國立臺灣大學生命科學院

基因體與系統生物學學位學程

博士論文

Genome and Systems Biology Degree Program

College of Life Science

National Taiwan University

Doctoral Dissertation

以網路型式量化食物網中物種的獨特性與功能多樣性

Quantifying species uniqueness and functional diversity in food webs: a network approach

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中華民國 111 年 8 月

August 2022

doi:10.6342/NTU202203106

國立臺灣大學（碩）博士學位論文
口試委員會審定書

以網路型式量化食物網中物種的獨特性與功能多樣性
Quantifying species uniqueness and functional diversity in food webs: a network approach

本論文係 林文賢 君（D02B48001）在國立臺灣大學基因體與系統生物學學位學程完成之博士學位論文，於民國 111 年 08 月 29 日承下列考試委員審查通過及口試及格，特此證明

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doi:10.6342/NTU202203106

摘要

在氣候劇烈變遷時代，生物多樣性的喪失儼然是一個迫切關注的議題，而如何量化生態系中物種的重要性和多樣性是生態研究中的兩個緊迫問題。由於物種的獵補關係而形成食物網，因此引發我們想從拓撲網路學角度量化物種重要性和生物多樣性。傳統上，物種網路的重要性即考慮了物種對整個食物網的影響以及其所處位置的中心性；近來，另一個物種重要性的評斷概念也逐漸被重視，那就是物種獨特性。在本論文中，我們提出了一個直覺的物種獨特性測量方法，以矩陣方式量化了食物網中物種彼此間的相互影響，進而計算物種間的距離與獨特性。本論文所產生的結果與過往研究方法所產生的結果近乎相同；然而避免重複使用計算的資訊、所耗費的計算時間也更少。此外，本論文也提供了一個基本框架，可用於接受不同的網路特質和距離度量以量化物種的獨特性。

生態系統的生物多樣性可以通過多種方式量化，其中之一即為「功能多樣性」，其可量化生態系統中物種特徵的異質性，此處「功能多樣性」包括物種特徵的豐富性, 多樣性與差異性。本論文中，提出了三種不同類型且基於網路基礎的「功能多樣性」測量方式。第一種是基於食物網的物種相互作用結構、第二種是基於各種拓撲中心性指數、第三種類型是基於物種在食物網中的獵食關係。此處也研究了基於網路的功能多樣性與食物網的網路屬性之間的關係，以及它們與傳統的基於生態特徵的功能多樣性指數的關係。本論文分析表明，連接性稀疏的食物網和具有高度模塊化結構的食物網往往具有高度基於網絡的功能多樣性。此外，基於網絡的功能多樣性指數與其傳統的基於特徵的對應物之間的適度相關性表明，我們的方法提供了生態系統功能多樣性的補充視圖。

doi:10.6342/NTU202203106

Abstract

The loss of biodiversity is a major concern in the era of global warming and climate change. How to quantify species' importance and biodiversity of an ecosystem are two pressing issues in ecological research. Since species interact trophically forming a food web, it is nature to quantify species importance and biodiversity from a network perspective. Traditionally, the network perspective of species importance considers the effect of a species on the whole food and the centrality of species' network position. Recently the concept of species uniqueness has been suggested as an alternative view on species importance. In this study, we propose a simple species uniqueness measurement. Our approach quantifies the effects between species, which constitute the interaction structure of a food web. Rows of such an interaction matrix are compared to compute distances between species, which are then used to calculate uniqueness values of species in a food web. Our approach produces results almost identical to that from a previous approach; however, ours requires less information and therefore requires much shorter computation time. Our approach also provides a basic framework for quantifying species uniqueness using different network-related information and distance measures.

Biodiversity of an ecosystem can be quantified in various ways. One of them, functional diversity, quantifies the heterogeneity in species traits in an ecosystem. Since species' network positions in a food web reflect their functional roles, we argue functional diversity of an

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ecosystem can also be measured from a network perspective. In this study, we propose three different types of network-based functional diversity measurement. The first type is based on the interaction structure of a food web, and the functional diversity of a food web is the average dissimilarity between species' interaction profiles. The second type is based on various centrality indices. Here, different centrality indices are applied to quantify the network position of species; and the functional diversity of a food web is quantified by several properties of species distribution in a multi-dimensional centrality trait space. The third type is based on the trophic role of species in a food web. Functional diversity here includes average trophic role dissimilarity between species, the number of trophic role groups, and how evenly species are partitioned into different trophic roles. Furthermore, we investigate the relationship between network-based functional diversity and several network properties of a food web, as well as their relationship with conventional trait-based functional diversity indices. Our analysis suggests that sparsely connected food webs and those with highly modular structures tend to have high network-based functional diversity. Also, the moderate correlation between network-based functional diversity indices and their conventional trait-based counterparts suggests that our approach provides a complementary view of an ecosystem's functional diversity.

doi:10.6342/NTU202203106

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Chapter 1 Introduction

One fundamental research question in ecology is how species interact and the consequences of such interactions. There exists a huge volume of literature that theoretically explores species interaction. In the simplest case, there are single-species models that examine how simple birth-death processes and self-regulation can produce a rich set of population dynamics, and these include exponential population growth, the sigmoid-shaped logistic growth curve, stable and chaotic fluctuations in population densities (May 1976, Hassell et al. 1976). Moving on to two-species interactions, some models examine the effect of competition between species and delineate the condition for two-species coexistence (Volterra 1926, Lotka 1932). There are also two-species models where one species assumes the role of a predator while the other plays the role of the prey. Such interaction can produce cyclic population dynamics for the two species, with the change in the population density of one species lagging behind that of the other (Volterra 1926, Lotka 1932, Maynard Smith and Slatkin 1973, Murdoch and Oaten 1975). Building on two-species interactions, some three-species models model the exploitive competition between two predators on a shared prey (May and Hassell 1981, Hogarth and Diamond 1984), as well as the apparent competition between two species that share the same natural enemy (Holt 1977, Bonsall and Hassell 1997). Furthermore, there are also models for three-species food chains (Spiller and Schoener 1994) and three-species intra-guild predation

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(Holt and Polis 1997). Research interests in those three-species systems often focus on the condition for species coexistence and the types of population dynamics they can exhibit.

Species in nature are embedded in a network of trophic interaction (i.e., a food web) that is much larger and has more complexity than those simple motifs explored by the above-mentioned models. Of course, one can scale up those simple models to the level of an ecosystem with a vast number of species, but the sheer amount of parameters involved makes the model difficult to explore and analyze. Instead of building more complex theoretical models and exploring model behavior in high dimensional parameter space, one useful and perhaps a more practical direction is to analyze the observed (empirical) network of trophic interaction between species and understand its organization and behavior; and this is the aim of food web research in ecology. To date, food web research investigates issues that generally fall into four categories: structural organization of food webs, the governing process shaping food webs, food web models, and quantifying species importance in food webs. We discuss each of those issues in turn before we outline the research topics explored in this thesis.

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1.1 *Structural organization of food webs*

Early food web research focuses on the structural properties of food webs (May 1972, Pimm 1980, 1982). Connectence is the most fundamental property that is the proportion of possible trophic links that are realized or observed in a food web. In general, connectence is low for many food webs, and it has a negative relationship with species richness (Briand 1983, Schoenly et al. 1991); in order words, larger food webs are more sparsely connected than smaller ones. Such a negative relationship can be explained from the perspective of food web stability, as it has been demonstrated that (larger) food webs are prone to collapse after the removal of a few species if their connectence is too high (May 1972, Pimm 1979a, 1979b, Chen and Cohen 2001). Another fundamental food web property is the number of trophic levels in a food web. Instead of piling up species to form a linear food chain comprising many trophic levels, food webs in nature seem to settle for, on average, 4 trophic levels. It has been suggested that the number of trophic levels is limited by the amount of resources or energy available to sustain an ecosystem. Matters and energy are progressively lost when passed on from lower to upper trophic levels (Vander Zanden et al. 1999, Post et al. 2000). Food webs also have other more complicated structures. For instance, species that engage in frequent trophic interactions tend to form a compartment in a food web; and the number of compartments in a food web is influenced by the heterogeneity of the habitat and is related to the phylogenetic relationship between species (Krause et al. 2003, Rezende et al. 2009). Another example is the trophic structure of a food web, where species performing similar trophic roles are aggregated into the

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same groups (Luczkovich et al. 2003, Lai et al. 2021). The trophic role of a species depends on how it transfers energy and organic matters; thus, it can be a basal species acting as the source node, a top predator species acting as a sink node, or various types of intermediate species connecting other species in different trophic levels. The assemblage or the composition of each trophic role group in a food web is found to be determined by the phylogenetic relatedness of the constituting species (Lai et al. 2021). Furthermore, the food web structure may also cause an interesting ecological phenomenon. For instance, the topological structure of wasp-waist marine ecosystems can serve as a constrain affecting the population dynamics of economically important fishes (Jordán et al. 2005). Another example is that food web structure can also determine the distribution of parasite diversity among host species in an ecosystem (Chen et al., 2008, Liu and Chen 2022).

1.2 *Governing processes shaping food webs*

One research question in food web research that has a long history is what process or processes govern the behavior of a food web. Since every species is linked directly or indirectly to basal species that act as the source of energy and organic matters, the bottom-up control effect from basal species is believed to be the dominant governing process (Pimm 1991). However, effects from top predators, namely the top-down control effect, can also be important (Paine 1980). For instance, the competitive exclusion principle predicts the competition between prey species for a shared resource often results in the dominance of the superior competitor (Hardin et al.

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1960). In contrast, the predatory effect from a predator species can mitigate the competition between prey species such that those prey species coexist in relatively similar abundances (Paine 1980). Moreover, for example, in many aquatic ecosystems, the top-down control can be even more important than the bottom-up control (Strong 1992); and there are also examples where both processes may be equally important as governing forces in food webs (Schmitz et al. 2000, Polis et al. 2000, Chase 2003). And in a different context, it has been shown recently that the environmental filtering process (rather than the competitive exclusion process) is the dominant force that shapes the assemblage of trophic role groups and the trophic structure of several food webs (Lai et al. 2021).

1.3 *Food web models*

Understanding the structural organization of food webs and their governing processes is undeniably important in food web research. Still, this information is merely descriptive, and they don't tell us how food webs are constructed from the first principle. Also, those structural properties calculated from food web datasets are point estimates of actual structural properties; therefore, there is a need to infer those actual values statistically. A food web model is useful in addressing those above-mentioned issues. Although May (1972) created random food webs to investigate the relationship between stability property and the connectence of food webs, those random food webs were generated in the framework of the Erdős–Rényi (ER) random graph model, which lacks any ecological realism. The first proper food web model

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incorporating ecological concepts is the cascade model of Cohen et al. (1990). In this model, species are distributed randomly on a linear line, with the trophic value of a species being its corresponding position (or coordinate) on that line. The model then assumes a species of higher trophic value can consume a lower species with a probability *p*. Such a simple model can capture, to a certain extent, some structural properties of real food webs (e.g., food chain lengths). Ten years after the cascade model, Williams and Martinez (2000) proposed the niche model for food webs. The niche model is an extension of the cascade model and assumes a linear dimension on which species can be distributed. Unlike the cascade model, the niche model assumes a species has a diet window, which can be placed randomly on the linear line, but the center of its diet window must not be higher than the trophic value of the species. As a consequence of this, the niche model is able to produce food web structures not observable in the cascade model (e.g., cannibalism). Since then, other types of food web models were also proposed. For example, Liu et al. (2012) construct a food web model with an intuitive rule: given a set of limited resources and a set of species, a species compete randomly with others for resources. Once it obtains a resource, it then becomes a resource for other species at higher trophic levels and so on. Another example is the work of Eklöf et al. (2012), who constructed a food web model by considering the evolutionary history of species. In essence, the model assumes that closely related species should have similar traits, and therefore their pattern of trophic interaction should be similar; species are then partitioned into several taxonomic groups,

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and trophic links are then being added between individuals of different groups probabilistically. Although those above-mentioned models are novel, whether they can produce random food webs similar to the real ones is still debatable. To this end, Liu et al. (2017) propose a statistical approach that generates bootstrap samples from a real food web; such an approach can construct the sampling distribution of various food web statistics, allowing for their statistical inference.

1.4 *Quantifying species importance in food webs*

One natural question in food web research is how to define or quantify species' importance. Such a question not only has a theoretical interest, but it also has practical values in other research fields such as conservation biology. To ecologists, how important a species is depends on how it affects others (Paine 1969). Species are embedded in a food web; therefore, it is nature to study how a species affect others by examining how its effect can propagate to others through a food web (Sih et al. 1985, Bondavalli and Ulanowicz 1999). There are methodologies for quantifying the effect of one species on another. The mixed trophic impact approach from the Ecopath with Ecosim (EwE) methodology is an example of this (Christensen and Walters 2004). EwE is a mass balance model of a food web with parameters quantified using real food web data, and the mixed trophic impact of a species on another quantifies how changes in the biomass of the former can affect the equilibrium biomass of the latter. In a much simpler manner (but at the expense of biological realism), Müller et al. (1999) propose an approach for

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quantifying indirect effects in host-parasitoid communities. By extending the approach of Müller et al. (1999), Jordán et al. (2003) quantify the probability of one species *i* affecting another species *j* via pathways up to a predefined length in a food web; and the effect of species *i* on the whole food web is the sum of those probabilities over all species (including itself). Such a simple approach has been used to measure the positional importance of species in a food web (Jordán et al. 2006, Chen et al. 2008, Endrédi et al. 2021). Since a food web is a type of network, the importance of species can also be quantified from a network perspective. To this end, the concept of node centrality from social network analysis (Wasserman and Faust 1994) has been applied to measure species' importance in food webs (Jordán et al. 2006, Estrada 2007). Node centrality can be measured in various ways. At the local level, there is degree centrality that simply counts the number of connections a node has. At the meso to a global scale, there are closeness centrality and betweenness centrality, which respectively measure node importance by considering how close a node is to others or how frequently a node appears on all shortest paths in a network. Armed with those various methods for quantifying species importance, several researches have shown that important species can have interesting consequences. For example, species occupying important or central network positions tend to have higher parasite diversity (Chen et al. 2008), and the removal of topologically important species tends to affect food web assemblage and causes the collapse of food webs (Estrada 2007, Dunne and Williams 2009). More recent researches have extended

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to investigate the relationship between the morphological traits and the network position of species in food webs, and this can help us further understand the biological nature of species importance in food webs (Olmo Gilabert et al. 2019, Endrédi et al. 2021).

In addition to using effect of species and their network positions as measures of species importance, a relatively new concept has emerged in the past decade. The uniqueness of a species from the network perspective was firstly proposed by Jordán et al. (2009). With a predefine cut-off threshold, the approach of Jordán et al. (2009) identifies those species that are within the range of a species trophic field as its strong interactors; and its uniqueness is defined in terms of the extent of overlap between its set of strong interactors with that of other species. A species is unique if it shares fewer strong interactors with other species, and the implication of this is that it may occupy a role or a network position in a food web not like other species do. Lai et al. (2012) investigate this concept of species uniqueness using several food web datasets and suggest that species in central network positions (or those that exert a huge effect on others) tend to be less unique. Their work reveals the redundant nature of food web structure as a possible mechanism for curbing the loss of important species. Lai et al. (2015) extend the methodology of Jordán et al. (2009) and propose a more complete measure of species uniqueness that quantify how well a species' sets of strong and weak interactors overlap with those of other species.

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1.5 *Research topics explored in this thesis*

In this thesis, we focus on two research topics regarding food webs. The first is on species uniqueness. The approaches of Jordán et al. (2009) and Lai et al. (2015) reply on the identification of interactors of each species under various cut-off effect thresholds, and they then quantify the overlap between species' sets of interactors. Such a procedure can be time-consuming, and the result can also depend on the cut-off effect thresholds. In fact, their approaches require one to quantify the interaction structure of a food web first (i.e., a matrix recording the effect of one species on another), and there is no reason why one cannot simplify the procedure by comparing the species' interaction profiles from the interaction matrix and then develop a uniqueness measure directly. Thus, we aim to develop a new and simple species uniqueness index in this study.

As for the second topic, we aim to quantify the diversity in species' network characteristics in a food web. From the brief review on food web research mentioned above, we know that each species can be characterized (e.g., its network effect, and its centrality values etc.) in different ways by using information from a food web. We aim to quantify the diversity in species food web characteristics, which can then be used as a diversity measurement for a food web (or an ecosystem in general). Such a concept is relevant to functional diversity in ecology. Traditionally, the most fundamental diversity measure of an ecosystem is species richness (MacArthur 1965, Hill 1973), and in the past few decades, different ways of viewing species

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richness were called for, and one of those is the functional diversity of an ecosystem (Villéger et al. 2008, Laliberté and Legendre 2010, Mammola et al. 2021). Ecologists argue that the function of a species is related to various morphological traits, and many have been using information derived from the species distribution in the multi-dimensional trait space as a proxy for functional diversity of an ecosystem. However, since trophic interaction is the most fundamental interaction species can perform, their positions in a food web must also reflect their functions (at least trophically). Therefore, we argue that information embedded in a food web must at least contain the functional diversity of an ecosystem to some extent. And this motivates us to investigate functional diversity of species from a network or food web perspective.

This thesis is organized as follows. In the second chapter, we summarize food web datasets that were analyzed in this study. In the third chapter, we present a new measure for species uniqueness based on the interaction structure between species in a food web. The fourth, fifth, and sixth chapters all deal with a network (or food web)-based measure of functional diversity, but they differ in the type of network information they use. The fourth chapter uses interaction profiles from the interaction structure of a food web; the fifth chapter uses information of species' centrality measurements; the sixth chapter considers diversity in species' trophic roles in a food web. Finally, the seventh chapter concludes with future research direction relevant to those presented in this thesis.

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Chapter 2 A basic description of food web datasets

2.1 Dataset sources

Throughout this thesis, we analyzed the same 92 food web datasets. Those food webs were produced by the Ecopath with Ecosim methodology (i.e., EwE (Christensen and Walters 2004)), and they are thus methodologically standard and comparable. All datasets are exactly the same as those in Endrédi et al. (2021), and they are available from EcoBase (http://ecobase.ecopath.org/) and from other sources as indicated in Heymans et al. (2014). We note that food webs produced from EwE methodology can have resolution problems. Higher trophic levels of a EwE food web tend to have better resolution than lower trophic levels. Specifically, species at the lower trophic levels tend to be aggregated into few number of large tropho groups; and in contrast, tropho groups at higher trophic levels often consist of few number of species.

2.2 Information in each dataset

Each food web dataset contains the trophic interactions between species (i.e., a food web) in the format of an edge list. For example, an edge of a food web is recorded as a row "A B *X*", which indicates that species A is consumed by species B with a weight *X*; the weight *X* is expressed in terms of the biomass transferred per unit area and per unit time from species A to species B (e.g., in grams of carbon per square meter per year). Also available for each food

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web is the trait information for many species; these traits are habitat type, mobility, and body size. Habitat type has two categories, benthic (i.e., living near the bottom of seas or lakes) and water column (i.e., living in the middle or the upper section of the seas or lakes). Note that habitat type is not an intrinsic property of a species; however, it may correlate with some intrinsic traits of a species. Mobility has four categories, sessile (i.e., lacking mobility and attached to other organisms or objects), drifter (i.e., passive moving), limited mobility (i.e. slow moving), and mobile (i.e. fast moving). Body size ranges from shorter than 0.001 cm to greater than 1000 cm.

2.3 The nature of ecosystems and their geographical distribution

These 92 food webs cover various aquatic ecosystems across the globe. The majority of them, or 64 out of 92, are from "sea" ecosystems covering various coasts, bays, gulfs, sounds, channels and straits. Four food webs are from "reef" ecosystems, and 16 are from "lagoon" ecosystems, while the remaining 8 food webs are from "estuary" ecosystems. Figure 2.1 shows the locations of the ecosystems from which those 92 food web data were collected on the world map. Eighty food webs are from locations in the northern hemisphere while the remaining 12 are from the southern hemisphere. Among these 92 food webs, 42 and 26 are from locations surrounding the Atlantic Ocean and the Pacific Ocean, respectively, while 8 are from the Indian Ocean, 6 from the Baltic Sea, 5 from the Mediterranean Sea, and 5 from the Adriatic Sea. Table 2.1 summarizes basic information on all 92 food webs. It contains information on the

doi:10.6342/NTU202203106

ecosystems from which food web data were collected, including food web ID, the name of the ecosystem, the country of origin, the geographic coordinates (i.e., latitude and longitude), and the type of the ecosystem (e.g., sea, reef, lagoon, or estuary).

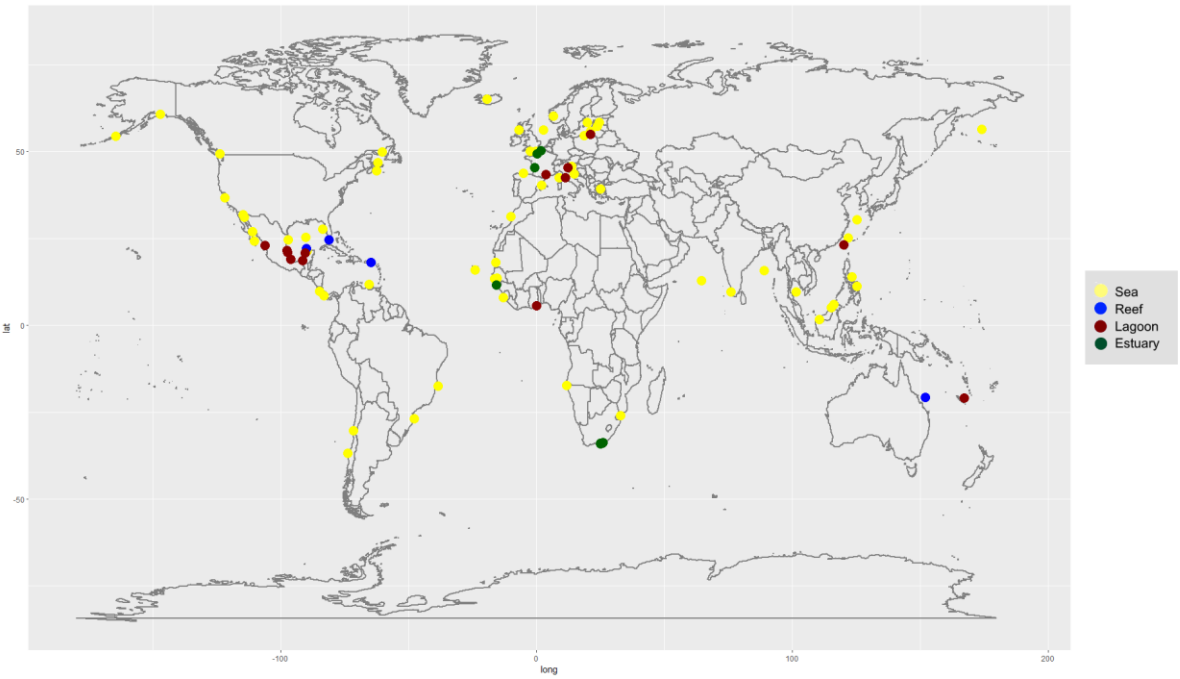

Figure 2. 1 Geographical distribution of food webs analyzed in this thesis.

doi:10.6342/NTU202203106

Table 2. 1 Food web summary

FoodWebID	Ecosystem Name	Country	Latitude	Longitude	Type
FW1	Cape Verde	Cape Verde	15.87	-24.08	sea
FW2	Gambia	Gambia	13.43	-16.53	sea
FW3	Sakumo Lagoon	Ghana	5.64	-0.03	lagoon
FW4	Guinea-Bissau	Guinea-Bissau	11.68	-15.70	estuary
FW5	Mauritania	Mauritania	18.06	-16.11	sea
FW6	Morocco	Morocco	31.31	-10.02	sea
FW7	Maputo	Mozambique	-26.04	32.73	sea
FW8	Northern Benguela	Namibia	-17.34	11.59	sea
FW9	Senegambien	Senegal	13.51	-15.58	sea
FW10	Sierre Leone 1990	Sierra Leone	7.90	-13.05	sea
FW11	Gamtoos Estuary	South Africa	-33.96	25.04	estuary
FW12	Kromme Estuary	South Africa	-34.14	24.84	estuary
FW13	Sundays Estuary	South Africa	-33.72	25.85	estuary
FW14	Swartkops Estuary	South Africa	-33.86	25.63	estuary
FW15	Great Barrier Reef-prawn	Australia	-20.79	151.76	reef
FW16	Bay of Bengal	Bangladesh	15.75	88.85	sea
FW17	Brunei	Brunei Darussalam	5.16	115.10	sea
FW18	East China Sea	China	30.43	125.25	sea
FW19	SE Arabian Sea	India	12.88	64.49	sea
FW20	Southwest coast of India	India	9.69	75.78	sea
FW21	West coast of Sarawak	Malaysia	1.69	110.55	sea
FW22	West coast of Sabah	Malaysia	6.04	115.97	sea
FW23	Loyalty Islands Atoll	New Caledonia	-20.87	167.10	lagoon
FW24	San Pedro Bay, Leyte	Philippines	11.18	125.08	sea
FW25	San Miguel Bay	Philippines	13.90	123.20	sea
FW26	Kuosheng Bay	Taiwan	25.21	121.67	sea
FW27	Lagoon Chiku-Taiwan	Taiwan	23.14	120.07	lagoon
FW28	Gulf of Thailand	Thailand	9.57	101.35	sea
FW29	Curonian Lagoon	Poland, Lituania	55.01	20.97	lagoon
FW30	Gulf of Riga	Estonia, Latvia	57.30	23.75	sea
FW31	Lithuanian Coast	Lituania	55.80	21.00	sea
FW32	Parnu Bay	Estonia, Latvia	58.32	24.42	sea
FW33	Puck Bay	Poland, Lituania	54.56	18.63	sea
FW34	Bay of Calvi	France	42.56	8.78	sea
FW35	Bay of Somme	France	50.21	1.61	estuary
FW36	Seine Estuary	France	49.43	0.29	estuary
FW37	Etang de Thau	France	43.38	3.60	lagoon
FW38	Gironde Estuary	France	45.42	-0.88	estuary
FW39	Aegean model	Greece	39.20	24.90	sea
FW40	Iceland	Iceland	65.05	-19.47	sea
FW41	Iceland - 1950	Iceland	65.05	-19.47	sea
FW42	Orbetello Lagoon	Italy	42.44	11.19	lagoon
FW43	Lagoon of Venice	Italy	45.38	12.28	lagoon
FW44	Venice Lagoon (Seagrass habitat)	Italy	45.38	12.28	lagoon
FW45	Miramare Natural Marine Reserve	Italy	45.69	13.71	sea
FW46	Venice Lagoon (Tapes habitat)	Italy	45.38	12.28	lagoon
FW47	North-Central Adriatic 1990s	Italy	43.53	14.69	sea
FW48	Sorfjord	Norway	60.25	6.60	sea
FW49	Catalan sea 2003	Spain	40.33	2.00	sea
FW50	Cantabrian Sea	Spain	43.80	-5.27	sea
FW51	Baltic Sea	Poland	58.32	19.86	sea
FW52	West Coast of Scotland	UK	56.27	-6.89	sea
FW53	Western English Chanel	UK	50.17	-2.61	sea
FW54	English Channel 1995	UK	50.11	-0.36	sea
FW55	North Sea 1880	UK	56.24	2.62	sea
FW56	North Sea 1991	UK	56.24	2.62	sea
FW57	Deep sea West Coast of Scotland	UK	56.27	-6.89	sea
FW58	Strait of Georgia	Canada	49.35	-123.88	sea
FW59	Eastern Scotian Shelf 1990s	Canada	44.41	-62.60	sea

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FW60	Northern Gulf of St. Lawrence	Canada	49.90	-60.46	sea
FW61	Southern Gulf of St. Lawrence	Canada	46.81	-61.97	sea
FW62	Tampamachoco Lagoon	Mexico	21.01	-97.35	lagoon
FW63	Celestun Lagoon	Mexico	20.82	-90.41	lagoon
FW64	Huizache-Caimanero	Mexico	22.95	-106.09	lagoon
FW65	Campeche Bank	Mexico	22.00	-90.01	reef
FW66	Tamiahua Lagoon	Mexico	21.61	-97.56	lagoon
FW67	Terminos Lagoon	Mexico	18.65	-91.56	lagoon
FW68	Terminos Lagoon (S&M)	Mexico	18.65	-91.56	lagoon
FW69	Alto Golfo de California	Mexico	31.76	-114.75	sea
FW70	Central Gulf of California	Mexico	26.86	-111.08	sea
FW71	Northern Gulf of California	Mexico	31.09	-114.33	sea
FW72	Sonda de Campeche	Mexico	22.00	-90.01	sea
FW73	Yucatan Continental Shelf	Mexico	21.39	-89.81	sea
FW74	Gulf of Mexico	Mexico	25.27	-90.28	sea
FW75	La Paz Bay	Mexico	24.24	-110.44	sea
FW76	Mandinga Lagoon	Mexico	19.01	-96.07	lagoon
FW77	Western Gulf of Mexico	Mexico	24.51	-97.13	sea
FW78	Prince William Sound_1980s	USA	60.69	-147.00	sea
FW79	Prince William Sound 1990s	USA	60.69	-147.00	sea
FW80	Aleutians Islands	USA	54.35	-164.57	sea
FW81	Western Bering Sea	USA	56.47	173.80	sea
FW82	Monterey Bay	USA	36.79	-121.95	sea
FW83	Looe Key Sanctuary	USA	24.58	-81.20	reef
FW84	West Florida Shelf	USA	27.67	-83.55	sea
FW85	Southern Brazil Shelf	Brazil	-17.41	-38.43	sea
FW86	South Brazil Bight	Brazil	-26.98	-47.97	sea
FW87	Tongoy Bay	Chile	-30.27	-71.55	sea
FW88	Central Chile	Chile	-36.79	-73.85	sea
FW89	Golf of Dulce	Costa Rica	8.44	-83.21	sea
FW90	Gulf of Nicoya	Costa Rica	9.73	-84.80	sea
FW91	Venzuela Shelf	Venzuela	11.69	-65.51	sea
FW92	Virgin Islands	Virgin Islands	18.15	-64.72	reef

doi:10.6342/NTU202203106

Chapter 3 Simplifying a trophic overlap-based measure for species uniqueness in food webs

3.1 Introduction

Identifying important species is of utmost importance since we are living in a world where species extinctions occur at an unprecedented speed, and conserving important species may have a desirable effect on curbing species extinction and the collapse of an ecosystem (Johnson et al. 2017, Ortiz et al. 2017, Mason et al. 2020). The most fundamental pattern of interaction between species can be summarized in a food web (Cohen 1978, Pimm 1982). Given that food webs are a type of a network, ecological researches in the past decades have employed network analysis to identify important species in various ecosystems (Jordán et al. 2006, Scotti and Jordán 2010, Endrédi et al. 2021).

The most well-known concept of species importance is node centrality which has its origin in sociology (Wassermann and Faust 1994, Jordán et al. 2006). It can be measured in various ways, but they all concern with how dominant a node is in a network. For instance, degree centrality measures the number of links a node has; closeness centrality quantifies how close a node is to all others in a network; betweenness centrality measures how frequent a node is incident to the shortest pathways in a network (Estrada 2007). More recently, an alternative approach to species importance starts to emerge, and it measures how unique a species is in its

doi:10.6342/NTU202203106

interaction pattern when compared to others in the same food web (Jordán et al. 2009, Lai et al. 2012, 2015). Again, borrowed from sociology, the REGE analysis (i.e., regular equivalence) has been employed to quantify the similarity between species' network positions in a food web (Luczkovich et al. 2003), and Lai et al. (2012) extent this concept to develop a new index for species uniqueness. Another approach that is more relevant to ecology than REGE-based analysis is the concept of trophic field overlap (TFO for short) (Jordán et al. 2009, Lai et al. 2015). In this approach, both direct and indirect effects between species are being quantified, and this results in a matrix describing the interaction structure between species (Müller et al. 1999, Rott and Godfray 2000, Jordán et al. 2003). Trophic field overlap between a focal species and all others is determined as the number of shared interactors between them, and the extent of this overlap is then used as the uniqueness value of the focal species.

Although conceptually appealing, the TFO-based uniqueness index requires users to specify effect cutoff thresholds for its calculation, and the computation can be very time-consuming. Here, in this chapter, we examine whether information directly from the interaction matrix can be used to compute the TFO-based uniqueness index in order to simplify its computation and shorten its computation time. Next, we describe in full the TFO-based uniqueness index.

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3.2 Trophic field overlap-based uniqueness index

Given a food web, we first quantify the one-step effect of species *i* on species *j* as (i.e., direct effect):

$$a_{ij} = \frac{1}{D_j}, \quad (3.1)$$

where D_j is the number of species connected to species *j*. All one-step effects can be organized in a matrix **A** where the ij^{th} element of this matrix is the one-step effect of species *i* on species *j*. Effects between species up to *n* steps (i.e., indirect effects) can be calculated through the self-multiplication of matrix **A**:

$$\mathbf{E}_n = \frac{1}{n}(\mathbf{A}^1 + \mathbf{A}^2 + \mathbf{A}^3 + \cdots \mathbf{A}^n), \quad (3.2)$$

where $\mathbf{A}^x$ is the matrix recording the effects between species in *x* steps. Thus, the ij^{th} element of matrix $\mathbf{E}_n$, namely $E_{n,ij}$, is the average effect of species *i* on species *j* up to *n* steps. Moreover, $\mathbf{E}_n$ can be regarded as the interaction matrix between species for the entire food web.

With an effect cutoff *T*, for each species *i,* we define two sets of interactors, S_i and W_i: if the average effect of species *i* on species *j* up to *n* steps is greater than or equal to *T* (i.e., $E_{n,ij}>=T$), then species *j* is species *i*'s strong interactor and belongs to S_i, otherwise a weak interactor (i.e., $E_{n,ij}<T$) and belongs to W_i. With an effect cutoff *T*, the extent of overlap between species *i*'s two sets of interactors and that of all other species is defined as:

$$TO_{T,i} = \sum_j n(S_i \cap S_j) + \sum_j n(W_i \cap W_j), \quad (3.3)$$

where $n(S_i \cap S_j)$ and $n(W_i \cap W_j)$ respectively are the numbers of strong interactors and weak

doi:10.6342/NTU202203106

interactors shared by species i and j. Doing this for T from 0 to 1 with a user predefined increment t (e.g., t=0.05) thus produces a trophic overlap (TO) profile, which shows how species i overlaps with all other species in their interactors for the entire range of T (Fig. 3.1). Furthermore, the summed $TO_{T,i}$ across all Ts, namely STO_i, is the uniqueness value for species i:

$$STO_i = \sum_T TO_{T,i}. \quad (3.4)$$

A unique species should in theory has a low *STO* value as it overlaps little with all other species for the entire range of T; and conversely, a species with a large *STO* value is not unique.

We analyzed the Great Barrier Reef ecosystem (i.e., the food web named "FW15" in Chapter 2), and plotted the TO profile for benthic autotrophs (i.e., "Benthau") with increment t=0.05, 0.025 and 0.00001. Fig. 3.1 shows how t can affect the resolution of the TO profile; and when the increment in T is small, TO profile shows details that are absent when the increment in T is large. This can also affect the STO values calculated for individual species. We plotted the STO values calculated for individual species when t=0.05 (i.e., $STO_{t=0.05}$) against that

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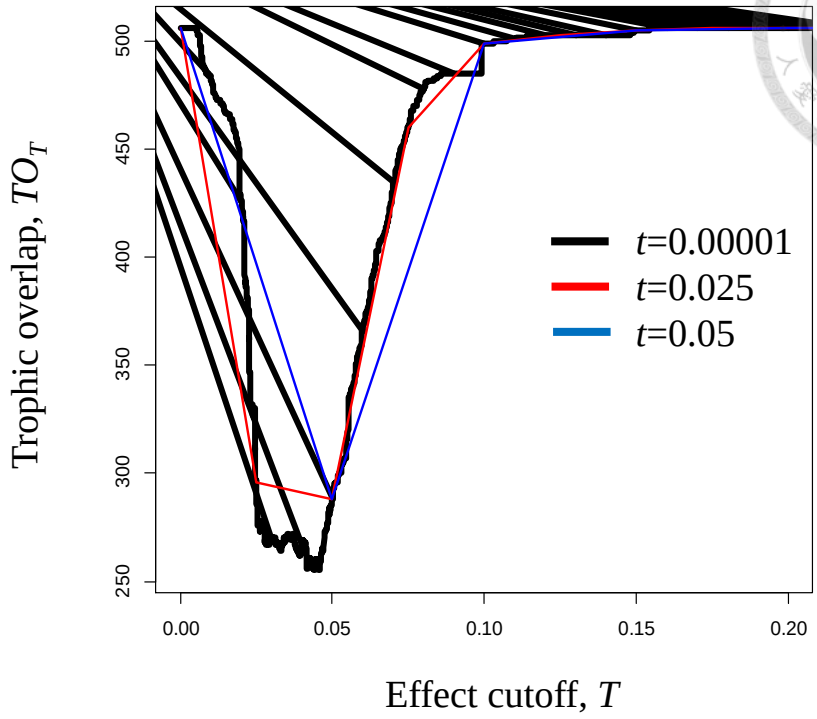

Figure 3. 1 Trophic overlap (TO) profiles for species "Benthau" from Great Barrier Reef food web using different increment values t (blue: t=0.05; red: t=0.025; and black: t=0.0001).

obtained with t=0.00001 (i.e., $STO_{t=0.00001}$), and observed little (Kendall's) rank correlation between those two sets of STO values (Fig. 3.2a). And when we plotted that obtained with t=0.025 (i.e., $STO_{t=0.025}$) against that for t=0.00001 (i.e., $STO_{t=0.00001}$), rank correlation becomes larger (Fig. 3.2b). All these suggest that in order to obtain stable STO values, increment in T, or the value of t, is preferably as small as possible, but this will inevitably add more to the computation time.

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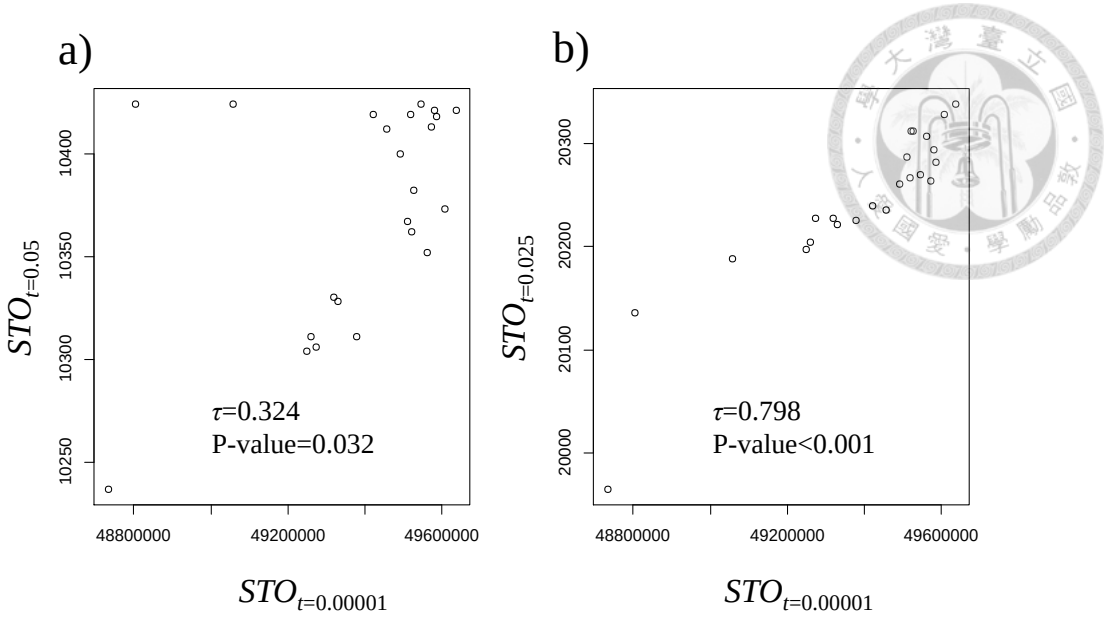

Figure 3. 2 Scatter plots showing the relationship between different sets of STO values obtained using different increment values *t*.

The essential part of the TFO-based index calculation is to compare the trophic fields between species; intuitively, if two species overlap greatly in their trophic fields, then their corresponding rows in the interaction matrix $\mathbf{E}_n$ should be similar. Thus, this prompts us to speculate on the possibility of whether the whole procedure can be simplified and reduced to the comparison between rows in the interaction matrix $\mathbf{E}_n$. To this end, we propose the following simplified approach.

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3.3 Using interaction matrix to compute species uniqueness index

We repeat the same procedure as above until we obtain the interaction matrix $\mathbf{E}_n$. Note that the i-th row of $\mathbf{E}_n$ represents the interaction profile of species i and it records the effects of species i on individual species in the same food web. We then compare every two rows of matrix $\mathbf{E}_n$ and calculate their distance or dissimilarity in two different ways. First is the Manhattan distance between the interaction profiles of species i and j:

$$d_{Manh,ij} = \sum_k |E_{n,ik} - E_{n,jk}|, \quad (3.5)$$

and after calculating for all species pairs, those distance values can be placed in a distance matrix $\mathbf{D}_{Manh}$. We then calculate the sum of the i-th row of matrix $\mathbf{D}_{Manh}$ to be the uniqueness value for species i:

$$Uq_{Manh,i} = \sum_j D_{Manh,ij}. \quad (3.6)$$

Second is the Euclidean distance between the interaction profiles of species i and j:

$$d_{Eucl,ij} = \sqrt{\sum_k (E_{n,ik} - E_{n,jk})^2}, \quad (3.7)$$

and again, after calculating for all species pairs, those distance values can be placed in a distance matrix $\mathbf{D}_{Eucl}$. Similarly, the sum of the i-th row of matrix $\mathbf{D}_{Eucl}$ is the uniqueness value for species i:

$$Uq_{Eucl,i} = \sum_j D_{Eucl,ij}. \quad (3.8)$$

Here, a species with a large value for Uq_{Manh} or Uq_{Eucl} is unique since the distance between its interaction profile and that of others is large. Note that for the TFO-based uniqueness index, a small value indicates a species is unique because it overlaps little with other species in terms

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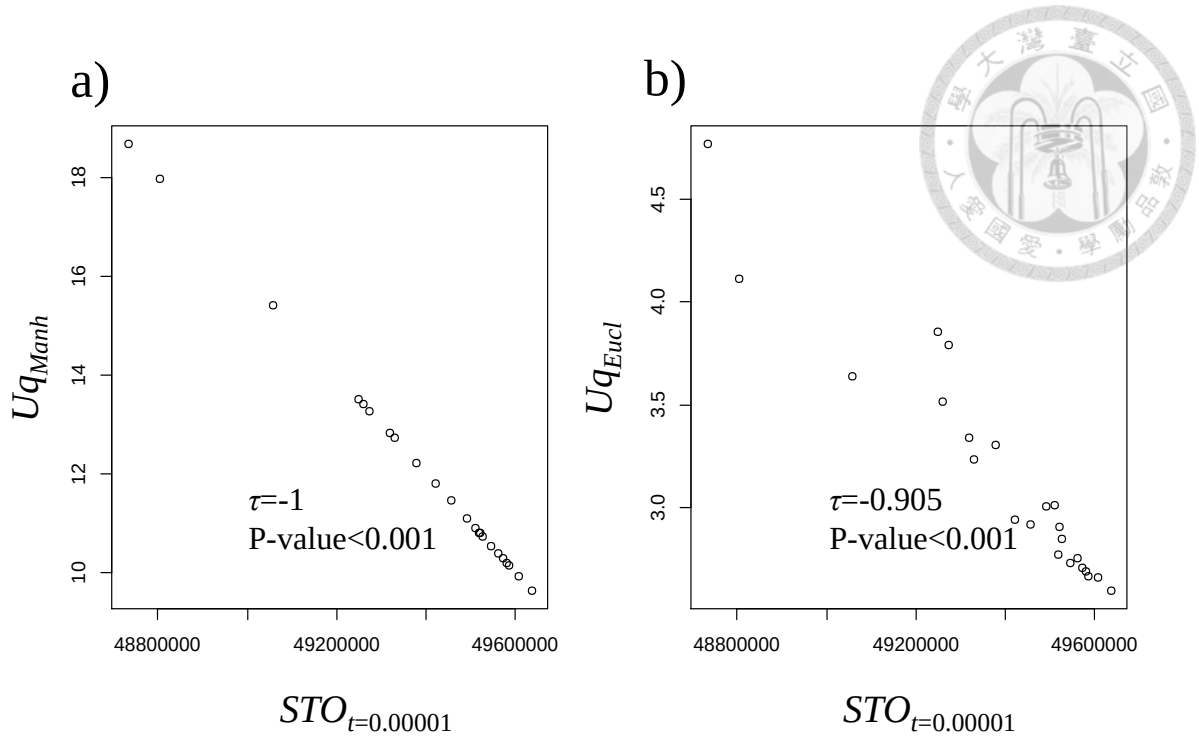

Figure 3. 3 Scatter plots showing the relationship between the TFO-based uniqueness index (i.e., $STO_{t=0.00001}$) and our interaction matrix-based uniqueness indices (i.e., Uq_{Manh} and Uq_{Eucl}).

of interactors.

Again, we applied our simplified approach of species uniqueness to the Great Barrier Reef ecosystem, and examined the relationship between $STO_{t=0.00001}$ (i.e., STO values when increment t=0.00001) and each of Uq_{Manh} and Uq_{Eucl}. Fig. 3.3a shows that the relationship between $STO_{t=0.00001}$ and Uq_{Manh} is perfectly linear and shows a perfect negative rank correlation. Although not perfect, the relationship between $STO_{t=0.00001}$ and Uq_{Eucl} is also linear and shows a strong negative rank correlation (Fig. 3.3b). To ascertain that this result is

doi:10.6342/NTU202203106

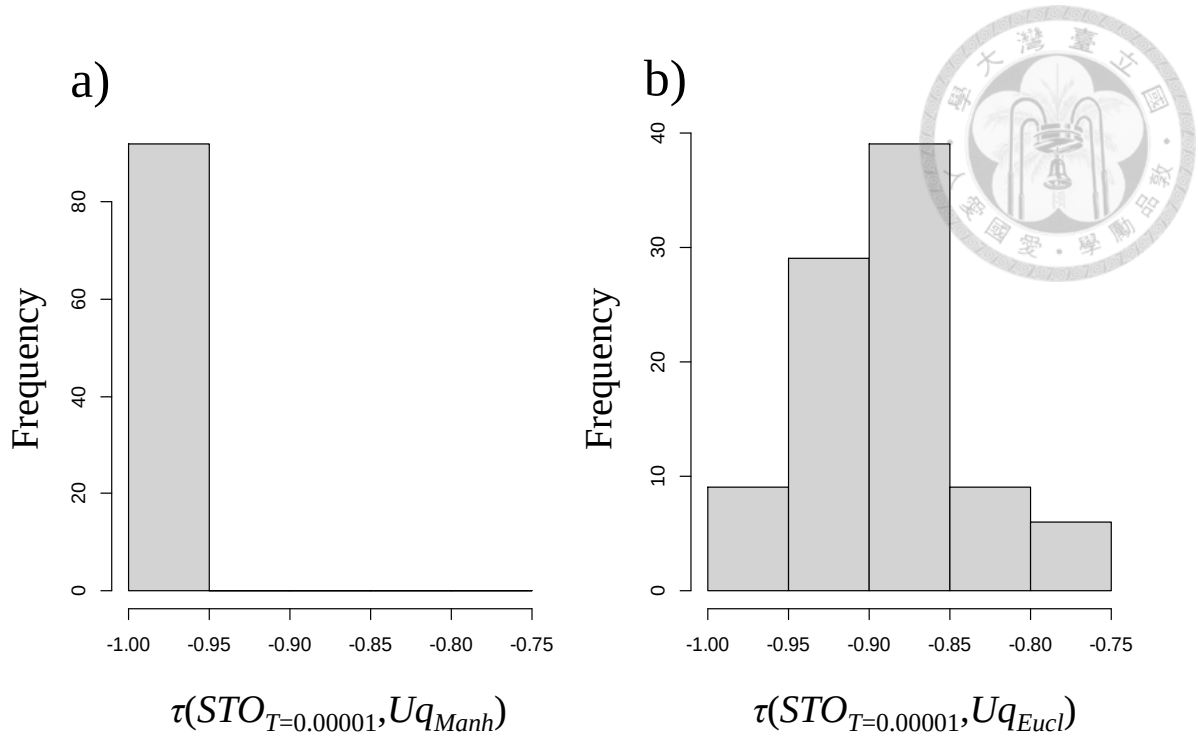

Figure 3. 4 Distribution of Kendall rank correlation coefficients between TFO-based uniqueness index (i.e., $STO_{t=0.00001}$) and the two interaction matrix-based uniqueness indices (i.e., Uq_{Manh} and Uq_{Eucl}) calculated for 92 food webs.

not exclusive to the dataset analyzed, we repeated the same analysis to 92 different food webs from Chapter 2. Of all the food web analyzed, 90 show a perfect negative rank correlation between $STO_{t=0.00001}$ and Uq_{Manh} (i.e., Kendall τ =1) and the remaining 2 food webs show an almost perfect negative correlation (i.e., Kendall τ =0.995) (Fig. 3.4a). As for the relationship between $STO_{t=0.00001}$ and Uq_{Eucl} , Kendall rank correlation coefficient varies from -0.762 to -1 for those 92 food webs examined, with a mean value of -0.890 (Fig. 3.4b). These results point to the possibility and plausibility of using the interaction matrix directly to quantify species uniqueness in the framework of trophic field overlap.

doi:10.6342/NTU202203106

3.4 Discussion and conclusion

In this chapter, we have revisited the TFO-based species uniqueness index and have proposed two possible ways to simplify its calculation. Species uniqueness rankings produced by our Manhattan distance-based index are almost identical to that produced by the TFO-based index. Although the agreement in species uniqueness ranking between our Euclidean distance-based index and the TFO-based index is not perfect, they still show a strong correlation. Based on these results, one might prefer the use of Manhattan distance over Euclidean distance in quantifying species uniqueness. However, since distances of different lengths in Euclidean space may correspond to the same Manhattan distance (and vice versa), we suggest both distance-based indices should be used in order to gain a more complete view on species uniqueness. We note that Euclidean distance is an intuitive measure of the shortest distance between two objects, and it has been widely used in social network analysis to quantify the similarity in the connection pattern between nodes (Burt and Bittner 1981, Faust and Romney 1985, Burt 1987). However, it has also been shown that Euclidean distance is not an appropriate measure of similarity between objects when the dimensionality is high, and Manhattan distance is often preferred (Aggarwal 2001). Given that a food web often consists of a large number of species, comparing the interaction profile of a species with that of all other species is akin to the process of finding distances between objects in a high-dimensional space. Therefore, on this note, one should be cautious when using Euclidean distance-based index to measure species uniqueness.

doi:10.6342/NTU202203106

We need to emphasize that our simplified approach does not make the TFO-based approach redundant or obsolete. In fact, using interaction matrix directly to quantify species uniqueness like we have done here ignores much information that otherwise could be of interest in some circumstances. For instance, one prominent feature of the TFO-based index is the use of TO profiles of different species, which is being omitted altogether in our simplified approach. Each species has a TO profile, and the shape of TO profile differs from species to species. A TO profile tells us how a species' trophic field overlaps with that of other species across the entire range of *T*. The shape of TO profile for some species changes drastically over small values of *T*, while some are more sensitive to changes at larger *T* values (Lai et al. 2015). Those TO profiles can be considered as species traits, which can be incorporated into the general framework of Schmera et al.(2009) for quantifying the functional diversity of an ecosystem. Furthermore, although our simplified approach omits the need to define an effect threshold for interaction strength, in practice, it is still valuable and informative to set one (with appropriate domain knowledge) if there is a need to identify the strong or weak interactors of a species. Such detailed information can be of use to, for example, conservation practice when one wishes to understand how an endangered species interacts with each other species in the same food web. In a nutshell, our proposed approach here offers a quick and simple calculation of species uniqueness using principles akin to TFO-based approach; however, if one opts to study species uniqueness in more detail, then we suggest using the TFO-based approach.

doi:10.6342/NTU202203106

Quantifying species uniqueness from the network perspective may have important implications in helping us better understand an ecosystem. Stable isotope analysis (Post 2002, Bearhop et al. 2004) is a widely used tool to quantify the flow of matter and energy between species, and this provides insights into the level of trophic diversity and redundancy within an ecosystem (Mondal and Bhat 2021). Our simplified approach to species uniqueness measurement can provide similar information. For instance, in a given food web, one can simply determine the extent of variation in species uniqueness value by calculating its coefficient of variation. A large variation indicates greater diversity in species' trophic roles in a food web, whereas a small variation implies redundancy in trophic roles.

The way we implemented in this study also offers a simple framework for quantifying species uniqueness. Firstly, one needs to construct a matrix where each row contains information about how a species interacts with or relates to all species in the same food web; here we used the interaction structure where each row records how a species affects every species up to a predefined number of steps. Other types of information can be used instead depending on one's research interest. For instance, one can use basic information such as whether a species is connected to others via predator-prey trophic links (i.e., the adjacency matrix representing a food web); or a matrix recording the length of the shortest path between species, and each row

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here records how far a species is from all other species in the food web. Secondly, similarity or dissimilarity matrices can be constructed by comparing every pair of rows of the matrix obtained from the first step. Here we calculated Manhattan and Euclidean distance matrices to measure the dissimilarity between the interaction profiles of every two species. Other measures, such as Pearson correlation coefficient, can be employed as an alternative approach for assessing the similarity or dissimilarity between species. And lastly, similarity or dissimilarity matrices from the second step can be interrogated to derive species uniqueness measures. Here we simply calculated the row sums of Manhattan and Euclidean distance matrices to be our species uniqueness indices. Other more complicated procedures can be used here; for instance, those similarity or dissimilarity matrices can be subjected to dimension reduction techniques (e.g., multi-dimensional scaling) or cluster analysis in order to identify unique species. Quantifying species uniqueness from the network perspective is still in its infancy, and all of above possibilities are potential directions for future research.

doi:10.6342/NTU202203106

Chapter 4 Functional diversity from a network perspective I: an interaction-based functional diversity index

4.1 Introduction

The biodiversity crisis is a major concern in the era of climate change (Pimm 2008, Bellard et al. 2012, Scheffers and Pecl 2019) as we are losing species at an unprecedented rate (Chase et al. 2020, Gabara et al. 2021). In consequence, quantifying biodiversity in ecosystems has been the focus of considerable research in recent decades. Biodiversity in its most fundamental sense is the number of species present in an ecosystem, but researchers have extended this concept by incorporating either abundance data (MacArthur 1965, Hill 1973, Jost 2006) or genetic diversity (Wennerström et al. 2017) in order to gain a better picture of biodiversity in nature. Furthermore, species have their own characteristics or traits, and these ultimately influence ecosystem functioning (Tilman et al. 1997, Flynn et al. 2011). Thus, it is also possible to measure biodiversity from the functional perspective, in terms of the diversity of the functional traits of species (Villéger et al. 2008, Schmera et al. 2009, Laliberté and Legendre 2010, Chiu and Chao 2014, Mammola et al. 2021).

Species are embedded in an intricate network of trophic interactions, namely a food web. How species interact in a food web reveals their functional roles (Jordán et al. 2006). For instance, the effect of one predator species on another predator species via a shared prey species can be

doi:10.6342/NTU202203106

quantified as a two-step effect, resulting in exploitative competition. Similarly, in a food chain consisting of four species, the effect of the top predatory species on a basal species via two intermediary species can be quantified as a three-step effect, measuring the extent of top-down control. Social network analysis has been applied to partition species based on their interaction pattern into functional units in order to reveal the fundamental structure of a food web (e.g., environs analysis (Fath and Patten1999) and regular equivalence analysis (White and Reitz 1983, Borgatti and Everett 1989, Luczkovich et al. 2003)). More recently, species with similar sets of interactors were assumed to have similar functional roles, and such a concept has been used to quantify the uniqueness of species in a food web (Jordán et al. 2009, Lai et al. 2012, 2015). All this suggest that species' functional roles depend on how they interact with each other in a food web.

In this chapter, we use species interaction patterns in a food web to quantify the diversity in their functional roles. The conventional concept of functional diversity is based on how species are distributed in a multi-dimensional space constructed by using trait information. In contrast, our approach here uses information on how species interact with each other in a food web. Our work here thus provides a complementary view to functional diversity of an ecosystem.

doi:10.6342/NTU202203106

4.2 Material and method

4.2.1 *Food web data analyzed in this study*

We analyzed 92 food webs in this study. Please refer to Chapter 2 for basic information on these food webs.

4.2.2 *Measuring functional diversity from the interaction structure of a food web*

Given a food web of N species and treating it as a network with undirected and unsigned edges, the method of Jordán et al. (2003) produces a square matrix **E** where an element E_{ij} is the effect of a row species i on a column species j up to n steps (i.e., equations (3.1) and (3.2) from Chapter 3). Specifically, E_{ij} is the probability of species j being affected by species i in one step, two steps, or up to n steps; and steps here refer to the number of links in a pathway linking species i and j. Treating the same food web as a network with directed and signed edges (i.e., a signed digraph), the method of Liu et al. (2010) can further partition matrix **E** into two matrices $\mathbf{E}^+$ and $\mathbf{E}^-$. An element E_{ij}^+ of $\mathbf{E}^+$ is the *magnitude* of the positive effect of species i on species j up to n steps; and it is the probability of species j being positively affected by species i in one step, two steps, or up to n steps. Similar interpretation applies to an element E_{ij}^- of $\mathbf{E}^-$ for negative effects. Examples of effects are as follows. Positive one-step effects are those from prey species on predator species; and negative two-step effects include those associated with exploitative competition (i.e., from a predatory species to another via a shared prey species) or apparent competition (i.e., from a prey species to another prey species via a shared predator species). We provide a detailed description on how to construct those matrices and demonstrate

doi:10.6342/NTU202203106

with a simple food web in Appendix 1. In this chapter, n is 3 throughout unless stated otherwise. $\mathbf{E}^+$ and $\mathbf{E}^-$ can be considered as the interaction structure of a food web. The i-th row of $\mathbf{E}^+$ is the positive interaction profile of species i which records its positive effects on all species in the food web, and similarly the i-th row of $\mathbf{E}^-$ is its negative interaction profile. These two rows then form a vector of length $2N$ which is the interaction profile of species i. Throughout this chapter, we use the terms "profile" and "pattern" interchangeably. We use Marczewski-Steinhaus index (i.e., complementary to the weighted Jaccard index) (Podani 2000, Schmera et al. 2009) to quantify the dissimilarity between the interaction profiles of species i and j:

$$d_{ij} = \frac{\sum_{k=1}^{N} |{E_{ik}}^{+} - {E_{jk}}^{+}| + \sum_{k=1}^{N} |{E_{ik}}^{-} - {E_{jk}}^{-}|}{\sum_{k=1}^{N} \max\{{E_{ik}}^{+}, {E_{jk}}^{+}\} + \sum_{k=1}^{N} \max\{{E_{ik}}^{-}, {E_{jk}}^{-}\}}, \quad (4.1)$$

where d_{ij} ranges from 0 to 1, and a large d_{ij} indicates high dissimilarity between the interaction profiles of species i and j. We then quantify the diversity in interaction profiles of a food web as:

$$IPD = \frac{\sum_{i=1}^{N} \sum_{j>i}^{N} d_{ij}}{(N^2 - N)/2}, \quad (4.2)$$

where the nominator is the summation of all pairwise dissimilarities and the denominator is the total number of species pairs (note that pairs ij and ji count only once and we don't include

doi:10.6342/NTU202203106

self-pairs). Thus, *IPD* is the average dissimilarity between two interaction profiles of a food web, and a large *IPD* value indicates high interaction diversity.

4.2.3 *Global network properties*

For a given food web, we calculated several global properties of the whole network in order to investigate whether and how *IPD* was correlated with them. These network properties are as follows.

a) Number of species (*N*): this is the number of species in the food web.

b) Number of trophic links (*L*): this is the number of prey-predator trophic links in the food web.

c) Connectance of a food web (*C*): this is the link density of a food web,

$$C = \frac{L}{N(N-1)/2}. \quad (4.3)$$

d) Diameter of a food web (*diam*): for this measure we determined all the shortest paths between all species pairs. The diameter of a food web is the length of the longest and shortest path.

e) Maximum trophic position (TP_{max}): we applied the approach of Levine (1980) to quantify the trophic position of each species in the food web. TP_{max} is the maximum value of those trophic positions.

f) Network cohesion (*coh*): we borrowed this concept directly from sociology (White and Harary 2001, Moody and White 2003). Specifically, we determined the number of nodes that

doi:10.6342/NTU202203106

need to be removed in order to make the original food web disintegrate into at least two components. We then divided this number by the number of species in the food web.

g) Number of clusters (*clu*): we applied the algorithm of Clauset et al. (2004) to identify the number of clusters in a given food web. In general, nodes belonging to the same clusters interact more frequently than nodes belonging to different clusters.

h) Network modularity (*mod*): after we partitioned nodes into several clusters, we then quantified the difference between the fraction of edges within clusters and the fraction of edges between clusters. We used this as a measure of network modularity (Clauset et al. 2004, Newman 2006).

4.2.4 *Conventional functional diversity indices*

To examine the uniqueness of our new measure, we need to investigate its relationship with conventional functional diversity indices. For every food web we analyzed, trait information for many species was also available (see Chapter 2). These traits were: habitat type, mobility, and body size (note that habitat type is not an intrinsic property of a species; however, we still include it as it may correlate with some intrinsic traits of a species). Thus, we also calculated the functional richness (*Tric*), evenness (*Teve*), dispersion (*Tdis*), and Rao's *Q* (*Traoq*) based on these three traits (Villéger et al. 2008, Laliberté and Legendre 2010). We used the R package "FD" version 4.2.0 to calculate those conventional functional diversity indices, and then examined their relationship with *IPD*.

doi:10.6342/NTU202203106

4.2.5 *Weight of trophic links*

Those 92 food web data also have information on the weight of each trophic link (i.e., in terms of the biomass transferred per unit area and per unit time, for example, in grams of carbon per square meter per year). We also quantified the interaction structure of each food web by considering each trophic link as a weighted edge (see Appendix 1), and calculated the weighted version of interaction profile diversity (i.e., IPD_w).

4.2.6 *Number of steps n*

There is one parameter in our methodology, namely the number of steps n up to which the interaction structure of a food web is quantified. We investigated how changing n (from 1 to 50) can affect the values of *IPD* and IPD_w. We note that the interpretation for large n may be less clear than that for small n. For instance, with n=2, inter-specific effects include those from exploitative competition and apparent competition. With n=50 however, its ecological meaning is unclear. Therefore, we suggest n should not be greater than the diameter of a food web.

4.3 Results

For each of those 92 food webs involved in this study, we quantified its interaction structure up to n=3 steps and then calculated its interaction profile diversity (i.e., *IPD*), as well as those other indices mentioned in the Material and Method section. We used Kendall rank correlation to determine the association between *IPD* and eight global network properties (Fig. 4.1). *IPD* correlates positively with diameter, the number of clusters and network modularity, and

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negatively with connectance and cohesion. As for the relationship with conventional functional diversity indices (Fig. 4.2), *IPD* shows weak-to-moderate positive correlation with functional richness (*Tric*), functional dispersion (*Tdis*) and Rao's *Q* (*Traoq*).

We also calculated the weighted version of interaction profile diversity (i.e., IPD_w) for each food web, and repeated the same correlation analysis as before. In general, IPD_w correlates with these eight global network indices in the same way as its un-weighted counterpart despite changes in the magnitude of their correlation coefficients (Fig. 4.3). Furthermore, IPD_w correlates with conventional functional diversity indices in a manner similar to that for

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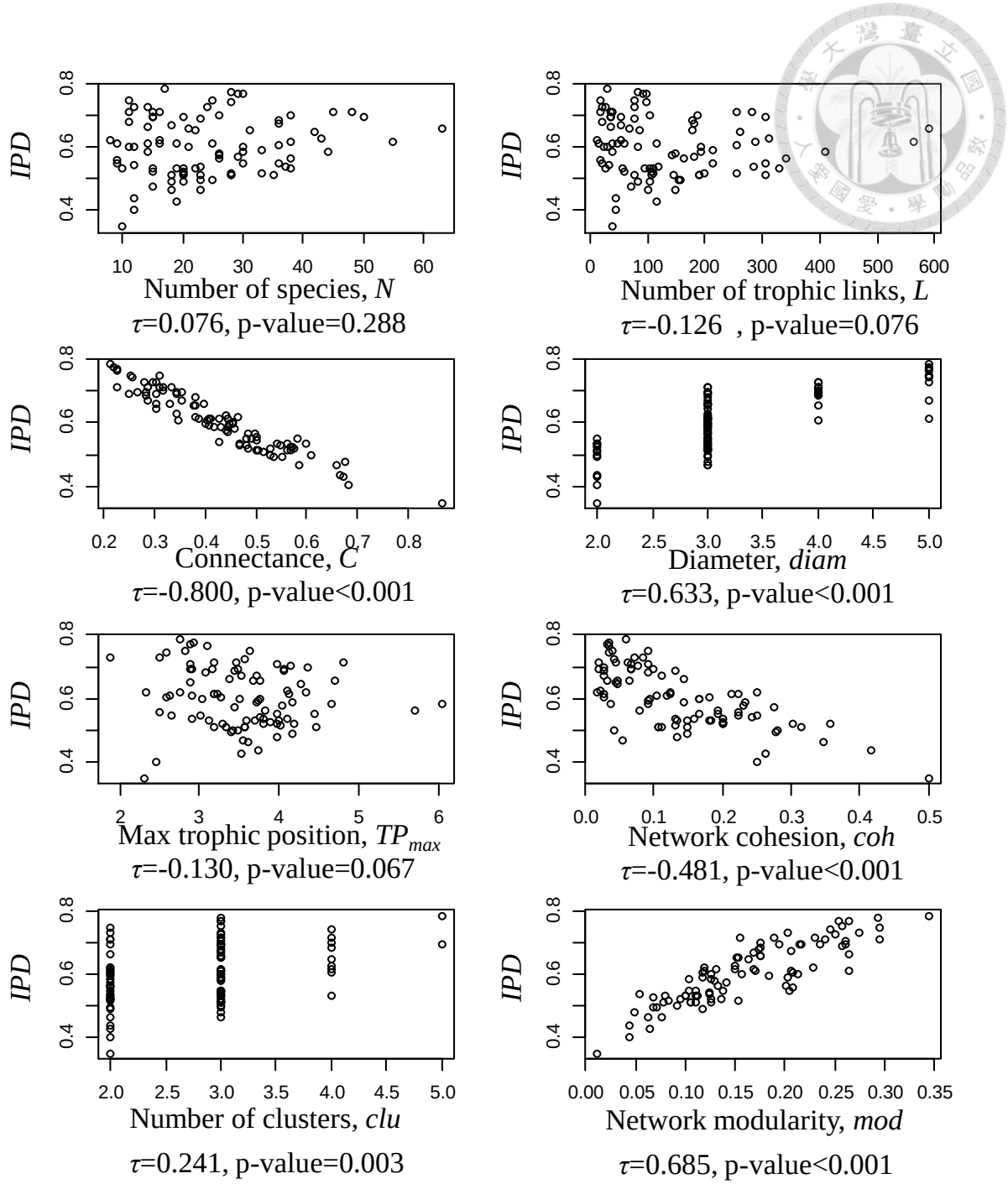

Figure 4. 1 Correlation between interaction profile diversity (i.e., *IPD*) and eight different network properties. τ is Kendall correlation coefficient.

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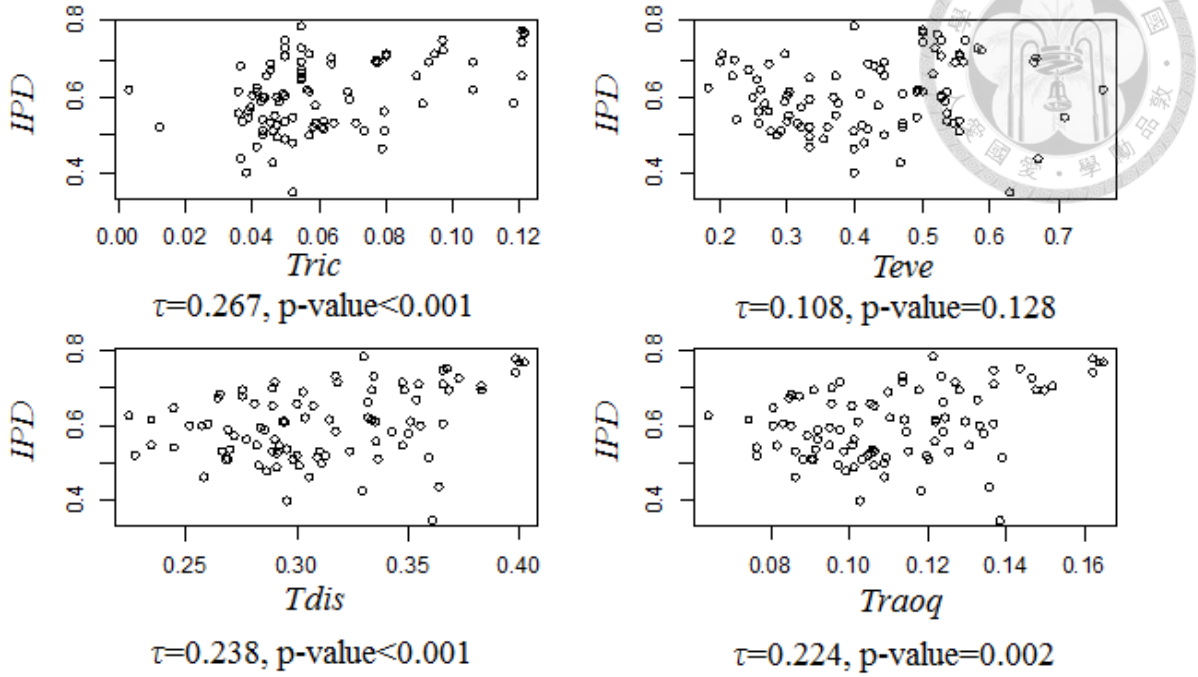

Figure 4. 2 Correlation between interaction profile diversity (i.e., *IPD*) and conventional functional diversity indices (i.e., *Tric*, *Teve*, *Tdis* and *Traoq*). τ is Kendall correlation coefficient.

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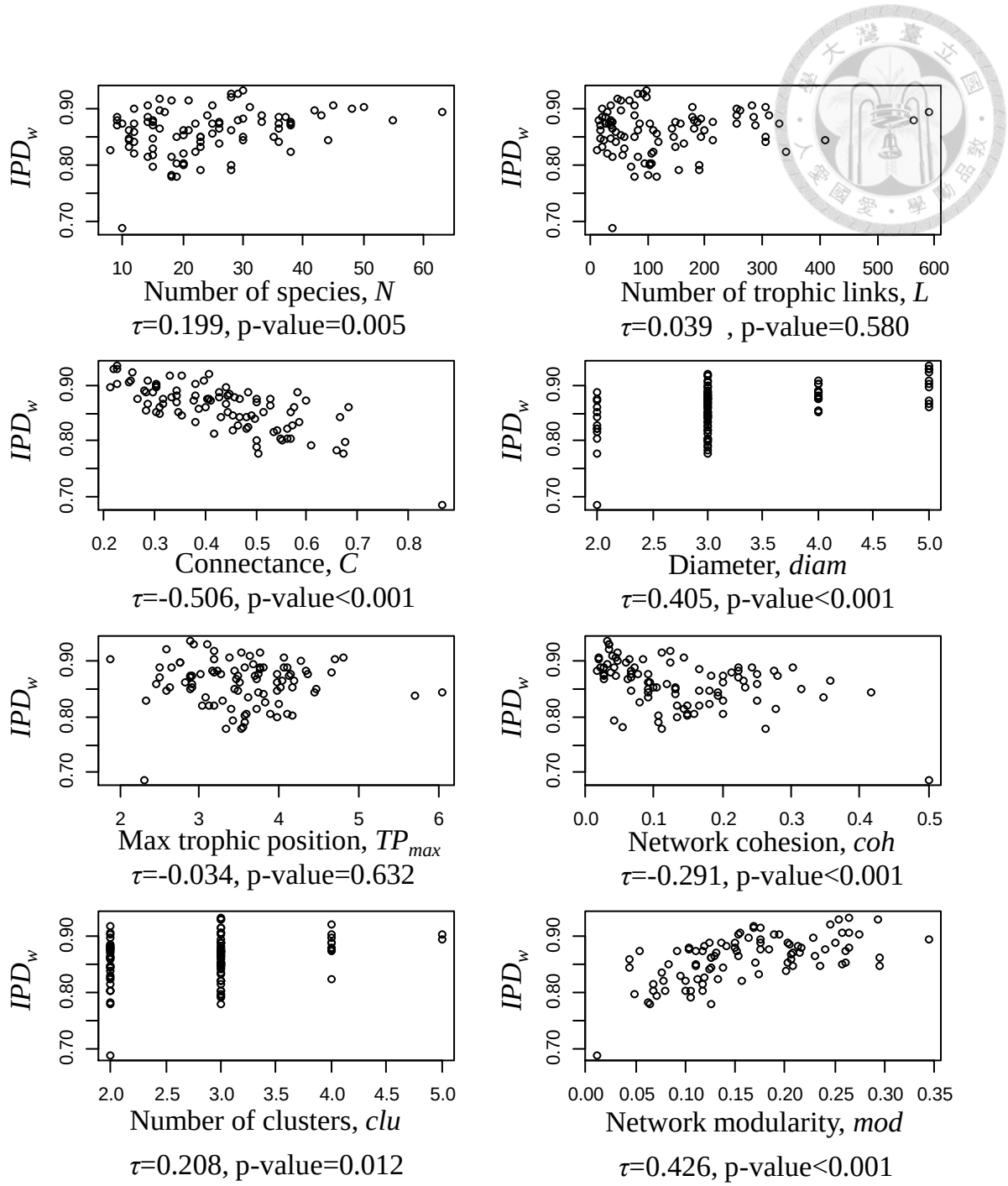

Figure 4. 3 Correlation between weighted version of interaction profile diversity (i.e., IPD_w) and eight different network properties. τ is Kendall correlation coefficient.

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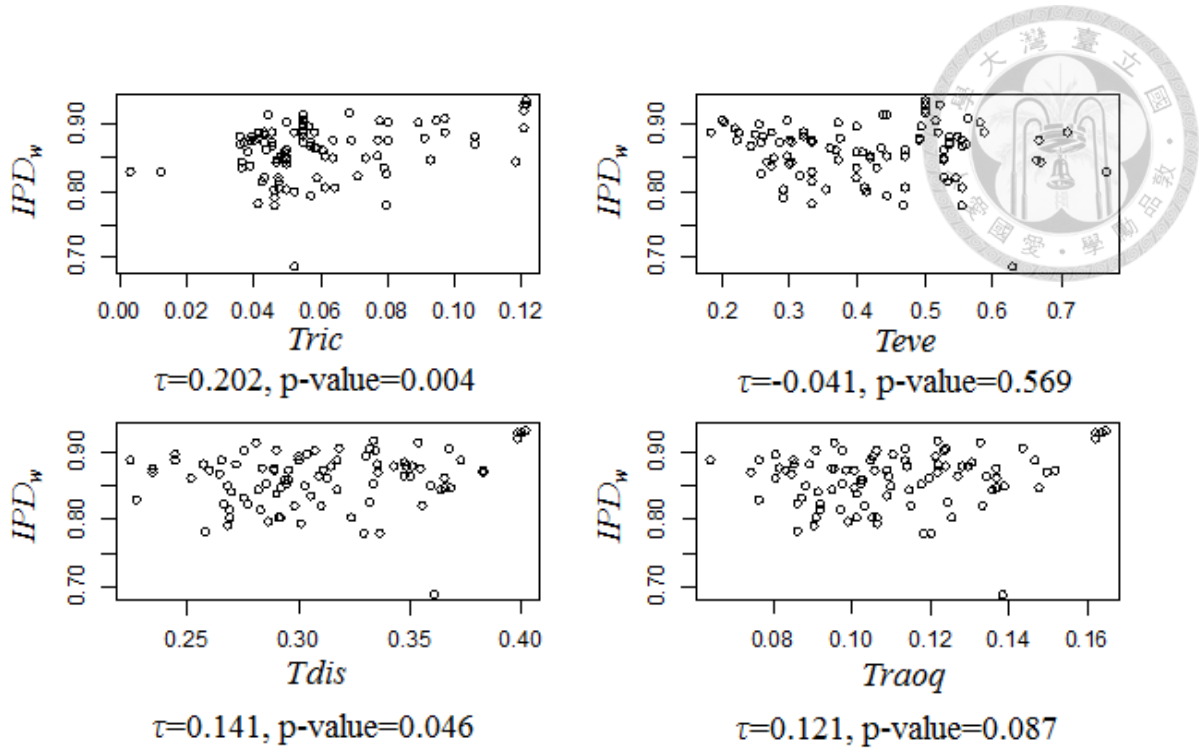

Figure 4. 4 Correlation between weighted version of interaction profile diversity (i.e., IPD_w) and other conventional functional diversity indices (i.e., *Tric*, *Teve*, *Tdis* and *Traoq*). τ is Kendall correlation coefficient.

IPD (Fig. 4.4).

We investigated how changing *n* (from 1 to 50) can affect the value of *IPD* for all 92 food webs. For all food webs, as *n* increases, *IPD* decreases and stabilizes to a fixed value, and the same trend is observed for IPD_w (Fig. 4.5). As for the relationship between both *IPDs* and each of those network properties examined, the sign of Kendall correlation coefficient remains the same, but its magnitude stabilizes to a fixed value as *n* increases (Fig. 4.6 and Fig. 4.7). We note that food web diameter varies from 2 to 5 for those 92 food webs we analyzed

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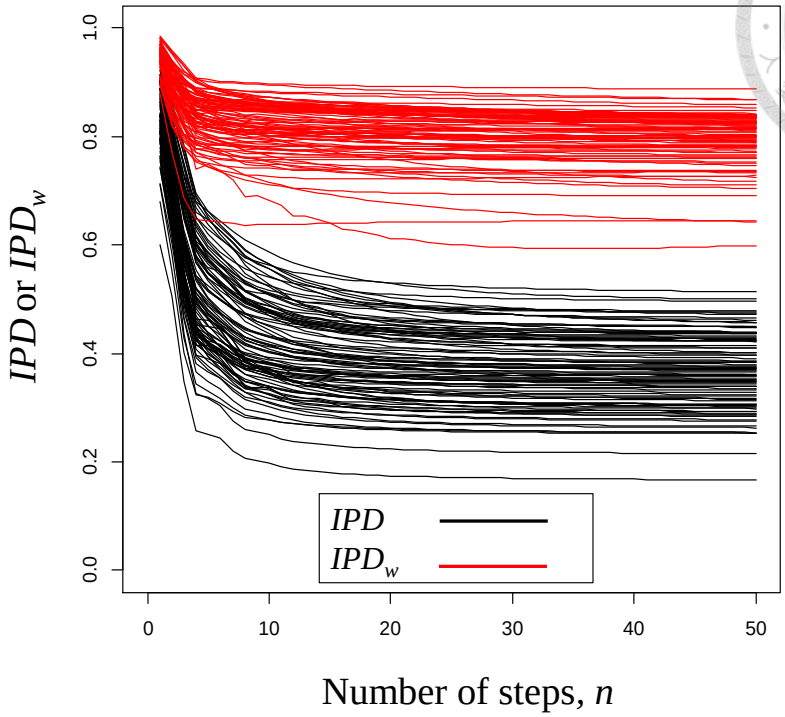

Figure 4. 5 Effect of changing the number of steps n on IPD and IPD_w.

(Please see the corresponding sub figure in Figure 4.1); and both IPD and IPD_w, as well as their correlation coefficients with other network properties, stabilize at n values that are much larger than the values of food web diameter (Fig. 4.5, Fig. 4.6 and Fig. 4.7).

4.4 Discussion

Some general pattern emerges from our analysis. First, our proposed diversity index correlates negatively with connectance and positively with network diameter. This information indicates that the more compactly organized a food web is, the less diverse is the

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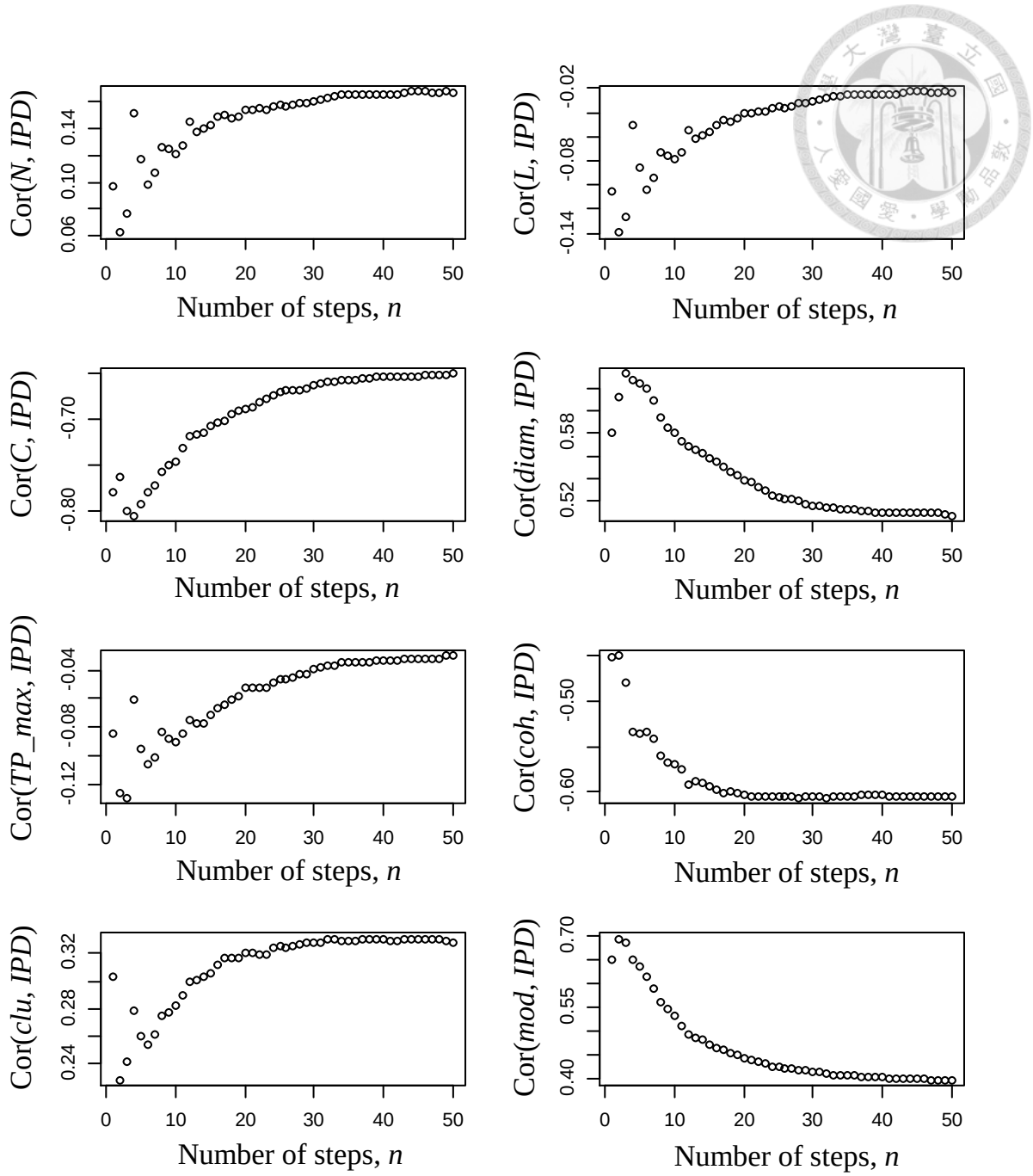

Figure 4. 6 Effect of changing the number of steps *n* on the correlation (Kendall) between *IPD* and various network properties.

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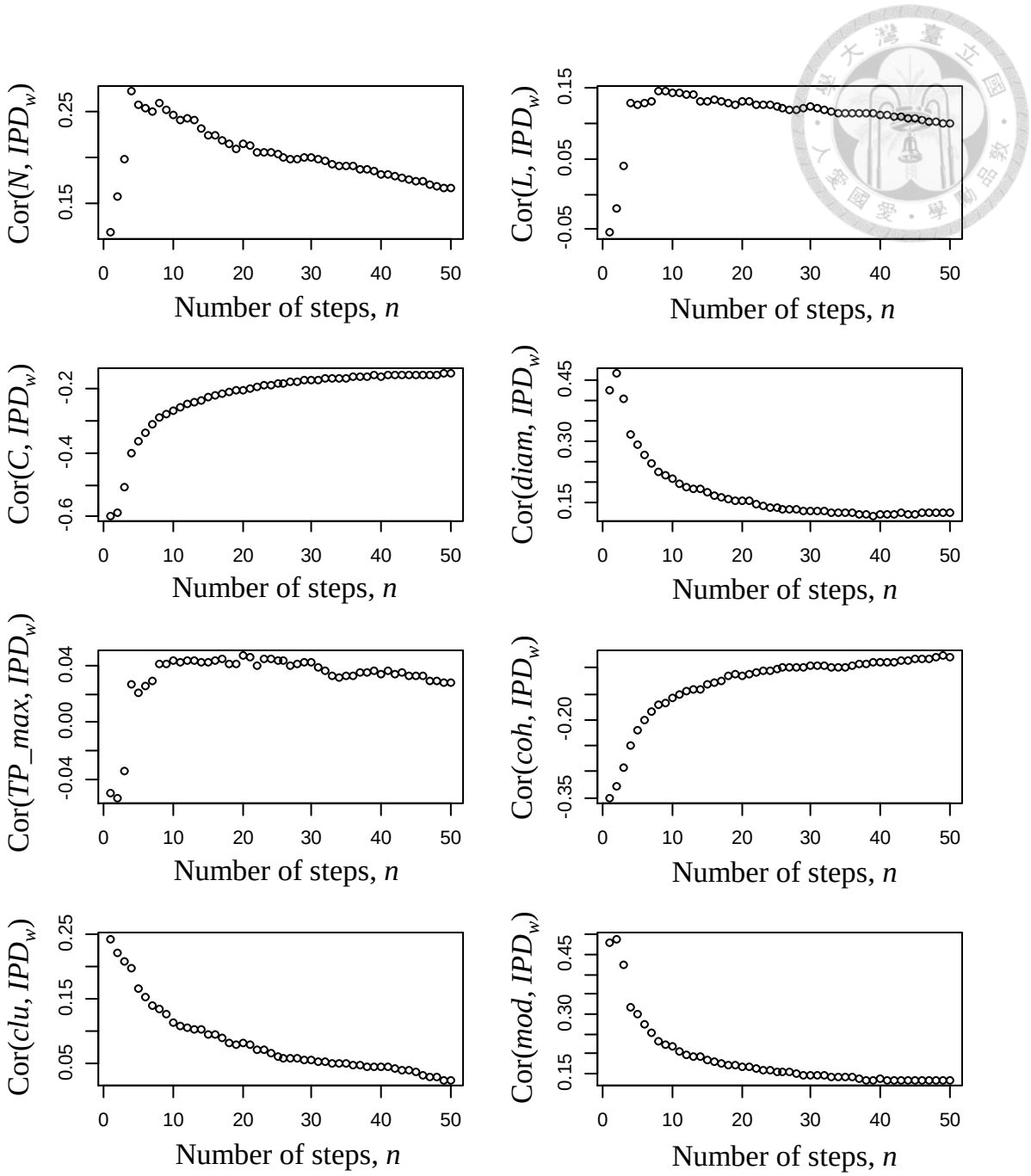

Figure 4. 7 Effect of changing the number of steps *n* on the correlation (Kendall) between IPD_w and various network properties.

interaction pattern of its constituent species. In a compactly organized food web, species are close in terms of network distance and there is little difference in their network positions. This

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results in similarity in their interaction patterns. In a sparsely connected food web, however, species are far apart in terms of network distance, and they occupy very different network positions. This then results in higher dissimilarity in their interaction patterns. Although the strong (negative) correlation between interaction diversity and connectance suggests that one can be used as a proxy of the other, we need to emphasize that they are based on very different concepts and provide different kinds of information. Connectance describes the structure of a food web and interaction diversity measures the dissimilarity between species' interaction patterns; these two types of information are important in their own right and do not make one another redundant. In fact, connectance should be viewed as a mechanism that explains the observed level of interaction diversity in a food web.

Second, our diversity index correlates negatively with network cohesion. This implies that a robust food web tends to have lower interaction diversity than a less robust food web. This is because, in a less diverse food web, species are similar in their interaction patterns. Therefore, if one species is lost, it is easily compensated for by other similar species. Thus, in a less diverse food web, the level of species redundancy should be higher. Positional redundancy (i.e., overlapping trophic roles) is prevalent in many food webs. As Lai et al. (2012) have demonstrated, existing ecosystems tend to be redundant in central or important species. They suggest that this pattern of organization is required to render an ecosystem resilient to species

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loss. Redundancy has also been found to be a common feature in other biological networks such as metabolic networks, gene networks, and biochemical networks (Stelling et al. 2002, Liu et al. 2007, Tian et al. 2020).

Third, interaction diversity is also positively associated with the number of clusters in a food web. Food webs are compartmentalized and consist of modules of interacting species (Guimerà et al. 2010, Stouffer and Bascompte 2011). Intuitively, a food web with many modules implies greater heterogeneity in its structural organization. There should therefore be greater diversity in the network position of species than in a food web with few modules. This then results in a natural and positive association between interaction diversity and the number of clusters in a food web. Moreover, we found that interaction diversity is positively correlated with network modularity. Network modularity measures how well-defined clusters are by examining how links are distributed within clusters relative to between clusters (Clauset et al. 2004, Newman 2006). Our results, therefore, imply that modules or clusters are better defined in a functionally more diverse food web.

Our analysis shows that interaction diversity has some positive correlation with trait-based functional diversity, but their relationship is far from perfect. Intuitively, a positive correlation is expected as species with similar traits may have similar interactions with other species;

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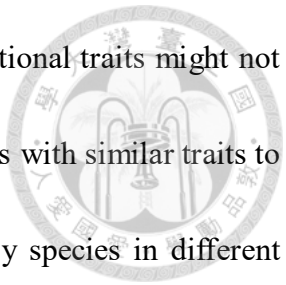

however, other factors may lower such a correlation. For instance, functional traits might not be strongly linked to feeding behavior; or competition may drive species with similar traits to interact with different species. Moreover, some traits can be shared by species in different trophic groups; or species in the same trophic group can differ greatly in characteristics such as body sizes. In addition, indirect interactions in a complex food web might alter the relationship between trophic functions and traits. All in all, our result suggests that interaction diversity provides a complementary view of functional diversity to those trait-based ones.

We conclude with possible research directions. First, we can combine the conventional concept of functional diversity with what we have proposed here. Many functional diversity indices in the literature are weighted measures where relative abundances of species are often taken into account (Laliberté and Legendre 2010, Mammola et al. 2021). We can borrow this concept and multiply each pairwise dissimilarity (i.e., equation (4.1)) by the relative abundance of the species pair involved, and then sum them up to obtain a weighted version of *IPD* or IPD_w. We note that IPD_w is already a weighted version of *IPD* by incorporating trophic weights. We speculate that species abundance and trophic weight may be related quantities; therefore, how to interpret a weighted version (based on relative abundance) of IPD_w warrants further investigation. Second, one can quantify the network characteristics of each species by using measures borrowed from social network analysis. For example, the position of a node in a

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network can be characterized by using degree-centrality, closeness centrality, betweenness centrality and others (Wasserman and Faust 1994, Jordán et al. 2006). Each of these can be considered as a trait for a species, and the conventional functional diversity measures can then be calculated directly on those traits; and these can potentially be measures for quantifying the diversity in species' network positions in a food web. In Chapter 5, we present new network-based measures of functional diversity by considering this new idea. Finally, we note that there are other ways of quantifying positional dissimilarity in networks (White and Reitz 1983, Borgatti and Everett 1989, Yodzis and Winemiller 1999). The approach we have adopted in this study is based on the ecological concept of species interactions. In Chapter 6, we will employ the concept of regular equivalence as an alternative approach to positional dissimilarity and develop other network-based measures of functional diversity.

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Chapter 5 Functional diversity from a network perspective II: a centrality-based functional diversity index

5.1 Introduction

Species' ecological functions are related to their morphological traits (Tilman et al. 1997, Flynn et al. 2011), and it has been suggested that trait diversity among species can be a proxy to functional diversity in an ecosystem (Villéger et al. 2008, Mammola et al. 2021). Each species can be characterized by several morphological traits (e.g., body size, weight, color and mobility), and conventional approaches to functional diversity mainly concern with how species are distributed in a multi-dimensional trait space (Petchey and Gaston 2002, Villéger et al. 2008). Several indices have been developed to measure different facets of functional diversity from such a distribution (Laliberté and Legendre 2010, Pla et al. 2011, Mammola et al. 2021). These include how to quantify the range or boundary of the trait space (Mason et al. 2003, Cornwell et al. 2006, Layman et al. 2007), how even and/or dispersed species are in this trait space (Mouillot et al. 2005, Villéger et al. 2008, Laliberté and Legendre 2010), and how similar species are in their morphological traits (Rao 1982, Botta-Dukát 2005).

One aspect of species function is how species interact with each other. A food web is the simplest representation of inter-specific interactions as it depicts who eats whom in an ecosystem (Pimm 1982). A food web, in essence, is a network where nodes and links

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respectively represent species and their trophic interactions, and species' network positions can be quantified in different ways by using methods borrowed from (social) network analysis (Wassermann and Faust 1994). These range from local measures that simply count the number of neighbors a node has to more global measures that use the information on the entire network (Jordán et al. 2006). We argue that a species can also have various traits in a network sense, and for convenience, we call those as their network traits. We further argue that how species are distributed within this multi-dimensional network trait space can also be a proxy to the network-based functional diversity in an ecosystem. Thus, following the research idea from the end of Chapter 4, we propose in this chapter a new network-based concept of functional diversity by combining conventional measurements of functional diversity with network analysis. To be more specific, for each of 92 food webs from Chapter 2, we quantify the network position of individual species in a food web by using several centrality indices, and regard them as various network traits. We then apply conventional methods of functional diversity on those network traits just like one would have done for morphological traits. For our convenience, we refer to the resulting network-based indices as centrality-based functional diversity indices. Furthermore, we conduct the same analysis as those in Chapter 4, and investigate the relationship between our new functional diversity indices and several global network properties. Finally, we also compare these centrality-based functional diversity indices with their interaction-based and morphological trait-based counterparts to assess their novelty.

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5.2 Material and method

5.2.1 *Food web data analyzed in this study*

We analyzed 92 food webs in this study. Please refer to Chapter 2 for basic information on these food webs.

5.2.2 *Centrality indices*

Centrality indices quantify from different perspectives the network position of each species in a food web. There are eight centrality indices in this study, and they were calculated by using R package igraph ver1.3.4. A brief description for those indices is as follows.

a) Degree centrality (*DC*) (Wassermann and Faust 1994). This is the number of neighbors a node has in a network. Here, it is the total number of predator and prey species of one species.

b) Closeness centrality (*CC*) (Wassermann and Faust 1994). This measures how close a node is to all other nodes in a network:

$$CC_i = \frac{1}{\sum_{j=1}^{N} d_{ij}}, \qquad (5.1)$$

where N is the number of nodes and d_{ij} is the length of the shortest path between node i and node j. A node with a large CC value indicates that it is close to many other nodes in the same network.

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c) Betweenness Centrality (*BC*) (Freeman 1977, Wassermann and Faust 1994). This index measures how frequently a node *i* appears on all shortest paths between node pairs:

$$BC_{ij} = \sum_{j>k} \frac{g_{jk,i}}{g_{jk}}, \quad (5.2)$$

where g_{jk} is the number of shortest paths between node pair *j* and *k*, and $g_{jk,i}$ is the number of these shortest paths that contain node *i*.

d) Eigenvector Centrality (*EC*) (Bonacich 2007). This is an extension of degree centrality. Degree centrality and eigenvector centrality differ in how neighbors contribute to a node's centrality. In the former, a node *i*'s neighbors contribute equally; but in the latter, each neighbor *j* contributes an amount proportional to *j*'s eigenvector centrality. Let **A** denotes the adjacency matrix representing a network with an element A_{ij}=1 if nodes *i* and *j* are connected, then eigenvector centrality for node *i* (EC_i) is:

$$\lambda\, EC_i = \sum_{j=1}^{N} A_{ij}\, EC_j, \quad (5.3)$$

or alternatively in matrix notation:

$$\lambda \mathbf{E} = \mathbf{AE}, \quad (5.4)$$

where **E** is an eigenvector vector containing eigenvector centrality of individual nodes and λ is the associated eigenvalue. In plain language, eigenvector centrality of a node simply describes its importance by taking into account how important its neighbors are.

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e) Alpha centrality (*AC*) (Katz 1953). Also known as Katz centrality, it measures the influence of a focal node on all others in the same network. Here, a node's influence diminishes with distance; thus, its immediate neighbors receive stronger influence than more distant ones. It can be formulated as:

$$AC_i = \sum_{k=1}^{\infty} \sum_{j=1}^{N} \alpha^k A_{ij}^k, \quad (5.5)$$

where k is the length of a given distance between node i and node j, while α is an attenuation factor.

f) Average nearest neighbor degree (*KNN*) (Newman 2002). This is simply the average degree centrality of a node *i*'s neighbors:

$$KNN_i = \frac{1}{DC_i} \sum_{j=1}^{N} A_{ij}\, DC_j, \quad (5.6)$$

where DC_i and DC_j are the degree centralities for node i and node j respectively. In essence, *KNN* measures the connectivity of the immediate neighborhood of a focal node.

g) Harmonic Centrality (*HC*) (Marchiori and Latora 2000). This is also a measure of how close a node is to all other nodes in a network. It is similar to closeness centrality, but here the lengths of shortest distances between nodes are being inversed first before the summation of those inversed values:

$$HC_i = \sum_{j=1, j\neq i}^{N} \frac{1}{d_{ij}}. \quad (5.7)$$

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h) Kleinberg's centrality (*KC*) (Kleinberg 1999). *KC* is obtained by calculating the principal eigenvector of the matrix $(\mathbf{A}^T)\mathbf{A}$, and nodes that serve as hubs in a network have high *KC* scores. Again, **A** is the adjacency matrix representing a network and $\mathbf{A}^T$ is its transpose.

5.2.3 *Relationship between centrality indices*

Several studies have examined the relationship between various centrality indices and have found that some indices are more closely related than others (Jordán et al. 2006, Oldham et al. 2019, Endrédi et al. 2021). These findings suggest that some centrality indices are redundant in terms of the information they can provide. Therefore, we needed to elucidate the relationship between those eight centrality indices in this study. This was a necessary step as some measures might be similar, and including similar measures in subsequent analysis might produce a biased result. As such we did the followings. For each food, we quantified the centrality values for each species by using all eight centrality indices as mentioned above. We then calculated Kendall's rank correlation coefficient between every two centrality indices. Doing this for all 92 food webs, we then investigated how the correlation between every two centrality indices varies across all 92 food webs. If those correlation coefficients don't vary much, then we can pool all results together and compute a correlation matrix, where each element of this matrix represents the averaged correlation coefficient between a particular pair of centrality indices across those 92 food webs. Such a correlation matrix was then subjected to hierarchical cluster

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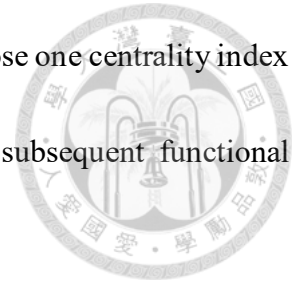
analysis to identify clusters of centrality indices. In the end, we then chose one centrality index from each cluster, and used the selected centrality indices for the subsequent functional diversity analysis.



5.2.4 *Functional diversity indices*

Those *M* chosen centrality indices were regarded as *M* network traits. We then carried out functional diversity analysis on *M* selected network traits. Here, each species is a data point in a *M*-dimensional trait space, and its position is defined by its *M* trait values (i.e., its coordinates). We used R package fundiversity Ver 0.2.1 to calculate the following functional diversity indices; each quantifies a different facet of functional diversity from the *M*-dimensional trait space.

a) Functional richness (*Cric*) (Mason et al. 2003, Cornwell et al. 2006, Layman et al. 2007). This is the volume of the convex hull encapsulating data points in the *M*-dimensional trait space.

b) Functional evenness (*Ceve*) (Mouillot et al. 2005, Villéger et al. 2008). A minimum spanning tree can be constructed linking all data points in the *M*-dimensional trait space. A tree branch linking two data points represents the trait distance between the two species involved. If all tree branches are of the same length, this indicates that species are evenly spaced out in the trait space. In contrast, if tree branches vary drastically, this indicates that species are clustered in certain part(s) of the trait space, or some sections of the trait space are void of species.

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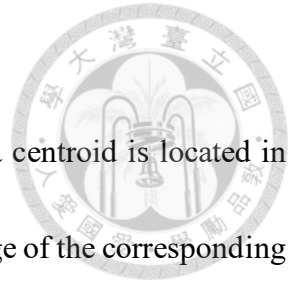

c) Functional dispersion (*Cdis*) (Laliberté and Legendre 2010). Here, a centroid is located in the *M*-dimensional trait space, where each of its coordinates is the average of the corresponding trait. Functional dispersion is the mean distance between this centroid and a data point.

d) Rao's *Q* (*Craoq*) (Rao 1982, Botta-Dukát 2005). This is an entropy-based measure. First, a distance matrix is constructed where an *ij*-th element is the Euclidean distance between species *i* and species *j* in the *M*-dimensional trait space. Rao's *Q* is the average distance between two species if we sample two species with replacement from the ecosystem.

5.2.5 *Global network properties*

Following the analysis from Chapter 4, we quantified eight global network properties and assessed their relationship with our centrality-based functional diversity indices. Details of those global network properties are in section 4.2.3, and briefly they are: number of species (*N*), number of trophic links (*L*), connectance (*C*), network diameter (*diam*), maximum trophic position (TP_{max}), network cohesion (*coh*), number of clusters (*clu*) and network modularity (*mod*).

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5.3 Results

5.3.1 *Relationship between centrality indices*

For each of 92 food webs, we calculated eight above-mentioned centralities indices for individual species. For each food web and for each centrality index, we standardized each value by subtracting from the mean and divided this by the standard deviation; we then pooled all standardized values from all 92 food webs together. Using these standardized values, we then examined the relationship between every pair of centrality indices (Fig. 5.1). From the pooled results, we can observe that the majority of pairs of centrality indices show certain amounts of association. However, there are exceptions. We can observe that alpha

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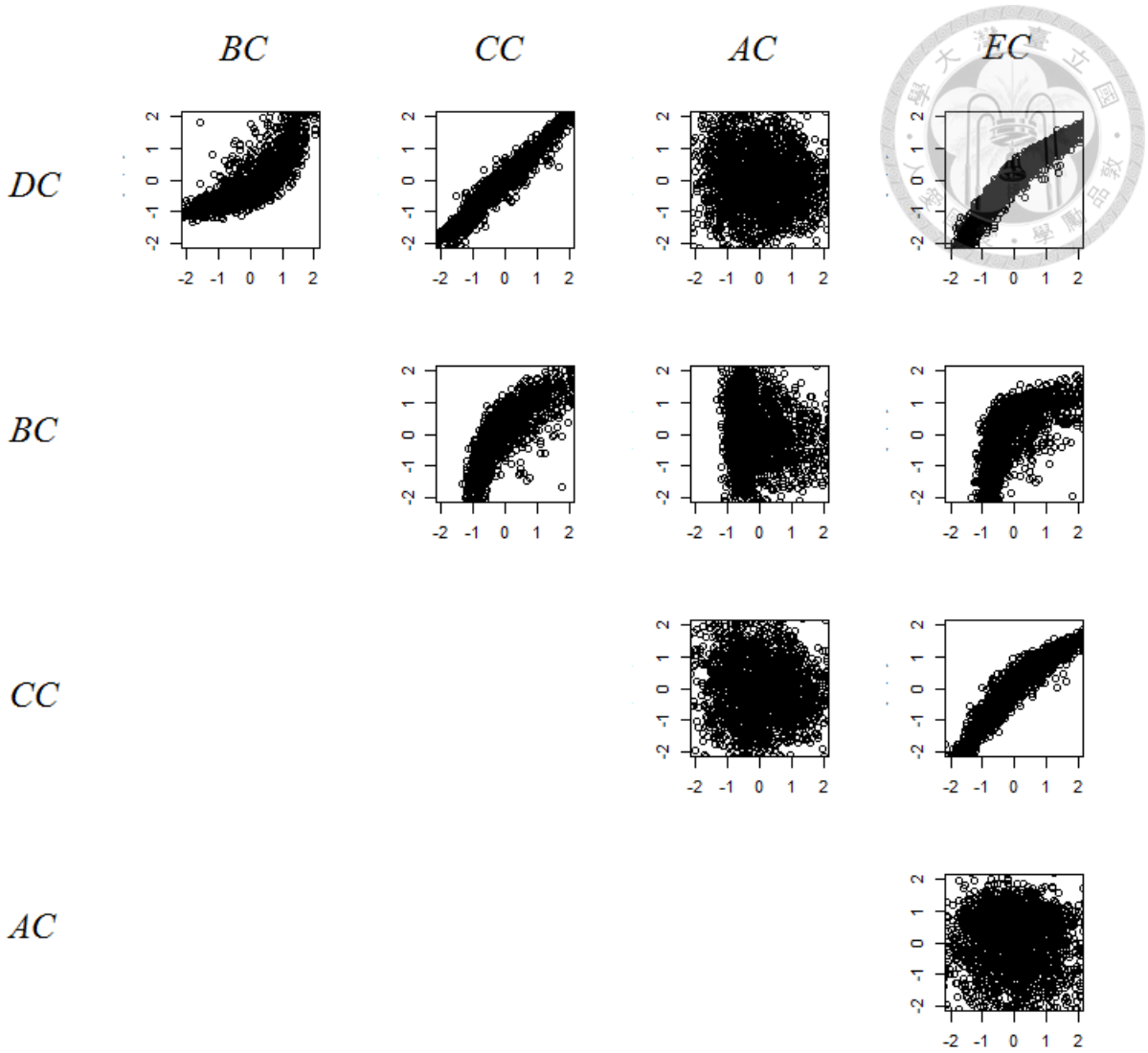

Figure 5. 1 Scatter plots showing the relationship between pairs of centrality indices.

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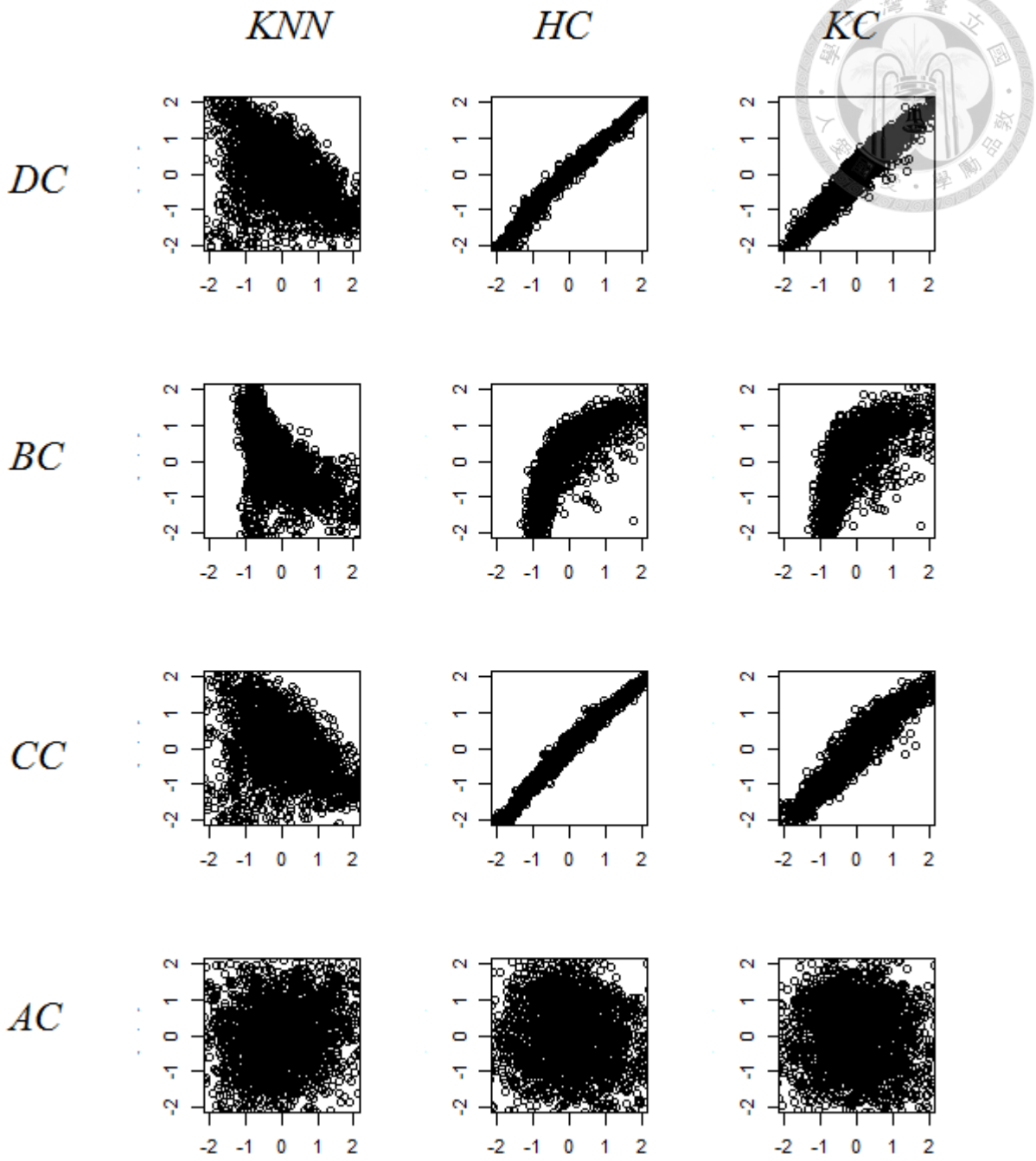

Figure 5.1 (continued) Scatter plots showing the relationship between pairs of centrality indices.

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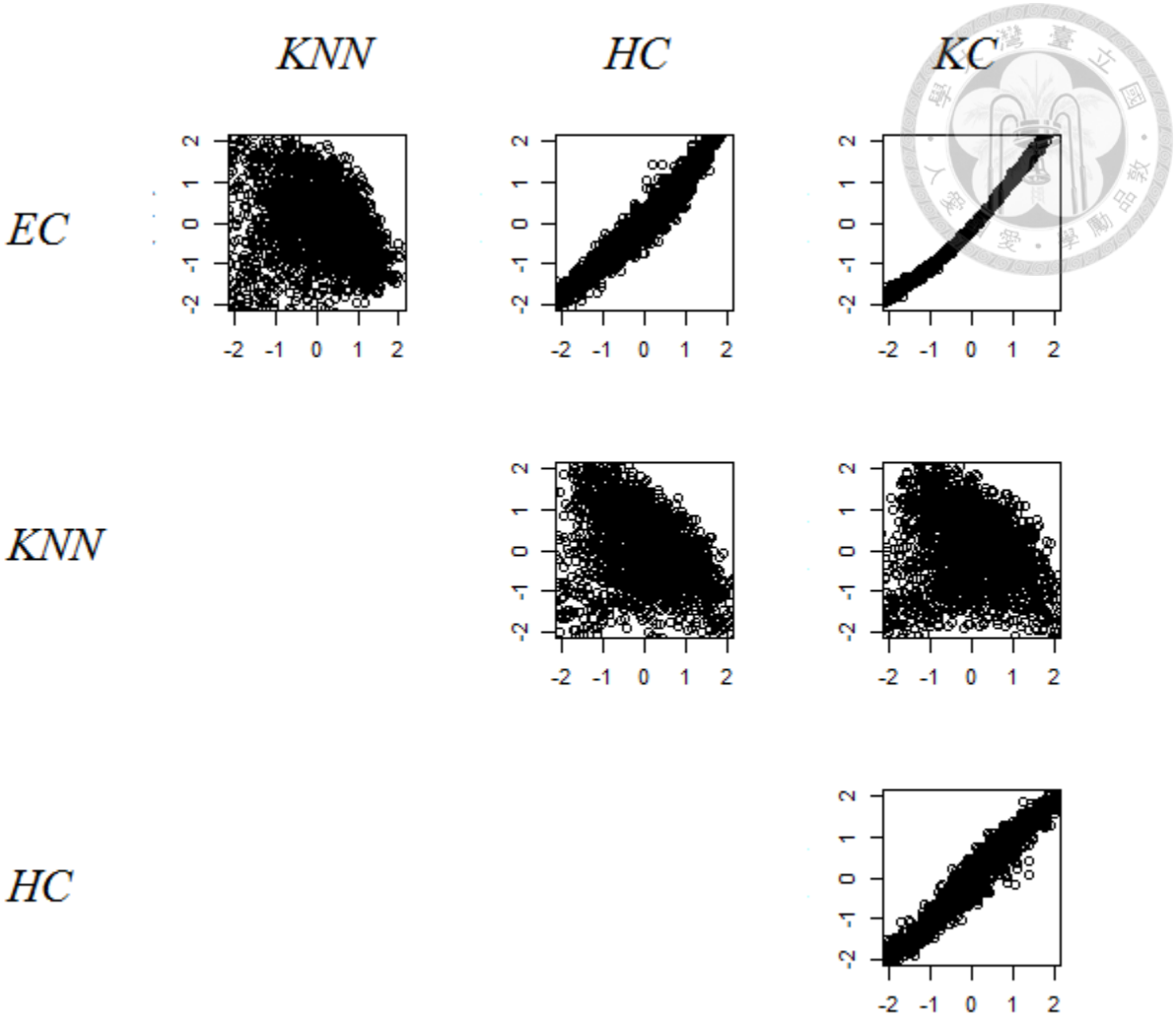

Figure 5.1 (continued) Scatter plots showing the relationship between pairs of centrality indices.

centrality (*AC*) and average nearest neighbor degree (*KNN*) show no association with other centrality indices.

For each food web, we also calculated Kendall rank correlation coefficient between every pair of centrality indices, and examined how each of these correlation coefficients varied across all 92 food webs (Fig. 5.2). We can observe that although most correlation coefficients

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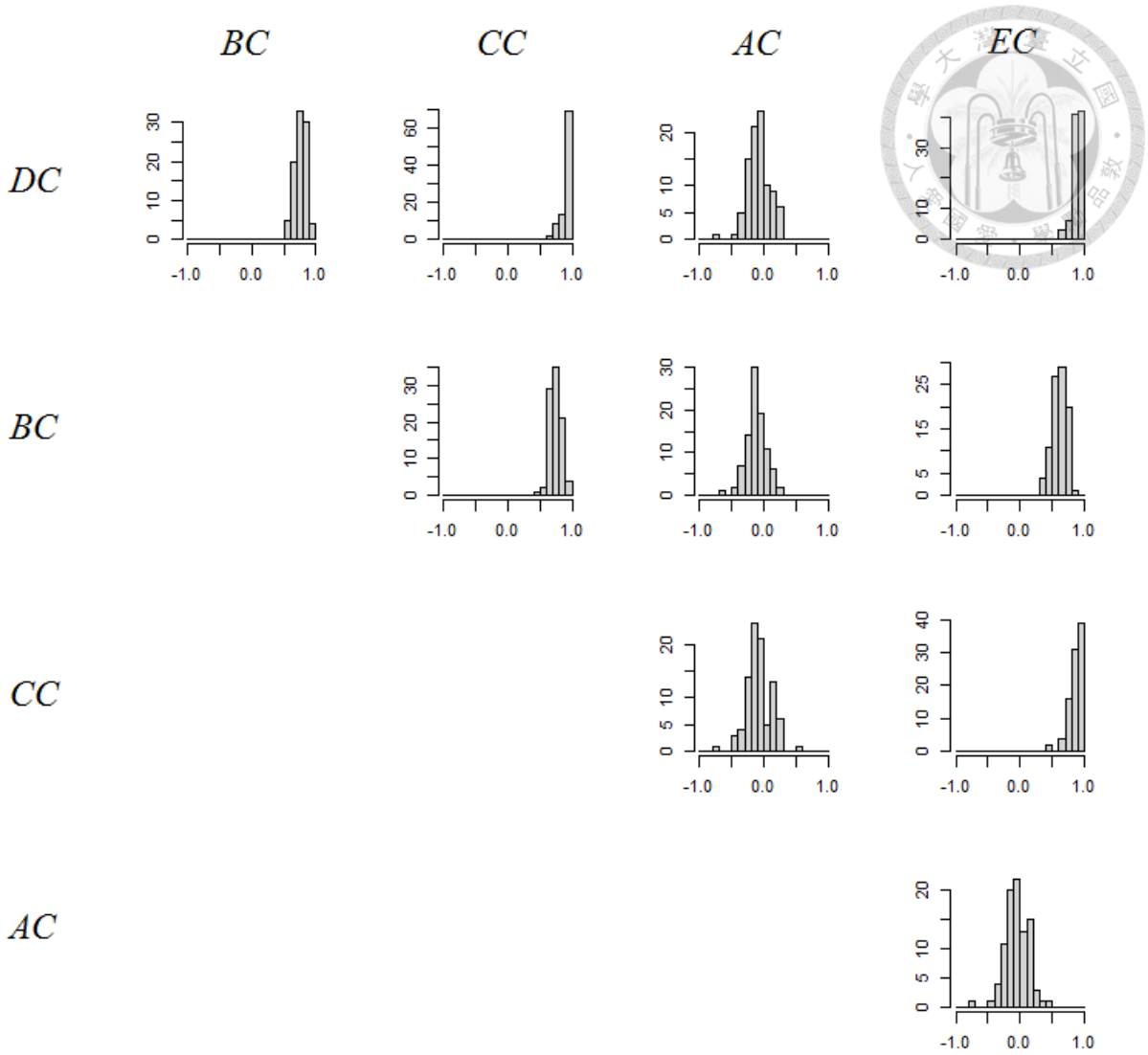

Figure 5. 2 Distribution of Kendall rank correlation coefficient between pairs of centrality indices.

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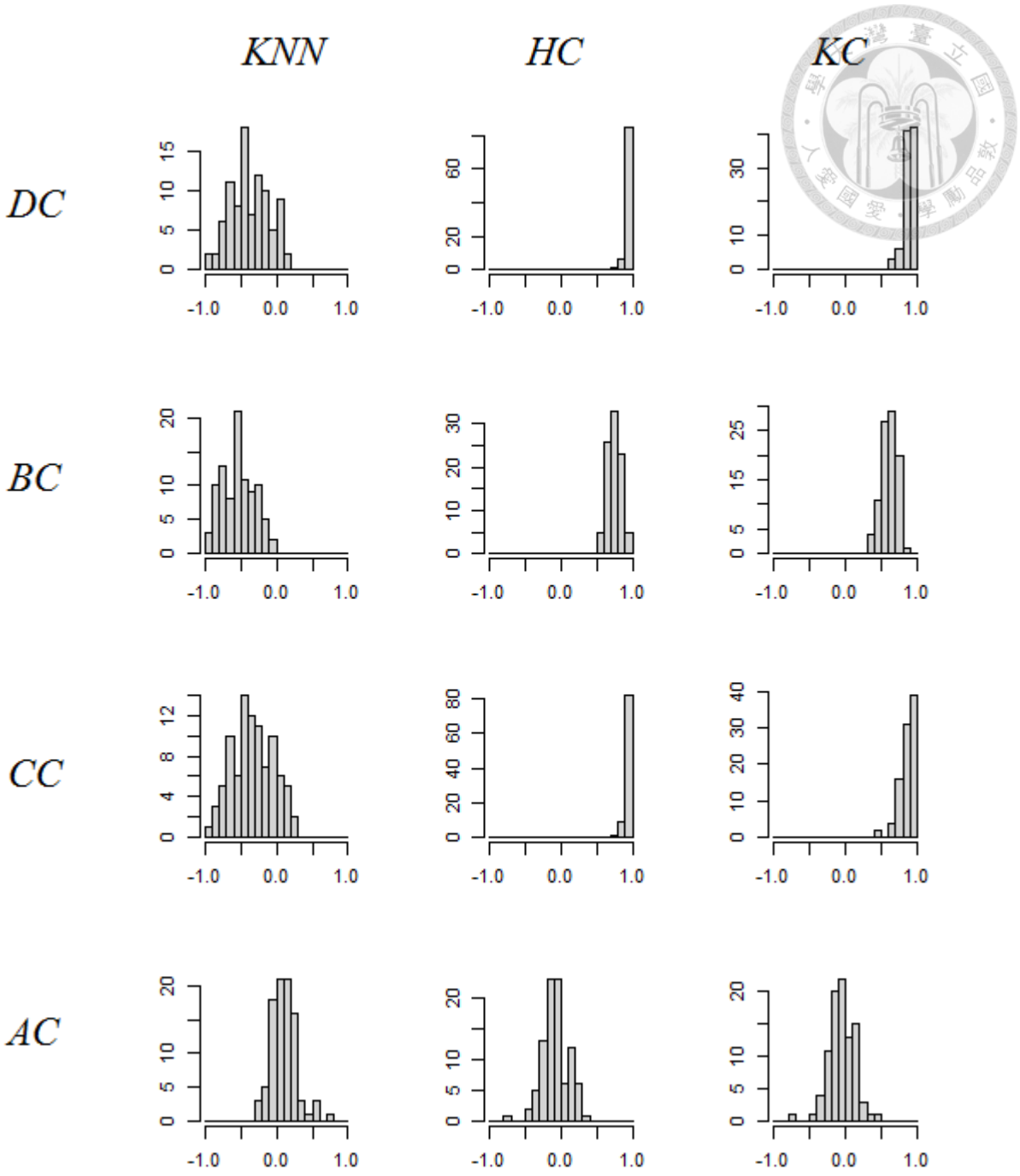

Figure 5.2 (continued) Distribution of Kendall rank correlation coefficient between pairs of centrality indices.

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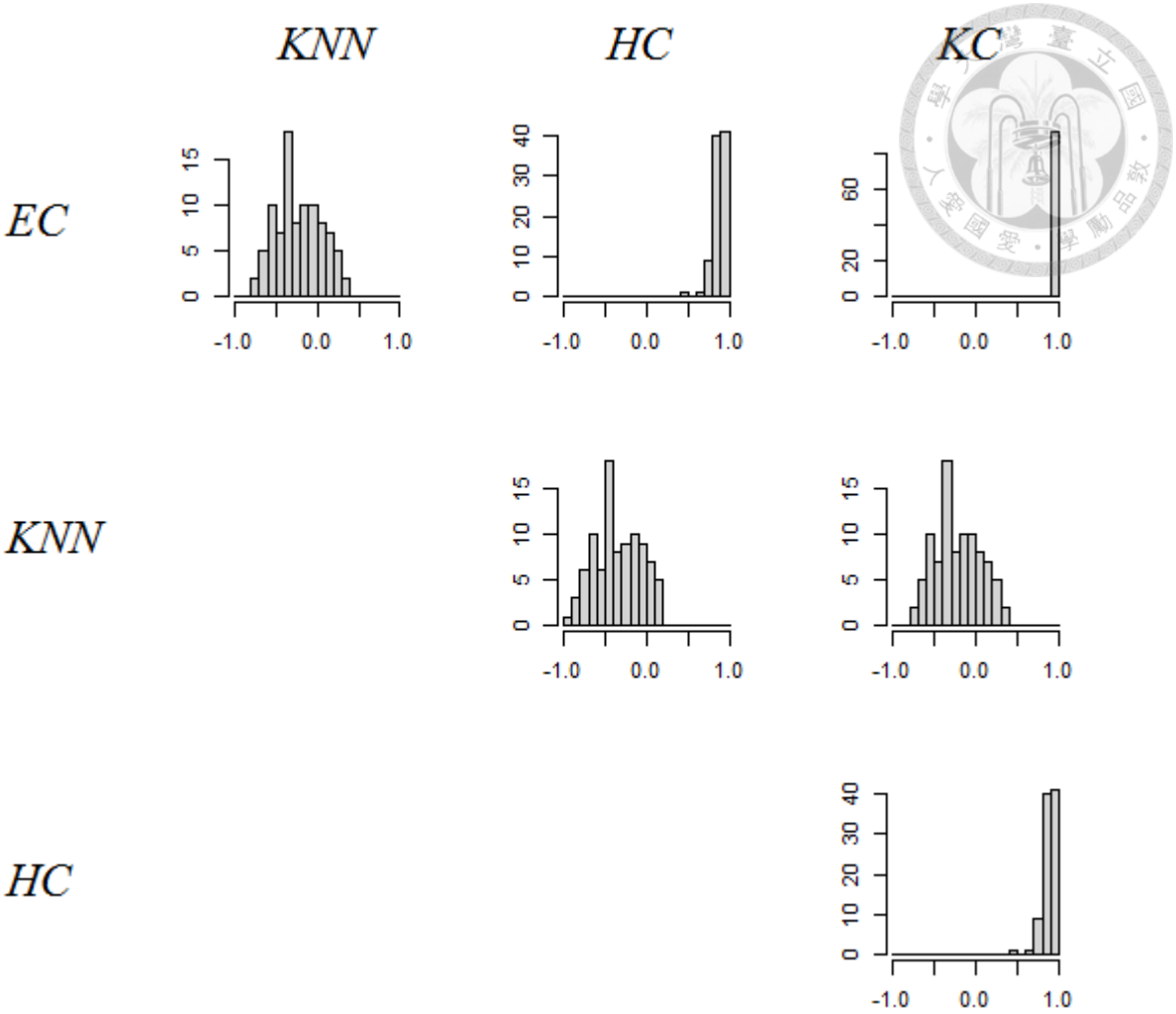

Figure 5.2 (continued) Distribution of Kendall rank correlation coefficient between pairs of centrality indices.

vary across all 92 food webs, they do center around particular values. However, there is only one exception, as correlation coefficients involving average nearest neighbor degree (*KNN*) seem to vary more than the majority of others. Thus, the relational trends between centrality indices seem to be consistent across all 92 food webs.

For each pair of centrality indices, we then calculated the average Kendall rank correlation

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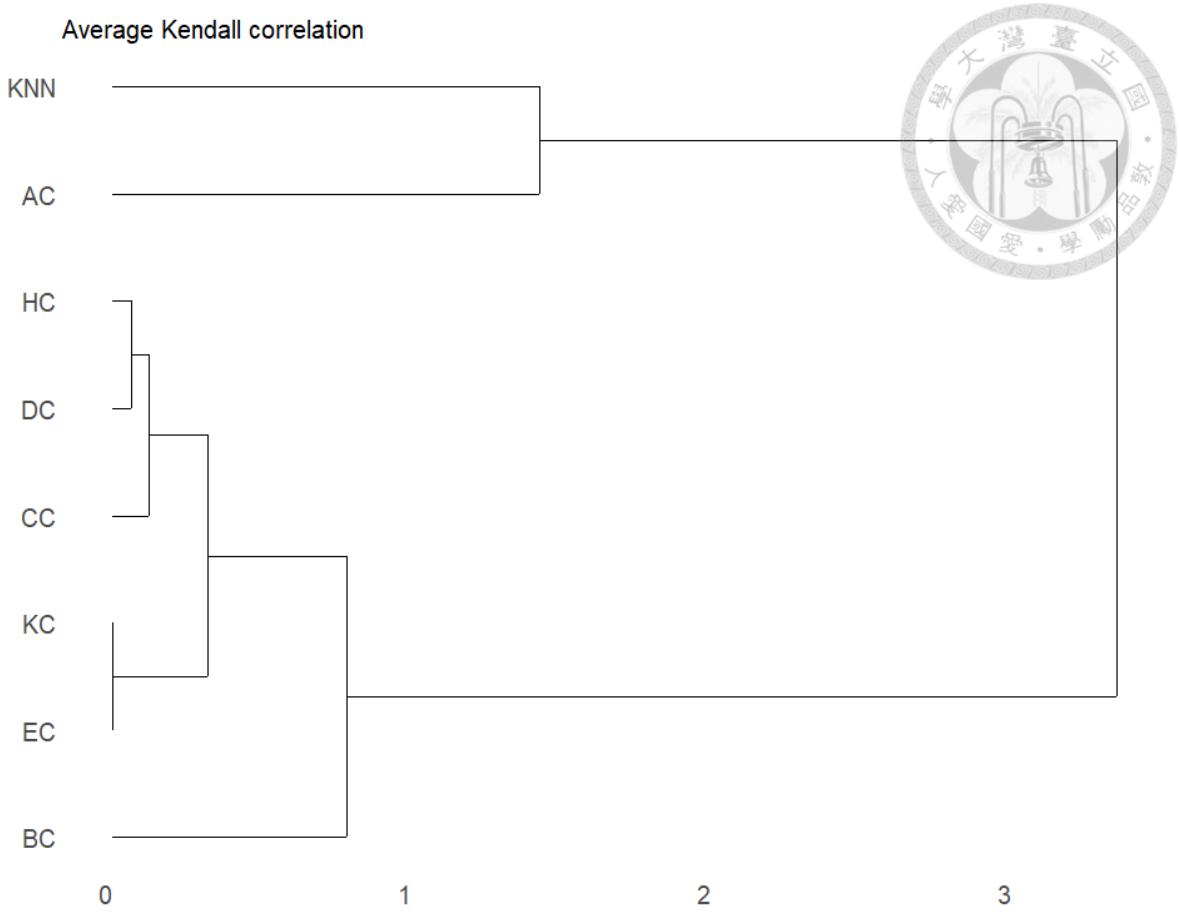

Figure 5. 3 A cluster tree showing the relationship between various centrality indices.

coefficient over those 92 food webs. This resulted in a correlation matrix, which was then subjected to hierarchical cluster analysis to identify clusters of related centrality indices (Fig. 5.3). We can observe that *DC*, *CC,* and *HC* are closely related and form a cluster; the same can be said for *EC* and *KC* which form another cluster. *BC*, *AC,* and *KNN* respectively form their own clusters. Thus, we chose one centrality index from each cluster to be included as species traits in the subsequent functional diversity analysis: specifically, we chose *DC*, *EC*, *BC,* and *AC*. We omitted *KNN* because strictly speaking it is not a centrality index; or to be more precise, *KNN* describes the neighborhood of a node, not how central a node is in a network.

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5.3.2 *Relationship between centrality-based functional diversity and network structure*

We quantified four centrality-based functional diversity indices and eight global network properties for all 92 food webs. Kendall rank correlation coefficients between functional diversity indices and global network properties are summarized in Table 5.1.

For functional richness, there are significant positive correlations with the number of species, number of trophic links, network diameter, maximum trophic position, number of clusters and network modularity. Functional richness correlates significantly and negatively with connectance and network cohesion.

Functional evenness shows a weak and positive correlation with connectance and network cohesion; however, it does not correlate significantly with the remaining six network properties.

Functional dispersion and Rao's Q show similar relational tends with network properties. They both correlate positively and significantly with the number of species, number of trophic links, network diameter, maximum trophic position, number of clusters and network

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Table 5. 1 Kendall rank correlation coefficients between centrality-based measures of functional diversity and eight global network properties after analyzing 92 food webs.

	Cric	*Ceve*	*Cdis*	*Craoq*
N	0.521 (<0.001)	-0.016 (0.821)	0.638 (<0.001)	0.610 (<0.001)
L	0.341 (<0.001)	0.058 (0.414)	0.438 (<0.001)	0.412 (<0.001)
C	-0.495 (<0.001)	0.177 (0.012)	-0.510 (<0.001)	-0.527 (<0.001)
diam	0.527 (<0.001)	-0.078 (0.337)	0.438 (<0.001)	0.480 (<0.001)
TP_max	0.231 (0.001)	0.127 (0.074)	0.254 (<0.001)	0.231 (0.001)
coh	-0.590 (<0.001)	0.264(<0.001)	-0.526 (<0.001)	-0.550 (<0.001)
clu	0.378 (<0.001)	-0.103 (0.210)	0.417 (<0.001)	0.419 (<0.001)
mod	0.309 (<0.001)	-0.113 (0.111)	0.293 (<0.001)	0.314 (<0.001)

modularity. Both functional diversity indices show significant negative correlations with connectance and network cohesion.

5.3.3 *Relationship between centrality-based functional diversity indices and other functional diversity indices*

We also examined the relationship between centrality-based functional diversity and interaction-based and trait-based functional diversity (from Chapter 4). Kendall rank correlation coefficients between various functional diversity indices are summarized in Table 5.2. We can observe that centrality-based functional richness, dispersion and Rao's *Q* correlate positively and significantly with interaction-based indices. In contrast, centrality-based functional evenness correlates negatively and marginally with interaction-based indices. As for the relationship between centrality-based and trait-based functional diversity, only centrality-based richness correlates positively and significantly with

Table 5. 2 Kendall rank correlation coefficients between centrality-based measures of functional diversity and interaction-based and trait-based measures of functional diversity after analyzing 92 food webs.

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	Cric	*Ceve*	*Cdis*	*Craoq*
IPD	0.408 (<0.001)	-0.158 (0.025)	0.388 (<0.001)	0.412 (<0.001)
IPD_w	0.327 (<0.001)	-0.149 (0.035)	0.371 (<0.001)	0.383 (<0.001)
Tric	0.358 (<0.001)	-0.097 (0.174)	0.329 (<0.001)	0.351 (<0.001)
Teve	-0.268 (<0.001)	-0.012 (0.863)	-0.358 (<0.001)	-0.324 (<0.001)
Tdis	-0.032 (0.656)	0.003 (0.962)	-0.108 (0.127)	-0.081 (0.251)
TraoQ	-0.044 (0.535)	0.005 (0.941)	-0.124 (0.079)	-0.097 (0.173)

its trait-based counterpart, whereas the others do not.

5.4 Discussions

Species interact trophically forming a food web. Their network positions in a food web reflect their trophic functions. Thus, it is intuitive to quantify the diversity of species' network positions in a food web and use this as a proxy to the functional diversity of an ecosystem. Network position can be measured using a host of centrality indices, and each focuses on a particular aspect of network position measurement (Jordán et al. 2006, Oldham et al. 2019). In this chapter, through the meta network analysis of 92 food webs, we selected four distinct centrality indices to be species network traits, and performed conventional functional diversity analysis on them. Out of those four centrality-based functional diversity indices, evenness is the only index that shows no relationship with the network structure of a food web. Functional richness, dispersion and Rao's *Q* are consistent in how they correlate with various network properties.

doi:10.6342/NTU202203106

First, large food webs, in terms of the numbers of species and trophic interactions, tend to have higher richness, dispersion and Rao's *Q*. In other words, more enormous food webs are diverse in species' network positions. This result is somehow expected as more nodes and links open up the opportunity to have various network positions in a network. Second, centrality-based functional richness, dispersion and Rao's Q reflect the structural organization of a food web. A compactly organized food web should have high connectance, shorter network diameter and lower maximum trophic position; and the result shows that those food webs tend to have lower centrality-based functional diversity. This finding suggests that species' network positions are more homogeneous in a compactly organized food web than those in a sparsely connected food web. Third, food webs that have many structural clusters and high network modularity tend to be more diverse in species' network positions. And lastly, a food web that is robust to species deletion tends to have lower centrality-based functional diversity. This suggests that species in a robust food web tend to have similar network positions, and a natural consequence of this is that the loss of one species can be compensated for by similar other species, rendering higher food web robustness.

Many of the relational trends mentioned above are also observed between interaction-based functional diversity and the network structure of a food web (Chapter 4 and Lin et al. 2022); In fact, both sets of results can be explained in a very similar fashion. Although the centrality-

doi:10.6342/NTU202203106

based functional diversity measurement correlates positively with the interaction-based one, their correlation is far from perfect. We note that both types of measures are network-related; the one developed in this chapter is based on the diversity of network positions while the other (i.e., Chapter 4) is based on the diversity in the interaction profiles of species in a food web. Furthermore, the one developed in this chapter is based on the topology of network structure, while the other incorporates ecological concepts such as competition and trophic cascade. Thus, both types of functional diversity measurements correlate through their network-based origin, but they differ in whether or not ecological concepts are incorporated. Having said this, we need to emphasize that centrality indices used in this chapter have little or no ecological origin in their development. There exist several indices that quantify the centrality of species in a food web (i.e., species importance) in a more ecology-orientated manner. For instance, direct and indirect effects of species on the whole food web (Jordán et al. 2003, Liu et al. 2010, 2020), keystone species indices (Jordán et al. 2006) and species trophic overlap indices (Yodzis and Winemiller 1999, Jordán et al. 2009, Lai et al.2015). All of these ecology-orientated centrality indices can also be incorporated into our framework of centrality-based functional diversity as the next step of future work.

Species with similar morphological traits intuitive should be similar in how they interact trophically with others; therefore, their network positions in a food web should be similar. By

doi:10.6342/NTU202203106

similar logic, an ecosystem consisting of species with very diverse morphological traits should be more diverse in species' network positions; thus, trait-based and centrality-based functional diversity indices should be positively correlated. After analyzing 92 food webs, we found that centrality-based richness is the only functional diversity measure that shows a positive and significant correlation with its trait-based counterpart. There are possible explanations for the discrepancy between our intuition and the observed results. For instance, competition between morphologically or phylogenetically similar species might drive them to evolve to have different ecological niches (Webb et al. 2002, Gerhold et al. 2015); this might result in very different patterns of trophic interaction and different network positions in a food web (Lai et al. 2021).

To summarize, in this chapter, we have quantified functional diversity from the perspective of species' network positions in a food web. Centrality-based functional diversity is positively related to the size of a food web, and is dependent on how a food web is organized. Future studies in this research field should consider other more complicated network traits. For instance, a food web can be treated as a signed and direct network, and there exist other centrality measures for signed digraphs (Liu et al. 2010, Everett and Borgatti 2014, Liu et al. 2020). Future studies should also consider network traits that incorporate ecological concepts (Jordán et al. 2006, Lai et al.2015). For instance, species have different top-down and/or

doi:10.6342/NTU202203106

bottom-up effects, as well as horizontal competition effects. Lastly, given that we are dealing with how species are distributed in a multi-dimensional trait space, multi-variate techniques such as principal component analysis and multi-dimensional scaling (Mammola et al. 2021) can be applied for analyzing centrality-based functional diversity.

doi:10.6342/NTU202203106

Chapter 6 Functional diversity from a network perspective III: a trophic role-based functional diversity index

6.1 Introduction

In a food web, two species that have the same connection pattern (i.e., share the same predator and prey species) bound to have the same interaction profiles (Chapter 4) and occupy the same network positions (Chapter 5). This sort of definition has one major shortcoming. Imagine, two basal species that don't have any consumer species in common will have different interaction profiles and network positions, but intuitively their ecological roles are the same; namely, they are basal species or producers of an ecosystem. Trophic role of a species can be considered as how a species deals with the transfer of organics maters and/or energy in a food web (Pimm 1982, Yodzis and Winemiller 1999). Species at the bottom of a food web are often producers or basal species that are the source of energy or organics matters. At the other end of the food web (i.e., the top), there are top predators acting as sink nodes as all energy or organic matters ultimately end up with them (we omit decomposers for simplicity). In between the top and the bottom layers of a food web, there is a bulk of consumer species with various (omnivorous) feeding patterns as they all perform the role of passing on energy or organic matters from one species to another via different pathways.

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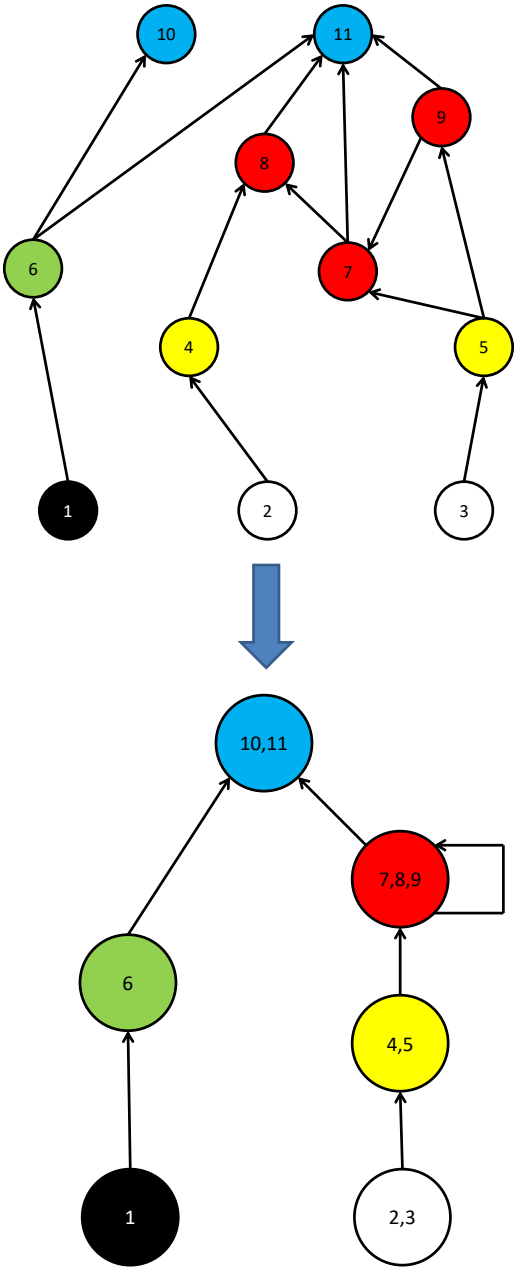

Figure 6. 1 Upper figure: a food web with species coloration that fulfills strict REGE definition. Lower figure: the simplified food web after species aggregation into the same color types.

To reveal the role of species in an otherwise complicated network of trophic interactions, Luczkovich et al. (2003) applied the concept of regular equivalence to several food webs and elucidated their fundamental structure. Regular equivalence (REGE for short) has its root in

doi:10.6342/NTU202203106

social network analysis (White and Reitz 1983, Borgatti and Everett 1989); it states that two nodes are regularly equivalent if they have links to the same types of nodes, as well as if they receive links from the same types of nodes. Note that REGE does not require these two nodes to have precisely the same connecting neighbors. Taken and derived from Luczkovich et al. (2003), Fig. 6.1 and Fig. 6.2 show a simple demonstration of REGE concept. The food web in Fig. 6.1 fulfills strict REGE definition; this is because species of the same type (e.g., color in this case) are connected to and from the same types of species. As a consequence, the food web can be reduced to a simpler one (i.e., the lower sub-figure of Fig. 6.1). Fig. 6.2 is a food web that falls short of strict REGE definition; this is because even though species 6, 7, 8, and 9 belong to the "red" group, species 6 has different connection pattern to that for species 7, 8 and 9. Although this food web can be reduced to a simpler one by grouping species of the same color together, links between the aggregated groups may only hold true for some species (dotted lines in the lower sub-figure of Fig. 6.2); for example, the link between the "black" group and the "red" group is only applicable to species 6, but not to species 7, 8 and 9. Due to the complexity of a food web (or a network in general), it is rarely we have species that are perfectly equivalent under REGE. In a more practical sense, the REGE analysis calculates the degree of regular equivalence between species pairs, which can be considered as similarity scores ranging from 0 to 1. Subtracting each similarity score from 1 thus produces a score that measures the dissimilarity in the role of two species.

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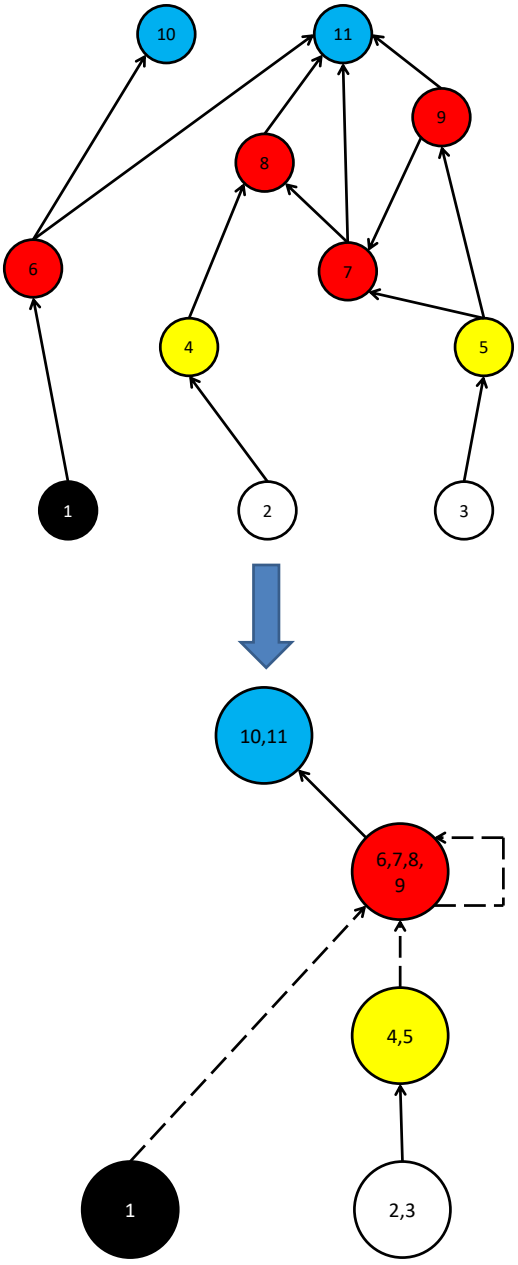

Figure 6. 2 Upper figure: a food web with species coloration that does not fulfills strict REGE definition. Lower figure: the simplified food web after species aggregation into the same color types.

Pooling all dissimilarity scores together gives us a dissimilarity matrix, which can then be used in a similar fashion as those in Chapter 4 to calculate the functional diversity of an ecosystem.

doi:10.6342/NTU202203106

This chapter extends the future research idea from Chapter 4 and explores the potential of REGE concepts in quantifying functional diversity from a network perspective. For our convenience, we call this type of network-based concept of functional diversity as trophic role or REGE-based functional diversity. Specifically, three measures of functional diversity are proposed in this chapter. The first is to calculate the average dissimilarity between the roles of a species pair in a food web. The second is to use REGE to partition species into an optimal number of trophic role groups, and this number can be treated as a proxy for network-based functional diversity. The third is an extension of the second measure where we also take into account the number of species, total abundance, or biomass for each trophic role group and calculate Shannon's diversity index as a proxy to network-based functional diversity.

This chapter is organized as follows. First, in the material and method section, we present the REGE algorithm and how this can be modified for food webs; this is then followed by the formulation of three REGE-based functional diversity indices. Second, in the result section, we first present the distributions of these REGE-based functional diversity indices after analyzing 92 food webs; and then we compare these results with that obtained from a random food web model. Also, in the result section, this chapter follows the same analysis as those in Chapters 4 and 5: we present the relationship between our new functional diversity indices and several global network properties, as well as their relationship with other network-based and trait-based

doi:10.6342/NTU202203106

functional diversity indices. Lastly, this chapter finishes with a general discussion.

6.2 Material and method

6.2.1 *Food web data analyzed in this study*

Again, we analyzed 92 food webs in this study. Please refer to Chapter 2 for basic information on these food webs.

6.2.2 *Measuring trophic role similarity between species*

Borrowed from social network analysis (White and Reitz 1983, Borgatti and Everett 1989), we present the REGE algorithm and show how the extent of regular equivalence between two nodes can be quantified for a directed network. REGE is an iterative algorithm, and let $\mathbf{R}^t$ be an $N*N$ matrix where the ij^{th} element R^t_{ij} represents the extent of regular equivalence between node i and node j at iteration t. The algorithm proceeds as follows:

1. At iteration 0, set $R^0_{ij}=1$ for all ijs, meaning all node pairs are perfectly equivalent.

2. At iteration $t+1$, R^{t+1}_{ij} is determined by the following steps:

    a) Considering outgoing links only, for each (outgoing) neighbor k of node i, we find which (outgoing) neighbor m of node j is most equivalent to k; in other words, given k, we find m by maximizing the value of R^t_{km}. We then define a quantity $X_{i,k,j}$, which denotes how well the outgoing link from node i to node k can be matched by an outgoing link from node j, and this quantity takes the value of R^t_{km}. Similarly, considering outgoing links only,

doi:10.6342/NTU202203106

for each (outgoing) neighbor *m* of node *j*, we find which (outgoing) neighbor *k* of node *i* is most equivalent to *m* by maximizing the value of R^t_{mk}. We also define a quantity $X_{j,m,i}$ which is equal to R^t_{mk}.

b) Considering incoming links only, for each (incoming) neighbor *h* of node *i*, we find which (incoming) neighbor *n* of node *j* is most equivalent to *h* by maximizing the value of R^t_{hn}. We also define a quantity $Y_{i,h,j}$, which denotes how well the incoming link from node *h* to node *i* can be matched by an incoming link to node *j*, and this quantity takes the value of R^t_{hn}. Similarly, considering incoming links only, for each (incoming) neighbor *n* of node *j*, we find which (incoming) neighbor *h* of node *i* is most equivalent to *n* by maximizing the value of R^t_{nh}; and we also define a quantity $Y_{j,n,i}$ which takes the value of R^t_{nh}.

3. The extent of regular equivalence between node *i* and node *j* at iteration *t*+1 is:

$$R_{ij}^{t+1} = \frac{\sum_k X_{i,k,j} + \sum_m X_{j,m,i} + \sum_h Y_{i,h,j} + \sum_n Y_{j,n,i}}{MAX(\sum_k X_{i,k,j} + \sum_m X_{j,m,i} + \sum_h Y_{i,h,j} + \sum_n Y_{j,n,i})}, \quad (6.1)$$

where the denominator is the maximum possible value of the numerator if node *i* and node *j* are perfectly equivalent; in other words, the denominator is the total number of links connected to and from node *i* and node *j*. We then repeat steps 2 and 3 until all REGE values stabilize, and define **R'** to be the final REGE matrix.

Luczkovich et al. (2003) extend the original REGE concept for food webs by incorporating

doi:10.6342/NTU202203106

species' dietary information. However, their method is slightly different from the original REGE concept. Specifically, when they compute the REGE similarity between two species, comparison is only made from the perspective of one of the two species; but in the original REGE algorithm, comparison is made from the perspective of both species. Thus, in this chapter, we combine both the original approach and that of Luczkovich et al. (2003). Our modified approach is as follows. First, we need to derive a dietary matrix **Z** from the original food web data. The ij^{th} element of **Z**, namely Z_{ij}, is the proportion of species j's diet that comes from species i. The REGE algorithm follows almost the same procedure as above, and for clarity, we re-iterate it with food web-specific modification as follows. Again, let $\mathbf{R}^t$ be the REGE matrix at iteration t. The algorithm proceeds as follows:

1. At iteration 0, set $R^0_{ij}=1$ for all ijs, meaning all species pairs are perfectly equivalent.

2. At iteration $t+1$, R^{t+1}_{ij} is determined by the following steps:

    a) Considering outgoing trophic links only, for each predator k of species i, we find which predator m of species j is most equivalent to k. Here equivalence has two components; one is based on the REGE value R^t_{km} while the other is based on the dietary values Z_{ik} and Z_{jm}; in other words, we find predator species m that not only has to be regularly as equivalent as possible to predator species k, but species m must also consume species j in a proportion similar to the way predator k consumes species i. Thus, all this amounts to finding a predator species m by maximizing the product of R^t_{km} and $\text{Min}(Z_{ik}, Z_{jm})/\text{Max}(Z_{ik}, Z_{jm})$, and

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then we equate $X_{i,k,j}$ to the value of this product. Similarly, considering outgoing trophic links only, for each predator m of species j, we find which predator k of species i is most equivalent to m by maximizing the product of R^t_{mk} and $\text{Min}(Z_{jm}, Z_{ik})/\text{Max}(Z_{jm}, Z_{ik})$; and we define a quantity $X_{j,m,i}$ which is equal to the value of this product.

b) Considering incoming trophic links only, for each prey h of species i, we find which prey n of species j is most equivalent to h by maximizing the product of R^t_{hn} and $\text{Min}(Z_{hi}, Z_{nj})/\text{Max}(Z_{hi}, Z_{nj})$; and we define a quantity $Y_{i,h,j}$ which is equal to the value of this product. In other words, we find a prey species n that is regularly as equivalent as possible to species h, and species j must consume prey species n in a proportion similar to species i consumes prey species h. Similarly, considering incoming trophic links only, for each prey n of species j, we find which prey species h of species i is most equivalent to n by maximizing the product of R^t_{nh} and $\text{Min}(Z_{nj}, Z_{hi})/\text{Max}(Z_{nj}, Z_{hi})$; and we also define a quantity $Y_{j,n,i}$ which takes the value of this product.

3. The extent of regular equivalence between species i and species j at iteration t+1 is still given by Eq. (6.1). Again, we repeat steps 2 and 3 until all REGE values stabilize, and define **R'** to be the final REGE matrix.

doi:10.6342/NTU202203106

6.2.3 *Three REGE-based functional diversity indices*

The REGE matrix **R'** is a similarity matrix, it can be converted to a dissimilarity matrix by subtracting each element of **R'** from 1, and this results in a dissimilarity matrix **D:**

$$\mathbf{D} = \mathbf{J} - \mathbf{R}', \quad (6.2)$$

where **J** is a matrix of ones that has the same dimension as **R'**. Below we propose three REGE-based functional diversity indices.

a) Average dissimilarity in species' trophic roles (*TRD*)

Here, from matrix **D**, calculating the average value of its upper (or lower) triangle gives the average dissimilarity in species' trophic roles:

$$TRD = \frac{\sum_{i=1}^{N}\sum_{j>i}^{N} D_{ij}}{(N^2-N)/2}. \quad (6.3)$$

A large *TRD* value indicates that species differ greatly in their trophic roles, whereas a small *TRD* value shows homogeneity in species' trophic roles.

b) Number of trophic role groups (*TRN*)

One can carry out hierarchical cluster analysis by using REGE matrix **R'** and partition species into different clusters or trophic role groups. Ideally, we would expect species pairs in the same trophic role groups to have large REGE values (i.e., they have similar trophic roles), whereas those pairs in different groups should have small REGE values (i.e., they have different trophic

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roles). The method of Luczkovich et al. (2003) finds the optimal number of trophic role groups in a food web as follows. First, given a partition of species into M trophic role groups, we define a binary dummy variable W_{ij} to indicate whether species pair ij are in the same groups or not (i.e., 1 for "yes" and 0 for "no"). Second, associated with each species pair ij is the REGE value R'_{ij} measuring the extent of regular equivalence between species i and species j. Third, we then carry out a regression analysis using W_{ij} as the explanatory variable and R'_{ij} as the dependent variable and then calculate the R-squared value. The R-squared value from a regression analysis indicates the percentage of the variation in R'_{ij} that can be explained by W_{ij}; thus, the optimal partition of species should correspond to the largest R-squared value, and TRN is the number of trophic role groups resulted from this analysis.

c) A Shannon diversity-based index (TRS)

After finding the optimal number of trophic role groups (i.e., TRN), we can employ the Shannon diversity index as a measure of network-based functional diversity:

$$TRS = \frac{-\sum_{i=1}^{TRN} p_i \ln(p_i)}{\ln(TRN)}, \qquad (6.4)$$

where TRN is the optimal number of trophic role groups and p_i is the proportion of certain quantity (e.g., total abundance, total biomass or total number of species) in the i^{th} group. In this study, we only have the total number of species in a food web available to us; thus, p_i is the proportion of a total number of species belonging to the i^{th} trophic role group:

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$$p_i = \frac{n_i}{N}, \quad (6.5)$$

where N is the total number of species in the food web, and n_i is the number of species in the i^{th} trophic role group. *TRS* in essence measures how evenly species are being distributed across different trophic role groups.

6.2.4 *Global network properties*

Again, following the analysis from Chapter 4, we quantified eight global network properties and assessed their relationship with our REGE-based functional diversity indices. Details of those global network properties are in section 4.2.3, and briefly they are: number of species (*N*), number of trophic links (*L*), connectance (*C*), network diameter (*diam*), maximum trophic position (TP_{max}), network cohesion (*coh*), number of clusters (*clu*) and network modularity (*mod*).

6.3 Results

We first present the result for one demonstrative food web, namely the Great Barrier Reef ecosystem (GBR) in Australia (i.e., the food web named "FW15" in Chapter 2), and then we present the result from our meta-analysis on all 92 food webs.

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6.3.1 *A demonstrative result using the GBR food web*

We subjected the GBR food web to REGE analysis and constructed a cluster tree showing the relationship between species (Fig. 6.3). We partitioned species into different numbers of trophic role groups, from 2 up to 16 groups; and for each partitioning, we carried out the regression analysis as mentioned in the material and method section to calculate the corresponding *R*-squared value. Fig. 6.4 shows the relationship between the number of trophic role groups and their respective *R*-squared values. We can observe that, for GBR food web, the largest *R*-square value occurs at nine trophic role groups (Fig. 6.4), and thus we partitioned species into nine groups according to this optimal partition (Fig. 6.3). We organized the GBR food web with species in the same trophic role grouped together in order to reveal the fundamental trophic structure of the GBR food web (Fig. 6.5). At the bottom of the GBR food web, there are Benthau, Decomp and Phyto forming the basal group (light green). At the top (or near the top) of the food web there are three groups: one for Turtle (purple) which mainly consumes the basal group (light green) and the lower-level group (green), one for Lgroup (brown) which mainly consumes lower (green) and mid-level groups (orange), and one for Lshark, Seabird and Scom (red) which almost consume everything

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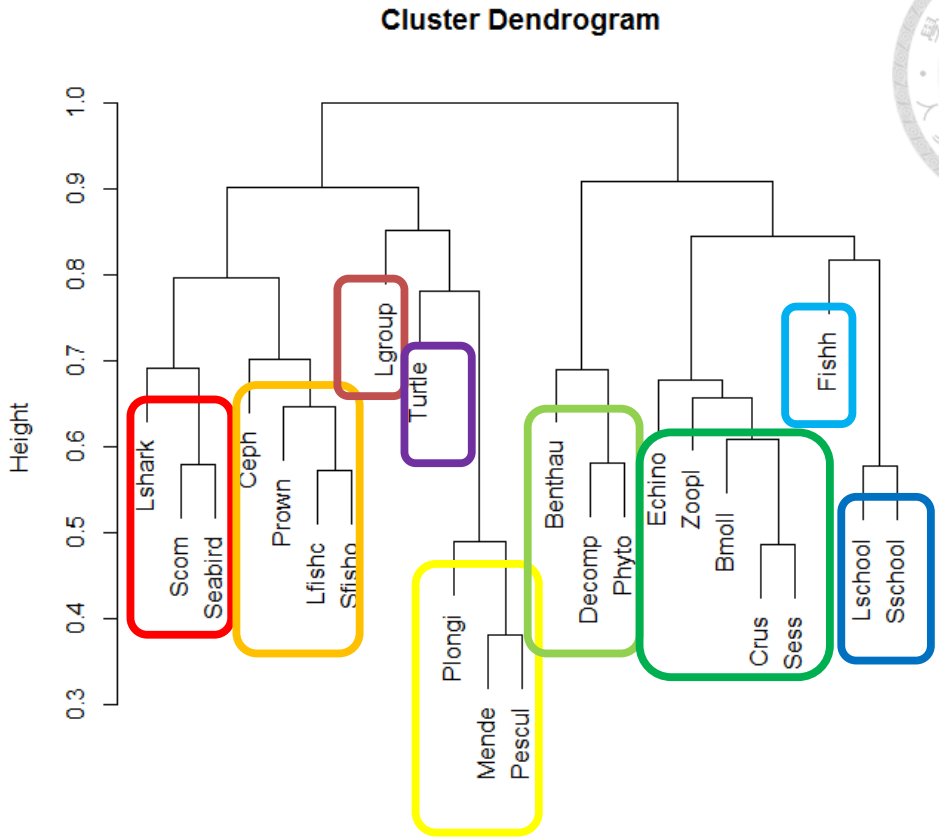

Keys:

Benthau: Benthic autotrophs
Bmoll: Benthic molluscs/worms
Ceph: Cephalopods
Crus: Crustaceans
Decomp: Decomposer/microfauna
Echino: Echinoderms
Fishh: Fish herbivore
Lfishc: Large fish carnivore
Lgroup: Large groupers
Lschool: Large schooling fish
Lshark: Large sharks/rays
Mende: M. endeavouri
Pescul: P. esculentus
Phyto: Phytoplankton
Plongi: P. longistylus
Prown: Other prawns
Scom: Scombrids/jacks
Seabird: Sea birds
Sess: Sessile animals
Sfisho: Small fish omnivore
Sschool: Small schooling fish
Turtle: Turtle
Zoopl: Zooplankton

Figure 6. 3 Cluster tree of GBR food web after carrying out REGE analysis. Color boxes represent the optimal partition of species into different trophic role groups.

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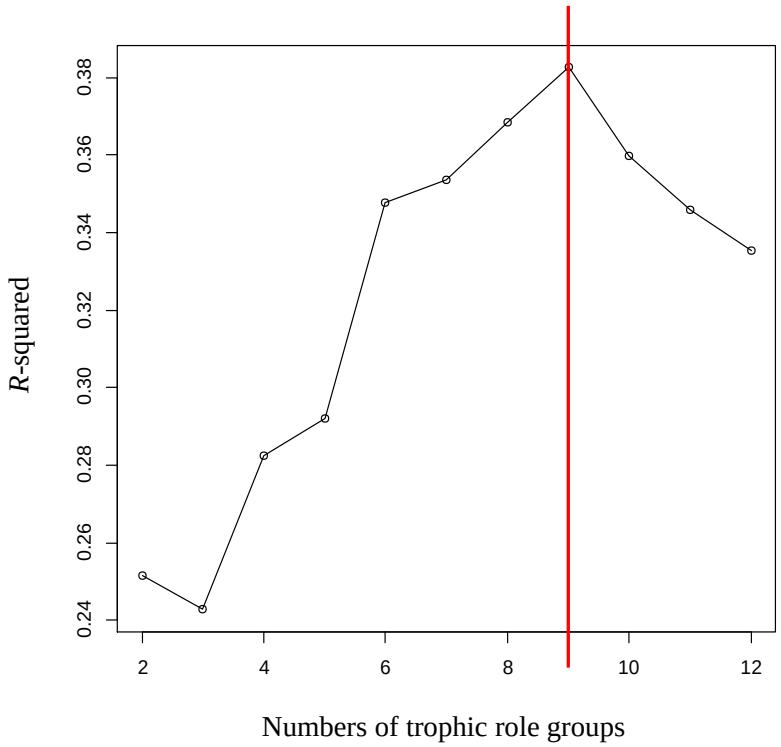

Figure 6. 4 Relationship between R-squared value and the number of trophic role groups for the GBR food web. Red line indicates the optimal number of groups.

except for the basal group and the turtle. The average REGE dissimilarity of the GBR food web (*TRD*) is 0.804, and the number of trophic role groups (*TRN*) is 9, with the evenness of species distribution in different trophic role groups (*TRS*) equal to 0.935.

6.3.2 *Distribution of TRD, TRN and TRS for all 92 food webs*

Fig.6.6a shows the distribution of *TRD* for all 92 food webs analyzed in this study. The distribution has a mean *TRD* of 0.817 and ranges from a minimum of 0.692 to a maximum of 0.942. Fig. 6.6b shows the distribution of *TRN* for the same 92 food webs and it is skewed to

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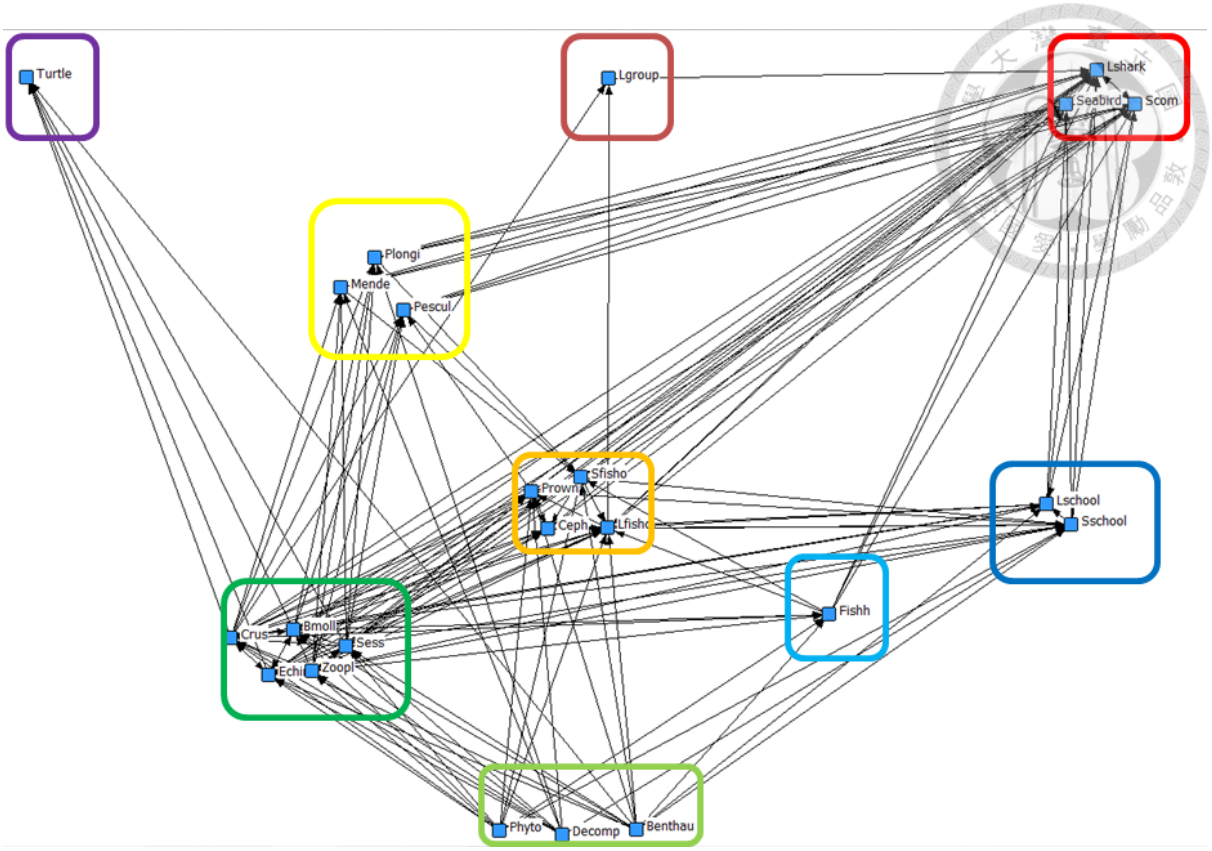

Keys:

Benthau: Benthic autotrophs	Lgroup: Large groupers	Scom: Scombrids/jacks
Bmoll: Benthic molluscs/worms	Lschool: Large schooling fish	Seabird: Sea birds
Ceph: Cephalopods	Lshark: Large sharks/rays	Sess: Sessile animals
Crus: Crustaceans	Mende: M. endeavouri	Sfisho: Small fish omnivore
Decomp: Decomposer/microfauna	Pescul: P. esculentus	Sschool: Small schooling fish
Echino: Echinoderms	Phyto: Phytoplankton	Turtle: Turtle
Fishh: Fish herbivore	Plongi: P. longistylus	Zoopl: Zooplankton
Lfishc: Large fish carnivore	Prown: Other prawns	

Figure 6. 5 A simplified representation of the GBR food web after aggregating species into various trophic role groups (indicated by different colors).

the left. This distribution has a median of 5 trophic role groups, and the minimum and the maximum are 3 and 14, respectively. Fig. 6.6c shows the distribution of *TRS* and it is slightly skewed to the right. The distribution has a median of 0.886, with the minimum and the maximum equal to 0.602 and 0.992, respectively.

doi:10.6342/NTU202203106

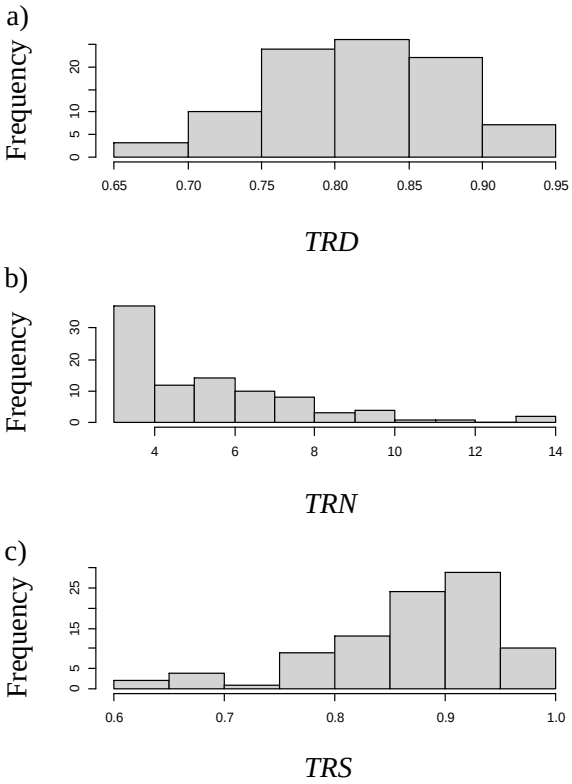

Figure 6. 6 Frequency distributions for *TRD*, *TRN* and *TRS* after analyzing 92 food webs.

6.3.3 *Comparison with a random food web model*

For each food web, we constructed random food webs by using the cascade model (Cohen et al. 1990, 1993) with the observed number of species and the observed connectance value. We then calculated *TRD*, *TRN* and *TRS* for those random food webs and compared them with the corresponding observed values. Fig. 6.7a shows the distribution of *TRD* after simulating the cascade model 100 times and the position of the observed *TRD* for all 92 food webs. We can see that the observed *TRD* is greater than the median of the simulated *TRD*s for all food webs; furthermore, the observed *TRD*s are all greater than the upper bounds of their respective 95%

doi:10.6342/NTU202203106

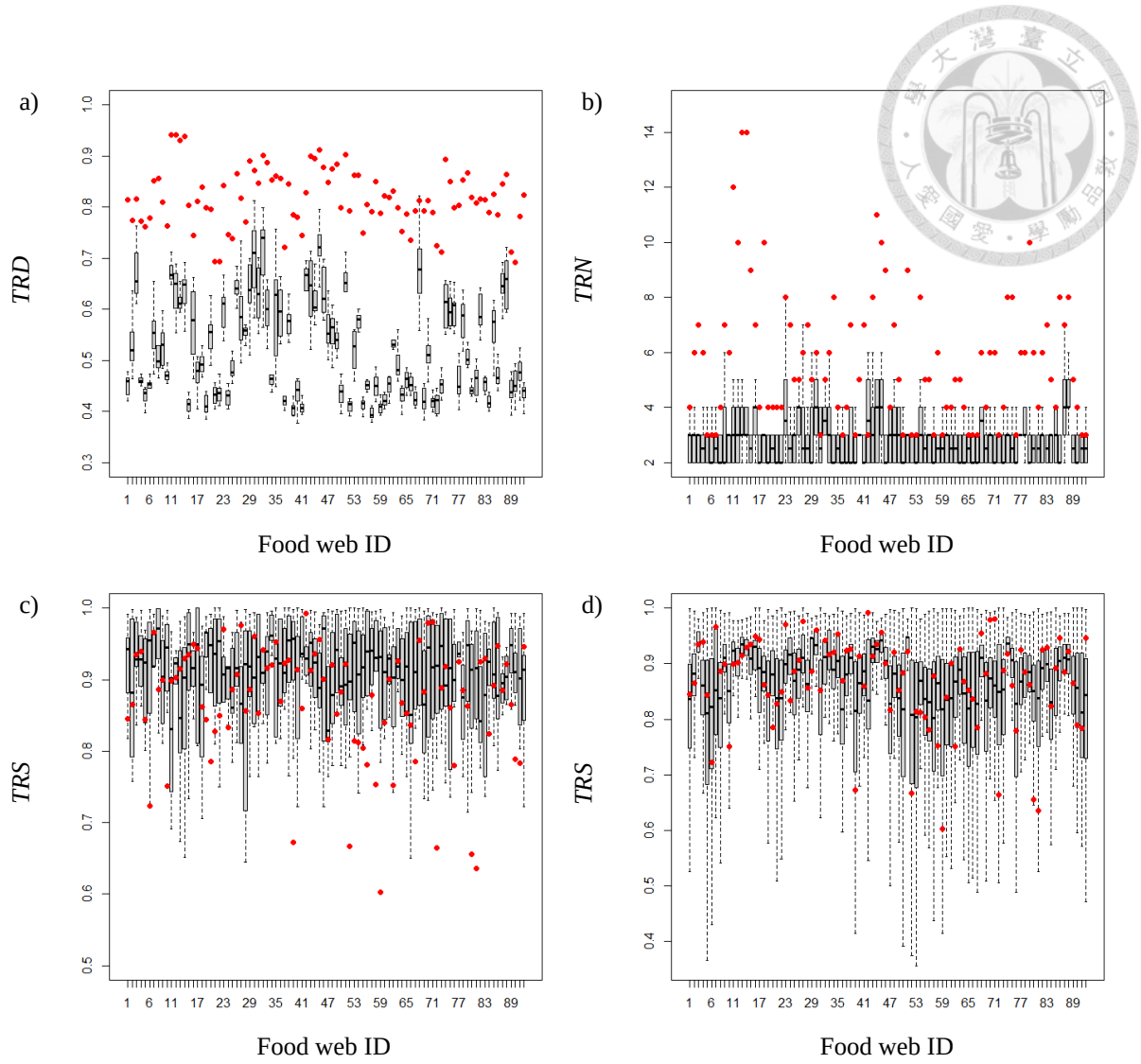

Figure 6. 7 Distributions for a) *TRD*, b) *TRN* and c) *TRS* after 100 simulations of the cascade model for each food web. d) is the distribution for *TRS* after 100 simulations of random species partition for each food web. Red dots are observed *TRD*, *TRN* and *TRS*.

confidence intervals. Fig. 6.7b shows the result for *TRN* where 88 food webs have the observed value greater than the median of the simulated ones; moreover, 73 food webs have their observed *TRN* greater than the upper bound of the 95% confidence interval. Fig. 6.7c shows the result for *TRS*, where 62 food webs have the observed value being greater than the median

doi:10.6342/NTU202203106

of the simulated values, and 30 food webs have a lower observed value than the median of the simulated value. In contrast to *TRD* and *TRN*, the *TRS* for 77 food webs falls within the 95% confidence interval and is indistinguishable from the simulated values.

Although the result for *TRS* indicates the observed value is well-predicted by the cascade model for most food webs, it remains to be seen whether the observed *TRS* of a food web is any different from the random assignment of species into different trophic role groups. To this end, we constructed a species partition model where species have an equal probability of being assigned to any trophic role group; in other words, we randomly assigned *N* species to *TRN* trophic role groups, and then calculated *TRS* value for this partition. We construed such a random partition model 100 times for each food web. Fig. 6.7d shows the distributions of simulated *TRS* for 92 food webs as well as the observed *TRS* values; and we can observe that most food webs have their observed *TRS* indistinguishable from the simulated values. In fact, the observed *TRS* for 87 food webs falls within the 95% confidence interval derived from the random partition model. This suggests that for almost all food webs analyzed in this study, the evenness of species distribution among trophic role groups is no different to a random partition model.

doi:10.6342/NTU202203106

Table 6. 1 Kendall rank correlation coefficients between REGE-based functional diversity indices and various global network properties after analyzing 92 food webs.

	TRD	*TRN*	*TRS*
N	-0.084 (0.244)	0.050 (0.514)	-0.337 (<0.001)
L	-0.243 (<0.001)	-0.110 (0.145)	-0.391 (<0.001)
C	-0.465 (<0.001)	-0.422 (<0.001)	-0.088 (0.217)
diam	0.433 (<0.001)	0.401 (<0.001)	0.065 (0.423)
TP_max	-0.162 (0.023)	-0.021 (0.777)	-0.213 (0.003)
coh	-0.238 (<0.001)	-0.341 (<0.001)	0.144 (0.044)
clu	0.078 (0.345)	0.325 (<0.001)	-0.043 (0.606)
mod	0.522 (<0.001)	0.325 (<0.001)	0.233 (0.001)

6.3.4 *Relationship with global network properties*

We calculated the Kendall rank correlation coefficients between the three REGE-based functional diversity indices and eight global network properties (Table 6.1). *TRD* and *TRN* show similar correlation patterns with global network properties. First, *TRD* and *TRN* seem to be independent of system size or the number of species (*N*). Second, they correlate negatively and significantly with connectance (*C*) and network cohesion (*coh*). Third, they correlate positively and significantly with network diameter (*diam*) and modularity (*mod*). Fourth, although both *TRD* and *TRN* show a negative correlation with the number of trophic links (*L*) and the maximum trophic position (*TP_max*), only correlations involving *TRD* are significant. Lastly, correlation coefficients between *TRD*, *TRN*, and the number of clusters (*clu*) are all positive, but only the one involving *TRN* is significant. In contrast to *TRD* and *TRN*, *TRS* shows rather different correlation patterns with global network properties. *TRS* shows a negative and significant correlation with the numbers of species (*N*) and trophic links (*L*) and

doi:10.6342/NTU202203106

Table 6. 2 Kendall rank correlation coefficients between REGE-based functional diversity indices and other network-based and trait-based indices after analyzing 92 food webs.

	TRD	*TRN*	*TRS*
Tric	0.208 (0.003)	0.418 (<0.001)	0.055 (0.442)
Teve	0.264 (<0.001)	0.191 (0.011)	0.402 (<0.001)
Tdis	0.400 (<0.001)	0.316 (<0.001)	0.327 (<0.001)
TraoQ	0.385 (<0.001)	0.321 (<0.001)	0.339 (<0.001)
IPD	0.566 (<0.001)	0.431 (<0.001)	0.167 (0.018)
IPD_w	0.460 (<0.001)	0.286 (<0.001)	0.018 (0.800)
Cric	0.179 (0.012)	0.302 (<0.001)	-0.149 (0.035)
Ceve	-0.006 (0.933)	-0.138 (0.067)	0.018 (0.798)
Cdis	0.164 (0.020)	0.237 (0.002)	-0.182 (0.010)
Craoq	0.172 (0.015)	0.270 (<0.001)	-0.167 (0.019)

maximum trophic position (*TP_max*); while it shows a weak and positive correlation with network cohesion (*coh*) and modularity (*mod*).

6.3.5 *Relationship with other functional diversity indices*

We also calculated the Kendall rank correlation coefficients between REGE-based indices and other functional diversity indices (Table 6.2). Again, *TRD* and *TRN* show similar correlation patterns as they have a significant and positive correlation with most other functional diversity indices; in particular, they show the strongest correlation with *IPD* (i.e., Kendall's τ=0.566 and 0.431) and no significant correlation with *Ceve*. *TRS* only shows a significant and positive correlation with *Teve*, *Tdis,* and *TraoQ*, whereas it either has a weak or non-significant correlation with other remaining functional diversity indices.

doi:10.6342/NTU202203106

6.4 Discussion

This chapter presents three network-based functional diversity indices using the information on the trophic role of species in a food web. First, *TRD* measures the average dissimilarity in the trophic roles of two species. Second, *TRN* is the number of trophic role groups that maximizes the between-group dissimilarity while at the same time minimizing the within-group dissimilarity. Third, *TRS* quantifies the evenness of species partition into trophic role groups. Like interaction-based (Chapter 4) and centrality-based (Chapter 5) functional diversity indices, *TRD* and *TRN* correlate with a certain network structure of a food web. Sparsely connected food webs and those with large diameter, high network modularity, and low robustness property, tend to have higher *TRD* and *TRN*. Like *Ceve*, which is also an evenness-related measure, *TRS* does not correlate with network structure of a food web in a manner that can be explained with a clear mechanism. One peculiar result from our analysis is the relationship between maximum trophic position (i.e., *TP_max*) and REGE-based functional diversity. Intuitively, a food web with many trophic levels should have a larger *TP_max* and also should have diverse trophic roles; therefore *TP_max* in theory should correlate positively with *TRD* or *TRN*. However, such relationships were not observed from our analysis. We speculate that in many food webs there are cross-level trophic links connecting various trophic levels, and this might reduce the dissimilarity between species' trophic roles. This might then obscure the relationship between *TP_max* and REGE-based functional diversity.

doi:10.6342/NTU202203106

We also compared the observed REGE-based functional diversity of real food webs with those derived from random food webs. Our results show that real food webs seem to have higher average trophic role dissimilarity and more trophic role groups than random food webs have. Rather surprisingly, it appears to be no difference between real and random food webs in terms of how evenly species are being partitioned into trophic role groups. In other words, trophic role groups in real food webs are more or less equal in size, or there is a lack of dominant trophic role groups in real food webs. This phenomenon can be explained from the perspective of food web robustness (Dunne and Williams 2009) and species redundancy (Lai et al. 2012) as follows. If a food web has trophic role groups that vary disproportionately in their group sizes such that some groups consist of only one species, then the loss of one species from those small groups will not be compensated for and this results in the collapse of the food web (due to the lack of certain trophic roles pertained to these extinct groups). In contrast, in a food web with equally abundant trophic role groups, the loss of one species can be easily compensated for by another species that performs the same trophic role, and this ensures the proper functioning and integrity of the food web.

Finally, we conclude with potential research directions. First, REGE is a very general concept that defines the trophic role of species, and this can be problematic. For instance, two top predators, one with many prey species whereas the other only has one, may still be in the

doi:10.6342/NTU202203106

trophic role group according to REGE. But clearly, the first predator bounds to exert wider competitive effects and top-down control on others than the second predator does. In other words, although these two predators perform the same trophic role, but their effects on other species are clearly different. How to incorporate information on species interaction (Lin and Liu 2021, Lin et al. 2022) into REGE-based functional diversity measurement remains as an open question. Second, many species of these 92 food webs analyzed in this study are trophy species (i.e., aggregation of several species). Aggregating species information and the resolution of food webs (Martinez 1991, Jordán et al. 2018) are two issues that need to be examined. These might not be serious issues for *TRD* and *TRS* as they both are not correlated with the number of species, but for *TRS* they can be problematic. Third, we note that there are other methods for measuring trophic role similarity/dissimilarity between species. For instance, the additive trophic similarity proposed by Yodzis and Winemiller (1999) measures the degree of overlap between the preys and the predators of two species. Future research on trophic role-based functional diversity measurement should consider such an approach.

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Chapter 7 Conclusion

In this thesis, we have explored two topics in food web research. The first topic is the development of a new measure for species uniqueness. This approach requires one to quantify the interaction structure of a food web, which records the average effect of one species on another up to a predefined number of steps; then, one computes a distance matrix by comparing row pairs of the interaction structure matrix, and the row sums of this distance matrix are then the uniqueness values of species in a food web. Such an approach produces results almost identical to that proposed by Lai et al. (2015) while omitting the need to predefine the cut-off effect threshold and reducing a significant amount of computation time. However, our approach is not without its shortcomings. Like the earlier approaches of Jordán et al. (2009) and Lai et al. (2015), our approach also needs to predefine the number of steps up to which indirect effects are to be quantified in order to construct the interaction structure of a food web. A future study should consider ways to avoid the need for this parameter, but how this can be achieved is not clear to us. One can consider the case where effects diminish with path length, but this still requires an attenuation parameter. Having said this, our approach outlines a basic framework for the future development for species uniqueness in food webs. For example, one can use network geodesic matrix instead of interaction structure matrix for the relationship between species, and other measures such as cosine similarity can be used to compute the distance

doi:10.6342/NTU202203106

matrix. A systematic approach to explore all those possibilities is essential to compare results derived from them. Furthermore, since species interact trophically in a food web, effects between species can be positive and negative. Future work on species uniqueness should consider how to incorporate signed effects.

The second topic of this thesis is the development of network-based functional diversity of an ecosystem. This thesis proposes three different types of measurement. The first is based on the interaction structure of a food web, where functional diversity is the average dissimilarity of two interaction profiles of a food web. The second is centrality-based. A set of centrality indices can be quantified for each species, and functional diversity is measured from properties of species distribution in this multi-dimensional centrality trait space. Specifically, these include the richness, evenness, and dispersion of this trait space, as well as Rao's Q, which measures the average dissimilarity in species' centrality traits. The third is trophic-role based. This approach proposes three indices: one quantifying the average dissimilarity in species' trophic role, one for the number of trophic role groups in a food web, and one measuring the evenness of species partition into different trophic role groups. Our analysis has shown that network-based functional diversity indices are correlated with certain structural properties of food webs. In general, sparsely connected food webs, those with long diameter, as well as food webs with lows robustness property and high network modularity, tend to have higher network-based

doi:10.6342/NTU202203106

functional diversity. We note food web datasets often have resolution issues, and this is can be a serious problem with EwE-based food webs as species at lower trophic levels are aggregated into a small number of large tropho groups. Our work in this thesis is based on those EwE food webs, and as a future research direction it is imperative to examine how sensitive our proposed indices are to changes in food web resolution. We also note that conventional functional diversity analysis often incorporates relative species abundance into diversity indices, and our proposed indices at the present do not use such information. Therefore, another future research direction is to incorporate species abundance data into network-based functional diversity measurement. Furthermore, recent food web researches have shown the importance of combining species trait information into the analysis of food webs (Olmo Gilabert et al. 2019, Endrédi et al. 2021); therefore, future research should follow similar footsteps and add trait information into network-based functional diversity indices. This thesis mainly focuses on the relationship between network-based functional diversity and various structural properties of food webs. There are also other ecology-related information available for those food webs analyzed. For instance, there are information on the geographical coordinates and the type of ecosystem from which a food web dataset was collected. Future extensions from this thesis should investigate whether there exists a longitudinal gradient in network-based functional diversity, and how different ecosystems types differ in their network-based functional diversity. Moreover, accompanied with EwE datasets are demographic information on various

doi:10.6342/NTU202203106

ecosystems; and future research can also examine how ecosystem properties (e.g., turn-over rate) are related with network-based functional diversity. Lastly, we also need to emphasize that the work presented in this thesis is based on food webs. There are other types of ecological networks that are also of ecological importance. For instance, there are various bipartite networks in ecology (e.g., host-parasite networks, flower-pollinator networks), and species interactions in those cases are very different to the trophic interactions in food webs. And as a possible future direction, one can extent concepts developed in this thesis to measure species uniqueness and systems functional diversity by considering different types of (non-trophic) interactions.

doi:10.6342/NTU202203106

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Appendix 1 Method used to quantify the interaction structure of a food web

In this appendix we provide a detailed description on how to quantify the interaction structure of a food web. First, we start with the methodology developed by Müller et al. (1999) and Jordán et al. (2003) for a food web treated as a network with undirected and unsigned edges. Second, borrowed from Liu et al. (2010, 2020), we then describe how the method of Müller et al. (1999) and Jordán et al. (2003) can be extended for a food web treated as a network with directed and signed edges. Lastly, we provide an example of how interaction structure is quantified by using a toy food web.

A.1 Interaction structure for a food web with undirected and unsigned edges

In this section, we treat each trophic link between two species as an edge without direction and sign.

Given a food web, let *i*-*j* be a link connecting species *i* to species *j*, then we define the one-step effect of species *i* on species *j* as:

$$a_{ij,1} = \frac{1}{D_j},$$

(A1)

doi:10.6342/NTU202203106

where D_j is the number of neighbors of species j (i.e., the degree of species j). To be more explicit, if species i is a neighbor of species j, then $a_{ij,1}$ is given by (A1); if species i is not a neighbor of species j, then $a_{ij,1}$ is zero. The interpretation of one-step effect $a_{ij,1}$ is as follows: if species j is affected by one species that is one step away from it (i.e., one trophic link away from species j), then the probability of this influence coming from species i is $a_{ij,1}$. Terms such as "affect" and "influence" here may refer to changes in the population size of a species cause changes in the population size of another species.

There are two simple rules in this method. First, effects are multiplicative. For a pathway consisting of more than one step (i.e., trophic link), we define the effect from the starting species on the ending species via this pathway as the product of the constituent one-step effects. For instance, consider a 2-step pathway *i*-*k*-*j*, the effect of species i on species j through species k is defined as:

$$a_{ik,1} \times a_{kj,1} = \frac{1}{D_k} \times \frac{1}{D_j}. \quad \text{(A2)}$$

Second, effects are additive. If there are m pathways of length l (i.e., l steps) connecting two species, then the effect of the starting species on the ending species in l steps is the sum of effects along those m pathways. For instance, if there are only three 2-step pathways linking species i and species j, via species k, h and g respectively, then the 2-step effect of species i on

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species *j* is:

$$a_{ij,2} = (a_{ik,1} \times a_{kj,1}) + (a_{ih,1} \times a_{hj,1}) + (a_{ig,1} \times a_{gj,1})$$

$$= (\frac{1}{D_k} \times \frac{1}{D_j}) + (\frac{1}{D_h} \times \frac{1}{D_j}) + (\frac{1}{D_g} \times \frac{1}{D_j}).$$

(A3)

The interpretation of (A3) is as follows: if species *j* is affected by one species that is two steps away from it (i.e., two trophic links away from species *j*), then the probability of this influence coming from species *i* is $a_{ij,2}$.

By using the same principle, one can quantify the effect of one species on another in one step, two steps, three steps and so on. The effect of species *i* on species *j* "up to" *n* steps is:

$$E_{ij} = \frac{1}{n}(a_{ij,1} + a_{ij,2} + a_{ij,3} \ldots + a_{ij,n}).$$

(A4)

The interpretation of (A4) is as follows: if species *j* is affected by one species that is one step, two steps, three steps or up to *n* steps away from it, then the probability of this influence coming from species *i* is E_{ij}.

One can construct a matrix **E** where the *ij*-th element is given by (A4). Matrix **E** here can be regarded as the interaction structure of a food web as it contains the effects between all species pairs. Furthermore, the *i*-th row of matrix **E** is the interaction profile of species *i*, which contains

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the effects of species *i* on all species in the same food web. Note that this matrix is not symmetrical, meaning the effect of species *i* on species *j* is not the same as the effect of species *j* on species *i*. Also, this method allows for a species affecting itself (i.e., self-effect, E_{ii}).

Furthermore, if we consider the weight of trophic links (i.e., in terms of the biomass transferred per unit area and per unit time, for example, in grams of carbon per square meter per year), we can also define the weighted one-step effect as follows:

$$a_{ij,1} = \frac{w_{ij}}{\sum_k w_{kj}}, \quad \text{(A6)}$$

where w_{ij} is the weight associated with the trophic link *i*-*j*; and w_{kj} is the weight for the trophic link between species *j* and its neighbor *k*. The above-mentioned method is still applicable to weighted food webs, and one simply uses (A6) for one-step effects instead of (A1).

A.2 Interaction structure for a food web with directed and signed edges

In this section, we assume a trophic link from a prey species to a predator species consists of two edges with opposite signs and in opposite directions. Specifically, there is a positive edge pointing from the prey species to the predator species, and this indicates the former affects the latter in a positive manner; in other word, increases (or decreases) in the population size of the prey species cause increases (or decreases) in the population size of the predator species. And

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then in the opposite direction, there is a negative edge pointing from the predator species to the prey species as the former affects the latter negatively; in other words, increases (or decreases) in the population size of the predator species cause decreases (or increases) in the population size of the prey species. Quantifying interaction structure here still follows the same principle outlined in Section A.1, and as we will see, effects defined in Section A.1 can be partitioned into positive and negative components.

We define one-step effects as before with additional information. Let $i \rightarrow j$ denotes the link from species i to species j, and let $S_{i \rightarrow j}$ be the sign of the link (i.e., $S_{i \rightarrow j}$ = + or -). Let D^{in}_j be the number of species connected to species j (i.e., the in-degree of species j), then the *magnitude* of the one-step effect from i on j is:

$$a_{ij,1} = \frac{1}{D_j^{in}}, \tag{A7}$$

and the sign of this effect is $S_{i \rightarrow j}$. The interpretation of this one-step effect is as follows: if species j is affected by one species that is one step away from it, then $a_{ij,1}$ is the probability that such an influence is from species i with the sign determined by $S_{i \rightarrow j}$.

Again, there are two rules in this method. First, effects are multiplicative. For a pathway consisting of more than one step, we define the *magnitude* of the effect from the starting species

doi:10.6342/NTU202203106

on the ending species via this pathway as the product of the *magnitudes* of the constituent one-step effects. For instance, consider a 2-step pathway $i \rightarrow k \rightarrow j$, the magnitude of the effect of species i on species j through species k is defined as:

$$a_{ik,1} \times a_{kj,1} = \frac{1}{D_k^{in}} \times \frac{1}{D_j^{in}}, \quad \text{(A8)}$$

and the sign of this effect is the product of signs of the constituent one-step effects (i.e., $S_{i \rightarrow k} \times S_{k \rightarrow j}$). Second, again, effects are additive; but here we only add effects of the same sign together. Assuming there are m pathways of length l (i.e., l steps) starting with species i and ending with species j, where p pathways resulting in positive effects and the remaining m-p pathways producing negative effects; then the effect of the starting species on the ending species in l steps (i.e., $a_{ij,l}$) is partitioned into the positive component (i.e., $a_{ij,l}^{+}$) and the negative component (i.e., $a_{ij,l}^{-}$). Specifically, the positive component is the sum of the magnitudes of those p positive effects, and the negative component is the sum of the magnitudes of those (m-p) negative effects. For instance, if there are only three 2-step pathways from species i to species j, they are $i \rightarrow k \rightarrow j$, $i \rightarrow h \rightarrow j$ and $i \rightarrow g \rightarrow j$, and all one-step effects involved are positive except for the link $g \rightarrow j$ (which is negative); then the magnitudes and the signs of those three 2-step effects are as follows.

The magnitude and the sign of the effect along pathway $i \rightarrow k \rightarrow j$ are:

$$a_{ik,1} \times a_{kj,1} = \frac{1}{D_k^{in}} \times \frac{1}{D_j^{in}},$$

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(A9)

$$S_{i\to k} \times S_{k\to j} = (+) \times (+) = (+);$$

(A10)

magnitude and the sign of the effect along pathway $i \to h \to j$ are:

$$a_{ih,1} \times a_{hj,1} = \frac{1}{D_h^{in}} \times \frac{1}{D_j^{in}},$$

(A11)

$$S_{i\to h} \times S_{h\to j} = (+) \times (+) = (+);$$

(A12)

and the magnitude and the sign of the effect along pathway $i \to g \to j$ are:

$$a_{ig,1} \times a_{gj,1} = \frac{1}{D_g^{in}} \times \frac{1}{D_j^{in}},$$

(A13)

$$S_{i\to g} \times S_{g\to j} = (+) \times (-) = (-).$$

(A14)

Therefore the 2-step effect of species i on species j (i.e., $a_{ij,2}$) can be partitioned into the positive component (i.e., $a_{ij,2}^{+}$) and the negative component (i.e., $a_{ij,2}^{+}$) as follows:

$$a_{ij,2} = a_{ij,2}{}^{+} + a_{ij,2}{}^{-}$$

(A15)

where

$$a_{ij,2}{}^{+} = \frac{1}{D_k^{in}} \times \frac{1}{D_j^{in}} + \frac{1}{D_h^{in}} \times \frac{1}{D_j^{in}}$$

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(A16)

and

$$a_{ij,2}{}^{-} = \frac{1}{D_g^{in}} \times \frac{1}{D_j^{in}}$$

(A17)

The interpretation of these two components is as follows: if species *j* is affected by one species that is two steps away from it, then the probability of this influence being positive and coming from species *i* is $a_{ij,2}{}^{+}$; and the probability of this influence being negative and coming from species *i* is $a_{ij,2}{}^{-}$.

Following the same principle, we can quantify the positive effect and the negative effect of one species on another in one step, two steps, three steps and so on. The magnitude of the positive effect of species *i* on species *j* "up to" *n* steps is:

$$E_{ij}{}^{+} = \frac{1}{n}(a_{ij,1}{}^{+} + a_{ij,2}{}^{+} + a_{ij,3}{}^{+} \ldots + a_{ij,n}{}^{+}).$$

(A18)

The interpretation of (A18) is as follows: if species *j* is affected by one species that is one step, two steps, three steps or up to *n* steps away from it, then the probability of this influence being positive and coming from species *i* is $E_{ij}{}^{+}$. Similarly, the magnitude of the negative effect of species *i* on species *j* "up to" *n* steps is:

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$$E_{ij}^{-} = \frac{1}{n}(a_{ij,1}^{-} + a_{ij,2}^{-} + a_{ij,3}^{-} \ldots + a_{ij,n}^{-}).$$

(A19)

The interpretation of (A19) is as follows: if species *j* is affected by one species that is one step, two steps, three steps or up to *n* steps away from it, then the probability of this influence being negative and coming from species *i* is E_{ij}^{-}.

One can construct two matrices $\mathbf{E}^{+}$ and $\mathbf{E}^{-}$, where the *ij*-th elements of those two matrices are given by (A18) and (A19) respectively. Matrices $\mathbf{E}^{+}$ and $\mathbf{E}^{-}$ together can be regarded as the interaction structure of a food web, as they respectively contain the magnitudes of positive and negative effects between all species pairs. The *i*-th row of $\mathbf{E}^{+}$ records the magnitudes of positive effects that species *i* exerts on all species in the same food web, while the corresponding row in $\mathbf{E}^{-}$ records the magnitudes of negative effects; therefore, those two rows together form the interaction profile of species *i*. Note that adding matrices $\mathbf{E}^{+}$ and $\mathbf{E}^{-}$ together produces **E**.

A.3 An example of quantifying interaction structure of a food web

Fig. A1 shows a toy food web consisting of seven species and eight trophic links. Each

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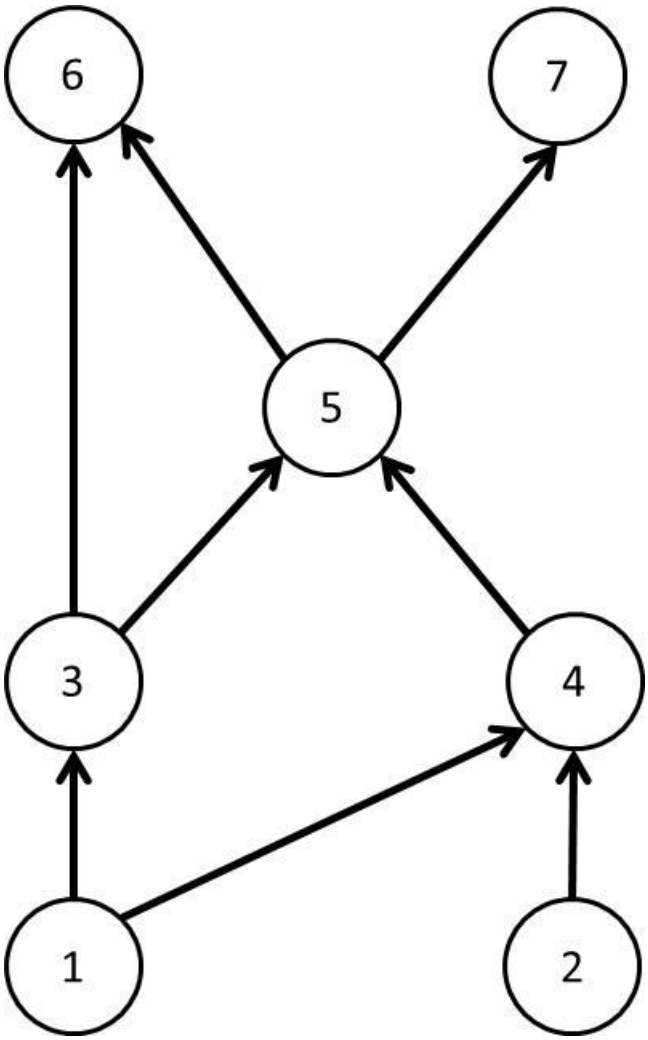

Figure A1. A toy food web

trophic link connects a prey species to a predator species (i.e., in the direction of the arrow). We first consider this food web as a network with undirected and unsigned edges, and quantify the interaction structure up to three steps.

Table 1 is a matrix representing the one-step effects, where the *ij*-th element represents the effect of species *i* (i.e., row species) on species *j* (i.e., column species). For instance, the

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Table 1. One-step effects for the toy food web in Fig. A1. Each element of the table is the effect of a row species on a column species.

Sp\Sp	1	2	3	4	5	6	7
1	0	0	0.333	0.333	0	0	0
2	0	0	0	0.333	0	0	0
3	0.500	0	0	0	0.250	0.500	0
4	0.500	1.000	0	0	0.250	0	0
5	0	0	0.333	0.333	0	0.500	1.000
6	0	0	0.333	0	0.250	0	0
7	0	0	0	0	0.250	0	0

Table2. Two-step effects for the toy foo web in Fig A1. Each element of the table is the effect of a row species on a column species.

Sp\Sp	1	2	3	4	5	6	7
1	0.333	0.333	0	0	0.167	0.167	0
2	0.167	0.333	0	0	0.083	0	0
3	0	0	0.417	0.250	0.125	0.125	0.250
4	0	0	0.250	0.583	0	0.125	0.250
5	0.333	0.333	0.167	0	0.542	0.167	0
6	0.167	0	0.083	0.083	0.083	0.292	0.250
7	0	0	0.083	0.083	0	0.125	0.250

one-step effect of species 5 on species 4 is 1/3=0.333, this is because species 4 has three neighbors, and species 5 is one of them. This can be interpreted as follows: if species 4 is affected by one species that is one step away from it, then the probability of this species being species 5 is 0.333. Also, note that the one-step effect of species 7 on species 4 is zero, as the former cannot reach the latter in one step.

Table 2 is a matrix representing the two-step effects, where the *ij*-th element is the effect of species *i* on species *j* in two steps. For instance, species 1 can reach species 5 in two steps via

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two pathways, namely 1-3-5 and 1-4-5. The effect of species 1 on species 5 via species 3 is the product of two one-step effects:

$$a_{13,1} \times a_{35,1} = \frac{1}{3} \times \frac{1}{4} = 0.083. \quad \text{(A20)}$$

Similarly, the effect of species 1 on species 5 via species 4 is:

$$a_{14,1} \times a_{45,1} = \frac{1}{3} \times \frac{1}{4} = 0.083. \quad \text{(A21)}$$

The 2-step effect of species 1 on species 5 is:

$$a_{13,1} \times a_{35,1} + a_{14,1} \times a_{45,1} = \frac{1}{3} \times \frac{1}{4} + \frac{1}{3} \times \frac{1}{4} = 0.167. \quad \text{(A22)}$$

Thus, if species 5 is affected by one species that is two steps away from it, then the probability of this species being species 1 is 0.167.

Table 3 summarizes the three-step effects, and each element of the matrix is calculated by using the same principle as that used to calculate values in Table 2. For instance, Species 7 can reach species 1 via two pathways of length three, one is 7-5-3-1, and the other is 7-5-4-1, therefore the effect of species 7 on species 1 in three steps is:

$$a_{75,1} \times a_{53,1} \times a_{31,1} + a_{75,1} \times a_{54,1} \times a_{41,1} = \frac{1}{4} \times \frac{1}{3} \times \frac{1}{2} + \frac{1}{4} \times \frac{1}{3} \times \frac{1}{2} = 0.083. \quad \text{(A23)}$$

Thus, if species 1 is affected by one species that is three steps away from it, then the probability

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of this species being species 7 is 0.167.

Table 3. Three-step effects for the toy food web in Fig. A1. Each element of the table is the effect of a row species on a column species.

Sp\Sp	1	2	3	4	5	6	7
1	0	0	0.222	0.278	0.042	0.083	0.167
2	0	0	0.083	0.194	0	0.042	0.083
3	0.333	0.250	0.083	0.042	0.260	0.271	0.125
4	0.417	0.583	0.042	0	0.302	0.125	0
5	0.083	0	0.347	0.403	0.083	0.354	0.542
6	0.083	0.083	0.181	0.083	0.177	0.083	0.083
7	0.083	0.083	0.042	0	0.135	0.042	0

Table 4. The interaction structure up to three steps for the toy food web in Fig. A1. The food web is treated as a network with undirected and unsigned edges. Each element of the table is the effect of a row species on a column species.

Sp\Sp	1	2	3	4	5	6	7
1	0.111	0.111	0.185	0.204	0.069	0.083	0.056
2	0.056	0.111	0.028	0.176	0.028	0.014	0.028
3	0.278	0.083	0.167	0.097	0.212	0.299	0.125
4	0.306	0.528	0.097	0.194	0.184	0.083	0.083
5	0.139	0.111	0.282	0.245	0.208	0.340	0.514
6	0.083	0.028	0.199	0.056	0.170	0.125	0.111
7	0.028	0.028	0.042	0.028	0.128	0.056	0.083

Adding Tables 1, 2 and 3, and then dividing each element of the resulting table by 3 produces Table 4, which is a matrix representing the effect of one species on another up to 3 steps. For instance, the effect of species 7 on species 1 is 0.028. This is the probability of species 7 affecting species 1 in one step, two steps or three steps. Table 4 represents the interaction structure of the toy food web and is equivalent to matrix **E** in the main text of this paper.

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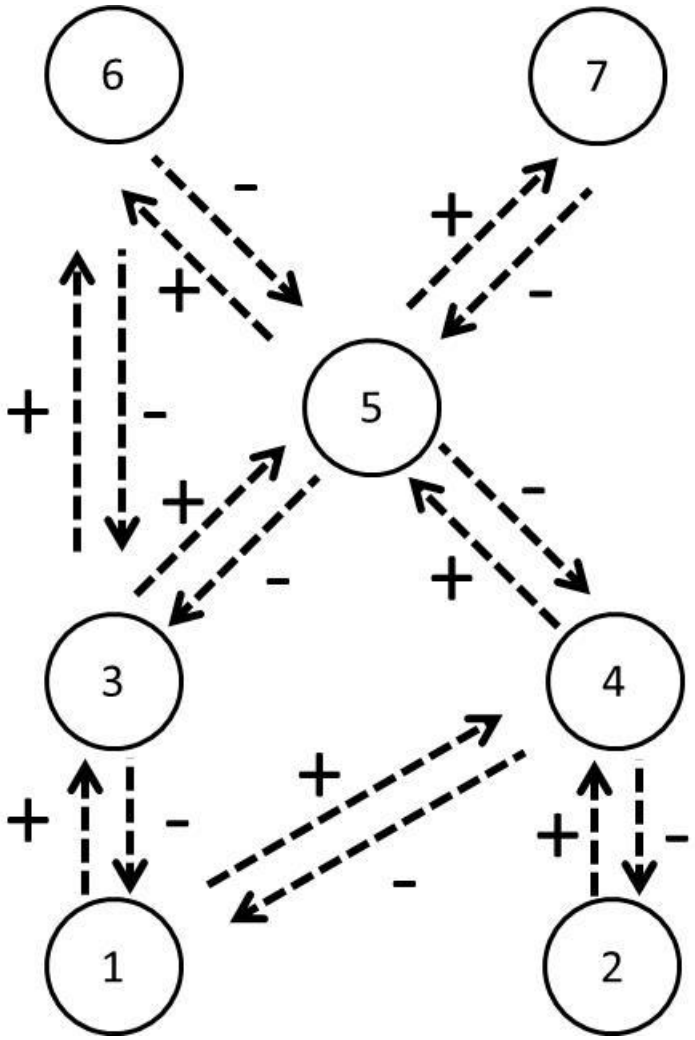

Figure A2. The toy network of Figure 1 as a signed diagraph.

Fig. A2 shows the toy food web in the form of a signed digraph (i.e., a network with directed and signed edges). Each trophic link in the toy food web is converted to two edges with opposite signs and pointing in the opposite directions. One-step effects now can be partitioned into two components, one for positive effects (Table 5.1), and one for negative effects (Table 5.2). For instance, species 5 has four edges pointing toward it, and one of them is negative and is from species 7; then the magnitude of negative one-step effect of species 7

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Table 5.1. The magnitudes of positive one-step effects for the toy food web in Fig. A2. Each element of the table is the effect of a row species on a column species.

Sp\Sp	1	2	3	4	5	6	7
1	0	0	0.333	0.333	0	0	0
2	0	0	0	0.333	0	0	0
3	0	0	0	0	0.250	0.500	0
4	0	0	0	0	0.250	0	0
5	0	0	0	0	0	0.500	1.000
6	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0

Table 5.2. The magnitudes of negative one-step effects for the toy food web in Fig. A2. Each element of the table is the effect of a row species on a column species.

Sp\Sp	1	2	3	4	5	6	7
1	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0
3	0.500	0	0	0	0	0	0
4	0.500	1.000	0	0	0	0	0
5	0	0	0.333	0.333	0	0	0
6	0	0	0.333	0	0.250	0	0
7	0	0	0	0	0.250	0	0

on species 5 is 1/4=0.25. This can be interpreted as follows: if species 5 is affected by one species in one step, then the probability of this influence being negative and coming from species 7 is 0.25. This can be considered as the effect of a predator species on a prey species. Note that the magnitude of positive one-step effect of species 7 on species 5 is 0. Another example, species 6 has two positive edges pointing toward it, and one of them is from species 3; then the magnitude of positive one-step effect of species 3 on species 6 is 1/2=0.5. In other words, if species 6 is affected by one species in one step, then the probability of this influence being positive and coming from species 3 is 0.5. This can be regarded as the effect of a prey

doi:10.6342/NTU202203106

species on a predator species. Also note that adding Tables 5.1 and 5.2 together produces Table 1 (i.e., Table 1 can be partitioned into Table 5.1 and 5.2).

Calculating two-step effects and partitioning them into positive effects and negative effects result in Table 6.1 and Table 6.2. For instance, we can calculate the two-step effect of species 4 on species 3 as follows. First, identify pathways (with direction) starting from species 4 and ending with species 3, and in this case there are two such pathways: one is 4→1→3, akin to the effect of one competitor on another competitor via a shared food item; and the other is 4→5→3, akin to apparent competition where one prey species can affect another via a common predator. For the effect of species 4 on species 3 via pathway 4→1→3, its magnitude and sign are:

$$a_{41,1} \times a_{13,1} = \frac{1}{2} \times \frac{1}{3} = 0.167. \quad \text{(A24)}$$

$$S_{4\to1} \times S_{1\to3} = (-) \times (+) = (-). \quad \text{(A25)}$$

For the effect of species 4 on species 3 via pathway 4→5→3, its magnitude and sign are:

$$a_{45,1} \times a_{53,1} = \frac{1}{4} \times \frac{1}{3} = 0.083. \quad \text{(A26)}$$

$$S_{4\to5} \times S_{5\to3} = (+) \times (-) = (-).$$

doi:10.6342/NTU202203106

(A27)

Therefore, in 2 steps, the effects of species 4 on species 3 are all negative, with a resultant magnitude of 0.167+0.083=0.25. This can be interpreted as follows: if species 3 is affected by

Table 6.1. The magnitudes of positive two-step effects for the toy food web in Fig. A2. Each element of the table is the effect of a row species on a column species.

Sp\Sp	1	2	3	4	5	6	7
1	0	0	0	0	0.167	0.167	0
2	0	0	0	0	0.083	0	0
3	0	0	0	0	0	0.125	0.250
4	0	0	0	0	0	0.125	0.250
5	0.333	0.333	0	0	0	0	0
6	0.167	0	0.083	0.083	0	0	0
7	0	0	0.083	0.083	0	0	0

Table 6.2. The magnitudes of negative two-step effects for the toy food web in Fig. A2. Each element of the table is the effect of a row species on a column species.

Sp\Sp	1	2	3	4	5	6	7
1	0.333	0.333	0	0	0	0	0
2	0.167	0.333	0	0	0	0	0
3	0	0	0.417	0.250	0.125	0	0
4	0	0	0.250	0.583	0	0	0
5	0	0	0.167	0	0.542	0.167	0
6	0	0	0	0	0.083	0.292	0.250
7	0	0	0	0	0	0.125	0.250

one species two steps away in the food web, then the probability of this influence being negative and is from species 4 is 0.25. Also, the effect of species 7 on species 3 is calculated as follows. There is only one pathway from species 7 to species 3, namely 7→5→3, and the magnitude and the sign for this effect are:

$a_{75,1} \times a_{53,1} = \frac{1}{4} \times \frac{1}{3} = 0.083,$

doi:10.6342/NTU202203106

(A28)

$$S_{7\to5} \times S_{5\to3} = (-) \times (-) = (+),$$

(A29)

and this can be regarded as the effect of a top predator on the prey of its prey. Note that adding Tables 6.1 and 6.2 together produces Table 2 (i.e., Table 2 can be partitioned into Tables 6.1 and 6.2).

Calculating three-step effects and partitioning them into positive effects and negative effects result in Table 7.1 and Table 7.2. Values in Tables 7.1 and 7.2 are calculated in a similar manner as those in Tables 6.1 and 6.2. For instance, to quantify the three-step effect of species 7 on species 1, we identify pathways of length 3 staring from species 7 and ending with species 1. In this case, there are two such pathways, they are 7→5→3→1 and 7→5→4→1. The magnitude and the sign for the effect along pathway 7→5→3→1 are:

$$a_{75,1} \times a_{53,1} \times a_{31,1} = \frac{1}{4} \times \frac{1}{3} \times \frac{1}{2} = 0.042,$$

(A30)

$$S_{7\to5} \times S_{5\to3} \times S_{3\to1} = (-) \times (-) \times (-) = (-),$$

(A31)

and for pathway 7→5→4→1 they are:

$$a_{75,1} \times a_{54,1} \times a_{41,1} = \frac{1}{4} \times \frac{1}{3} \times \frac{1}{2} = 0.042,$$

doi:10.6342/NTU202203106

(A32)

$$S_{7\to5} \times S_{5\to4} \times S_{4\to1} = (-) \times (-) \times (-) = (-),$$

(A33)

Thus, the three-step effect of species 7 on species 1 is negative with a magnitude of 0.083, and this can be considered as the top-down effect of species 7 on species 1. Similarly, adding Tables 7.1 and 7.2 together produces Table 3 (i.e., Table 3 can be partitioned into Table 7.1 and 7.2).

Table 7.1. The magnitudes of positive three-step effects for the toy food web in Fig. A2. Each element of the table is the effect of a row species on a column species.

Sp\Sp	1	2	3	4	5	6	7
1	0	0	0	0	0	0.083	0.167
2	0	0	0	0	0	0.042	0.083
3	0.333	0.250	0.042	0.042	0	0	0
4	0.417	0.583	0	0	0	0	0
5	0.083	0	0.347	0.403	0.042	0	0
6	0	0	0.181	0.083	0.177	0.042	0
7	0	0	0.042	0	0.135	0.042	0

Table 7.2. The magnitudes of negative three-step effects for the toy food web in Fig. A2. Each element of the table is the effect of a row species on a column species.

Sp\Sp	1	2	3	4	5	6	7
1	0	0	0.222	0.278	0.042	0	0
2	0	0	0.083	0.194	0	0	0
3	0	0	0.042	0	0.260	0.271	0.125
4	0	0	0.042	0	0.302	0.125	0
5	0	0	0	0	0.042	0.354	0.542
6	0.083	0.083	0	0	0	0.042	0.083
7	0.083	0.083	0	0	0	0	0

Adding Tables 5.1, 6.1 and 7.1, and then dividing each element of the resulting table by three

doi:10.6342/NTU202203106

produces Table 8.1, which is a matrix representing the magnitudes of positive effects between species up to three steps. For instance, the positive effect of species 6 on species 1 is 0.056; this is the probability of species 1 being positively affected by species 6 in one step, two steps or three steps. Note that Table 8.1 is the positive component of the interaction structure for the toy food web, and it is equivalent to matrix $\mathbf{E}^+$ in the main text of this paper. Similarly, for negative effects, adding Tables 5.2, 6.2 and 7.2, and then dividing each element of the

Table 8.1. The positive component of the interaction structure for the toy food web in Fig. A2. The food web is treated as a network with directed and signed edges. Each element of the table is the effect of a row species on a column species.

Sp\Sp	1	2	3	4	5	6	7
1	0	0	0.111	0.111	0.056	0.083	0.056
2	0	0	0	0.111	0.028	0.014	0.028
3	0.111	0.083	0.014	0.014	0.083	0.208	0.083
4	0.139	0.194	0	0	0.083	0.042	0.083
5	0.139	0.111	0.116	0.134	0.014	0.167	0.333
6	0.056	0	0.088	0.056	0.059	0.014	0
7	0	0	0.042	0.028	0.045	0.014	0

Table 8.2. The negative component of the interaction structure for the toy food web in Fig. A2. The food web is treated as a network with directed and signed edges. Each element of the table is the effect of a row species on a column species.

Sp\Sp	1	2	3	4	5	6	7
1	0.111	0.111	0.074	0.093	0.014	0	0
2	0.056	0.111	0.028	0.065	0	0	0
3	0.167	0	0.153	0.083	0.128	0.090	0.042
4	0.167	0.333	0.097	0.194	0.101	0.042	0
5	0	0	0.167	0.111	0.194	0.174	0.181
6	0.028	0.028	0.111	0	0.111	0.111	0.111
7	0.028	0.028	0	0	0.083	0.042	0.083

resulting table by 3 produces Table 8.2, which is a matrix representing the magnitudes of

doi:10.6342/NTU202203106

negative effects up to 3 steps. For instance, the magnitude of the negative effect of species 6 on species 7 is 0.111; and this is the probability of species 7 being negatively affected by species 6 in one step, two steps or three steps. Note that Table 8.2 is the negative component of the interaction structure for the toy food web, and it is equivalent to matrix $\mathbf{E}^-$ in the main text of this paper. Also note that adding Tables 8.1 and 8.2 produces Table 4 (i.e., Table 4 can be partition into Tables 8.1 and 8.2, or Matrix **E** can be partition into $\mathbf{E}^+$ and $\mathbf{E}^-$).

In summary, **E** records the unsigned effect of one species on another up to *n* steps, and each row is the interaction profile of one particular species. **E** can be partition into $\mathbf{E}^+$ and $\mathbf{E}^-$, where $\mathbf{E}^+$ and $\mathbf{E}^-$ record respectively the magnitudes of positive effects and negative effects between species up to *n* steps. The *i*-th row of $\mathbf{E}^+$ and the *i*-th row of $\mathbf{E}^-$ together form a vector of length $2\times N$ (*N* is the number of species in the food web), and this is the interaction profile of species *i*. Furthermore, the first half of this vector records the magnitudes of positive effects that species *i* exerts on every species up to *n* steps, and the second half of this vector records the magnitudes of the negative effects.

doi:10.6342/NTU202203106