A unified framework for nonparametric causality detection

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Abstract (250 words)

Most complex systems in the real world are driven by multiple interactions among

components. Identifying these interactions is critical for understanding, forecasting, and

controlling system-level phenomena. Transfer entropy (TE) and convergent cross mapping

(CCM) are two approaches for nonparametric causality detection based on time-series data

that enable the identification of interactions with the minimal need for system intervention.

However, the theoretical relationship between TE and CCM has not been formally explained.

Here, we provide a theoretical formulation that links TE and CCM, based on different

definitions of causal influence, in an information-theoretic framework. Furthermore, from the

formulation, we propose a novel nonparametric causality test, named unified

information-theoretic causality (UIC), which has lower data requirements than those of TE

(due to robustness to noise) and lower false-positive rates than those of CCM. Numerical

experiments confirmed that UIC outperforms TE and CCM in terms of the performance of

causality detection for both linear and nonlinear dynamical systems. Finally, we demonstrate

the practical importance of the conditional test based on UIC using numerical simulations

with indirect causality and empirical data for microbial communities in irrigated water

samples from rice fields. Our results contribute to a unified understanding of nonparametric

causality tests in time series and the accurate reconstruction of complex real-world systems.

Significance Statement (120 words)

Complex systems with multiple interacting components are common in a wide range of

scientific fields, including economics, sociology, engineering, epidemiology, and ecology.

Identifying interactions among components is necessary for understanding and predicting

system-level phenomena. To this end, nonparametric causality tests based on time-series data

have attracted attention. In this study, we provide a theoretical framework that integrates two

major nonparametric causality tests, transfer entropy and convergent cross mapping.

Furthermore, from the integrated framework, we propose a novel nonparametric causality test,

named unified information-theoretic causality, which shows greater accuracy and efficiency

compared with conventional methods. Our method enables the reconstruction of large

interacting systems from multivariate time-series data and can provide insight into

system-level phenomena, such as critical transitions.

Main Text

Introduction

Detection of cause–effect relationships among variables, events or objects is a

fundamental topic in both natural and social sciences. Most attempts at causality detection are

easily influenced by confounding factors (Spirtes et al. 2000) and nonlinear dynamics

(Sugihara et al. 2012). These issues are particularly challenging in large systems where

intervention is technically or ethically difficult or even impossible (Runge et al. 2019a). In

recent years, nonparametric tests for time series have attracted attention as promising

methods for detecting potential causal relations with the minimal need to intervene in the

target system (Sugihara et al. 2012, Runge et al. 2019b). Time-series data have two essential

characteristics for establishing Granger's statistical concepts of causality: (1) the cause

necessarily occurs before the effect, and (2) the cause contains information about the effect

when accounting for confounding variables (Granger 1969, Hlaváčková-Schindler et al.

2007).

Nonparametric causality tests based on time-series data have been proposed from the

perspectives of information theory and dynamical systems theory. In this study, we focus on

two widely-used methods: transfer entropy (TE; Schreiber 2000) and convergent cross

mapping (CCM; Sugihara et al. 2012). TE is an information-theoretic causality test, known as

a nonparametric generalization of Granger causality (Barnett 2009). TE has a clear

mathematical definition of causal influence, which is advantageous for theoretical advances

(Frenzel & Pompe 2007, Oizumi et al. 2016) and practical applications (Runge et al. 2012,

Runge et al. 2019a). CCM is a nonparametric causality test developed mainly for nonlinear

dynamical systems (Sugihara et al. 2012, Ye et al. 2015). The most important feature of CCM

is the use of time-delay embedding theorems (Takens 1981), which allow for the detection of

causal relations without addressing confounding variables embedded by state space

reconstruction (Sugihara et al. 2012). However, few studies have compared TE and CCM

despite their shared aim of causality detection (but see Edinburgh et al. 2021). As the

performance of these methods can be reversed depending on the system, it is essential to

clarify the mathematical connection between TE and CCM in order to understand their

advantages and disadvantages and to detect correct cause–effect relationships in various

systems.

Here, we provide a theoretical formulation that links TE and CCM in an

information-theoretic framework. Furthermore, based on the formulation, we propose a novel

nonparametric causality test, named unified information-theoretic causality (UIC). UIC

incorporates the advantages of both TE and CCM, including (1) a clear mathematical

definition of causal influence, (2) noise robustness for causal variables in nonlinear

dynamical systems, and (3) efficient computation of statistical significance. Because UIC and

TE have equivalent measures of causal influence, theoretical extensions of TE can be easily

applied to UIC. Considering the previously developed extension of TE (Frenzel & Pompe

2007), we also introduce a conditional test based on UIC and apply this test to an artificial

model system and an empirical microbial system. In most numerical experiments, UIC

outperformed TE and CCM for both linear and nonlinear dynamical systems, consistent with

the theoretical results.

Unified Framework for Causality Tests

Setting. We consider a multivariate time-series with $x = \{x_t\}$ as the effect variable and

$y = \{y_t\}$ as the cause variable and test whether y_{t-p} has a causal influence on x_t with

time lag $p > 0$. Under generic conditions, x_t can be embedded by y_{t-p} and $x_t^{(E,\tau)} =$

$\{x_{t-\tau}, x_{t-2\tau} \dots, x_{t-E\tau}\}$ based on the time-delay embedding theorem (Takens 1981, Deyle &

Sugihara 2011). Note that, in most real-world cases, the embedding dimensions ($E > 0$) and

time interval ($\tau > 0$) are not known *a priori* and need to be estimated (Chang et al. 2017).

TE and CCM. In the above setting, we give the definitions of TE and CCM following their

original formulations. Using the joint distribution $p(x, y)$ and the conditional probability

$p(x|y)$, TE measures causal influence as the flow of information from a cause variable to an

effect variable as follows (Schreiber 2000):

$$\text{TE}\left(y_{t-p} \to x_t \middle| x_t^{(E,\tau)}\right) = \sum_t p\left(y_{t-p}, x_t, x_t^{(E,\tau)}\right) \log \frac{p\left(x_t \middle| y_{t-p}, x_t^{(E,\tau)}\right)}{p\left(x_t \middle| x_t^{(E,\tau)}\right)}. \quad (1)$$

98 Thus, the causal influence from y_{t-p} to x_t is tested by rejecting the null hypothesis,

99 $\text{TE}\left(y_{t-p} \to x_t \middle| x_t^{(E,\tau)}\right) = 0$. CCM evaluates the predictive performance of cross mapping (i.e.,

100 a non-parametric regression model based on the nearest neighbor method) to test for causal

101 influence. Under the assumption of Gaussian noise, the predictive performance $\mathcal{X}(L, P)$ is

102 defined as follows (Sugihara et al. 2012):

$$\mathcal{X}(L, P) = \sum_{t \in P} p\left(y_{t-p}, x_t, x_t^{(E,\tau)}\right) \log p(x_L, y_L) \int dW \, p\left(y_{t-p} \middle| y_L, W\right) p\left(W \middle| x_t, x_t^{(E,\tau)}, x_L\right),$$

where L and P are the sets of time indices for state space reconstruction (i.e., model

training) and prediction (i.e., model cross-validation), respectively. $x_L = \{x_t | t \in L\}$ and

$y_L = \{y_t | t \in L\}$. W denotes the model parameters (e.g., projection weights). Note that

$p\left(\boldsymbol{W}\middle|x_t, \boldsymbol{x}_t^{(E,\tau)}, \boldsymbol{x}_L\right)$ and $p\left(y_{t-p}\middle|\boldsymbol{y}_L, \boldsymbol{W}\right)$ describe the process where nearest neighbors are

searched from the effect variable and the process where the predictive performance of the

cause variable is evaluated based on the searched nearest neighbors, respectively. Sugihara et

al. (2012) measured causal influence by the improvement in predictive performance with

increasing training data (so-called "convergence") as follows:

$$\text{CCM}\left(y_{t-p} \to x_t \middle| \boldsymbol{x}_{t-\tau}^{(E)}\right) = \mathcal{X}(\boldsymbol{L}, \boldsymbol{P}) - \mathcal{X}(\boldsymbol{L}_{\min}, \boldsymbol{P}), \quad (2)$$

111   where $\boldsymbol{L}_{\min}$ is the set of time indices of training data at the minimum size ("minimum

112   library length" in previous studies; Chang et al. 2017). As the training data size approaches

113   zero, we can prove that the expectation of causal influence defined by Eqn. (2) is equivalent

114   to that of the following mutual information (see Appendix S1):

$$\text{CCM}^{\text{IT}}\left(y_{t-p} \to x_t \middle| \boldsymbol{x}_t^{(E,\tau)}\right) = \sum_t p\left(y_{t-p}, x_t, \boldsymbol{x}_t^{(E,\tau)}\right) \log \frac{p\left(y_{t-p}\middle|x_t, \boldsymbol{x}_t^{(E,\tau)}\right)}{p\left(y_{t-p}\right)}, \quad (3)$$

115   which is considered the information-theoretic definition of the CCM causal influence.

117   **Unified Information-theoretic Causality.** Using the information-theoretic definitions, here

118   we clarify the theoretical connection between TE and CCM. We define the following novel

119   measure of causal influence, hereafter referred to as unified information-theoretic causality

120   (UIC):

$$\text{UIC}\left(y_{t-p} \to x_t \middle| \boldsymbol{x}_t^{(E,\tau)}\right) = \sum_t p\left(y_{t-p}, x_t, \boldsymbol{x}_t^{(E,\tau)}\right) \log \frac{p\left(y_{t-p}\middle|x_t, \boldsymbol{x}_t^{(E,\tau)}\right)}{p\left(y_{t-p}\middle|\boldsymbol{x}_t^{(E,\tau)}\right)}. \quad (4)$$

Based on the Bayes' rule, $p(y|x, z)p(x|z) = p(x|y, z)p(y|z)$, we can immediately prove the

equivalence between TE and UIC from Eqns. (1) and (4). If there are enough data to

accurately estimate the conditional probabilities, we will have the same value of causal

influence for TE and UIC. It is also obvious from Eqns. (3) and (4) that CCM and UIC are

equivalent only if y_{t-p} and $\{x_{t-\tau}, x_{t-2\tau} ..., x_{t-E\tau}\}$ are independent. In general, CCM tends

to perform better for nonlinear systems because this independence can be more satisfied due

to long-term unpredictability. CCM is more likely to detect false causality than TE and UIC

(Runge et al. 2019b, Edinburgh et al. 2021) because y_{t-p} may have causal influence on x_t

via $\{x_{t-\tau}, x_{t-2\tau} ..., x_{t-E\tau}\}$ (i.e., the previous states of x_t).

In CCM and UIC, $\boldsymbol{x}$ and $\boldsymbol{y}$ show complete separation as conditional and predicted

variables for conditional probabilities. This variable separation is not trivial for

nonparametric causality tests for two reasons. First, it relates to noise robustness because

noise of conditional variables has a significant effect on the estimation of causal influence,

particularly in nonlinear dynamical systems. As CCM and UIC do not include any cause

variables (i.e., $\boldsymbol{y}$) as conditional variables, they show greater robustness to noise than that of

TE. Second, variable separation allows us to efficiently generate surrogate data (see

Appendix S3 for details), which are required to evaluate the statistical significance of causal

influences (Runge et al. 2018). These theoretical expectations are indeed confirmed in the

following numerical experiments.

Numerical Experiments. Using artificial model systems, we compared the detection

performance of three causality tests. Synthetic time-series were generated by numerical

simulations from two dynamical systems with varying noise: a nonlinear logistic model and

linear vector autoregression (VAR) model (Materials and Methods). The performance of

causality tests was evaluated by the area under the receiver-operator characteristic curve

(AUC). We found that UIC outperforms TE and CCM for both nonlinear and linear systems

(Fig. 1). The performance of CCM was similar to that of UIC for the nonlinear system (Fig.

1a). However, for the linear system, with an increasing number of time points, the

improvement in performance was slower for CCM than for TE and UIC (Fig. 1b) because

false positives do not decrease in CCM; even with an infinite number of observations, CCM

did not necessarily detect true causality (i.e., a lack of statistical consistency). Consistent with

its theoretical definition, TE was quite sensitive to the noise levels of causal variables for the

nonlinear dynamical system and thus requires a considerable number of time points for robust

causality detection (Fig. 1a).

Development of Conditional Causality Tests: Conditional UIC

In most large real-world systems, the causal relation between two variables can be

detected by causality tests even when there are no direct relations between them. There are

two possible scenarios for the misidentification of causal relations. In the first scenario, the

causal relation is indirectly mediated by third variables; for example, when y_{t-2} affects

z_{t-1}, which affects x_t, we find the causal influence of y_{t-2} on x_t. In the second scenario,

target variables are strongly driven by external forces, which are never embedded by

time-delayed variables. In this case, an external force z_{t-2} affects both y_{t-1} and x_t,

resulting in the spurious detection of a causal relation of y_{t-1} on x_t. The misidentifications

of causality are ameliorated by conducting the causality test conditional on third variables. In

the following section, we introduce the conditional UIC test based on previous studies of TE

(Frenzel & Pompe 2007).

Conditional UIC. The measure of causal influence conditional on third variables, $\mathbf{z}$, is

defined as follows:

$$\text{UIC}\left(y_{t-p} \to x_t \,\middle|\, \mathbf{x}_{t-\tau}^{(E)}, \mathbf{z}_t\right) = \sum_t p\left(y_{t-p}, x_t, \mathbf{x}_t^{(E,\tau)}, \mathbf{z}_t\right) \log \frac{p\left(y_{t-p} \,\middle|\, x_t, \mathbf{x}_t^{(E,\tau)}, \mathbf{z}_t\right)}{p\left(y_{t-p} \,\middle|\, \mathbf{x}_t^{(E,\tau)}, \mathbf{z}_t\right)}. \quad (5)$$

The difference from unconditional UIC defined by Eqn. (4) is that the conditional

probabilities include $\mathbf{z}_t$ as conditional variables. By conducting two causal tests:

$$\text{UIC}\left(y_{t-p} \to x_t \,\middle|\, \boldsymbol{x}_{t-\tau}^{(E)}\right) > 0 \ \text{ and } \ \text{UIC}\left(y_{t-p} \to x_t \,\middle|\, \boldsymbol{x}_{t-\tau}^{(E)}, \boldsymbol{z}_t\right) = 0, \quad (6)$$

we can examine whether the causal influence of y_{t-p} on x_t is indirectly mediated by $\boldsymbol{z}_t$

or not.

Applications. First, we applied the conditional UIC test to a four-species food chain model to

demonstrate the identification of direct and indirect effects (Ye et al. 2015). In the food chain

model, one species directly affects another species at time-lag 1 along a transitive causal

chain (Materials and Methods). Using conditional UIC tests expressed by conditions (6), we

successfully detected the direct causal relations at time lag 1 (red circle in Fig. 2; $P < 0.05$

using a surrogate-based significance test). However, when using only unconditional UIC tests,

we detected many indirect effects (blue circle in Fig. 2) in addition to direct effects.

Next, we applied the conditional UIC test to bacterial DNA time-series data collected

from an experimental rice field (Ushio 2022). These time-series data were obtained by

quantifying DNA copy numbers for over 1000 taxa from irrigated water in experimental rice

plots. In this application, we chose 20 abundant bacterial taxa with sufficient temporal

fluctuations (Table S1; see Materials and Methods for more details). Conditional UIC

detected 16 direct interactions and 28 indirect interactions among these bacterial taxa. To

investigate the effects of identifying direct and indirect interactions on dynamical properties,

we further estimated the signs and strengths of these interactions by S-map (Sugihara 1994,

Deyle et al. 2016). We evaluated the dynamic stability of the system (Ushio et al. 2018) in

two situations: (1) the system is incorrectly assumed to be driven by both direct and indirect

interactions (Fig. 3a) and (2) the system is correctly assumed to be driven by only direct

interactions (Fig. 3b). In this analysis, the sign was reversed for 4 of 16 direct interactions

due to a failure to distinguish between indirect and direct interactions. These interactions had

weak (i.e., near-zero) strengths, and their estimates may be influenced by other strong

interactions. Using the conditional UIC, the system was identified as more stable because the

reconstructed network eliminated suspicious indirect interactions (lower panels in Fig. 3),

suggesting that the present time-series analysis method underestimates the system stability

due to the inability to effectively distinguish between direct and indirect interactions.

Discussion

In this paper, we develop a unified framework for nonparametric causal tests based on

information-theoretic formulations and propose a novel causality test (i.e., UIC), establishing

the theoretical connection between TE and CCM. Numerical experiments reveal that UIC

shows higher robustness to noise in time-series data and have lower data requirements than

TE and CCM (Fig. 1). Importantly, UIC outperforms TE and CCM in both linear and

nonlinear dynamical systems. These results support the real-world applications of UIC

because we do not know *a priori* whether TE or CCM is an appropriate causality test in

weakly nonlinear systems.

In addition to its high performance, our method has two key advantages over

conventional approaches. First, previous theoretical advances in information theory (e.g.,

Hlaváčková-Schindler et al. 2007, Oizumi et al. 2016) and dynamical systems theory (e.g., Ye

& Sugihara, 2016, Ma et al. 2018) can be applied to UIC. As such, our framework enables

theoretical and applied developments in causality tests by combining the insights of both

theories. Second, our method enables efficient computations of statistical significance.

Specifically, we can reduce the computational requirements for searching nearest neighbors

for state space reconstruction, which is the greatest computational challenge in nonparametric

causality tests (Appendix S3). Because recent studies have focused on large systems with

thousands of components or more (e.g., Ushio 2022), efficient computation is important for

real-world applications.

Interestingly, despite the mathematical equivalence of their definitions, TE and UIC

show distinct statistical behavior. This arises from the following three characteristics of the

nonparametric causality tests we studied: (1) the use of time-delayed variables for state space

reconstruction, (2) the need to search nearest neighbors to obtain nonparametric estimators,

and (3) the need to separately calculate two (conditional) probabilities and their ratio to

obtain causal influence. In contrast to (1) and (2), the last characteristic may depend on the

algorithm used in nonparametric causality tests. For example, the Frenzel-Pompe algorithm

(Frenzel & Pompe 2007) gives an identical value for causal influence for both TE and UIC.

Although comparing computational algorithms is beyond the scope of our study, we stress the

caveat that TE and UIC might have similar statistical behavior when implemented using other

computational algorithms.

To understand complex systems in the real world, it is critical to identify interactions

among components. For example, under anthropogenic stress, ecosystems sometimes exhibit

unexpected regime shifts, including decreases in net primary production (Gherardi & Sala

2015, Gilarranz et al. 2022) and mass bleaching of corals (Hughes et al. 2018), due to

transitions in dynamical structure emergent from interacting components (Scheffer et al.

2009). With improved ecosystem monitoring techniques (Besson et al. 2022), nonparametric

causality detection allows us to capture such critical transitions, providing a basis for

preventing unexpected regime shifts and supporting ecosystem management to maintain

biodiversity and ecosystem functions. Our method can improve the application of causality

detection to real-world complex systems, thereby contributing to human well-being in a

changing world.

Materials and Methods

Numerical Experiments. To compare the performance of causality tests, we generated

synthetic time-series data from two dynamical systems with noise: (1) a nonlinear

two-component logistic model:

$$x_t = x_{t-1}(3.5 - 3.5\ x_{t-1} - \beta\ y_{t-1}), \qquad X_t = x_t + \varepsilon_t^X$$

$$y_t = y_{t-1}(3.8 - 3.8\ y_{t-1} - 0.02\ x_{t-1}), \qquad Y_t = y_t + \varepsilon_t^Y$$

250   and (2) a linear two-component VAR model:

$$x_t = 0.1\ x_{t-1} + \beta\ y_{t-1} + \varepsilon_t^X, \qquad X_t = x_t$$

$$y_t = 0.1\ y_{t-1} + \varepsilon_t^Y, \qquad Y_t = y_t$$

where the observed time-series $X = \{X_t\}$ and $Y = \{Y_t\}$ were obtained from true model

dynamics of $x = \{x_t\}$ and $y = \{y_t\}$, respectively. The causal influences are controlled by

the parameter β. Then, we conducted two numerical experiments. In the first experiment, we

performed model simulations with different noise levels for effect variables (ε_t^X) and cause

variables (ε_t^Y). We used $\mathrm{sd}(\varepsilon^X)/\mathrm{sd}(x) = 0.01$ or 0.5 and $\mathrm{sd}(\varepsilon^Y)/\mathrm{sd}(y) = 0.01$ or 0.5 for

the logistic model and $\mathrm{sd}(\varepsilon^X) = 1.0$ or 2.0 and $\mathrm{sd}(\varepsilon^Y) = 1.0$ or 2.0 for the VAR model

(upper panels in Fig. 1). In the second experiment, we varied the number of time points in

time-series data, $T = 10, 20, \ldots, 300$ at the same noise level (lower panels in Fig. 1). Each

experiment was repeated 1000 times without causality ($\beta = 0$) and 1000 times with causality

($\beta > 0$) and the performance of causality tests was evaluated in terms of the area under the

receiver-operator characteristic curve (AUC). In the experiments with causality, we used $\beta =$

0.1 for the logistic model and $\beta = 0.5$ for the VAR model.

To demonstrate the identification of direct and indirect effects, we also conducted

numerical experiments using a four-component-chain logistic model (Fig. 2, Appendix Fig.

S1):

$$x_t = x_{t-1}(3.9 - 3.9\ x_{t-1}),$$

$$y_t = y_{t-1}(3.6 - 3.6\ y_{t-1} - 0.40\ x_{t-1}),$$

$$z_t = z_{t-1}(3.6 - 3.6\ z_{t-1} - 0.40\ y_{t-1}),$$

$$w_t = w_{t-1}(3.8 - 3.8\, w_{t-1} - 0.35\, z_{t-1}),$$

where $x = \{x_t\}$, $y = \{y_t\}$, $z = \{z_t\}$ and $w = \{w_t\}$ were used as observed time-series

without noise.

Empirical microbial community data. The rice growth experiments were conducted in five

experimental plots, started on 23 May 2017 and finished on 22 September 2017 (Ushio 2022;

https://doi.org/10.5281/zenodo.6510542). Irrigated water samples were collected from each

plot every day during the experimental period, and the environmental DNA copy numbers for

1197 taxa in water samples were quantified. Among 1197 taxa, we chose 20 abundant

bacteria with sufficient temporal fluctuations (belonging to the phylum Proteobacteria;

Appendix Table S1) to examine causal influences. Proteobacteria was the most abundant and

most diverse phylum in this experiment, and these 20 Proteobacteria were detected frequently

in July. The DNA dynamics of these proteobacteria are shown in Appendix Fig. S2. The DNA

copies were standardized by the maximum number of DNA copies of each taxon (i.e., scaled

from 0 to 1). Using all time-series data for 20 Proteobacteria, we conducted causality tests

based on unconditional and conditional UIC and estimated the sign and strength of the

detected causal relations by S-map (Sugihara 1994). Then, we evaluated the dynamic stability

of the bacterial community assuming the system is driven by the detected causal relations

(Ushio et al. 2018).

Analysis. All analyses were conducted using R version 4.2.2 (R core team 2022). We utilized

the *RTransferEntropy* package (version 0.2.14, Behrendt 2019) and *rEDM* package (version

0.7.4, Ye 2023) for TE and CCM tests, respectively. We implemented UIC algorithms (see

Appendix S4 for more details) in the *rUIC* package (version 0.9.0), obtained from

https://github.com/yutakaos/rUIC. the *pROC* package (version 1.18.0, Robin 2011) also was

used to compute AUC.

Data, Material, and Software Availability. Code has been deposited in GitHub

(https://github.com/yutakaos/archives/tree/master/analysis/2023_uic). Previously published

data for microbial communities were obtained from https://doi.org/10.5281/zenodo.6510542

(Ushio 2022).

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Figure 1 | Simulation experiments to compare the detection performance of transfer entropy

(TE, red), convergent cross mapping (CCM, green), and unified information-theoretic

causality (UIC, blue) in (a) nonlinear logistic model systems and (b) linear VAR model

systems. In the upper panels, areas under the receiver-operator characteristic curve (AUC) are

compared for different noise levels of effect (X) and cause (Y) variables. In the lower panels,

we examine the relation between data requirements (i.e., the number of time points in

time-series data) and AUC at the same noise level. Lines are obtained by fitting simulation

results (points) by generalized additive models.

Figure 2 | Identification of direct and indirect effects based on conditional UIC in a

four-species food chain model. In this model, species directly affect their prey at time-lag 1.

The causality tests were performed for species pairs with direct effects (diagonal panels) and

with indirect effects (off-diagonal panels). For each species pair, species X and Y were used

as effect and cause variables, respectively. Red and blue circles indicate direct and indirect

effects detected by significance tests, while black circles indicate no causal effects. Causal

influences (vertical axes) are estimated by unconditional UIC (also see Appendix Fig. S1).

Figure 3 | Application of conditional UIC to empirical bacterial community data. (a)

Unconditional UIC detects 44 interactions between 20 Proteobacteria taxa. Each node size

indicates the abundance of each bacterial DNA. Blue and red arrows represent positive and

negative interactions estimated by S-map, respectively. The dynamic stability estimated from

these interactions exhibits large temporal fluctuation. Colors in the scatter plots indicate

different experimental plots. (b) Conditional UIC finds only 16 direct interactions among 44

interactions. The dynamic stability indicates that the system is more stable when estimated

from only direct interactions.