this data, it becomes possible to estimate past changes in ecosystem resilience. Here we prototype and test an algorithm in R [36] for reconstructing ecological networks (eco-nets) from palaeoecological data using network inference [37–40]. This technique for characterising interspecific interactions comes from microbial metagenomics, where it provides an alternative to the unreliable proxy of relative abundance correlations. Network inference instead uses multilinear regression to infer the interaction matrix of a discrete-time Lotka-Volterra ecosystem model from abundance data (Figure 1a), with nodes representing individual species or functional groups and edges their interactions, and is less dependent on regular temporal resolution [38].

We then explore ecosystem resilience using two different approaches. Firstly, we perform local stability analysis on the inferred interaction matrix with a rolling temporal window, in order to track changes in λ_d. We test this on two different datasets of eutrophication-induced regime shifts: output from a commonly-used lake ecosystem model (PCLake+) for a hypothetical lake on a whole-ecosystem level, and empirical community-level data from lake Erhai where a critical transition was observed in 2001. For comparison, we also calculate time-series metrics (TSMs: AR1, standard deviation (SD), skewness, and kurtosis), biodiversity, and for empirical data sequential disorder-biodiversity correlation.

Secondly, we develop a novel neural network-based method of resilience analysis. Analyses of Lotka-Volterra systems demonstrate how an ecosystem can retain a distributed 'memory' of past states as a result of a process akin to unsupervised Hebbian learning in a neural network [41,42]. In Hopfield Networks, frequent correlations between neurones (nodes) lead to an increase in their connection strength (edges) – a process described colloquially as "*neurons that fire together, wire together*" [43–46]. Over time this allows the emergence of distributive associative memory of training input that can be recovered when given degraded input. Power et al. [41] proposed that eco-nets experience similar dynamics, with species (nodes) that frequently co-occur developing stronger interactions (edges), allowing emergence of a distributed associative "ecological memory" (eco-memory) of past environmental forcing (training input) that acts as a stable attractor (Figure 1b). Although memory strength has no direct metric, one can calculate its energy, which is minimised at metastable points. We estimate eco-net energy, E_N, by treating the interaction matrix reconstructed by our network-inference algorithm as the weight matrix [41] of a continuous Hopfield Network [43–46]. We expect low E_N for eco-nets that have 'learnt' from stable environmental conditions, and higher E_N when destabilisation shifts the eco-net away from its learned state. To test these expectations, we calculate E_N for both test-cases and compare to other resilience metrics. Detailed methods and scripts are available in the Supplementary Material.

2. Results and Discussion

2.1. PCLake+

We first apply the algorithm to output from a default setup of PCLake+ [47], an extension of the widely-used PCLake model of lake eutrophication, as a test-bed with well-known dynamics and drivers for generating realistic artificial data (with 14 functional groups representing the whole ecosystem, and phosphorus input increased along its nonlinear but non-hysteretic load-response curve to induce eutrophication- see Supplementary Material). The impact of nutrient enrichment is clearly visible in lake conditions, biodiversity, local stability (λ_d), and eco-net energy (E_N) as three distinct phases (Figure 2a-d, left). In phase 1, λ_d increases shortly after input begins, in conjunction with declining E_N interrupted by a temporary peak at ~50-55 years ago (ya). However, following a plateau in both E_N and λ_d in phase 2, λ_d re-stabilises after a second peak (~35 ya) and E_N strongly decreases. E_N begins to recover following the transition, while λ_d remains moderately high relative to pre-eutrophication levels. This pattern indicates complex eco-memory dynamics starting decades before the transition, with destabilisation away from memorised conditions (increasing λ_d, i.e. weakened net-negative feedbacks) accompanied and followed by a multi-phase "relearning" process (decreasing E_N) as the eco-net adapts and restructures (increasing biodiversity) in response to new conditions. Increasing the accumulation rate does not alter the overall signal but reduces the resolution of deeper features (Supplementary Figure S1), indicating this methodology is not overly sensitive to temporal resolution.

2.2. Lake Erhai

Lake Erhai in south-western China has undergone eutrophication after decades of nutrient-enrichment, similar to our PCLake+ scenario. Data consist of relative diatom abundances sampled at regular radioisotope-dated intervals down sediment cores [27,48]. We focus on diatoms as they are well-preserved and belong to the same trophic level, but as they form only one functional group this means that unlike PCLake+ the whole ecosystem is not directly analysed. However, we posit that the community-level diatom λ_d acts as a proxy for whole-ecosystem resilience, as diatoms play a key role in the trophic loops involved in eutrophication [29] and are ecologically sensitive to water quality [49,50].

Although real-world data exhibits more complexity than model results, we can observe similar phases of activity to PCLake+ (Figure 2a-d, right). Phase 1 begins with nutrient-enrichment starting ~60-50 ya [48]. This is reflected by a shift to negative disorder-biodiversity correlation indicative of destabilisation, declining E_N, and culminates with a λ_d peak. In phase 2 both λ_d and E_N plateau prior to the observed transition at ~8 ya, after which E_N recovers, λ_d slightly drops, biodiversity sharply drops, and disorder-biodiversity correlation recovers. These patterns are broadly similar to the PCLake+ results, with phase 1 marked by declining E_N and increasing λ_d, suggesting the eco-net destabilising and relearning decades before the transition, and a recovery in E_N and stable λ_d post-transition. This similarity suggests diatoms can act as a community-level proxy for the whole lake ecosystem. However, the λ_d and E_N trends are not as clear during phase 1 as for PCLake+, suggesting that the data are not sufficiently resolved to fully capture this phase (unlike disorder-biodiversity correlation). There is also no post-transition E_N decline in lake Erhai, which may result from slower forcing (Supplementary Figure S2) or has yet to be observed. Biodiversity increases during destabilisation in both cases, but only during phase 2 in lake Erhai.

2.3. Time-series metrics comparison

TSM are shown for comparison as a legacy method. As a consistently sampled model lake with constant temporal resolution, PCLake+ provides idealised conditions for observing TSM during eutrophication (Figure 2e). During phase 1 AR1, skewness, and kurtosis rapidly peak and SD begins to steadily increase, whilst in phase 2 all metrics apart from SD decline. Lake Erhai shows only early peaks in skewness and kurtosis at ~92-75 ya before phase 1, which may represent an unknown precursor event. Following this, SD steadily increases while kurtosis decreases, AR1 and skewness slightly increase during phase 1, and in phase 2 AR1 stabilises while skewness declines. Both examples suggest SD consistently increases during destabilisation, but variable temporal resolution obscures this in real-world data (Supplementary Figure S1). However, due to the methodological limitations described earlier, TSM are not considered robust for lake Erhai without further sensitivity and significance testing.

3. Further Development

Several methodological limitations can be improved with future development. The algorithm works best with long, minimally-sparse datasets that resolve equilibrium population dynamics, but many palaeorecords do not meet these requirements. Further development will improve the algorithm's capacity to analyse short or sparse datasets using innovative techniques from metagenomic network inference [38]. We also assume these ecosystems fit a generalised Lotka-Volterra model, in which all abundance changes are caused by linear pairwise interspecific interactions and other processes simplified into a broad noise term. However, nonlinear interactions are expected in some ecosystems [37,51–55] and potentially allow a better representation of multiple alternative stable states [56,57], but are harder to parameterise. Future work will assess the feasibility of allowing nonlinear functional responses. The assumed model includes only biotic elements, with life-environment interactions implicit. Incorporating life-environment feedbacks explicitly would allow more realistic feedback loops critical to resilience to emerge (such as anoxia-driven phosphorus release from sediment), but the eco-net cannot simply be extended to include abiotic elements as the environment is assumed to be its training input. Possible solutions include neural networks that allow training input that is dynamic (e.g. continuous-time recurrent neural networks) and interacts with the eco-net (e.g. multi-layer or adversarial networks).

4. Conclusions

With refinement, our findings suggest that network-based methods can allow changes in past ecosystem resilience to be reconstructed from palaeoecological abundance datasets from various settings, and are less sensitive to data quality than time-series metrics. “Ecological memory” has only been applied to a simplified ecosystem model before now [41,42], but the development here of eco-net energy allows us to explore eco-memory in more realistic models and empirical data for the first time. Eco-memory opens a new dimension for understanding ecosystem resilience, with the formation of eco-memory potentially increasing resilience by allowing past stable eco-network 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 ecosystem resilience.

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Figures

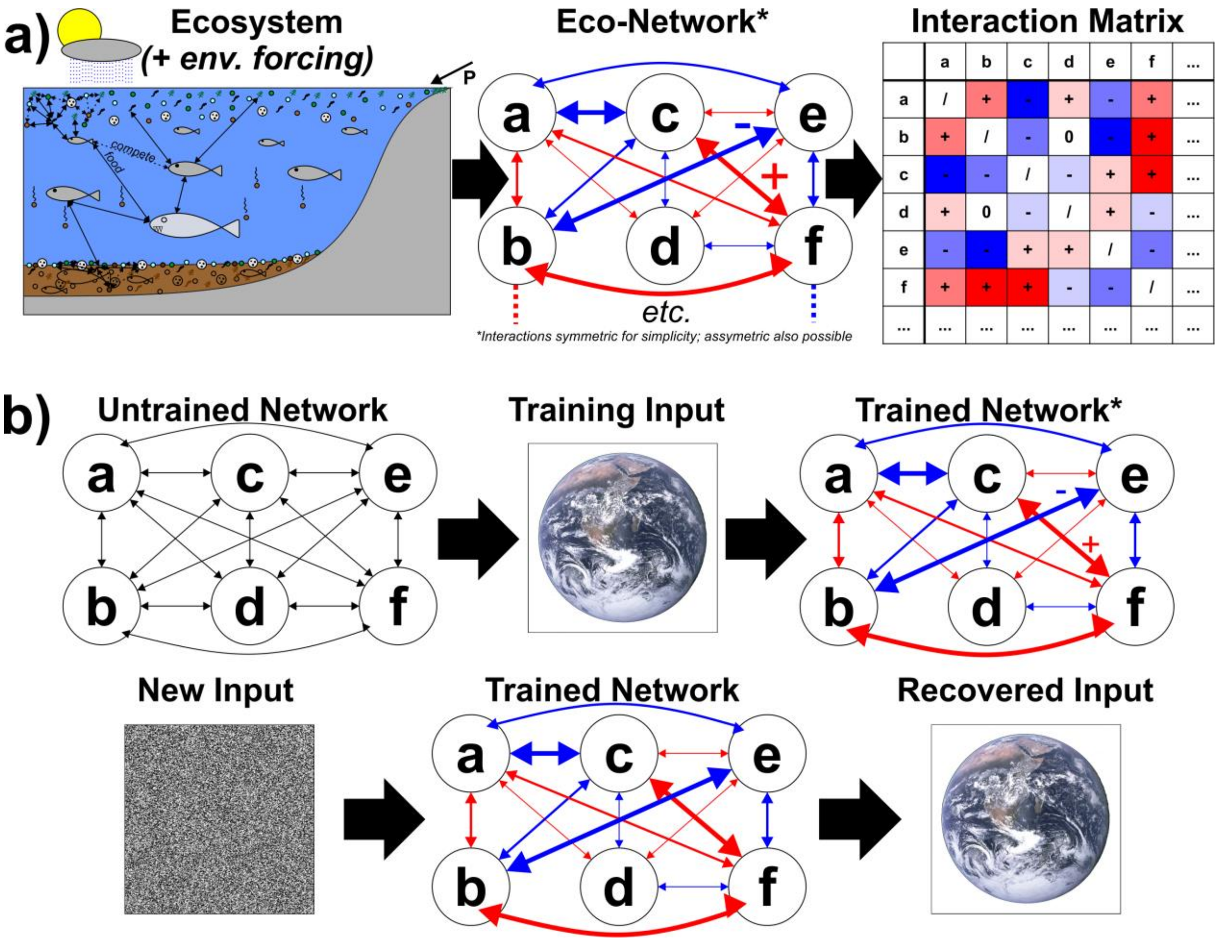
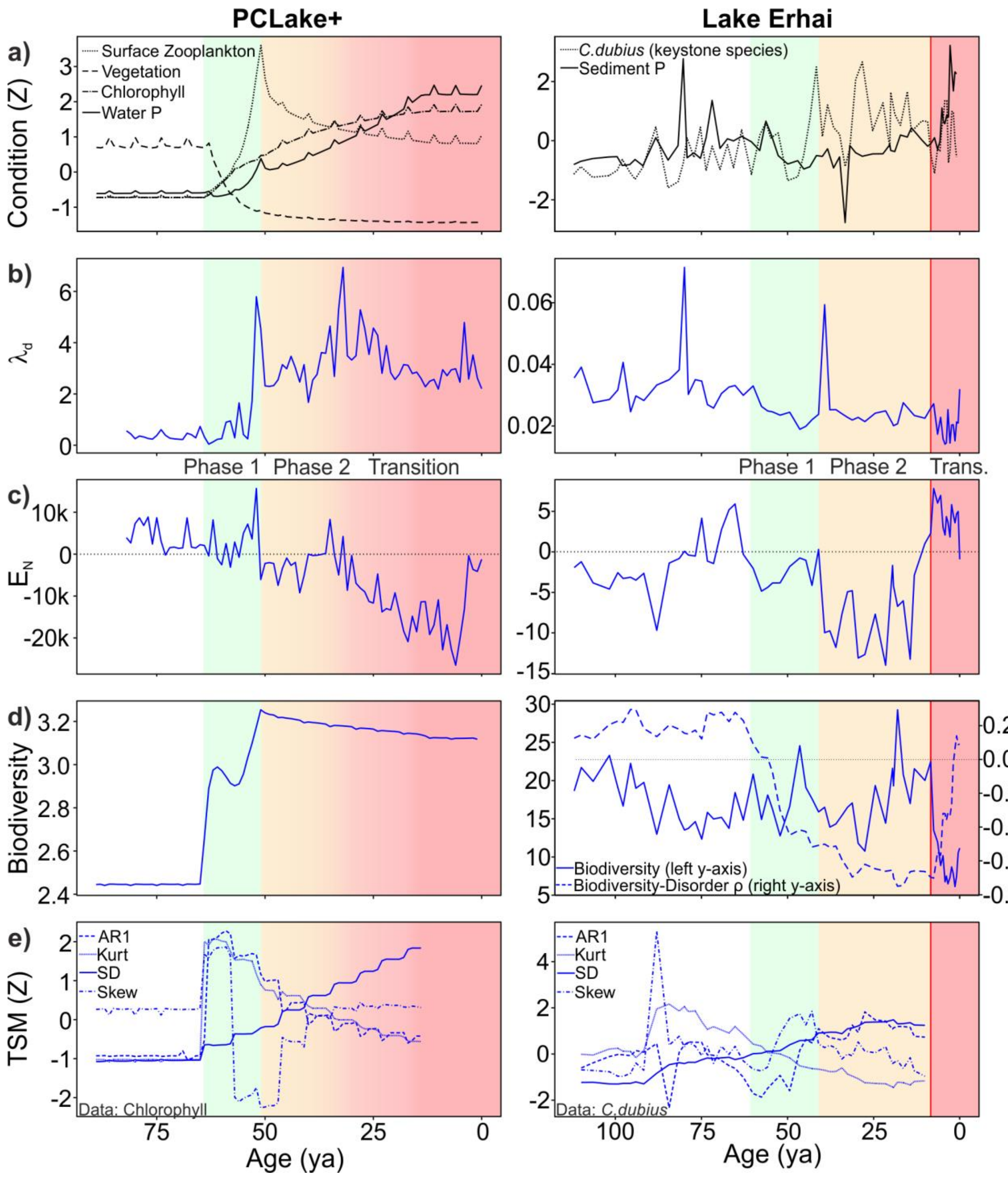


Figure 1: Schematics illustrating: (a) how ecosystem interactions (left) are represented as an eco-network (middle –lettered nodes represent individual species or functional groups, and edges their interactions), the structure of which forms an interaction matrix (right) suitable for resilience analysis (N.B. only symmetric interactions are shown; asymmetric interactions are common); and b) how networks can be trained using input (i.e. exogenous drivers; the Earth representing environmental forcing) which can be recovered when given new input (i.e. new drivers; white noise representing random forcing).



221

Figure 2: Results for PCLake+ (left) and lake Erhai (right), showing: (a) lake conditions (normalised concentrations/abundances – vegetation-zooplankton shift and increased chlorophyll in PCLake+ and increased keystone abundance in Erhai indicates eutrophication), (b) local instability λ_d, (c) eco-net energy E_N, (d) biodiversity (inverse Simpson index) and (Erhai only) disorder-biodiversity correlation [27], and (e) normalised time-series metrics (TSM; for comparison only). Interpreted transition phases (1=green box, initial destabilisation; 2=orange, pre-transition) and observed regime shifts (red box; gradient indicates smooth non-hysteretic transition, vertical line indicates critical transition) are marked.

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