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TECHNICAL ADVANCE

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Long-term warming destabilizes aquatic ecosystems through weakening biodiversity-mediated causal networks

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Abstract

Understanding how ecosystems will respond to climate changes requires unravelling the network of functional responses and feedbacks among biodiversity, physicochemical environments, and productivity. These ecosystem components not only change over time but also interact with each other. Therefore, investigation of individual relationships may give limited insights into their interdependencies and limit ability to predict future ecosystem states. We address this problem by analyzing long-term (16–39 years) time series data from 10 aquatic ecosystems and using convergent cross mapping (CCM) to quantify the causal networks linking phytoplankton species richness, biomass, and physicochemical factors. We determined that individual quantities (e.g., total species richness or nutrients) were not significant predictors of ecosystem stability (quantified as long-term fluctuation of phytoplankton biomass); rather, the integrated causal pathway in the ecosystem network, composed of the interactions among species richness, nutrient cycling, and phytoplankton biomass, was the best predictor of stability. Furthermore, systems that experienced

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stronger warming over time had both weakened causal interactions and larger fluctuations. Thus, rather than thinking in terms of separate factors, a more holistic network view, that causally links species richness and the other ecosystem components, is required to understand and predict climate impacts on the temporal stability of aquatic ecosystems.

KEYWORDS

biodiversity–ecosystem functioning, causal network, phytoplankton, stability, warming

1 | INTRODUCTION

Climate change has already begun to dramatically alter ecosystems (Walther et al., 2002), and there is growing concern about its ultimate effects on ecosystem health and resilience (Cardinale, Duffy, Gonzalez, Hooper, & Perrings, 2012; Fussmann, Schwarzmuller, Brose, Jousset, & Rall, 2014; Tilman, Reich, & Knops, 2006). However, the mechanisms underlying the impacts of climate change on ecosystem resilience remain unclear, with long-term predictions that can conflict with each other. For example, some studies suggest that increased temperatures will cause decreases in biodiversity (Urrutia-Cordero et al., 2017; Verbeek, Gall, Hillebrand, & Striebel, 2018) that will destabilize ecosystems (Hooper et al., 2005) and increase volatility in community biomass (Benincà, Dakos, Nes, Huisman, & Scheffer, 2011); in contrast, other evidence suggests that warming may stabilize ecosystems by altering species metabolism in ways that reduce the strength of interspecific interactions (Fussmann et al., 2014).

This lack of consensus arises in part because experimental studies investigate one causal mechanism at a time, such as the effect of biodiversity on total biomass (Giller et al., 2004; Steudel et al., 2012; Tilman, Isbell, & Cowles, 2014). Although this approach reveals how the key ecosystem functions (e.g., total biomass) respond to biodiversity changes, it does not easily accommodate the dependency of these responses on other factors (e.g., various environmental drivers) and is difficult to be extrapolated to large-scale manipulations of multiple interdependent processes due to mutual interactions or feedbacks (Hughes, Byrnes, Kimbro, & Stachowicz, 2007; Loreau, 2010). Analysis of observational data can sometimes better describe the statistical relationships between ecosystem properties such as species richness, total biomass (Grace et al., 2016), and stability (Ptacnik et al., 2008). However, these analyses often use linear correlative methods that are not designed for investigating the complex interactions and feedbacks in nonlinear dynamical systems, making it difficult to account for interactions and ecosystem properties that change with time (Deyle, May, Munch, & Sugihara, 2016; Sugihara et al., 2012). Therefore, an integrated, holistic, and dynamical perspective is required (Chapin III et al., 2000) to disentangle the complex impacts of climate warming on dynamical ecosystems (Dee et al., 2017; Snelgrove, Thrush, Wall, & Norkko, 2014).

We address this problem with a method specifically designed for quantifying causality network in nonlinear dynamical ecosystems, CCM (Sugihara et al., 2012). CCM is a causality analysis based on Takens' theorem for dynamical systems (Sauer, Yorke, & Casdagli, 1991; Takens, 1981), which infers the causal relationship among variables from their empirical time series (see Section 2). With CCM, we reconstructed the causal network among species richness, total biomass, and environmental variables using long-term monthly time series of phytoplankton and environmental variables from 10 aquatic ecosystems spanning a wide range of geography and habitats (Figure S1). The environmental variables consisted of nutrients and water temperature (Tables S1–S3). Following previous studies, we adopted chlorophyll-*a* concentration as a proxy for phytoplankton community biomass in aquatic systems (Cardinale, 2011; Lewandowska et al., 2016), and defined ecosystem stability as the temporal stability (1/coefficient of variation) of phytoplankton biomass (Narwani & Mazumder, 2012; Steiner, Long, Krumins, & Morin, 2005). Here, we focused on the stability of phytoplankton biomass, as phytoplankton represent the basis of the aquatic food web. We determined that the systems experiencing the strongest warming exhibited the lowest ecosystem stability (Figure 1). That is, long-term warming weakened the temporal stability of phytoplankton biomass. This long-term effect of warming was also observed in a global ocean dataset (Figure S2). We noticed that the systems Lake Mendota and Monona (Me and Mo) were leveraged, influential observations for the analysis in Figure 1; nevertheless, when global ocean data were included, a general negative relationship between ecosystem stability and warming rate was revealed (Figure S2). To further test the robustness of the negative warming impacts revealed in Figure 1, we performed a series of robust analyses, including building more reliable confidence interval from bootstrapped samples (Figure S3a), examining influences of data removals on model fittings (Figure S3b), and using an alternative warming measure derived from nonaveraged water temperature data (Figure S3c,d). Based on these analyses, we inferred that there was a general negative relationship between warming rate and ecosystem stability. Then, to better understand the mechanisms behind this pattern, we herein provided a novel framework using CCM to investigate which causal links are associated with stability across various aquatic systems.

Causal interaction links inferred from CCM were denoted as $X \rightarrow Y$ for a cause X and an effect Y. A chain of connected links is a *causal*

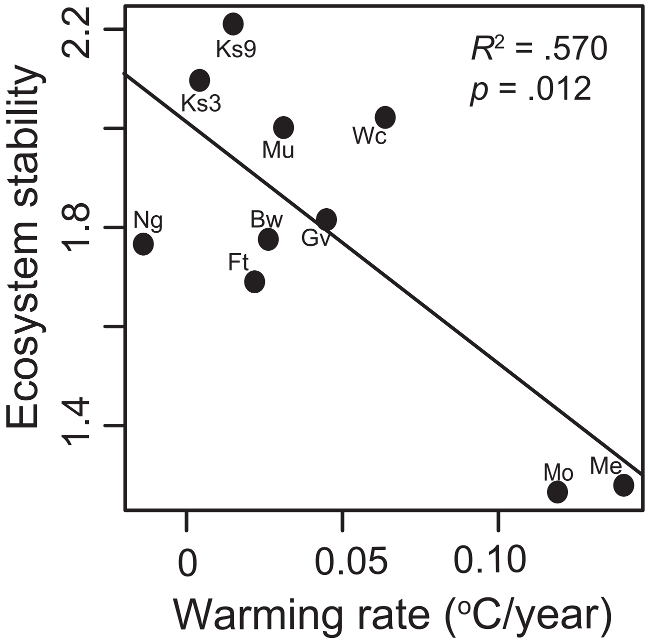

FIGURE 1 Ecosystems experiencing stronger warming are less stable (larger fluctuations in phytoplankton biomass). Ecosystem stability is measured as 1/CV of phytoplankton biomass. Ecosystem stability significantly decreased with warming rate. See Table S1 for the full name of each monitoring system. Robustness analyses for this negative relationship are provided in Figure S3

pathway, and its *linkage strength* is computed as the geometric mean of the strength associated with each of the directed links (Section 2). We used the resulting networks (Figure 2) of links between phytoplankton species richness, biomass, and the physiochemical environment to examine whether specific causal pathways were associated with ecosystem stability and to investigate how these pathways differed across the gradient of warming that is expected at global scale (Belkin, 2009; Schneider & Hook, 2010). Specifically, we investigated the following questions: (a) what ecological properties or causal pathways are associated with stability? and (b) what are the differential impacts of long-term warming across various systems?

2 | MATERIALS AND METHODS

2.1 | Data

The 10 aquatic ecosystems studied were Lake Geneva (1974–2012), Lake Biwa (1978–2009), Lake Kasumigaura Stations 3 and 9 (1977–2009), Lake Mendota (1995–2012), Lake Monona (1995–2011), Lake Müggelsee (1994–2013), Narragansett Bay (1999–2014), Western Channel (1992–2009), and Feitsui Reservoir (1986–2017; Figure S1). The stations in Lake Kasumigaura are independent monitoring stations with distinct bottom depths and limnological characteristics (Table S1). Detailed characteristics of each system are listed in Tables S1–S3. For each system, time series data included: (a) phytoplankton species richness; (b) total phytoplankton biomass; (c) phosphorus stock (phosphate concentration); (d) nitrogen stock (nitrate concentration); and (e) physical factors (e.g., water temperature). In systems with depth-resolved measurements, data were depth-integrated averages in the euphotic zone; otherwise, only surface layer measurements were used. This yielded a total of 2,854 and 2,790 data points for phytoplankton species richness and total biomass, respectively, across the 10 sites. We used chlorophyll-*a* concentration as a proxy for total phytoplankton biomass. The chlorophyll-*a* concentration was measured by a standard spectrophotometric approach, so that the approximated biomass is independent of species richness derived from species composition data, following recommendations in the literature (Cardinale, 2011; Ptacnik et al., 2008; Ye et al., 2019). The availability of variables differed among systems (Tables S3); thus, only variables and interactions measured by similar approaches (e.g., measuring chlorophyll-*a* concentration as a proxy for total phytoplankton biomass) in all ecosystems were considered in the cross-system comparisons. For example, we used phosphate instead of total phosphorus to study the effects of nutrients on ecosystem stability, because the latter was not measured in all systems. Other ecosystem functions, such as primary production, decomposition, and respiration, were not consistently observed across systems and therefore were excluded from this study.

2.2 | Quantification of causal networks via CCM

Convergent cross mapping (Sugihara et al., 2012) was used to reconstruct the causal networks consisting of multiple causal interactions among key ecosystem components, including species richness, total biomass, and physicochemical factors. The essential ideas of CCM are described in brief animations: tinyurl.com/EDM-intro, whereas the detailed implementations of CCM are given in the Supporting Information. The strength of causal links was quantified by CCM based on cross-mapping skill ρ (i.e., correlation coefficient between observations and CCM predictions) using the maximal training set (BozorgMagham, Motesharrei, Penny, & Kalnay, 2015; Sugihara et al., 2012).

For the strengths of causal links (i.e., linkage strength) to be comparable among systems, we needed to account for differences in cross-map skill due to differences in the relative amount of noise in the time series observed in each system. Thus, we scaled linkage strength by the maximum cross-map ρ obtained in each system; the resulting standardized linkage strengths (SLS) ranged between 0 and 1 and gave the relative importance (but not absolute strength) of each link with respect to the strongest causal link in that system. Note that the reconstruction and standardization of causal networks were computed separately for each system.

2.3 | Linkage strength of a pathway

For network pathways consisting of multiple individual links, we quantified the strength as the geometric mean of the SLS for all links in the pathway (analogous to loop weight, Neutel, Heesterbeek, &

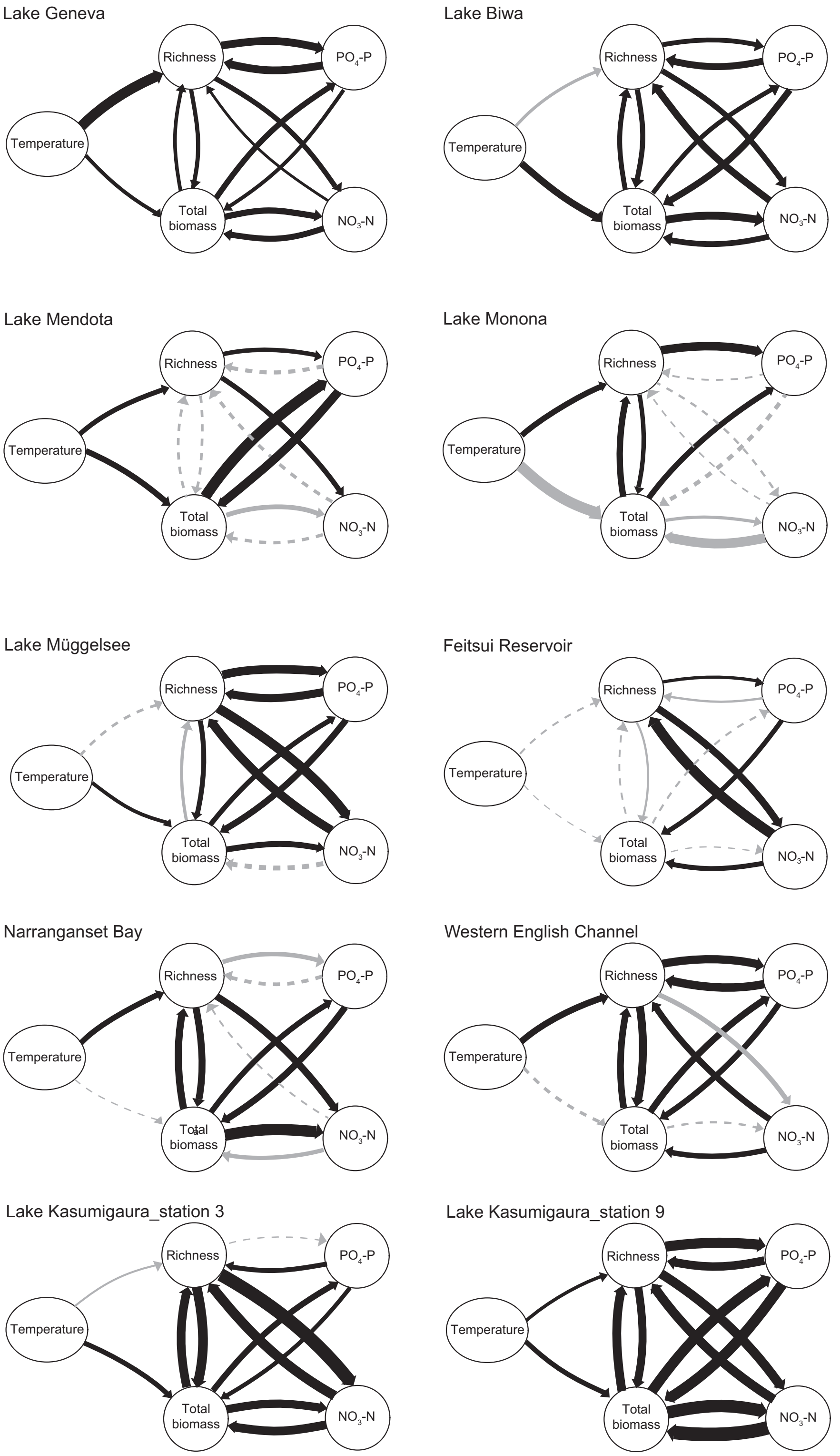

FIGURE 2 Summary causality network for each of the 10 ecosystems reconstructed by CCM. Arrow thickness indicated linkage strength estimated by CCM. The black and gray solid arrows are the causal links showing significant ($p < .05$) and marginally significant ($p < .1$) convergence in CCM, respectively. The gray dashed arrows indicate the causal links not showing significant convergence ($p > .1$) in CCM

de Ruiter, 2002). For example, the strength of the causal pathway, nutrient→species richness→phytoplankton biomass, was computed as the geometric mean of the SLS values for nutrient→richness and richness→phytoplankton biomass. We recognized that links of causal pathways within a network are not independent (Anneville et al., 2019; Sugihara et al., 2012); nevertheless, the average interaction strength quantified for a pathway represented a reasonable approximation of joined regulatory strength along the pathways and reflected the real-world situation where links among a network are rarely independent (Levine, Bascompte, Adler, & Allesina, 2017).

2.4 | Ecosystem stability

Following previous studies (Downing, Brown, Perrin, Keitt, & Leibold, 2008; Narwani & Mazumder, 2012), ecosystem stability was quantified for each ecosystem as the inverse coefficient of variation (1/CV) of phytoplankton biomass. Namely, 1/CV is computed as μ/σ, where μ is the long-term mean calculated from the original time series and σ is the temporal standard deviation calculated from the detrended and deseasoned time series. Detrending and deseasoning were performed as described in Supplementary Methods (section: Implementation of convergent cross-mapping), except that no variance normalization was performed, in order to maintain the original variability of time series (Tilman et al., 2006).

2.5 | Evaluation of ecosystem attributes associated with stability

We used a cross-system comparison to explore associations between ecosystem stability and the linkage strength of various network pathways (either individual links or a combination of connected links). Again, the linkage strength of a pathway was either the SLS of an individual link or the geometric mean for all SLS values for links that comprised the pathway. We used AIC to compare various linear regression models that linked ecosystem stability to linkage strengths of different pathways. In total, the 12 links common to all ecosystems (Table S4) and their 2^{12}–1 combinations were examined. In summary, we: (a) selected the best combination (among all candidates) using the criterion of minimizing AIC and (b) tested the statistical hypothesis only once for the selected variable and then reported the *p* value. As such, we conducted only one test for the selected causal pathway as if we were doing a classic stepwise regression, but not multiple tests. However, the main difference is that we retained only one independent variable (i.e., geometric mean of the individual SLS values) throughout the selection process to avoid the pitfall of over-fitting and the associated inflated Type 1 error when adding many variables in multivariate regression (Freedman & Freedman, 1983). This heuristic approach does not aim to test a pre-existing hypothesis; instead, it aims to formulate a new hypothesis from complex causal networks (i.e., causal pathway) that mostly likely explains the cross-system patterns regarding stability. Consequently, we do not falsify the possibility that the other causal pathways were also influential to ecosystem stability.

As a comparison, we also evaluated other factors hypothesized to strongly influence system stability, such as species richness and environmental variables including nutrients (Downing et al., 2008), water temperature (Paerl & Huisman, 2008), and morphometrics (Mayora, Devercelli, & Giri, 2013; e.g., depth). The relationship between system stability and these factors was quantified by a linear regression model using both temporal mean and variability (CV) as explanatory variables.

2.6 | Warming effects on ecosystem stability and linkage strength

We measured the warming rate (intensity of long-term warming) of surface water temperature in each system using the Theil–Sen median-based trend estimator that is robust to episodic extreme events and gives stable estimations of long-term trend in the presence of outliers (Mohsin & Gough, 2010). Then, we examined associations between warming rate, measures of ecosystem stability, and network linkage strength.

2.7 | Computation

All analyses were done with R (ver. 3.1.2). The CCM analyses modeling was implemented using rEDM (Ye, Clark, Deyle, Keyes, & Sugihara, 2013). Documentation of all analytical procedures and R codes is available at GitHub (https://github.com/biozoo/GCB_SI_Rscript).

3 | RESULTS AND DISCUSSION

3.1 | Ecosystem causal networks

Details of causal networks for the 10 ecosystems, where links represent quantitative causal interactions by applying the CCM analysis to time series of the corresponding variables, are shown (Figure 2). In aggregate (Figure S4), the detected causal interactions between key ecosystem properties were common to most systems. Curiously, we did not identify a causal effect of phosphate concentration on total phytoplankton biomass in every lake (Figure 2; Figure S4). This seemingly counterintuitive result likely occurred because phosphorous is not always a limiting factor for phytoplankton growth (Anneville, Souissi, et al., 2002; Matsuzaki, Suzuki, Kadoya, Nakagawa, & Takamura, 2018); in such cases, fluctuations in phytoplankton biomass would not respond to changes in phosphate concentration. Indeed, in Lakes Mendota and Monona, where the average phosphate concentrations were 65.71 and 46.35 μg/L, respectively (and much higher than in the other lakes; Table S1), phosphate did not significantly influence phytoplankton biomass.

3.2 | Determinants of ecosystem stability

To investigate the factors (or processes) affecting ecosystem stability across systems, we examined both ecosystem state variables (e.g., species richness or nutrient) and ecosystem processes (i.e., the causal pathways). First, although ecosystem properties such as nutrients (Hautier et al., 2014; Ptacnik et al., 2008), water temperature (Paerl & Huisman, 2008), and morphometrics (depth and area; Mayora et al., 2013) have been hypothesized to be related to ecosystem stability, ecosystem stability was not associated with either the mean or variability of any of environmental factors (Table S5). Similarly, even though species richness is usually considered an important determinant of ecosystem health and resilience (Hooper, 1997; Tilman et al., 2014), there was no significant positive relationship with the cross-system pattern of stability (rarefacted and mean species richness in Figure 3a and Figure S5, respectively). The lack of positive

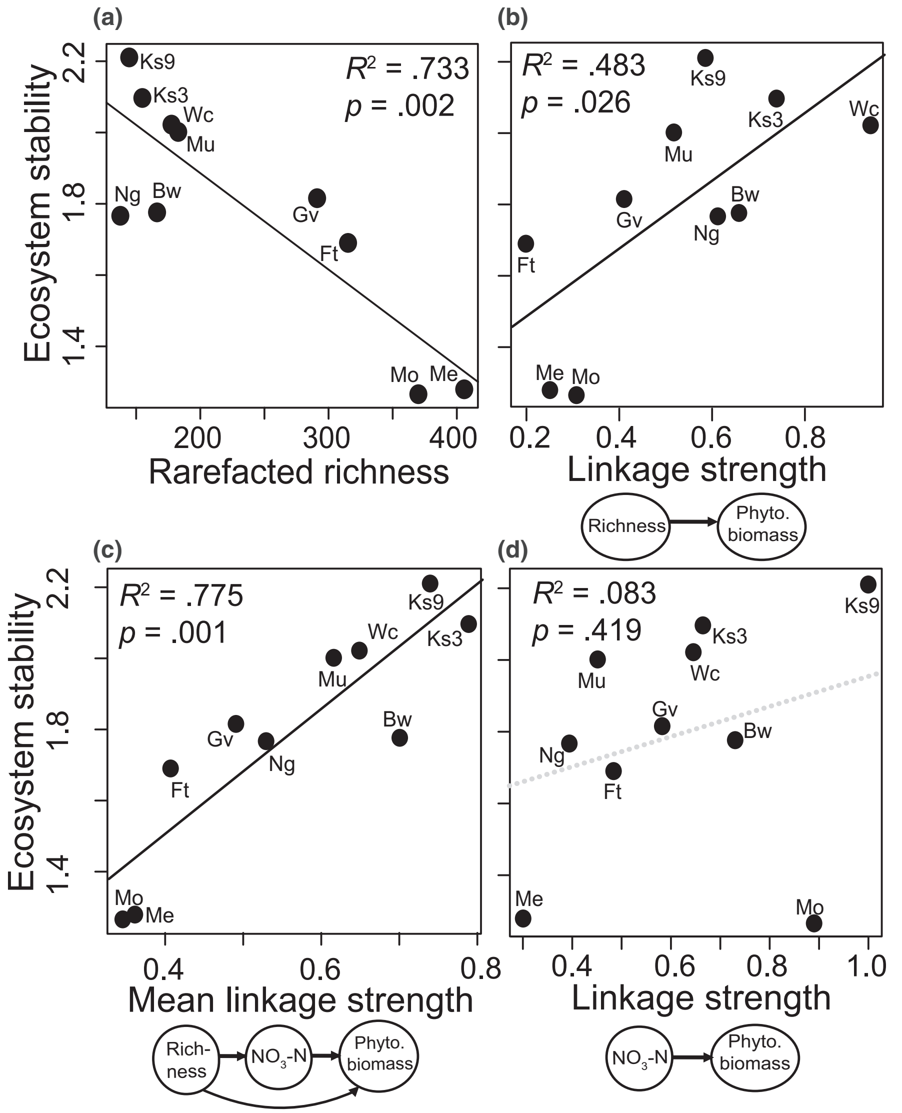

FIGURE 3 Ecosystem stability depends on species richness effect on phytoplankton biomass and the species richness-nutrient-biomass causal pathway. (a) Rarefacted species richness shows a confusing negative relationship to stability. Rarefaction of species richness followed Chao's rarefaction approach (Chao et al., 2013) which accounts for sampling effort by calculating rarefaction curves of accumulated species richness against total sampling years that approximates sampling effort. (b) The strength of species richness effect on phytoplankton biomass was positively associated with stability. (c) Combining the nutrients and species richness into a single causal pathway further improved explanatory power (R^2). (d) However, stability cannot be explained by the direct effect of nutrients on phytoplankton biomass. The gray dash line labels the result, showing a nonsignificant relationship

relationship between species richness and temporal variability was also revealed in a previous study, especially when there was high environmental variability (Romanuk & Kolasa, 2002).

Secondly, from the causal networks of individual systems (Figure 2), we examined which interaction pathways were associated with stability. Despite no evidence that higher species richness per se contributes to ecosystem stability, the effect of species richness on phytoplankton biomass (i.e., the SLS of species richness→phytoplankton biomass) was positively associated with stability (Figure 3b; Table S4). Again, ecosystem properties such as species richness and phytoplankton biomass are not static but are state variables of a dynamical system; thus, their interdependencies can determine ecosystem stability, regardless of whether the state variable (e.g., species richness) is high or low. When compared across various systems of substantial variation in habitat type, *linkage strength*, as a measure of the strength of regulatory causal pathways, may therefore be a more general predictor of ecosystem stability. This finding was consistent with existing hypotheses that species richness acts as a dynamical regulator of ecosystem functions (Hillebrand & Matthiessen, 2009). This relationship was robust to alternative measures of diversity index (Figure S6), as well as system-specific noise (Figure S7) and time series lengths (Figure S8).

Among all the causal pathways, the linkage strength for the regulatory pathway that included nitrate, species richness, and biomass (i.e., species richness→nitrate→phytoplankton biomass + species richness→phytoplankton biomass) was the best predictor of ecosystem stability according to AIC (Figure 3c). This association remained significant, even after excluding the two systems with the lowest values of stability and appeared visually distinct (i.e., Me and Mo in Figure 1). The same analysis using phosphate instead of nitrate produced a similar pattern, although the results were weaker (Figure S9). These results supported the mechanism that species richness stabilizes phytoplankton biomass through regulating nutrient cycling (Cardinale, 2011).

3.3 | Warming effects on causal networks

Our analysis also provided insights into how a warming climate affects and will continue to affect ecosystem processes. Ecosystems undergoing stronger warming usually have weaker species richness effect on phytoplankton biomass (Figure 4a), echoing previous experimental results in grasslands (De Boeck et al., 2008). Even so, just as the findings that including nutrients in the causal pathway better explained ecosystem stability (recall Figure 3c), there was a stronger response to warming for the causal pathway that included nutrients (Figure 4b; $R^2 = .417$, compared to .187 when only considering species richness effect on phytoplankton biomass). This reinforced the view that long-term warming weakens the ability of the community to buffer against nutrient fluctuations, resulting in decreased stability. Moreover, the responses of these ecosystem processes to warming were stronger when restricting the data to freshwater systems ($R^2 = .408$ and .610, respectively; Figure S10), implying freshwater and marine ecosystems might respond to warming differently (Thackeray et al., 2010). More data from marine systems are needed to confirm the significance of this apparent difference. Certainly, more datasets from other types of aquatic systems are needed to confirm our mechanistic explanation, since our key results were based on only 10 datasets.

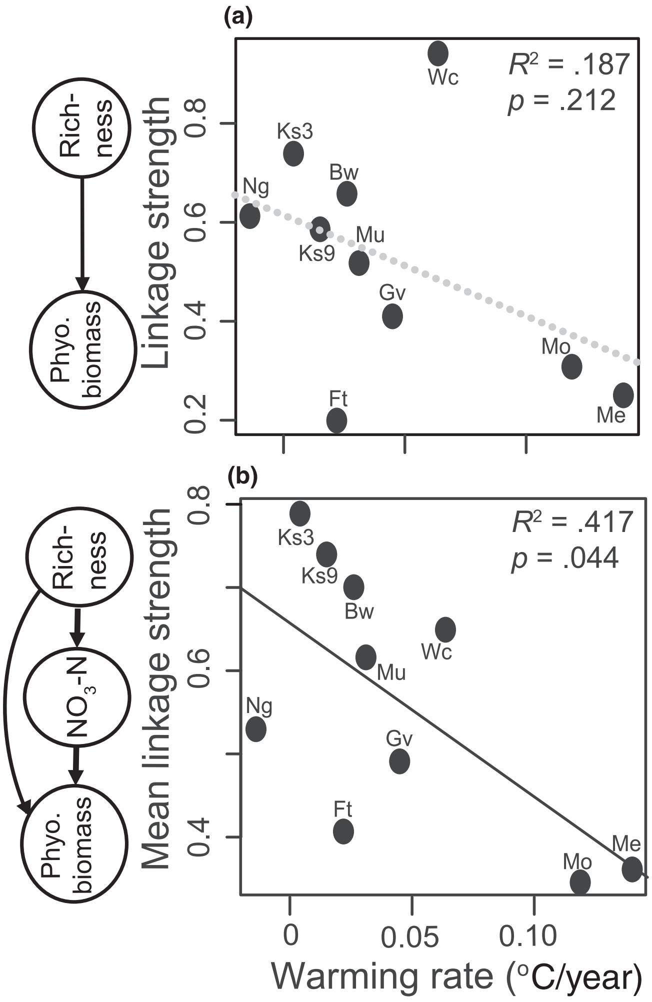

FIGURE 4 The effect of warming rate on linkage strength and ecosystem stability. The linkage strengths of species richness effect on phytoplankton biomass (a) and the species richness-nitrate-biomass pathway (b) were weaker under stronger warming. The gray dash line labels the result, showing a nonsignificant relationship

3.4 | Robustness of the statistical associations

Although the use of only 10 datasets limited the statistical power of our analyses, this problem could be alleviated if the same analyses were repeated using numerous time series subsets randomly subsampled from the original time series over decades (Figure S11). This approach improves the statistical power, although it also sacrifices some estimating precisions and causes minor autocorrelations due to overlapped subsets. Based on the random subset analysis (Figure S11), we determined that main conclusions drawn from the 10 long-term monitoring sites remain hold. This consistency indicated that our proposed mechanisms operated throughout the sampling periods.

Another statistical issue that warranted attention was the accuracy of estimates. For example, all measurements, including causal strength, ecosystem stability, and warming rate, were not estimated with equal accuracy across systems because the time series length varied among systems. In addition, there were measurement errors in the estimated independent variables (e.g., causal strength). These did not agree with the assumptions in ordinary regression assuming equal variances in the dependent variables and no measurement error in the independent variables. To tackle these issues, we performed the weighted least square regression that down-weighed the estimates derived from short time series (i.e., less accurate) and applied the ranged major axis regression that is more suitable for analyzing the dataset containing measurement errors in the independent variables (Legendre & Legendre, 2012). Again, the results (Figure S12) obtained from these more sophisticated analyses were consistent with the findings based on ordinary regression, both suggesting that warming destabilized ecosystem dynamics by weakening regulatory causal pathways.

3.5 | Stabilizing mechanisms of causal pathways mediated by species richness

What mechanisms drive the stabilizing effect of regulatory causal pathways? One hypothesis is that ecosystems become more stable because species respond to environmental changes differently (Elmqvist et al., 2003) when the strength of the causal pathways mediated by species richness is strong. If so, then asynchrony in species abundance fluctuations should also be associated with the linkage strength of the pathways driven by species richness. Indeed, that is what we observed; temporal asynchrony in species abundance was positively associated with stability as well as the linkage strength of species richness effects (Figure S13). In fact, a stronger linkage strength of species richness effect on phytoplankton biomass revealed by CCM implied that phytoplankton biomass responded more strongly to changing species richness (Sugihara et al., 2012).

This strong response was likely due to low functional redundancy or high functional uniqueness in the communities (Cardinale, 2011) and might result in differential responses among species to their environment (Elmqvist et al., 2003). Therefore, the stabilization of regulatory causal pathways was manifested in the form of asynchronous fluctuations among species in response to changing nutrient conditions. This mechanism also explained a real example in Lake Geneva, in which a return to a mesotrophic state resulted in extirpation of some phytoplankton species whereas other species flourished, with only minor changes to the net phytoplankton biomass (Anneville, Ginot, & Angeli, 2002). Here, there was general support for the regulatory role of species richness on nutrient fluctuations across multiple aquatic ecosystems. Nevertheless, further theoretical analysis is needed to clarify the detailed mechanisms and test the role of functional redundancy to temporal stability (e.g., compensatory dynamics).

3.6 | Roles of nutrients in stabilizing causal pathways

Furthermore, what is the role of nutrients in ecosystem stability? As previously mentioned, there was no direct correlation between stability and long-term averages of nutrients (Table S5), indicating that any influence of nutrients had to be on dynamic processes. When examining the causal network, the linkage strength for the effect of nutrients on phytoplankton biomass was not significantly associated with stability (Figure 3d). However, nutrient inputs have been implicated as an important driver of species turnover (Jochimsen, Kümmerlin, & Straile, 2013) and species richness (Lehtinen, Tamminen, Ptacnik, & Andersen, 2017), suggesting that species richness is likely a necessary intermediary for the influence of nutrients on stability. Indeed, the linkage strength between nutrients and species richness was a marginally significant predictor of stability (Table S4).

Nevertheless, it is noteworthy that the analyzed dataset lacked nutrient data measuring total contents (e.g., total phosphorous) for every system. Total phosphorous is less likely exhausted below detection limits in comparison to more bioactive mineral nutrients, and thus more appropriate for reflecting the trophic state of aquatic systems (Jochimsen et al., 2013). However, measurements of total nutrient contents were often lacking in marine and some freshwater systems (Table S3), making cross-system comparison restricted. Therefore, further examination considering various types of nutrients is encouraged in future study.

3.7 | Reconstruction of causal networks using nonlinear approaches

CCM effectively quantifies the causal network in nonlinear dynamical systems where relationships between any two variables depend on other state variables (Clark & Luis, 2020). In nonlinear systems, linear associations will appear, then disappear or change sign—so-called *mirage correlations* (Sugihara et al., 2012). Mirage correlations are common in long-term monitoring stations wherein linear correlations are ephemeral (e.g., the correlation between species richness and phytoplankton biomass changes with the time period analyzed—see Supplementary Methods and Figure S14). Therefore, nonlinear methods (e.g., CCM) accounting for dynamic interactions and context dependency are more suitable to detect and quantify these causal links in dynamical ecosystems. Based on our findings, we inferred that explicitly resolving the causal pathways connecting species richness and the other key ecosystem components offered a better understanding on the temporal stability of phytoplankton biomass and can be extended to other types of ecosystems (e.g., grassland or microbial ecosystems) with better long-term monitoring (Anneville et al., 2019; Ye et al., 2019) or short-term monitoring with massive spatial replicates (Clark et al., 2015).

3.8 | Final remarks

In constructing causal networks for 10 aquatic systems using empirical time series data, our study established several important links between ecological theory and empirical observations. First, we concluded that regulatory causal pathways were responsible for species richness effects on ecosystem stability. Moreover, there was support for the portfolio effect as a mechanism: asynchrony in species abundances implied that species-specific responses to stochasticity (and nutrient fluctuations in particular) modulated dynamics of phytoplankton biomass. The weakening of regulatory causal pathway under warming could be a consequence of preferential removal of species with certain functional traits (De Boeck et al., 2008), for example, large body size (Daufresne, Lengfellner, & Sommer, 2009); however, further study is necessary to determine the detailed mechanism(s). Although our results were specific to aquatic planktonic systems, our approach established a roadmap for further study. Are these regulatory pathways present in other ecosystems? Are the impacts of warming detectable on shorter timescales (e.g., monthly or yearly) compared to an aggregated influence over decades? Moreover, we computed temporal variability (1/CV) because it is the most commonly used stability measure (Narwani & Mazumder, 2012; Ptacnik et al., 2008), but we acknowledge that stability is a multifaceted concept (Kéfi et al., 2019), and so different measures may well implicate different processes. By leveraging both time series data and methods for reconstructing causal networks, we can provide insights into these topics. Furthermore, we hope that our approach provided a useful exemplar for investigating ecological processes that have long been hypothesized (Anneville, Ginot, et al., 2002) or are critical to maintain ecosystem health (e.g., productivity and respiration; Yvon-Durocher, Jones, Trimmer, Woodward, & Montoya, 2010).

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTION

C.-W.C., C.-h.H., T.M., and G.S. conceived the research idea. C.-W.C. analyzed the data with help from C.-h.H., E.R.D., T.M., G.S., S.S., and H.Y. O.A., R.A., Y.-R.C., S.I., M.K., S.-i.S.M., F.-K.S., and J.-T.W. collected the data. C.-W.C., C.-h.H., T.M., G.S., and H.Y. wrote the manuscript with critical comments from co-authors.

DATA AVAILABILITY STATEMENT

We confirm that this manuscript is not under consideration by another journal and has not been published elsewhere. The accessibility of the time series data is provided in Table S2. Documentation of all analytical procedures and R codes are provided in the github, https://github.com/biozoo/GCB_SI_Rscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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