

博 士 論 文

Understanding of population dynamics and complex
community structure through quantification of
interspecific interactions via Empirical Dynamic Modeling

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Chapter1. General Introduction

In natural environments, ecological communities are composed of multiple species. Within these communities, interspecific interactions are intricately intertwined among populations, forming complex networks. These interactions encompass various types, including predator-prey relationships, competition, and mutualism. Importantly, the strength and direction of interspecific interactions can be modulated by environmental conditions (e.g., Liu and Gaines 2022).

Ecological roles of interspecific interactions are recognized as a key factor in determining population dynamics (Dhondt 2023). Empirical studies focusing on these interactions have been conducted for decades. One of the earliest and most influential experiments was conducted by Gause (1934), who demonstrated the competitive exclusion principle using mathematical model and laboratory experiments. From this, it is called the competitive exclusion principle, which posits that stable coexistence is impossible when multiple species occupy the same ecological niche.

Previous experimental study has been used to evaluate the dynamics of communities and the role of interspecific interactions in linking populations and communities. Notably, predator-mediated interactions have been shown to influence species coexistence and community diversity. For example, Morin (1983) manipulated the densities of two salamander species (*Notophthalmus viridescens dorsalis* and *Ambystoma tigrinum*) in 22 artificial pond mesocosms to investigate their effects on the community structure of six larval anuran species. Similarly, Resetarits and Fauth (1998) used mesocosms to simulate natural pond communities and demonstrated that the presence and density of predators allowed competitively inferior amphibian larvae to persist.

These studies highlight the critical role of predators in maintaining community structures. Here, Behavioral observations (Hori 1993) and stomach content analyses (Takamura 1984; Nshombo 1987; Nshombo et al. 1985) have been employed to understand community structure and stability in fish communities dominated by cichlids which community is highly species diversity shaped by adaptive radiation.

The concept of keystone species has also been central to understanding which species sustain the community. Paine (1966) investigated the effects of removing the top predator, the sea star *Pisaster*, from a rocky intertidal food web in Mukkaw Bay. The removal led to the dominance of *Mytilus*, a mussel species previously preyed by *Pisaster*, which subsequently excluded other species and formed a monoculture. This experiment revealed that a single predator species could regulate the entire community which led to defining such ecologically influential species as keystone species.

General Issues in Previous Research on Interspecific Interactions

In natural communities, the strength and direction of interspecific interactions fluctuate over long

time scales in response to environmental conditions, making them difficult to track through observational methods (Liu & Gaines, 2022). It remains unclear whether observable interactions directly influence population dynamics, and their strength is rarely quantified. Moreover, observational studies often require long-term tracking of species-specific behaviors and traits, which is inefficient and resource intensive (Murray et al. 2023, Vanovac et al. 2021). The high diversity of species and the complexity of interaction networks in natural communities further hinder comprehensive assessments. Observational evaluations typically capture only transient interactions (e.g., CaraDonna et al. 2017), which necessitate an expanded interpretation of their effects on community structure, although such interpretation remains inherently ambiguous (Toju et al. 2024).

Research on Interspecific Interactions with Empirical Dynamic Modeling (EDM)

To overcome the limitations of traditional observational approaches (e.g., Paine, 1966; Estes and Palmisano, 1974) for estimating interspecific interactions, which demand substantial observational effort and extensive field setups in natural environments, I employ Empirical Dynamic Modeling (EDM), a time-series analysis framework proposed by Sugihara et al. (2012) that has gained increasing attention in ecological research. EDM enables the estimation of causal relationships and interaction strengths between species using time-series data derived from population censuses. This approach allows for the quantification of interspecific interactions and their influence on population dynamics.

For example, Kawatsu and Kishi (2018) applied EDM to test whether observed behavioral interactions, which specifically include resource competition and reproductive interference, between two *Bruchus* species affected their population dynamics. Using time-series data collected from laboratory competition experiments, it inferred causal relationships between the species and linked these to behavioral observations, demonstrating that behavioral traits can drive changes in population dynamics via interspecific interactions.

Environmental drivers of variation of interspecific interaction have also been explored using EDM. Liu and Gaines (2022) investigated how environmental factors such as the Multivariate ENSO Index (MEI), Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), and sea surface temperature (SST) influence interspecific interactions between kelps and sea urchins. Their findings revealed that NPGO significantly affected kelp interactions, and that bottom-up environmental forcing played a role as critical as top-down herbivory in shaping kelp forest dynamics. Their study identified which environmental variables most strongly influenced population dynamics.

Ushio et al. (2018) examined the role of time-varying interaction strength in community stability. Using time-series data from fish communities in Maizuru Bay, they applied EDM to estimate interspecific interactions and their temporal dynamics. Their results showed that dominantly weak interactions during summer were associated with higher community stability and reduced fluctuations,

highlighting the importance of dynamic interaction strength in maintaining ecosystem resilience.

Population dynamics are influenced by changes in interspecific interactions, and these changes are suggested to be driven by environmental factors. However, whether environmental factors can directly control interspecific interactions and thereby regulate population dynamics, as well as the sequence of these processes, remains unclear. The concept of keystone species has long been used to understand ecosystem structure and stability (e.g., Paine 1966). However, as Whittaker and Cottee-Jones (2012) pointed out that the definition of keystone species has often been overstated and inconsistently applied with various species being labeled as keystones based on non-standardized criteria. This ambiguity stems from the difficulty of conducting quantitative experiments in natural settings and the difficulty of comprehensive understanding of interspecific interactions based on observations (Hughey et.al. 2018, Costa et al. 2022).

Namely, to estimate key species such as keystone species, standardized criteria are required that rely on quantitative evaluation of interspecific interaction strength with varying time variation, as exemplified by EDM, while using simple surveys such as counting number of individuals.

My studies in this dissertation

In Chapter 2, I examined whether environmental conditions could influence population dynamics by altering the strength of interspecific interactions. This study aimed to experimentally demonstrate whether manipulating environmental factors could directly control interspecific interactions that affect population-level outcomes.

To solve this question, I conducted a competition experiment using two species of *Bruchus* beetles with four different cage sizes, which were as controlled by environmental conditions. Time series data for number of populations were collected to enable causal inference using Empirical Dynamic Modeling (EDM). The hypothesis was that cage size would affect the frequency of encounters between individuals of different species, thereby modulating the strength of reproductive interference and influencing the duration of species coexistence.

In Chapter 3, I aimed to comprehensively map the interspecific interaction network within a highly diverse and complex community shaped by adaptive radiation, and to identify key species which are maintaining community structure and stability. The study focused on the cichlid fish community in Lake Tanganyika, one of the world's ancient lakes. This ecosystem is characterized by exceptional species diversity and ecological specialization resulting from adaptive radiation. Hori et al. (1993) reported various interspecific interactions in this system, including predation, aggression, and unique behaviors such as chasing, as well as the food habits of each species based on stomach content analysis and behavioral observations.

Due to the complexity and diversity of these interactions, it is difficult for observational approaches

sorely to understand comprehensively the interaction network. To address these limitations, I combined Empirical Dynamic Modeling (EDM) with behavioral observations. EDM was applied to long-term time-series data collected over 20 years of underwater census surveys conducted by Professors Hori and Ochi between 1995 and 2014. Convergent Cross Mapping (CCM), one of the EDM methods, enabled the detection of indirect effects that are not easily captured through behavioral observation.

The primary purpose of this dissertation is to clarify how environmental conditions influence population dynamics through interspecific interactions and to understand the structure and stability of interaction networks in complex communities. To address these questions, this study applies Empirical Dynamic Modeling (EDM) to both controlled experiments and long-term observational data.

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Chapter2. Time series analysis showing how different environmental conditions affect the interspecific interactions of *Callosobruchus maculatus* and *Callosobruchus chinensis*

Introduction

Ecologists have long established that interspecific interactions are important determinants of population dynamics and the stability of communities (e.g., May 1972). Experimental studies have attempted to evaluate the effects of interspecific interactions on population dynamics by manipulating interaction strength via changing environment conditions that often affect population densities (e.g., Drolet et al. 2013; Quammen 1984). For example, Paine (1966) demonstrated that the experimental removal of the top predator (Asteroidea) in the tidal community increased the size of the prey (bivalve) community, resulting in the dominance of single prey species. Thus, changing the biological environmental factors of bivalve communities (i.e., predator abundance) could modify the strength of interspecific competition and alter community dynamics. Toquenaga and Fujii (1991) examined resource competition at the larval stage for two bruchid species (*Callosobruchus analis* and *Callosobruchus phaseoli*) that exhibit different competition modes (contest: *C. analis*, scramble: *C. phaseoli*). By using two resource patches (*Vigna angularis* and *Vigna radiata*) of different size and controlling initial densities of competing species, the authors assumed that the encounter rate of individuals, and hence interaction strength, were altered monotonically with these conditions.

These early studies examining the effect of interspecific interactions on community dynamics often did not directly measure the strength of interspecific competition, but assumed that interspecific competition and trophic interactions should increase monotonically with community size or encounter rate. However, this assumption holds in limited conditions. In general, the interaction strength of one species (hereafter ‘effect’ species with density X) on population of another species (‘causal’ species with density Y) at the population level is formalized as interaction coefficient $\times f(X, Y)$ where f represents the density-dependence form. When $f(X, Y)$ follows the Lotka Volterra form, i.e., $f(X, Y) = XY$ and the environmental manipulation does not change the interaction coefficient, the interaction strength from causal species to effect species proportionally changes with the density Y (Leger and Espeland 2010). Also, when interaction coefficient is changed by environmental manipulation with constant densities, the interaction strength changes proportionally with the degree of environmental manipulation (e.g. habitat complexity), independently of the density dependence form of f (Fonteyn and Mahall 1981). However, if environmental manipulation alters individual behavior, it will result in the changes in interaction coefficient as well as functional form of f , leading to the unexpected changes in interaction strength. In addition, in a long-term experiment with multiple generations, the population density continuously changes with time, and thus the relationship between environmental manipulation and interaction strength may change with time. These and other studies with similar

designs clearly advanced our understanding of how interspecific interactions affect population dynamics; however, interspecific interaction strength and its impacts on population and community dynamics were not directly measured but inferred by the assumptions mentioned above. Consequently, the fundamental assumption behind the experimental test that changes to the density or encounter rate actually strengthen interspecific interactions remains untested.

One of the frequently employed approaches for quantifying interaction strength relies on observing animal behavior (e.g., Schellhorn 1999). Although the behavioral approach is effective to identify the type of interactions (e.g. interference and prey 103 predator), it is difficult to make clear the relationship between observed behavioral change and its impact on population dynamics. For example, behavioral observations show the presence of prey-predator interactions between two species at the individual level. However, it is difficult to elucidate how prey-predator encounters affect the population density of each interacting species. Among the sources of predator growth (or prey mortality), observed prey-predator interactions might only have negligible importance. Therefore, individual-level behavioral interactions do not necessarily represent important population-level interactions.

Another, relatively new, approach for quantifying interaction strength at the population level uses the time-series of population dynamics. Empirical Dynamic Modeling (EDM) is one example of a time-series analysis framework used to determine non-linear systems (Chang et al. 2017; Sugihara et al. 2012). It has been applied to evaluate population dynamics in both natural and experimental systems (e.g., Kawatsu et al. 2021; Kawatsu and Kishi 2018; Ushio et al. 2018). In particular, Convergent Cross Mapping (CCM), one of the methods of EDM, is used to detect causal-effect relationships between populations from time-series abundance data, even with temporally fluctuating interaction strength (Sugihara et al. 2012). This analysis uses information of the causal variable that is left as a footprint in the data of the effect variable. Thus, the dynamics for Y has information of X when X affects Y. For example, CCM showed that apparent negative interactions between two commercial fish species (Matsuda et al. 1992) were explained by opposing effects of water temperature on them (Sugihara et al. 2012). Furthermore, Chang et al. (2020) demonstrated that the forecast skill of CCM could be used to measure the strength of ecological interactions (e.g., effect of species richness on total biomass) in marine and freshwater systems. Thus, applying CCM to experimental time series could be used to bridge the gap between manipulating environmental conditions and the outcome of population dynamics.

Two *Callosobruchus* seed beetle species, *Callosobruchus chinensis* and *C. maculatus*, are used as a model system for investigating interspecific interactions under laboratory conditions (Bellows and Hassell 1984; Ishii and Shimada 2008; Kishi 2015). Existing studies showed that the competition between these two species is mediated by two mechanisms that occur at different life stages. The first

mechanism is resource competition, which occurs within resource patches (beans) at the larval stage. The second mechanism is reproductive interference (Kishi et al. 2009), which is mediated by the interspecific mating between *C. maculatus* females and *C. chinensis* males. While *C. maculatus* is superior to *C. chinensis* (Kishi et al. 2009) in the former type of competition, *C. chinensis* is superior in the latter, physically injuring *C. maculatus* females (Crudginton and Siva-Jothy 2000) and incapacitating them from laying eggs (Kyogoku and Nishida 2013; Kyogoku and Sota 2015). Existing studies using CCM to investigate interspecific interactions in *Callosobruchus* species showed that larval resource competition and adult reproductive interference jointly influence the abundance of adults (Kawatsu and Kishi 2018; Kyogoku et al. 2019). Thus, the cage experimental system of *Callosobruchus* species is viable for CCM application.

Here, I evaluated how the interactions of two species of *Callosobruchus* seed beetle changed with cage sizes. Specifically, I aimed to provide evidence of the demographic link among environmental manipulation, strength of interspecific interactions, and competition outcome. This was achieved by applying CCM to the obtained time series for the experimental system of *Callosobruchus* seed beetle species. The strength of resource competition is expected to be affected by the amount of resources, while the strength of reproductive interference would be affected by intersexual encounter rates (Ishii and Shimada 2008; Kyogoku and Sota 2017). Therefore, with a fixed amount of resources, I hypothesized that larger cage size, which reduces encounter rates, would reduce the strength of reproductive interference without affecting the strength of resource competition. Based on this information, I considered that the impact on population dynamics could be evaluated by the coexistence period. More specifically, I tested whether: 1) cage size alters the strength of interspecific interactions, and 2) the coexistence period of the two species was affected by the strength of interspecific interactions. Following Chang et al. (2020) I used the forecast skill in CCM analysis to measure the strength of ecological interactions. I predicted that encounter frequency with co-cultured species would decrease with increasing cage size, and would reduce the impact of reproductive interference, prolonging coexistence time.

Methods

Insects

The lifecycle of *Callosobruchus chinensis* and *C. maculatus* lasts approximately one month. The adults of both species survive one week without any food or water, during which they mate, and adult females lay eggs on the surface of beans (Kishi 2009). Then, hatched larvae and pupae grow up inside a bean before emerging.

I used the beans of *Vigna angularis* (adzuki) as oviposition substrate and larval food. Adults do not consume this plant. Adults were placed in no food conditions during the experiments. I used two strains (jC-F and msC15) for *C. chinensis* and one strain (hQ) for *C. maculatus*. (all strains were provided by Dr. Dobata and Mr. Ohtake of Kyoto University, Japan). The jC-F strain has been maintained for more than 80 years under laboratory conditions (Harano and Miyatake 2005). msC15 strain was established from six males and 11 females, collected in Okayama, Japan during 2015 (Shigeto Dobata, personal communication). hQ strain was established at the University of Tokyo (Japan) in 1989 (for details see, Miyatake and Matsumura 2004).

Competition experiments

I prepared four sizes of cages for my experiments: small (8.5 cm × 3.5 cm × 6 cm width x height x depth, respectively), medium (12 cm × 4.5 cm × 13.5 cm), large (18.5 cm × 7 cm × 13.5 cm), and huge (21 cm × 8 cm × 15 cm) (Fig. 1). The body and lid of the cages were made from polypropylene and polyethylene, respectively. I made an air vent covered with fine mesh at the center of a lid to prevent beetles from suffocating (Fig. 1). I separated cage bottoms into four compartments, partitioned with a polyvinyl chloride plate of 3 cm height to prevent mixing beans of different ages. I introduced one of two strains of *C. chinensis* (jC-F or msC) as the initial population to cages containing *C. maculatus*. Each replicate of competition experiments was initiated with four male-female pairs for each species. I also introduced 10 g of beans in one of the compartments. Afterwards, I counted the numbers of living adults every week. Dead individuals were removed. At the time of this census, I provided 10 g of new beans. In week 2, 3, and 4, I introduced beans to empty compartments. From week 5, I replaced the oldest beans with new ones. I repeated these steps every week until one of the species became extinct. I defined extinction as the absence of adults (dead or alive) for five consecutive weeks. Likewise, I finished the observation when the two species had coexisted for over 40 weeks. I made 16 replications for each cage size (Table S1). These cages were kept in an incubator during the experiment (60% relative humidity, 30°C, and 12 h lights 12 h dark).

Analyses

Effects of cage size on population dynamics

First, I checked if the population dynamics (coexistence period) were affected by cage size using a generalized linear model (GLM) with Poisson distribution. It was appropriate to use Poisson distribution for the response variable, because the coexistence period was a nonnegative integer. To calculate the coexistence period, I needed to specify the timing of the extinction. After the first week of an observation when one or other species was absent (i.e., apparent extinction), I continued

observations, and only concluded that extinction occurred at the first week of apparent extinction when absence was confirmed four more weeks. To avoid zero-inflated data, I did not use data from these additional four weeks (i.e., zero) for further analyses.

Preliminary setting of time series analysis

The whole dataset consisted of 16 replicates of the time series from each cage size (small, medium, large, and huge), generating 48 time series in total. I first combined all 16 replicates for each cage size, to obtain four time series. I applied EDM to this first set of data to confirm nonlinearity and bidirectional interspecific interactions in each cage size. I followed the method from previous EDM studies (Hsieh et al. 2008; Kawatsu and Kishi 2018). Second, taking into account variation in the coexistence periods between replications, I only combined a small number of replicates of the time series in descending order of the coexistence periods. I ensured that each combined time series included more than 35 time points, which were necessary for the EDM analysis (Sugihara et al. 2012). Then, the average value of the coexistence periods and EDM parameters (see the following sections) was calculated for the combined time series replicates for further analysis (Table 1). I used this second set of data to determine how cage size affected interspecific interaction strength, and how it, in turn, affected the coexistence period.

Determining embedding dimension and nonlinearity

The EDM analysis is based on Takens theorem, which states that the attractor (a set of state vectors) of a nonlinear deterministic system can be reconstructed with the lagged time series of a single time series (Takens 1981). Thus, it is necessary to use EDM to determine the optimal embedding dimension E^* (i.e., number of time lags used for attractor reconstruction) for each species. I used simplex projection, which is a nonlinear forecasting method that assesses the self-prediction skill with different embedding dimensions (Sugihara and May 1991). I searched for the optimal embedding dimension E^* that had the highest prediction skill (i.e., the largest correlation coefficient ρ between the prediction and observation) in a range of 1 to 10.

I then checked the nonlinearity of the time series data with univariate S-map (sequential locally weighted global linear map; Sugihara 1994, Deyle et al. 2016). This method is also based on Takens theorem, performing nonlinear forecasting by fitting a locally-weighted linear model. The nonlinearity of the data was evaluated using parameter θ , which represents how strongly the regression is localized to the region nearby the prediction target on the reconstructed attractor. When $\theta > 0$, a greater weight is given to the neighboring points on the reconstructed attractor when fitting a local linear model, and indicates that the time-series data have a nonlinear behavior. The

local linear map was constructed by varying θ between 0 and 8, with a default interval setting. The relationship was checked between θ and the forecast skill (ρ). I also calculated delta- ρ : the difference in the forecast skill(ρ) between $\theta = 0$ and when ρ was maximized, as an index of the degree of nonlinearity. Then, I only applied CCM to the time series when ρ was maximized with $\theta > 0$ for both species.

Convergence Cross Mapping (CCM)

CCM analysis allows me to test causality between different time series. Specifically, the causal effect of X on Y (i.e., X and Y are the causal and effect variables, respectively) is investigated by predicting X_{t+tp} with the reconstructed attractor of Y , which is called “ Y cross-maps (or xmap) X ”. The parameter tp stands for the time required to prediction, and usually has negative values in cause-effect relationships, indicating when the interaction occurred (Ye et al. 2015). The prediction skill of cross-mapping is evaluated with the correlation coefficient ρ , which increases and converges with an increase in the size of library time series when there is significant causality between two variables. I varied library length from $E^* + 1$ to the whole time series data.

In addition to the above procedure, I performed CCM analysis with the ‘surrogate’ data of the causal variable to avoid false-positive causality. Specifically, I generated surrogate data by randomizing the phases of a Fourier transform (i.e., the data preserve the power spectra or autocorrelation of the original causal variable; Ebisuzaki 1997). I generated phase-shuffled data of a causal variable, and calculated the prediction skill of the effect variable’s cross-mapping surrogate data at the maximum library length. I judged the causality between the two bean beetles as significant if ρ of original data was higher than that 95 percentile of surrogate data (Kawatsu and Kishi 2018). The arguments of the function *ccm()* were set as follows, unless otherwise noted. To specify time series data, I set the effect variable and causal variable to *lib_column* and *target_column*, respectively. For example, when considering Y cross map X , X was the causal variable and was used as the target, whereas Y was the effect variable, which was used as the library. The increment in library size for cross map prediction set in *lib_sizes()* were set as the integer value of the length of the time series divided by the corresponding E^* of the library using the function *floor()*. I set the arguments for bootstrap as *num_sample* = 100, *replace* = F, and *RNGseed* = 1.

Time-delayed CCM and interspecific interaction

Kawatsu and Kishi (2018) demonstrated that CCM analysis distinguishes the two competitive interactions (i.e., resource competition at the larval stage and reproductive interference at the adult stage), focusing on the difference in the time lags of causality. Resource competition inside a bean reduces the number of larvae, which is reflected in fewer adults in the next generation. Reproductive

interference reduces the longevity of (reflected in the time series data with no delay) and fecundity (resulting in lower adult abundance in the next generation) of adult females. Thus, it is expected that the prediction skill is highest at $tp = 0$ if reproductive interference is the dominant competitive interaction. In contrast, the highest prediction skill occurs at $tp = -4$ if resource competition is dominant (Kawatsu and Kishi 2018). In the analysis, I checked causality with CCM for $tp = 0$ to -4 to estimate these interactions.

Comparison of interspecific interaction strengths between cage sizes

I used the cross-map skill ρ as the proxy of interaction strength to test if species interaction was influenced by the environmental condition (i.e., cage size). BozorgMagham et al. (2015) reported that comparison of bidirectional cross-map skills could be used to determine the causal-effect interaction. Several studies used the cross map skill ρ at the maximum library length as the index of interaction strength (Ye et al. 2019; Chang et al. 2020). However, interaction strength can also be assessed by the degree of improvement in prediction skill with increasing the library length. Therefore, it is also reasonable to use the difference in ρ value between at maximum library length and the minimum library length. In addition, the cross-map skill strikingly depends on how much noise is contained in time-series, both of the library and prediction target. Then, a certain standardization is necessary for cancelling the noise effects and focusing on the deterministic drivers of population dynamics to compare different systems (Chang et al. 2020). Here, the standardization by the prediction-skill of simplex projection is a promising approach. This is because CCM is a natural extension of simplex projection by including the second variable effects, making is plausible to interpret the prediction-skill of simplex project as a proxy of intraspecific density dependence or interaction strength. Thus, I used the following quantity as the index of relative strength of interspecific interaction,

$$\frac{\rho_{max} - \rho_{min}}{\rho_{self,max} - \rho_{self,min}}$$

where ρ_{max} and ρ_{min} are the cross-map skill at maximum and minimum library length, respectively; $\rho_{self,max}$ and $\rho_{self,min}$ are the prediction-skill of library time-series with simplex projection at maximum and minimum library length, respectively. $\rho_{max} - \rho_{min}$ represents the proxy of interspecific interaction strength, while $\rho_{self,max} - \rho_{self,min}$ represents the proxy of intraspecific density-dependence or interaction strength.

For example, the relative interspecific interaction strength from *C. chinensis* to *C. maculatus* was calculated from the ratio of $\rho_{max} - \rho_{min}$ of *C. maculatus* cross-mapping *C. chinensis* to

the $\rho_{self,max} - \rho_{self,min}$ of *C. chinensis* (hereafter, termed “relative interaction strength of *C. chinensis*”; the relative strength from *C. maculatus* was termed “the relative interaction strength of *C. maculatus*”). Through 100 permutations, I obtained 100 values for the relative interaction strength of each combined time series, and I then calculated the averages and the standard errors. These averages and standard errors were used in the linear regression analysis. The arguments of *ccm()* for calculating ρ_{max} , ρ_{min} , $\rho_{self,max}$ and $\rho_{self,min}$ were the same as those when the causality was tested with *ccm()*, except for the argument *target_column* and *E** for each cage size. When calculating ρ_{self} for each cage size, I set focal species data as both *lib_column* and *target_column* in the argument of *ccm()*. I also standardized ρ values using another method, which was based on common library length. However, this method did not effectively standardize the interaction strength (see “Standardized cross map skills based on common-library length for each cage size” and Fig. S1 in the Supplement). I regressed the relative interaction strength for each species (i.e., averaged values) against cage size using ordinary least squares (OLS). Because the accuracy of the averaged values varied between the combined time series, I also applied weighted least squares (WLS) to weight the estimates of relative interaction strength by the inverse of the standard errors.

Effects of interspecific interactions on coexistence

I used a GLM to investigate the effect of the relative interaction strength on coexistence periods. I hypothesized that the coexistence period would be explained by the relative interaction strength and cage size. In the arguments of the function for GLM analysis *glm()*, I first included the interaction terms. The formula was set as (coexistence period) ~ (relative interspecific interaction strength) * (cage size). The family was set as Gamma (link = identify). Since I used the second set of data for GLM analysis (see Preliminary setting of time series analysis), the response variable, i.e., the averaged coexistence period was a positive continuous variable. This was why using Gamma distribution was appropriate. In the first step, I applied GLM separately to each of the unidirectional interspecific interactions (i.e., effect of *C. chinensis* on *C. maculatus* and that of *C. maculatus* on *C. chinensis*) and with each *tp* (0, -1, -2, -3, and -4). Statistically significant explanatory variables (relative interspecific interaction strength, cage size, and/or their interactions) were specified in the best models for each model. In other words, the best model for each of unidirectional interaction strength with each *tp* would include cage size only, interaction strength only, both of these variables, or both of these variables with their interactions. In the second step, I built a single full model that included all statistically significant ($P < 0.05$) variables among all interspecific interaction strengths with both directions with different *tps* and cage size that were selected in the first step. Then, the best model from this full model was selected. Models were selected using the function *stepAIC()*, where variables were selected based on Akaike’s Information Criterion (AIC). I interpreted that the remaining variables in the selected best

model were important factors explaining the length of coexistence, irrespective of statistical significance.

Results

Effect of cage size on coexistence time

In most of the replications of my competition experiments, *C. maculatus* eliminated *C. chinensis* (Table S1). In my experiment, the coexistence period was longer in larger cages (GLM: $= 8.478 \times 10^{-11}$ Fig. 2). The average period of coexistence for each cage size was 15.62, 21.06, 24.12, and 26.31 weeks, for small, medium, and huge sizes, respectively.

Prevalence of nonlinearity and bidirectional interactions

When EDM was applied to the time series that combined all 16 replicates from each cage size (the first set of data), the population dynamics of both species were nonlinear in all replicates. The optimal embedding dimensions E^* for *C. maculatus* population dynamics were (Small, Medium, Large, Huge) = (5, 8, 5, 8), whereas those for *C. chinensis* were (Small, Medium, Large, Huge) = (10, 10, 9, 9) (Fig. S2). The weights of nonlinearity (θ^*) for *C. maculatus* were (Small, Medium, Large, Huge) = (4, 2, 3, 2). Similarly, those for *C. chinensis*, were (Small, Medium, Large, Huge) = (4, 2, 3, 2) (Fig. S3). Since my time series data demonstrated nonlinearity, I used *rEDM* functions to analyze the time series data with the estimated θ^* values. Similarly, I detected bidirectional causality (i.e., bidirectional interspecific interactions) for each cage size between *C. maculatus* and *C. chinensis* (Fig. S4). These interspecific interactions were also detected for all examined tp (Fig. S43). Each species affected the other species at each life stage (larval stage $tp = -1, -2, -3$) and at the adult stage of the current generation ($tp = 0$) and previous generation ($tp = -4$).

Effect of cage size on interactions

When EDM was applied to the time series that combined a small number of the replicates (the second set of data), some of the dynamics were linear (Table 1). I only applied CCM to the combined time series when the population dynamics of both species were nonlinear. However, I obtained no statistically significant linear relationship between the relative interspecific interaction strength and cage size (Fig. 3 and 4, Table 2 and 3) when using OLS or WLS regression ($P > 0.05$). Even when I regarded cage size as four discrete levels, there was no difference in the interaction strength between cages of different sizes (using *anova (lm())*, Table S2 $P > 0.05$).

For the combined datasets, other properties of the population dynamics estimated by EDM analysis (Table 1) may change with cage size. However, the relationship between the dimensionality (E^*), nonlinearity (θ^*), delta- ρ (Hsieh et al. 2008) and the cage size did not show clear trends except for the delta- ρ and the cage size for *C. chinensis* (Fig. S5).

Effect of interspecific interaction strength on coexistence

There was not statistically significant negative relationship between the coexistence period and relative interspecific interaction strength of *C. maculatus* (i.e., effect of *C. maculatus* on *C. chinensis*) for all tp s in the selected models (GLM: $P = 0.013, 0.012, 0.012, 0.013$, and 0.017 , Fig. 5, Table S3). The interaction term of the relative interspecific interaction strength and volume did not remain in the selected models (Table S3). In contrast, there was a statistically significant positive relationship between the coexistence period and relative interspecific interaction strength of *C. chinensis* (i.e.,

effect of *C. chinensis* on *C. maculatus*) for $tp = 0, -1, -2$ and -34 (GLM: $P = 8.0213 \times 10^{-3}$, 1.4980×10^{-2} , and 1.6126×10^{-2} , Fig. 6, Table S4). The relationships depended on cage size for $tp = 0, -2$ (i.e., interaction terms remained in the selected models but statistically insignificant for the term itself). With increasing cage size, the slope was shallower (i.e., weaker relationship between the interaction strength and coexistence period) (Fig. 6). Based on these results, I included cage size, the interspecific interaction strength of *C. maculatus* ($tp = 0, -1, -2, -3$ and -4), and that of *C. chinensis* with $tp = -1, -2$, and -3 in the single full model. The selected model from the full model included cage size and the relative interspecific interaction strengths of *C. chinensis* (Table S5).

Discussion

My experiments demonstrated that environmental condition (in this case, cage size) affected the coexistence period of the populations of two competing *Callosobruchus* species. However, EDM showed that the effect of the cage size on species coexistence was not explained by differences in interspecific interaction strength. Rather, interspecific interaction strength was highly variable among replicates for each cage size and across cage sizes. In fact, the effect of interspecific interaction strength on coexistence depended on the cage size. In my experimental setting, *C. chinensis* was competitively inferior to *C. maculatus*, because it was competitively excluded at the end of the experiments in most replicates. The inferiority of *C. chinensis* weakened the interspecific effect of *C. chinensis* on *C. maculatus* increased, lengthening the coexistence period (Fig. 6). Along with the positive influence of cage size on coexistence, the contribution of the interspecific effects of *C. chinensis* on *C. maculatus* to coexistence became smaller. The hypothesis did not support because the

result of research showed that environment condition did not control the strength of interspecific interactions directly. Environmental factors could influence coexistence through mechanisms other than interspecific interactions. I could not elucidate the mechanisms of how cage size affected the coexistence period. I used different cage sizes to generate differences in encounter rates between individuals of the two species, and so alter interspecific interaction strength; however, such effects were, at most, too weak to be statistically significant (Fig. 3). Similarly, there were no relationships between intraspecific interaction strength ($\rho_{self,max} - \rho_{self,min}$) and cage size (not shown). The stability of population dynamics could also be affected by cage size; however, the stability indices (non-linearity parameter θ ; Telschow et al. 2017, Table 1) did not change with cage size (Fig. S5). One may argue that a larger cage size increased the dimensionality of nonlinear dynamics (Munch et al. 2022) and made the variability between replicates greater (Figs 5 and 6), resulting in weaker effects of interaction strength on coexistence period. However, the dimensionality (E^*) and degree of nonlinearity (evaluated by $\Delta\theta$; the difference in the forecast skill between $\theta = 0$ and the optimal θ) did not change with cage size (Fig. S5). Due to the lack of a general trend between these dynamical aspects and cage size, the correlation between interaction strength and coexistence period suggests causality since cage size is unlikely to mediate the observed correlation. In addition, it is worth noting a technical aspect of applying CCM to population dynamics in various spatial scales. The interaction strength can be underestimated in a large spatial scale (in large and huge cage sizes of my experimental setting) where populations would behave in a subdivided way acting as metapopulations (Grziwotz et al. 2018; Sugihara et al. 1990). This might lead to the unclear pattern between cage size and interaction strength in my experiment (Figs.3 and 4).

Other than EDM, more basic analyses can also be used to interpret my results (Fig.S6 and Table S6 for the raw dataset of population dynamics). Here, I considered two possibilities. Firstly, the time to extinction and then the coexistence period depended on the degree of temporal fluctuations of population dynamics. Since the relationship between them depended on cage sizes (Fig. S7), it does not simply imply that less stable population is more likely to go extinct (Pimm et al. 1988) and does not give me specific insights regarding the biological mechanisms behind. Secondly, the coexistence period may be related to a founder effect. Since each experimental population started with four pairs of males and female individuals only, replicates started with less reproductive individuals (or any other stochasticity leading to lower population growth) would likely go extinct earlier. The coexistence period was longer (or shorter) with a greater early stage population size (at the fifth week) of competitively inferior species, *C. chinensis* (or competitively superior species, *C. maculatus*) (Fig. S8), which is in line with the founder effect's expectation.

The observed effect of cage size on the coexistence period might also be explained by the oviposition behavior of the two species. Larger cages had had larger surface areas, with resources being more widely spread, and show with shallower depth (Fig. 1), because resource abundance was fixed across

cage sizes. There is a clear difference in adult oviposition behavior between *C. maculatus* and *C. chinensis*. *Callosobruchus maculatus* lays eggs much deeper in substrate than *C. chinensis* (Watanabe 1985). Therefore, the shallower depth of beans (resources) would have improved resource availability for *C. chinensis*. Theoretically, the resource availability can affect both density-dependent and independent growth; however, I recorded no (or weak) signals in CCM (i.e., density-dependent effect), implying that such effects improved the density-independent growth rate of *C. chinensis*. This phenomenon might explain how larger cage sizes led to the longer persistence of *C. chinensis* with *C. maculatus*. Accordingly, the shallower slopes in Fig. 6 could be interpreted as the contribution of interspecific interactions (i.e., density-dependent effect) being weaker when the density independent growth of *C. chinensis* is better.

The relationship between interspecific interaction strength and the coexistence period corresponded well to the established competitive asymmetry of the two *Callosobruchus* species (Kawatsu and Kishi 2018). *C. chinensis* is superior with respect to reproductive interference (RI), because *C. maculatus* is affected by the interspecific sexual interaction, whereas *C. chinensis* is not. The best model included the effect of *C. chinensis* with and without time lag ($tp = -1, -3$). It is reasonable to hypothesize that the stronger effect of RI from competitively inferior *C. chinensis* to *C. maculatus* probably appeared immediately in the adult abundance of the same generation without any influence of time lag ($tp = 0$) via impacts on longevity (Kishi et al. 2009), and in the next generation with time lag ($tp = -4$) via influences on fecundity. However, the selected interaction with $tp = -1$ could be equally possible when adult males of *C. chinensis* that were counted in a census shortens the longevity of *C. maculatus* females and thereby reduce the number of *C. maculatus* adults in the next census. The interaction with $tp = -3$ could be also possible because both $tp = -3$ and $tp = -4$ (i.e., effects of *C. chinensis* adults that were present three and four weeks ago) approximately correspond to one generation (~4 weeks).

In conclusion, my experiments and EDM showed that the stronger reproductive interference effect of *C. chinensis* on *C. maculatus* contributed to longer coexistence of competitively inferior *C. chinensis* with *C. maculatus*. This experimental study provides a good example of the direct effect of interaction strength on population dynamics and species coexistence. Unexpectedly, the effect of changing habitat size itself on species coexistence was not realized by altering the intra- and inter-specific interaction strength of coexisting species, but was directly achieved through altering resource availability for competitively inferior *C. chinensis*. My results also demonstrate the difficulty of changing habitat size to alter interaction strength without significantly affecting resource availability in my system. Environmental conditions and interaction strength could, alternatively, be linked by using the natural variability of environmental variables, and applying EDM to the long-term time series of both populations and environmental variables in natural systems (e.g., Liu and Gaines 2022). To alter interaction strength directly, future studies need more sophisticated experimental settings, including controlling both the depth and horizontal spatial distribution of resource layers.

Figures and Tables

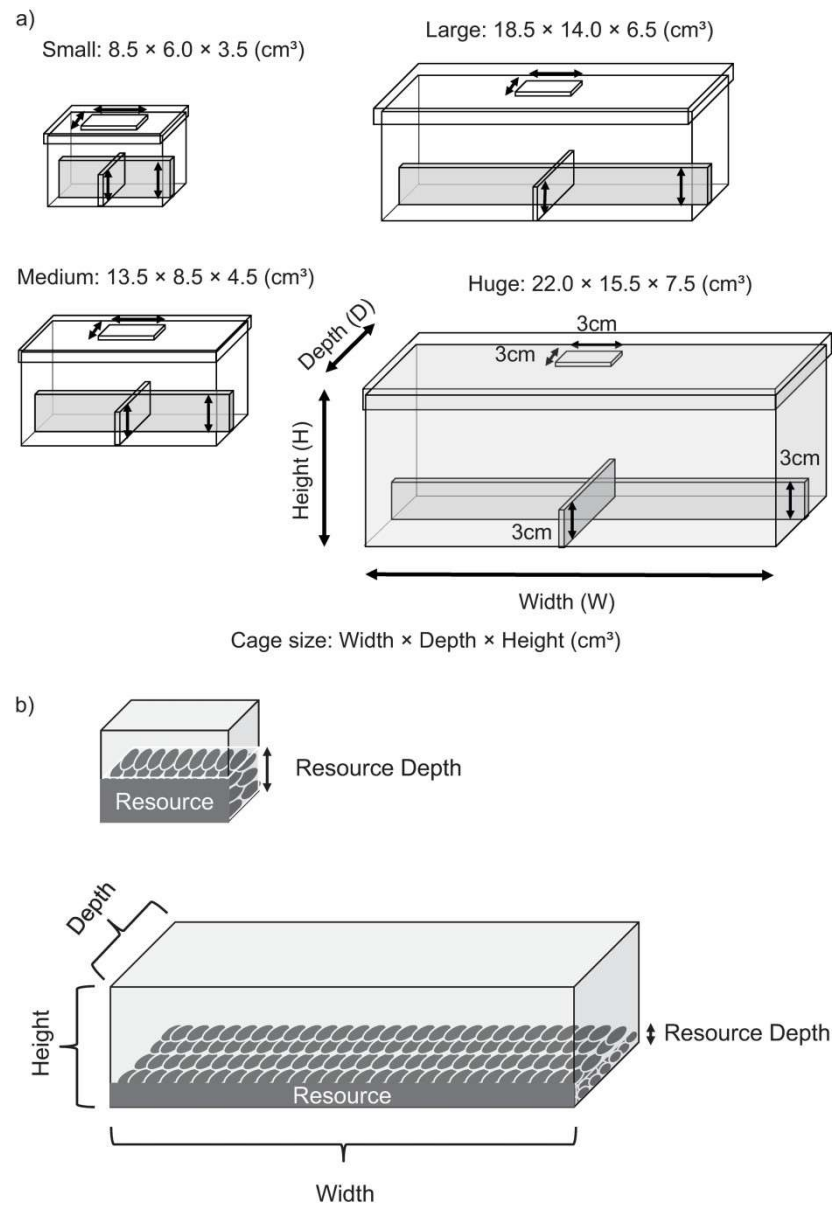


Figure 1. Cage sizes in my competitive experiment. (a) Cage sizes in my experiment. I used four cage sizes. These cages were made from polypropylene and polyethylene. An air vent was made at the center of lid. I made replicates of each cage. Details are provided in Table S1. (b) Images of resource conditions in cages. I used the same weight of resources (10 g), so the thickness of the resource ($\leftrightarrow$) differed across cage sizes.

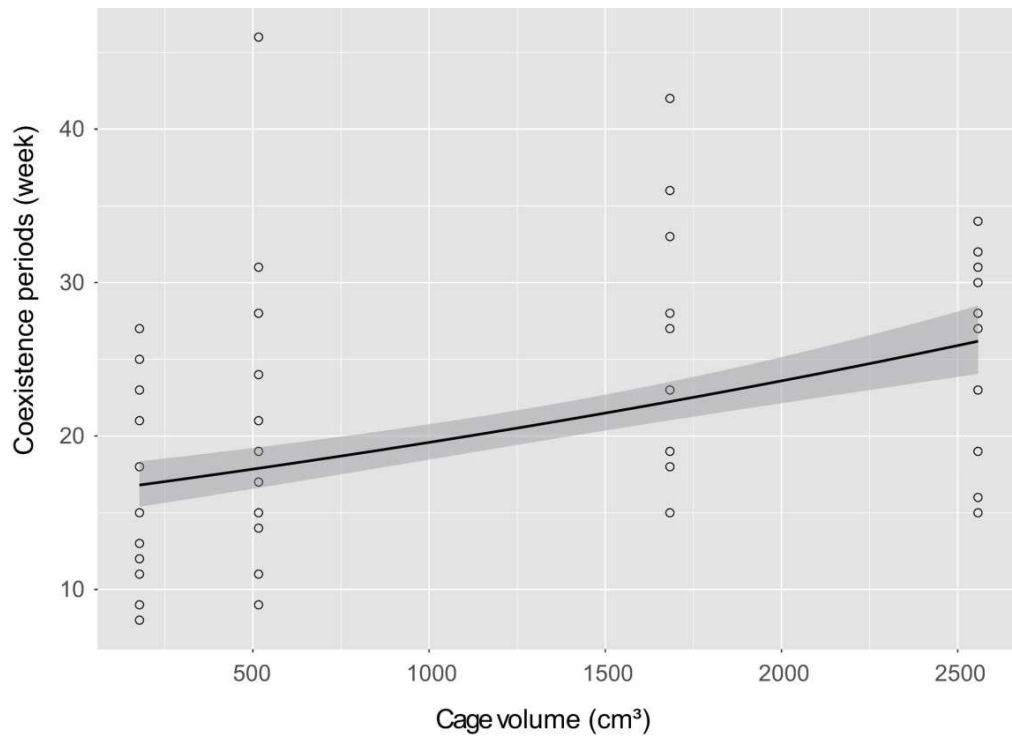


Figure 2. Results of the *Callosobruchus* beetle competition experiments. The solid line and shaded area represent the regression line and its 95 % confidence interval, respectively. Coexistence periods was extended when cage volume was larger (GLM: with Poisson distribution: coefficient = 1.863×10^{-4} , $P = 8.478 \times 10^{-11}$).

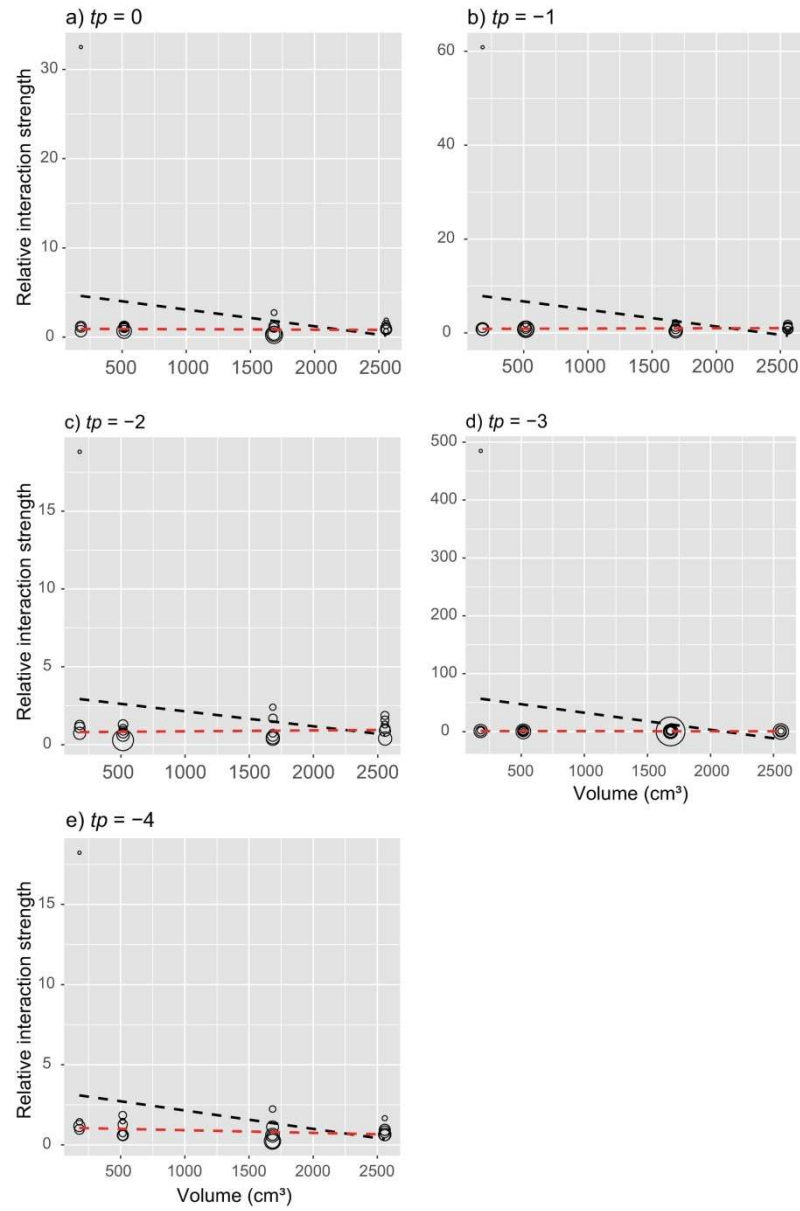


Figure 3. Relationship between cage volume and relative interaction strength of *Callosobruchus maculatus* on *Callosobruchus chinensis*. Points are sized relative to the weight of each point estimate, which is the inverse of the standard error of the forecast skill (ρ). Black and blue lines represent a relationship fitted using ordinary least squares and weighted least squares, respectively. None of the relationships were significant ($P > 0.05$).

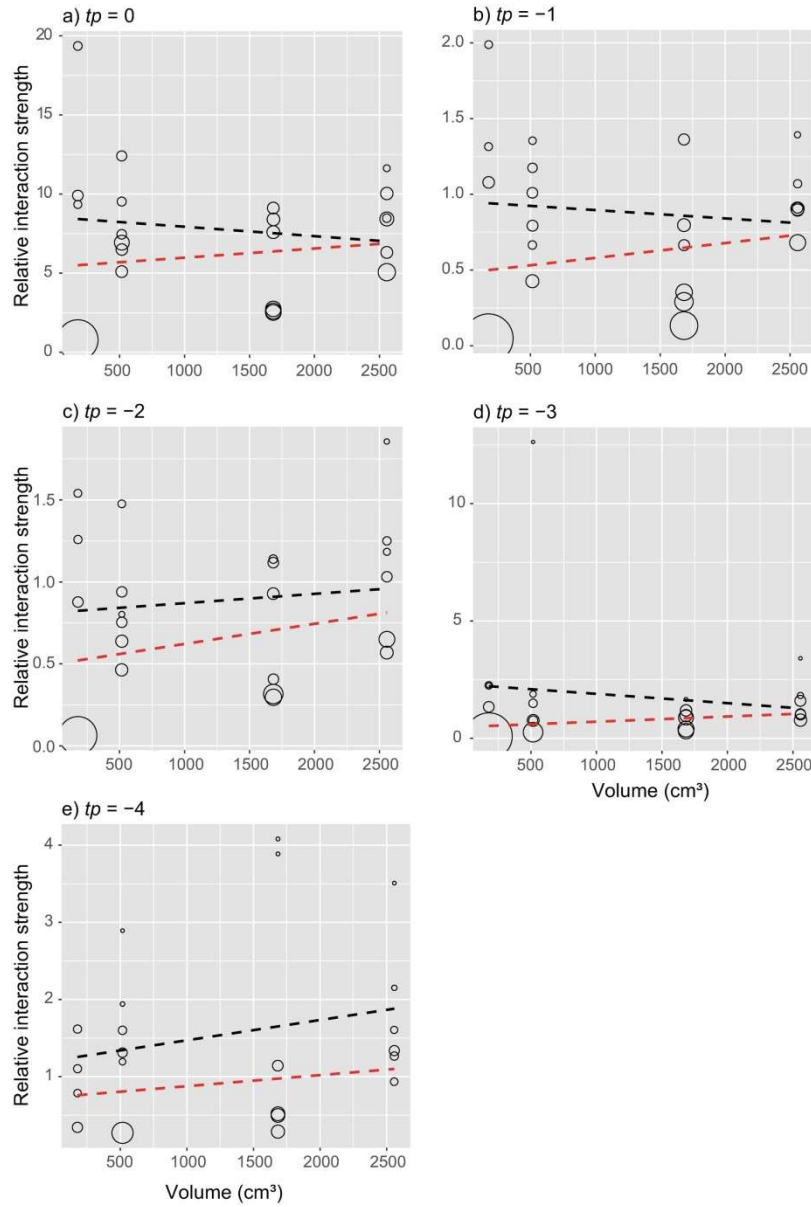


Figure 4. Relationship between cage volume and relative interaction strength of *Callosobruchus chinensis* on *Callosobruchus maculatus*. Points are sized relative to the weight of each point estimate, which is the inverse of the standard error of the forecast skill (ρ). Black and blue lines represent a relationship fitted using ordinary least squares and weighted least squares, respectively. None of the relationships were significant ($P > 0.05$).

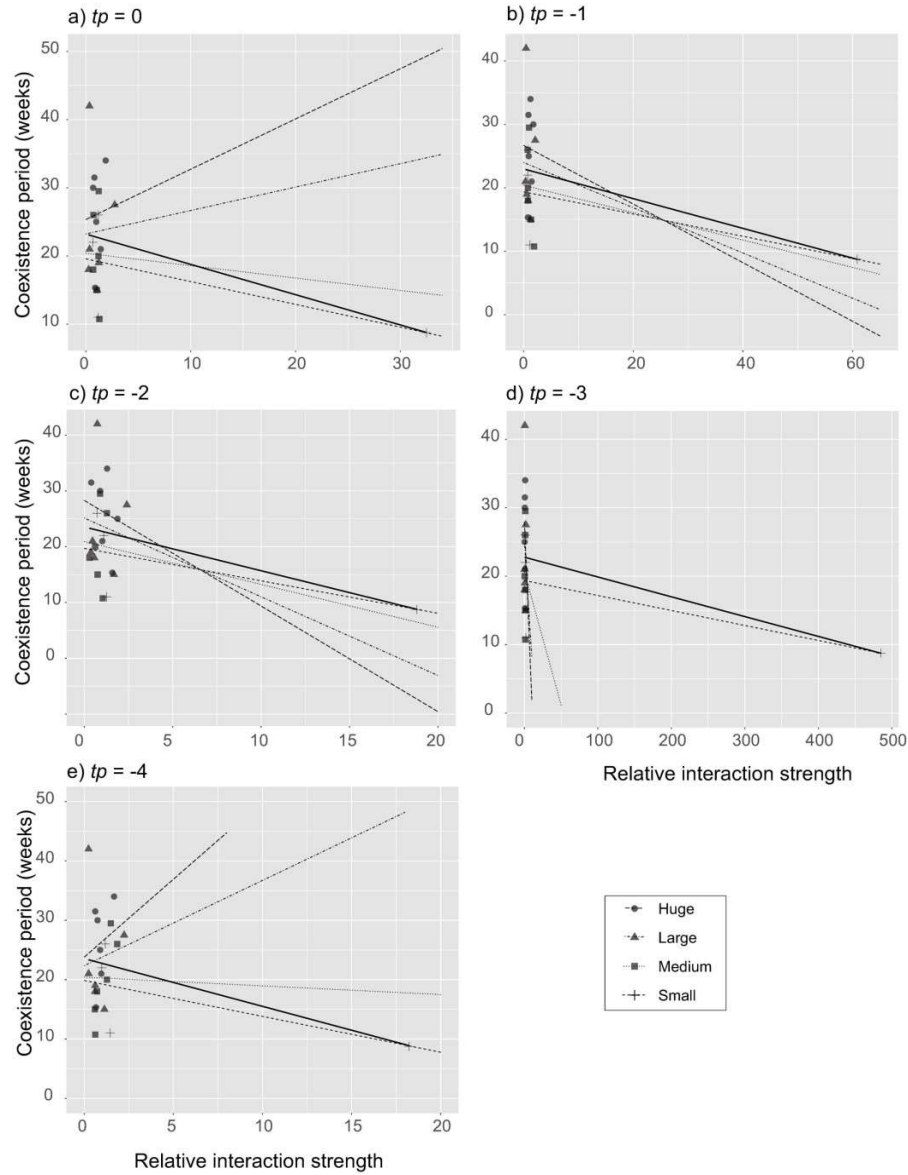


Figure 5. Relationship between cage size, relative interspecific interaction strength of *C. maculatus* (effect of *C. maculatus* on *C. chinensis*), and coexistence period. GLM was used to check if the interaction effect existed (Table S3). x-axis is the relative strength, y-axis is the coexistence period (week). Each color in the legend represents the volume of each cage size. None of the relationships were significant ($P > 0.05$). Thus, they were not included in the full model for detecting the best model with AIC (Table S5).

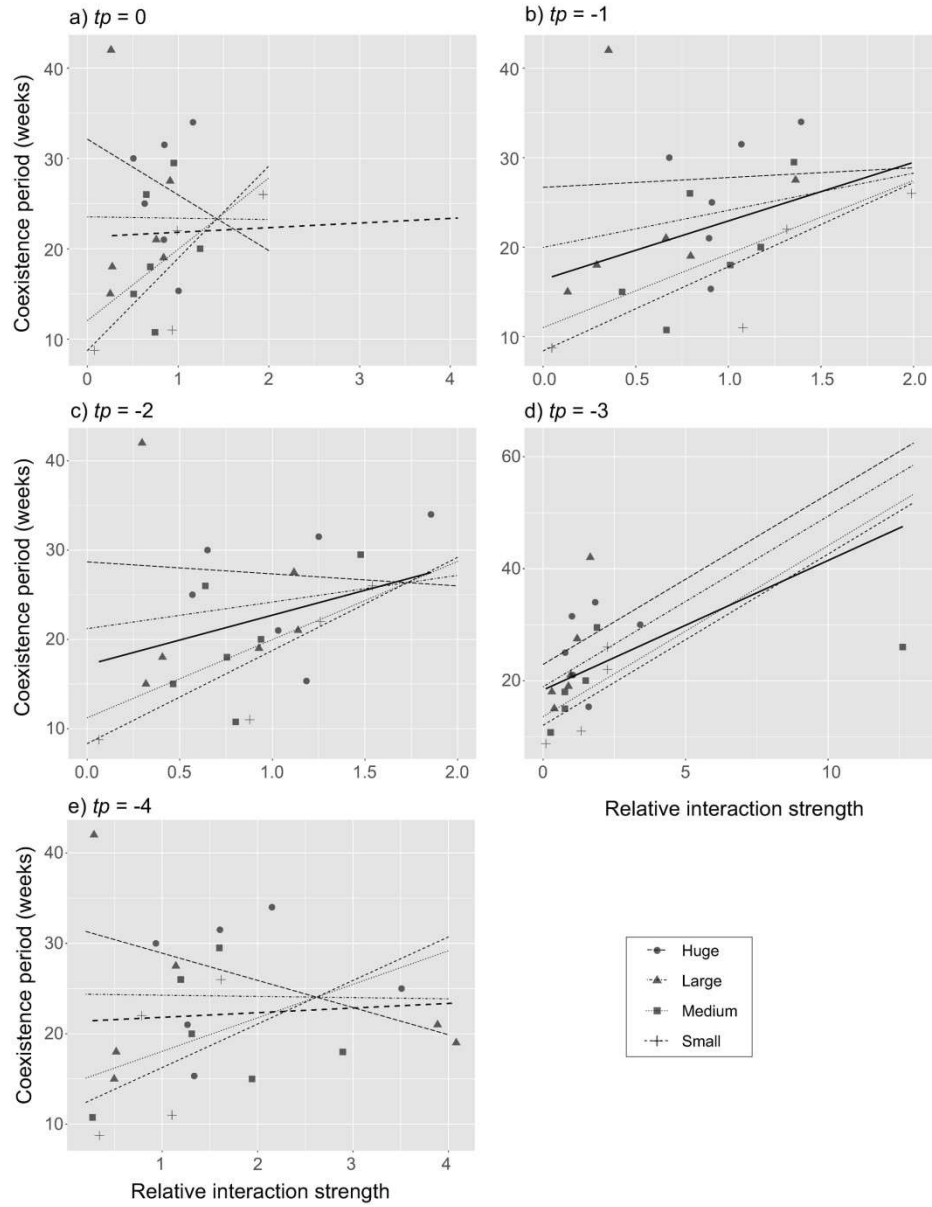


Figure 6. GLM results showing the relative strength of *Callosobruchus chinensis* for the interaction effects. GLM detected an interaction effect (Table S4). X-axis is relative strength, y-axis is coexistence period (week). Each color in the legend represents the volume of each cage size. These solid-line and broken-lines on tps were significant and non-significant ($P > 0.05$; Table S4). Thus, significant relationships on $tp=0, -1, -2$ and -4 were included in full model for detecting the best model with AIC (Table S5).

Table 1. Details on the combined time series data and summary of EDM (Empirical Dynamic Modeling) analysis for each replicate. I summarized the EDM results for the combined time series data of each replicate. Number of NAs (Not Available) is how many NAs were inserted between time series data to combine short time series data for replicates. I adopted the larger optimal embedding dimension (E^*) for the number of NAs, which was calculated for each species and replicate by simplex_projection for combining. Cc and Cm represent the population dynamics of *Callosobruchus chinensis* and *Callosobruchus maculatus*, respectively. Rho (ρ) represents the correlation coefficient from univariate S-map analysis.

Small	S1	S1	S2	S2	S3	S3	S4	S4	S4	S5	S5	S5	S6	S6	S6	S6
Original ID	23	4	24	9	25	34	5	18	35	36	48	49	13	33	57	56
Number of NAs	9		8		5		6		4		3					
Embedding dimension for a replicate: Cm, Cc	8,5	9,5	8,5	4,4	5,3	5,5	4,6	2,1	4,5	4,1	1,1	4,2	1,2	1,3	1,3	1,1
Coexistence periods (week)	27	25	23	21	18	15	13	12	12	11	11	11	9	9	9	8
Average of coexistence periods	26.00		22.00		16.50		12.33		11.00		8.75					
Embedding dimension for combined time series data: Cm, Cc	5,10		4,3		10,3		5,7		3,4		8,4					
Nonlinearity for combined time series data: Cm, Cc	4,1		2,8		0,0		2,0		8,3		0.003,3					
The difference of ρ_{ho} between $\theta = 0$ and the best θ : Cm, Cc	0.108,0.019		0.109,0.354		0,0		0.137,0		0.561,0.711		2.55 $\times 10^{-18}$,0.425					
Medium	M1	M2	M2	M3	M3	M4	M4	M5	M5	M6	M6	M6	M7	M7	M7	M7
Original ID	38	20	19	21	51	3	22	39	6	37	40	50	16	58	12	59
Number of NAs	0	10		10		8		5		6		5				
Embedding dimension for a replicate: Cm, Cc	7,8	7,9	10,8	5,5	6,10	4,8	4,3	1,1	4,5	5,1	1,6	4,2	4,5	4,2	1,1	1,2
Coexistence periods (week)	46	31	28	28	24	21	19	19	17	15	15	15	14	11	9	9
Average of coexistence periods	46.00	29.50		26.00		20.00		18.00		15.00		10.75				
Embedding dimension for combined time series data: Cm, Cc	7,8	8,8		9,7		5,10		8,5		6,5		8,5				
Nonlinearity for combined time series data: Cm, Cc	3,0	2,3		1,5,4		2,0.75		0.75,3		3,3		1,8				
The difference of ρ_{ho} between $\theta = 0$ and the best θ : Cm, Cc	0.097,0	0.174,0.147		0.052,0.065		0.061,0.020		0.026,0.180		0.152,0.089		0.011,0.216				
Large	L1	L2	L3	L3	L4	L4	L5	L5	L6	L6	L7	L7	L8	L8	L8	L8
Original ID	52	15	2	26	28	27	53	42	43	44	7	10	17	41	60	61
Number of NAs	0	0	10		9		9		8		5		6			
Embedding dimension for a replicate: Cm, Cc	8,2	9,8	8,2	7,10	7,6	6,9	4,9	4,3	4,5	8,3	5,2	4,5	1,6	5,4	4,3	4,2
Coexistence periods (week)	42	36	33	28	28	27	23	19	19	19	18	18	15	15	15	15
Average of coexistence periods	42.0	36.0	30.5		27.5		21.0		19.0		18.0		15.0			
Embedding dimension for combined time series data: Cm, Cc	8,2	9,8	4,10		9,10		4,9		5,9		5,1		5,5			
Nonlinearity for combined time series data: Cm, Cc	3,6	4,0	0,0		6,1,5		2,8		2,1,5		1,5,8		2,4			
The difference of ρ_{ho} between $\theta = 0$ and the best θ : Cm, Cc	0.165,0.165	0.109,0	0,0		0.080,0.144		0.109,0.032		0.248,0.118		0.061,0.201		0.119,0.379			
Huge	H1	H2	H2	H3	H3	H4	H4	H5	H5	H6	H6	H7	H7	H8	H8	H8
Original ID	1	47	54	14	29	30	31	32	45	46	55	63	11	64	8	62
Number of NAs	0	10		10		10		10		10		8		5		
Embedding dimension for a replicate: Cm, Cc	6,7	6,5	10,3	8,8	10,1	4,6	8,10	10,9	5,7	10,3	4,5	4,2	8,1	4,3	1,5	4,5
Coexistence periods (week)	34	32	31	30	30	28	28	27	27	27	23	23	19	16	15	15
Average of coexistence periods	34	31.5		30.0		28.0		27.0		25.0		21.0		15.333		
Embedding dimension for combined time series data: Cm, Cc	6,7	10,4		10,9		6,6		5,8		5,6		5,9		4,5		
Nonlinearity for combined time series data: Cm, Cc	6,1,5	2,8		6,3		0,3		2,0		1,1		1,6		2,2		
The difference of ρ_{ho} between $\theta = 0$ and the best θ : Cm, Cc	0.054,0.043	0.137,0.021		0.141,0.030		0,0.158		0.095,0		0.005,0.019		0.028,0.087		0.143,0.033		

Table 2. Effect of volume on the relative strength of *C. maculatus*. Linear model (lm) was implemented to check that volume affected the relative strength for *Callosobruchus maculatus* (ρ) using OLS (Ordinary Least Squares) and WLS (Weighted Least Squares). I could not confirm a significant difference for volume. * represents a confirmed significant difference ($P < 0.05$) for explanatory variables. tp represents the time delay used for Cross Convergent Mapping analysis.

OLS						WLS					
$tp = 0$	Estimate	Std. Error	t value	$Pr(> t)$	Adjusted R -squared	$tp = 0$	Estimate	Std. Error	t value	$Pr(> t)$	Adjusted R -squared
(Intercept)	4.957	2.471	2.005	0.059	0.0234	(Intercept)	9.3955×10^{-1}	2.576×10^{-1}	3.647	0.002*	(Negative)
Volume	-1.867×10^{-3}	1.522×10^{-3}	-1.226	0.234		Volume	-4.844×10^{-5}	1.644×10^{-4}	-0.295	0.771	
$tp = -1$	Estimate	Std. Error	t value	$Pr(> t)$	Adjusted R -squared	$tp = -1$	Estimate	Std. Error	t value	$Pr(> t)$	Adjusted R -squared
(Intercept)	8.489	4.686	1.812	0.085	0.0241	(Intercept)	8.6755×10^{-1}	3.539×10^{-1}	2.452	0.024*	(Negative)
Volume	-3.557×10^{-3}	2.886×10^{-3}	-1.232	0.232		Volume	5.862×10^{-5}	2.325×10^{-4}	0.252	0.804	
$tp = -2$	Estimate	Std. Error	t value	$Pr(> t)$	Adjusted R -squared	$tp = -2$	Estimate	Std. Error	t value	$Pr(> t)$	Adjusted R -squared
(Intercept)	3.009	1.418	2.186	0.041*	0.0099	(Intercept)	5.862×10^{-5}	2.325×10^{-4}	0.252	0.804	
Volume	-9.602×10^{-4}	8.732×10^{-4}	-1.100	0.285		Volume	5.951×10^{-5}	1.975×10^{-4}	0.301	0.766	
$tp = -3$	Estimate	Std. Error	t value	$Pr(> t)$	Adjusted R -squared	$tp = -3$	Estimate	Std. Error	t value	$Pr(> t)$	Adjusted R -squared
(Intercept)	62.045	37.843	1.64	0.117	0.0276	(Intercept)	1.043	6.050×10^{-1}	1.723	0.1	(Negative)
Volume	-2.944×10^{-2}	2.331×10^{-2}	-1.263	0.221		Volume	-2.315×10^{-4}	3.547×10^{-4}	-0.653	0.521	
$tp = -4$	Estimate	Std. Error	t value	$Pr(> t)$	Adjusted R -squared	$tp = -4$	Estimate	Std. Error	t value	$Pr(> t)$	Adjusted R -squared
(Intercept)	3.299	1.35	2.443	0.024*	0.0412	(Intercept)	1.088	2.795×10^{-1}	3.893	0.001*	0.0027
Volume	-1.148×10^{-3}	8.319×10^{-4}	-1.380	0.183		Volume	-1.673×10^{-4}	1.627×10^{-4}	-1.028	0.316	

Supporting Information

Standardized cross map skills based on a common-library length for each cage size

This method was used to standardize the index of interspecific interaction strength for each cage size. In addition to the method described in the main text, I implemented a separate method to standardize interaction strength. I used the ρ value at the common library size (= 106), which is the length of the shortest time series (i.e., small cage size). The value at the common library size (= 106) depends on that at the minimum library size, and how it increases with increasing library size. To exclude the effect of the value from the maximum library size for each cage size, I used an increment in the ρ value (i.e., the differences in ρ values from the common length [= 106]) as the index of interaction strength.

The absolute values of the interaction strength defined by our method were expected to be lower when population dynamics is more strongly influenced by random noise. To focus on the deterministic drivers of population dynamics, I calculated the ratio of the increments of ρ from the interspecific interaction to that from the intraspecific interaction as the index of the relative strength of interspecific interactions. Namely, the ratio was the index used to determine the result of competitive examination. I also used common library length (= 106) for the intraspecific interaction.

However, this method generated many outliers. The increment for the intraspecific interaction tended to be very small; consequently, the division of the increment for the interspecific interaction by such small values led to values that were too large. Thus, this method was not considered appropriate for the standardizing the interaction strength.

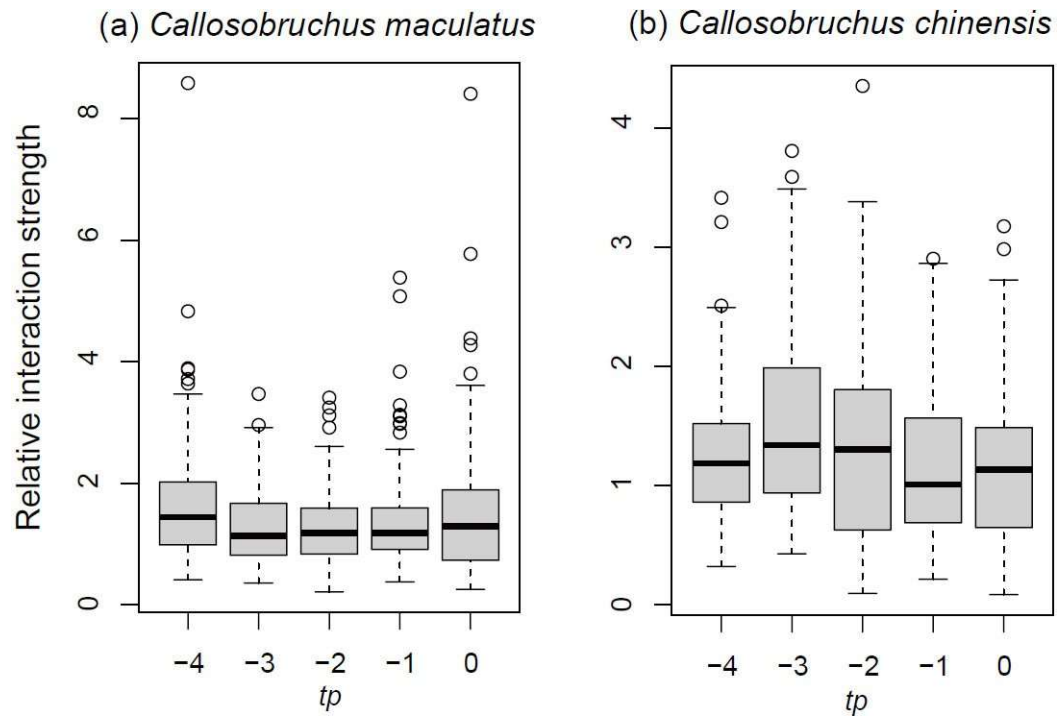


Figure S1. Examples of the distributions for the relative strength. (a) *Callosobruchus chinensis* and (b) *Callosobruchus maculatus*. The developed method aimed to standardize the relative strength using the common library length (106), but this method was inappropriate.

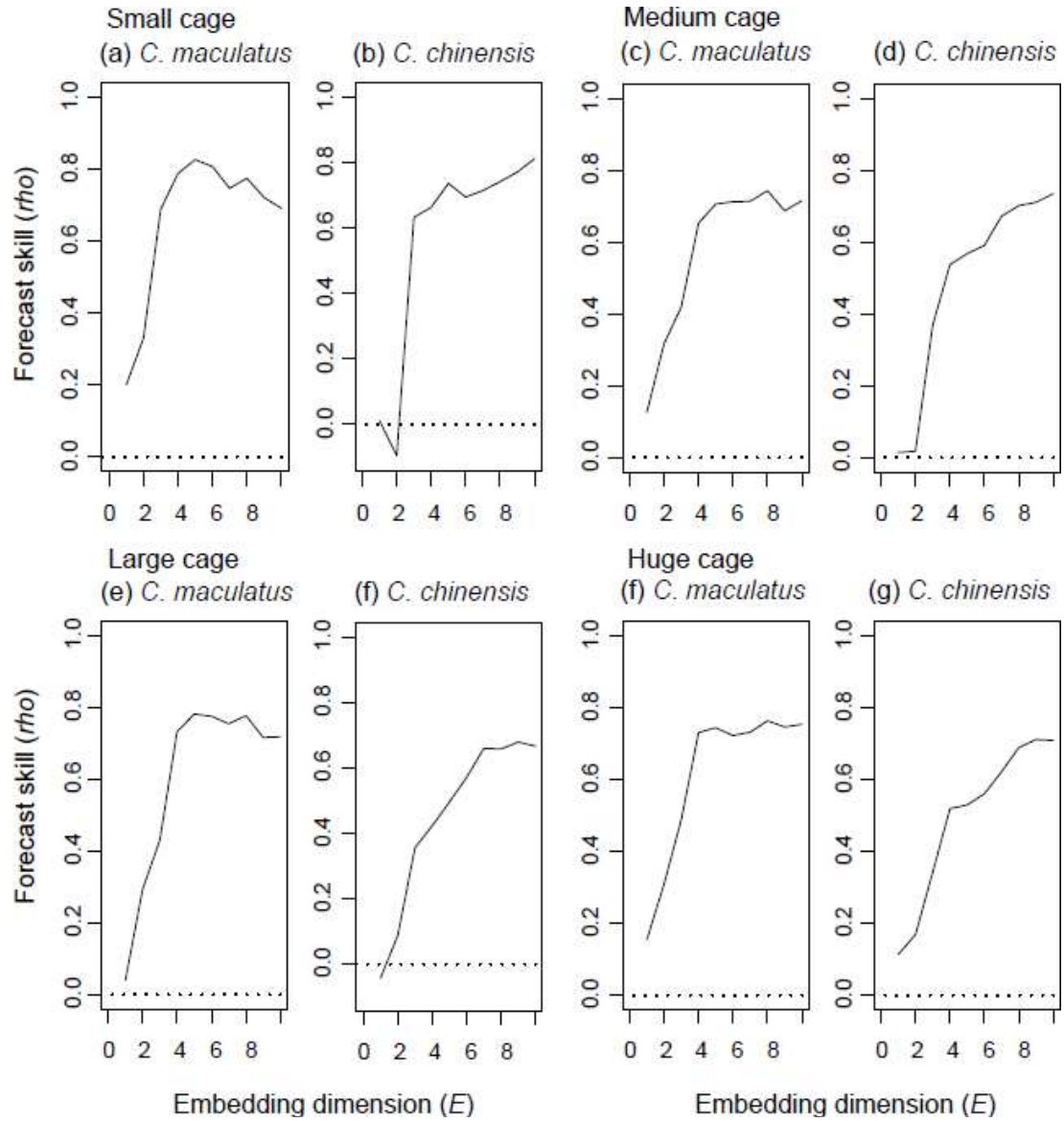


Figure S2. Detection of the optimal embedding dimension (E^*) for each cage size using the function `simplex()`. Horizontal and vertical axes represent the embedding dimension and forecast skill (ρ), respectively. I tested each dimension between 1 and 10, with an interval 1. I determined the optimal embedding dimension (E^*) using the highest ρ , which was calculated with the function `simplex()`. I could check nonlinearity for all combined time series data by `smap()` with each E^* .

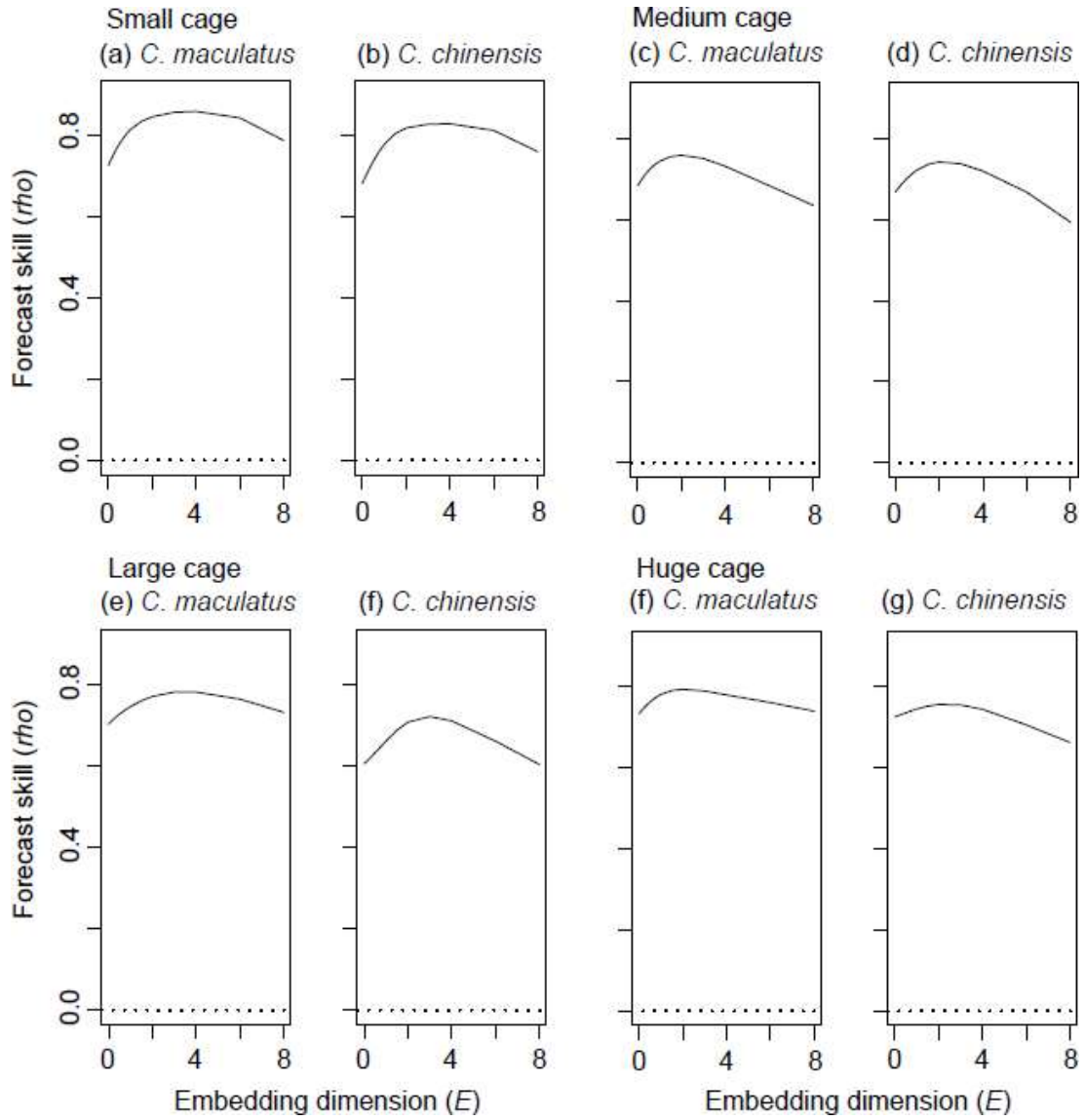


Figure S3. Detection of the weight of nonlinearity (θ) for each cage size using the function *smap* (). Horizontal and vertical axes are the θ and forecast skill (ρ), respectively. The time series data were driven by linear dynamics when the forecast skill was the highest at $\theta = 0$. Therefore, the time series data from each cage size showed nonlinear dynamics. I could check causality between all combined time series data with CCM.

Table S1. Details of the competitive experiment (*Callosobruchus. Chinensis*: *C.c*, *Callosobruchus. Maculatus*: *C.m*). I examined 64 cages. The longest observation period lasted 46 weeks in cage No. 38 (Medium). The shortest observation period lasted 8 weeks in cage No. 56 (Small).

Cage Size	Cage No.	Strain of <i>C.c</i>	Coexistence Weeks	Result of competition	Cage Size	Cage No.	Strain of <i>C.c</i>	Coexistence Weeks	Results of competition
Small	4	jc-F	25	<i>C.m</i>	Small	5	msC	13	<i>C.m</i>
Small	9	jc-F	21	<i>C.m</i>	Small	13	msC	9	<i>C.m</i>
Small	18	jc-F	12	<i>C.m</i>	Small	33	msC	9	<i>C.m</i>
Small	23	jc-F	27	<i>C.m</i>	Small	34	msC	15	<i>C.m</i>
Small	24	jc-F	23	<i>C.m</i>	Small	35	msC	12	<i>C.m</i>
Small	25	jc-F	18	<i>C.m</i>	Small	36	msC	11	<i>C.m</i>
Small	48	jc-F	11	<i>C.m</i>	Small	56	msC	8	<i>C.m</i>
Small	49	jc-F	11	<i>C.m</i>	Small	57	msC	9	<i>C.m</i>
Medium	3	jc-F	21	<i>C.m</i>	Medium	6	msC	17	<i>C.m</i>
Medium	16	jc-F	14	<i>C.m</i>	Medium	12	msC	9	<i>C.m</i>
Medium	19	jc-F	28	<i>C.m</i>	Medium	37	msC	15	<i>C.m</i>
Medium	20	jc-F	31	<i>C.m</i>	Medium	38	msC	46	Coexistence
Medium	21	jc-F	28	<i>C.m</i>	Medium	39	msC	19	<i>C.m</i>
Medium	22	jc-F	19	<i>C.m</i>	Medium	40	msC	15	<i>C.m</i>
Medium	50	jc-F	15	<i>C.m</i>	Medium	58	msC	11	<i>C.m</i>
Medium	51	jc-F	24	<i>C.m</i>	Medium	59	msC	9	<i>C.m</i>
Large	2	jc-F	33	<i>C.m</i>	Large	7	msC	18	<i>C.m</i>

Large	15	jc-F	36	<i>C.m</i>	Large	10	msC	18	<i>C.m</i>
Large	26	jc-F	28	<i>C.m</i>	Large	17	msC	15	<i>C.m</i>
Large	27	jc-F	27	<i>C.m</i>	Large	41	msC	15	<i>C.m</i>
Large	28	jc-F	28	<i>C.m</i>	Large	42	msC	19	<i>C.m</i>
Large	52	jc-F	42	Coexistence	Large	43	msC	19	<i>C.m</i>
Large	53	jc-F	23	<i>C.m</i>	Large	44	msC	19	<i>C.m</i>
Huge	1	jc-F	34	<i>C.m</i>	Large	60	msC	15	<i>C.m</i>
Huge	14	jc-F	30	<i>C.c</i>	Large	61	msC	15	<i>C.m</i>
Huge	29	jc-F	30	<i>C.c</i>	Huge	8	msC	15	<i>C.c</i>
Huge	30	jc-F	28	<i>C.m</i>	Huge	11	msC	19	<i>C.m</i>
Huge	31	jc-F	28	<i>C.m</i>	Huge	45	msC	27	<i>C.m</i>
Huge	32	jc-F	27	<i>C.m</i>	Huge	46	msC	27	<i>C.m</i>
Huge	54	jc-F	31	<i>C.m</i>	Huge	47	msC	32	<i>C.m</i>
Huge	55	jc-F	23	<i>C.c</i>	Huge	62	msC	15	<i>C.m</i>
					Huge	63	msC	23	<i>C.m</i>
					Huge	64	msC	26	<i>C.m</i>

Table S2. Comparison of linear models for OLS and WLS with the function *anova(lm())*. The models were used to assess the relationship between cage volume (cm^3) and relative interaction strength for (a) *C.m* and (b) *C.c*. There were none of significant difference in any model. Thus, none of difference was between OLS and WLS with *lm*.

(a) Effect of *C. m* on *C. c*

OLS					
<i>tp</i> = 0	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	200.74	66.91	1.6069	0.2228
Residuals	18	749.55	41.64	NA	NA
<i>tp</i> = -1	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	718.55	239.52	1.5971	0.2250
Residuals	18	2699.48	149.97	NA	NA
<i>tp</i> = -2	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	65.63	21.88	1.6223	0.2193
Residuals	18	242.71	13.48	NA	NA
<i>tp</i> = -3	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	4.82×10^5	1.61×10^5	1.6488	0.2135
Residuals	18	1.75×10^6	9.75×10^3	NA	NA
<i>tp</i> = -4	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	66.60	22.20	1.7969	0.1839
Residuals	18	222.38	12.36	NA	NA
WLS					
<i>tp</i> = 0	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	7.54	2.51	0.4034	0.7523
Residuals	18	112.11	6.23	NA	NA
<i>tp</i> = -1	Df	Sum Sq	Mean Sq	F value	Pr(>F)

Volume class	3	7.35	2.45	0.1641	0.9191
Residuals	18	268.50	14.92	NA	NA
$tp = -2$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	10.32	3.44	0.3136	0.8153
Residuals	18	197.44	10.97	NA	NA
$tp = -3$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	17.70	5.90	0.1603	0.9217
Residuals	18	662.69	36.82	NA	NA
$tp = -4$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	12.98	4.32	0.6923	0.5686
Residuals	18	112.45	6.25	NA	NA

(b) Effect of *C. c* on *C. m*

OLS					
$tp = 0$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	0.50	0.17	1.0574	0.3916

Residuals	18	2.86	0.16	NA	NA
$tp = -1$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	0.74	0.25	1.1597	0.3524
Residuals	18	3.82	0.21	NA	NA
$tp = -2$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	0.48	0.16	0.7615	0.5303
Residuals	18	3.74	0.21	NA	NA
$tp = -3$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	13.58	453	0.6646	0.5846
Residuals	18	124.77	6.93	NA	NA
$tp = -4$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	1.97	0.65	0.4798	0.7004
Residuals	18	24.57	1.37	NA	NA
WLS					
$tp = 0$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	9.12	3.04	0.8753	0.4722
Residuals	18	62.49	3.47	NA	NA
$tp = -1$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	20.94	6.98	1.4846	0.2524
Residuals	18	84.63	4.70	NA	NA
$tp = -2$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	11.75	3.92	1.1233	0.3659
Residuals	18	62.74	3.49	NA	NA

$tp = -3$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	20.68	6.89	0.9943	0.4179
Residuals	18	124.77	6.93	NA	NA
$tp = -4$	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Volume class	3	16.19	5.40	1.1479	0.3567
Residuals	18	84.61	4.70	NA	NA

Table S3. Effect of the relative strength for *Callosobruchus maculatus*. Generalized linear model (GLM) and stepwise model selection were used to assess whether the relative strength affected the number of coexistence weeks. * represents significant difference ($P < 0.05$) for explanatory variables. I confirmed the negative relationship for all tp between the relative strength and Volume. The interaction term (Relative strength:Volume) did not remain in the best models for all tp .

$tp = 0$	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	19.014	2.767	6.871	1.484×10^{-6}	*
Volume	2.943×10^{-3}	1.823×10^{-3}	1.615	1.229×10^{-1}	
Relative strength	-3.319×10^{-1}	1.214×10^{-1}	-2.735	1.314×10^{-2}	*
$tp = -1$	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	18.868	2.725	6.924	1.335×10^{-6}	*
Volume	2.928×10^{-3}	1.820×10^{-3}	1.609	1.242×10^{-1}	
Relative strength	-1.757×10^{-1}	6.355×10^{-2}	-2.764	1.236×10^{-2}	*
$tp = -2$	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	19.222	2.806	6.850	1.548×10^{-6}	*
Volume	2.967×10^{-3}	1.809×10^{-3}	1.640	1.173×10^{-1}	
Relative strength	-5.863×10^{-1}	2.122×10^{-1}	-2.762	1.239×10^{-2}	*
$tp = -3$	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	18.725	2.700	6.934	1.309×10^{-6}	*
Volume	2.914×10^{-3}	1.829×10^{-3}	1.594	1.275×10^{-1}	
Relative strength	-2.165×10^{-2}	7.910×10^{-3}	-2.737	1.311×10^{-2}	*

$tp = -4$	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	129.311	2.880	6.712	2.048×10^{-6}	*
Volume	2.896×10^{-3}	1.853×10^{-3}	1.563	1.346×10^{-1}	
Relative strength	-5.985×10^{-1}	2.282×10^{-1}	-2.623	1.675×10^{-2}	*

Table S4. Effect of relative strength for *Callosobruchus chinensis*. Generalized linear model (GLM) and stepwise model selection were used to assess whether the relative strength affected the number of coexistence weeks. * represents significant difference ($P < 0.05$) for explanatory variables. I confirmed the positive relationship between the relative strength and coexistence weeks for all tp but it was statistically significant for $tp = -1$, -2 , and -3 only. Volume was always selected and statistically significant. The interaction term (Relative strength:Volume) did not remain in the best models except for $tp = -2$.

$tp = 0$	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	10.571	3.666	2.884	9.5169×10^{-3}	*
Volume	4.897×10^{-3}	1.189×10^{-3}	2.595	1.7765×10^{-2}	*
Relative strength	6.677	3.966	1.684	1.0863×10^{-1}	
$tp = -1$	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	8.824	2.980	2.961	8.0213×10^{-3}	*
Volume	4.994×10^{-3}	1.752×10^{-3}	2.851	1.0223×10^{-2}	*
Relative strength	7.724	3.000	2.574	1.8569×10^{-2}	*
$tp = -2$	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	6.791	3.296	2.060	5.4117×10^{-2}	*
Volume	8.559×10^{-3}	3.386×10^{-3}	2.528	2.1066×10^{-2}	*
Relative strength	11.319	4.209	2.690	1.4980×10^{-2}	*
Volume:Relative strength	-4.951×10^{-3}	3.234×10^{-3}	-1.489	1.5370×10^{-1}	
$tp = -3$	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	11.221	2.451	4.579	2.0516×10^{-4}	*
Volume	4.561×10^{-3}	1.615×10^{-3}	2.823	1.0854×10^{-2}	*

Relative strength	3.053	1.156	2.640	1.6126×10^{-2}	*
$tp = -4$	Estimate	Std. Error	t value	$\Pr(> t)$	
(Intercept)	17.032	3.256	5.231	4.7565×10^{-5}	*
Volume	3.654×10^{-3}	1.961×10^{-3}	1.863	7.7929×10^{-2}	*
Relative strength	1.450×10^{-1}	1.674	8.664×10^{-2}	9.3186×10^{-1}	

Table S5. The best model was selected with Akaike's Information Criterion (AIC) using the "stepAIC" function. I assessed whether the best model had Relative strength in the explanatory variables. I included the variables that were confirmed to be statistically significant in the best GLM model for each tp . The best model had volume and relative interaction strength for *C.chinensis* on $tp = -1$ and -3

Full model	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	13.270	6.803	1.951	0.0748	
Volume	0.005	0.002	2.512	0.0273	*
Relative strength for <i>C. m</i> on <i>C. c</i> with $tp=0$	1.903	7.713	0.247	0.8092	
Relative strength for <i>C. m</i> on <i>C. c</i> with $tp=-1$	-3.606	5.720	-0.631	0.5402	
Relative strength for <i>C. m</i> on <i>C. c</i> with $tp=-2$	-3.428	5.239	-0.654	0.5253	
Relative strength for <i>C. m</i> on <i>C. c</i> with $tp=-3$	0.439	0.476	0.923	0.3743	
Relative strength for <i>C. m</i> on <i>C. c</i> with $tp=-4$	0.172	7.249	0.023	0.9819	
Relative strength for <i>C. c</i> on <i>C. m</i> with $tp=-1$	10.147	9.144	1.110	0.2884	
Relative strength for <i>C. c</i> on <i>C. m</i> with $tp=-2$	-5.458	9.045	-0.603	0.5574	
Relative strength for <i>C. c</i> on <i>C. m</i> with $tp=-3$	1.179	1.096	1.076	0.3032	
Best model	Estimate	Std. Error	t value	Pr(> t)	
(Intercept)	7.668	2.535	3.025	0.0073	*
Volume	0.005	0.002	3.257	0.0044	*
Relative strength for <i>C. c</i> on <i>C. m</i> with $tp=-1$	6.142	2.786	2.204	0.0408	*
Relative strength for <i>C. c</i> on <i>C. m</i> with $tp=-3$	1.360	0.848	1.604	0.1261	

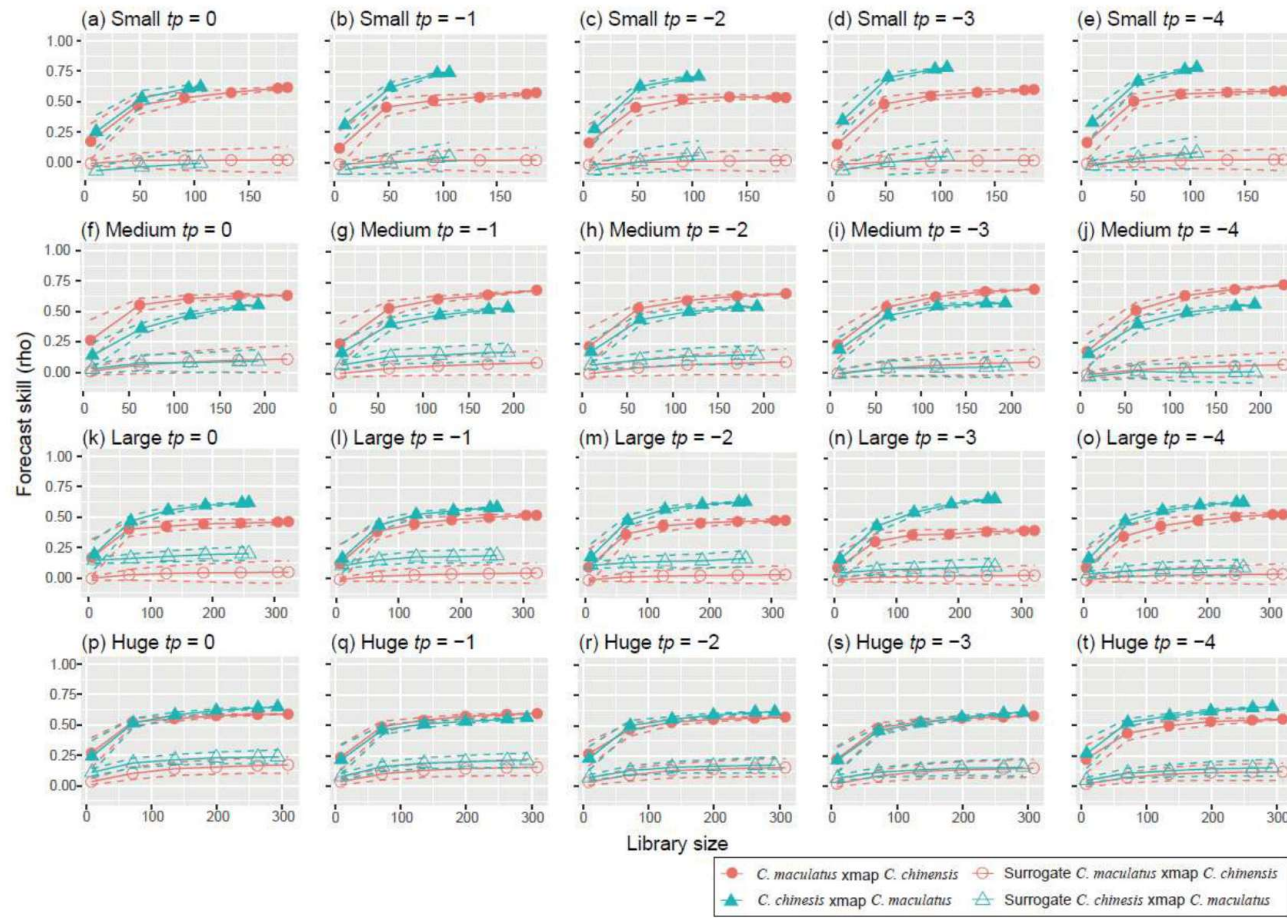


Figure S4. CCM outputs on the causality of competition between the two *Callosobruchus* beetle species. X axes are library size, y axes are ρ . Red lines are *Callosobruchus maculatus* cross-map *Callosobruchus chinensis*, whereby *Callosobruchus chinensis* affects *Callosobruchus maculatus*; blue lines are *Callosobruchus chinensis* cross-map *Callosobruchus maculatus*, whereby *Callosobruchus maculatus* affects *Callosobruchus chinensis*. Dashed red and blue line are standard deviation of them. Pink and light blue line are the null models of the red and blue lines, respectively. ρ becomes saturated with increasing library size when a relationship has causality between two beetles. CCM detected bi-directional causality in each cage size and tp .

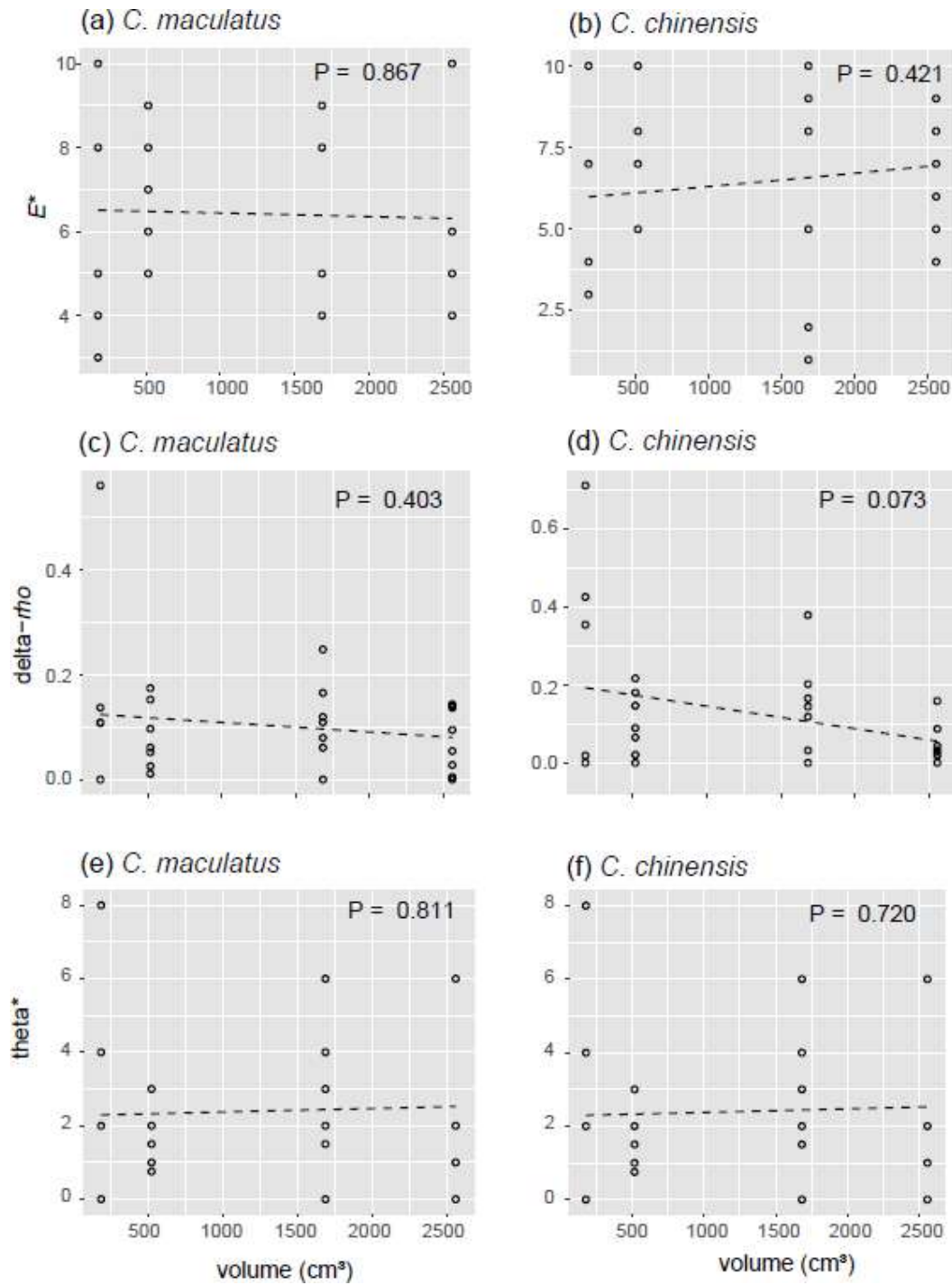


Figure S5. Relationship between cage size and parameters of EDM (E^* , $\delta\rho$ and θ^*) with lm and GLM. (a) and (b) were analyzed by GLM with Poisson distribution. (c) to d (f) were analyzed by lm. The dashed lines represent the regression lines but without statistical significance ($P \geq 0.05$).

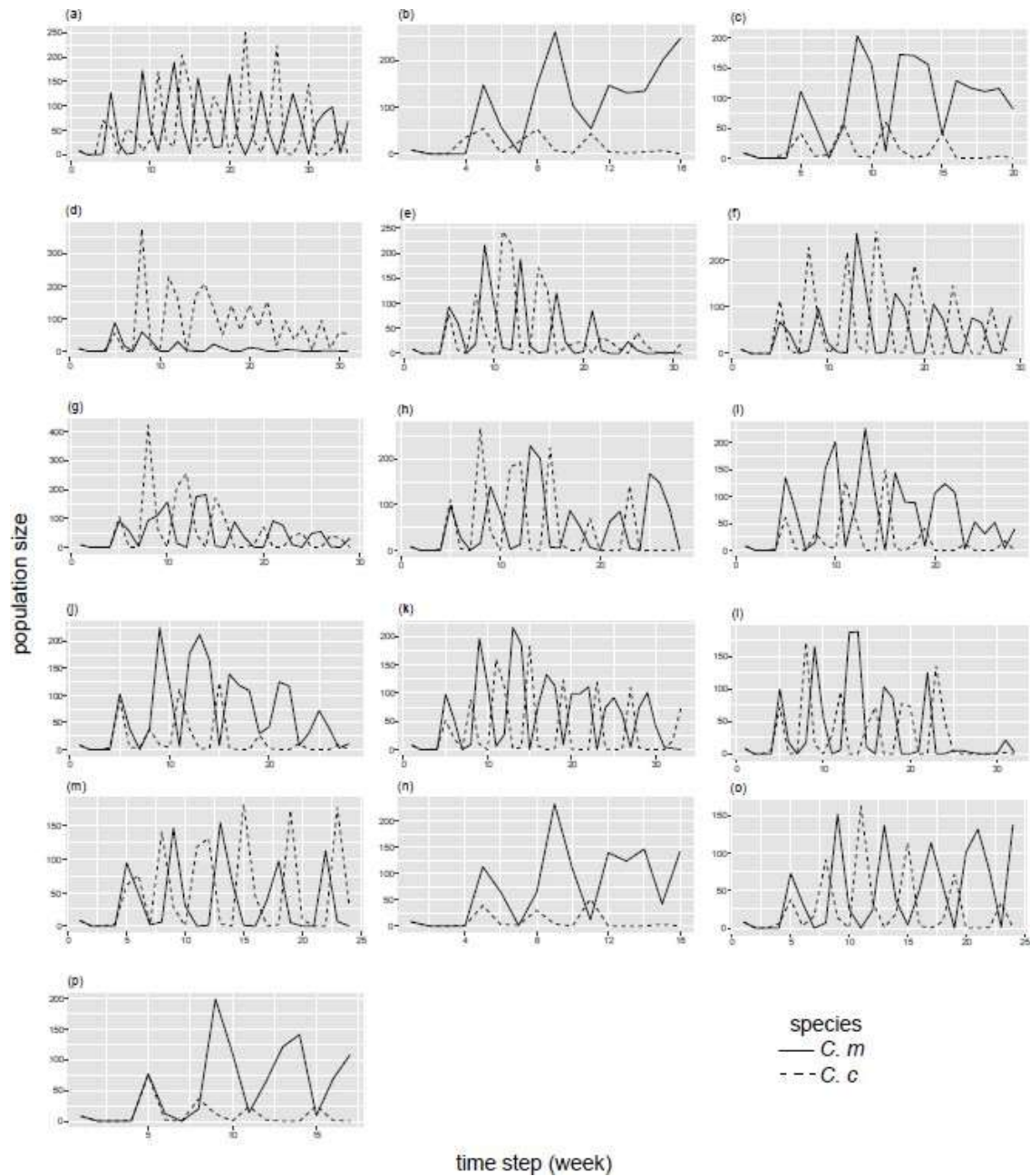


Figure S6. Examples of the population dynamics for the competition experiments with two *Callosobruchus* species in the huge cage size. Solid lines and dashed lines were *C. maculatus* and *C. chinensis*, respectively. *C. chinensis* excluded *C. maculatus* in (d), (e), (k) and (m) replicates (see also Table S1 for more detail).

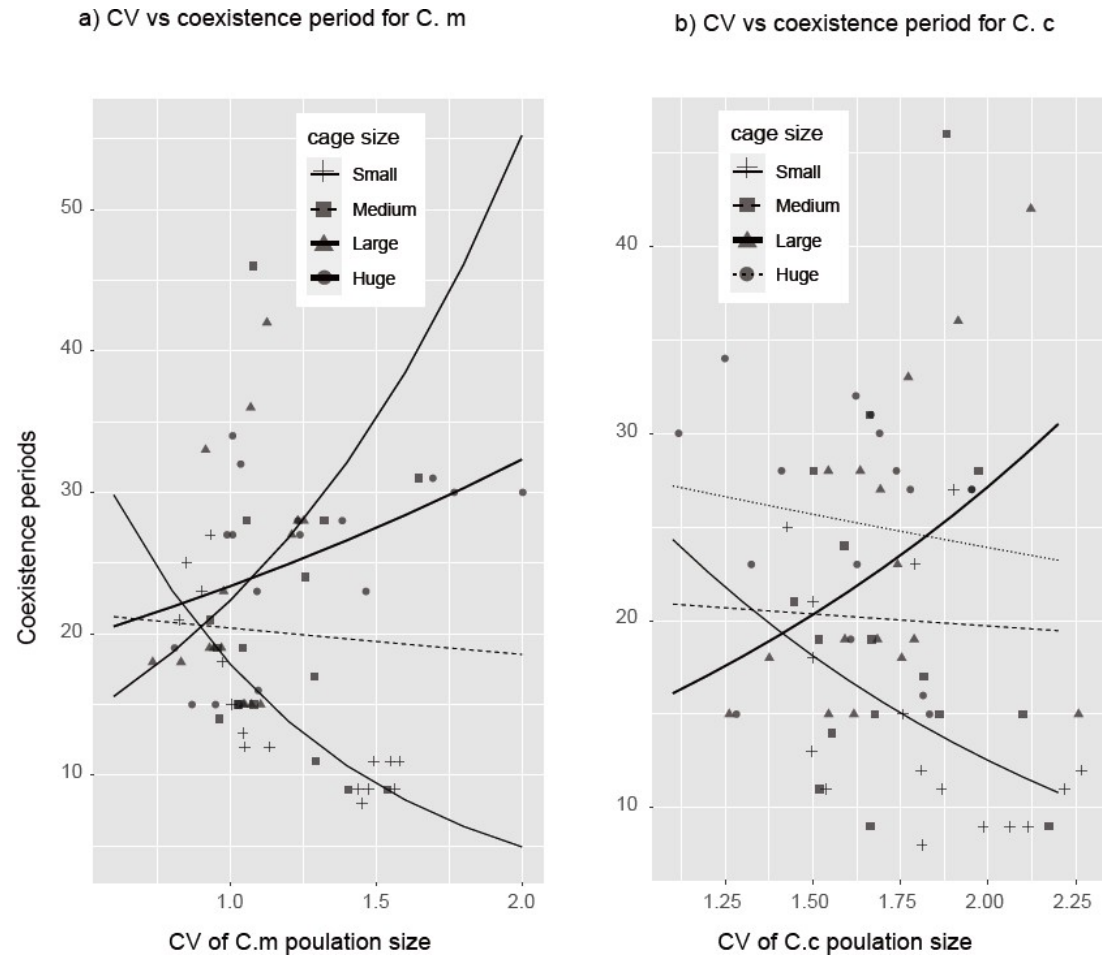
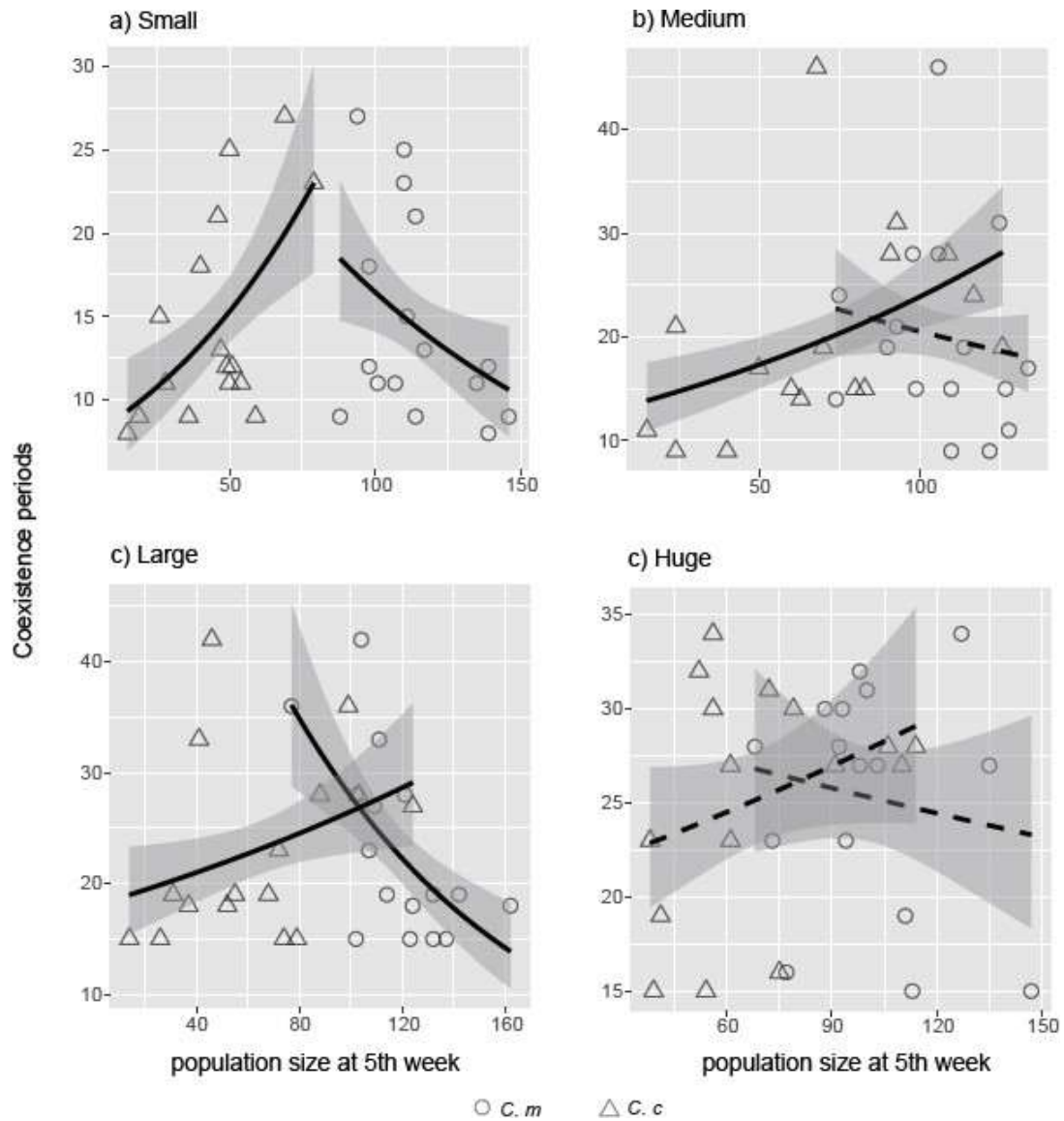


Figure S7. Relationship between coefficient of variation (CV) and coexistence periods. CV was calculated with the standard division and the mean of population size for each cage size. There were statistically significant relationships between the CVs of population dynamics in Small, Large, Huge cage sizes and the coexistence period for *C. m* while those in Small and Large cage sizes and the coexistence period for *C. c* (see also Table S6 for more detail).



FigS8. Relationship between initial population size (2nd generation: 4weeks later) and coexistence periods. There were statistically significant relationships ($P < 0.05$) on (a) Small (each species), (b) Medium (*C.chinensis*) and (c)Large (each species) replicates.

Table S6. Relationship between coefficient of variation (CV) and coexistence periods (week) for (a) *C.maculatus* and (b) *C.chinensis*. These relationships were checked by GLM with Poisson distribution. There were statistically significant relationships ($P < 0.05$) on Small, Large and Huge cage size for *C.maculatus* and on Small and Large cage size for *C.chinensis*.

(a) *C.maculatus*

Small	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	4.165	0.338	14.536	7.1644×10^{-48}	*
Coefficient of variation	-1.284	0.252	-5.101	3.3731×10^{-7}	*
Medium	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	3.112	0.319	9.724	1.9920×10^{-22}	*
Coefficient of variation	-0.096	0.267	-0.358	7.2018×10^{-1}	
Large	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	2.203	0.403	5.471	4.4725×10^{-8}	*
Coefficient of variation	0.904	0.382	2.367	1.7939×10^{-2}	*
Huge	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	2.827	0.186	15.231	2.2068×10^{-2}	*
Coefficient of variation	0.324	0.141	2.295	2.1717×10^{-2}	*

(b) *C.chinensis*

Small	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	4.002	0.456	8.774	7.1644×10^{-18}	*
Coefficient of variation	-0.737	0.256	-2.882	3.9482×10^{-3}	*

Medium	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	3.109	0.456	6.813	9.5589×10^{-12}	*
Coefficient of variation	-0.064	0.263	-0.240	8.0797×10^{-1}	
Large	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	2.142	0.367	5.846	5.3550×10^{-9}	*
Coefficient of variation	0.580	0.209	2.778	5.4733×10^{-3}	*
Huge	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	3.461	0.321	10.786	3.9981×10^{-27}	*
Coefficient of variation	-0.143	0.199	-0.721	4.7061×10^{-1}	

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Chapter3. Complex network of interspecific interactions among Tanganyikan cichlids revealed by empirical dynamic modeling

Introduction

Understanding entangled interspecific interactions is a fundamental step toward uncovering the mechanisms that maintain highly diverse communities. Interspecific interactions drive the population dynamics of the involved species and, consequently, determine the stability of the community. Classical ecological studies on interspecific interactions have relied on well-defined mathematical frameworks, such as the Lotka–Volterra equations, which describe the coexistence of two species with competitive or predator–prey relationships (Lotka, 1925; Volterra, 1926). Extending such pairwise models to multispecies communities, Mougi and Kondoh (2012) theoretically showed that a moderate mixture of antagonistic and mutualistic interactions can stabilize community dynamics. More recently, empirical dynamic modeling (EDM; Sugihara et al., 2012) has been developed as a dynamical-systems–based framework that reconstructs interactions directly from time-series data without assuming predefined equations. By embedding empirical population trajectories into reconstructed state spaces, EDM provides a theoretical extension that allows the estimation of causal relationships among species and between species and environmental drivers. Applications include pairwise analyses, such as those between Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) in relation to sea surface temperature, as well as community-level reconstructions, as demonstrated by Ushio et al. (2018), who analyzed a 12-year dataset of 15 dominant species in Maizuru Bay, Japan, to reconstruct a dynamic interaction network and assess temporal changes in interspecific relationships. While these theoretical and analytical approaches can detect the presence and strength of interspecific interactions, they cannot reveal the proximate mechanisms underlying those links. Direct behavioral observations provide such mechanistic insights.

Direct field observations of interspecific behaviors have also provided crucial insights into how species interactions shape ecological communities. For example, studies of territorial defense, aggressive interference, and specialized foraging strategies in cichlid fishes of the African Great Lakes have demonstrated how observable behaviors can structure species coexistence (e.g., Hori, 1997; Seehausen et al., 2008). More broadly, behavioral observations across taxa, including birds, mammals, and insects, have revealed the proximate mechanisms of interactions such as predation, competition, and mutualism that are often hidden in population time series (Lima & Dill, 1990; Schmitz et al., 1997). However, such observations are temporally and spatially restricted, tend to capture only conspicuous behaviors, and cannot by themselves account for the long-term population-level consequences of repeated interactions. Moreover, they are limited in detecting indirect effects mediated by third-party species. These strengths and limitations emphasize both the value of

behavioral data and the need for complementary approaches. To overcome some of these limitations, manipulative field experiments have been employed as another powerful approach to evaluate the role of focal species in natural communities. Classic removal experiments demonstrated the dramatic influence of a single predator on community structure (Paine, 1966), and many subsequent studies have applied similar manipulations to reveal the impact of keystone species and to quantify the strength of species interactions. Such experiments remain a gold standard for establishing causality because they can directly demonstrate the effects of one species on others under controlled conditions. However, they are generally constrained to relatively simplified systems or a limited subset of species (Bennett, 1990). In species-rich natural communities, the logistical difficulty of manipulating multiple interacting taxa, combined with ethical and conservation concerns, makes these approaches impractical. Thus, while manipulative experiments provide invaluable evidence in certain contexts, they cannot easily be scaled to the complexity of diverse ecological assemblages.

In addition to direct interactions, ecological communities are structured by indirect effects mediated by third-party species. Such interactions can arise through chains of direct behaviors—for example, when competition between two species is modified by the presence of a shared predator—or through more cryptic mechanisms, as when keystone species or ecosystem engineers alter the relationships among many others. Indirect effects are often as influential as direct ones in determining community stability and resilience, yet they are notoriously difficult to detect through either behavioral observations or manipulative experiments alone. Capturing both direct and indirect interactions, therefore, requires methods that can operate at the scale of whole networks, while still providing mechanistic insights into the processes involved. This motivates an integrative approach: empirical dynamic modeling of long-term population dynamics to reconstruct causal network structure, combined with direct behavioral observations to characterize the proximate mechanisms underlying those causal links. In this study, I applied EDM to a 20-year underwater census of Tanganyikan cichlids to estimate a network of interspecific interactions, and compared the inferred relationships with known trophic guilds and behavioral observations.

Lake Tanganyika, located in the Great Rift Valley of East Africa, harbors one of the most diverse assemblages of cichlid fishes, providing an exceptional model system for analyzing species interaction networks. The lake supports more than 200 endemic cichlid species coexisting in sympatry (Muschick et al., 2012; Konings, 2019; Ronco et al., 2021). Such extraordinary diversity results in a dense web of interspecific interactions, including competition, predation, interference, and facilitation. Resource use is highly partitioned, with species specialized on trophic niches such as herbivory, piscivory, omnivory, and scale-eating (e.g., Fryer & Iles, 1972; Kawanabe et al., 1997). This ecological diversification generates complex networks of both overlapping and complementary interactions that can be quantitatively analyzed. From an evolutionary perspective, the Tanganyikan cichlid assemblage is a classic example of adaptive radiation, in which morphological, ecological, and behavioral traits

have diversified repeatedly within lineages (Seehausen, 2006; Salzburger, 2018). This makes it possible to link network structure with evolutionary processes such as convergence, parallel evolution, and niche differentiation.

Based on direct observations, Hori et al. (1993) quantitatively summarized a wide range of interspecific behaviors among coexisting fishes. These included predation (Liem & Liem, 1978; Hori et al., 1983), nonlethal scale eating (Hori, 1993), aggressive interactions toward both resource competitors (e.g., territoriality; Kohda, 1991, 1998) and predators (prey counter-attack; Kohda & Mboko, 1994), as well as "following behaviors", in which follower species obtain food more efficiently while the followed species gain no benefits (Hori et al., 1993). The same divers who described behavioral interactions (Hori & Ochi) had also monitored the population dynamics of fishes (individual counts for each species) on a littoral rocky shore continuously for 20 years (see Takeuchi et al., 2010; Hata & Ochi, 2016), which enables EDM analysis to find causal relationships between species. Such long-term underwater censuses have rarely been conducted in other communities (but see Ushio et al., 2018 for a study in a coastal area). I visualized a network of interspecific interactions of this diverse fish community using EDM analysis, namely, convergent cross mapping (CCM) followed by S-map coefficient analysis, identified the hub species that interact with other species more than the other species (Toju et al., 2018), and compared the EDM results with trophic guilds, prey–predator/scale-eating interaction data, as well as aggressive behavior data, which were provided by the previous studies (Hori, 1983, 1987, 1997; Hori et al., 1983, 1993).

Methods

Time-series data from underwater survey

I used underwater census data collected annually from 1995 to 2014 in a 10 m × 40 m quadrat established on a rocky littoral zone at Kasenga Point (8°43'S, 31°08'E), along the southern shore of Lake Tanganyika. The quadrat spans depths of 2 to 13 m, where littoral cichlid diversity peaks. It was subdivided into 400 subquadrats (1 m² each), and individual counts of all fish species were recorded by experienced researchers (Hori & Ochi; Takeuchi et al., 2010; Hata & Ochi, 2016; Table S1, Figure S1). For this study, I additionally analyzed unpublished data from 2009 to 2014.

EDM analysis requires more than 35 time points to reliably estimate causal interactions within a community (Sugihara et al., 2012). However, my time series data consisted of only 20 time points, because the survey was conducted once per year over a 20-year period. To extend the time series from 20 to 40 points (necessary for reliable EDM estimation; Sugihara et al., 2012), I divided the original quadrat into western and eastern halves (each 5 m × 40 m with 200 subquadrats). Time series from these subareas were concatenated, assuming comparable environmental conditions. To avoid artefactual transitions, I excluded cross-predictions between the final point of the western data and the

initial point of the eastern data, as proposed by Hsieh et al. (2008).

Of the 59 taxa (hereafter referred to as “species” for simplicity) observed (55 cichlids and 4 non-cichlids), I retained 36 species for analysis by excluding 23 species whose individual counts per 5 m × 40 m were consistently below 10 across all 40 time points prior. Individuals were originally classified into four size classes (SS, S, M, L), and only S, M, and L were used as these represent adult stages. Prior to EDM, all time series were standardized to zero mean and unit variance (Hsieh et al., 2008). This standardization minimizes potential biases from differences in population size among species and facilitates the integration of multiple short time series.

Trophic guilds of fish species

Trophic guilds were determined based on the stomach content analysis conducted by Hori from 1988 to 1989 (Figure S2). Hierarchical clustering using Ward’s minimum variance method was applied to a dissimilarity matrix derived from dietary overlap, yielding seven trophic guilds: fry-feeder, scale-eater, shrimp-eater, piscivore, omnivore, and two types of herbivores (grazer and browser).

Empirical dynamic modeling (EDM) analysis

The EDM analysis conducted in this study comprised the following four main components: (1) simplex projection (Sugihara and May 1990, Hsieh et al. 2005) to determine the optimal embedding dimension, (2) univariate sequential locally weighted global linear maps (S-map; Sugihara 1994) to assess the nonlinearity and predictability of individual time series, (3) convergent cross mapping (CCM; Sugihara et al. 2012) to identify causal relationships between species, and (4) multivariate S-map (Dixon et al. 1999, Deyle and Sugihara 2011) to quantify dynamic interactions among species (see Chang et al., 2017 for details).

(1) Simplex projection was conducted to determine the optimal embedding dimension (E^*) for population dynamics data of each species by evaluating its short-term forecasting skill. This method identifies E nearest neighbors of the state (Y_t) in the reconstructed state space for each time point t , and predicts the next state (Y_{t+1}) based on the subsequent values of those neighbors. E^* was determined as the E value with the highest correlation coefficient (*i.e.*, the forecast skill by simplex projection). Four species out of the remaining 36 species were excluded from further analysis in this study because the highest correlation coefficient was less than or equal to zero.

(2) Univariate S-map was conducted to assess the nonlinearity for population dynamics data of each species, which serves as a prerequisite for the subsequent CCM analysis. In this method, the parameter θ determines how strongly the regression is localized around each target point in the reconstructed E^* dimensional state space. The optimal θ^* was determined as the θ that maximizes the correlation coefficient of the observation vs. forecasting of the S-map. The population dynamics with $\theta^* > 0$ were regarded as nonlinear. Five species out of the remaining 32 species with $\theta^* \leq 0$ were

excluded for further analysis in this study.

(3) CCM, a time series analysis to detect the causality between two time series data (Sugihara et al., 2012) based on Takens' embedding theorem (Takens, 1981), was conducted to identify causal relationships between all pairs of population dynamics data for the remaining 27 species. Although CCM can assess causality with a time lag parameter (tp), this study focused on concurrent causality for the sake of simplicity ($tp = 0$). The significance of causality was evaluated based on the prediction skill (ρ), which is theoretically expected to increase with the library size (i.e., the number of time points used for prediction) when a true causal relationship exists. Causality was considered significant when the minimum ρ was greater than 0, and the ρ value of the maximum library size exceeded the 95% confidence interval of ρ values obtained using the minimum library size.

(4) Multivariate S-map was used to quantify the causal relationships that were significantly detected by CCM. This method calculates S-map coefficients at each time point to represent the strength of the causal relationship, thereby revealing the temporal variation in both the sign and strength of interspecific interactions. Note that necessary NAs were inserted to prevent S-map predictions between the final time point of the western data and the initial time point of the eastern data.

Interspecific interaction network constructed by CCM

I constructed a directed interaction network using significant CCM links, outgoing causality links and incoming recipient links. The means of the absolute values of S-map coefficients over the entire period were used as the strength of each causal relationship. The sign of each interaction (positive or negative) was determined according to the majority of the S-map coefficient signs across the 38 time points (Figure S3). In this directed network, the number of positive and negative incoming and outgoing links (positive and negative in-degree and out-degree, respectively) was counted for each species.

To evaluate determinants of interaction degree, I performed an analyses of variance (ANOVA), using in-degree and out-degree as response variables. Explanatory variables include their trophic guild (categorical) and their mean abundance across all sampling periods (continuous). Correlation coefficients between the positive and/or negative in-degree and out-degree for each species were calculated and tested using Pearson's correlation coefficient. Furthermore, to account for phylogenetic relationships in these analyses, a phylogenetic tree of cichlid species was constructed based on the mitochondrial ND2 gene sequence, and phylogenetic generalized least squares (PGLS) analyses were conducted.

Testing for scale-free properties

After reconstructing interspecific networks using CCM, we next examined their global structure by

testing whether degree distributions exhibit a scale-free form, a property widely discussed in complex networks including ecological and food-web studies. Scale-free organization is particularly important because it can shape network robustness: such networks are generally resilient to random loss of nodes but highly vulnerable to targeted removal of hubs (Dunne et al., 2002). Degree distributions were analyzed following the statistical framework of Clauset et al. (2009) and Broido & Clauset (2019). The lower cutoff ($x_{\min}$) was determined by minimizing the Kolmogorov–Smirnov statistic. The scaling exponent α was estimated by maximum likelihood, and the goodness-of-fit p-value (p_{gof}) was computed by Monte Carlo resampling with re-estimation of $x_{\min}$. Alternative models (truncated power law, lognormal, exponential, stretched exponential) were also fitted, and Vuong’s likelihood ratio tests were used to compare them with the pure power law. Networks were then classified into “strong”, “weak”, “super-weak”, or “non-scale-free” categories according to Broido & Clauset (2019). All analyses were performed in Python 2.7 using their original scripts with minor modifications.

Hub species

Hub species of the interaction network were identified based on the betweenness centrality (C_B), which quantifies how often a given node (species) lies on the shortest paths between other species in the network (Freeman, 1977). To assess factors influencing species’ roles in the interaction network, I used analysis of variance (ANOVA) with betweenness centrality as the response variable. Explanatory variables were trophic guild (categorical) and mean individual abundance (continuous) across all sampling periods.

Behavioral observation

To compare with CCM-based estimates of species interactions, I used direct underwater observational data on predation and scale-eating, as well as aggressive behaviors, documented by Hori (1983, 1987, 1997) and Hori et al. (1983, 1993). These behaviors are visually distinctive and thus relatively easy to record in the field. For example, during predatory behavior, predators often approach their prey with sudden movements like dashing or chasing, and the moment of capturing the prey is especially clear (Liem & Liem, 1978; Hori et al., 1983). Scale-eating behavior also shows a clear pattern, as it involves quickly approaching another fish and scraping off its scales (Takahashi et al., 2007; Takeuchi et al., 2012). Aggressive behavior often occurs during competition for territory or food, and it includes actions such as displaying, chasing, and physical contact like bumping or biting, which makes it easy to recognize signs of aggression (Kohda, 1991).

Computation

All statistical analyses were performed in R 4.2.3 (R core team, 2023). Simplex projection, the S-map method, and CCM were performed using the package rEDM 0.6.9 (<https://cran.r->

project.org/web/packages/rEDM/index.html). I draw networks using igraph 1.5.1 and plot.igraph2 (<https://github.com/jevansbio/igraphhack>). All the datasets and scripts are provided via github (<https://github.com/TKawaseScript/complex-interaction>).

Results

CCM detected a total of 125 significant causal relationships among the examined 27 fish species (out of 702 potential relationships of 351 species pairs) on a littoral rocky shore of Lake Tanganyika (Figure 1). Among the 27 fish species, one species (*Cyathopharynx* spp.) did not exhibit any significant causal relationship (Table S1). These 125 relationships were classified into 67 positive relationships (54%) and 58 negative relationships (46%), according to the majority of the signs (positive/negative) of S-map coefficients over the 38 time points (Tables S2, S3, Figure S3). As a result, 25 species (out of the 26 species examined) were positively linked with 1–8 species and composed a positive relationship network (Figure 1a). Twenty-five species of different composition were negatively linked with 1–7 species and composed a negative relationship network (Figure 1b).

The in-degree, out-degree, and total degree distributions of the directed network were all classified as ‘non-scale-free’ because the power-law fits were statistically implausible ($p(\text{gof}) < 0.1$ in all cases), the tail sizes were very small ($n_{\text{tail}} = 12\text{--}15$), and in two cases the estimated scaling exponents fell outside the canonical range ($2 < \alpha < 3$, Figure S4, Table S4). In addition, alternative models such as the lognormal and exponential provided superior fits. Significant correlations were detected between various combinations of in-degree and out-degree, including negative or both (negative and positive) out-degree and positive, negative, or both in-degree (Figure 2). Most of these significant correlations were also supported by phylogenetic general least squares (PGLS) analyses. These results suggest that certain species tend to have disproportionately more in-degree and out-degree than others, influencing the population dynamics of many species—regardless of whether the effects are positive or negative—and, in turn, being affected by a similarly wide range of positive and negative influences by other species. For the number of interspecific interactions estimated by CCM, ANOVA was performed on out-degree using a full model that included mean abundance of the causal species, its trophic guild, and their interaction. The results showed that only the main effect of mean abundance was significant (Table S5a, Figure S5a). In contrast, for in-degree, significant effects were found for both mean abundance of the recipient species and the interaction between the mean abundance and their trophic guilds (Table S5b, Figure S5b). Betweenness centralities of species were not significantly related to mean population sizes, but were significantly related to trophic guilds, and the interaction between mean population size and trophic guild (Table S6, Figure S6).

I examined whether interspecific interactions in the network estimated by CCM occurred within the

same trophic guild (intraguild) or between different trophic guilds (interguild). Among the guilds, the most species-rich was the omnivores (9 species), which exhibited numerous intraguild interspecific interactions, with many of the causal effects being negative (Table S7). In addition, they showed the largest number of interguild interactions, frequently exerting positive effects on species belonging to other guilds. Conversely, they were often subject to negative interguild effects from species in other guilds. The shrimp eaters, the second most species-rich guild, exhibited the next highest number of intraguild interactions after the omnivores, but many of their effects were positive. The fry feeders (3 species) exerted both positive and negative interguild effects on many species of other guilds, while receiving more positive than negative interguild effects from them. The browsers (3 species), in contrast, were particularly subject to negative interguild effects from many species belonging to other guilds (Figures S7, S8, Table S7).

Based on betweenness centrality, five species, *Aulonochromis dewindti* (fry-feeder), *Tropheus moorii* (browser), *Lamprologus calipterus* (fry-feeder), *Neolamprologus fasciatus* (piscivore), and *Perissodus microlepis* (scale-eater), were selected as the top five hub species in this order in the network of interspecific interactions constructed by CCM (Figure 3).

A comparison between the CCM-based network derived from 20-year population dynamics and the field-observed behavioral interaction networks reveal a marked discrepancy between them. The CCM-based network included a greater number of interactions (125 in total), which were distributed across a wider range of species and trophic guilds, compared to the more limited prey–predator and agonistic interaction networks observed in the field. Moreover, most significant relations detected by CCM were not supported by field observations of interspecific behaviors (Figure 4). Only 5 of 67 positive relationships were supported by compatible prey→predator interaction, and only 5 of 58 negative relationships were supported by compatible predator→prey (4), victim→aggressor (2, overlapping with predator→prey), aggressor→victim (1) interactions. For five positive and one negative relationships, contradictory interspecific behaviors were observed in the field survey.

Discussion

Network structure

In this study, CCM successfully characterizes the network of interspecific interactions within a fish community on a littoral rocky shore of Lake Tanganyika, where most fish species are endemic and belong to a species flock derived from an adaptive radiation (Figures 1, 3). The 20-year field observation and the extensive population dynamics datasets enabled this analysis. My analysis provided no evidence for scale-free organization in the studied networks. This finding is in line with the comprehensive survey by Broido & Clauset (2019), who reported that 63% of biological networks

are not scale-free and that food-web networks in particular often show weak or no evidence for scale-free structure. Thus, my results reinforce the view that scale-free patterns are not a universal property of ecological networks, but instead that degree heterogeneity may arise from alternative processes or constraints. Nevertheless, the presence of high-degree nodes indicates potential hub species whose loss could disproportionately affect network stability, emphasizing the ecological relevance of network structure even in the absence of scale-free scaling.

Network hub species

Aulonochromis dewindti, *Tropheus moorii*, *Lamprologus callipterus*, *Neolamprologus fasciatus*, and *Perissodus microlepis* were identified as hub species rather than keystone species in the CCM network, as they both affect the populations of numerous species and are simultaneously affected by many others. Surprisingly, five hub species have various trophic guilds, *i.e.*, fry-feeder, browser, piscivore, and scale-eater, and are not necessarily ordinary keystone species such as top-predator, dominant prey species. Firstly, *A. dwendti* is among the most dominant species on rocky shores of Lake Tanganyika (Sturmbauer et al., 2008; Mushagalusa et al., 2014). At my study site, the density was also high and variable, averaging 32.8 ± 34.5 individuals/200 m² (average $\pm$ SD). Mature males (>10 cm in standard length, SL) exhibit territorial behavior, defending large mating territories (5.0 m²) where they construct nests and prey on fish fry (Figure S2; Konings, 2019). In contrast, females form groups that hover about 50 cm above the substrate and primarily feed on shrimp and other benthic invertebrates (Hori, 1987). As a maternal mouth-brooder, females retain fertilized eggs with their buccal cavities for protection. These pronounced behavioral disparities between sexes likely drive divergent ecological interactions with sympatric species. Moreover, the high abundance of *A. dwendti* juveniles may make them a critical prey resource for various piscivores and fry-feeders. Conversely, fluctuations in predator populations reliant on this resource could influence *A. dwendti* demography, suggesting species-specific demographic linkages.

A browser, *T. moorii*, was selected as a hub species. This dominant herbivore in shallow rocky areas strictly defends its feeding territories, chasing away intruding species (Yamaoka, 1983; Takamura, 1983, 1984, Yanagisawa & Nishida, 1991). This territorial behavior may negatively impact other sympatric species by limiting their resource access (Hata et al., 2014; Hata et al., 2015; Hata & Ochi, 2016). At the same time, this territorial species can be negatively impacted by various intruding species. *Lamprologus callipterus* is known as a shell-brooding species; however, my quadrat did not include the shell bed (Takeuchi et al., 2010). Consequently, the individuals observed in this study were primarily immature males that formed foraging groups (Yuma & Kondo, 1997). These groups can grow in size, and as they do, their diet expands to include shrimp and the fry of various substrate-brooding cichlids (Konings, 2019, Figure S2). *Neolamprologus fasciatus* is a piscivorous species that

feeds on various cichlid species, as observed directly (Figure 1c and Figure S2). On the other hand, subadults feed mainly on shrimp (Hori, 1983; Yuma et al., 1998). Therefore, this species may have strong interactions with prey species and competing species for prey fish and shrimp. For the scale-eating *P. microlepis*, it is well-documented that this dominant species in shallow rocky areas feeds on the scales of various species, as observed directly (Fig. 1c; Hori, 1987, 1997; Hori et al., 1993) and through DNA analyses of stomach contents (Kovac et al., 2019). Interactions estimated by CCM suggest that scale-eating does not have a lethal effect but can negatively impact prey fish populations, primarily by disturbing reproduction and/or reducing their condition.

Intraguild interactions and interguild interactions

The most species-rich guild, the omnivores, exhibited frequent intraguild interactions, most of which were negative (Figure S8d). Omnivores such as *Lamprichthys tanganicus*, females of *Ophthalmotilapia ventralis*, and *Paracyprichromis* spp. are pelagic species that primarily feed on plankton (Coulter & Tiercelin, 1991; Konings, 2019). Although no direct interference behaviors were observed among these species, their use of overlapping resources suggests strong competition within the guild. In contrast, in interguild interactions, omnivores often exerted positive effects on other guilds. For example, they served as prey resources, or in some cases were observed to drive away scale-eaters and piscivores (Figure 1c, d), thereby providing both direct and indirect benefits to other guild members. Omnivores were, however, more likely to receive negative effects from other guilds. Thus, from a bidirectional perspective, they exhibited an asymmetry: positive as causative species, negative as recipients. This pattern reflects their role as central hubs in the food web, making them more exposed to diverse competitive and antagonistic relationships. Shrimp eaters exhibited relatively frequent intraguild interactions, but most of these were positive (Figure S8a). This suggests the existence of complementary relationships within the guild, such as resource partitioning through different foraging behaviors (Hori, 1987, 1997). Unlike the strongly competitive relationships observed among omnivores, the presence of multiple shrimp eaters may contribute to community stability. Although fry feeders comprised only three species, they exhibited distinctive interaction patterns at the network level (Figure S8b). The hub species *A. dwendti* exerted positive effects on five species and negative effects on four, while receiving positive effects from seven species and negative effects from four. Because fry feeders prey heavily on the offspring of other species, they tend to benefit from resources provided by other guilds. Thus, despite their small species number, fry feeders established diverse connections throughout the network. In contrast, *L. attenuatus*, also a fry feeder, exerted positive effects on four species. These effects cannot be explained by direct behavioral observations and are more likely attributable to indirect interactions. Browsers (three species) received negative effects from many other guilds, most of which were directed toward a hub species, *T. moorii*. This indicates that browsers are particularly susceptible to resource competition and predation pressure,

suggesting a vulnerable position within the overall network. In summary, each guild played distinct roles characterized by the balance of intraguild versus interguild interactions and the polarity of their effects. Omnivores functioned as competitive yet facilitative hubs, shrimp eaters as a cooperative guild through complementary interactions, fry feeders as resource-dependent beneficiaries, and browsers as a vulnerable guild prone to negative impacts. These differences provide important insights into understanding the stability and resilience of the community as a whole.

Comparison of network structure between CCM network using time-series population data and networks constructed by accumulating direct observations

The network estimated using CCM captures both direct and indirect interactions (Sugihara et al., 2012), thereby revealing comprehensive interspecies interactions, including indirect interactions that are not directly observed. My comparison between the CCM-inferred interaction network and field-observed behavioral networks revealed both marked discrepancies and informative overlaps. The CCM-based network detected a much larger number of interactions across a broader range of species and trophic guilds than were observed in the field. This difference reflects the contrasting perspectives of the two approaches: while field surveys capture only overt predation and agonistic behaviors, CCM infers causal relationships from long-term population dynamics (Sugihara et al., 2012; Deyle et al., 2016), thereby revealing not only direct interactions but also indirect or hidden processes that are difficult to observe in real time. Such processes may include resource competition, facilitation, shared responses to environmental drivers, or trophic cascades (Wootton, 1994; Polis & Strong, 1996; Bascompte, 2009).

Despite the overall low concordance, several cases showed agreement between the two approaches. Among the 67 positive CCM links, five corresponded prey→predator relationships observed in the field, and notably, four of these involved the scale-eating cichlid *P. microlepis* as the predator (Figures 4, S8e). Because lethal predation events are rare and difficult to capture in situ, they are seldom observed directly. In contrast, scale-eating strikes occur more frequently and are thus more easily recorded during behavioral surveys. This pattern suggests that CCM may detect many prey–predator interactions that were simply missed in field observations, while scale-eating providing one of the few cases where observational and time-series approaches converged. Conversely, apparent contradictions also emerged, particularly in cases where CCM inferred positive links. For instance, in the relationship *G. pfefferi*→*P. microlepis*, field surveys documented not only prey→predator interactions through scale-eating but also aggressor→victim behaviors, with prey actively attacking or repelling scale-eaters. In such case, CCM detection likely reflects the demographic consequences of defensive aggression, which may outweigh the direct effects of predation in shaping long-term population

dynamics.

For negative CCM links, five of 58 inferred relationships corresponded to species interactions documented by field observations (Figure 4). In most of these cases, the causal direction inferred from population dynamics was consistent with observed predator→prey or aggressor↔victim interactions. Taken together, these results underscore that discrepancies between CCM and direct observations should not be interpreted simply as errors, but rather as evidence that different types of interactions (predation, aggression, competition, facilitation) operate at different frequencies, life stages, or levels of detectability. The complementarity of the two approaches thus provides a more holistic picture of the interaction network: field observations ground inferences in observable behaviors, while CCM reveals hidden or indirect influences that strongly shape population trajectories. Incorporating time-lagged methods (Ye et.al 2015) may help disentangle synchronization driven by strong one-way forcing from genuine bidirectional causality, and further allow the identification of transitive causal chains within the interaction network. Future work combining CCM with diet analyses, life-stage specific monitoring, and experimental manipulations will be crucial to disentangling the relative contributions of predation, aggression, and indirect effects in maintaining the complex web of interactions in this community (Montoya et al., 2006; Berlow et al., 2009). Global warming has been shown to cause a decline in the productivity of fish communities in Lake Tanganyika (Cohen et al., 2016). In addition, degradation of fish communities is of concern owing to sediment inflow into the lake caused by human activities (McGlue et al., 2021) and overfishing (Phiri et al., 2023). In my study, I inferred a species interaction network from long-term population dynamics data and identified its hub species. By paying particular attention to these hub species and the overall network, I suggest that it may be possible to safeguard the community, since—as demonstrated by Solé & Montoya (2001)—the loss of hub species greatly increases network vulnerability, whereas protecting them can reduce the risk of cascading species diversity loss and help maintain ecosystem stability.

Figures and Tables

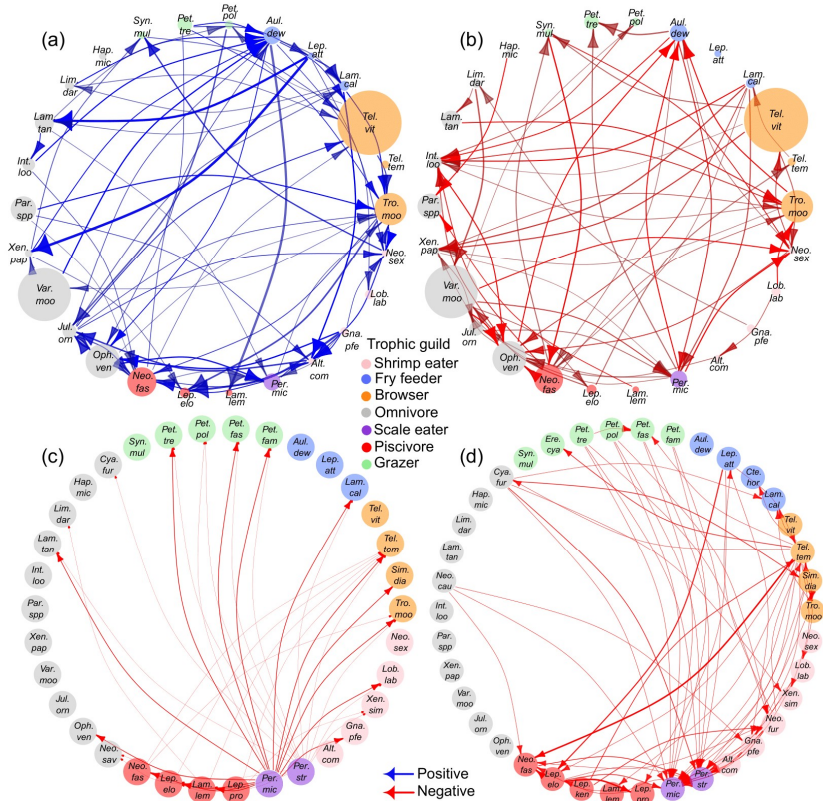


Figure 1. Networks of positive (blue arrows) and negative (red) interspecific interactions among fish species in a rocky littoral area of Lake Tanganyika. a–b: CCM-estimated positive (a) and negative (b) causal relationships, where the sizes and colors of the node circles indicate the average individual number and trophic guilds of the species, respectively. Directions, widths, and brightness of the edge arrows reflect causality directions, causality strengths (absolute cumulative sum of S-map coefficients), and ratios of positive or negative S-map coefficients over the 38 time points, respectively. c–d: The directions (arrows) and frequency (line width) of predation (c) and aggressive behaviors (d) among fishes observed directly in the lake (Hori 1993). Species are indicated by the first three letters of the genus and species names.

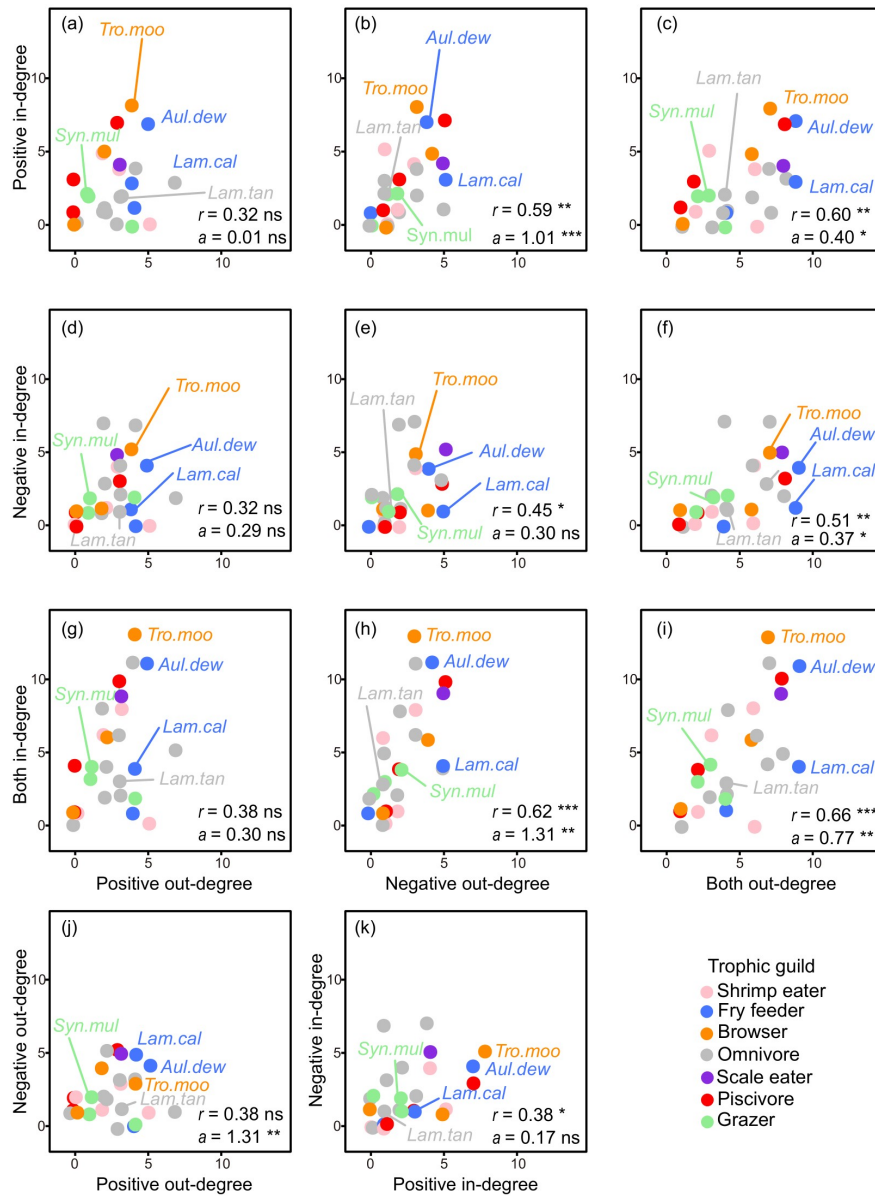


FIGURE 2

Figure 2. Pairwise scatter plots of the number of input and output (in-degree and out-degree, respectively) of positive and/or negative relationships for each of the 26 CCM-examined fish species in a rocky littoral area of Lake Tanganyika. Plot colors indicate trophic guilds. Simple correlation coefficients (r) for all 26 species and phylogenetic generalized least squares coefficients (α) for 24 cichlid species (excluding the non-cichlid species *Synodontis multipunctatus* and *Lamprichthys tanganicus*) are shown with significance levels (ns: $p \geq 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$). Species names are abbreviated as in Figure 1.

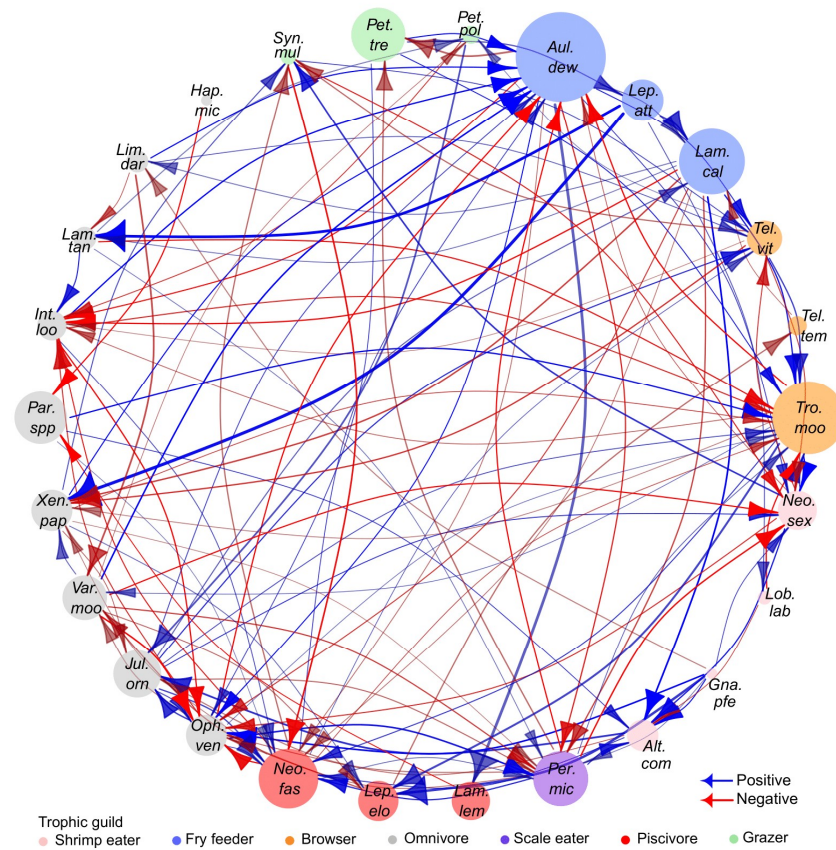


Figure 3. The top five hub species (*Aulonochromis dewindti*, *Tropheus moorii*, *Lamprologus calipterus*, *Neolamprologus fasciatus*, and *Perissodus microlepis*) in the CCM-estimated network of positive (blue arrows) and negative (red arrows) causal relationships among 26 fish species in a rocky littoral area of Lake Tanganyika. The size of each node indicates its betweenness centrality index, while the other node and edge properties are the same as in Figure 1a–b.

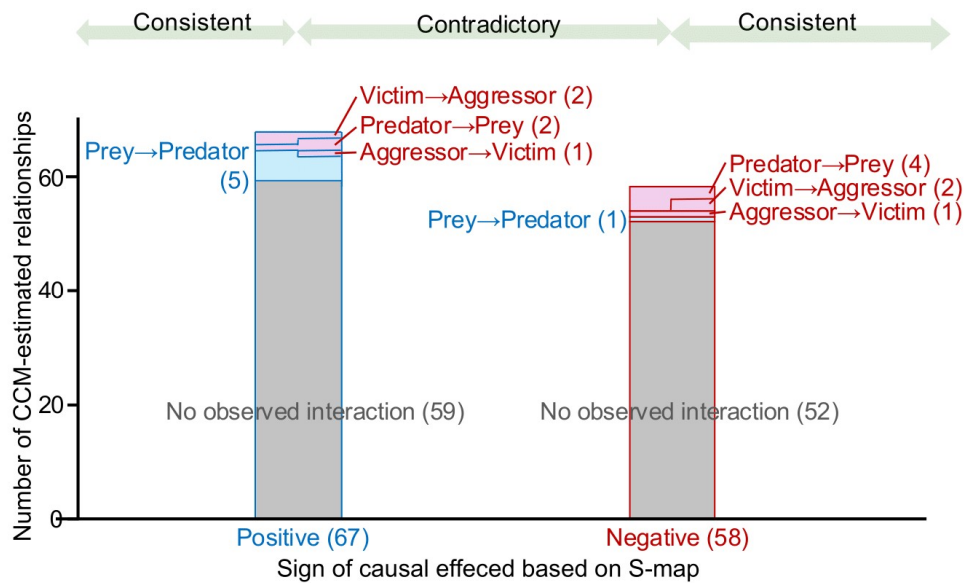


Figure 4. Stacked bar graph of CCM-estimated positive and negative interspecific relationships, with only a small portion supported by direct behavioral observations from Hori (1993). The blue area denotes interactions with a positive effect on the recipient species, while the red area indicates those with a negative effect. Relationships involving two observed behaviors are divided vertically. Observed relationships that are consistent with CCM estimates are listed on the left and right sides of the bars, whereas contradictory relationships are shown between the bars.

Supporting Information

Table S1. List of 59 fish species observed in the 20-year underwater census survey in a rocky littoral area of Lake Tanganyika, along with their tribes, abbreviated species names used in this study, trophic guilds, and 20-year mean abundance (N) and the standard deviations (SD). Trophic guilds are summarized according to the stomach content analysis in the same region (Supplement FIGURE S2; Hori 1990). For species excluded from the CCM analysis, issues encountered during the analysis steps, such as linearity detection or problems with projection, are indicated. For the species that passed all processes and reached CCM and subsequent analyses, the betweenness centrality index is provided.

Species name	Tribe	Abbreviation	Trophic guild	N	SD	Reasons to exclude from CCM	Betweenness centrality
<i>Altolamprologus compressiceps</i>	Lamprologini	<i>Alt.com</i>	Shrimp eater	3.4	2.2 (Passed)		14.8
<i>Aulonocranus dewindti</i>	Ectodini	<i>Aul.dew</i>	Fry feeder	32.8	34.5 (Passed)		135.8
<i>Cyathopharynx</i> spp.	Ectodini	<i>Cya.spp</i>	Omnivore	2.8	4.2 (Passed)		-
<i>Ctenochromis horei</i>	Haplochromini	<i>Chr.hor</i>	Fry feeder	0.6	1.5 Max. $N < 10$		-
<i>Cyprichromis</i> sp.	Cyprichromini	<i>Cyp.spp</i>	Omnivore	72.1	164 Linearity detected		-
<i>Cunningtonia longiventralis</i>	Ectodini	<i>Cun.lon</i>	No data	0.7	1.4 Max. $N < 10$		-
<i>Eretmodus cyanostictus</i>	Eretmodini	<i>Ere.cya</i>	Grazer	34	16.8 Linearity detected		-
<i>Gnathochromis pfefferi</i>	Haplochromini	<i>Gna.pfe</i>	Shrimp eater	7.5	4.6 (Passed)		0.0
<i>Haplotaxodon microlepis</i>	Perissodini	<i>Hap.mic</i>	Omnivore	4.8	8.9 (Passed)		0.0
<i>Interochromis loocki</i>	Haplochromini	<i>Int.loo</i>	Omnivore	19.7	15.8 (Passed)		12.7
<i>Julidochromis ornatus</i>	Lamprologini	<i>Jul.orn</i>	Omnivore	23.3	16.5 (Passed)		36.9
<i>Lepidolamprologus attenuatus</i>	Lamprologini	<i>Lep.att</i>	Fry feeder	3.8	6.1 (Passed)		27.5
<i>Lamprologus callipterus</i>	Lamprologini	<i>Lam.cal</i>	Fry feeder	11.6	10.7 (Passed)		71.5
<i>Lepidolamprologus cunningtoni</i>	Lamprologini	<i>Lep.cun</i>	No data	0.1	0.3 Max. $N < 10$		-
<i>Limnotilapia dardennii</i>	Haplochromini	<i>Lim.dar</i>	Omnivore	9.8	7 (Passed)		6.3
<i>Lepidolamprologus elongatus</i>	Lamprologini	<i>Lep.elo</i>	Piscivore	12.3	10.4 (Passed)		25.6
<i>Lepidolamprologus kendalli</i>	Lamprologini	<i>Lep.ken</i>	Piscivore	0.3	0.5 Max. $N < 10$		-
<i>Lobochilotes labiatus</i>	Haplochromini	<i>Lob.lab</i>	Shrimp eater	9.9	3.3 (Passed)		1.1
<i>Lamprologus lemairii</i>	Lamprologini	<i>Lam.lem</i>	Piscivore	3.1	2.3 (Passed)		23.0
<i>Lepidolamprologus mimicus</i>	Lamprologini	<i>Lep.mim</i>	Piscivore	0.4	1 Max. $N < 10$		-
<i>Lepidolamprologus profundicola</i>	Lamprologini	<i>Lep.pro</i>	Piscivore	0.7	0.9 Max. $N < 10$		-
<i>Lamprichthys tanzanicus</i>	non_cichlid	<i>Lam.tan</i>	Omnivore	36.6	35.8 (Passed)		6.9
<i>Lates</i> sp.	non_cichlid	<i>Lat.M</i>	Piscivore	0.3	0.7 Max. $N < 10$		-
<i>Mustacembelus</i> spp.	non_cichlid	<i>M.spp</i>	No data	4.7	2.6 Projection failed		-
<i>Neolamprologus buescheri</i>	Lamprologini	<i>Neo.bus</i>	Omnivore	0	0.2 Max. $N < 10$		-
<i>Neolamprologus caudopunctatus</i>	Lamprologini	<i>Neo.cau</i>	Omnivore	10.5	12.9 Projection failed		-
<i>Neolamprologus cylindricus</i>	Lamprologini	<i>Neo.cyl</i>	Shrimp eater	3	1.9 Max. $N < 10$		-
<i>Neolamprologus fasciatus</i>	Lamprologini	<i>Neo.fas</i>	Piscivore	64.1	16.7 (Passed)		58.4
<i>Neolamprologus fuscifer</i>	Lamprologini	<i>Neo.fur</i>	Shrimp eater	1	0.9 Max. $N < 10$		-
<i>Neolamprologus mustax</i>	Lamprologini	<i>Neo.mus</i>	Shrimp eater	0.4	0.6 Max. $N < 10$		-
<i>Neolamprologus obscurus</i>	Lamprologini	<i>Neo.obs</i>	Shrimp eater	0.5	0.9 Max. $N < 10$		-
<i>Neolamprologus petricola</i>	Lamprologini	<i>Neo.pet</i>	Shrimp eater	0.6	0.9 Max. $N < 10$		-
<i>Neolamprologus prochilus</i>	Lamprologini	<i>Neo.pro</i>	Shrimp eater	0.7	0.9 Max. $N < 10$		-
<i>Neolamprologus pulcher</i>	Lamprologini	<i>Neo.pul</i>	Omnivore	24.2	11 Linearity detected		-
<i>Neolamprologus savoyi</i>	Lamprologini	<i>Neo.sav</i>	Omnivore	31.6	13.9 Linearity detected		-
<i>Neolamprologus sexfasciatus</i>	Lamprologini	<i>Neo.sex</i>	Shrimp eater	3.8	4 (Passed)		23.9
<i>Neolamprologus tetracanthus</i>	Lamprologini	<i>Neo.tet</i>	Fry feeder	0.4	0.7 Max. $N < 10$		-
<i>Ophthalmotilapia ventralis</i>	Ectodini	<i>Oph.ven</i>	Omnivore	78	37.4 (Passed)		26.6
<i>Paracyprichromis</i> spp.	Cyprichromini	<i>Par.spp</i>	Omnivore	54.3	88 (Passed)		45.0
<i>Pseudosimochromis curvifrons</i>	Haplochromini	<i>Pse.cur</i>	Browser	0.9	1.8 Max. $N < 10$		-
<i>Petrochromis famula</i>	Haplochromini	<i>Pet.fam</i>	Grazer	1.4	1.6 Max. $N < 10$		-
<i>Petrochromis fasciolatus</i>	Haplochromini	<i>Pet.fas</i>	Grazer	4.7	17 Projection failed		-
<i>Perissodus microlepis</i>	Perissodini	<i>Per.mic</i>	Scale eater	31	18.6 (Passed)		49.3
<i>Petrochromis polyodon</i>	Haplochromini	<i>Pet.pol</i>	Grazer	7.8	4.4 (Passed)		3.5
<i>Petrochromis horii</i>	Haplochromini	<i>Pet.hor</i>	Grazer	0.1	0.4 Max. $N < 10$		-
<i>Plicodius straeleni</i>	Perissodini	<i>Per.str</i>	Scale eater	2.2	2.1 Max. $N < 10$		-
<i>Petrochromis trewavasae</i>	Haplochromini	<i>Pet.tre</i>	Grazer	24.7	8.1 (Passed)		47.6
<i>Simochromis diagramma</i>	Haplochromini	<i>Sim.dia</i>	Browser	18	17.4 Linearity detected		-
<i>Synodontis multipunctatus</i>	non_cichlid	<i>Syn.mul</i>	Grazer	5.3	4.7 (Passed)		2.0
<i>Tropheus moorii</i>	Haplochromini	<i>Tro.moo</i>	Browser	77.4	25.7 (Passed)		88.0
<i>Telmatochromis temporalis</i>	Lamprologini	<i>Tel.tem</i>	Browser	6.8	5.4 (Passed)		4.2
<i>Telmatochromis vittatus</i>	Lamprologini	<i>Tel.vit</i>	Browser	159.6	47.2 (Passed)		19.0
<i>Variabilichromis moorii</i>	Lamprologini	<i>Var.moo</i>	Omnivore	129.2	30.6 (Passed)		31.7
<i>Xenotilapia papilio</i>	Ectodini	<i>Xen.pap</i>	Omnivore	5.6	3.3 (Passed)		26.6
<i>Xenotilapia sinu</i>	Ectodini	<i>Xen.sin</i>	Shrimp eater	0.3	0.8 Max. $N < 10$		-
<i>Xenotilapia spiloptera</i>	Ectodini	<i>Xen.spi</i>	Omnivore	26	12.4 Projection failed		-
<i>Xenotilapia flavipinnis</i>	Ectodini	<i>Xen.flu</i>	Omnivore	0.2	1 Max. $N < 10$		-
<i>Xenotilapia boulengeri</i>	Ectodini	<i>Xen.bou</i>	No data	0.2	0.6 Max. $N < 10$		-
<i>Xenotilapia</i> sp.	Ectodini	<i>Xen.sp</i>	Omnivore	0	0.3 Max. $N < 10$		-

Table S2. List of CCM-estimated relationships among 26 fish species in a rocky littoral area of Lake Tanganyika, along with the trophic guilds of causative species and the means and ranges of S-map coefficients. Each relationship was classified as negative or positive based on the majority of S-map coefficients from 38 timepoints being negative or positive, respectively. Behavioral relationships directly observed by underwater survey (Hori 1993, unpublished) were provided. The rightmost column indicates whether a reverse-direction link was estimated by CCM for species pairs.

Species pair		Trophic guild		S-map coefficients					Observed relationship	Reverse link
Causative	Recipient	Causative species	Recipient species	Mean	Min	Max	Majority sign	Majority ratio		
<i>Alt.com</i>	<i>Jul.orn</i>	Shrimp eater	Omnivore	0.71	-0.38	2.73	Positive	0.82	None	Absent
<i>Alt.com</i>	<i>Neo.fas</i>	Shrimp eater	Piscivore	0.14	-0.29	0.49	Positive	0.76	None	Absent
<i>Alt.com</i>	<i>Oph.ven</i>	Shrimp eater	Omnivore	-0.08	-0.47	0.34	Negative	0.66	None	Absent
<i>Aul.dew</i>	<i>Int.loo</i>	Fry feeder	Omnivore	-0.23	-0.60	0.09	Negative	0.97	None	Present
<i>Aul.dew</i>	<i>Lam.cal</i>	Fry feeder	Fry feeder	0.24	-0.72	2.32	Positive	0.55	None	Absent
<i>Aul.dew</i>	<i>Lam.lem</i>	Fry feeder	Piscivore	1.34	-7.21	8.05	Positive	0.63	None	Absent
<i>Aul.dew</i>	<i>Neo.fas</i>	Fry feeder	Piscivore	-0.12	-1.12	0.38	Negative	0.55	None	Present
<i>Aul.dew</i>	<i>Neo.sex</i>	Fry feeder	Shrimp eater	0.11	-0.17	0.57	Positive	0.76	None	Present
<i>Aul.dew</i>	<i>Oph.ven</i>	Fry feeder	Omnivore	0.19	-0.11	0.39	Positive	0.95	None	Present
<i>Aul.dew</i>	<i>Per.mic</i>	Fry feeder	Scale eater	-0.35	-1.56	1.36	Negative	0.87	None	Present
<i>Aul.dew</i>	<i>Pot.tre</i>	Fry feeder	Grazer	-0.67	-5.57	2.72	Negative	0.61	None	Present
<i>Aul.dew</i>	<i>Tel.vit</i>	Fry feeder	Brower	0.18	-0.30	0.50	Positive	0.87	None	Absent
<i>Gna.pfe</i>	<i>Alt.com</i>	Shrimp eater	Shrimp eater	0.20	-0.04	0.47	Positive	0.95	None	Absent
<i>Gna.pfe</i>	<i>Lim.dar</i>	Shrimp eater	Omnivore	-0.25	-5.23	5.05	Negative	0.50	None	Absent
<i>Gna.pfe</i>	<i>Lep.elo</i>	Shrimp eater	Piscivore	1.14	-1.08	5.92	Positive	0.79	None	Absent
<i>Gna.pfe</i>	<i>Neo.sex</i>	Shrimp eater	Shrimp eater	0.07	-0.48	0.42	Positive	0.74	None	Absent
<i>Gna.pfe</i>	<i>Oph.ven</i>	Shrimp eater	Omnivore	0.54	0.13	1.00	Positive	1.00	None	Absent
<i>Gna.pfe</i>	<i>Per.mic</i>	Shrimp eater	Scale eater	0.03	-1.34	1.41	Positive	0.55	Aggressor-Victim Prey-predator	Absent
<i>Hap.mic</i>	<i>Par.spp</i>	Omnivore	Omnivore	-0.28	-0.36	-0.07	Negative	1.00	None	Absent
<i>Int.loo</i>	<i>Aul.dew</i>	Omnivore	Fry feeder	0.39	0.22	0.79	Positive	1.00	None	Present
<i>Int.loo</i>	<i>Neo.fas</i>	Omnivore	Piscivore	0.13	-0.51	0.58	Positive	0.68	None	Present
<i>Int.loo</i>	<i>Oph.ven</i>	Omnivore	Omnivore	-0.37	-0.81	0.02	Negative	0.97	None	Present
<i>Int.loo</i>	<i>Tro.moo</i>	Omnivore	Brower	-0.25	-0.62	0.14	Negative	0.84	None	Present
<i>Jul.orn</i>	<i>Aul.dew</i>	Omnivore	Fry feeder	0.13	-0.45	0.82	Positive	0.74	None	Absent
<i>Jul.orn</i>	<i>Lam.cal</i>	Omnivore	Fry feeder	0.24	-1.14	1.61	Positive	0.63	None	Absent
<i>Jul.orn</i>	<i>Neo.fas</i>	Omnivore	Piscivore	0.38	-0.85	1.61	Positive	0.74	None	Absent
<i>Jul.orn</i>	<i>Neo.sex</i>	Omnivore	Shrimp eater	0.12	-0.86	0.70	Positive	0.82	None	Absent
<i>Jul.orn</i>	<i>Oph.ven</i>	Omnivore	Omnivore	0.17	-0.54	0.74	Positive	0.74	None	Present
<i>Jul.orn</i>	<i>Per.mic</i>	Omnivore	Scale eater	-0.21	-1.64	1.05	Negative	0.61	None	Present
<i>Jul.orn</i>	<i>Tro.moo</i>	Omnivore	Brower	0.11	-0.34	0.95	Positive	0.71	None	Absent
<i>Jul.orn</i>	<i>Tel.vit</i>	Omnivore	Brower	0.27	-0.53	1.11	Positive	0.84	None	Absent
<i>Lep.att</i>	<i>Lam.cal</i>	Fry feeder	Fry feeder	0.58	-1.29	2.40	Positive	0.76	None	Absent
<i>Lep.att</i>	<i>Lob.lab</i>	Fry feeder	Shrimp eater	0.15	-6.16	10.27	Positive	0.66	None	Absent
<i>Lep.att</i>	<i>Lam.tan</i>	Fry feeder	Omnivore	1.30	-0.02	1.98	Positive	0.97	None	Absent
<i>Lep.att</i>	<i>Xen.pap</i>	Fry feeder	Omnivore	1.54	-1.04	4.25	Positive	0.95	None	Absent
<i>Lam.cal</i>	<i>Alt.com</i>	Fry feeder	Shrimp eater	0.61	0.12	1.05	Positive	1.00	None	Absent
<i>Lam.cal</i>	<i>Int.loo</i>	Fry feeder	Omnivore	-0.36	-0.76	0.01	Negative	0.97	None	Absent
<i>Lam.cal</i>	<i>Lim.dar</i>	Fry feeder	Omnivore	0.17	-5.67	8.30	Positive	0.55	None	Absent
<i>Lam.cal</i>	<i>Lam.tan</i>	Fry feeder	Omnivore	0.10	-0.30	0.79	Positive	0.58	None	Absent
<i>Lam.cal</i>	<i>Neo.fas</i>	Fry feeder	Piscivore	-0.08	-1.26	0.71	Negative	0.55	None	Absent
<i>Lam.cal</i>	<i>Oph.ven</i>	Fry feeder	Omnivore	-0.21	-0.65	0.28	Negative	0.79	None	Absent
<i>Lam.cal</i>	<i>Per.mic</i>	Fry feeder	Scale eater	-0.41	-2.04	0.65	Negative	0.74	Prey-Predator	Absent
<i>Lam.cal</i>	<i>Tro.moo</i>	Fry feeder	Brower	0.36	-0.21	0.92	Positive	0.92	Victim-Aggressor	Absent
<i>Lam.cal</i>	<i>Xen.pap</i>	Fry feeder	Omnivore	-0.49	-2.86	0.94	Negative	0.76	None	Absent
<i>Lim.dar</i>	<i>Aul.dew</i>	Omnivore	Fry feeder	0.26	0.12	0.38	Positive	1.00	None	Absent

<i>Lim.dar</i>	<i>Lam.tan</i>	Omnivore	Omnivore	-0.04	-0.39	0.33	Negative	0.66	None	Absent
<i>Lim.dar</i>	<i>Tel.vit</i>	Omnivore	Browser	0.09	-0.29	0.45	Positive	0.66	None	Absent
<i>Lim.dar</i>	<i>Var.moo</i>	Omnivore	Omnivore	-0.64	-2.47	0.74	Negative	0.71	None	Absent
<i>Lep.elo</i>	<i>Tel.tem</i>	Piscivore	Browser	-0.36	-4.79	5.83	Negative	0.58	Predator-Prey Victim-Aggressor	Absent
<i>Lep.elo</i>	<i>Var.moo</i>	Piscivore	Omnivore	-0.35	-2.56	1.49	Negative	0.66	None	Present
<i>Lob.lab</i>	<i>Alt.com</i>	Shrimp eater	Shrimp eater	-0.05	-0.21	0.26	Negative	0.74	None	Absent
<i>Lob.lab</i>	<i>Tro.moo</i>	Shrimp eater	Browser	-0.30	-0.52	-0.05	Negative	1.00	None	Absent
<i>Lam.lem</i>	<i>Par.spp</i>	Piscivore	Omnivore	-0.09	-0.14	-0.02	Negative	1.00	None	Absent
<i>Lam.tan</i>	<i>Int.loo</i>	Omnivore	Omnivore	0.26	-0.29	0.75	Positive	0.84	None	Absent
<i>Lam.tan</i>	<i>Per.mic</i>	Omnivore	Scale eater	0.07	-1.67	0.83	Positive	0.55	Prey-Predator	Absent
<i>Lam.tan</i>	<i>Pet.pol</i>	Omnivore	Grazer	0.24	-2.55	2.78	Positive	0.50	None	Absent
<i>Lam.tan</i>	<i>Tro.moo</i>	Omnivore	Browser	-0.30	-0.59	0.10	Negative	0.92	None	Absent
<i>Neo.fas</i>	<i>Aul.dew</i>	Piscivore	Fry feeder	0.09	-0.23	0.35	Positive	0.74	None	Present
<i>Neo.fas</i>	<i>Int.loo</i>	Piscivore	Omnivore	-0.22	-0.52	0.13	Negative	0.90	None	Present
<i>Neo.fas</i>	<i>Oph.ven</i>	Piscivore	Omnivore	-0.38	-1.02	0.09	Negative	0.92	None	Present
<i>Neo.fas</i>	<i>Per.mic</i>	Piscivore	Scale eater	0.10	-0.61	1.86	Positive	0.58	Prey-Predator	Present
<i>Neo.fas</i>	<i>Syn.mul</i>	Piscivore	Grazer	-0.39	-1.96	1.10	Negative	0.58	None	Present
<i>Neo.fas</i>	<i>Tro.moo</i>	Piscivore	Browser	-0.06	-0.35	0.34	Negative	0.68	Predator-Prey	Present
<i>Neo.fas</i>	<i>Tel.vit</i>	Piscivore	Browser	0.04	-0.56	0.41	Positive	0.63	None	Absent
<i>Neo.fas</i>	<i>Xen.pap</i>	Piscivore	Omnivore	-0.05	-1.65	1.43	Negative	0.53	None	Absent
<i>Neo.sex</i>	<i>Alt.com</i>	Shrimp eater	Shrimp eater	0.34	-0.13	0.74	Positive	0.92	None	Absent
<i>Neo.sex</i>	<i>Aul.dew</i>	Shrimp eater	Fry feeder	-0.03	-0.15	0.30	Negative	0.66	None	Present
<i>Neo.sex</i>	<i>Oph.ven</i>	Shrimp eater	Omnivore	-0.21	-0.64	0.20	Negative	0.84	None	Absent
<i>Neo.sex</i>	<i>Syn.mul</i>	Shrimp eater	Grazer	0.59	-0.78	2.06	Positive	0.82	None	Present
<i>Neo.sex</i>	<i>Tro.moo</i>	Shrimp eater	Browser	0.16	-0.31	0.45	Positive	0.76	None	Present
<i>Neo.sex</i>	<i>Tel.vit</i>	Shrimp eater	Browser	-0.17	-0.68	0.38	Negative	0.79	None	Present
<i>Oph.ven</i>	<i>Aul.dew</i>	Omnivore	Fry feeder	-0.33	-0.57	-0.13	Negative	1.00	None	Present
<i>Oph.ven</i>	<i>Int.loo</i>	Omnivore	Omnivore	-0.22	-0.54	0.13	Negative	0.82	None	Present
<i>Oph.ven</i>	<i>Jul.orn</i>	Omnivore	Omnivore	0.43	-2.11	2.27	Positive	0.79	None	Present
<i>Oph.ven</i>	<i>Neo.fas</i>	Omnivore	Piscivore	0.10	-0.73	0.80	Positive	0.68	None	Present
<i>Oph.ven</i>	<i>Per.mic</i>	Omnivore	Scale eater	0.56	-0.21	1.49	Positive	0.92	Prey-Predator	Present
<i>Oph.ven</i>	<i>Tro.moo</i>	Omnivore	Browser	0.02	-0.19	0.27	Positive	0.55	None	Absent
<i>Oph.ven</i>	<i>Var.moo</i>	Omnivore	Omnivore	-0.23	-2.72	1.98	Negative	0.53	None	Present
<i>Par.spp</i>	<i>Alt.com</i>	Omnivore	Shrimp eater	0.07	-0.27	0.27	Positive	0.79	None	Absent
<i>Par.spp</i>	<i>Neo.fas</i>	Omnivore	Piscivore	0.03	-0.83	0.54	Positive	0.50	None	Absent
<i>Par.spp</i>	<i>Tro.moo</i>	Omnivore	Browser	0.38	-0.08	0.82	Positive	0.97	None	Absent
<i>Per.mic</i>	<i>Alt.com</i>	Scale eater	Shrimp eater	0.16	-0.17	0.41	Positive	0.84	None	Absent
<i>Per.mic</i>	<i>Aul.dew</i>	Scale eater	Fry feeder	-0.31	-0.64	-0.05	Negative	1.00	None	Present
<i>Per.mic</i>	<i>Jul.orn</i>	Scale eater	Omnivore	-0.28	-3.85	5.60	Negative	0.53	None	Present
<i>Per.mic</i>	<i>Neo.fas</i>	Scale eater	Piscivore	0.32	-0.17	1.31	Positive	0.87	Predator-Prey	Present
<i>Per.mic</i>	<i>Neo.sex</i>	Scale eater	Shrimp eater	-0.45	-1.12	0.08	Negative	0.97	None	Absent
<i>Per.mic</i>	<i>Oph.ven</i>	Scale eater	Omnivore	-0.04	-0.31	0.27	Negative	0.63	Predator-Prey	Present
<i>Per.mic</i>	<i>Pet.tre</i>	Scale eater	Grazer	-0.43	-3.03	1.44	Negative	0.58	Predator-Prey Victim-Aggressor	Absent
<i>Per.mic</i>	<i>Tro.moo</i>	Scale eater	Browser	0.07	-0.34	0.41	Positive	0.63	Predator-Prey Victim-Aggressor	Absent
<i>Pet.pol</i>	<i>Int.loo</i>	Grazer	Omnivore	-0.13	-0.52	0.31	Negative	0.79	None	Absent
<i>Pet.pol</i>	<i>Jul.orn</i>	Grazer	Omnivore	0.68	-0.93	7.46	Positive	0.68	None	Absent
<i>Pet.tre</i>	<i>Aul.dew</i>	Grazer	Fry feeder	0.20	-0.08	0.48	Positive	0.97	None	Present
<i>Pet.tre</i>	<i>Lep.att</i>	Grazer	Fry feeder	0.30	-0.44	1.35	Positive	0.71	None	Absent
<i>Pet.tre</i>	<i>Oph.ven</i>	Grazer	Omnivore	0.09	-0.18	0.45	Positive	0.74	None	Absent
<i>Pet.tre</i>	<i>Tro.moo</i>	Grazer	Browser	0.14	-0.13	0.39	Positive	0.90	None	Absent

<i>Syn.mul</i>	<i>Neo.fas</i>	Grazer	Piscivore	-0.58	-1.37	0.15	Negative	0.95	None	Present
<i>Syn.mul</i>	<i>Neo.sex</i>	Grazer	Shrimp eater	-0.22	-0.73	0.13	Negative	0.90	None	Present
<i>Syn.mul</i>	<i>Tel.vit</i>	Grazer	Browser	0.12	-0.32	0.49	Positive	0.74	None	Present
<i>Tro.moo</i>	<i>Aul.dew</i>	Browser	Fry feeder	-0.37	-0.55	0.03	Negative	0.97	None	Absent
<i>Tro.moo</i>	<i>Int.loo</i>	Browser	Omnivore	-0.07	-0.41	0.30	Negative	0.63	None	Present
<i>Tro.moo</i>	<i>Lep.elo</i>	Browser	Piscivore	0.83	-1.02	3.07	Positive	0.74	None	Absent
<i>Tro.moo</i>	<i>Neo.fas</i>	Browser	Piscivore	0.19	-0.41	0.60	Positive	0.79	Prey-Predator	Present
<i>Tro.moo</i>	<i>Neo.sex</i>	Browser	Shrimp eater	0.30	0.01	0.75	Positive	1.00	None	Present
<i>Tro.moo</i>	<i>Var.moo</i>	Browser	Omnivore	0.00	-1.99	1.23	Positive	0.61	None	Absent
<i>Tro.moo</i>	<i>Xen.pap</i>	Browser	Omnivore	-0.10	-1.10	0.90	Negative	0.50	None	Present
<i>Tel.tem</i>	<i>Lam.cal</i>	Browser	Fry feeder	-0.01	-2.12	0.97	Negative	0.61	Aggressor-Victim	Absent
<i>Tel.vit</i>	<i>Int.loo</i>	Browser	Omnivore	-0.01	-0.76	0.44	Negative	0.50	None	Absent
<i>Tel.vit</i>	<i>Neo.sex</i>	Browser	Shrimp eater	-0.21	-0.89	0.33	Negative	0.74	None	Present
<i>Tel.vit</i>	<i>Pet.pol</i>	Browser	Grazer	0.00	-1.40	1.08	Positive	0.53	None	Absent
<i>Tel.vit</i>	<i>Syn.mul</i>	Browser	Grazer	-0.33	-3.68	2.28	Negative	0.61	None	Present
<i>Tel.vit</i>	<i>Tro.moo</i>	Browser	Browser	0.38	-0.48	1.00	Positive	0.76	None	Absent
<i>Tel.vit</i>	<i>Xen.pap</i>	Browser	Omnivore	-0.40	-2.20	1.24	Negative	0.82	None	Absent
<i>Var.moo</i>	<i>Aul.dew</i>	Omnivore	Fry feeder	0.51	0.21	0.90	Positive	1.00	None	Absent
<i>Var.moo</i>	<i>Lep.elo</i>	Omnivore	Piscivore	-0.16	-2.54	3.80	Negative	0.61	None	Present
<i>Var.moo</i>	<i>Neo.sex</i>	Omnivore	Shrimp eater	-0.29	-0.65	-0.03	Negative	1.00	None	Absent
<i>Var.moo</i>	<i>Oph.ven</i>	Omnivore	Omnivore	-0.50	-0.86	-0.13	Negative	1.00	None	Present
<i>Var.moo</i>	<i>Per.mic</i>	Omnivore	Scale eater	-0.31	-1.22	0.64	Negative	0.76	None	Absent
<i>Var.moo</i>	<i>Pet.pol</i>	Omnivore	Grazer	0.00	-0.65	0.47	Negative	0.55	None	Absent
<i>Var.moo</i>	<i>Xen.pap</i>	Omnivore	Omnivore	0.16	-0.50	1.09	Positive	0.61	None	Absent
<i>Xen.pap</i>	<i>Aul.dew</i>	Omnivore	Fry feeder	0.22	-0.01	0.43	Positive	0.97	None	Absent
<i>Xen.pap</i>	<i>Jul.orn</i>	Omnivore	Omnivore	-0.08	-1.93	2.89	Negative	0.61	None	Absent
<i>Xen.pap</i>	<i>Lep.elo</i>	Omnivore	Piscivore	0.13	-2.42	2.68	Positive	0.58	None	Absent
<i>Xen.pap</i>	<i>Per.mic</i>	Omnivore	Scale eater	-0.01	-0.57	0.50	Negative	0.50	None	Absent
<i>Xen.pap</i>	<i>Syn.mul</i>	Omnivore	Grazer	0.22	-0.87	1.31	Positive	0.68	None	Absent
<i>Xen.pap</i>	<i>Tro.moo</i>	Omnivore	Browser	-0.08	-0.35	0.24	Negative	0.74	None	Present

Table S3. A subset of CCM-estimated relationships from Table S2 that align with the observed behavioral interactions (Hori 1993, unpublished) among 26 fish species in a rocky littoral area of Lake Tanganyika, along with the means and ranges of S-map coefficients

Fish species		Trophic guild		S-map coefficient					Observed relationship	Consistency
Causative species	Recipient species	causative	Recipient	Mean	Min	Max	Majority sign	Majority ratio	Causative→Recipient	
<i>N_fasciatus</i>	<i>P_microlepis</i>	Piscivore	Scale-eater	0.10	-0.61	1.86	positive	0.58	Prey-Predator	Consistent
<i>O_ventralis</i>	<i>P_microlepis</i>	Omnivore	Scale-eater	0.56	-0.21	1.49	positive	0.92	Prey-Predator	Consistent
<i>T_moorii</i>	<i>N_fasciatus</i>	Browser	Piscivore	0.19	-0.41	0.60	positive	0.79	Prey-Predator	Consistent
<i>L_tanganicanus</i>	<i>P_microlepis</i>	Omnivore	Scale-eater	0.06	-1.66	0.83	positive	0.55	Prey-Predator	Consistent
<i>G_pfefferi</i>	<i>P_microlepis</i>	Shrimp-eater	Scale-eater	0.03	-1.34	1.41	positive	0.55	Aggressor-Victim	Contradictory
<i>P_microlepis</i>	<i>N_fasciatus</i>	Scale-eater	Piscivore	0.32	-0.17	1.31	positive	0.87	Prey-Predator	Consistent
<i>P_microlepis</i>	<i>T_moorii</i>	Scale-eater	Browser	0.07	-0.34	0.41	positive	0.63	Predator-Prey	Contradictory
<i>L_callipterus</i>	<i>T_moorii</i>	Fry-feeder	Browser	0.36	-0.21	0.92	positive	0.92	Victim-Aggressor	Contradictory
<i>L_callipterus</i>	<i>P_microlepis</i>	Fry-feeder	Scale-eater	-0.41	-2.04	0.65	negative	0.74	Prey-Predator	Contradictory
<i>N_fasciatus</i>	<i>T_moorii</i>	Piscivore	Browser	-0.06	-0.35	0.34	negative	0.68	Predator-Prey	Consistent
<i>P_microlepis</i>	<i>O_ventralis</i>	Scale-eater	Omnivore	-0.04	-0.31	0.27	negative	0.63	Predator-Prey	Consistent
<i>L_elongatus</i>	<i>T_temporalis</i>	Piscivore	Browser	-0.36	-4.79	5.83	negative	0.58	Predator-Prey	Consistent
<i>P_microlepis</i>	<i>P_trewavasae</i>	Scale-eater	Grazer	-0.43	-3.03	1.44	negative	0.58	Victim-Aggressor	Consistent
<i>T_temporalis</i>	<i>L_callipterus</i>	Browser	Fry-feeder	-0.01	-2.12	0.97	negative	0.61	Predator-Prey	Consistent
									Aggressor-Victim	Consistent

Table S4. Summary of power-law fitting results for each network. n is the sample size; x_{min} , the lower cutoff of the power-law tail; n_{tail} , the number of observations in the tail; α , the maximumlikelihood exponent estimate; KS , the Kolmogorov-Smirnov distance between the empirical tail and the fitted model; and p (gof), the goodness-of-fit p-value obtained by the Clauset-ShaliziNewman procedure. The best model column indicates the model with the highest log-likelihood among power law (PL), truncated power law (TPL), log normal (LOGN), exponential (EXP), and stretched exponential (STEX).

Degree distribution	n	x_{min}	n_{tail}	α	KS	p (gof)	Best model
Total degree	26	11	12	4.016	0.294	0.070	LOGN
In-degree	24	4	15	2.570	0.293	0.017	EXP
Out-degree	26	6	12	4.948	0.263	0.080	LOGN

Table S5. Results of the analysis of variance (Anova) analysis explaining the number of input and output CCM-estimated relationships for each species, with trophic guilds and mean individual number as explanatory variables (full model) for causality (a) or recipient (b). Df, degree of freedom.

(a)	Df	Deviance	Resid. Df	Resid. Dev	Pr (>Chi)
NULL	NA	NA	25	37.636	NA
Population mean	1	5.117	24	32.519	0.024 *
Trophic guild	6	10.8757	18	21.644	0.092
Population mean: Trophic guild	5	5.857	13	15.788	0.32

(b)	Df	Deviance	Resid. Df	Resid. Dev	Pr (>Chi)
NULL	NA	NA	25	78.246	NA
Population mean	1	8.887	24	69.359	0.003 **
Trophic guild	6	5.665	18	63.693	0.462
Population mean: Trophic guild	5	25.274	13	38.419	0 ***

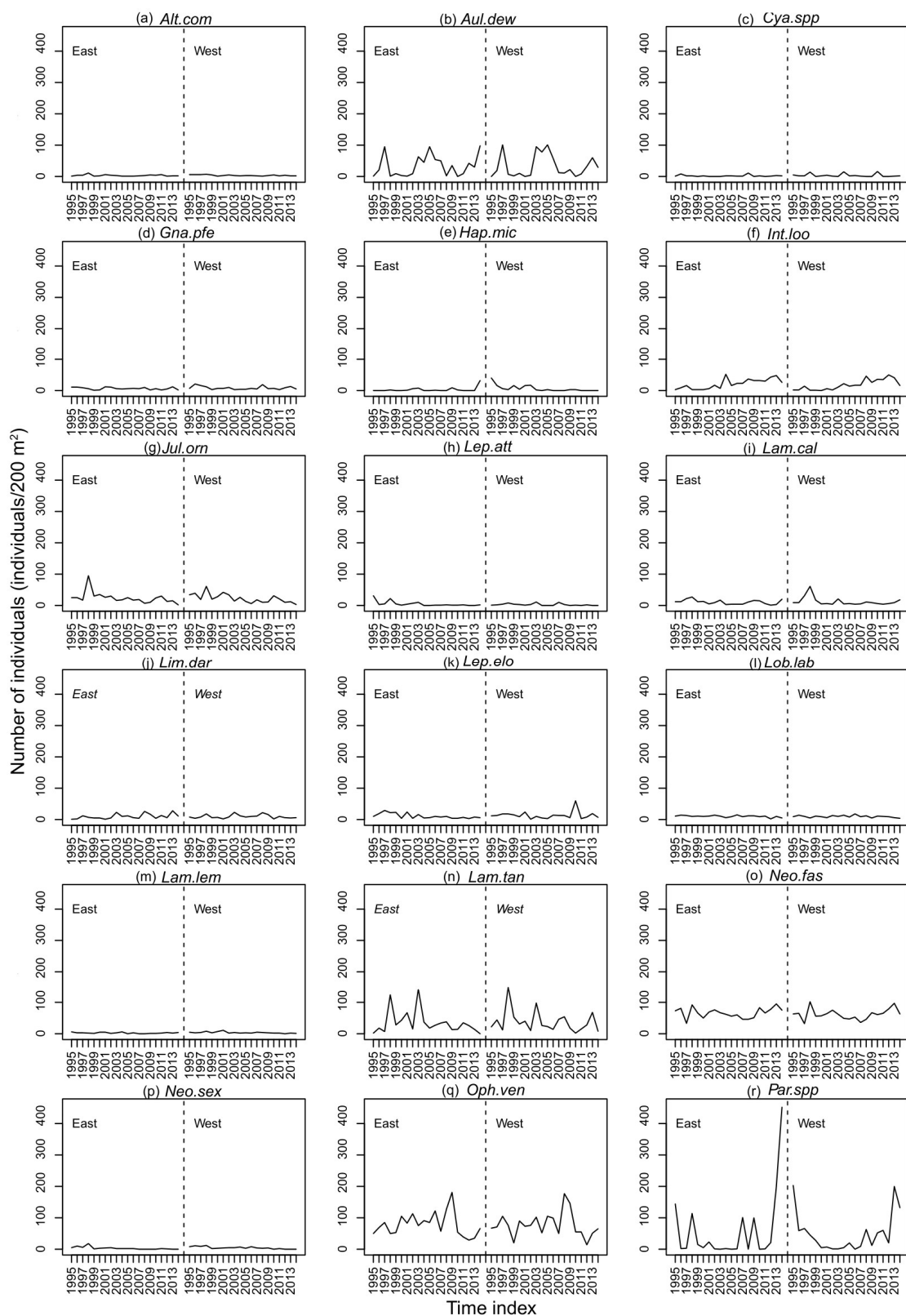
Table S6. Analysis of variance (ANOVA) explaining the betweenness centrality, with trophic guilds and mean abundance as explanatory variables.

	Df	Sum Sq	Mean Sq	<i>F</i> value	<i>P</i> value
Mean abundance	1	1268.63	1268.63	2.88	0.113
Trophic guild	6	10510.33	1751.72	3.98	0.018 *
Mean abundance: Trophic guild	5	7217.06	1443.41	3.28	0.039 *
Residuals	13	5717.69	439.82	NA	NA

Table S7. Numbers of positive and negative causal relationships among trophic guilds of cichlid fishes in Lake Tanganyika, estimated by convergent cross mapping (CCM). (a) Relationships where each trophic guild acts as the causative species. (b) Relationships where each trophic guild acts as the recipient species. Values are separated into intra-guild and inter-guild interactions, with totals shown in the rightmost column.

(a) Causative species							
Trophic guild	Number of species	Intra-guild		Inter-guild		Total	
		Positive	Negative	Positive	Negative		
Fry feeder	3	2	0	11	9	22	
Scale eater	1	0	0	3	5	8	
Shrimp eater	4	3	1	7	6	17	
Piscivore	3	0	0	3	8	11	
Omnivore	9	4	8	22	10	44	
Grazer	3	0	0	6	3	9	
Browser	3	1	0	5	8	14	

(b) Recipient species							
Trophic guild	Number of species	Intra-guild		Inter-guild		Total	
		Positive	Negative	Positive	Negative		
Fry feeder	3	2	0	9	5	16	
Scale eater	1	0	0	4	5	9	
Shrimp eater	3	3	1	7	4	15	
Piscivore	3	0	0	11	4	15	
Omnivore	8	4	8	10	19	41	
Grazer	3	0	0	4	5	9	
Browser	3	1	0	12	7	20	



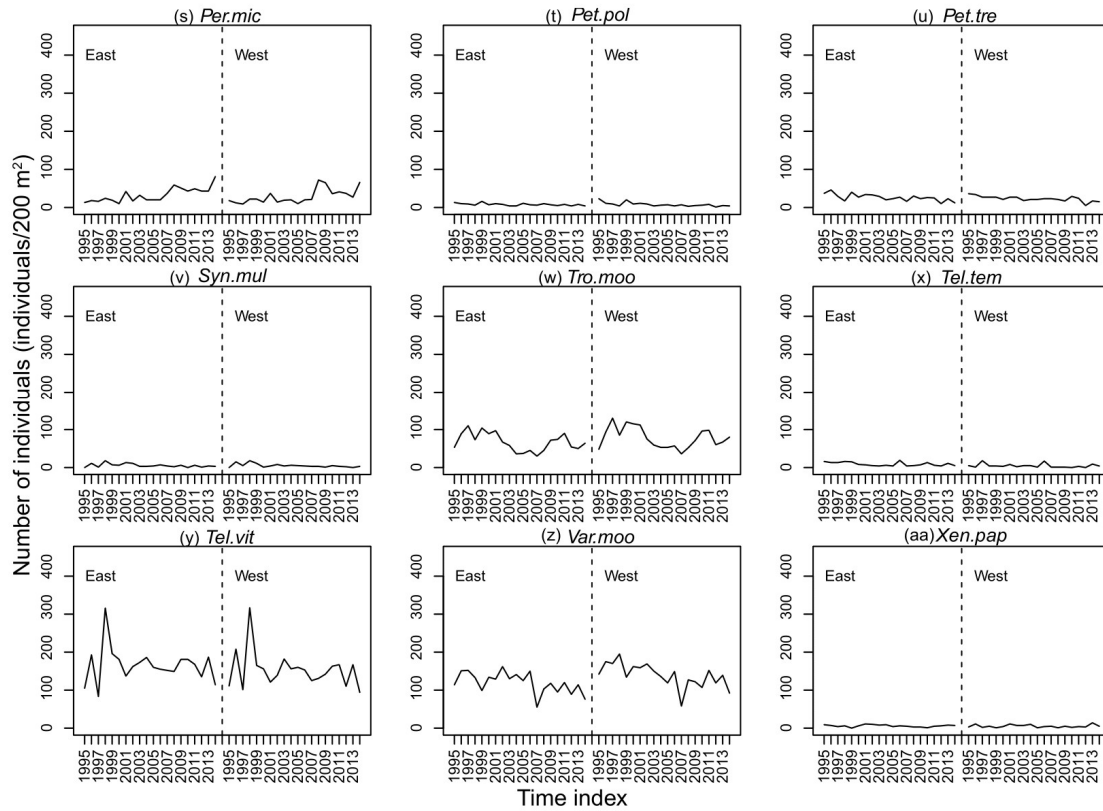


Figure S1. Changes in the abundances (individuals per 200 m²) of 26 fish species examined by CCM, observed over a 20-year underwater census in a rocky littoral area of Lake Tanganyika. Data from the western half of the study area were concatenated after those from the eastern half (indicated by vertical dotted lines) for use in EDM analyses (CCM and S-map), with NAs inserted at the junction (see text).

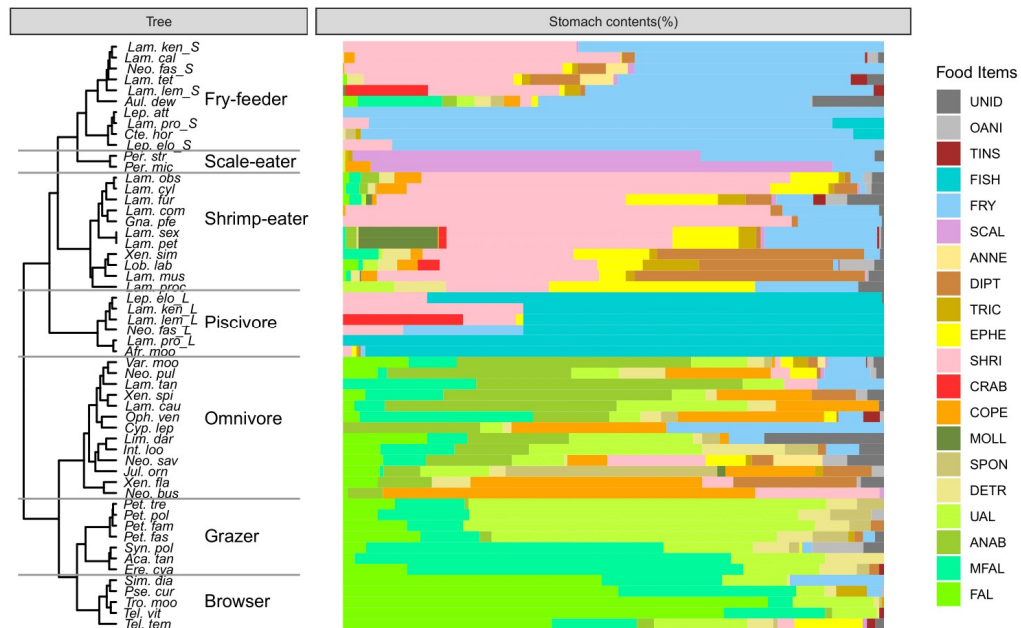
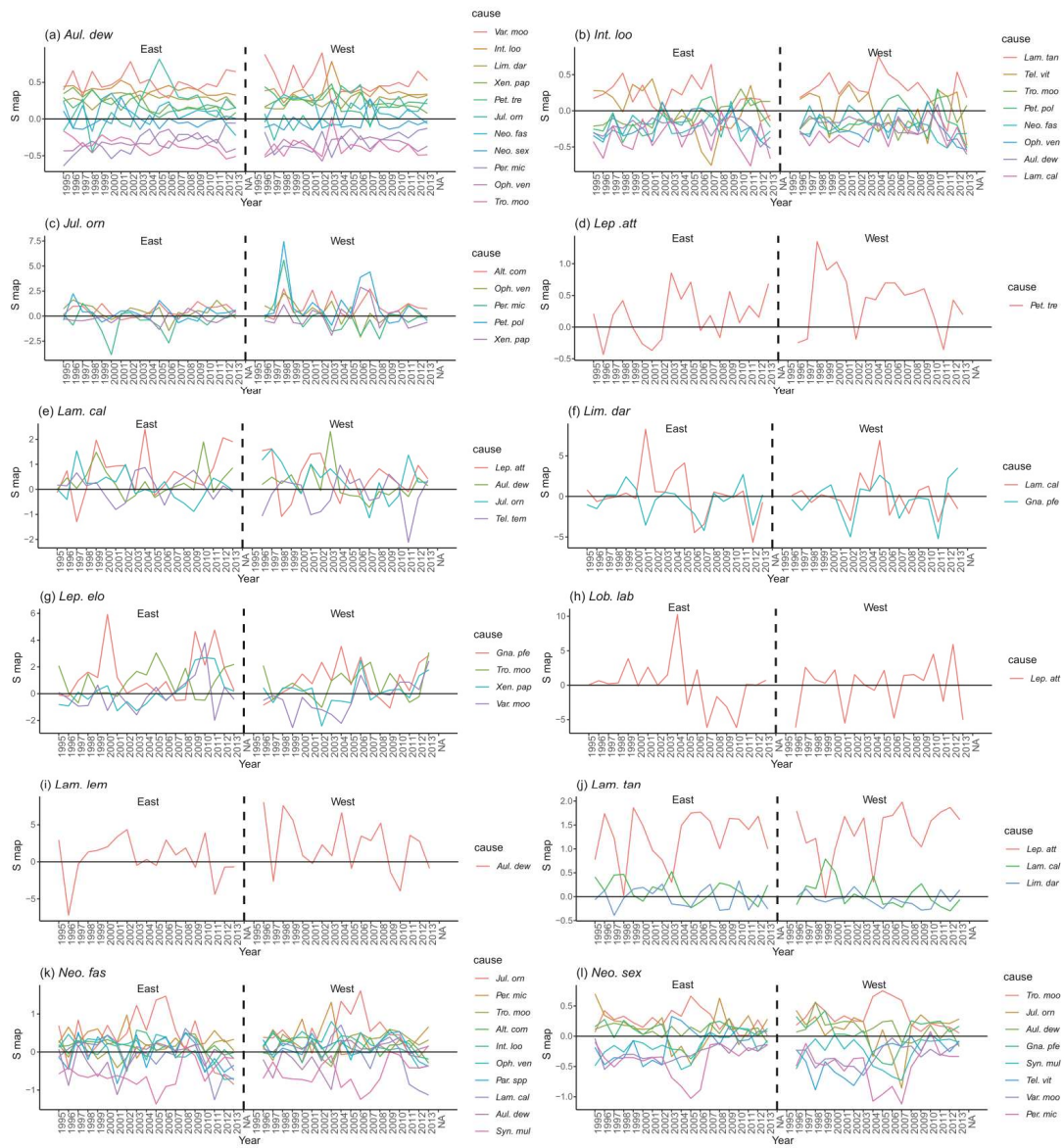


Figure S2. Food habits of Tanganyican cichlids collected in Mpulung, Zambia, based on their stomach contents. Stomach contents analyses were conducted by Hori (1990). To construct the hierarchical clustering tree, we applied hierarchical clustering to our dissimilarity matrix using the Ward's minimum variance method. UNID, unidentified; OANI, other animals; TINS, terrestrial insects; FISH, adult and subadult fish; FRY, fish fry; SCAL, fish scales; ANNE, annelids; DIPT, dipteran larvae; TRIC, tricopteran larvae; EPHE, ephemeropteran larvae; SHRI, shrimps; CRAB, crabs; COPE, copepods; MOLL, molluscs; SPON, sponge; DETR, detritus; UAL, unicellular algae; ANAB, Anabaena, Microcystis, Aphanocapsa; MFAL, micro filamentous algae; FAL, filamentous algae. Species are shown by abbreviations and full names are provided in Table S1.



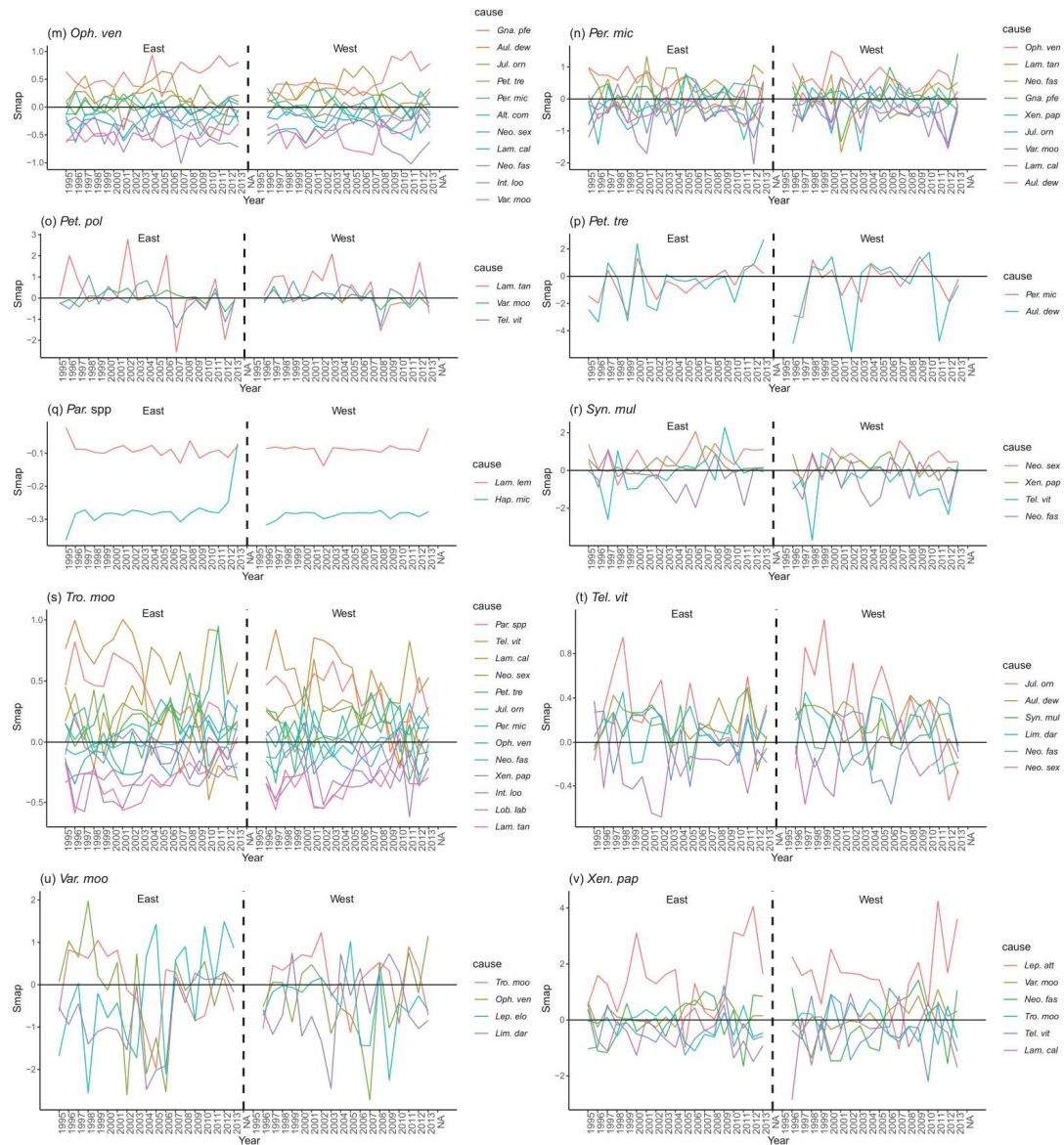


Figure S3. Changes in S-map coefficients, an index for the relationship strength, toward each of 26 recipient species (a–v) observed in the 20-year underwater census survey in a rocky littoral area of Lake Tanganyika. Lines of different colors indicate different species, from which CCM analysis detected significant effects to the focal recipient species. Time-series data from the western half of the study area were connected after those from the eastern half (vertical dotted lines) to calculate S-map coefficients, with NAs inserted at the connection (see text).

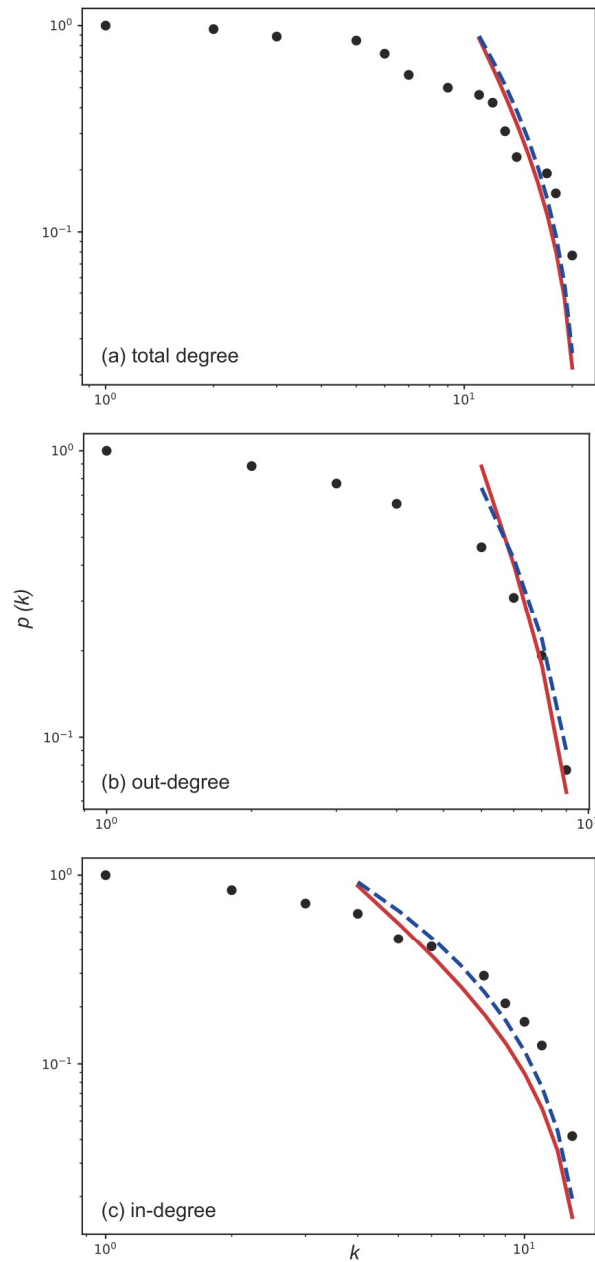


Figure S4. Scatter plots showing the number of CCM-estimated relationships for each species (k) and their proportion $P(k)$ among 26 fish species inhabiting a rocky littoral area of Lake Tanganyika. Panels show (a) total degree, (b) out-degree, and (c) in-degree. Red solid lines indicate linear regressions fitted from the degree at which the power-law model provided the most plausible fit. Blue dashed lines indicate linear regressions based on truncated power-law fits.

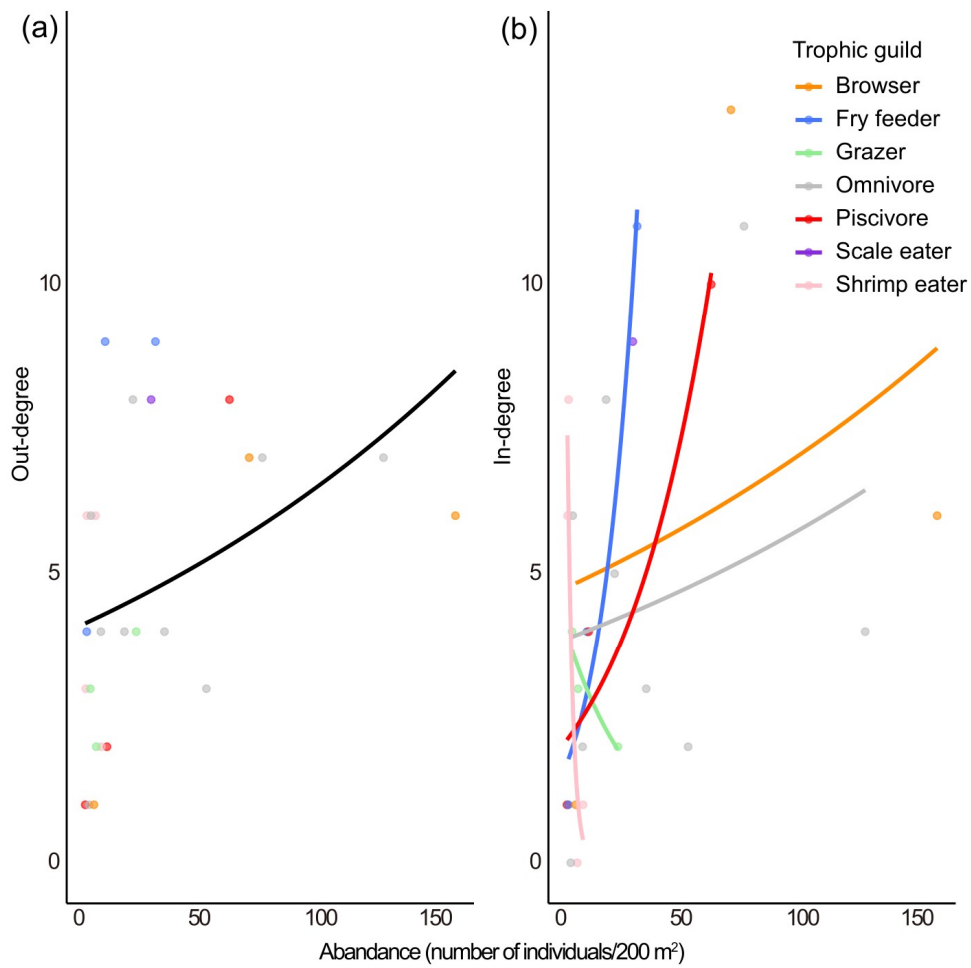


Figure S5. Out-degree (a), in-degree (b), and mean abundance of 26 fish species in the CCM-estimated interaction network from a rocky littoral area of Lake Tanganyika. Colors represent trophic guilds. Regression lines from generalized linear models (GLMs) with a Poisson distribution are shown; the black line represents the overall regression across all trophic guilds (indicating no significant differences among trophic guilds), while the colored lines represent separate regressions for each trophic guild.

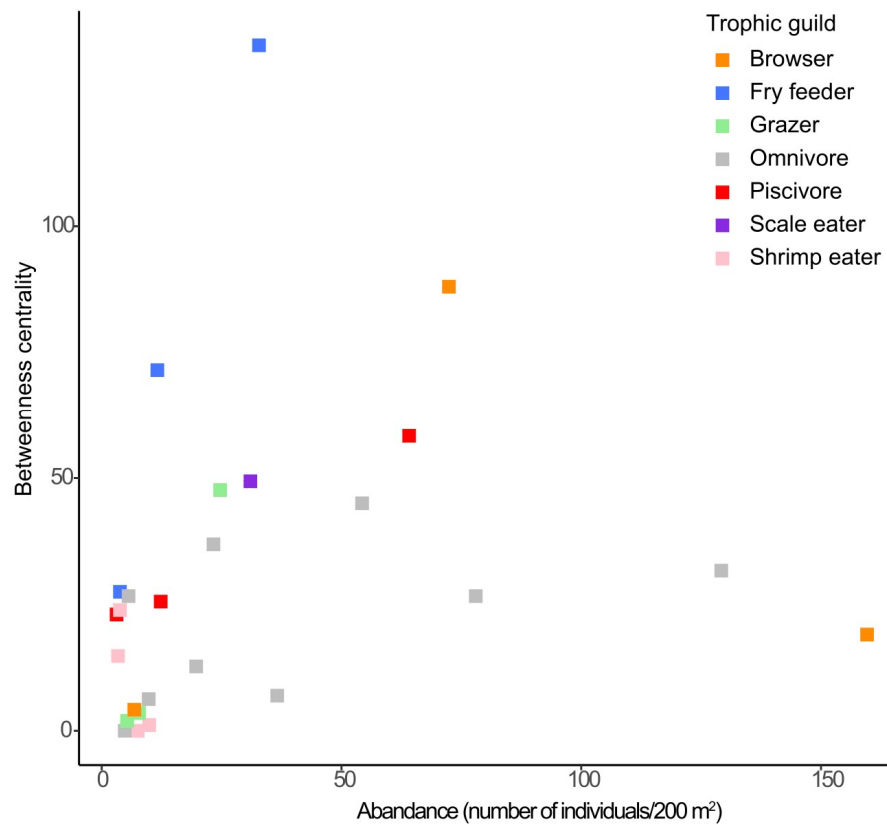


Figure S6. Betweenness centrality and mean abundance of 26 species in the CCM-estimated interaction network from a rocky littoral area of Lake Tanganyika. Colors indicate trophic guilds.

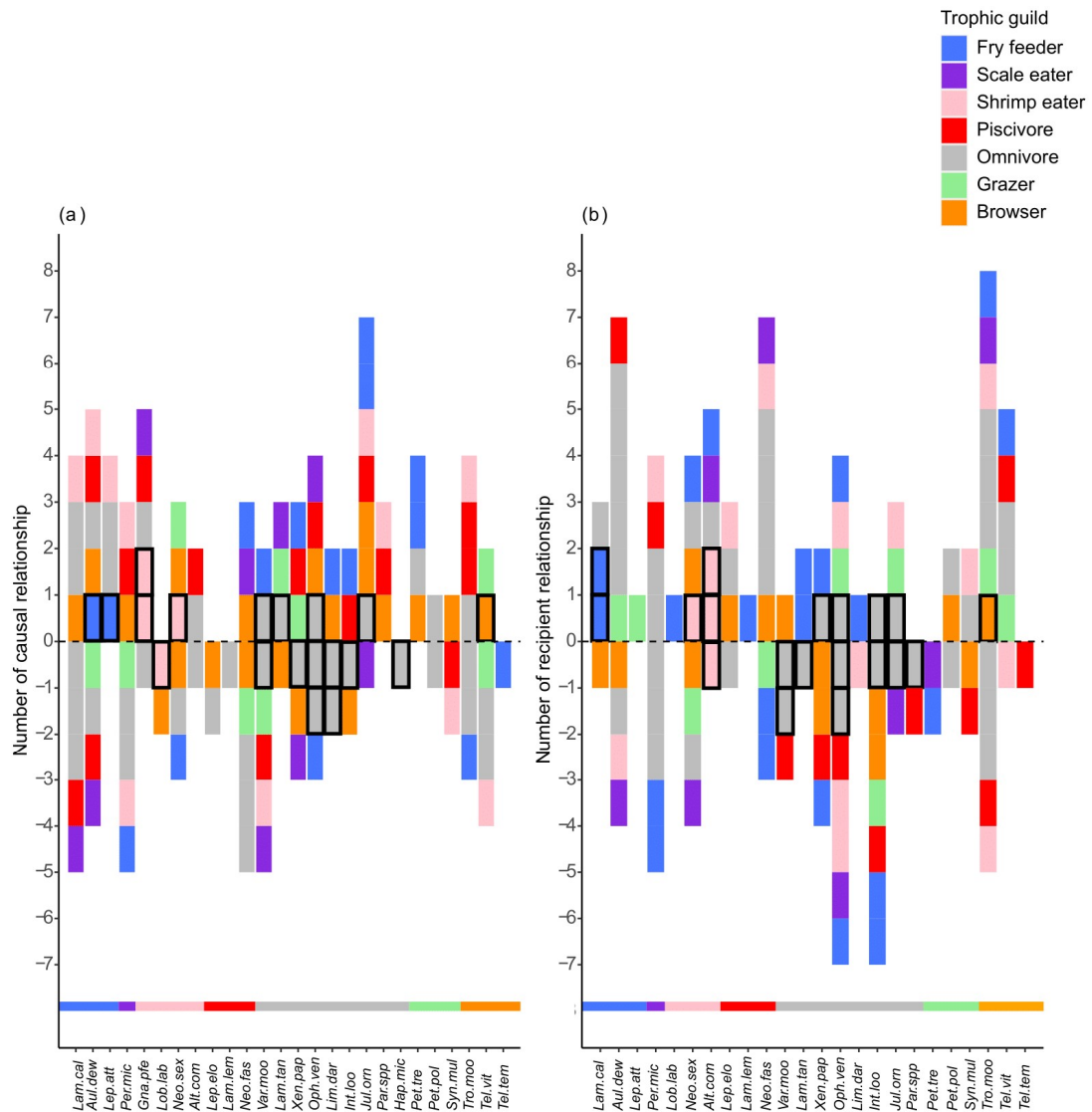
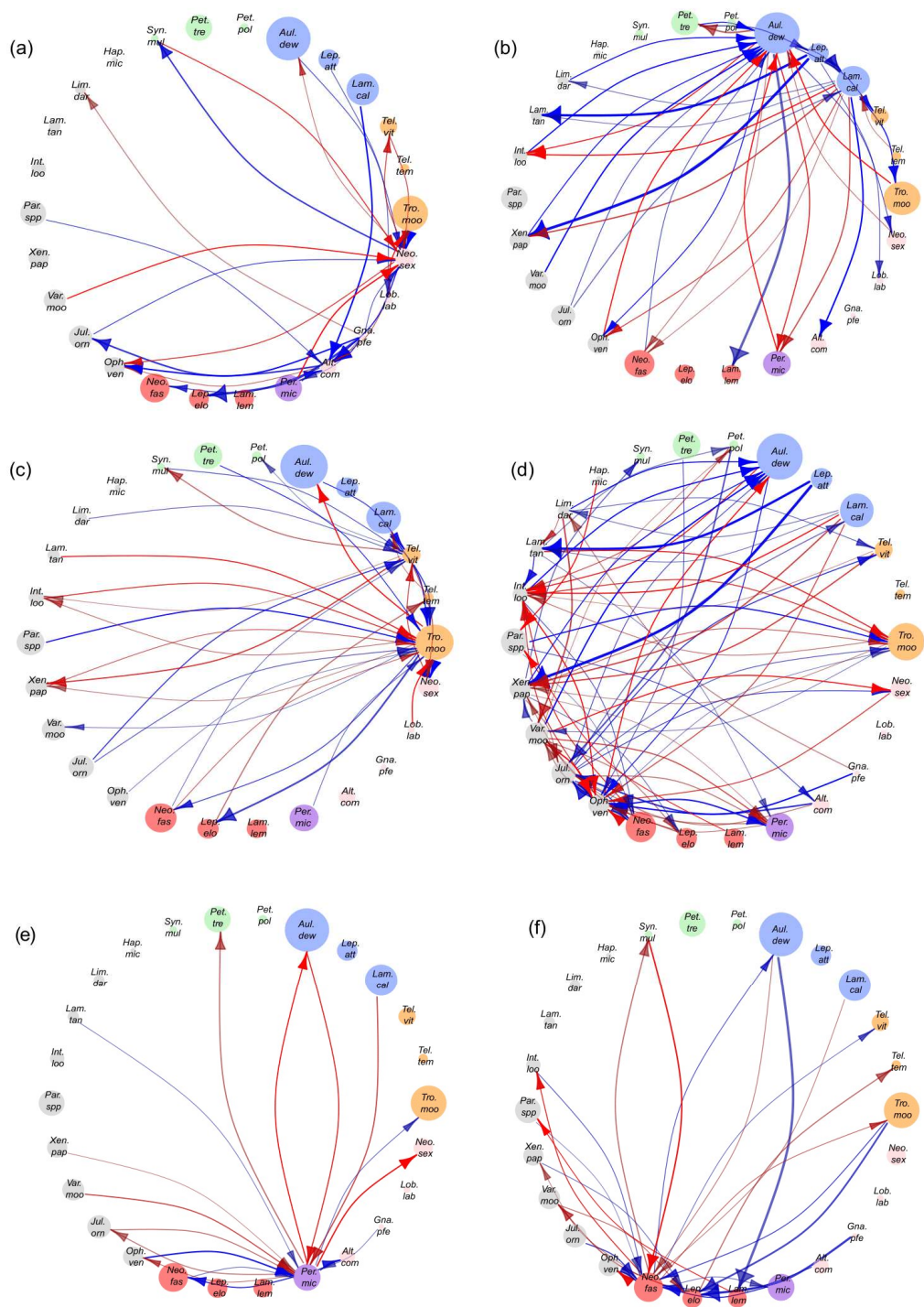


Figure S7. Numbers of CCM-estimated relationships originating from each causative species (a) and received by each recipient species (b). Positive and negative relationships are stacked upward and downward, respectively. The colors of the stacked bars indicate the trophic guilds (see Fig. S3) of the species at the opposite end of each relationship (i.e., recipients in (a), causative species in (b)). The trophic guilds of the species on the X-axis are represented by the color of the horizontal bars above the axis.



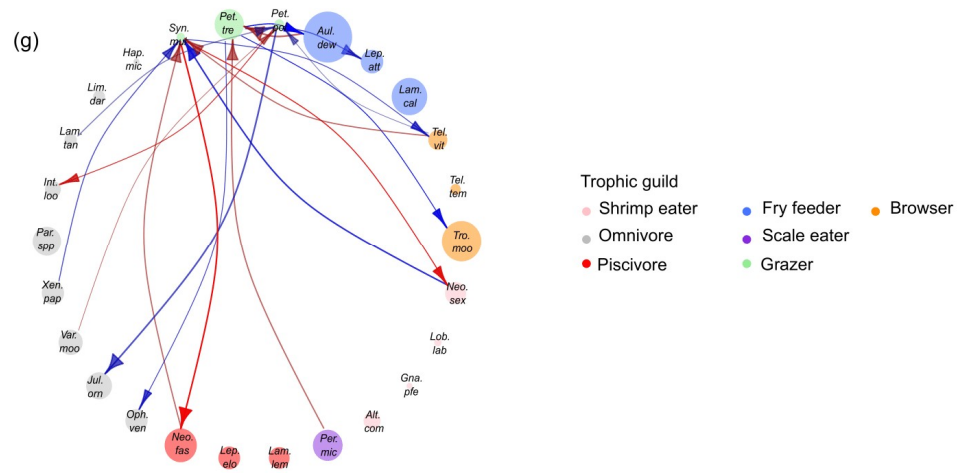


Figure S8. Species interaction networks among cichlid species belonging to each trophic guild, as estimated by CCM. (a) Shrimp eater, (b) Fry feeder, (c) Browser, (d) Omnivore, (e) Scale eater, (f) Piscivore, and (g) Grazer. The settings for nodes and edges are the same as in Fig. 3.

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Chapter 4. General discussion

This paper aimed to investigate interspecific interactions which is effect on population dynamics through both experimental and field-based approaches. By employing Empirical Dynamic Modeling (EDM), which is a time-series-based analytical framework, the study enabled the quantitative evaluation of causality and interaction strength, which are often difficult to capture using traditional observation-based methods (e.g.; Paine 1966, Estes and Palmisano 1974). In doing so, it addressed the limitations of conventional approaches which were counting data for individuals solely for estimating interspecific interactions by revealing temporally dynamic interspecific interactions.

The chapter 2nd showed interactions among population dynamics, inter specific interactions with fluctuating over time and under changing environmental conditions. Observational approaches provide detailed insights into specific interspecific interactions (Paine 1966, Hockaday et al. 2023). By comparing these observations with interactions inferred through Empirical Dynamic Modeling (EDM), the chapter 3rd was able to indicate important interactions with key species in the natural community. Interspecific interaction strength is temporally variable. Therefore, traditional observational methods that rely on one-off or short-term approaches are inadequate for estimating the long-term effects of interspecific interactions on population dynamics.

To solve these challenges, this study introduced EDM as a tool for reconstructing interaction networks from long-term population time series data and to elucidate the influence of environmental factors on population dynamics through interspecific interactions. Specifically, EDM was applied to two distinct systems: a controlled laboratory competition experiment with *Bruchid* beetles, and a long-term field observation of fish community for cichlid species in Lake Tanganyika. These complementary approaches allowed for the evaluation of EDM's applicability and effectiveness across different conditions, which were the nature and laboratory experiment.

The results showed the importance of integrating observational data with statistical approaches such as EDM to comprehensively evaluate interspecific interactions that influence population dynamics. This complementary framework demonstrated that even in environments where direct observation is difficult, EDM can efficiently and comprehensively assess interaction networks.

Furthermore, the study contributed to the identification of key species within community for *Cichlid* species with understanding of interaction network structures and provided insights into how environmental factors can influence population dynamics via interspecific interactions. These results showed the potential of EDM as a powerful tool for advancing ecological research beyond the constraints of traditional observational methods.

Summary of Chapter 2

Time series analysis showing how different environmental conditions affect the interspecific interactions of *Callosobruchus maculatus* and *Callosobruchus chinensis* the results of the EDM analysis and competition experiments demonstrated that environmental changes that specifically variations in cage size indirectly influenced interspecific interaction strength and consequently altered population dynamics. Although the environmental factor did not directly control the interaction strength, the findings support, at least partially, the long-standing hypothesis that environmental conditions can shape interspecific interactions and determine population-level outcomes.

In the competition experiment, changes in cage size led to predictable shifts in coexistence duration, suggesting that population dynamics can be modulated by environmental conditions. The initial hypothesis posited that cage size would alter the frequency of encounters between species, thereby affecting reproductive interference. However, the change in cage volume unexpectedly influenced resource bulk and surface area, which in turn may have affected oviposition behavior and resource competition intensity.

One possible explanation for this outcome is that changes in cage size may have unintentionally altered oviposition behavior due to differences in resource bulk and surface area. These changes could have reduced the intensity of resource competition, thereby increasing the relative importance of reproductive interference in shaping population dynamics. In other words, although reproductive interference was expected to be the primary mechanism driving coexistence, the experiment may have instead modulated resource competition, indirectly affecting the strength of interspecific interactions and the observed population dynamics.

These results showed that cage size can influence fundamental ecological conditions such as resource availability and encounter rates that support interspecific interactions. The experiment used cage size as an environmental variable and species whose interaction mechanisms characterized through long-term observation, providing a controlled context for testing ecological hypotheses (e.g., Drolet et al. 2013; Quammen 1984).

Despite these results showed that direct evidence was not found that environmental manipulation alone could control the strength of interspecific interactions. This result showed difficulty experimentally regulating interaction strength through environmental factors and emphasized the need for integrative approaches that consider indirect pathways and behavioral responses.

Summary of Chapter 3

This study successfully identified interspecific interactions with EDM that influence population dynamics in natural ecosystems based solely on time-series data. This approach allowed for a comprehensive mapping of interaction networks without requiring advanced expertise to estimate interspecific interactions from behavioral observations.

By incorporating S-map coefficients, which estimate time-varying interaction strengths, this approach

can estimate interaction strengths with obscure temporal dynamics (Deyle et al. 2016). This enabled a more accurate assessment of how interspecific interactions fluctuate over time and influence population dynamics and structure for interspecific interactions.

Here, I confirmed whether the interaction network with CCM was scale-free. The degree distribution of interspecific interactions did not conform to a scale-free pattern; instead, alternative models such as lognormal and exponential provided better fits, suggesting that interactions are more evenly distributed across the community rather than being dominated by a few highly connected species. Out-degree was positively correlated with the mean abundance of causative species, indicating that more abundant species tend to influence a greater number of others. In contrast, in-degree increased with the abundance of recipient species but showed substantial variation across trophic guilds.

Especially, omnivorous species exhibited the richest intra- and inter-guild interactions. Within their own guilds, they tended to exert negative effects, while across guild boundaries, they often had positive effects. This dual role suggests that omnivores may act as modulators of community dynamics, balancing competitive pressures within guilds and facilitating coexistence across guilds.

Future Perspectives

The growing application of EDM has opened new avenues for evaluating interspecific interactions in ways previously unattainable. It enables the estimation of time-varying interaction strength and its impact on population dynamics, offering a powerful tool for disentangling complex ecological processes.

By combining short time-series datasets which can not apply with EDM (Sugihara et al. 2012), this study successfully applied Empirical Dynamic Modeling (EDM) to both laboratory competition experiments and field observations, enabling the quantitative evaluation of interspecific interactions across different ecological contexts. This demonstrates the flexibility and robustness of EDM, even when data availability is limited.

Future methodological developments such as Spatial Convergent Cross Mapping (Clark et al. 2015) allow for the integration of short time series data under consistent dynamical systems which may further improve the applicability of interaction inference. These approaches hold promises for expanding the applicability of EDM in experimental and observational research for interactions.

Traditionally, identifying keystone species has required manipulative experiments, such as the removal of target species from ecosystems, as exemplified by Paine (1966). However, such methods risk disrupting ecosystem integrity and demand substantial logistical effort, including site maintenance and repeated species removal. In contrast, the approach used in this study, which infers key species from time-series data alone, offers a relatively efficient and non-invasive alternative to traditional observation-based methods.

As in the case of the cichlids examined in the third chapter, some species change trophic guilds according to growth stage. Changing trophic guilds may lead to alterations in interspecific interactions. By obtaining data for each growth stage, it would be possible to estimate the interaction strengths specific to different growth stages that were not addressed in the present study, and this approach may contribute to a better understanding of interspecific interaction networks in natural environments. A comparison with direct behavioral observations revealed that only a small subset of the links estimated by CCM corresponded to observed predator–prey or antagonistic interactions. This discrepancy highlights the complementary nature of observational and data-driven approaches. While behavioral observations provide detailed insights into specific interactions, CCM offers a broader and more integrative view of the interaction network, including indirect and non-obvious relationships.

By integrating EDM with behavioral observation, this study provides a general framework for identifying ecologically influential species and understanding community resilience in complex ecosystems. It demonstrates the power of time-series analysis in uncovering hidden structures within ecological networks and contributes to a deeper understanding of how biodiversity is maintained in systems shaped by evolutionary processes such as adaptive radiation.

This framework may contribute to a deeper understanding of complex interaction networks structured by changing trophic guild by across stages and help identify key species within communities (Xu et al. 2025). These insights are essential for advancing predictions of the structure of communities in the nature and for informing conservation strategies in dynamically changing environments (Van Meerbeek and Haesen 2025).

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