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This monograph shall inform you about up to date methodologies and recent results in landscape research. It is intended as a guide for researchers, teachers, students, decision makers, stakeholders interested in the topic of landscape science and related disciplines. It provides information basis for decision makers at various levels, from local up to international decision bodies, representing the top level of landscape science in a very short form.

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Chapter III/64: QUANTIFYING INTERACTION NETWORKS AND STABILITY PROPERTIES OF PLANKTON FOOD WEBS USING MULTIVARIATE FIRST ORDER AUTOREGRESSIVE MODELLING

Глава III/64: Количественное определение взаимодействия и свойств устойчивости пищевых цепей планктона с использованием многовариантного авторегрессионного моделирования первого порядка

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ABSTRACT. Lakes and reservoirs have been identified as sentinels of global change as they integrate changes in the surrounding landscape. While univariate indicator variables are relatively well assessed, the lack of knowledge on temporal changes in species interactions under pressure has been identified as a major gap in the bio-monitoring sciences. Multivariate autoregressive models can be used to assess direction and strength of both direct and indirect interactions in complex communities over time. This model framework also allows calculation of network stability properties (variance, resilience and reactivity). Moreover, the interaction matrix can be further analyzed for classical network structure properties (closeness- and betweenness centrality). These measures are useful indicators of changes in ecosystem stability and help identify biotic keystone groups and/or groups of species that are particularly vulnerable to changes in the landscape.

Резюме. Озера и водохранилища являются стражами глобальных изменений, поскольку они интегрируют в себе изменения в окружающем ландшафте. В то время как одномерные индикаторные переменные относительно хорошо изучены, недостаток знаний об изменениях в видовом взаимодействии под антропогенным давлением является большим пробелом в науках о биологическом мониторинге. Многомерные авторегрессионные модели могут быть использованы для оценки динамики направления и силы как прямых, так и косвенных взаимодействий в сложных сообществах. Эта модельная структура также позволяет рассчитывать свойства устойчивости сети (дисперсия, устойчивость и реактивность). Более того, матрица взаимодействия может быть дополнительно проанализирована для свойств классической структуры сети (центральность по близости и посредничеству). Эти меры являются важными индикаторами изменений в стабильности экосистем и помогают определить биотические ключевые группы и/или группы видов, которые особенно уязвимы к изменениям ландшафта.

KEYWORDS: community stability, interaction networks, long-term research, network centrality
Ключевые слова: стабильность сообщества, сети взаимодействия, долгосрочные исследования, сетевая центральность

INTRODUCTION

Constituting the lowest points in the landscape, lakes and reservoirs integrate changes in the catchment and atmosphere, and can be regarded as sentinels of past and current environmental changes across regions [1,2]. Physical, chemical and biological variables that are sensitive to climate and land-use changes have been identified as sentinel indicators, ranging from e.g., ice phenology to dissolved nutrient concentrations to community composition [1,2]. Long-term monitoring data for such sentinel indicators are necessary to extract information as to how aquatic landscapes respond to a rapidly changing world; for example, through the assessment of decadal temperature changes in a global set of lakes [3].

While temporal changes in physical and chemical variables in lakes and reservoirs have been relatively well explored, especially during growing seasons, less is known as to how plankton interactions, community composition and network topography change over time and under environmental pressure [4]. This lack of direct, observational data on species interactions and community network response to stress has been identified as a major gap in the bio-monitoring sciences [5]. When long-term empirical data are available, multivariate first order autoregressive, or MAR(1), models can be used to quantify the direction and strength of species interactions and community stability properties in complex communities (reviewed by [6]). Moreover, the resulting interaction matrix can help characterize network structure and identify keystone species or groups [7]. These stability and network structure properties of MAR(1) models provide useful biological indicators that can be applied for e.g. conservation management and underlines the general importance of the maintenance of well-designed long term monitoring programs.

MAR(1) models have predominantly been used to asses interaction networks in freshwater and marine ecosystems, likely because the short generation time of plankton allows for the assessment of many generations' worth of dynamics over comparably few years. The model framework has been used to analyze biotic and abiotic drivers of community dynamics [6,8]. Several studies have explored the effect fish predation pressure on lower trophic levels and assessed the direct and indirect pathways through which changes in predation pressure cascaded through interaction networks [9,10]. MAR(1) models have also been used to assess the role of predation pressure on phytoplankton and ciliate population dynamics [11] and on disease transmission [12], the effects of biotic invasions on pelagic food web structure [13], the effects of climate change and eutrophication on the structure of plankton communities and food webs in lakes [14-16], the effects of carbon and nutrient manipulations on pelagic networks [17], and the interactive effects of environmental drivers on species interactions [18]. MAR(1) models have also allowed to uncover interactions that were previously overlooked or underestimated in their importance to shape interaction networks [7,19].

MAR(1) MODEL APPLICATION

An comprehensive guide for data preparation and analysis steps, including an introduction to the R package "MAR1" has been published by Scheef and coauthors [20]. In a nutshell, to avoid over-parameterization of the MAR(1) models, it may be necessary to group plankton species data, whereby the choice of grouping depends on the specific aims of a study. Biotic groups and environmental variables can then be categorized either as variates or covariates for inclusion in the MAR(1) model [21]. Variables that can affect their own dynamics and/or the dynamics of other groups are considered as variates. Covariates are variables that can affect the dynamics of variates but are unlikely to be influenced by themselves. These covariates are generally abiotic variables such as temperature or relatively static biotics such as fish predation pressure. Seasonality may also need to be accounted for; for example, by adding a time 'dummy' variable as covariate [9]. The choice of time intervals to which the data are aggregated can influence the outcome of the model. Longer intervals (e.g., monthly intervals) have been shown to efficiently capture time-lagged responses of biotic interactions in lake networks, but may also increase the chance to capture signals of indirect effects [19]. Data can be log-transformed to linearize non-linear relationships between groups (as many trophic relationships are non-linear; [9]), and z-scoring allows direct comparison of the interaction coefficients among groups [20]. The MAR(1) model needs to be initiated by prior characterization of all potential interactions. Often, the choice is to allow only biologically plausible interactions [21], with or without restrictions as to the sign of interactions (negative or positive interactions). However, depending on the research question, it may also be of interest to allow the full suite of potential interactions to explore all potential outcomes [20]; however, this will lead to a higher number of parameters fitted to the model. Therefore, care should be taken to allow and/or restrict interactions based on ***a priori*** knowledge of a given system.

The principle of MAR(1) models is analogous to most autoregressive models: for a given time point (t), the biomass of each variate is predicted by multiple linear regression, using data of all other variates and covariates from the previous time point as predictors (for details, see [9,21]). Hence, MAR(1) models assume linear relationships, often approximated by linearizing input data. Advances in MAR(1) models include the development of the moving window MAR(1) (mwMAR), which quantifies the interaction network on a moving data window and allows tracking changes in interaction strength over time [22]. Other model frameworks have been developed to allow the analysis of nonlinear relationships and changes in attractor directly such as S-maps [23].

Network stability measures. Network stability indicators derived from MAR1 models are based on measurements relative to deviations from an "equilibrium" state, i.e., the stationary distribution of a community under environmental noise. The stability indicators (Figure 1) are expressed as (i) variance, (ii) return rate, and (iii) reactivity (for a detailed derivation, see 21). 'Variance' (Figure 1a) is expressed as the ratio of stationary distribution variance to environmental variance. Unstable systems with low resilience (i.e., slow return to its stationary distribution) and low resistance (i.e., high reactivity) tend to fluctuate more strongly as species interactions amplify the system response to environmental variation [21]. 'Resilience' (Figure 1b) is the return rate to 'equilibrium' after a perturbation (e.g., heat wave). Resilience increases as return rate increases [21]. 'Reactivity' (Figure 1c) describes the potential maximal reaction strength of a system to a perturbation. Unstable systems exhibit larger deviations from the stationary distribution after perturbations. Resistance increases as reactivity decreases [21]. These stability indicators are directly comparable across systems, as they are not affected by the magnitude of fluctuations in system variables [6] and thereby allow to assess the stability of ecosystems over time or space.

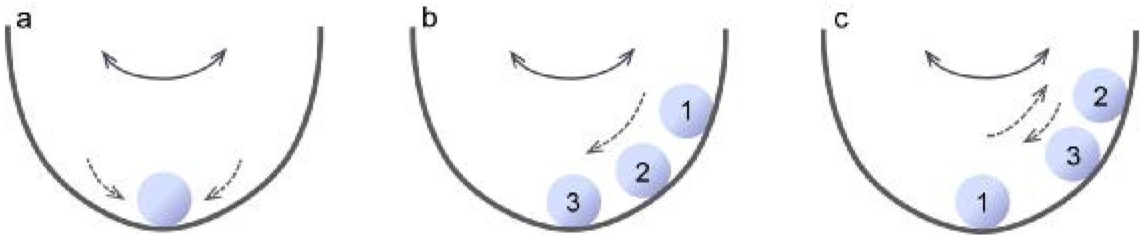

Figure1: Simplified balls in cup illustration of three stability measures modified from Figure 2 in Ives et al (21) for a) variance, b) return rate, and c) reactivity with a disturbance (solid arrows) and a stability measure response (dashed arrows). In unstable systems, variance (a) is higher as the ball spends more time away from the center, return rate (b) is lower as the force to return to the center is lower, and reactivity (c) is higher as the ball is moved further away from the center after a disturbance.

Network structure measures. The MAR(1) model interaction matrices can be used as a network analysis input to calculate network structure properties, quantifying the influence that every group exerts on the entire network. Betweenness and closeness centrality (Figure 2) can be used to identify keystone groups. However, this is based on the assumption that well-connected groups (i.e., strongly linked to multiple other groups) in the network are major interactors, and should therefore exert a greater influence on the structure and stability of the network than other groups [24,25]. Closeness centrality (Figure 2, yellow vertices) describes how strongly a change in one vertex influences the entire network. This indicator quantifies the distance of each vertex to every other vertex in the network. A vertex with a direct connection to every other vertex in the network has a high closeness value, whereas a vertex connected to other vertices through many intermediaries has a low closeness value [26]. Betweenness centrality (Figure 2, blue vertex) assesses vertices that connect separated modules of the network (e.g., sub-networks). This indicator is derived from the number of shortest paths passing through a given vertex (intermediary; [26]).

Advantages and disadvantages. MAR(1) models provide quantitative estimates of interaction strengths, enabling the identification of direct and strong links but also of indirect "long and weak" links [24]. While most models reported in the literature only allow biologically plausible interactions, MAR(1) models can be used to uncover previously unrecognized or overlooked interactions; hence the exclusion of, and restrictions (e.g., on the sign) of interactions should be considered with care. MAR(1)-based interaction coefficients represent maintained interactions (across seasons and years) among groups. Hence, interactions that are important for a short period per year, or those that are not consistent among years, tend to be eliminated during the model searching process. Applying MAR(1) to short time series can reduce the potential to capture the signal of environmental long-term change and render interaction coefficients more sensitive to stochastic variability. Moreover, the interpretation of interactions using MAR(1) needs to take into account that seemingly direct interactions could also result from indirect effects (e.g., consumers increasing nutrient cycling; [27]) or from an unobserved explanatory variable shared between groups.

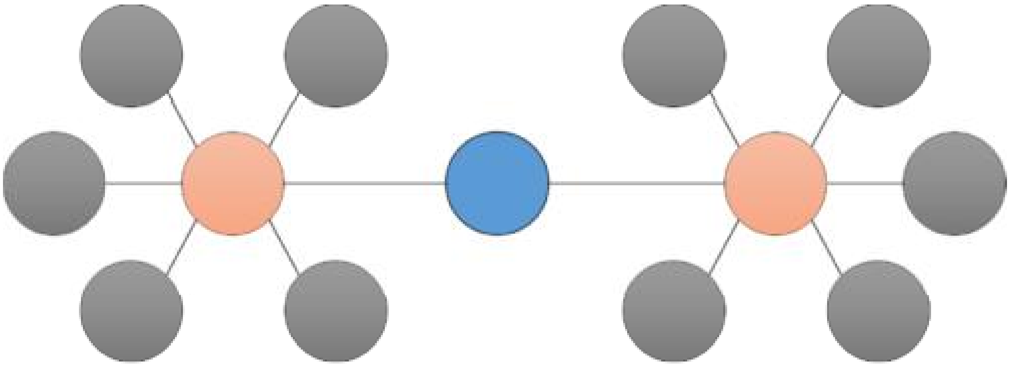

Figure 2: Simplified and idealized graphical illustration of a network structure with two sub-networks, including a visualization of network members having high betweenness (blue vertex) and closeness (yellow vertices) centrality values. The vertices can have different lengths and thickness representing the interactions strength between members; e.g., MAR(1) model interaction matrices.

CONCLUSIONS

1. The application of MAR(1) or mwMAR models can help better understand how the structure of interaction networks and the stability of ecological communities respond to anthropogenic pressures. Ultimately, the application of such model framework in biomonitoring programs can improve our ability to predict changes in aquatic landscapes.
2. MAR(1)-derived stability and centrality measures may be used as integrated ecological indicators in landscape research, with the aim of detecting changes in ecosystem stability (to prevent tipping points, for instance) and identifying particularly vulnerable components of the network.

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