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Quantifying change in pelagic plankton network stability and topology based on empirical long-term data

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ABSTRACT

Over the last 34 years, Lake Müggelsee has experienced concurrent warming and nutrient reduction. While the effects of environmental change on single taxonomic or physical–chemical variables have been relatively well researched in isolation, understanding how environmental change propagates through the ecological network remains a major challenge. Capitalizing on the long-term monitoring program of the German Long-Term Ecosystem Research Network site Lake Müggelsee (1979-ongoing), we identified three time periods (1979–1995; 1996–2005; 2006–2013) which differed significantly in phytoplankton biomass and relative plankton community composition. Using multivariate first order autoregressive (MAR1) modeling on 13 pelagic plankton groups and four abiotic variables, we quantified interaction networks and indicators of stability and centrality for each period. Our results suggested that the Müggelsee network was bottom-up regulated in all periods and that stability increased over time. Moreover, in all three networks, non-trophic and indirect interactions appeared to be as commonly present as trophic and direct interactions. Using network centrality measures of betweenness and closeness, we identified keystone plankton groups and groups particularly responsive to environmental change based on variation in centrality ranks over time. Given a more comprehensive understanding of the interaction network at hand, MAR1 model-derived stability and centrality measures may potentially be used as integrated ecological indicators to monitor changes in stability of lake ecosystems and to identify particularly vulnerable components of the network.

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1. Introduction

Lake ecosystems are considered important sentinels of environmental change as they integrate alterations in the catchment and atmosphere (Adrian et al., 2009; Williamson et al., 2009). Key response variables acting as sentinel variables include a wide range of physical, chemical and biological indicators that are sensitive to climate and land-use change (Adrian et al., 2006, 2009). While the effects of anthropogenic pressure on key response variables are reasonably well understood in isolation, it remains a challenge to predict how global change affects the interactions among such variables and, thus, the ecological network of a lake and its stability. The lack of ground-truthed data on species interactions and community network response to stress has been identified as major gap in the bio-monitoring sciences (Gray et al., 2014). To better understand and predict how global change will affect community structure and stability and hence also associated ecosystem processes, it is necessary to assess how ecological networks change over time and under pressure (McMeans et al., 2015).

Here, we make use of the long-term research program installed at the German Long-Term Ecosystem Research Network (LTER-D) site Müggelsee (Germany) to explore how changes in the phyto- and zooplankton biomass and community composition due to anthropogenic pressure affect the structure and stability of the pelagic interaction network utilizing multivariate first order autoregressive modeling (MAR1) and ecological network analysis. MAR1 modeling (Ives et al., 2003) allows the identification and quantification of network interactions and the derivation of stability metrics of ecological networks from long-term data (Hampton et al., 2013; Ives et al., 1999; Scheef et al., 2013). The resulting interaction matrix can also be used to inform ecological network analysis. MAR1 models have predominantly been used to elucidate trophic networks in both freshwater and marine systems, likely because short generation times of plankton allow capturing

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Table 1
Ecological indicators used in this study to describe changes in the Müggelsee network stability and topology.

Ecological indicator	Description	Ecological significance	Key references
Variance	The lower the stationary distribution variance in relation to the environmental variance, the more stable the system. The determinant of the interaction matrix ('DetB') shows how much group (or species) interactions increase the variance of the stationary distribution relative to that of the environmental noise (i.e. stability increases with decreasing DetB).	Unstable systems with low resilience (slow return to its stationary distribution) and low resistance (high reactivity) tend to fluctuate more strongly as species interactions amplify the system response to environmental variation.	Ives et al. (2003)
Resilience	The dominant eigenvalue of the Kronecker product B⊗B ('maxeigen KrB') limits the return rate of the community to its stationary distribution after a perturbation. Resilience increases as return rate increases (i.e. 'maxeigen KrB' decreases)	More stable systems return to their 'equilibrium' state more quickly after a perturbation (e.g. heat waves, storms etc.) than less stable ones.	Ives et al. (2003)
Reactivity	The maximum eigenvalue of the interaction matrix B ('maxeigen BxB') represents the potential maximal reaction strength of a system to a perturbation. Resistance increases as reactivity decreases.	Less stable systems show larger deviations from the stationary distribution after perturbations.	Ives et al. (2003)
Closeness centrality	This indicator emphasizes the distance from each vertex to every other vertex in the network. A vertex with direct connections to every other vertex in the network will have a high closeness value, whereas a vertex which is connected to other vertices through many intermediaries will have a low closeness value.	Closeness centrality focuses on the strength of influence over the entire network. Changes in organisms with high closeness centrality values influence the network dynamics more than changes in organisms with lower values.	Jordán et al. (2008), Vasas and Jordán (2006)
Betweenness centrality	This indicator is derived from the number of shortest paths passing through a given vertex (intermediary). To calculate betweenness centrality, all the shortest paths between any two vertices in the network are found and then the number of these shortest paths that go through each vertex is counted.	Groups with high betweenness centrality are not necessarily connected directly to all other vertices. High betweenness groups are considered important because they provide (the only) link between otherwise unconnected network vertices.	Jordán et al. (2008), Vasas and Jordán (2006)

hundreds of generations' worth of dynamics within few years. The method has been implemented to assess the food-web structure in deep lakes under changing climate and eutrophication (Hampton et al., 2006, 2008), the effect of predation on phytoplankton and ciliate population variability (Huber and Gaedke, 2006) and on disease transmission (Duffy, 2007), to appraise the response of pelagic networks to changes in fish predation pressure (Beisner et al., 2003; Ives et al., 1999) and to carbon and nutrient manipulations (Klug and Cottingham, 2001). As MAR1 models provide quantitative estimates of interaction strengths they allow the identification of direct and strong links but also of indirect "long and weak" links (Jordán, 2009).

Network stability indicators derived from MAR1 models are based on measurements of deviation from an "equilibrium" state, here the stationary distribution of a community under environmental noise. The stability indicators are expressed as variance of the stationary distribution in relation to the environmental variance (hereafter "variance"), return rate after perturbation ("resilience") and short term response to perturbation ("reactivity"), for a detailed derivation see Ives et al. (2003), for a short description see Table 1. These stability indicators are directly comparable across systems as they are not affected by the magnitude of fluctuations in system variables (Hampton et al., 2013) and hence also allow tracking stability of ecosystems over time. Most ecological networks in the literature describe networks aggregated over time or space and thus do not provide information about the variability in stability of networks in evolving natural systems (but see Francis et al., 2014). The application of MAR1 models and their derived indicators on sequential time periods can improve our assessment and predictive power on the response and stability of ecological networks under anthropogenic pressure. Tracking the variability in interaction strength among keystone groups in a network, or the overall stability of the network over time may even serve as a leading indicator for ecosystem resilience and as advance warning for regime shifts (Francis et al., 2014; Kuiper et al., 2015).

The quantitative interaction matrix resulting from MAR1 models can be passed on to classic ecological network analysis to assess network properties such as closeness- and betweenness centrality. The centrality indicators can identify vertices (species, or groups of species) that are either particularly well-connected or that connect otherwise disconnected compartments of the network and therefore take a keystone position in the network (Jordán et al., 2008). Changes in the position and dynamics of keystone species or groups are likely to cascade through the network as these groups are linked to many other groups in the network (Vasas and Jordán, 2006). Comparison of successive time period networks also allows tracking changes in the centrality scores and therefore the identification of groups that are particularly sensitive to environmental changes over time (Jordán and Osváth, 2009).

The aim of this study is to explore how long-term changes in lake nutrient status and a warming trend affected the internal trophic (bottom up or top down) and non-trophic (competition, facilitation or indirect effects) interactions of the pelagic plankton as well as overall network stability and topology. We identified three periods between 1979 and 2013 which differed in phytoplankton biomass (period 1 versus periods 2 and 3) and plankton community composition (periods 2 and 3). These periods were analyzed for their interaction networks properties, including stability indicators and measures of network centrality. Our study is of exploratory nature, making use of the Müggelsee long-term dataset to assess interactions among pelagic plankton groups based on their temporal autocorrelation and is geared toward revealing potentially overlooked keystone groups and key interactions in the plankton network as well as changes in network stability and centrality measures over time.

2. Methods

2.1. Study site

Lake Müggelsee is a shallow (mean depth 4.9 m, max depth 8 m), eutrophic lake situated southeast of the city of Berlin (Germany, 52°26′ N, 13°39′ E). The lake is polymictic and usually fully mixed due to the wind fetch of its relatively large surface area of ~750 ha (Driescher et al., 1993). The River Spree enters the lake from southeast and the outflow is situated in the north-west of the lake. This results in an average retention time of about 6–8 weeks (Köhler

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