

# The Architecture of Antagonistic Networks

by

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# Declaration

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# Abstract

Designing a mechanistic model that can give rise to realistic architecture of ecological networks is central to the understanding of how species assemble and function in ecosystems. As species are constantly adjusting their diets in an antagonistic network, we here incorporate this adaptive behaviour of diet choice into a bipartite network model, with the effect of antagonistic interactions between species depicted by Holling's type II functional response. Predictions of this model fit extremely well with the observed levels of nestedness, modularity and node-degree distributions for 61 real host-parasitoid and plant-herbivore networks. We further examined two specific scenarios of our model (species with identical [neutral] demographic parameters and interactions with identical [neutral] benefit in the network) and found that the demography-neutral scenario over-estimated observed modularity, whilst the benefit-neutral scenario over-estimate observed nestedness. Relationships between nestedness, modularity and connectance were found strong. Moreover, in contrast to the common belief of the high modularity in antagonistic networks, most real networks (> 80%) are significantly nested, whilst nearly 40% of the real networks are surprisingly less compartmentalized than random networks generated from null models. Regardless of the controversy on whether antagonistic networks are nested or compartmentalized, the proposed model captured the essence of the dynamic nature of structural emergence in antagonistic networks. Due to its predictive power, this model was further used to investigate robustness in antagonistic networks. Predictions showed that the robustness of a network is determined by many factors, such as connectance, resource degree distribution, resource-consumer ratio, diversity, nestedness and compartmentalisation. Surprisingly, the manner of network response to species loss was independent of the sequence followed while removing species from a network. Variations were only noticed in the intensity of the effect resulting from the removals. In addition, we also showed that species extinction procedures which ignore the interaction switch underestimate the effect of any loss of species in these networks. We must therefore value our knowledge of possible adaptive processes in the ecosystem as they may be important for resolving the diversity-stability debate.

# Opsomming

Die ontwerp van 'n meganistiese model wat aanleiding kan gee tot realistiese argitektuur van ekologiese netwerke is sentraal tot die begrip van hoe spesies bymekaar kom en funksioneer in ekosisteme. Soos spesies voortdurend hul dieet aanpas in 'n antagonistiese netwerk, het ons hierdie aanpasbare gedrag van dieet keuse in 'n bipartiet netwerk model ingewerk, met die effek van antagonistiese interaksies tussen spesies wat uitgebeeld word deur Holling se tipe II funksionele reaksie. Voorspellings van hierdie model pas baie goed met die waargenome vlakke van *nestedness*, modulariteit en node-graad uitkerings vir 61 ware gasheer-parasiet en plant-herbivoor netwerke. Verder het ons twee spesifieke gevalle van ons model (spesies met identiese [neutrale] demografiese parameters en interaksies met identiese [neutrale] voordeel in die netwerk) ondersoek en gevind dat die demografie-neutrale geval waargenome modulariteit oorskat, terwyl die voordeel-neutraal geval waargenome *nestedness* oorskat. Verhoudings tussen *nestedness*, modulariteit en konektiwiteit is sterk bevind. Verder, in teenstelling met die algemene verwagting van hoe modulariteit in antagonistiese netwerke, is oorhoofse werklike netwerke (> 80%) aansienlik geneste, terwyl byna 40% van die werklike netwerke is verbasend minder gekompartimenteerd as ewekansige netwerke gegenereer uit null modelle. Ongeag van die omstrede oor of antagonistiese netwerke geneste of gekompartimenteerd is, die voorgestelde model vang die essensie van die dinamiese aard van die strukturele opkoms in antagonistiese netwerke. As gevolg van sy voorspellende krag, is hierdie model verder gebruik om robuustheid te ondersoek in antagonistiese netwerke. Voorspellings het getoon dat die robuustheid van 'n netwerk word bepaal deur verskeie faktore, soos konektiwiteit, hulpbron-graad verspreiding, hulpbron-verbruiker verhouding, diversiteit, *nestedness* en kompartementasie. Verrassend, die wyse van die netwerk reaksie op die verlies van spesies was onafhanklik van die reeks wat gevolg het toe die spesies verwyder is uit 'n netwerk. Variasies is slegs opgemerk in die intensiteit van die effek van die verskuiwings. Benewens, ons het ook aangetoon dat die prosedures van spesies se uitsterwing wat die interaksie skakelaar geignoreer het, onderskat die effek van 'n verlies van spesies in hierdie netwerke. Ons moet dus die waarde van ons kennis van die moontlike aanpassing prosesse in die ekosisteme in agneem, aangesien dit belangrik kan wees vir die oplossing van die diversiteit-stabiliteit debat.

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# Dedications

I dedicate this thesis to my family: my parents Godwin and Amy Mugasi, my husband Fredrick Wabwire and his family and my siblings Sylvia Tuhumwire, Samantha Mugasi, Shiber Namara, Sharper Mugasi and Surrender Mugasi.

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# Chapter 1

## Introduction

### 1.1 Problem introduction

Antagonism is defined as an interaction in which one species benefits at the expense of the other. The most obvious ecological interactions associated with antagonism are parasitism, herbivory and predation (Piazzon *et al.*, 2011; Nuismer *et al.*, 2007). Parasitism depicts that one of the interacting species lives on or in its interacting partner (host) from which it obtains its nourishment at some stages of its life. Almost half of the animals on earth are parasitic (Dobson *et al.*, 2008; Price, 1977). Parasites may or may not kill their hosts but either way they cause harm. Herbivory too, involves the interaction where the dependent partner does not kill its resource completely but rather exploits it and reduces its abundance. In contrast, predation involves the complete killing of resource (prey) species. Although not as common, mimicry (a species imitates another as a way of defending against its consumers or as a way to have access to alternative resources; Fordyce, 2006) is one other form of antagonism that can be exhibited by either the resource or consumer species in any interactions. In fact, many species associations in ecosystems are driven by antagonistic interactions. In food webs, for example, most resource species' energy is extracted through antagonism. Species invasions too, although known for enhancing biodiversity in some cases (Davis *et al.*, 2005), often cause species loss and thus can be categorised as antagonistic interactions (Kiers *et al.*, 2010). In addition, it has been noted that due to human activities, some mutualistic interactions can become antagonistic (Kiers *et al.*, 2010); for example, the use of fertilisers may reduce or completely stop the plant-rhizosphere mutualism and lead to severe antagonism among the microbes. Much as antagonism has been associated with negative effects especially on resource species, it has also been credited for positively shaping and maintaining the diversity of some ecosystems. For instance, invasive species that could cause the loss of some native species, can be controlled by their natural predators or parasites through antagonistic interactions (Morin, 1999).

Antagonism has also manifested in other systems. For example, the immune responses to pathogens (Fordyce, 2006) and the interaction between the Human Immunodeficiency Virus (HIV) and CD4-T cells in an infected human body is antagonistic. It happens that when the virus infects a human body, it establishes its life cycle within a cell. The virus then replicates itself and eventually kills the cell (Warnke *et al.*, 2007). Interestingly, the viruses do not attack all cells in the body but rather prefer some to others (Gregson, 2007), resembling the antagonistic interactions between predators and their prey. In light of their diverse manifestation, an understanding of antagonistic interactions and their role in forming diverse architectural (structural) patterns in ecosystems is central to our knowledge on the emergence of complex adaptive systems. Indeed, evidence is available that antagonistic interactions are vital in the functionality of various communities (Dobson *et al.*, 2008; Price, 1977), and understanding their evolutionary processes enables us to better manage ecosystems.

Many mathematical models have been proposed to explain the dynamics which are observed in antagonistic communities. However, although much insight has been gained from these models, there has not been a satisfactory model for the emergence of community structure. Most of these models are developed from the Lotka-Volterra model (Getz, 2011), assuming that the prey always has plenty sufficient resources, the predator entirely depends on the prey for survival and the rate at which each population changes is proportional to its size (Fred and Castillo-Chavez, 2000). These assumptions imply that in the absence of the predator, the prey grows exponentially, while in the absence of the prey the predator declines exponentially. Although these models brought insight in understanding the behaviour of species in such a system, their analysis showed that solutions were more sensitive to perturbations than expected. Therefore, it was regarded unrealistic and hence needed modification in order to predict the behaviour of predator-prey systems.

The first attempt, to my knowledge, was replacing the exponential growth of the prey population by a logistic growth. This implies that the prey species grow logistically in the absence of their predators. Even then, the predator population growth rate is assumed to increase with prey density. Holling's proposed functional responses therefore serve to control the predator population. The incorporation of the Holling type II functional response has proved to predict the behaviour of most systems (Liu *et al.*, 2006; Smout *et al.*, 2010; Ko and Ryu, 2006; Fryxell and Lundberg, 1994; Poisot *et al.*, 2012; Cai and Lin, 2007). It assumes that the prey consumption rate increases with increased prey density until predator population saturates. On realising that any interacting species are affected by other dynamic processes (also known as limiting factors) within their habitats, Tilman (1986) defined what he called "A consumer-resource approach to community structure", in which he suggests ways of incorporating some of the limiting factors by considering the effect they have on the system. These approaches are increasingly being used to study

the architecture (structure) and stability of interaction networks (Vincent *et al.*, 1996; Zhang *et al.*, 2011; Okuyama and Holland, 2008).

Describing complex ecosystems as networks of interacting components has proved fruitful—revealing many distinctive patterns and dynamic behaviours of ecological systems. Of the patterns, species degree distribution, compartmentalisation and nestedness have attracted much attention owing to their implications for the functionality and stability of communities. Species degree distribution depicts the proportion of species that interacts with a given number of other species. In mutualistic networks, the degree distribution follows a power law (Jackson, 2008) while in antagonistic networks, it is usually uniform (Boccaletti *et al.*, 2006; Dunne *et al.*, 2002a). Evidence has shown that networks whose degree distribution follows a power law are vulnerable to species loss (Boccaletti *et al.*, 2006). In contrast, uniform degree distribution often increases species persistence (Estrada, 2007; Dunne *et al.*, 2002b), implying that the species degree distribution is crucial for ecosystem stability. Compartmentalisation is characterised by the organisation of species into clusters that interact more with the species within the same cluster than across clusters (Guimera *et al.*, 2010) while nestedness depicts that species interacting with specialist form only a subset of those interacting with generalists (Bascompte *et al.*, 2003). The two patterns (compartmentalisation and nestedness) have been detected in many systems such as mutualistic networks of pollination and seed dispersal (Bascompte *et al.*, 2003; Bastolla *et al.*, 2009; Olesen *et al.*, 2007), antagonistic networks of parasitism and predation (Krasnov *et al.*, 2012; Vacher *et al.*, 2008; Thebault and Fontaine, 2010) and multi-trophic food webs (Dunne *et al.*, 2002a; Kondoh *et al.*, 2010; Meskens *et al.*, 2011). These patterns of ecological networks can have profound effects on the functionality and stability of communities (Bastolla *et al.*, 2009; Stouffer and Bascompte, 2011; Thebault and Fontaine, 2010). For instance, nested structure can reduce species persistence in mutualistic networks (James *et al.*, 2012) and destabilize the community (Allesina and Tang, 2012). However, contending works show that nested mutualistic networks can foster high species richness (Bastolla *et al.*, 2009) and enhance resilience against perturbations (Burgos *et al.*, 2007; Fortuna and Bascompte, 2006; Memmott *et al.*, 2004). In contrast, compartmentalization tends to stabilize antagonistic networks (Fortuna *et al.*, 2010) by containing the effect of perturbations within modules (Guimera *et al.*, 2010; Stouffer and Bascompte, 2011).

As a matter of fact, species often switch their interacting partners as a response to changes in their environment and resource availability (van Baalen *et al.*, 2001; Murdoch, 1969; Staniczenko *et al.*, 2010; Tilman, 1986; Kimbrell and Holt, 2005). This behaviour has shown to favour stability particularly in antagonistic networks and food webs as a whole. Moreover, an interaction switch can be further explained by the diet choice according to optimal foraging theory where a predator will only include a subset of potential preys to

its diet instead of all possible preys, in order to maximise the efficiency of energy intake (Stephens and Krebs, 1986; Vincent *et al.*, 1996). In instances where networks have been disturbed, Kondoh (2003) noted that the long term persistence of ecological communities can be enhanced by consumer switching. In fact, studies that have investigated the robustness of networks, defined as the proportion of species that have to be removed in order to result in a total loss of  $\geq 50\%$  of the species (Dunne *et al.*, 2002b), without considering switching as an adaptive process (Dunne *et al.*, 2002b; Eklöf, 2006; Estrada, 2007), have been questioned.

In this study therefore, we investigate the species degree distribution in real antagonistic networks and analyse its implication for network structure. We introduce the interaction switch into a modified Lotka-Volterra model for depicting the population dynamics of an antagonistic network. The effect of antagonistic interactions is depicted by Holling's type II functional response, consistent with optimal foraging theory. The predictive power of this model is tested using the real networks of antagonistic interactions. We also investigate the response of antagonistic networks to species loss by exploring network robustness, when allowing species to switch their interacting partners.

## 1.2 Project motivation

Antagonists are ubiquitous. Dobson *et al.* (2008) pointed out that more than half of all animals on earth exhibit some form of antagonism. Interactions such as herbivory, parasitism and predation, have been shown to be of particular importance for ecosystem function and stability (Dobson *et al.*, 2008; Price, 1977), and often drive the co-evolutionary arms race between interacting species (Geffeney *et al.*, 2002; Spottiswoode and Stevens, 2010; Musser *et al.*, 2002; Zhang *et al.*, 2013). In California, antagonism is used to control the extravagant growth of the plant *Hypericum perforatum* (St John's wort), which could have led to biodiversity loss. In agriculture, using biological methods to control pests (that is using natural enemies of pests to keep the pest abundance at low levels) is increasingly being advocated for. Further more, the interactions between disease pathogens and both animal and plant cells are antagonistic. Importantly, the human population depends a lot on ecosystems for economical, physical and health benefits. We therefore believe that considering antagonistic interactions at community (network) level and understanding the mechanisms and processes that give rise to the structure of antagonistic networks is fundamental for maintaining biodiversity and for better managing of ecosystem functioning and services, especially when facing the current global environmental changes.



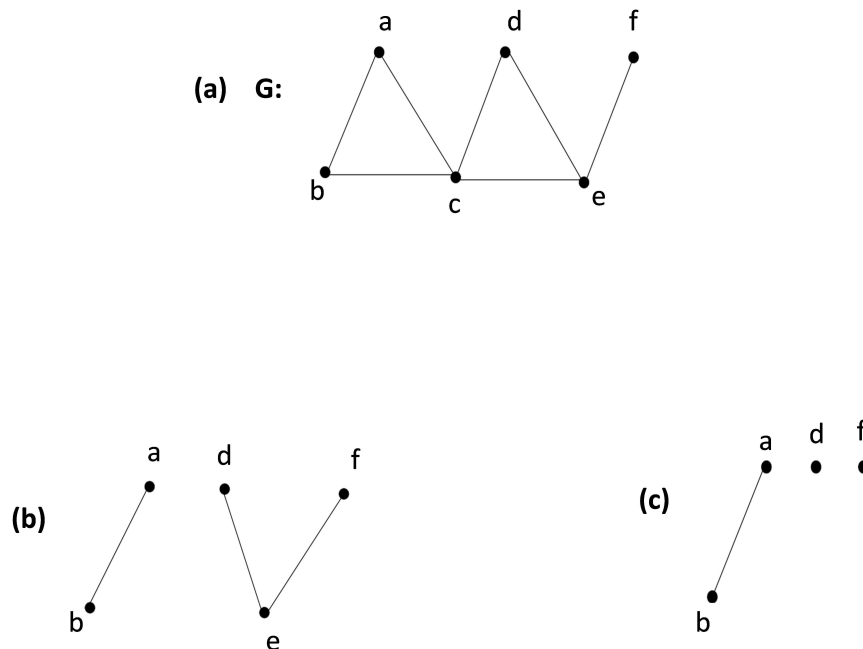
## 1.3 Preliminary terminology

This section introduces a number of terms (from a graph theory point of view) that will be used to define other terms in this thesis. We define the terms from the graph theory view point because graphs are used to diagrammatically represent networks. In other words, the terms “graph” and “network” can be used interchangeably most of the times in this thesis.

### 1.3.1 Graphs

**Definition 1.** A graph  $G$  is a finite non-empty set of objects called vertices together with a set of unordered pairs of distinct vertices of  $G$  called edges (Chartrand and Zhang, 2012).

The cardinality of the vertex set of  $G$  is called the **order** of  $G$  while the cardinality of its edge set is called the **size** of  $G$ . In a graph  $G$ ,  $u$  and  $v$  are **adjacent** to each other if  $\{u, v\}$  is an edge in the graph  $G$  and the edge  $\{u, v\}$  is said to be **incident** with  $u$  and  $v$ . Also, two adjacent vertices are referred to as neighbours of each other. Let  $V(G)$  and  $E(G)$  denote the vertex and edge sets of  $G$  respectively, then a graph  $H$  is called a **subgraph** of  $G$  if  $V(H) \subseteq V(G)$  and  $E(H) \subseteq E(G)$ . If  $V(H) \subset V(G)$  and  $E(H) \subset E(G)$ , then  $H$  is a **proper subgraph** of  $G$ .



**Figure 1.1:** Illustrations for characteristics of a graph. (a) shows a graph  $G$ . (b) shows the graph  $G$  without vertex  $c$  while (c) shows  $G$  without the set of vertices  $\{c, e\}$ .

In Figure 1.1,  $G$  is a graph of order 6 and size 7. Vertex  $d$  is adjacent to  $e$  while the edge  $\{d, e\}$  is incident with vertices  $d$  and  $e$ . The graphs in Figure 1.1 (b) and (c) are proper

subgraphs of  $G$ .

We however can say more about the vertices of  $G$ . The **degree** of a vertex is refers to the number of edges that are incident with it. If the degrees of the vertices of a graph are listed in a sequence, that sequence is called the **degree sequence** of the graph. For the graph  $G$  in Figure 1.1, the degree of vertex  $c$  is 4 and the degree sequence is 2,2,4,2,3,1, respectively for vertices  $a, b, c, d, e$  and  $f$ .

In a graph, if we start at a vertex  $u$  and proceed to its neighbour  $u_1$ , then to the neighbour of  $u_1$  and so on up to some vertex  $v$  without traversing any vertex more than once, the sequence of the traversed vertices describes a  $u - v$  **path**. The **length** of such a path is the number of edges encountered. In the graph  $G$ ,  $(b, a, c, d, e)$  is a  $b - e$  path of length 4. We can however find a  $b - e$  path of shorter length such as  $(b, c, e)$ . The average shortest path length of a graph is termed as the **characteristic path length**,  $l$ , of the graph. It is given by

$$l = \frac{1}{s(s-1)} \sum_{i,j \in F, i \neq j} d_{ij}, \quad (1.3.1)$$

where  $s$  is the order of the graph  $F$  and  $d_{ij}$  denotes the shortest path length between vertices  $i$  and  $j$ .

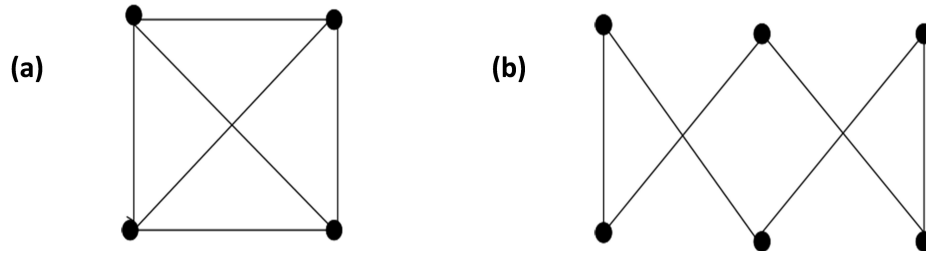
A graph  $G$  is **connected** if for any two vertices  $u$  and  $v$  in  $G$ , there exists a  $u - v$  path. Otherwise, the graph is said to be **disconnected**. If  $H$  is a connected subgraph of  $G$  and is not a proper subgraph of any other connected subgraph of  $G$ , the  $H$  is a **component** of  $G$ . For example, the graph in Figure 1.1 (b) has two components that resulted from removing vertex  $c$  from  $G$ . In fact such a vertex whose removal makes a connected graph disconnected, is called a **cut vertex**. Also, the set of vertices whose removal disconnects a connected graph is called a **vertex cut**. In the graph  $G$  of Figure 1.1, the vertex  $c$  is a cut vertex while the set  $\{c,e\}$  is a vertex cut.

**Definition 2.** A graph is called a regular graph if all vertices have the same degree.

If every vertex of a graph has degree  $k$ , then the graph is called  **$k$ -regular**. For instance, the graphs in Figure 1.2 are regular.

Suppose that  $V(G) = \{v_1, v_2, \dots, v_n\}$  is the vertex set of  $G$  and  $E(G) = \{e_1, e_2, \dots, e_n\}$  its edge set,  $G$  can be represented as a  $n \times n$  matrix known as the **adjacency matrix**  $A(G)$  such that

$$a_{ij} = \begin{cases} 1 & \text{if } v_i v_j \in E(G) \\ 0 & \text{if } v_i v_j \notin E(G), \end{cases}$$



**Figure 1.2:** Examples of regular graphs. (a) is a 3-regular graph while (b) is 2-regular.

where  $a_{ij}$  denotes an entry of the matrix. For the graph  $G$  in Figure 1.1, the adjacency matrix is

$$A = \begin{pmatrix} 0 & 1 & 1 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 \\ 1 & 1 & 0 & 1 & 1 & 0 \\ 0 & 0 & 1 & 0 & 1 & 0 \\ 0 & 0 & 1 & 1 & 0 & 1 \\ 0 & 0 & 0 & 0 & 1 & 0 \end{pmatrix}.$$

**Definition 3.** A graph  $G$  is bipartite if it is possible to partition its vertex set  $V(G)$  into two subsets  $V_1$  and  $V_2$  such that every element of its edge set  $E(G)$  joins a vertex in  $V_1$  to a vertex in  $V_2$  (Chartrand and Zhang, 2012).

For instance, Figure 1.2 (b) is bipartite. If the cardinalities of  $V_1$  and  $V_2$  are  $r$  and  $s$  respectively, the adjacency matrix describing the bipartite graph  $G$  takes the form

$$\begin{pmatrix} 0 & B \\ B^T & 0 \end{pmatrix},$$

where  $B$  is an  $r \times s$  matrix. It is obvious that the matrix  $B$  uniquely represents the bipartite graph  $G$  and therefore, through out this thesis, we define an interaction matrix of a bipartite network as the matrix  $B$ .

### 1.3.2 Matrix multiplication

Throughout this thesis, the matrix multiplication used will be the Hadamard product of matrices unless otherwise stated.

**Definition 4.** Let  $A = (a_{ij})$  and  $B = (b_{ij})$  be  $n \times m$  matrices. Then the Hadamard product between these two matrices, denoted by  $A \odot B$ , is a  $n \times m$  matrix (Caro-Lopera et al., 2012) given by

$$A \odot B = (a_{ij}b_{ij})$$

## 1.4 Thesis Outline

Having given a brief introduction to this project, its motivation and preliminary terminology, the forthcoming part of the thesis will be as follows;

Chapter 2 constitutes a more detailed overview of models, measures and indices regarding the structures of antagonistic networks, and the impact of the structural patterns on the stability and functionality of the ecosystem. We hope to introduce a number of studies on network structures, with intentional emphasis on ecological networks.

Chapter 3 constitutes published data on antagonistic networks. The networks are further analysed in terms of various structural properties.

In Chapter 4, we develop a model that depicts the evolutionary dynamics of the structural patterns in antagonistic networks. We also evaluate the predictive power of our model using the real networks analysed in Chapter 3, giving detailed information on statistical tests.

In Chapter 5, we use our model to investigate ecosystem function and stability. Specifically, we investigate the role of connectance in forming the nestedness-modularity relationship and the factors that enhance network robustness to the loss of generalist species, specialist species and random removal of species from a network.

In Chapter 6, we give the general conclusions from this study and identify knowledge gaps from which we yield recommendations for future work.

# Chapter 2

## Literature Review

### 2.1 Introduction

This chapter serves as a brief overview of the literature on the dynamics and structure of antagonistic communities. First, we introduce the classic Lotka-Volterra model for depicting the population dynamics of interacting species, and specify its underlying assumptions and modifications. Second, we discuss the use of graph-based (network-based) approaches in modelling interacting individuals in a system in a broader sense, and later narrow it to ecological systems. We further discuss the architectural (structural) patterns displayed by ecological communities (networks), the relationships between the architectural patterns and other network properties such as connectance and degree's distribution, and their implication for the functionality of these communities. We highlight the use of the combination of the Lotka-Volterra model and network approach to explain some of the observed community properties. We finally emphasise the importance of interaction switching as an adaptive process among species, and why we believe that this switching process can explain the observed architectural patterns in ecological bipartite antagonistic networks.

### 2.2 Consumer-resource models

A traditional way to introduce consumer-resource models is to first consider a single species, normally assumed to be isolated from the rest of the species. The dynamics of the population of such a species are described by the so called 'logistic equation', given by

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right), \quad (2.2.1)$$

where  $R$  is the abundance of the population,  $r$  is the per capita rate of increase and  $K$  is the carrying capacity (Morin, 1999). The model assumes that the only factor that

constrains the growth rate of such a species is the intraspecific competition that exists between individuals of the same population; implying that in the absence of competition, the species' population would grow exponentially. Can we find a single species that lives so independent of others in any ecosystems? Of course, such communities are very rare in the natural world – if they exist. It is evident that ecosystems consist of different species that interact differently, affecting each other's dynamics. For example, predator-prey, host-parasite, plant-herbivore, plant-pollinator and seed-disperser interactions are evidence that species do not live in isolation and therefore, the logistic equation on its own cannot model the dynamics of communities with such interactions. Interspecific interactions have been mostly modelled by using the Lotka-Volterra model. This model assumes that the resource species  $R$  are prey to a consumer species  $C$ , which entirely depends on that resource for survival. In other words, the population of this consumer species will decline exponentially in the absence of resource species. Originally, Lotka and Volterra assumed that the population of prey species grows exponentially in the absence of their consumers and hence described the dynamics using Equation (2.2.2).

$$\begin{aligned}\frac{dR}{dt} &= rR - aRC \\ \frac{dC}{dt} &= eaRC - dC,\end{aligned}\tag{2.2.2}$$

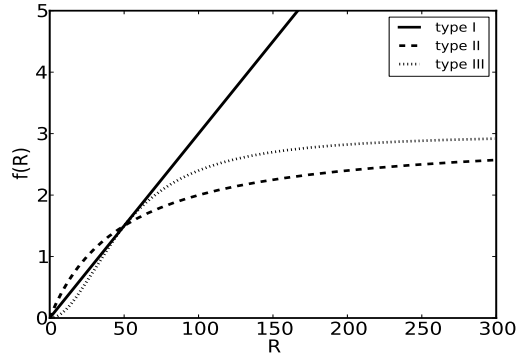
where  $C$  is the population abundance of the consumer species,  $a$  is the per capita attack rate,  $e$  is the rate at which consumed resources are converted into consumer individuals, and  $d$  is the consumer's mortality rate whenever they lack resources. The assumption that resources grow without limit proved to be unrealistic due to the fact that whenever a species abundance grows high, the individuals start to compete for the available resources. So, the model can be improved by replacing the exponential growth with the logistic growth of resource species in Equation (2.2.1). Then, the improved Lotka-Volterra model becomes

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - aRC\tag{2.2.3}$$

$$\frac{dC}{dt} = eaRC - dC.\tag{2.2.4}$$

The term  $aR$  can be referred to as the functional response due to the feeding of consumers. Holling and Buckingham (1976) proposed three different types of functional response, of which  $aR$  is called “linear or type I functional response”. Figure 2.1 is a summary of these functional responses.

The type I, II and III functional responses are defined as  $f(R) = aR$ ,  $f(R) = \frac{\omega_1}{D+R}R$  and  $\frac{\omega_2}{D^2+R^2}R^2$  respectively (see Figure 2.1), where  $D$  can be determined experimentally (Morin, 1999). Type I functional response indicates a constant rate of increase while types II and III increase in a decelerating manner to the point that their increase rates approach a constant.



**Figure 2.1:** The three types of Holling's functional response.  $R$  indicates the resource abundance

The two-species' consumer-resource models have been useful especially in obtaining analytical solutions and carrying out stability analyses. For example, using the Jacobian matrix  $J$  for Equation (2.2.3)

$$J = \begin{pmatrix} r - \frac{2rR}{K} - ac & aR \\ eaC & eaR - d \end{pmatrix},$$

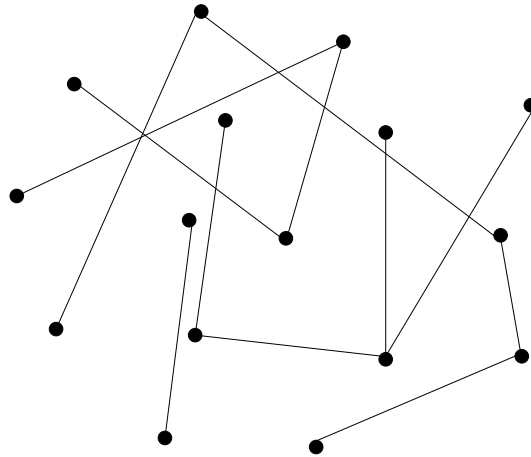
the linearisation process enables the stability analysis based on the sign of the eigenvalues obtained from the characteristic equation of the linearised system. In a three-species scenario, the Routh-Hurwitz criteria is used to determine the signs of the coefficients of the characteristic equation, as a way of investigating stability. However, once the number of interacting species becomes large, the analytical abilities are hampered. Nonetheless, the use of these models together with the analysis of data that describes interactions between species as graphs, has been insightful for understanding the ecosystem.

## 2.3 Network approach

The use of network-based approaches to describe pairwise interactions between various entities can be dated to the time of Leonhard Euler, the Swiss mathematician who solved the Königsberg bridge problem (Chartrand and Zhang, 2012). Most of these approaches refer to a graph as a network of these entities and therefore, this section introduces the concept of a network in a broad sense, tackling a few network models and properties.

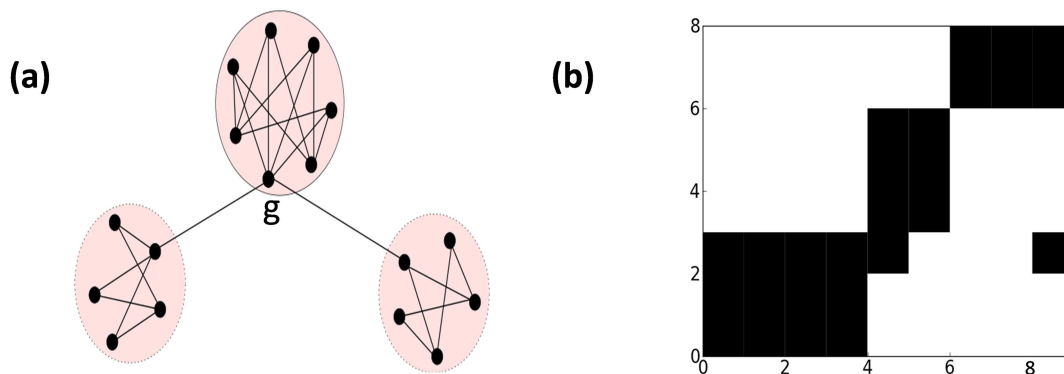
### 2.3.1 Network's representation

We define a network as a group of vertices or nodes (entities) joined together by edges or links (interactions) that represent different connections between vertices. These edges can be directed, undirected, or even weighed in addition to being directed or undirected. The connections can represent friendships, business partnerships, publication co-authorships, roads between cities; etc. To illustrate the idea, Figure 2.2 is an example of a simple network.



**Figure 2.2:** An example of a network

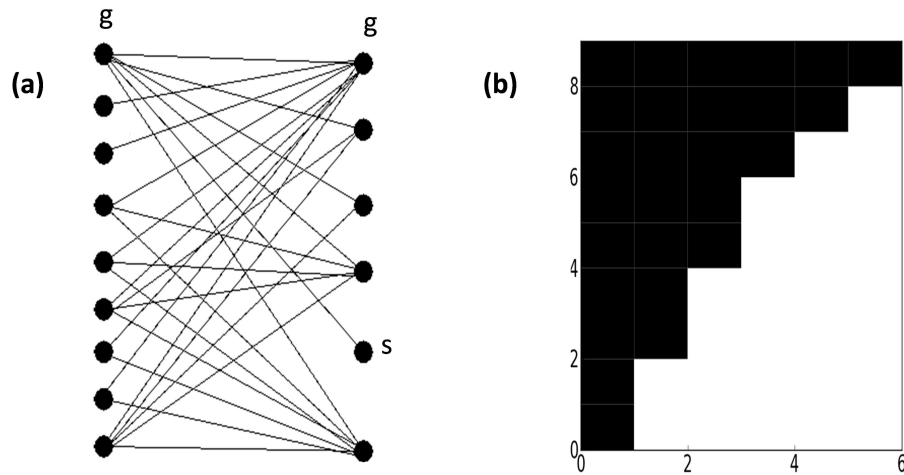
During the study of real networks, it has often been observed that these networks display certain structures that could be vital for the functionality of the networks themselves. For example;



**Figure 2.3:** An example of a compartmentalised network. (a) shows a network with 3 compartments while (b) shows the adjacency matrix plot.  $g$  indicates the generalist (most interactive node)

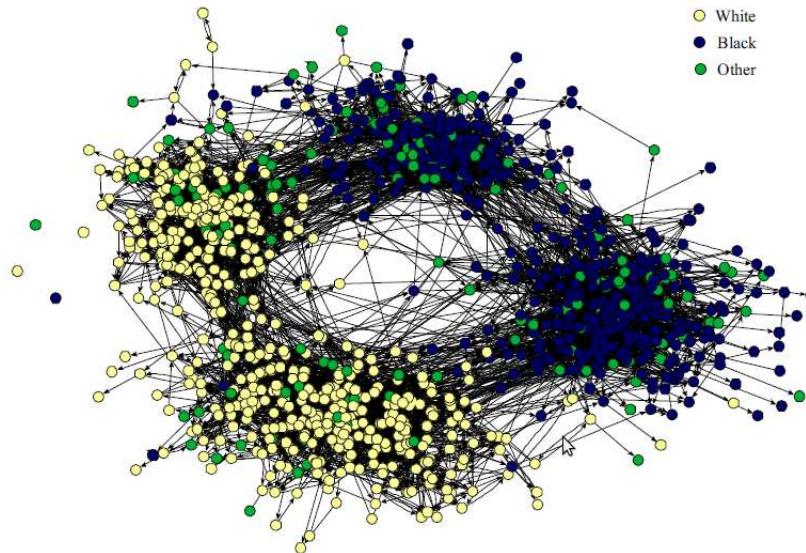
In Figure 2.3, there are 3 sub-networks that seem to function more or less independently although they all belong to the same network. This architecture (structure) is commonly known as compartmentalisation. Entities are connected more within their groups than across other groups. In addition, there are entities connected more than others (such as  $g$ ) yet there are those that seem to be more specialised (connected to only one or two other entities). Figure 2.4 gives light on such a scenario in a bipartite network (a network consisting of two groups with no interactions between nodes of the same group). This organisation where the more specialised entities interact with entities that interact with





**Figure 2.4:** A hypothetically perfectly nested network. (a) shows the nested network while (b) is the matrix representation of the bipartite network.  $g$  and  $s$  are the generalist and specialist entities respectively.

the generalist entities is what is termed as nestedness. Although simple drawings help us to visualise these structures easily, most networks are more complex than the networks in Figures 2.3 and 2.4. Take an example of the friendship network presented by Newman (2003).



**Figure 2.5:** “Friendship network of children in a U.S. school. Friendships are determined by asking the participants, and hence are directed, since A may say that B is their friend but not vice versa. Vertices are color coded according to race, as marked, and the split from left to right in the figure is clearly primarily along lines of race. The split from top to bottom is between middle school and high school, i.e., between younger and older children.” Picture courtesy of James Moody.

Friendships in a school often seem random however, Figure 2.5 clearly shows that students were friends according to race and age. Other complex networks such as th2.5 include sexual networks, citation networks, telephone networks, metabolic networks, the food web, to name but a few. The study of such networks and community interactions has been crucial in the fields of sociology, technology, physics, biology and ecology. Bridging the gap between the different disciplines has led to insightful discoveries in either fields. For instance, (i) it is well documented that the distribution of number of edges per node (degree distribution) in most networks follows a power law (Boccaletti *et al.*, 2006); (ii) recently, Fortuna *et al.* (2010) argued that the correlation between the degree of nestedness and the degree of compartmentalisation is not always negative as it has been known for a long time, but is rather dependent on the network connectance (the proportion of observed links or edges in a network, *sensu* Williams, 2011); (iii) the observed architectural patterns have a fundamental impact on the stability and functionality of different systems (Bastolla *et al.*, 2009; Stouffer and Bascompte, 2011; Thebault and Fontaine, 2010).

## 2.3.2 Descriptors and measures of a network

### 2.3.2.1 Connectance

Connectance is defined as the proportion of links that are observed in a network (Williams, 2011). For a given network, connectance( $C$ ) is calculated as

$$C = \frac{l}{s^2},$$

where  $l$  denotes the number of links and  $s$  the number of nodes in the network. If the network does not allow vertices to link to themselves, the connectance is given by

$$C = \frac{l}{s(s-1)}.$$

For a connected bipartite network however,

$$C = \frac{l}{nm},$$

where  $n$  and  $m$  denote the number of nodes in the two groups or 'partite' sets in the network (Williams, 2011). Much as one would imagine that  $0 \leq C \leq 1$ , some of the values in that range are meaningless. For example, a connectance of zero implies that the network has no links. Also, for any connected network, there exists a minimum number of links to ensure that all nodes are connected. The minimum number of links required for any graphs containing  $s$  nodes to be connected is  $s - 1$  hence  $C_{min} \leq C \leq 1$  where

$$C_{min} = \frac{s-1}{s^2}$$

This implies that for a bipartite network,

$$C_{min} = \frac{n + m - 1}{nm}.$$

Connectance is such an important property that it has been said to foster quite a number of other properties such as the degree distribution, nestedness, compartmentalisation, which are known to have important implications for stability in various systems.

### 2.3.2.2 Degree distribution

The degree distribution of a network can be roughly defined as the proportion of nodes with a given number of links (Shirley and Rushton, 2005) or the frequency distribution of degrees in a network. Early analyses of networks which were basically in the field of social sciences revealed that the degree distribution normally follows a power law (Jackson, 2008). This discovery has had a lot of implications such as vulnerability of these networks to the loss of nodes (Boccaletti *et al.*, 2006; Dunne *et al.*, 2002*b*). For instance, after losing a node, networks with skewed degree distribution are always at risk of losing many other nodes (Dunne *et al.*, 2002*b*; Boccaletti *et al.*, 2006). In fact, most of the studies on network properties are centred around this property. It is assumed that the shape of the degree distribution shows how co-evolutionary processes constrain the number of specialists and generalists in a network (Williams, 2011). As a consequence, various models have been proposed to generate this structure. In Section 2.3.3, we will give examples of some of the models that have been used to predict the degree distribution of a network.

### 2.3.2.3 Modularity

As the availability of data on various networks has increased both in number and complexity, the development of measures as a way of quantifying the structure of these networks has become both a tool and a need for us to extract as much information as possible from these data sets. Although a number of measures have been proposed to quantify the level of compartmentalisation in a network, the measure due to Newman and Girvan (2004) has been the most widely used. Fortuna *et al.* (2010) pointed out that this measure may fail to detect well-defined small communities in large networks, however, we chose to use it because we excluded large networks from the study. This measure assumes that nodes in the same module have more links between them than one would expect for a random network. The measure  $Q$  is given by

$$Q = \frac{1}{2l} \sum_{ij} \left( A_{ij} - \frac{k_i k_j}{2l} \right) \delta(C_i, C_j), \quad (2.3.1)$$

where  $A_{ij}$  is 1 if  $i$  and  $j$  have a link between them and 0 otherwise,  $l$  is the total number of links in the network,  $\frac{k_i k_j}{2l}$  is the expected number of links between nodes  $i$  and  $j$  ( $k_i$  and  $k_j$

are the degrees of the nodes),  $C_i$  denotes the community (module) in which node  $i$  belongs and  $\delta(C_i, C_j) = 1$  when  $i$  and  $j$  belong to the same module and 0 otherwise. Different algorithms have been developed based on Equation (2.3.1) although their optimisation techniques are different. In this study, we use the software NETCARTO, which uses the simulated annealing as the modularity optimisation technique (Guimera and Amaral, 2005a,b).

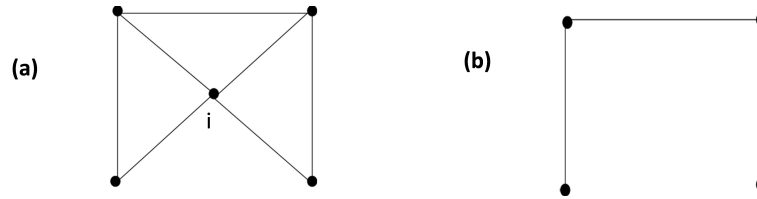
#### 2.3.2.4 *Simulated annealing*

Simulated annealing is a stochastic optimisation technique that enables one to obtain a desired configuration of a system (Guimera and Amaral, 2005b). For instance, we may desire to minimise a given cost function. Starting with a system in a known configuration, standard rearrangement operations are applied until a rearranged configuration that improves the cost function is discovered (Kirkpatrick *et al.*, 1983). The rearranged configuration then becomes the new configuration of the system. The search for a better configuration continues until no further improvement can be made. Often, this search gets stuck in local optimum. Therefore, the process is carried out several times, starting from different randomly generated configurations (Kirkpatrick *et al.*, 1983). From all trials, the best result is saved as the final solution.

For instance, in their algorithm, Guimera and Amaral (2005b) introduce a computational temperature,  $T$ . The high-cost configurations of the system are explored when  $T$  is high and the low-cost ones when  $T$  is low. Starting with high temperature and then gradually decreasing it, the system eventually settles in a certain minimum. To maximise modularity, the cost function,  $C = -M$ , is considered. At each temperature, some nodes are moved from one module to another and hence updating the cost function. Finally, the configuration that minimises the cost function  $C$  is the modularity.

#### 2.3.2.5 *Clustering coefficient*

For the sake of the comparative study that will be presented in Chapter 3, we here present another measure of the level of compartmentalisation in a graph (network). Suppose that a node  $i$  has at least two neighbours in a graph  $G$ . This measure first focusses on determining whether neighbours of a node are neighbours to each other. In other words, how likely is  $a_{jm} = 1$  for two neighbours  $j$  and  $m$  of  $i$ , where  $a_{jm}$  denotes an entry in the adjacency matrix of the graph  $G$ . The likelihood is obtained by counting the number of edges  $e_i$  in a subgraph, say  $G_i$ , consisting of the neighbours of  $i$  (Boccaletti *et al.*, 2006). The local clustering coefficient  $c_i$  is then given by the ratio of  $e_i$  to the total number of possible edges in that subgraph  $G_i$  ( $\frac{k_i(k_i-1)}{2}$ ), where  $k_i$  is the number of nodes neighbouring  $i$ . That is,



**Figure 2.6:** Calculation of the clustering coefficient of a graph. (a) shows a graph say  $G$  while (b) shows the graph  $G_i$  consisting of neighbours of node  $i$ .

$$c_i = \frac{2e_i}{k_i(k_i - 1)}.$$

The clustering coefficient  $C$  of the whole graph is given by the average of all local clustering coefficients hence

$$C = \frac{1}{N} \sum_{i=1}^N c_i,$$

where  $N$  denotes the order (number of nodes) of the graph.

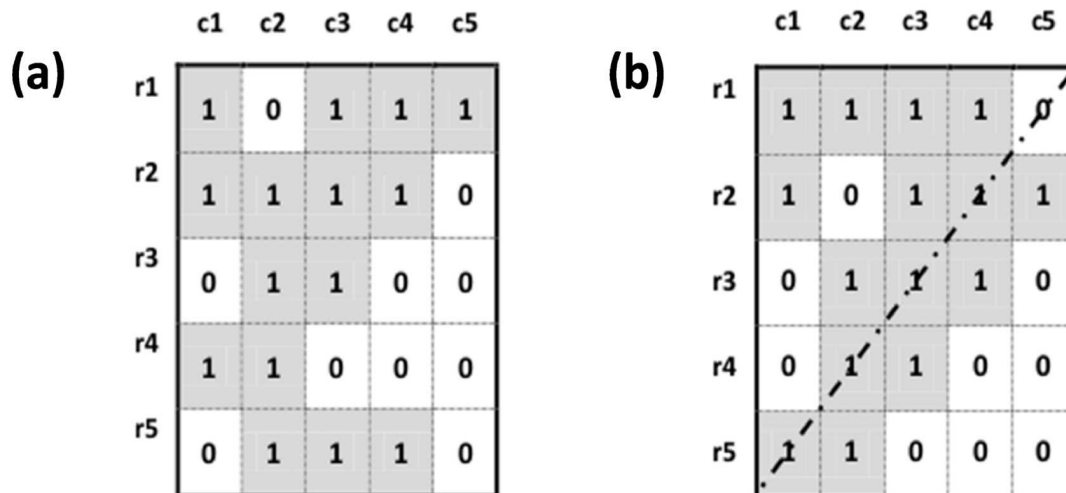
### 2.3.2.6 Nestedness

Like with the modular structure, different authors have suggested various measures of nestedness among which the matrix temperature (Atmar and Patterson, 1993) has been used the most (Almeida-Neto *et al.*, 2008). The matrix temperature quantifies whether the observed arrangement of 1's and 0's deviates from an isocline that describes perfect nestedness. Figure 2.7 illustrates the computation of the matrix temperature. Stud-

ies have shown that the matrix temperature is not sufficient for nestedness detection (Almeida-Neto *et al.*, 2008). This is because this measure focusses on specific matrix properties (eg. unexpected presences or absences), which may lead to type I statistical errors. Recently, a new measure of nestedness which relaxes the weaknesses of the matrix temperature has been proposed by Almeida-Neto *et al.* (2008). This new measure is based on two fundamental properties as per the meaning of nestedness: (i) the decreasing fill (DF) and (ii) the paired overlap (PO). Consider a matrix with  $m$  rows and  $n$  columns. Let row  $i$  be located at an upper position from  $j$ , column  $k$  at a left position from column  $l$  and let the marginal total (column or row sum) be denoted by  $MT$ . Then,

$$DF_{xy} = \begin{cases} 100, & \text{if } MT_y < MT_x \\ 0, & \text{Otherwise,} \end{cases}$$

where  $x$  and  $y$  are either rows  $i$  and  $j$  or columns  $k$  and  $l$ . The paired overlap is defined as the percentage of 1's in  $y$  located at identical positions to those in  $x$ . For any left-to-right column pair (or up-to-down row pair), the authors of the new measure of nestedness define the degree of paired nestedness as



**Figure 2.7:** Calculation of the matrix temperature. (a) is an interaction matrix whose level of nestedness is to be measured. (b) is a rearrangement of (a) via the matrix temperature algorithm. The diagonal dashed line represents the boundary of perfect nestedness

$$N_{paired} = \begin{cases} 0, & \text{if } DF_{xy} = 0 \\ PO_{xy}, & \text{if } DF_{xy} = 100. \end{cases}$$

Nestedness is then measured as the average of  $N_{paired}$  over all possible row and column pairs. It is given by

$$NODF = \frac{\sum N_{paired}}{\frac{n(n-1)}{2} + \frac{m(m-1)}{2}}$$

for an  $m \times n$  matrix, where  $\frac{n(n-1)}{2} + \frac{m(m-1)}{2}$  represents all possible pairs. Figure 2.8 illustrates the calculation of NODF for the interaction matrix in Figure 2.7 (a).

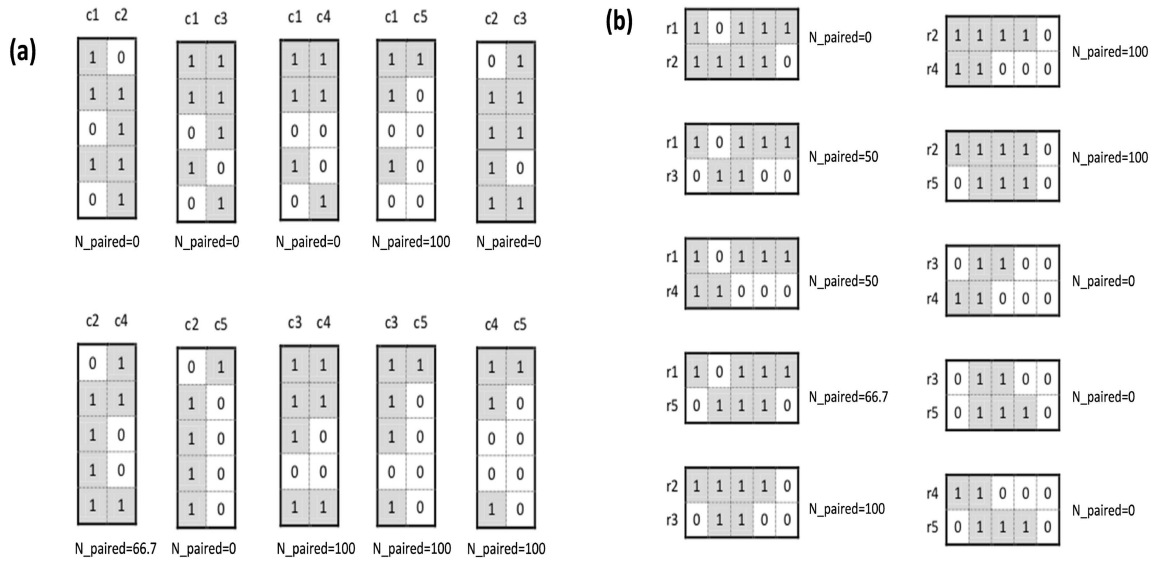
We chose to use this measure due to its consistence in quantifying the level of nestedness as reported by (Almeida-Neto *et al.*, 2008). One of the authors, R. Guimera, wrote the software package ANINHADO, which will be used for quantifying nestedness throughout this thesis.

### 2.3.3 Some network models

Although a few intrinsic properties of networks have been known, the mechanisms generating them are still unclear. We here present some of the basic models that have been proposed to mimic the growth of networks.

#### 2.3.3.1 Random networks

Consider a set of nodes  $v_1, v_2, \dots, v_n$ . If every two nodes have an edge between them, the total number of edges would be  $\frac{n(n-1)}{2}$ . To construct a network with  $L$  links, Erdos and Renyi



**Figure 2.8:** Calculation of NODF. Panels represent all possible row and column pairs from the matrix in Figure 2.7 (a) and the corresponding values of  $N_{paired}$ .

(1960) proposed that such a network can have the property that all nodes pairs have the same probability of having a link between them. This network model assumes that all nodes in a network are equally important. Using only the number of nodes and edges to describe a network is so ambiguous that a number of different networks can be created from the same description. Although the analysis of this model revealed that it did not capture a lot about the real world networks (Boccaletti *et al.*, 2006), it motivated research into the use of network models to analyse real network patterns. Some of the suggestions intended to improve this model include the use of a non Poisson degree distribution (Boccaletti *et al.*, 2006).

### 2.3.3.2 Small world networks

This model was motivated by the fact that by then, network models assumed to be either regular (all nodes having the same degree) or random (like the random network model above). Watts and Strogatz (1998) argued that social, biological and technical networks lay mid way between the two models. Starting with a regular network (all nodes with same degree), they defined a rewiring rule by which the initial network evolved into what they termed as “a small world” (a network with a short characteristic path length; see Equation (1.3.1)). In their rule, each edge of the  $k$ -regular (each node with degree  $k$ ) network on  $n$  nodes was randomly rewired with probability  $p$ . This simple rule generated networks that had the small world property and high clustering coefficients; two properties that have been observed in various real world networks. Owing to the evolutionary behaviour of networks, procedures based on the addition of nodes into an existing network have been proposed to capture the structures of real networks (Boccaletti *et al.*, 2006).

### 2.3.3.3 Scale free networks

After exploring a large data set of large networks, Barabasi and Albert (1999) showed that the probability  $p(k)$  that a node in a network interacts with  $k$  other vertices decays as a power law, i.e.,  $p(k) \approx k^{-\gamma}$ . This feature could not be captured by any of the random models. They noted that the random and small world models made an unrealistic assumption that networks are static (the number of nodes does not change). In addition, the two models assumed that all nodes in a network are equally important (having the same probability of having an edge). The argument presented by Barabasi and Albert (1999) was based on two processes that they believed could be controlling the development of networks: (i) the network growth and (ii) the preferential attachment. Of course, every network grows by addition of nodes but also, a node with many edges has a higher chance of having more links added to it. Unlike the two previous models, the probability of a node with  $k_j$  edges already is given by  $p(k_j) = \frac{k_j}{\sum k_i}$ , where  $k_i$  denotes the degree of node  $i$ . Basing on this reasoning, they constructed networks that display the power law degree distribution, a property that has been investigated in various real world networks to date. In fact, in the next chapter, we investigate whether antagonistic networks fall under this group of networks.

## 2.4 Ecological Networks

In ecology, networks are composed of species with different types of interactions between them. We here discuss two of such interactions, mutualistic and antagonistic, with detailed focus on the latter.

### 2.4.1 Mutualistic networks

Morin (1999) defines an interaction network as mutualistic if all participants benefit from that interaction. The main examples of such networks are pollination and seed-dispersal networks. These examples are fundamental for ecosystem function owing to the fact that they often happen at the bottom of the food web. Studies about the structure of such networks have revealed that they display power law degree distribution and high levels of nestedness (Bascompte and Jordano, 2007; Bascompte *et al.*, 2003; Piazzon *et al.*, 2011). This has often been attributed to their low connectance which is in fact constrained by phylogenetic (such as life histories) and phenotypic (such as species morphology) properties. For instance, a bird with a small beak may not disperse a large fruit and similarly an insect with a short tongue may not pollinate a flower with a long corolla. The structural properties of these networks are therefore indicative of the co-evolutionary processes, and indeed have great implications for the stability and functioning of these networks



(Bascompte and Jordano, 2007).

### 2.4.2 Antagonistic networks

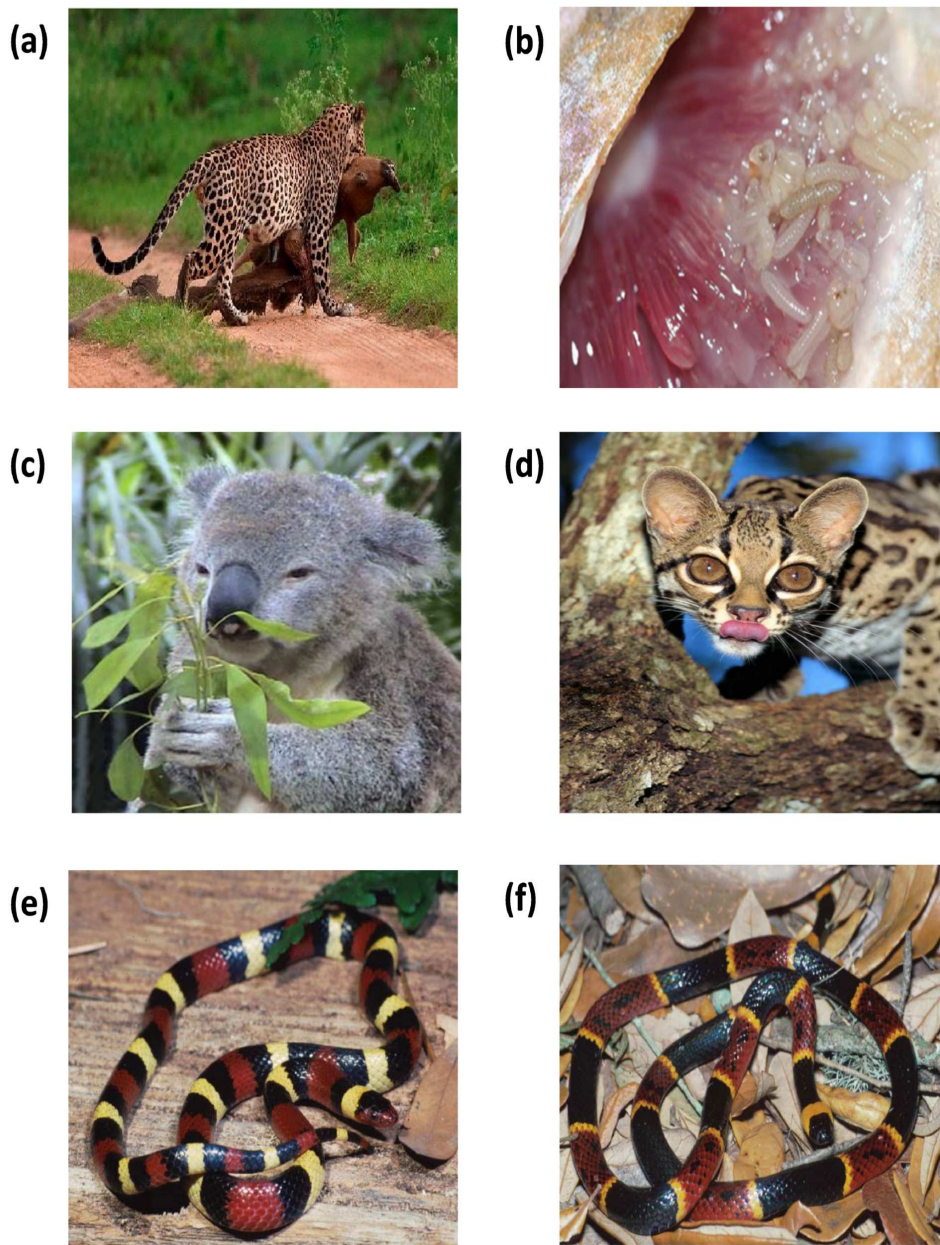
The interest of this study lies in networks that are bipartite and antagonistic in nature. Bipartite networks comprise of two types of nodes (consumers and resources) with edges between them and no edges between nodes of the same type. Antagonistic networks consist of mainly predator-prey (see Figure 2.9 (a)), host-parasite (see Figure 2.9 (b)) and plant-herbivore (see Figure 2.9 (c)) networks. Mimicry too can be categorised as antagonistic in a sense that some predators use it to exploit their preys (see Figure 2.9 (d)) while some preys use it to hide from their predators (see Figure 2.9 (e)).

#### Properties of Antagonistic Networks

Most networks have been defined as “small world” and “scale free”, however, studies have shown that ecological networks such as antagonistic networks do not necessarily display these properties (Dunne *et al.*, 2002a). This is because most ecological networks have much shorter path lengths, few compartments and are even more connected than other non-ecological real world networks. Although evidence shows that the degree distribution of ecological networks differs from being random, it does not have a specific form that it follows (Dunne *et al.*, 2002a). Some networks display power law, others truncated power law, exponential, and some uniform degree distributions. The difference in this property has been attributed to network complexity, usually measured by connectance. Networks with low connectance display power law degree distribution, the intermediately connected display exponential degree distribution while the highly connected display uniform degree distribution (Dunne *et al.*, 2002a). It is not surprising though, that less connected networks display power law degree distributions, considering the fact that most of the networks that have been studied aside from the ecological ones have many nodes but with few links between them. The few links therefore constrain the number of generalists in a network, hence the power law distribution.

Antagonistic networks have so much been associated with a modular (compartmentalised) structure, which is said to be indicative of the evolutionary dynamics there in. Recently, Thebault and Fontaine (2010) used a consumer-resource model to study the stability of antagonistic networks and found that resilience and persistence are correlated with the level of modularity in these networks. However, a clear understanding of the emergence of this structure is still lacking.

Whether antagonistic networks are nested or not is still a controversial issue in the literature. Some studies show that antagonistic networks are not nested (Thebault and Fontaine, 2010; Genini *et al.*, 2012; Meskens *et al.*, 2011) while others have proved the opposite



**Figure 2.9:** Examples of antagonistic interactions. Panels (a) courtesy of Vinay S. Kumar, (b) and (c) courtesy of Hsueh-Cheng Ho show predator-prey, host-parasite and plant-herbivore interactions respectively: A male leopard preying on an Indian bison, fish gills attached by parasites and a Koala bear feeding on a plant. (d) courtesy of J. H. Pete Carmichael shows a cat that mimics monkey sounds to lure its prey while the mimicry displayed by panels (e) and (f) is mainly for defence (Harper Jr and Pfennig, 2008). The non-venomous scarlet king snake in panel (e) mimics the venomous coral snake in panel (f) with the hope that predators will leave it alone.

(Bellay *et al.*, 2011; Fortunato, 2010; Kondoh *et al.*, 2010; Patterson *et al.*, 2009; Pires *et al.*, 2011; Piazzon *et al.*, 2011). However, certain studies clarify that the difference can be attributed to the use of different null models (Fortuna *et al.*, 2010; Timi and Poulina, 2008). We will therefore discuss the concept of null models in Section 2.4.3.

### 2.4.3 Null models

The use of null models has yielded great insight into the structure of ecological networks and the mechanisms that foster the development of different structures such as nestedness and compartmentalisation (Gotelli and Graves, 1996). A null model is defined as “a pattern generating model that is based on randomisation of ecological data or random sampling from a known or imagined distribution” (Gotelli and Graves, 1996). As mathematical models aim to include important mechanisms to capture reality, null models deliberately exclude these potential mechanisms in order to test the impact of these mechanisms on the system. We here present a number of null models that have been used in order to investigate the significance of modularity or nestedness.

#### 2.4.3.1 Erdo’s random graph (Er or R)

The Erdos-Renyi random graph presented in Section 2.3.3.1 is a null model. It assumes that all nodes of a graph are equally important and therefore randomly assigns presences or 1’s in an interaction matrix. This model generates networks whose connectance is the same as for the network whose structure is to be tested.

#### 2.4.3.2 Probabilistic model (CE or P)

This model assumes that the probability of having an interaction is proportional to the degree of both nodes in the interaction (Bascompte *et al.*, 2003). In particular, the probability of a link between a consumer and a resource is taken to be the arithmetic mean of the interacting probabilities of the focal consumer and resource species (Kondoh *et al.*, 2010). In other words, nodes with more links have a higher chance of being added more. For example, according to this null model, in the matrix

$$\begin{pmatrix} 0 & 0 & 0 & 1 \\ 1 & 1 & 1 & \boxed{0} \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \end{pmatrix},$$

the circled position has a higher probability of being assigned a presence (or 1) if one more link was required. In fact, that probability is  $\frac{3+3}{2}$ . This model generates networks whose connectance may not necessarily be the same as for the network that is to be tested.

### 2.4.3.3 Fixed model

This null model can be implemented in three different ways hence three different models. It can generate networks which have: (i) the same column sums ( $F_c$ ), (ii) the same row sums ( $F_r$ ) or (iii) the same row and column sums simultaneously ( $F$ ) as for the network whose structural significance is to be tested (Gotelli, 2000). The following matrix illustrates how column and row sums are maintained in these models.

$$\left( \begin{array}{cccc} 0 & 0 & 0 & 1 \\ 1 & \overset{F}{\rightleftarrows} & 1 & 1 & 0 \\ 0 & \overset{F}{\rightleftarrows} & 0 & 0 & 1 \\ 0 & 0 & 0 & \overset{F_r}{\rightleftarrows} & 1 \\ F_c \left( \begin{array}{c} 0 \\ 1 \end{array} \right) & 0 & 0 & 0 & 0 \end{array} \right)$$

For model  $F$ , the exchange of 1's for 0's and vice versa happens simultaneously for both positions in the matrix. In other words, an array of  $\{1,0\}$  is exchanged with one of  $\{0,1\}$ . The three versions of the model respectively imply that the number of resources per consumer, the number of consumers per resource and the number of interacting partners per species do not change. For this reason, all the models maintain the connectance of the network whose structure is to be tested. We notice that the third version ( $F$ ) is the most conservative of them all since it maintains the row and column sums simultaneously. Consequently, it is not prone to type II error, unlike the other models (Gotelli, 2000). A lot of null models have been proposed but the scope was limited to only the ones we refer to in the forthcoming chapters. However, more details and examples can be found in Gotelli (2000).

### 2.4.4 Switching in antagonistic interaction

In the first section of this chapter, we demonstrated that antagonistic interactions can be modelled by consumer-resource models. However, most of these models have focused on the effects of a particular interaction behaviour such as predation, leaving out species adaptation mechanisms. Although natural selection and evolutionary history are important for determining who interacts with whom (Nuismer *et al.*, 2007; Prado and M., 2004; Vazquez *et al.*, 2009), evidence has shown that interacting species often switch their partners in response to environmental changes and the availability of resources (Tilman, 1986; Pasteur, 1982; Abrams and Matsuda, 1993; van Baalen *et al.*, 2001; Murdoch, 1969). For instance, in a predator-prey network, the predator often switches between the prey species

depending on how much it benefits from the interaction with an individual prey species. On the other hand, the prey too may devise means of minimising the predator exploitation, hence forcing the predator to switch. These interaction switches reflect the adaptive behaviour of species and could play a significant role in the development of network architecture. Recently, Zhang *et al.* (2011) present a model for depicting mutualistic interactions in which species switch their partners to maximise fitness. In this model, a random network evolves into a nested network, with the predicted nestedness fitting observations from 81 empirical networks. Their results highlighted an interaction switch as an important behavioural strategy for species to adjust their roles in ecosystems.

### 2.4.5 Robustness

Traditionally, the stability of dynamical systems is determined by the analysis of its trajectories, considering both local and asymptotic behaviours. Unfortunately, once the dimensionality of the system becomes large, these kinds of analysis techniques become complicated or even impossible. Recently, it has become common to find various stability analysis techniques and measures that cater for scenarios where the traditional techniques fail. Robustness is one of such measures that have been used to quantify the response of networks (communities) to the loss of nodes (species). Although it has been defined in detail differently by different authors depending on the specific system under study, all definitions have quantified it as a function of the number of secondary extinctions that result from the removal of nodes from a network. Take an example of Dunne *et al.* (2002b). They define robustness as the fraction of species that needs to be removed to result in a greater than or equal to 50% total loss of species in a food web.

Dunne *et al.* (2002b)'s study aimed at processes that could enhance robustness in food webs, which is the ultimate goal of any conservation ecologist. To achieve their target, they compiled 16 food webs from literature and analysed the networks' responses to the removal of species (imitating species loss). They had previously noted that unlike other networks, food webs lacked the small world property hence their response to perturbation could be different. In their algorithm, they sequentially removed nodes from the network and after each node removal, species that had no links were declared extinct. This process was carried out considering four criteria.

- random removal of species
- removal of generalist species
- removal of specialist species
- removal of generalists that are not basal species

Their analysis initiated and revealed insights into the impact of species loss on a network. For example, they highlighted that (i) the removal of generalist species causes more secondary extinctions than the removal of specialists (ii) robustness increases with connectance (iii) depending on the species' function in the network, its removal can be catastrophic. To examine the claims made by Dunne *et al.* (2002b), Estrada (2007) analysed networks with the same connectance but with different degree distributions and expansibility (the absence of cut vertices or a vertex cut [see Section 1.3.1] in the food web, whose removal separates the network into large isolated clusters) and in fact found that connectance alone cannot determine robustness. In addition to high connectance, networks needed to have uniform degree distribution and good expansibility in order to be highly robust. Although it turned out that networks with high connectance had a higher chance of having uniform degree distributions and good expansibility, it was not always the case. Therefore, it is not only how many links there are in a network but also how these links are distributed (Brose, 2011).

Although such observations have created a clearer picture of network attributes that foster robustness, the sequential removal of species has received a number of criticisms (Thierry *et al.*, 2011; de Visser and Olf, 2011). This is because the usage of these sequences indirectly assumed that species lack adaptive measures in response to perturbation and that the species abundance remains unchanged. Of course, species adapt to changes in their environment hence affecting their abundance. To address the aforementioned gaps, a number of studies have tried to include the interaction switch in modelling the response of different ecosystems to the removal of species, and to track the changes in species abundance. However, as far as we know, studies that have investigated the change in species abundance have not considered the adaptive behaviour (Eklof, 2006) and *vice versa* Thierry *et al.* (2011); de Visser and Olf (2011). Nevertheless, these studies have revealed that the topological approach (declaring species extinct based on the number of links that they have) underestimates the effect of species extinctions, implying that considering the species population dynamics is necessary if we are to understand the robustness of networks to the loss of species. We therefore intend to address this issue by simulating species extinctions using the topological approach, but allowing the species abundance to play a role in the adaptive process.

# Chapter 3

## Data collection and analysis

### 3.1 Introduction

The scarcity of data has been one of the controlling factors that could have led to controversial results in the analysis of ecological networks (Dunne *et al.*, 2002a). Fortunately, with the improvement in technology, a lot of data has been collected and published. This chapter serves as a mirror into the kind of data that has been collected for analyses and comparisons in this thesis. Properties such as modularity, nestedness, connectance and the degree distribution observed in real networks are quantified where applicable, and the relationships between these properties are discussed.

### 3.2 Data collection

All the networks were obtained from published materials, and their data was collected from both terrestrial and aquatic habitats. In particular, we obtained host-parasite networks from both types of habitats while plant-herbivore networks were only aquatic. The herbivore networks were obtained by extracting out the first two trophic levels (leaving out the unidentified species) of the predator-prey food webs on the interaction web data base . Although most of the networks on the interaction web data base ([www.nceas.ucsb/interactionweb/index.html](http://www.nceas.ucsb/interactionweb/index.html)) are recorded as presence/absence matrices, some networks are presented as species abundance, frequency or prevalence. Nevertheless, we obtained presence/absence matrices for all data sets either directly or by replacing frequencies or abundances by presences. In total, we obtained 61 networks, 33 host-parasite and 28 plant-herbivore (see appendix A for details).

### 3.3 Diversity and connectance

The data in this study includes networks that contain the number of species (also known as network diversity) within the range of 18–130, the number of interactions in the range of 33–736 and connectance (defined for bipartite networks) in the range of 9.87–55.56%. These ranges lie within those commonly used in ecological data analyses and so we believe that the data is valid and reliable. In fact, most of the data has been used for analyses in recent publications (Krasnov *et al.*, 2012; Fortuna *et al.*, 2010).

### 3.4 Degree distribution

In most network studies, such as social, biological or even ecological, there has been a tendency of investigating whether the network degree distribution fits to a power law, thereby investigating the scale-free property. It is indeed an important network property due to its implications for community structure (such as its influence on network robustness as seen in Section 2.4.5). However, as observed from literature, many ecological networks do not possess this property. This section is devoted to fit different models to describe the degree distribution followed by each of the 61 networks. For each network, we fit the different models to the degree distribution of the whole network, the resource species' degree distribution and the consumer species' degree distribution. Connectance being a vital network property, we also investigate its relationship with the degree distribution.

#### 3.4.1 Degree distribution Models

##### 3.4.1.1 Power law distribution

The power law distribution is given by

$$p(k) = Ck^{-\alpha} \quad \forall k > k_{min},$$

where  $C$  is the normalising constant,  $k_{min}$  is the minimum possible value of  $k$  and  $\alpha$  is the scaling constant (Seal, 1952). Considering that the distribution with  $\alpha \leq 1$  is infeasible, we assume that  $\alpha > 1$ . As a result, the discrete power law distribution satisfies the equation,

$$\sum_{k=k_{min}}^{\infty} p(k) = 1. \quad (3.4.1)$$

Solving Equation (3.4.1) when  $k_{min} = 1$  gives

$$C = \frac{1}{\zeta(\alpha)},$$



where

$$\zeta(\alpha) = \sum_{n=1}^{\infty} \frac{1}{n^{\alpha}},$$

and the function  $\zeta(\alpha)$  is the Riemann zeta function (Clauset *et al.*, 2009). The maximum likelihood parameter estimation method was employed to estimate  $\alpha$ . Given the normalising constant  $C$ , the log likelihood function  $L$  for the power law is given by

$$\begin{aligned} L &= \log \prod_{i=1}^n \frac{k_i^{\alpha}}{\zeta(\alpha)}, \\ &= -n \log \zeta(\alpha) - \alpha \sum_{i=1}^n \log k_i, \end{aligned} \quad (3.4.2)$$

where  $k_i$  represents the observed degree for species  $i$ . To fit this distribution, we numerically found the value of  $\alpha$  that maximises the log likelihood function 3.4.2 by taking its derivative, which is given by

$$\frac{\partial L}{\partial \alpha} = -n \frac{\zeta'(\alpha)}{\zeta(\alpha)} - \sum_{i=1}^n \log k_i. \quad (3.4.3)$$

If the right hand side of Equation (3.4.3) is equal to zero, the solution to the obtained equation gives the estimate for  $\alpha$ .

### 3.4.1.2 Truncated power law distribution

The truncated power law distribution is given by

$$p(k) = C k^{-\alpha} e^{-\frac{k}{\lambda}} \quad \forall k > k_{min},$$

where  $C$  is the normalising constant,  $k_{min}$  is the minimum possible value of  $k$ ,  $\alpha$  is the scaling constant and  $\lambda$  is the truncation parameter (Seal, 1952). Similarly, if we consider  $k_{min} = 1$ ,

$$\int_1^{\infty} C k^{-\alpha} e^{-\frac{k}{\lambda}} dk = 1.$$

Using substitution and integration by parts gives

$$C = \frac{1}{\lambda^{1-\alpha} \Gamma(1-\alpha, \frac{1}{\lambda})},$$

where  $\Gamma()$  is the upper incomplete gamma function, which is given by

$$\Gamma(1-\alpha, \frac{1}{\lambda}) = \int_{\frac{1}{\lambda}}^{\infty} k^{-\alpha} e^{-k} dk.$$

The truncated power law distribution being a continuous function needs to be discretised in order to be used to fit the discrete data. We therefore define the discrete case as

$$\begin{aligned} p(k=x) &= \int_{x-0.5}^{x+0.5} p(k) dk, \\ &= \frac{1}{\lambda^{1-\alpha} \Gamma(1-\alpha, \frac{1}{\lambda})} \int_{x-0.5}^{x+0.5} k^{-\alpha} e^{-\frac{k}{\lambda}} dk. \end{aligned}$$

Using substitution and integration by parts gives

$$p(k=x) = \frac{\Gamma(1-\alpha, \frac{x-0.5}{\lambda}) - \Gamma(1-\alpha, \frac{x+0.5}{\lambda})}{\Gamma(1-\alpha, \frac{1}{\lambda})}.$$

For mathematical convenience and for consistency, we compute the log likelihood of the continuous function however, discrete data values are used. This is because the normalising constant is calculated for the continuous function hence,

$$\begin{aligned} L &= \log \prod_{i=1}^n \frac{k_i^{-\alpha} e^{-\frac{k_i}{\lambda}}}{\lambda^{1-\alpha} \Gamma(1-\alpha, \frac{1}{\lambda})}, \\ &= \sum_{i=1}^n \log \frac{k_i^{-\alpha} e^{-\frac{k_i}{\lambda}}}{\lambda^{1-\alpha} \Gamma(1-\alpha, \frac{1}{\lambda})}, \end{aligned} \quad (3.4.4)$$

where  $k_i$  are the observed degrees. The parameters  $\alpha$  and  $\lambda$  were estimated as their values that maximise Equation (3.4.4)

### 3.4.1.3 Exponential distribution

The exponential distribution is defined as

$$p(k) = C e^{-\lambda k} \quad \forall k > k_{min},$$

where  $C$  is the normalising constant,  $k_{min}$  is the minimum possible value of  $k$ , and  $\lambda$  is the rate parameter. Taking  $k_{min} = 1$ , the normalising constant

$$C = \lambda e^{\lambda}.$$

The log likelihood of the exponential function is therefore given by

$$\begin{aligned} L &= \log \prod_{i=1}^n p(k), \\ &= \sum_{i=1}^n (\log \lambda + \lambda - \lambda k_i), \\ &= n \log \lambda + n\lambda - \lambda \sum_{i=1}^n k_i. \end{aligned}$$

We calculated the maximum likelihood estimate for  $\lambda$  by taking the derivative of the likelihood function.

$$\frac{\partial L}{\partial \lambda} = \frac{n}{\lambda} + n - \sum_{i=1}^n k_i.$$

The solution to  $\frac{\partial L}{\partial \lambda} = 0$  gives

$$\hat{\lambda} = \frac{1}{\bar{k} - 1} \quad \text{where} \quad \bar{k} = \sum_{i=1}^n \frac{k_i}{n}.$$

We discretise the function in order for it to fit discrete data as follows.

$$\begin{aligned} p(k=x) &= \int_{x-0.5}^{x+0.5} p(k) dk, \\ &= \lambda e^{\lambda} \int_{x-0.5}^{x+0.5} e^{-\lambda k} dk, \\ &= e^{\lambda} (e^{-\lambda(x-0.5)} - e^{-\lambda(x+0.5)}). \end{aligned}$$

#### 3.4.1.4 Negative binomial distribution

The negative binomial distribution we consider here is of the form

$$p(k) = \binom{k-r-1}{r-1} p^r (1-p)^k \quad \forall k \in \{1, 2, 3, \dots\},$$

where

$$\binom{x}{y} = \frac{x!}{y!(x-y)!},$$

$r > 0$  is a positive discrete parameter and  $p \in [0, 1]$ . Given that the minimum value of  $k$  for the data is 1, we consider a zero-truncated negative binomial distribution. This implies that we fit a probability mass function of the negative binomial type up to some constant  $C$ ; that is

$$p'(k) = Cp(k).$$

Like in the previous distributions, since  $p'(k)$  is probability mass function,

$$\begin{aligned} \sum_{k=1}^{\infty} p'(k) &= 1, \\ \Rightarrow C \sum_{k=1}^{\infty} p(k) &= 1, \\ \Rightarrow C \left[ \sum_{k=0}^{\infty} p(k) - p(0) \right] &= 1, \\ \Rightarrow C[1 - p^r] &= 1, \end{aligned}$$

hence

$$C = \frac{1}{(1 - p^r)}.$$

As a result, the probability mass function of a zero-truncated negative binomial is given by

$$p(k) = \frac{1}{(1 - p^r)} \binom{k - r - 1}{r - 1} p^r (1 - p)^k \quad \forall k \in \{1, 2, 3, \dots\}.$$

The existence and uniqueness of the maximum likelihood estimates for  $r$  and  $p$  are well defined as long as the second sample moment is greater than the sample mean and the estimator does not exist if the second sample moment is less or equal to the sample mean Aragón *et al.* (1992). For each network that satisfied the condition, the zero-truncated negative binomial distribution was fitted otherwise, it was left out. The maximum likelihood function is given by

$$L = -\log(1 - p^r) + \log \Gamma(k + 1) + \log \Gamma(r) + r \log p + k \log(1 - p),$$

where  $\Gamma(x)$  is a gamma function and is given by

$$\Gamma(x) = (x - 1)! \quad , \quad x \in \mathbf{N}.$$

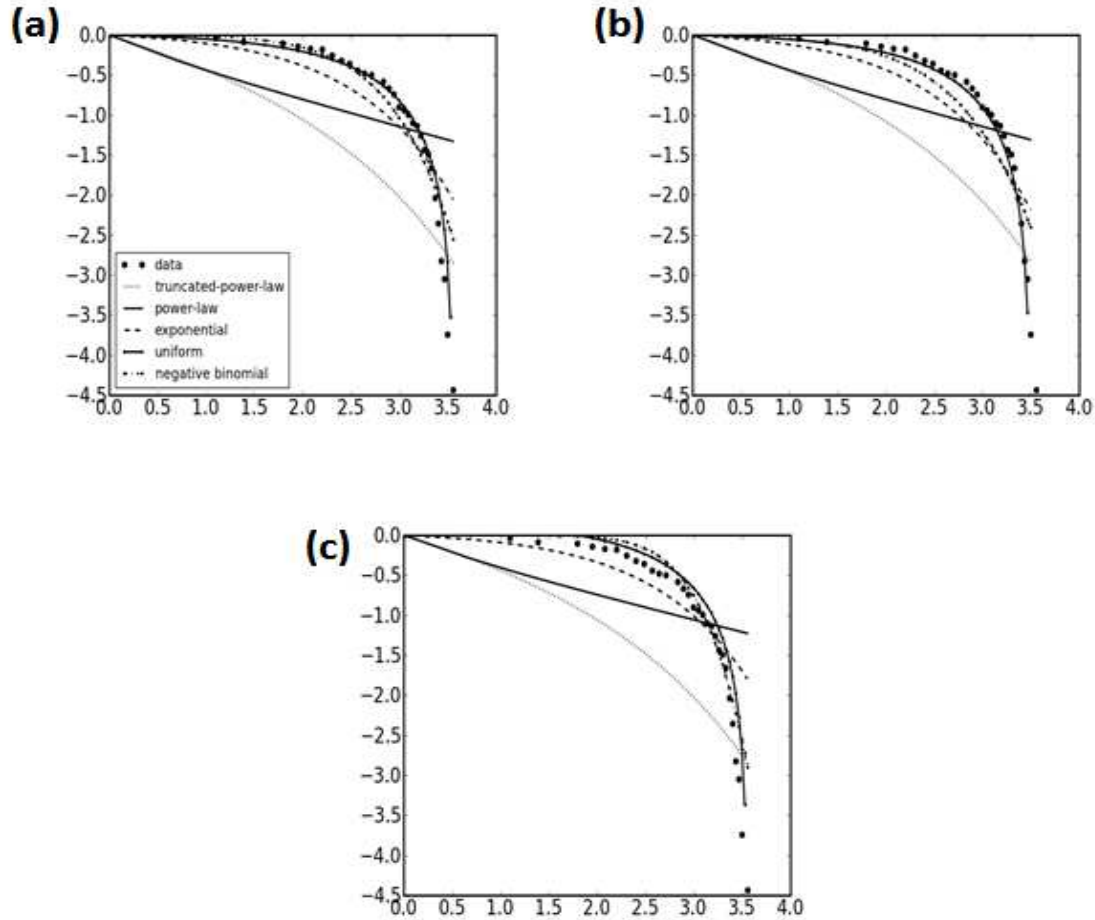
A direct estimation of  $r$  was impossible due to the fact that it is not bounded. We therefore considered its inverse  $\frac{1}{r}$  which is bounded by 0 and 1.

#### 3.4.1.5 Uniform distribution

The uniform distribution is given by

$$p(k) = \begin{cases} \frac{1}{b - a} & , \quad a \leq k < b \\ 0, & \text{otherwise.} \end{cases}$$

Given the form of the uniform distribution, it is a normalised function by default (its normalising constant is 1). For convenience, the continuous form of the distribution was used, however, discrete values were used for fitting. We estimated the parameters  $a$  and  $b$  to be the data minimum and maximum values respectively. Figure 3.1 shows an example of a network whose cumulative degree distribution was fitted with the five different models above.



**Figure 3.1:** An example of a network fitted with the five degree distribution models. Panels (a), (b) and (c) are the log-log plots of the complementary cumulative distribution of the network degree distribution, the consumers' degree distribution and the resources' degree distribution respectively corresponding to network PH11 (see appendix A).

### 3.4.2 Degree distribution model selection

All the above distributions were fitted to data numerically and the distribution that best depicted the data was reported as its degree distribution. The best fit was determined by the computation of the corrected Akaike Information Criterion ( $AIC_c$ ) score for each of the model distributions (Burnham and Anderson, 1992). It is given by

$$AIC_c = 2\beta - 2 \ln(L) + \frac{2\beta(\beta + 1)}{s - \beta - 1},$$

where  $L$  is the maximum value of the likelihood function for a specific model,  $\beta$  is the number of parameters in the model and  $s$  is the total number of species in a network. One needs to note that the  $AIC_c$  score is not used to reject or accept a model but rather to compare different models. In other words, it only provides a relative goodness of the fit.  $AIC_c$  scores were computed for the general network, consumer species alone and resource species alone.

### 3.4.3 Summary of the degree distribution results

After determining the degree distribution for each of the networks, the results were recorded in the order of the network connectance as shown in Table 3.1.

Generally, most of the antagonistic networks in this study did not display power law degree distributions regardless of whether the network is considered as a whole or the consumer or resource species degree distribution considered independently. 8.2% of the networks have power law degree distribution, 15.3% truncated power law, 31.15% exponential, 12.02% negative binomial and 33.33% uniform degree distribution. This implies that the degree of species in bipartite antagonistic networks are mostly uniformly or exponentially distributed.

In order to understand the details of these distributions, we divided the networks into three groups depending on their connectance ( $Co < 19\%$ ,  $19\% \leq Co < 30\%$  and  $Co \geq 30\%$ ) and in fact, distributions were concentrated or dominant in specific ranges of connectance. The truncated power law distribution dominated in the range of connectance  $Co < 19\%$  as observed in Table 3.2, the exponential distribution in the range  $19\% \leq Co < 30\%$ , and the uniform distribution in networks with high connectance ( $Co \geq 30\%$ ). We also investigated the ranges in which each of the distributions is concentrated. The power law was equally concentrated in the ranges  $Co < 19\%$  and  $19\% \leq Co < 30\%$ , the exponential distribution was concentrated in the ranges  $19 \leq Co < 30$ , the truncated power law in the range  $Co < 19\%$  while the negative binomial and the uniform distributions were concentrated in the range  $Co \geq 30\%$  (see Table 3.3). Of course it was unexpected that the power law distribution was equally concentrated in the ranges  $Co < 19\%$  and  $19\% \leq Co < 30\%$  however this could be explained. Compared to many networks that display power law degree distribution, almost all the networks analysed here have high connectance. Moreover, the 50% represents 2 out of 4 networks that displayed power law distribution. When we investigated the the degree distributions for the resource or consumer species alone, we noted that in most cases, the degree distribution for resource species was different from that for the consumer species hence the possibility of the network degree distribution being different from either.

The resource species in networks whose connectance lay in the range  $Co < 19\%$  had the exponential degree distribution dominating while the uniform degree distribution dominated in the rest of the ranges ( $19\% \leq Co < 30\%$  and  $Co \geq 30\%$ ; see Table 3.4). This could imply that resource species are generally uniformly distributed. All the distributions were concentrated in the range  $Co < 19\%$  except for the uniform distribution which was concentrated in the range  $Co \geq 30\%$  as shown in Table 3.5.

The consumer species in networks whose connectance lay in the ranges  $Co < 19\%$  and  $19\% \leq Co < 30\%$  were dominated by the exponential distribution while in  $Co \geq 30\%$ ,

**Table 3.1:** The degree distribution for 61 real networks. ID denotes the network code where HP stands for host-parasite while PH plant-herbivore. R denotes the number of resource species in a network, C the number of consumer species, L the number of links in the network and Co the connectance. The degree distribution fit is represented by Dist for the whole network, R dist for the resource species alone and C dist for the consumer species alone where pl, tpl, exp, NB and UN denote the power law, truncated power law, exponential, negative binomial and uniform distribution respectively. The networks are arranged in order of their connectance, from the least to the highly connected

ID	R	C	L	Co	Dist	R dist	C dist
HP5	33	97	316	9.87	tpl	tpl	NB
PH1	40	37	153	10.34	tpl	exp	pl
HP28	23	35	87	10.81	tpl	pl	exp
PH2	26	16	52	12.5	pl	pl	pl
PH7	35	16	72	12.86	tpl	exp	exp
PH23	35	21	95	12.93	NB	exp	pl
HP13	22	37	106	13.02	NB	pl	exp
PH16	45	30	176	13.04	NB	NB	tpl
PH27	54	24	173	13.35	tpl	exp	tpl
PH17	26	16	57	13.7	tpl	tpl	exp
PH8	25	16	55	13.75	tpl	exp	pl
HP20	21	44	139	15.04	tpl	exp	exp
HP23	16	34	82	15.07	exp	exp	exp
PH18	21	35	117	15.92	exp	exp	tpl
HP3	14	51	114	15.97	pl	pl	UN
PH26	52	22	184	16.08	tpl	NB	tpl
PH24	28	23	108	16.77	tpl	exp	tpl
HP10	20	44	151	17.16	tpl	exp	UN
HP17	11	20	38	17.27	tpl	exp	pl
HP4	17	53	158	17.54	tpl	tpl	UN
PH12	47	30	255	18.09	NB	NB	tpl
PH3	32	28	166	18.53	exp	UN	exp
PH6	11	19	39	18.66	tpl	exp	exp
HP24	28	33	178	19.26	NB	tpl	exp
HP11	14	23	63	19.57	exp	UN	UN
HP22	18	31	112	20.07	exp	exp	exp
PH4	47	30	298	21.13	exp	UN	exp
HP8	19	26	107	21.66	exp	tpl	UN
PH28	6	88	116	21.97	pl	UN	pl
HP2	10	40	91	22.75	tpl	exp	UN
HP27	19	22	96	22.97	exp	exp	UN
HP29	30	35	244	23.24	exp	exp	exp
HP30	28	25	172	24.57	exp	UN	exp
HP7	15	20	74	24.67	exp	UN	exp
PH20	46	24	278	25.18	exp	UN	exp
PH15	37	26	267	27.75	NB	NB	exp
HP26	9	13	33	28.21	UN	UN	UN
PH10	46	33	439	28.92	NB	UN	NB
HP33	18	42	219	28.97	exp	UN	UN
PH9	41	26	314	29.46	exp	exp	exp
PH25	5	64	95	29.69	pl	pl	exp
HP12	15	22	100	30.3	NB	UN	UN
HP15	9	22	60	30.3	exp	exp	exp
PH14	55	32	541	30.74	NB	UN	exp
PH5	51	31	490	30.99	UN	UN	NB
PH13	44	36	493	31.12	NB	NB	exp

**Table 3.1 continued**

ID	R	C	L	Co	Dist	R dist	C dist
PH19	61	37	717	31.77	UN	UN	NB
HP32	15	29	139	31.95	NB	UN	UN
HP25	23	26	209	34.95	UN	NB	UN
HP6	6	25	53	35.33	tpl	UN	UN
HP21	17	18	116	37.91	UN	UN	UN
HP14	7	22	59	38.31	exp	UN	UN
HP16	16	21	129	38.39	UN	UN	UN
HP1	7	29	78	38.42	tpl	UN	UN
PH21	44	20	344	39.09	UN	UN	UN
HP18	11	16	69	39.2	NB	UN	UN
HP31	15	14	86	40.95	UN	UN	UN
PH11	47	37	736	42.32	UN	UN	UN
PH22	55	14	372	48.31	exp	UN	UN
HP9	23	9	108	52.17	exp	UN	UN
HP19	9	9	45	55.56	UN	UN	UN

**Table 3.2:** Dominant degree distribution in networks. For a specific range of connectance, the values in the table indicate the percentage of networks that display a specific degree distribution when the whole network is considered

Range	pl	tpl	exp	NB	UN
$Co < 19\%$	8.7	60.87	13.04	17.39	0
$19\% \leq Co < 30\%$	11.11	5.56	61.11	16.67	5.56
$Co \geq 30\%$	0	10	20	25	45

**Table 3.3:** Where a specific network degree distribution is concentrated. For a specific distribution, the values in the table indicate the percentage of networks that lie in a specific range of connectance when the whole network is considered

Range	pl	tpl	exp	NB	UN
$Co < 19\%$	50	82.35	16.67	33.33	0
$19\% \leq Co < 30\%$	50	5.88	61.11	25	10
$Co \geq 30\%$	0	11.76	22.22	41.67	90

**Table 3.4:** Dominant degree distribution among resource species. For a specific range of connectance, the values in the table indicate the percentage of networks that display a specific degree distribution when resource species alone are considered

Range	pl	tpl	exp	NB	UN
$Co < 19\%$	17.37	13.04	52.17	13.04	4.35
$19\% \leq Co < 30\%$	5.56	11.11	27.78	5.56	50.0
$Co \geq 30\%$	0	0	5	10	85

the uniform distribution dominated (see Table 3.6). The power laws (pl and tpl) were concentrated in the range  $Co < 19\%$ , the exponential in the range  $19\% \leq Co < 30\%$  and the negative binomial and uniform distributions concentrated in the range  $Co \geq 30\%$  (see Table 3.7). In general, high connectance implied uniform or negative binomial



**Table 3.5:** Where a specific resource degree distribution is concentrated. For a specific resource degree distribution, the values in the table indicate the percentage of networks that lie in a specific range of connectance.

Range	pl	tpl	exp	NB	UN
$Co < 19\%$	80	60	66.67	50	3.7
$19\% \leq Co < 30\%$	20	40	27.78	16.67	33.33
$Co \geq 30\%$	0	0	5.56	33.33	62.96

**Table 3.6:** Dominant degree distribution among consumer species. For a specific range of connectance, the values in the table indicate the percentage of networks that display a specific degree distribution when consumer species alone are considered

Range	pl	tpl	exp	NB	UN
$Co < 19\%$	21.74	26.09	34.78	4.35	13.04
$19\% \leq Co < 30\%$	5.56	0	55.56	5.56	33.33
$Co \geq 30\%$	0	0	15	10	75

**Table 3.7:** Where a specific consumer degree distribution is concentrated. For a specific consumer degree distribution, the values in the table indicate the percentage of networks that lie in a specific range of connectance.

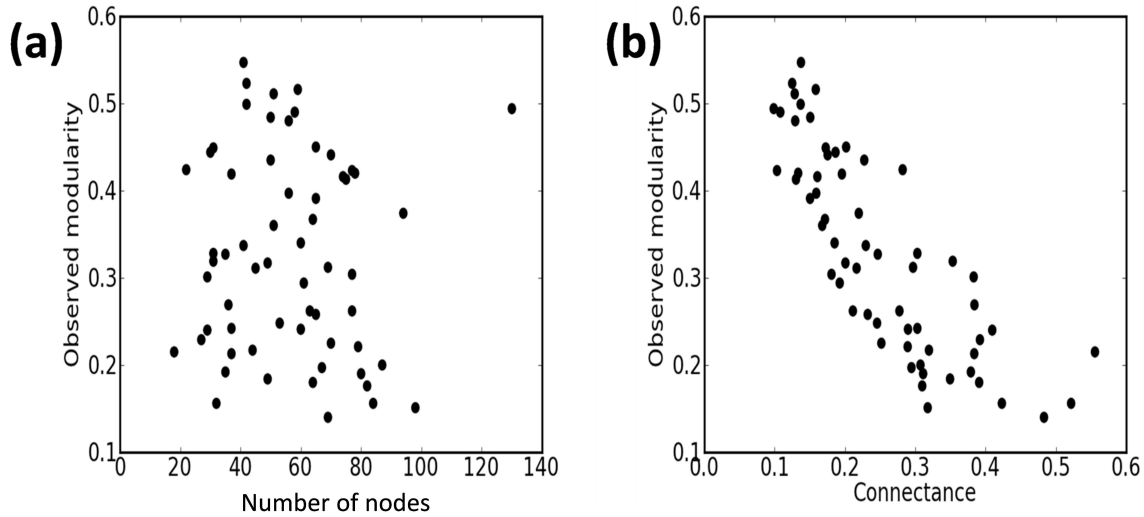
Range	pl	tpl	exp	NB	UN
$Co < 19\%$	83.33	100	38.1	25.0	12.5
$19\% \leq Co < 30\%$	16.67	0	47.62	25	25
$Co \geq 30\%$	0	0	14.29	50	62.5

degree distribution, low connectance implied power law or truncated power law degree distribution and “medium” connectance implied exponential degree distribution.

### 3.5 Modularity

The level of compartmentalisation was quantified using the modularity measure described in Section 2.3.2.3. Using the software NETCARTO, the modularity of networks ranged from 0.140–0.547 (see Table 3.8). Knowing that it is not enough to make conclusions based on just the quantity of a property but rather its statistical significance compared to randomness (Guimera *et al.*, 2004; Gotelli, 2000), we investigated the significance of modularity in these networks using the fixed null model (F) as described in Section 2.4.3. Although the average modularity of the networks was quite high ( $M=0.327$ ), generally, the networks were not significantly modular compared to random networks. Eleven of the 61 networks were significantly more modular than null model networks, 26 were not significantly different from null model networks while 24 were significantly less modular than null model networks. This was largely unexpected that it prompted us to carry

out a literature search on studies that have quantified modularity or nestedness and their significance when included. The findings are summarised in Table 3.9. Regardless of the insignificance, we observed a pronounced relationship between the modularity and connectance (Figure 3.2 (b)) in these networks.

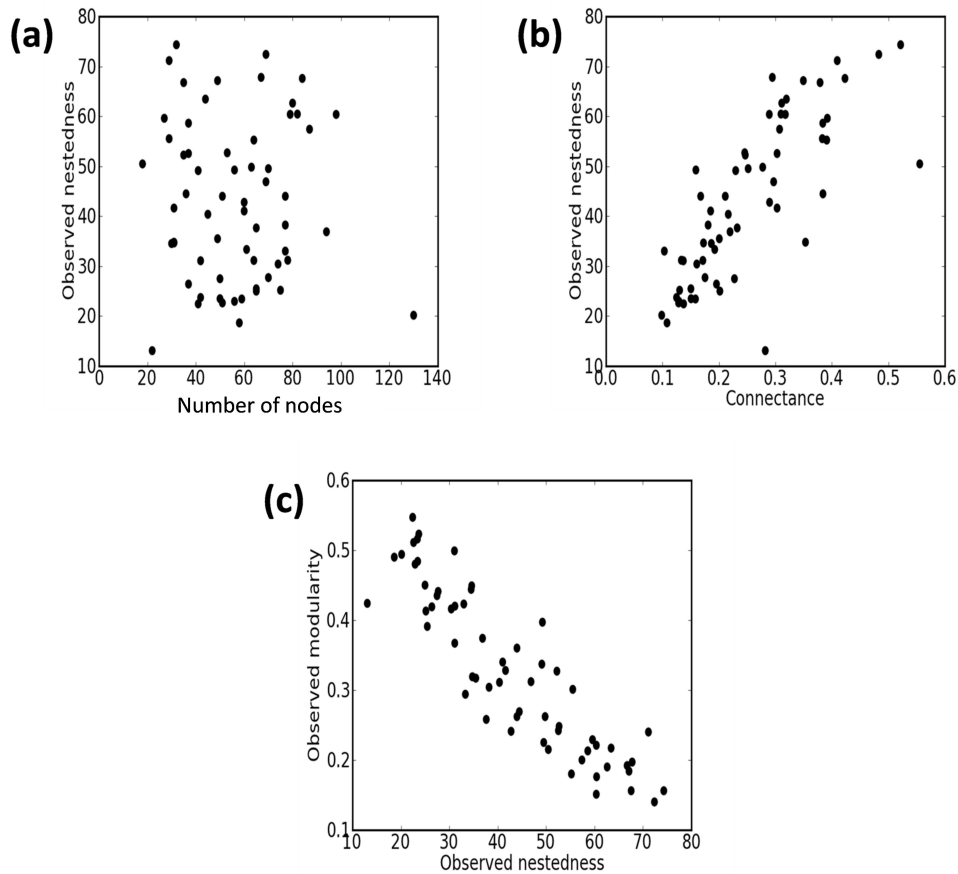


**Figure 3.2:** Modularity–connectance and –diversity relationships in real networks. (a) shows the relationship between modularity and diversity while (b) the modularity–connectance relationship from the 61 real networks

Figure 3.2 (b) suggests that generally, modularity reduces with network connectance but its dependence on the number of nodes is not as obvious (see Figure 3.2 (a)). The relationship between modularity and connectance is not a surprise because one would expect that the more connected a network is, the harder it gets to separate it into seemingly independent sub networks, hence low modularity.

### 3.6 Nestedness

The level of nestedness in these networks was quantified using the software ANINHADO, which is based on the NODF measure described in Section 2.3.2.6. The level of nestedness (measured as NODF) ranged from 13.07–74.31 (see Table 3.8), with an average of  $NODF=42.97$ . Like with modularity, we investigated the significance of nestedness but using both the Erdos-Renyi (Er) and probabilistic (P) null models as described in Section 2.4.3. Most of the networks were significantly nested regardless of the null model used. In fact, the fixed and probabilistic null models depicted 55 and 49 networks respectively as significantly nested.



**Figure 3.3:** NODF–diversity, –connectance and –modularity relationships. (a) shows the NODF–diversity, (b) NODF–connectance and (c) NODF–modularity relationships from the 61 real networks

Although the relationship between NODF and network diversity (number of nodes) was not clear (see Figure 3.3 (a)), Figure 3.3 (b) suggests that NODF increases with connectance, which indicates a pronounced relationship between nestedness and connectance. This implies that modularity and nestedness (measured as NODF) are negatively correlated. And, indeed, from Figure 3.3 (c), modularity seems to be negatively correlated with NODF, indicating that the more interactive species are with one another in a network, the less modular and the more nested they are likely be.

**Table 3.8:** The modularity and nestedness of 61 real networks. ID denotes the network code where HP stands for host-parasite while PH plant-herbivore. OM denotes the observed modularity, ON observed NODF. N(ER) and N(CE) are the random and probabilistic null model outcomes for the NODF; M(F) is the fixed null model outcome for the modularity.

ID	OM	ON	N(ER) <i>p</i> -value	N(CE) <i>p</i> -value	M(F) <i>p</i> -value
HP1	0.269	44.47	0.17	0.61	0.9984
HP2	0.435	27.47	0.18	0.58	0.0087
HP3	0.45	24.99	0	0.05	0.1977
HP4	0.441	27.7	0	0.02	0
HP5	0.494	20.16	0	0	0
HP6	0.319	34.78	0.68	0.87	0.9686
HP7	0.327	52.23	0	0	0.7611
HP8	0.311	40.37	0	0	0.9726
HP9	0.156	74.31	0	0	1
HP10	0.367	31.13	0	0	0.4247
HP11	0.419	26.4	0.08	0.37	0.6102
HP12	0.242	52.54	0	0	0.9999
HP13	0.516	23.42	0	0.02	0
HP14	0.301	55.51	0	0.04	0.6141
HP15	0.328	41.62	0.02	0.39	0.242
HP16	0.213	58.61	0	0	0.9996
HP17	0.449	34.63	0	0.03	0.9319
HP18	0.229	56.59	0	0.06	0.9989
HP19	0.215	50.46	0.7	0.8	0.9896
HP20	0.391	25.46	0	0.03	0.6554
HP21	0.192	66.74	0	0	1
HP22	0.317	35.48	0	0.03	0.9878
HP23	0.484	23.47	0	0.11	0.0793
HP24	0.294	34.33	0	0	0.9842
HP25	0.184	67.16	0	0	1
HP26	0.424	31.07	0.45	0.62	0.3228
HP27	0.337	49.12	0	0	0.2676
HP28	0.49	18.64	0	0.08	0.881
HP29	0.258	37.64	0	0.02	0.7486
HP30	0.248	52.68	0	0	0.9946
HP31	0.24	71.14	0	0	0.5675
HP32	0.217	63.43	0	0	1
HP33	0.241	42.77	0	0.04	0.9713
PH1	0.423	33	0	0	0.2912
PH2	0.523	23.71	0	0.06	0.6985
PH3	0.34	41.03	0	0	0.117
PH4	0.262	43.98	0	0	0.9581
PH5	0.176	60.43	0	0	1
PH6	0.444	34.52	0	0.05	0.8997
PH7	0.511	22.63	0	0.04	0.4721
PH8	0.547	22.44	0.01	0.13	0.0307
PH9	0.197	67.78	0	0	1
PH10	0.221	60.38	0	0	0.0475
PH11	0.156	67.57	0	0	0.9945
PH12	0.304	38.22	0	0	0.117
PH13	0.19	62.62	0	0	0.9953

**Table 3.8 continued**

ID	OM	ON	N(ER) <i>p</i> -value	N(CE) <i>p</i> -value	M(F) <i>p</i> -value
PH14	0.2	57.4	0	0	0.7422
PH15	0.262	49.8	0	0	0.0409
PH16	0.413	25.17	0	0	0.0082
PH17	0.499	31.07	0	0	0.3745
PH18	0.397	49.24	0	0	0.0192
PH19	0.151	60.37	0	0	1
PH20	0.225	49.51	0	0	1
PH21	0.18	55.23	0	0	1
PH22	0.14	72.38	0	0	1
PH23	0.48	22.94	0	0.03	0.1611
PH24	0.36	43.98	0	0	0.741
PH25	0.312	46.88	0	0.02	0.937
PH26	0.416	30.41	0	0	0
PH27	0.42	31.17	0	0	0.0012
PH28	0.374	36.87	0	0.01	0.1867

### 3.7 Discussion

The degree distribution, among other network properties, has attracted the attention of conservation biologists due to its implications for community robustness. Different types of networks (such as mutualistic and antagonistic) often display different degree distribution patterns, although there exists networks of the same type following different degree distributions. For example, while the degree distribution of bipartite mutualistic networks mostly follows power laws, whether as a network (considering both the resource and consumer species together) or as resource or consumer species, results from this study have shown that antagonistic networks display a variety of degree distributions. But mostly, they are either uniformly or exponentially distributed, consistent with previous studies (Dunne *et al.*, 2002a). As a consequence, antagonistic networks could be more robust to the loss of species as compared to mutualistic networks that display skewed degree distribution.

Connectance being one of the key network properties that determine ecosystem functionality, it has in many instances showed remarkable influence on the degree distribution pattern (Estrada, 2007; Dunne *et al.*, 2002a). The very highly connected among the networks in this study had uniform degree distribution, in agreement with previous studies (Estrada, 2007; Dunne *et al.*, 2002b). Intuitively, if a network has got many links, it is most probable that each species will have a high degree hence uniform distribution. In Chapter 5, we will investigate the impact of connectance and degree distribution patterns on robustness, with special focus on bipartite antagonistic networks.

Although antagonistic networks have often been regarded as being compartmentalized (Genini *et al.*, 2012; Krasnov *et al.*, 2012; Alcantara and Rey, 2012) as shown in Table 3.9, we had a rather surprising result when comparing the structures of the 61 real net-

**Table 3.9:** Literature findings on the modularity and nestedness of antagonistic networks. CP: Compartmentalized and ND: nested architecture of antagonistic networks in literature of the past ten years. Network types: HP, host-parasite; PH, plant-herbivore; FW, food web; IR, individual-resource; PP, plant-plant [parasitic]; MU, mutualistic networks(eg. Pollination networks (PN)). Measures of modularity, M and Qd (for directed networks), are given in Newman and Girvan (2004); the metrics of nestedness, NODF (N) and matrix temperature (T; also Tr stands for the relative nestedness based on T) are given in Almeida-Neto *et al.* (2008). Null models: F, fixed row and column marginal totals (SIM9 as described in Gotelli (2000); Fc; Fr, fixed column or row marginal totals respectively as defined in Gotelli (2000); P, the probability of an interaction is assigned proportional to the average of corresponding row and column marginal totals; R, randomly placed interactions; Rd, randomly placed interactions, with directions and root node properties preserved. Numbers in the first column give the total number of networks in the study; characters and numbers (when available) in brackets of other columns show the null model and the number of significant networks. References: 1: Krasnov *et al.* (2012); 2: Fortuna *et al.* (2010); 3: Thebault and Fontaine (2010); 4: Piazzon *et al.* (2011); 5: Kondoh *et al.* (2010); 6: Bellay *et al.* (2011); 7: Cagnolo *et al.* (2011); 8: Genini *et al.* (2012); 9: Meskens *et al.* (2011); 10: Pires *et al.* (2011); 11: Vacher *et al.* (2008); 12: Graham *et al.* (2009); 13: Patterson *et al.* (2009); 14: Timi and Poulina (2008); 15: Dunne *et al.* (2002a); 16: Alcantara and Rey (2012).

Type	Network structure		Conclusion	Ref
	CP	ND		
HP(27)	M(F,24)	-	HP is significantly modular	1
HP(39)	M(F,26; P,15)	T(F,5; P,27)	Low connectance enhances M and N; general conclusions depend on the null model used	2
PH&PN(57)	M(P)	N(P)	PN are as modular as PH, however, they are more nested than PH	3
HP&MU(59)	-	N(P,R,Fr)	Antagonistic networks are as nested as mutualistic ones	4
FW(31)	-	N(P,20)	No significant difference of nestedness between antagonistic and mutualistic networks	5
HP(1)	M(F,1)	N(F,1)	HP is both modular and nested due to low connectance	6
HP&PH(2)	M(F,2)	N(F,0)	Both PH and HP are significantly modular although PH is more modular than HP	7
HP (1)	M(P,1)	N(P,0)	HP is significantly modular but not nested	8
FW (1)	M(P,1)	T&Nr(P,0)	FW is significantly modular d but not nested	9
IR(10)	M(P,0)	N(P,10)	IR is significantly nested but less modular than null model expectation	10
HP(1)	C(R&P,1)	-	HP are clustered [modular]. The nested structure is observed only in compartments	11
HP(29)	-	N(P,17)	Antagonistic and mutualistic networks are nested at the same level	12
HP(31)	-	T(R,31; Fc,31&P,16)	Nestedness is best developed in HP	13
HP(31)	-	T&Nr	Significance of nestedness depends on the measure and null model used	14
FW(16)	C(R,5)	-	Some real FWs are less clustered [modular] than random FWs; others more clustered	15
FW&PP(19)	M(Rd,8), Qd(Rd,15)	-	Modularity was significant but only slightly higher than null model expectation	16

works with those of random networks. Most of the networks studied here are not significantly modular. Moreover, of the 17 networks shared by Krasnov *et al.* (2012) and Fortuna *et al.* (2010), all networks were reported significantly compartmentalized in the former study but only 14 were reported significant in the latter study, even though the same null model was used. Of the 27 networks shared here with Krasnov *et al.* (2012), 21

are less compartmentalized than null model expectation, and only one network showed a significant sign of modularity; yet Krasnov *et al.* (2012) reported 24 of the 27 networks as significantly modulated [note that the null model F via the swap algorithm in NETCARTO is different from the null model used in Krasnov *et al.* (2012)]. Clearly, the conclusion of whether a network is significantly compartmentalized depends largely on the selected null model. Pires *et al.* (2011) analyzed 10 individual-resource networks (individuals of the same species interacting with different resource species) and found none compartmentalized (but all nested). Of the 61 real networks examined here, 11 of the 28 plant-herbivore networks are compartmentalized (39%), compared to only 4 being compartmentalized of the 33 host-parasite networks (12%), consistent with the conclusion that plant-herbivore networks are more compartmentalized than host-parasite networks (Cagnolo *et al.*, 2011).

Although many studies have shown that antagonistic networks are not nested (Thebault and Fontaine, 2010; Genini *et al.*, 2012; Meskens *et al.*, 2011), recent studies have reported that antagonistic networks display a nested architecture (Bellay *et al.*, 2011; Fortuna *et al.*, 2010; Kondoh *et al.*, 2010; Patterson *et al.*, 2009; Pires *et al.*, 2011; Piazzon *et al.*, 2011). Results from this study have demonstrated that antagonistic networks are significantly nested. It is however important to note that the probability of detecting nestedness depends on the metric and null model used (Timi and Poulina, 2008). For instance, we showed that the Er model depicted a higher number of significantly nested networks compared to the CE model. In addition, of the 22 networks shared here in and Fortuna *et al.* (2010), 14 of them are significantly nested when using NODF while 16 are significantly nested when using *Temperature* measure. After reviewing the literature (Table 3.9), we think categorizing antagonistic networks as being nested represents the majority poll in the literature. Nested structure could be best developed in host-parasite networks due to long-term infestation (Patterson *et al.*, 2009) and is common in consumer-resource communities (Kondoh *et al.*, 2010). Indeed, further evidence shows no difference in nestedness between antagonistic and mutualistic networks (Graham *et al.*, 2009; Kondoh *et al.*, 2010; Piazzon *et al.*, 2011), with a clear consensus showing the latter being nested (Bascompte *et al.*, 2003).

# Chapter 4

## Model Development and Simulations

### 4.1 Introduction

Having analysed the structure of real antagonistic networks, we here construct a model that can depict the observed structural patterns. We use a modified version of the Lotka-Volterra model to simulate population dynamics in antagonistic networks. This model assumes Holling's type II functional response however, it ignores the interspecific competition between species as its impact on population dynamics is often much weaker compared to cross-trophic antagonistic interactions, (Cai and Lin, 2007; Fryxell and Lundberg, 1994; Ko and Ryu, 2006; Krivan and Sikder, 1999; Liu *et al.*, 2006; Thebault and Fontaine, 2010). Therefore, the model emphasizes indirect competition via resource competition. Due to the fact that species switch their interaction partners in order to maximize their fitness, we incorporate this interaction switch into the modified Lotka-Volterra model in order to capture the emergence of structural patterns in such networks. We investigate two specific scenarios; (i) whether an interaction switch can sufficiently explain the levels of modularity, nestedness and degree distribution that are observed in real networks and (ii) how species demographic rates and benefits affect the network structure. We test the predictive power of this model by using the 61 real networks whose structure we know from Chapter 3.

### 4.2 Model Development

In an antagonistic network consisting of  $n$  resource species ( $R$ ) and  $m$  consumer species ( $C$ ), suppose that a consumer  $j$  has a total time  $T_j$  for foraging. This time is used for both searching and handling resources, where handling includes catching, eating and digesting the resources. If we denote the time spent on handling resources by  $T_h$ , the searching time, denoted by  $T_s$  is given by

$$T_s = T_j - T_h.$$



At this stage, we impose the assumption that the total number of resource species  $i$  that the consumer  $j$  encounters is proportional to the time it has for searching ( $T_s$ ). As a result, if  $X_{kj}$  is the number of species  $k$  handled by  $j$ ,

$$T_s = T_j - h \sum_{k=1}^m X_{kj}.$$

where  $h$  is the per capita handling time for any one resource. Notice that we assumed that the per capita handling time for all species is the same and this was just for simplicity. Let  $a_{ij}$  denote whether consumer  $j$  encounters prey  $i$  and  $v_{ij}$  denote the probability that an interaction takes place once  $j$  encounters  $i$ . Then, the number of resource species handled by the consumer  $j$  is given by

$$X_{ij} = a_{ij}v_{ij} \left[ T_j - h \sum_{k=1}^m X_{kj} \right] R_i, \quad (4.2.1)$$

where  $R_i$  denotes the abundance of resource species  $i$ . Before presenting the general solution for Equation (4.2.1), consider the same equation for only two resource species  $X_1$  and  $X_2$ , being searched by one consumer. Then, Equation (4.2.1) for this system will be

$$\begin{aligned} X_1 &= a_1v_1(T - hX_1 - hX_2)R_1, \\ X_2 &= a_2v_2(T - hX_1 - hX_2)R_2. \end{aligned} \quad (4.2.2)$$

Substituting the first equation of the System (4.2.2) into the second one gives

$$X_2 = \frac{a_2v_2R_2(T - hX_1)}{1 + a_2v_2R_2h}. \quad (4.2.3)$$

Similarly, substituting Equation (4.2.3) into the first equation of (4.2.2) gives

$$X_1 = \frac{a_1v_1R_1T}{1 + h(a_1v_1R_1 + a_2v_2R_2)}.$$

In general, solving System (4.2.1) for  $X_{ij}$  gives

$$X_{ij} = \frac{a_{ij}v_{ij}T_jR_i}{1 + h \sum_{k=1}^m a_{kj}v_{kj}R_k}.$$

Thus the number of prey species  $i$  encountered by  $j$  per unit time is

$$\frac{X_{ij}}{T_j} = \frac{a_{ij}v_{ij}R_i}{1 + h \sum_{k=1}^m a_{kj}v_{kj}R_k}.$$

We further assumed that the resource species grow according to their density-dependent process minus the rate at which they reduce due to consumers foraging on them. It was also assumed that the consumers solely depend on their resources for survival thus their

dynamics are described by the functional response to foraging on the resources minus their mortality rate. Under these assumptions,

$$\begin{aligned} \frac{1}{R_i} \frac{dR_i}{dt} &= r_i - c_i R_i - \sum_{j=1}^m \frac{a_{ij} v_{ij} C_j}{1 + h \sum_{k=1}^m a_{kj} v_{kj} R_k}, \\ \frac{1}{C_j} \frac{dC_j}{dt} &= -d_j + \sum_{i=1}^n \frac{b_{ji} a_{ij} v_{ij} R_i}{1 + h \sum_{k=1}^m a_{kj} v_{kj} R_k}, \end{aligned} \quad (4.2.4)$$

where  $C_j$  denotes the abundance of the consumer species  $j$ ,  $r_i$  and  $c_i$  are the intrinsic growth rate and the density-dependent coefficient of resource species  $i$  respectively,  $d_j$  is the mortality rate of the consumer species  $j$  and the last terms in both the resource and consumer systems describe the resource loss rates due to predation and the consumer functional responses respectively. As consumers interact with resources, they obtain information about how much benefit is gained once they interact with certain resources. This information too constrains the functional response of the consumer hence the term  $b_{ji}$  in the consumer's functional response. This term denotes the benefit that a consumer species  $j$  gains from interacting with prey species  $i$ . Throughout this thesis, the matrices  $\{a_{ij}\}$ ,  $\{v_{ij}\}$  and  $\{b_{ji}\}$  will be referred to as the interaction, preference and benefit matrices respectively.

### 4.3 Model Simulation

We numerically solved the above model using the Euler method (Sever, 1987) with a time step of 0.01. The values of initial population sizes, intrinsic growth rates, density-dependent coefficients and the entries of the preference matrix were randomly assigned between 0 and 1; the entries of the benefit matrix were randomly assigned between 0 and 0.2 (the exact number of the upper bound has no meaning but only to ensure species co-existence in the network). The entries of the diet matrix were initially randomly assigned to be either 0 or 1, with the number of interactions being equal to the observation from the real networks and also ensuring no isolated species in the network. This diet matrix was then updated at each time step according to two rules of interaction switch.

#### 4.3.1 Main rule of interaction switch

During each time step, we randomly selected two consumers: one dropped from its diet the resource species that contributed the least to its fitness (i.e. per capita growth rate,  $b_{ji} a_{ij} R_j$ , and the other randomly added a new resource species into its diet. This rule of dropping the least contributors and randomly adding new resource species in consumer's diet ensures the increase of their fitness (Zhang *et al.*, 2011).

### 4.3.2 Alternative rule of interaction switch

In the alternative rule of interaction switch, we selected one consumer. It dropped an interaction with a resource species which contributes the least to its per capita growth rate and then randomly added a new species to its diet. In other words, this rule ensures the replacement of less beneficial species with other species. The initial matrices for this interaction switch rule were generated in two ways; (i) the column sums (the number of resources that each consumer interacts with) were the same as those in observed networks; (ii) the interactions were randomly assigned as in the main interaction switch.

The performance of the above model and their two specific scenarios were evaluated using 61 real networks (33 host-parasitoid and 28 plant-herbivore), collected from published materials and recorded as interaction matrices. For each real network, we ran the model with an initial interaction matrix (i.e. the diet matrix) and all other model parameters were randomly assigned as aforementioned. Each simulation corresponds to a specific real network. We tracked the interaction matrices, their modularity and nestedness measurements over time, from  $t = 0$  to 300, with each time unit equalling  $n+m$  steps in the Euler method. The predicted modularity and nestedness were the average of 250 matrices after  $t = 50$  when the dynamics has reached its stable equilibrium; the predictions were then compared with the observed nestedness and modularity from the real networks. Modularity was calculated by using the software NETCARTO based on simulated annealing (see Section 2.3.2.4 as the modularity optimisation technique (Guimera and Amaral, 2005*b,a*) while nestedness was measured based on the overlap and decreasing fill (NODF) using the software ANINHADO 3.0 (Almeida-Neto *et al.*, 2008). Reduced major axis (RMA) was used to compare observed with simulated nestedness and modularity while Kolmogorov-Smirnov test was used to compare observed with simulated node- degree distributions.

## 4.4 Results from the main rule of interaction switch

The summary of the architecture as predicted by the general model for each of the 61 real networks are presented in Table 4.1.

### 4.4.1 Modularity by general model

Through the interaction switch via diet choice, the modularity of a network that was initialized with a random diet matrix gradually converged to a stable equilibrium similar to the observed modularity of the real network (Figure 4.1). Generally, the predicted levels of modularity for the 61 real networks were not significantly different from their observed values (reduced major axis [RMA]: regression slope = 0.97,  $t$ -test:  $t = -1.099$ ,  $p = 0.276$ , see Figure 4.2 (a), Table 4.1). Surprisingly, the trajectory of network structure was not

**Table 4.1:** Summary of the predictions from the general model. ID specifies the network, with HP for host-parasite and PH for plant-herbivore networks. RS: the number of resource species; CS: the number of consumer species; I: the number of interactions; OM: the observed modularity; IM: the modularity of initial random matrix; PM: the average predicted modularity for the 250 matrices after  $t = 50$  from the general model; ON: observed nestedness measured by NODF; IN: the NODF of the initial random interaction matrix; PN: the average of predicted NODFs for the 250 matrices after  $t = 50$  from the general model; SD: the standard deviation of either modularity or nestedness.

ID	RS	CS	I	OM	IM	PM	SD	ON	IN	PN	SD
HP1	7	29	78	0.269	0.304	0.271	0.013	44.47	39.38	61.86	2.96
HP2	10	40	91	0.435	0.431	0.391	0.014	27.47	23.5	46.41	1.51
HP3	14	51	144	0.45	0.387	0.358	0.011	24.99	21.57	42.17	1.12
HP4	17	53	158	0.441	0.4	0.355	0.011	27.7	18.66	38.64	1.05
HP5	33	97	316	0.494	0.415	0.399	0.008	20.16	11.4	24.26	0.48
HP6	6	25	53	0.319	0.345	0.333	0.016	34.78	36.45	56.59	2.94
HP7	15	20	74	0.327	0.366	0.329	0.016	52.23	25.54	45.38	3.38
HP8	19	26	107	0.311	0.364	0.324	0.012	40.37	23.37	42.57	2.1
HP9	23	9	108	0.156	0.199	0.168	0.01	74.31	54.02	70.13	4.17
HP10	20	44	151	0.367	0.39	0.357	0.011	31.13	19.93	37.35	1.39
HP11	14	23	63	0.419	0.428	0.4	0.017	26.4	19.56	35.95	2.65
HP12	15	22	100	0.242	0.309	0.277	0.012	52.54	36.02	54.03	2.47
HP13	22	37	129	0.516	0.405	0.376	0.012	23.42	18.22	32.65	1.35
HP14	7	22	59	0.301	0.357	0.279	0.015	55.51	31.2	63.64	3.53
HP15	9	22	60	0.328	0.354	0.333	0.015	41.62	31.49	60.19	2.97
HP16	16	21	129	0.213	0.243	0.208	0.011	58.61	39.24	63.44	2.98
HP17	11	20	38	0.449	0.542	0.52	0.02	34.63	15.17	27.65	2.23
HP18	11	16	69	0.229	0.274	0.252	0.012	56.59	38.43	65.18	4.16
HP19	9	9	45	0.215	0.217	0.182	0.014	50.46	55.46	71.66	6.47
HP20	21	44	139	0.391	0.442	0.383	0.012	25.46	15.22	31.96	1.22
HP21	17	18	116	0.192	0.252	0.218	0.011	66.74	40.04	60.57	3.04
HP22	18	31	112	0.317	0.39	0.337	0.013	35.48	23.87	41.37	1.68
HP23	16	34	82	0.484	0.506	0.45	0.016	23.47	14.46	29.37	1.45
HP24	28	33	178	0.294	0.344	0.305	0.011	34.33	20.54	38.45	1.59
HP25	23	26	209	0.184	0.249	0.198	0.024	67.16	36.69	59.65	2.27
HP26	9	13	33	0.424	0.362	0.358	0.02	31.07	27.41	45.95	4.57
HP27	19	22	96	0.337	0.358	0.326	0.022	49.12	24.17	45.04	2.33
HP28	23	35	87	0.49	0.516	0.51	0.016	18.64	13.32	21.37	1.13
HP29	30	35	244	0.258	0.287	0.254	0.01	37.64	23.92	43.07	1.33
HP30	28	25	172	0.248	0.298	0.275	0.01	52.68	25.18	46.13	2.06
HP31	15	14	86	0.24	0.254	0.221	0.011	71.14	39.66	63.85	3.76
HP32	15	29	139	0.217	0.278	0.244	0.011	63.43	34.29	57.42	2.01
HP33	18	42	219	0.241	0.28	0.244	0.021	42.77	31.51	53.34	1.56
PH1	40	37	153	0.423	0.494	0.442	0.011	33	11.78	20.58	1.32
PH2	26	16	52	0.523	0.551	0.542	0.022	23.71	15.58	16.27	2.42
PH3	32	28	166	0.34	0.344	0.32	0.01	41.03	20.78	36.68	1.78
PH4	47	30	298	0.262	0.301	0.259	0.008	43.98	20.93	38.85	1.57
PH5	51	31	490	0.176	0.219	0.177	0.007	60.43	27.54	49.29	1.14
PH6	11	19	39	0.444	0.493	0.481	0.021	34.52	15.89	30.4	2.64
PH7	35	16	72	0.511	0.563	0.499	0.019	22.63	12.98	17.82	2.06

Table 4.1 continued

ID	RS	CS	I	OM	IM	PM	SD	ON	IN	PN	SD
PH8	25	16	55	0.547	0.52	0.505	0.021	22.44	16.28	19.33	2.21
PH9	41	26	314	0.197	0.237	0.205	0.009	67.78	31.21	50.79	1.5
PH10	46	33	439	0.221	0.232	0.194	0.007	60.38	29.43	50.56	1.48
PH11	47	37	736	0.156	0.161	0.128	0.006	67.57	43.6	68.74	1.02
PH12	47	30	255	0.304	0.335	0.289	0.009	38.22	18.89	34.9	1.41
PH13	44	36	493	0.19	0.218	0.176	0.006	62.62	30.41	54.2	1.16
PH14	55	32	541	0.2	0.225	0.17	0.007	57.4	32.17	51.89	1.28
PH15	37	26	267	0.262	0.263	0.217	0.009	49.8	28.07	47.73	1.48
PH16	45	30	176	0.413	0.413	0.38	0.012	25.17	16.13	25.14	1.58
PH17	26	16	57	0.499	0.559	0.507	0.022	31.07	14.08	19.44	2.53
PH18	21	35	117	0.397	0.436	0.38	0.015	49.24	15.57	33.48	1.54
PH19	61	37	717	0.151	0.199	0.163	0.007	60.37	32.19	56.32	0.83
PH20	46	24	278	0.225	0.277	0.245	0.008	49.51	27.01	44.49	1.57
PH21	44	20	344	0.18	0.207	0.168	0.008	55.23	39.48	59.52	1.8
PH22	55	14	372	0.14	0.183	0.143	0.007	72.38	49.26	67.12	1.37
PH23	35	21	95	0.48	0.5	0.459	0.016	22.94	14.27	21.36	2.41
PH24	28	23	108	0.36	0.423	0.383	0.013	43.98	18.83	31.75	2.02
PH25	5	64	95	0.312	0.474	0.421	0.019	46.88	25.99	38.12	1.06
PH26	52	22	184	0.416	0.385	0.35	0.011	30.41	18.84	26.77	1.81
PH27	54	24	173	0.42	0.447	0.381	0.014	31.17	13.56	23.16	1.66
PH28	6	88	116	0.374	0.592	0.525	0.043	36.87	15.76	27.5	0.6

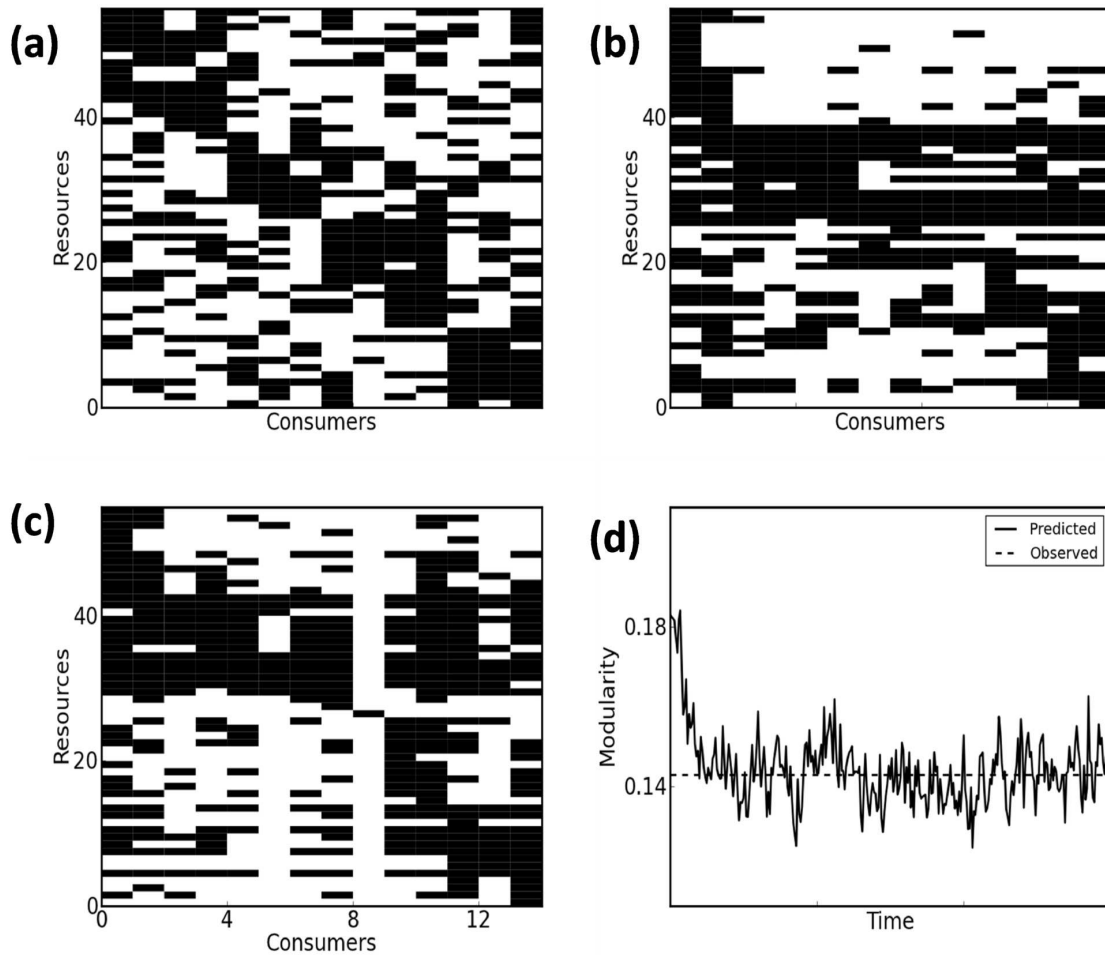
evolving towards a higher level of modularity; rather, the predicted networks showed a significantly lower modularity than these initial random networks ( $t$ -test:  $t = 19.053$ ,  $p < 0.001$ , see Figure 4.2 (b), Table 4.1). These results were consistent regardless of the initial network structure.

#### 4.4.2 Nestedness by the general model

Like with modularity, the predicted NODFs of the 61 real networks did not significantly differ from observations (RMA: regression slope = 0.93,  $t$ -test:  $t = -1.84$ ,  $p = 0.07$ , also see Figures 4.3, 4.4 (a) and Table 4.1) but were significantly higher than the nestedness of those initial random networks ( $t = -18.169$ ,  $p < 0.001$ , see Figure 4.4 (b) and Table 4.1). Similarly, these results were consistent regardless of the initial network structure.

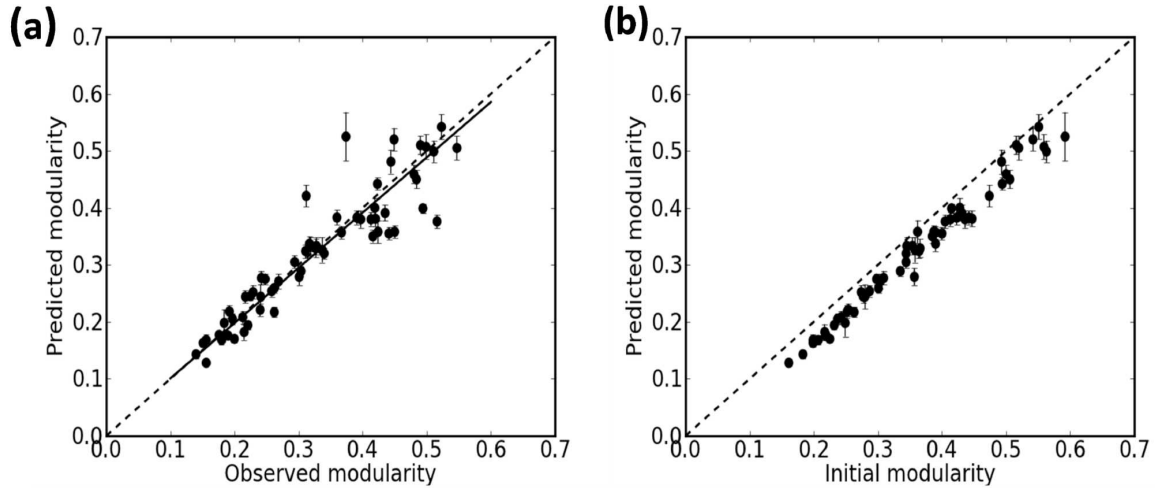
### 4.5 Neutral models

According to the optimal foraging theory (Stephens and Krebs, 1986; Vincent *et al.*, 1996), the abundance and benefit of resources are the key determinants for consumer's diet choice and, thus, the structures of an antagonistic network. To assess the effects of these two determinants on network structures and dynamics, we investigated two specific cases of the above general model: benefit-neutral and demography-neutral interactions. In the first case (benefit-neutral), we assign 0.1 to all entries in the benefit matrix, 0.5 to all entries in the preference matrix, keeping the handling time at 0.1 for all species. In the second case, we assign 1 to all demographic parameters (intrinsic growth rates  $r_i$ , the



**Figure 4.1:** The dynamics of modularity in antagonistic networks. Simulations started from a random interaction matrix, with the number of consumers, resources and interactions similar to the real network of PH22 (Table 4.1). Panels (a), (b) show snapshots of interaction matrices at the beginning and at  $t = 250$  (each time unit equals  $m + n$  steps) while panel (c) shows the interaction matrix of the real network of PH22; panel (d) illustrates the dynamics of the level of modularity predicted by the general model. Dashed lines represent the modularity of the real network.

density dependent coefficients  $c_i$  and the mortality rates  $d_j$ ), keeping the handling time at 0.1 for all species. The two value assignments ensure that the interaction switch is totally dependent on the demographic variations and variation in benefits respectively. By comparing the network structures from these two specific scenarios with the predictions from the general model, we are able to assess the role of abundance (controlled by the demographic parameters) and benefit (controlled by the benefit and preference matrices) in moulding nested and compartmentalized structures in antagonistic networks.



**Figure 4.2:** Relationship between observed and predicted levels of modularity. Panels (a) and (b) show observed modularity and the initial modularity of random interaction matrices vs. predicted modularity from the general model. Predictions of the general model are the average of 250 interaction matrices after  $t = 50$  in the simulation (with standard deviation presented as error bars). Dashed lines indicate perfect fit (i.e. predictions equal to observations or initial equal to predicted levels modularity).

#### 4.5.1 Demography neutral model

Results show that the demography neutral model significantly over estimated the level of modularity in the networks compared to the general model ( $t$ -test:  $t = 17.347$ ,  $p < 0.001$ , see Figure 4.5 (a) and (b)). This indicated that variations in benefits positively affect the

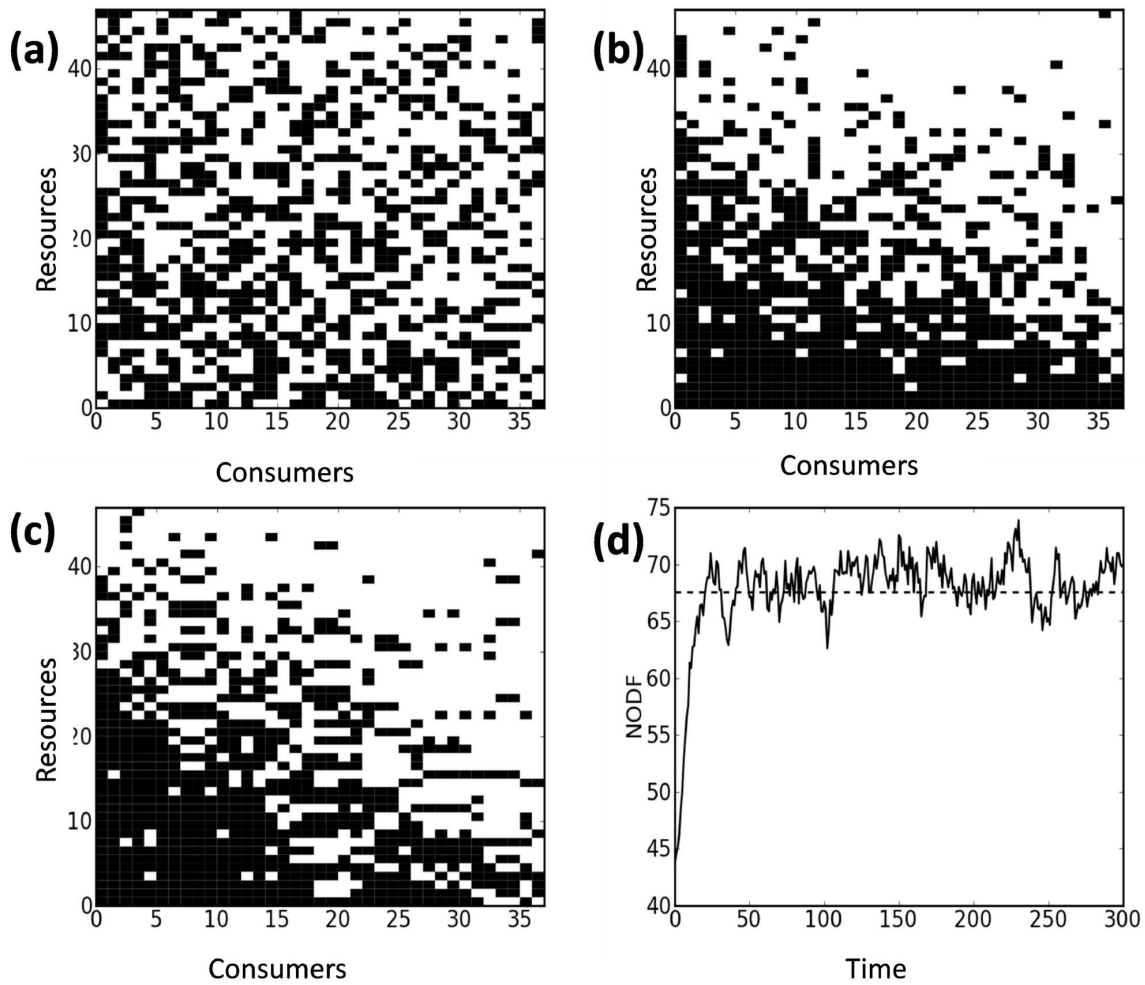
**Table 4.2:** Predictions from neutral models and Kolmogorov-Smirnov tests. The values specify modularity (M) and nestedness (N), as well as their standard deviation (SD), predicted from the demographic neutral model (D) and the benefit neutral model (B). Comparisons of the real node-degree distributions with predictions from the general model are tested by the Kolmogorov-Smirnov test: indicated by \* when initial degree distributions in the simulations significantly differed from the observations for resource species (left-hand stars in the ID column) or consumer species (right-hand stars in the ID column) ( $p$ -value  $< 0.05$ ), and by # when predicted resource and consumer degree distributions significantly differed from the observed node-degree distributions of resources (left) and of consumers (right), respectively.

ID	M(D)	SD	M(B)	SD	N(D)	SD	N(B)	SD
HP1	0.295	0.011	0.264	0.015	42.94	2.96	61.86	6.22
HP2	0.413	0.01	0.366	0.016	25.1	1.51	46.41	7.11
HP3	0.382	0.01	0.348	0.015	23.59	1.12	42.17	7.09
HP4*	0.393	0.01	0.376	0.053	21	1.05	38.64	5.78
HP5*	0.421	0.007	0.389	0.035	12.57	0.48	24.26	2.71
HP6	0.354	0.014	0.309	0.017	36.87	2.94	56.59	8.11
HP7	0.352	0.015	0.328	0.032	30.7	3.38	45.38	5.74
HP8*#	0.368	0.041	0.318	0.023	26.7	2.1	42.57	4.24
HP9	0.232	0.07	0.192	0.072	52.68	4.17	70.13	3.8
HP10	0.371	0.046	0.334	0.053	21.69	1.39	37.35	4.82
HP11	0.428	0.021	0.401	0.023	23.27	2.65	35.95	6.04
HP12	0.296	0.012	0.267	0.015	36.58	2.47	54.03	5.13

Table 4.2 continued

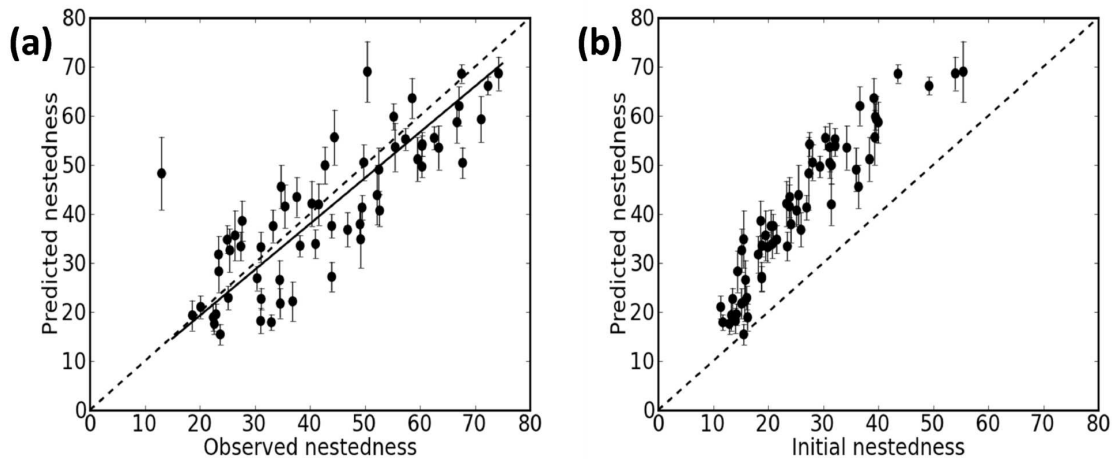
ID	M(D)	SD	M(B)	SD	N(D)	SD	N(B)	SD
HP13#	0.39	0.048	0.366	0.041	19.82	1.35	32.65	4.22
HP14	0.334	0.082	0.284	0.06	42.64	3.53	63.64	6.98
HP15	0.349	0.036	0.303	0.015	33.96	2.97	60.19	5.9
HP16	0.245	0.027	0.208	0.013	44.58	2.98	63.44	4.45
HP17	0.532	0.029	0.465	0.081	17.43	2.23	27.65	4.82
HP18	0.268	0.014	0.235	0.014	44.16	4.16	65.18	6.25
HP19	0.245	0.073	0.204	0.064	54.69	6.47	71.66	6.86
HP20	0.41	0.024	0.377	0.029	18.34	1.22	31.96	4.4
HP21	0.249	0.017	0.217	0.014	44.15	3.04	60.57	4.55
HP22	0.372	0.013	0.34	0.015	24.71	1.68	41.37	5.83
HP23	0.466	0.047	0.432	0.052	17.48	1.45	29.37	4.38
HP24*	0.327	0.052	0.301	0.039	24.44	1.59	38.45	3.78
*HP25	0.233	0.01	0.204	0.011	41.08	2.27	59.65	4.27
HP26	0.382	0.045	0.347	0.049	32.71	4.57	45.95	6.99
HP27	0.351	0.017	0.316	0.015	27.29	2.33	45.04	5.04
HP28	0.521	0.053	0.48	0.072	12.19	1.13	21.37	3.28
*HP29*#	0.288	0.045	0.273	0.061	29.22	1.33	43.07	3.26
*HP30*	0.313	0.042	0.283	0.053	29.54	2.06	46.13	4.08
HP31	0.249	0.029	0.218	0.027	46.68	3.76	63.85	5.08
HP32	0.273	0.009	0.241	0.012	37.54	2.01	57.42	4.83
HP33	0.275	0.036	0.243	0.032	35.1	1.56	53.34	4.31
*PH1	0.459	0.011	0.427	0.039	14	1.32	20.58	1.95
PH2	0.55	0.022	0.537	0.023	15.2	2.42	16.27	2.21
*PH3	0.347	0.011	0.312	0.011	23.92	1.78	36.68	3.1
*PH4*	0.287	0.007	0.257	0.01	26.84	1.57	38.85	2.85
*PH5	0.213	0.005	0.188	0.007	35.35	1.14	49.29	2.47
PH6	0.5	0.02	0.469	0.024	20.71	2.64	30.4	4.84
PH7	0.513	0.017	0.494	0.022	16.33	2.06	17.82	2.29
PH8	0.523	0.019	0.503	0.02	15.96	2.21	19.33	2.64
*PH9	0.238	0.006	0.207	0.009	34.74	1.5	50.79	2.69
*PH10	0.223	0.005	0.196	0.008	33.86	1.48	50.56	2.65
*PH11	0.158	0.003	0.128	0.008	45.3	1.02	68.74	2.96
*PH12	0.32	0.009	0.286	0.01	23.21	1.41	34.9	2.92
*PH13	0.21	0.005	0.179	0.007	35.53	1.16	54.2	2.52
*PH14	0.214	0.004	0.182	0.011	34.58	1.28	51.89	2.83
*PH15	0.256	0.007	0.225	0.009	33.72	1.48	47.73	3.17
PH16	0.401	0.011	0.374	0.011	18.19	1.58	25.14	2.33
PH17	0.518	0.02	0.5	0.022	16.56	2.53	19.44	2.44
*PH18	0.413	0.012	0.382	0.015	19.86	1.54	33.48	4.24
*PH19	0.193	0.004	0.161	0.008	35.72	0.83	56.32	2.2
*PH20	0.272	0.007	0.232	0.01	30.16	1.57	44.49	2.98
*PH21	0.201	0.006	0.167	0.009	42.96	1.8	59.52	2.68
*PH22	0.178	0.005	0.134	0.009	48.01	1.37	67.12	2.24
PH23	0.47	0.016	0.443	0.016	17.23	2.41	21.36	2.23
PH24	0.4	0.014	0.368	0.014	21.65	2.02	31.75	3.78
*PH25	0.474	0.004	0.408	0.04	25.95	1.06	38.12	5.45
PH26	0.375	0.011	0.348	0.014	21.78	1.81	26.77	2.03
*PH27	0.41	0.011	0.376	0.014	18.26	1.66	23.16	2.25
PH28	0.59	0.003	0.465	0.062	15.74	0.6	27.5	5.33





**Figure 4.3:** The dynamics of nestedness in antagonistic networks. Simulations started from a random interaction matrix, with the number of consumers, resources and interactions similar to the real network of PH11 (Table 4.1). Panels (a) and (b) show snapshots of interaction matrices at the beginning and at  $t = 250$  (each time unit equals  $m + n$  steps) while panel (c) shows the interaction matrix of the real network of PH11; panel (d) illustrates the dynamics of the level of nestedness predicted by the general model. Dashed lines represent the nestedness of the real network.

level of modularity in antagonistic networks. This model however underestimates the level of nestedness ( $t = -16.705$ ,  $p < 0.001$ , see Figure 4.5 (c) and (d)), which is not a surprising result, owing to the observed negative correlation between modularity and nestedness.



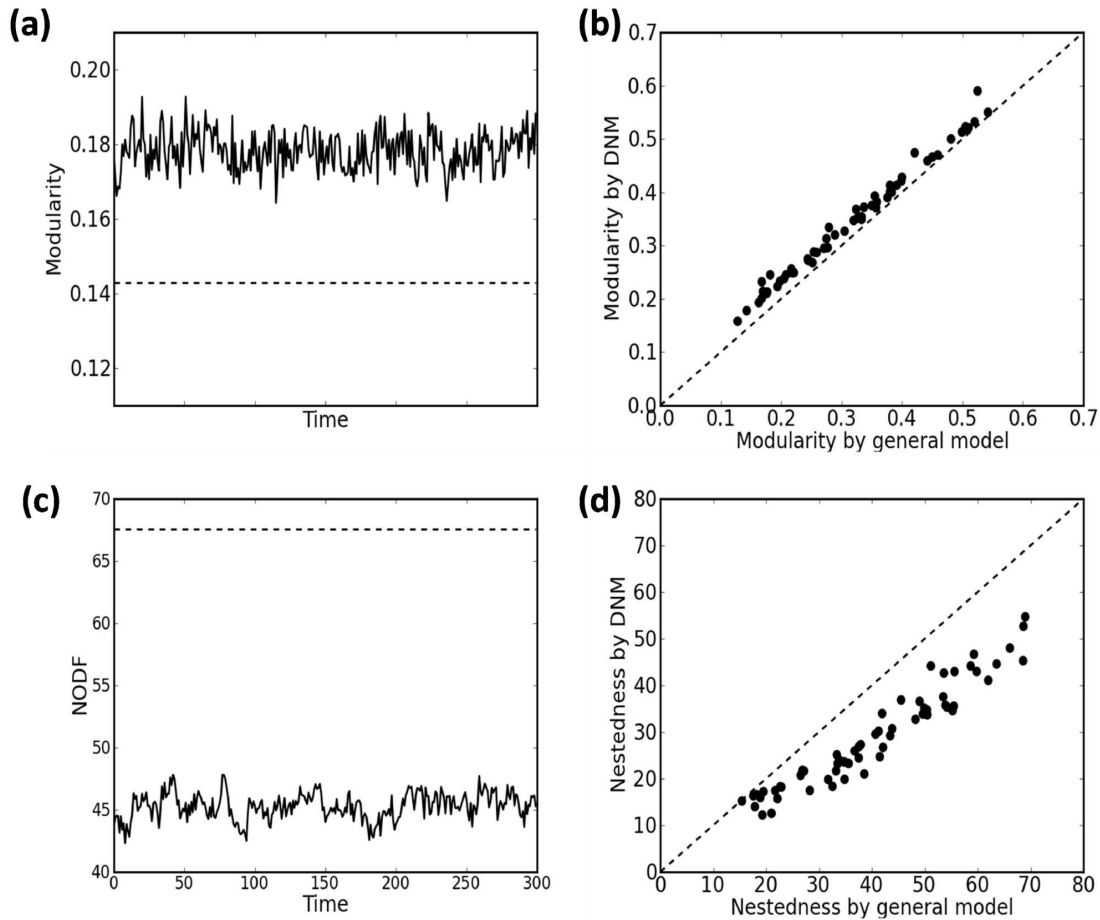
**Figure 4.4:** Relationship between observed and predicted levels of nestedness. Panels (a) and (b) show observed nestedness and the initial nestedness of random interaction matrices vs. predicted nestedness from the general model. Predictions of the general model are the average of 250 interaction matrices after  $t = 50$  in the simulation (with standard deviation presented as error bars). Dashed lines indicate perfect fit (i.e. predictions equal to observations or initial equal to predicted levels of nestedness).

### 4.5.2 Benefit neutral model

On the other hand, the benefit neutral model significantly under estimated the level of modularity in the networks ( $t$ -test:  $t = -3.167$ ,  $p = 0.002$ , see Figure 4.6 (a) and (b)). This indicated that unlike the variations in benefits, variations in demographic parameters negatively affects the modularity of antagonistic networks. On the other hand, this model over estimated the level of nestedness compared to the basic model ( $t = 4.768$ ,  $p < 0.001$ , see Figure 4.6 (d)).

## 4.6 Predicted relationships

The model predicted the observed relationships between nestedness and modularity and connectivity. The modularity of a network is negatively correlated with its nestedness (Figure 4.7 (a)). The increase of connectance (the proportion of links in the interaction matrix; see Williams, 2011) can lead to the increase of nestedness (Figure 4.7 (b)) and, thus, the decrease in modularity. Furthermore, the Kolmogorov-Smirnov test revealed no significant difference between the observed and predicted node-degree distributions (NDD; Figure 4.7 (c) and (d), Table 4.2). Specifically, the observed NDDs for some of the 61 real networks (21 for resource species and 7 for consumer species) differed from the NDDs of the initial random networks. At the equilibrium, none of the predicted NDDs for plant species showed significant difference from the observations (Table 4.2), and only three of the 61 predicted NDDs for consumer species differed significantly from the observation

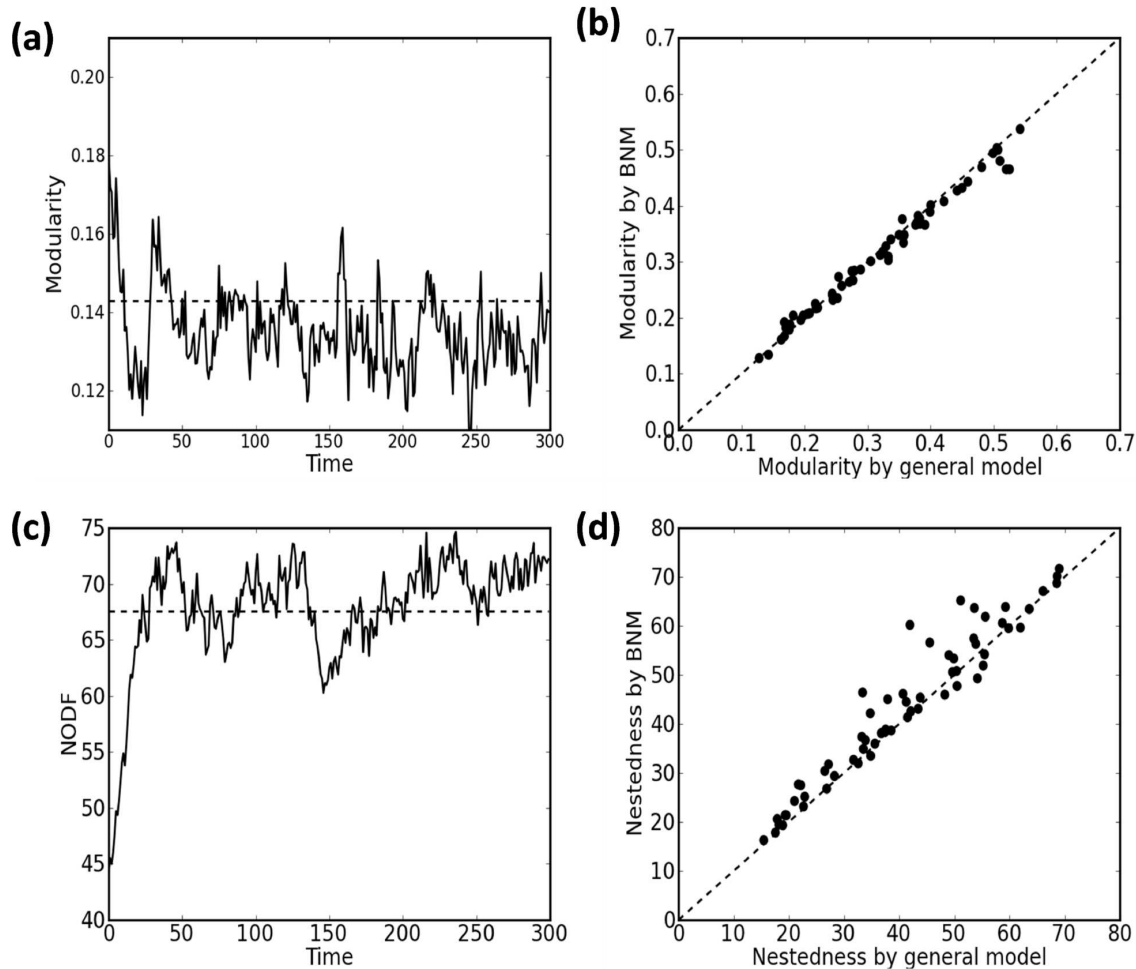


**Figure 4.5:** Structural dynamics by the demography-neutral model. Simulations started from a random interaction matrix, with the number of consumers, resources and interactions similar to the real network of PH22 for modularity and PH11 (Table 4.1) for nestedness. Panels (a) and (c) show the dynamics of the level of modularity and nestedness predicted the demography-neutral model while panels (b) and (d) show the relationship between observed and predicted levels of modularity and nestedness. Dashed lines indicate observed levels in the case of dynamics [panels (a) and (c)] and perfect fit in the case of relationships [panels (b) and (d)].

(Table 4.2). Evidently, the model successfully predicted the observed NDDs.

## 4.7 Results from Alternative rule of interaction switch

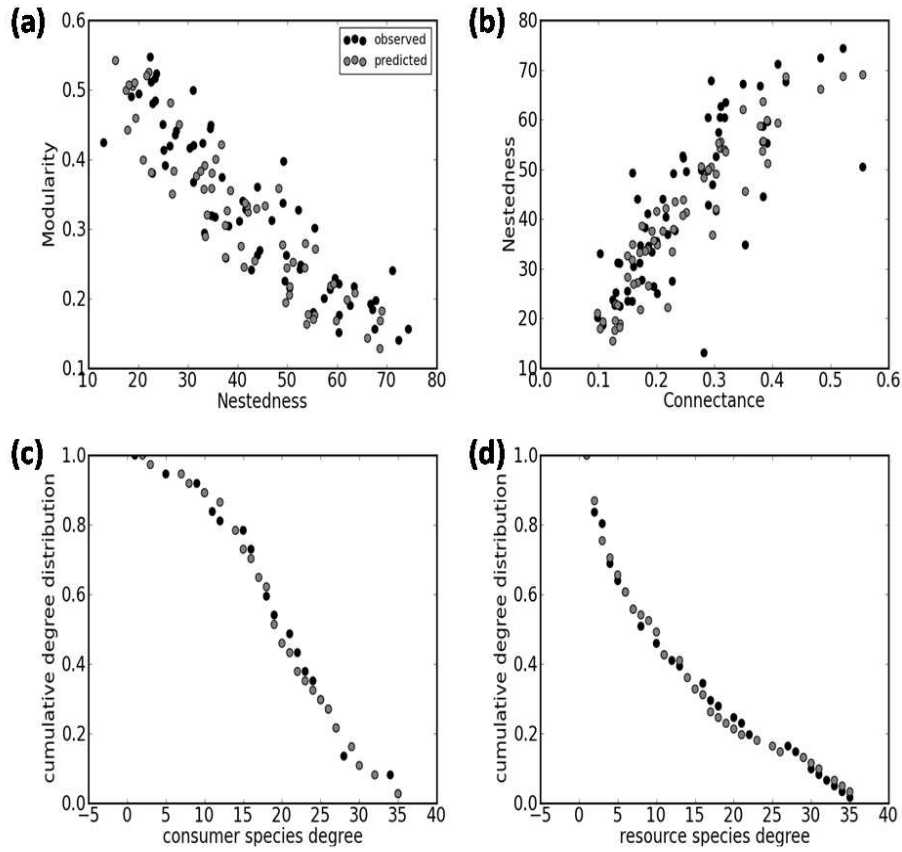
We will just give a brief summary of the results that were obtained from the alternative rule of interaction switch. Models with both fixed and random initial matrices successfully predicted the level of modularity but not nestedness while the benefit-neutral model predicted the observed nestedness better than the general model. The summary of the results is given in Figures 4.8, 4.9, 4.10 and Table 4.7.



**Figure 4.6:** Structural dynamics by the benefit-neutral model. Simulations started from a random interaction matrix, with the number of consumers, resources and interactions similar to the real network of PH22 for modularity and PH11 (Table 4.1) for nestedness. Panels (a) and (c) show the dynamics of the level of modularity and nestedness predicted the benefit-neutral model while panels (b) and (d) show the relationship between observed and predicted levels of modularity and nestedness. Dashed lines indicate observed levels in the case of dynamics [panels (a) and (c)] and perfect fit in the case of relationships [panels (b) and (d)].

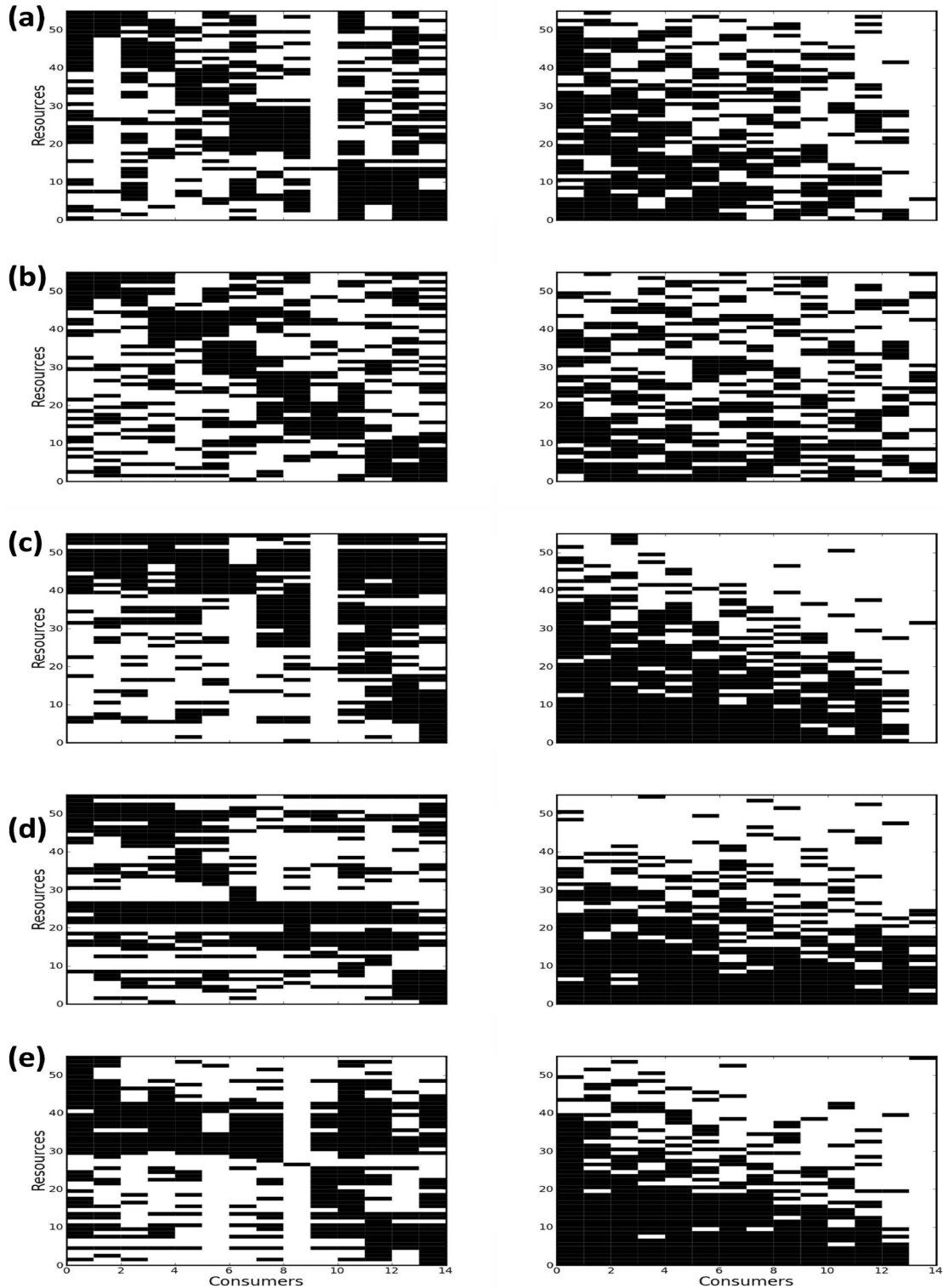
## 4.8 Discussion

Diet choice via interaction switch in the model affects a species' fitness through the functional response. This is in line with the optimal foraging theory which predicts that a consumer only utilizes a portion of available resources to maximize the energy intake rate through optimally allocating searching and handling time (Stephens and Krebs, 1986). Accordingly, consumers will choose to interact with those more beneficial resources, rather than waste time on handling low-beneficial resources. The increase in abundance of one high-beneficial resource species could lead to a consumer abandoning some low-beneficial resources from its diet (Stephens and Krebs, 1986; Tilman, 1986; Vincent *et al.*, 1996). The rule of the interaction switch implemented here captures exactly the consumer's nature for optimal foraging by constantly replacing the resource species that contributes the

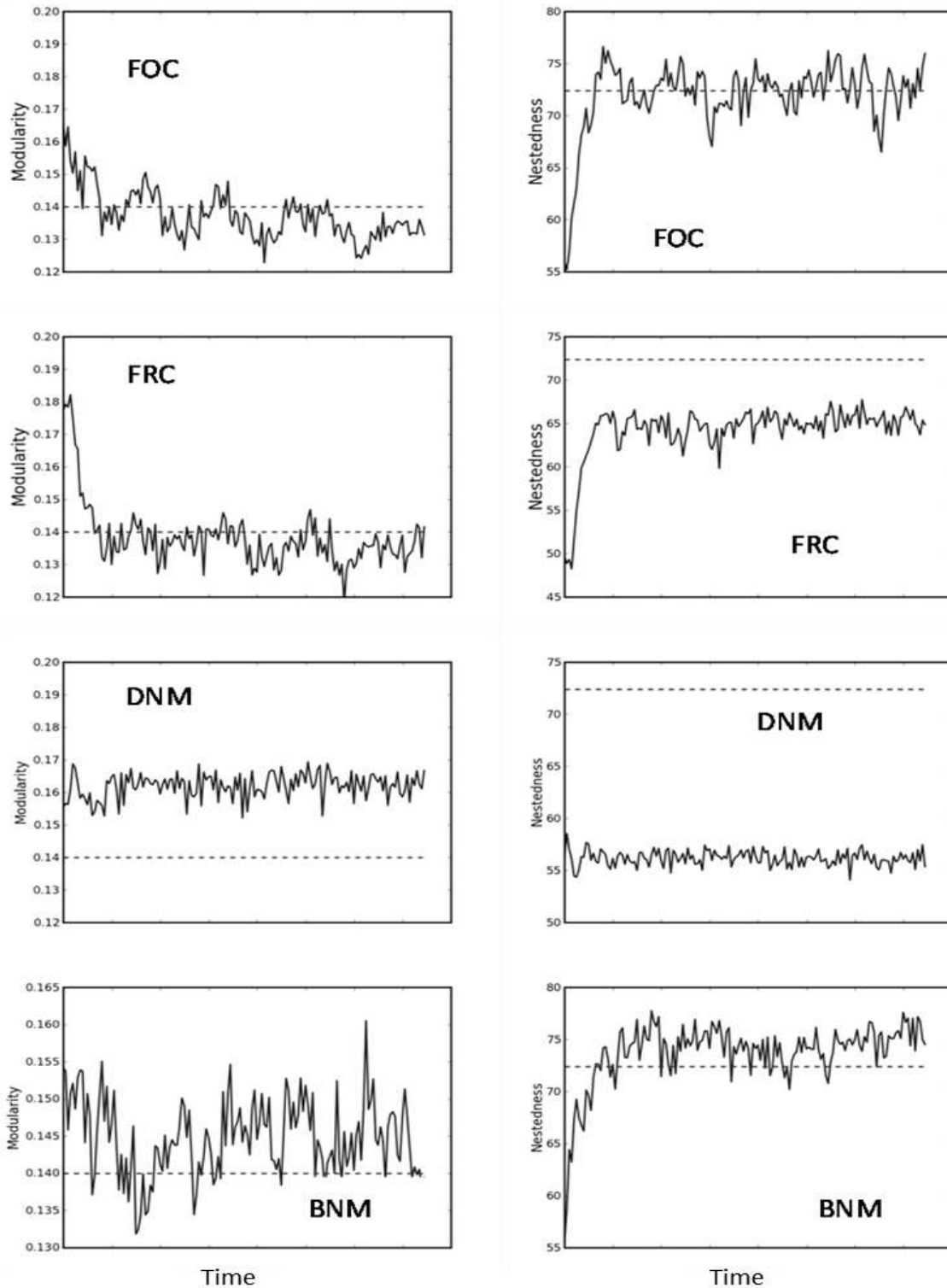


**Figure 4.7:** Relationships between different architecture. Panels (a) and (b) show modularity–nestedness and nestedness–connectance relationships while panels (c) and (d) show an example of the predicted vs. observed node-degree distributions of consumers and resources, respectively, for the real network PH19 (see Table 4.1). Black points indicate observations; grey points predictions from the general model.

least with a random new resource. The interaction switch depends on both the benefit ( $b_{ji}a_{ij}v_{ij}$ ) and the abundance ( $P_j$ ) of a consumer’s interacting resource species. The role of benefit and abundance was further exemplified in the benefit- and demography-neutral scenarios of the model (Figure 4.6, 4.5), which over-estimated the observed nestedness and modularity, respectively. As there is a strong negative correlation between nestedness and modularity (Figure 4.7 (a)), this suggests that similar resource quality in communities promotes the hierarchical structure of nestedness and diminishes the possible existence of stable functional clusters, whilst differential resource qualities can lead to the divide of a community into functional clusters. Importantly, the simple Lotka-Volterra model with an interaction switch successfully predicted the observed structures of real antagonistic networks. Other slightly modified rules of the interaction switch also yield excellent predictions of the structure of antagonistic networks (Figures 4.8, 4.9, 4.10 and Table 4.7),



**Figure 4.8:** Snapshots of interaction matrices via the alternative switching rule. The left panel represents compartmentalized structures of interaction matrices, while the right panels represent nested structures. (a) represents network structures of the fixed initial matrices; (b) represents network structures of the random initial matrices; (c) the interaction matrices at the 106th time in the simulation starting with a fixed initial matrix; (d) the interaction matrices at the 106th time in the simulation starting with a random initial matrix; (e) the observed real interaction matrices of the network PH22 (Table 4.1)



**Figure 4.9:** Structural dynamics predicted via alternative switching rule. The dynamics of modularity (left) and nestedness (right) of the network PH22 (Table 4.1) predicted by the general model with the alternative interaction switch and fixed initial matrices (FOC), by the general model with the alternative interaction switch and random initial matrices (FRC), by the benefit neutral model with fixed initial matrices (BNM), and by the demographic neutral model with fixed initial matrices (DNM). The dotted lines indicate the observed levels of modularity or nestedness.

**Table 4.3:** Summary of the model performance with alternative switching rule ( $t$ -statistic,  $p$ -value and the slope from the reduced major axis regression of row predictions vs. column ones for each entry). The bottom left represents comparisons of modularity and the top right of nestedness (NODF). OBS: observations; FOC: the fixed observed column sum; FRM: the fixed random column sum model; DNM: demographic neutral model; BNM: benefit-neutral model. IFRC and IFOC are the initial random matrices generated at the beginning of simulations using the FRC and FOC respectively

	OBS	FOC	FRC	DNM	BNM	IFRC	IFOC
OBS		2.934	6.229	10.393	1.348	12.653	11.189
		0.005	0.001	<0.001	0.183	<0.001	<0.001
		0.949	1.081	1.333	0.931	1.536	1.364
FOC	-1.957		5.977	9.508	-2.975	5.977	9.862
	0.055		<0.001	<0.001	0.004	<0.001	<0.001
	1.01		1.15	1.418	0.99	1.624	1.451
FRC	-0.596	5.145		4.794	-7.793	11.399	5.334
	0.553	<0.001		<0.001	<0.001	<0.001	<0.001
	1.022	1.012		1.233	0.861	1.412	1.262
DNM	2.462	15.446	8.997		-11.466	8.354	1.729
	0.017	<0.001	<0.001		<0.001	<0.001	0.089
	0.985	0.975	0.964		0.698	1.145	1.023
BNM	-2.791	-3.526	-7.317	-19.517		12.646	11.751
	0.007	<0.001	<0.001	<0.001		<0.001	<0.001
	0.971	1.041	0.95	0.985		1.64	1.466
IFRC	6.125	17.438	16.436	9.297	19.58		-7.714
	<0.001	<0.001	<0.001	<0.001	<0.001		<0.001
	0.981	0.971	0.96	0.996	1.011		0.894
IFOC	2.403	12.695	7.187	0.145	15.35	-6.648	
	0.019	<0.001	<0.001	0.885	<0.001	<0.001	
	0.957	0.948	0.937	0.972	0.987	0.976	

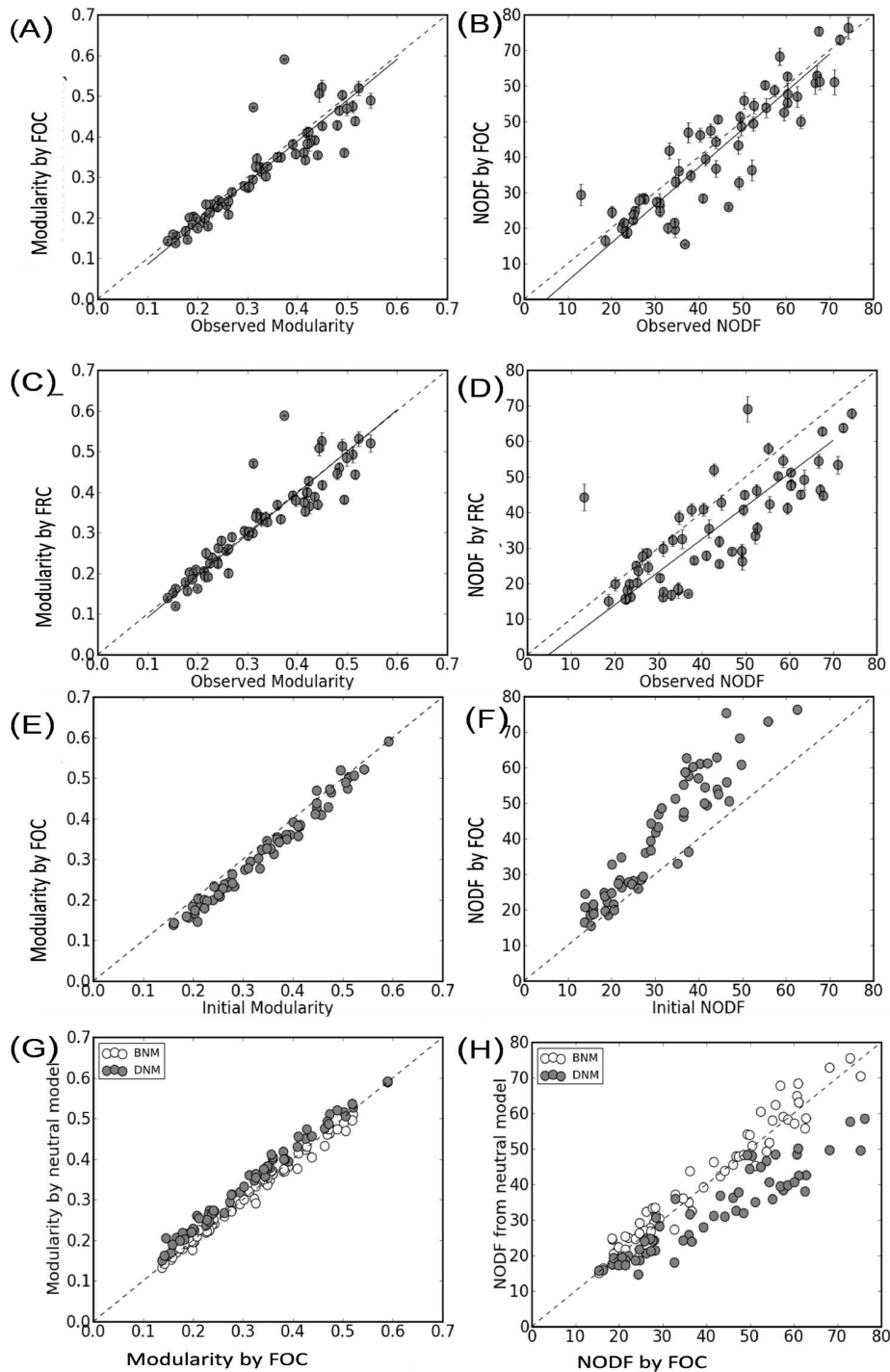
suggesting it an important mechanism for structure emergence in trophic networks.

Interaction switches not only foster stability but also enhance persistence in predator-prey systems (van Baalen *et al.*, 2001; Tilman, 1986). With the interaction switch, the abundance of species might fluctuate without necessarily leading to extinction when facing perturbations (van Baalen *et al.*, 2001). The interaction switch is, therefore a strong force for structuralizing and stabilizing ecosystems (Zhang *et al.*, 2011; Kondoh, 2006). Modulated and nested structures gradually emerge in antagonistic networks from random networks, and these two structures have been shown to enhance persistence and resilience in antagonistic networks, respectively (Thebault and Fontaine, 2010): compartmentalization enhances the containment of perturbations within modules by blocking their effect further spreading in the rest of the network (Guimera *et al.*, 2010; Prado and M., 2004; Stouffer and Bascompte, 2011), whilst nestedness can evidently enhance resilience in both cross-trophic and mutualistic networks (Thebault and Fontaine, 2010). The interaction switch allows the network to rebalance itself back to the equilibrium and is, therefore, a vital adaptive behaviour that buffers ecosystems against perturbations (Staniczenko *et al.*, 2010). Human activities have drastically changed how species interact and how ecosys-



tems function (Baskaran *et al.*, 2012; Staniczenko *et al.*, 2010); The model we developed here provides a novel framework for future studies on the role of how blocking or facilitating certain species interactions (by humans) could alter the ecosystem structures and its robustness.

Classic models of ecological communities (e.g. May, 1973) often assume static interspecific interactions (i.e. a constant interaction matrix), leading to a rigid system and the diversity-stability debate (McCann, 2000): a dynamic system that depicts a large number of species by differential equations is destined to be unstable (Allesina and Tang, 2012). This rigid depiction obviously violates the dynamic and adaptive nature of species and ecosystems during the course of evolution and succession. Species do select and adjust which other species to interact with in response to changes in ambient environment and resource availability (van Baalen *et al.*, 2001; Murdoch, 1969; Staniczenko *et al.*, 2010; Tilman, 1986; Kimbrell and Holt, 2005). We here provided a methodology for introducing adaptive behaviors into a classic Lotka-Volterra model of ecological communities. By allowing species to readjust their diets via updating the interaction matrix at each time step, our model successfully explained the simultaneous emergence of three network structures. A random network can evolve into a realistic compartmentalised or nested network, with realistic node-degree distributions, fitting the observed network architecture surprisingly well. This dynamic network model via diet choice thus captured the essence of the structural emergence in an antagonistic network.



**Figure 4.10:** Relationships between observation and predictions via alternative switching rule for the 61 real networks. (A) and (C) show observed vs. predicted modularity from the general model with fixed and random initial matrices, respectively; (B) and (D) show observed vs. predicted nestedness from the general model with fixed and random initial matrices, respectively; (E) is the modularity of fixed initial matrices vs. predictions from the general model using these fixed initial matrices; (F) is the nestedness of fixed initial matrices vs. predictions from the general model using these fixed initial matrices; (G) and (H) show predictions from the demographic neutral model (DNM) and benefit neutral model (BNM) vs. predictions from the general model with fixed initial matrices. Predictions are the average of 100 interaction matrices after  $t = 50$  in the simulation (with the standard deviation presented as error bars). Dashed lines indicate perfect fitting ( $y = x$ ).

# Chapter 5

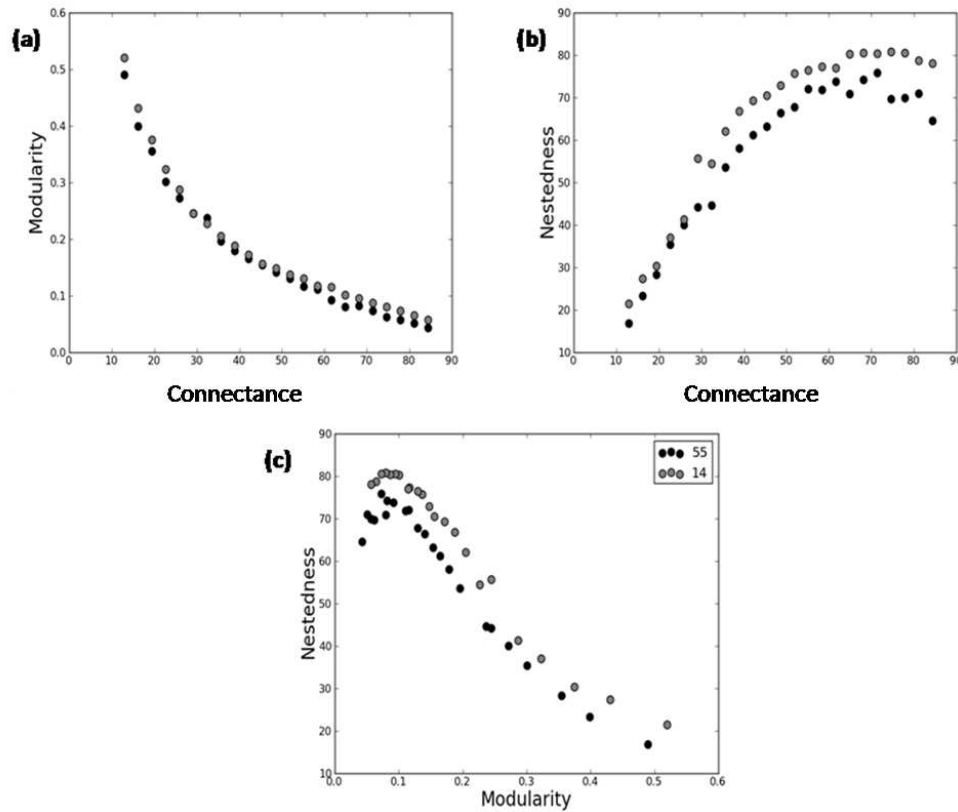
## Model application

### 5.1 Modularity–Nestedness relationship

Due to the fact that the real networks studied in this thesis were unable to reveal the positive correlation between modularity and nestedness at low connectances (as claimed by Fortuna *et al.* (2010)), we used the model proposed in Section 4.2 to create networks of the same diversity but with varying levels of connectance in order to investigate this relationship. Using the same number of resource and consumer species of network HP22 (see Table 4.1), we generated networks whose connectance ranged from 0.12–0.84. For each of the networks, the simulation algorithm in Section 4.3 was employed in order to depict their respective architecture. We also briefly investigated whether the consumer–resource ratio has any effect on the relationship between modularity and nestedness. Using diversity (total number of species) similar to that of HP22, we created another set of networks by interchanging the number of resource species with the number of consumer species and vice versa. We relied on this algorithm to reveal the expected relationships due to the fact that it successfully generated the architectural patterns that are observed in antagonistic networks.

#### 5.1.1 Results and discussion

The modularity and connectance were negatively correlated (see Figure 5.1 (a)) while nestedness and connectance were positively correlated although their relationship seemed to change at high levels of connectance (see Figure 5.1 (b)). Modularity and nestedness were negatively correlated for the biggest range of values of connectance (see Figure 5.1 (c)), as expected. However, in contrast to Fortuna *et al.* (2010), the positive correlation between modularity and nestedness seemed to be depicted at high levels of connectance as seen in the figure. This could have been partly because we could not have connectance levels as low as in Fortuna *et al.* (2010) otherwise some of the networks would be degenerate, a case that we intended to avoid. Also, the connectance of host–parasite networks in



**Figure 5.1:** Modularity vs. nestedness in relation to connectance. Simulations started with number of resource and consumer species as either 55 and 14 respectively or 14 and 55. Black points indicate predictions that started with 55 resource species and 14 consumer species (as in HP22) while grey ones indicate simulations that started with 14 resources and 55 consumers. Panels (a) and (b) show the modularity-connectance and nestedness-connectance relationships while panel (c): modularity-nestedness relationship.

Fortuna *et al.* (2010) were not as high as for the networks studied here. In addition, the relationship seems to be dependent on the consumer-resource ratio however, the sample space here is too small for us to make such a claim. We believe though that this is worth looking into in future.

## 5.2 Robustness and architecture

The loss of species in different ecosystems has proved to have catastrophic effects on the structure and functionality of these ecosystems (Estrada, 2007) such as changes in connectance and biodiversity. For a long time, studies have attempted to explain the response of food webs to species' loss (de Visser and Olf, 2011; Estrada, 2007; Dunne *et al.*, 2002b). Owing to the fact that the methodology in most of the investigations has been questioned (Brose, 2011), this section is dedicated to studying network response to the loss of generalists, specialists and to random loss of species. Unlike most studies, we allow species to switch their interacting partners in response to species' loss. The rule of an

interaction switch used here is as described in Section 4.3.1. In other words, we combine the behavioural adaptation with population dynamics, there by allowing species to adapt to or cope with species loss in their environment. We also analyse the post extinction architecture of the networks.

### 5.2.1 Methodology

The model proposed in Section 4.2 was used to investigate the relationship between robustness and different network properties. Before the removal of species, the model was run up to the time  $t = 150$  to get the network architecture to equilibrium. It was after then that we started the sequential removal of resource species. For the removal of generalist species, a resource species which had the highest number of interactions was removed from the network. The network was then allowed some time to reorganise via the interaction switch. The time allowed for species to reorganise was proportional to the diversity of the network in order for each species to have a chance to respond to the change in their environment. A species was declared extinct if it had no interacting partner. The remaining network was then considered to be the network obtained after each “adaptation period”, after which the architecture and diversity were recorded. Robustness was measured as the proportion of resource species that needed to be removed before at least 50% of the consumer species went extinct. This definition is a little different from the one by Dunne *et al.* (2002b) [the proportion of species that needed to be removed before at least 50% of all the species in the food web went extinct], however, the interpretation is not different.

We employed the same process as for the removal of generalists to mimic the removal of specialist species (species with the minimum number of interactions) and the random removal of species. In the case of removal of generalist species, all the 61 networks were investigated. It was from the resulting responses that 6 networks, representing different architectural patterns and network responses, were chosen to investigate network responses following the random removal of species and the removal of specialist species.

We compared the results from scenarios that included the interaction switch as an adaptive process with those from scenarios where species were not allowed to switch. For the cases where no switching was allowed, after the removal of any species, the consumer species that did not have any resources were declared extinct but resource species were not allowed to go extinct as a result of not having any interaction partners. These comparisons were intended to investigate the influence of an interaction switch on network response to the loss of species.

**Table 5.1:** Summary of the predictions of robustness vs. architecture. ID specifies the network, with HP for host-parasite and PH for plant-herbivore networks. I: the number of interactions; RC: the resource to consumer ratio; Co: the connectance; NODF: the nestedness measure; MOD: the modularity measure; RDD: the resource degree distribution and Rob: robustness.

ID	I	RC	Co	NODF	MOD	RDD	Rob
HP1	78	0.24	38.42	45.25	0.294	UN	42.9
HP2	91	0.25	22.75	37.25	0.388	UN	20
HP3	144	0.27	20.17	39.23	0.346	exp	21.4
HP4	158	0.32	17.54	31.8	0.376	exp	17.6
HP5	316	0.34	9.87	23.17	0.402	exp	12.9
HP6	53	0.24	35.33	48.01	0.321	UN	50
HP7	74	0.75	24.67	53	0.309	exp	42.9
HP8	107	0.73	21.66	39.01	0.332	UN	25
HP9	108	0.56	52.17	69.89	0.15	UN	60
HP10	151	0.45	17.16	40.58	0.347	exp	15.8
HP11	63	0.61	19.57	28.96	0.421	UN	23.1
HP12	100	0.68	30.3	48.53	0.292	UN	46.7
HP13	129	0.59	15.85	28.89	0.384	exp	15
HP14	59	0.32	38.31	52.1	0.287	UN	42.9
HP15	60	0.41	30.3	45.16	0.312	UN	33.3
HP16	129	0.76	38.39	56.21	0.204	UN	43.8
HP17	38	0.55	17.27	25.57	0.489	UN	20
HP18	69	0.69	39.2	62.23	0.227	UN	45.5
HP19	45	1	55.56	83.8	0.149	UN	44.4
HP20	139	0.48	15.04	30.55	0.383	exp	20
HP21	116	0.94	37.91	54.38	0.229	UN	47.1
HP22	112	0.58	20.07	41.82	0.34	exp	18.8
HP23	82	0.47	15.07	21.02	0.471	Un	20
HP24	178	0.85	19.26	30.2	0.324	UN	30.8
HP25	209	0.88	34.95	54.13	0.209	UN	54.5
HP26	33	0.69	28.21	38.03	0.397	UN	33.3
HP27	96	0.86	22.97	47.86	0.318	NB	37.5
HP28	87	0.66	10.81	16	0.513	exp	10
HP29	244	0.86	23.24	44.63	0.252	UN	36
HP30	172	1.12	24.57	47.09	0.253	UN	40
HP31	86	1.07	40.95	63.35	0.231	UN	50
HP32	139	0.52	31.95	62.92	0.252	NB	40
HP33	219	0.43	28.97	45.77	0.245	NB	38.9
PH1	153	1.08	10.34	17.53	0.446	exp	20
PH2	52	1.63	12.5	20.67	0.497	UN	11.1
PH3	166	1.14	18.53	35.46	0.333	NB	30.8
PH4	298	1.57	21.13	40.29	0.249	UN	30.6
PH5	490	1.65	30.99	52.59	0.182	NB	43.2
PH6	39	0.58	18.66	19.81	0.539	UN	20
PH7	72	2.19	12.86	16.58	0.491	UN	20.8

## 5.2.2 Results

The results from investigations concerning robustness are summarised in Table 5.1

Table 5.1 continued

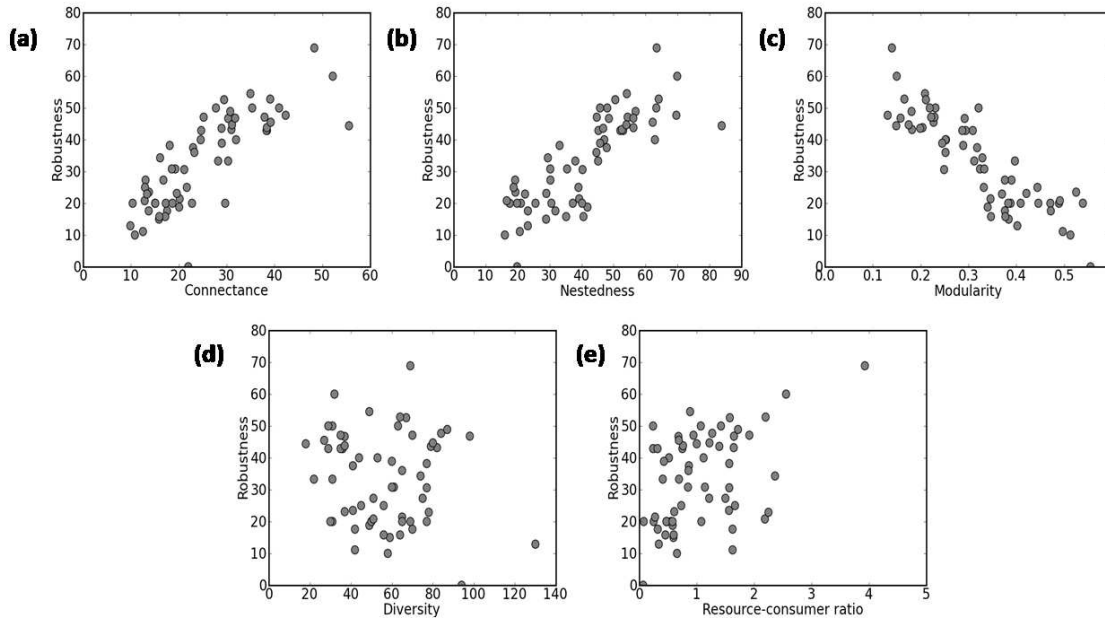
ID	I	CR	CON	NODF	MOD	RDD	Rob
PH8	55	1.56	13.75	19.3	0.525	UN	23.5
PH9	314	1.58	29.46	50.53	0.211	UN	52.6
PH10	439	1.39	28.92	46.75	0.199	NB	43.6
PH11	736	1.27	42.32	69.62	0.131	NB	47.7
PH12	255	1.57	18.09	33.11	0.289	exp	38.2
PH13	493	1.22	31.12	54.01	0.175	UN	44.7
PH14	541	1.72	30.74	56.88	0.181	UN	48.9
PH15	267	1.42	27.75	45.76	0.219	UN	50
PH16	176	1.5	13.04	19.21	0.39	NB	27.3
PH17	57	1.63	13.7	23.2	0.472	UN	17.6
PH18	117	0.6	15.92	35.15	0.377	exp	15.8
PH19	717	1.65	31.77	56.17	0.158	NB	46.8
PH20	278	1.92	25.18	44.74	0.222	UN	47.1
PH21	344	2.2	39.09	64.1	0.166	UN	52.8
PH22	372	3.93	48.31	63.47	0.14	UN	68.9
PH23	95	1.67	12.93	18.74	0.444	UN	25
PH24	108	1.22	16.77	30.24	0.376	exp	27.3
PH25	95	0.08	29.69	40.15	0.409	UN	20
PH26	184	2.36	16.08	29.44	0.329	NB	34.3
PH27	173	2.25	13.35	22.31	0.37	UN	22.9
PH28	116	0.07	21.97	19.82	0.555	exp	0

### 5.2.2.1 Robustness

Generally, robustness to the removal of generalist species increased with connectance and nestedness (see Figure 5.2 (a) and (b)) but decreased with increase of modularity [see Figure 5.2 (c)]. However, the dependence on diversity and consumer-resource ratio was not as obvious [see Figure 5.2 (d) and (e)].

We also noted that networks whose resource species were uniformly distributed were more robust to the removal of resource species (generalists, specialists, or randomly) than those that had skewed resource degree distributions (RDD; see Table 5.1). In fact, of the 14 networks whose RDD followed an exponential distribution, only 2 had their robustness greater than 30 (see Table 5.2). One of the two could have had its robustness enhanced by its high level of nestedness while the other could have been due to high resource–consumer ratio, diversity and relatively low modularity. However, we noticed that different combinations of the different properties lead to different responses to species loss.

The 6 networks we chose happened to have uniform RDD. This enabled us to investigate how the factors other than the RDD (resource degree distribution) influenced robustness. Figure 5.3 illustrates a robust network, whose robustness can be attributed to its high diversity, connectance, nestedness and its resource to consumer ratio. However, Figure 5.3 (b) shows a network with high diversity and resource–consumer ratio but very sensitive to species loss. This implies that even when the resources are uniformly distributed in a network, it is not enough to have high diversity and resource–consumer ratio. The level of connectance can still alter the expected response to species loss. In fact, Figure



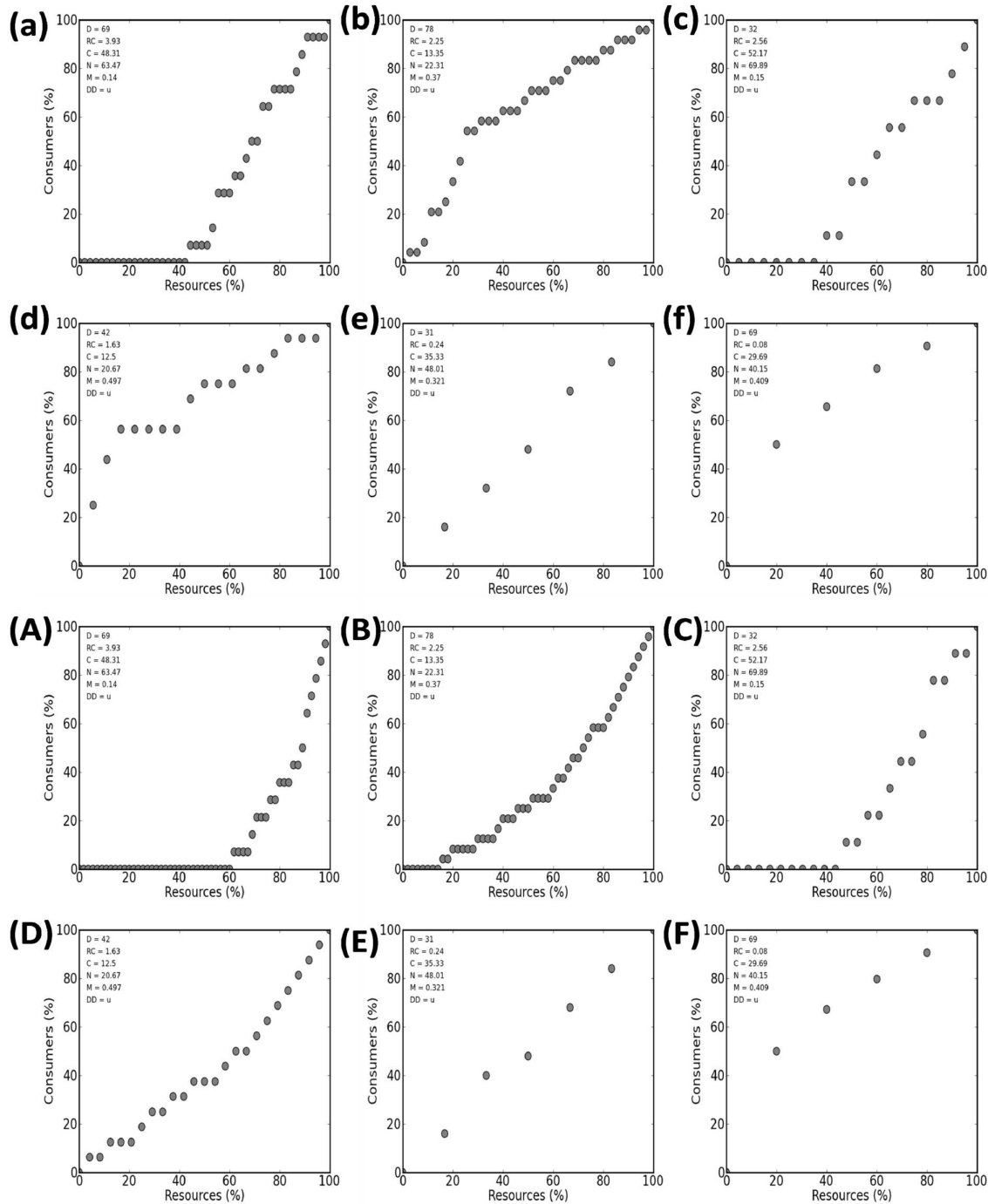
**Figure 5.2:** Robustness vs. architecture. For each simulation, the model proposed in Section 4.2 was ran up  $t=150$ , after which generalist species were sequentially removed. Panels (a), (b), (c), (d) and (e) show the relationship between robustness and connectance, nestedness, modularity, diversity and resource-consumer ratio.

5.3 (c) shows a small network that is; not as diverse, but its resource-consumer ratio, nestedness and connectance are high hence robust. At this stage, one may be tempted to conclude that small networks with more resources than consumers are robust to species loss, however, Figure 5.3 (d) shows a small network whose resource-consumer ratio is high but due to its very low connectance and nestedness, it is not robust to species' loss. The variability in these cases implied that the degree distribution alone can not determine the network response to extinctions.

Of course the results so-far may cause us to believe that the most important of all the properties is connectance. Yes, it turned out to be true most of the times but not always. In the case where both modularity and nestedness were high, the story changed. For example, Figure 5.3 (g) shows a network which had relatively medium level of connectance, uniform RDD but both NODF and modularity were relatively high. One would expect this network to be robust due to its high NODF, uniform RDD and high connectance but to the contrary, it was very sensitive to species loss. The fact that this network had few resource species could be the reason for the uniform RDD and lead to vulnerability as each resource supported a number of consumers. In other words, the network response to perturbation can not be predicted from only one factor but rather from a combination of factors.

The response to the random removal of species did not differ from generalist removal scenarios in terms of different networks but rather in the intensity of the effect (see





**Figure 5.3:** Robustness to the removal of generalists in 6 networks [PH22, PH27, HP9, PH2,HP6 and PH25 in Table 4.1]. D stands for diversity, RC: resource-consumer ratio, C: connectance, N: NODF, M: modularity and DD: resource degree distribution. The different structures of networks were quantified just before the beginning of the first removal of species (at  $t=150$ ). Points show the percentage of consumer extinctions that result from the removal of a certain percentage of resource generalists. Panels (a), (b), (c), (d), (e) and (f) represent simulations which included the interaction switch while (A), (B), (C), (D), (E) and (F) represent those that did not.

Figure 5.4). Networks seemed to be more robust to random removals than to the removal of generalist species. To the removal of specialist species, networks were very robust that

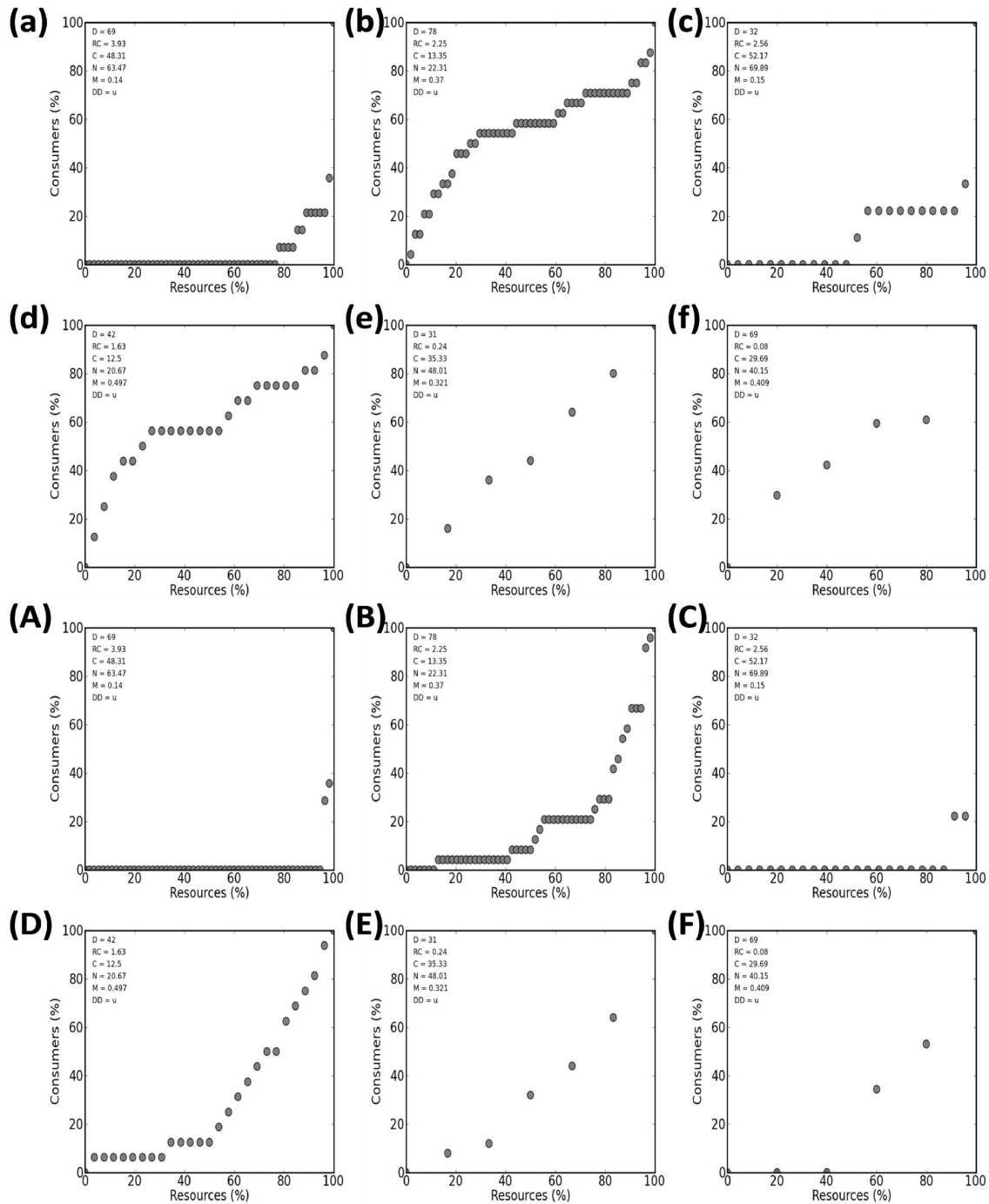
most of the network did not get to the point of totally collapsing, hence were terminated. The two that reached that point ( see Figure 5.5) were the most sensitive in the generalist and random removal scenarios.

Comparison between scenarios that allowed species to switch their interacting partners and those that did not showed that ignoring the effect of such adaptive processes underestimates the effect of extinctions. For each of the networks and removal sequences, the effect of species loss depicted by the model which included the adaptive behaviour, was more catastrophic than the corresponding cases with the model that ignores the interaction switch and population dynamics. This could be due to the fact that once a species is lost, the later assumes that the species which directly interact with the lost species will be the only ones to be affected by the loss. On the other hand, the model proposed in Section 4.2 acknowledges that other species in the network will be affected indirectly by the loss. This is because the species that lost interaction partners may switch to other resource species for survival hence affecting their abundance and function.

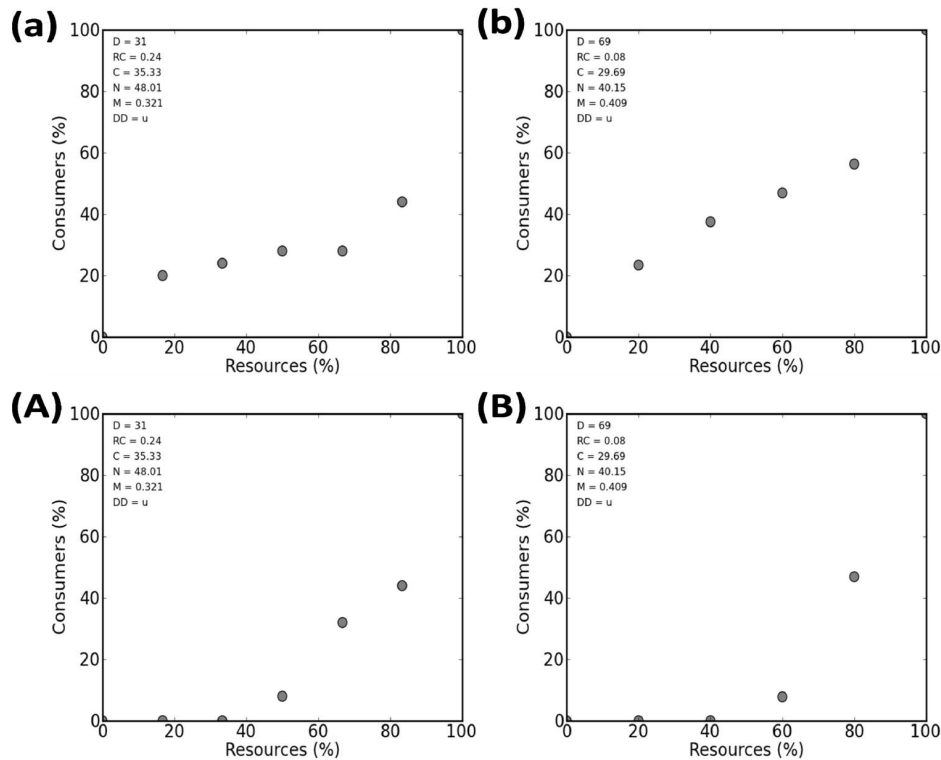
### 5.2.2.2 Effect of species removal on connectance

Due to its influence on other network properties, connectance was used as the main property to discuss post extinction dynamics.

Connectance in most networks was very sensitive to the removal of the generalist species that at the early species' removals, its level increased enormously. This could be attributed to the fact that a generalist resource species supports a number of consumers that its removal leads to the loss of a vast majority of consumers. We noted however that the change in connectance was different for networks whose resource–consumer ratio was high. In such networks, the removal of a generalist resource species could reduce the number of links but not the diversity as much since the consumers still had some resources to survive on. As a result, the level of connectance reduced. In other words, a reduction in connectance after an extinction implies robustness. We also noted that in networks whose resource–consumer ratio was high and connectance was low, connectance increased after the removal of a generalist. This was because the many resources support a few consumers which are specialists; implying that the removal of a species leads to the loss of those specialist consumers. Moreover such networks proved to be sensitive to species loss. Generally, the loss of generalists implied reduction in connectance, reduction in nestedness and increase in modularity, consistent with the relationship among the three properties. On the other hand, an increase in connectance, after an extinction, implies instability in the system, i.e., higher reduction in diversity compared to the number of links lost.



**Figure 5.4:** Robustness to random removal of species in 6 networks [PH22, PH27, HP9, PH2,HP6 and PH25 in Table 4.1]. D stands for diversity, RC: resource-consumer ratio, C: connectance, N: NODF, M: modularity and DD: resource degree distribution. The different structures of networks were quantified just before the beginning of the first removal of species (at  $t=150$ ). Points show the percentage of consumer extinctions that result from the random removal of a certain percentage of resource species. Panels (a), (b), (c), (d), (e) and (f) represent simulations which included the interaction switch while (A), (B), (C), (D), (E) and (F) represent those that did not.

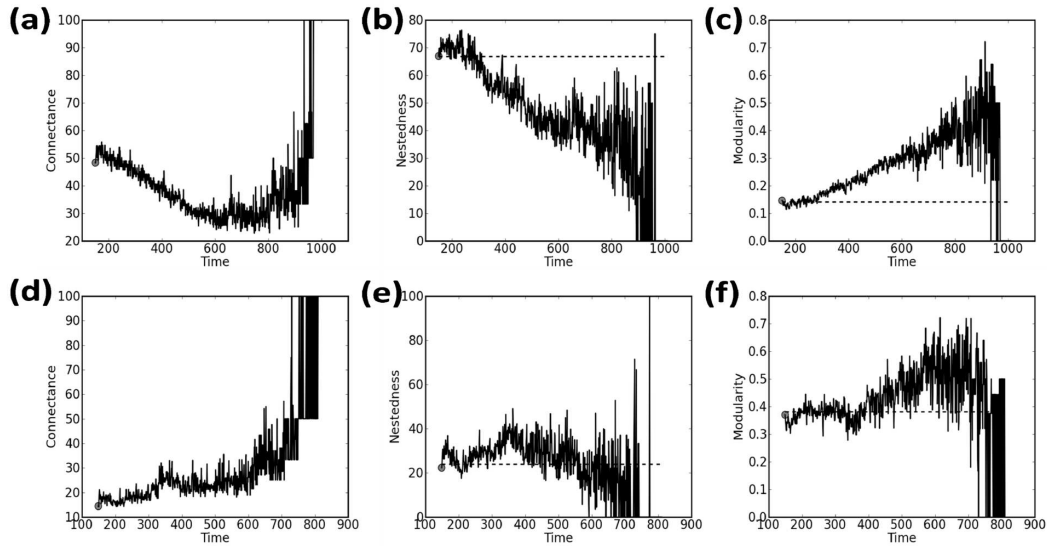


**Figure 5.5:** Robustness to the removal of specialists in 2 networks [HP6 and PH25 in Table 4.1]. D stands for diversity, RC: resource-consumer ratio, C: connectance, N: NODF, M: modularity and DD: resource degree distribution. The different structures of networks were quantified just before the beginning of the first removal of species (at  $t=150$ ). Points show the percentage of consumer extinctions that result from the removal of a certain percentage of resource generalists. Panels (a) and (b) represent simulations which included the interaction switch while (A) and (B) represent those that did not.

### 5.3 Discussion

Although de Visser and Olf (2011) realised that increased human impact generally led to the loss of poorly connected species, other studies (Eklof, 2006; Dunne *et al.*, 2002b) have shown that their loss does not induce as many secondary extinctions as those induced by the loss of generalists species. In fact, results from this study are in agreement with Eklof (2006) not only in terms of the effect of the loss of generalist species but also in terms of the role played by network connectance in determining the robustness of a network. Compared to other sequential species removals, we noted that the main difference is in the intensity of consequences, otherwise the manner of response for a specific network is almost the same regardless of the species lost.

Although network connectance is vital for robustness (Dunne *et al.*, 2002b) due to its implication for species degree distribution, nestedness and modularity, we showed that the other network properties too influence robustness. Networks that are highly nested, less modular but with high resource–consumer ratio, in addition to high connectance and uniform degree distribution, were the most robust. In other words, network robustness is



**Figure 5.6:** The dynamics of different architecture after extinctions. For (a), (b) and (c), simulations started from a random interaction matrix, with the number of consumers, resources and interactions similar to the real network of PH22 (Table 4.1). For (d), (e) and (f), simulations started from a random interaction matrix, with the number of consumers, resources and interactions similar to the real network of PH27 (Table 4.1). From  $t=150$ , generalist species were sequentially removed and the panels show the dynamics of connectance, nestedness and modularity.

affected by a number of factors, consistent with the study by Estrada (2007).

Results from this study demonstrate that adaptation mechanisms and population dynamics can not be ignored if we want to get a much clearer view of what to expect in a time like this, when a number of species are threatened by human behaviour. Thierry *et al.* (2011) showed that the interaction switch as a species rewiring mechanism could increase the robustness especially in networks of low connectance. The fact that simulations that incorporated an adaptive behaviour depicted higher extinction was unexpected. One possible explanation for this result is that species that loose interaction partners may experience selection pressures and hence extend these pressures to other species via the interaction switch. This way, ignoring the adaptive behaviour may eventually overestimate the robustness of a network experiencing such a dilemma.

## Chapter 6

# Conclusions and recommendations

The detection of the architecture of networks is very sensitive to the measure and null model used. Conclusions from recent literature on the structure of antagonistic networks has proved to be so controversial, resulting from the usage of different structural measures and null models for testing significance. Results from this thesis showed that most antagonistic networks are not significantly modular but nested than random (modularity tested against the fixed null model while nestedness against the Erdos-Renyi and probabilistic null models). With all these controversial findings, aiming for robust measures and specifying explicit procedures for null model selection is still crucial for understanding the structure of our ecosystem.

Importantly, we provided a new way of introducing adaptive behaviours into a classic Lotka-Volterra model of ecological communities. By allowing species to be able to readjust their diets via updating the interaction matrix at each time step, the model implemented in this thesis successfully explained the simultaneous emergence of three network structures. A random network can evolve into a realistic compartmentalised or nested network, with realistic node-degree distributions, fitting the observed network architecture surprisingly well. This dynamic network model via diet choice thus captured the essence of the structural emergence in an antagonistic network.

By allowing species to adaptively respond to changes in their environment, we demonstrated that biodiversity loss affects a larger number of other species than expected. Specifically, if we assume that the ecosystem consists of numerous isolated small clusters and that any calamity experienced by any cluster does not affect others, we are likely to underestimate the magnitude of the consequences of biodiversity loss. The removal of species following any of the removal sequences (generalist, specialists and random) resulted in more secondary extinctions when species were allowed to switch to new diets than when they were not allowed to. We must therefore value our knowledge of possible adaptive processes as they may have important implications for network robustness thus

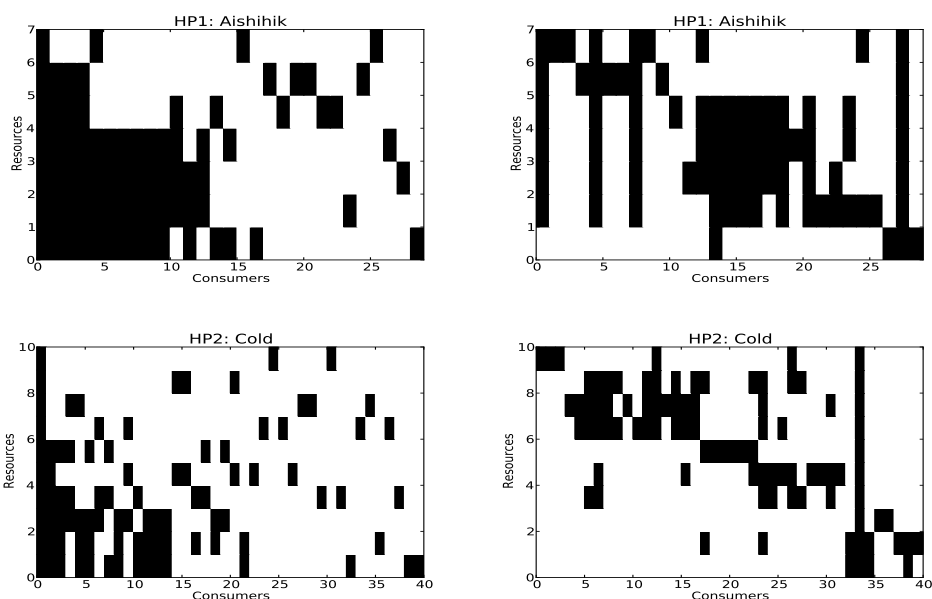
biodiversity maintenance and ecosystem function.

Following the findings from this thesis, we, thus, envisage a paradigm shift in resolving the diversity-stability debate, from depicting and analysing an ecosystem as a rigid system with a constant interaction matrix to a complex adaptive system with a constantly updated interaction matrix via adaptive behaviours such as interaction switch (and even an ever-evolving benefit matrix via mutation).

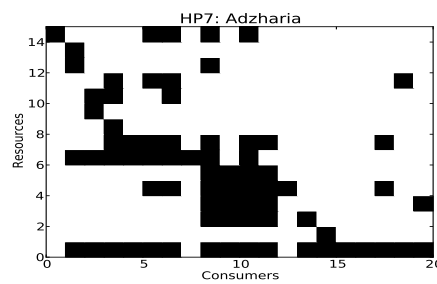
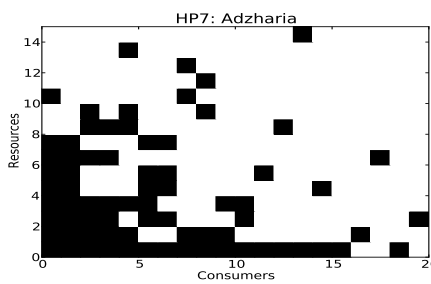
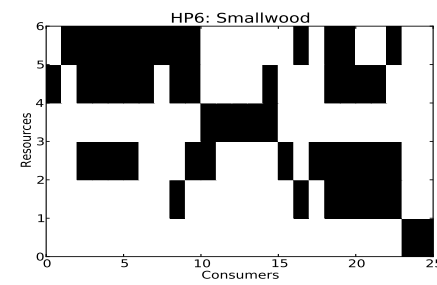
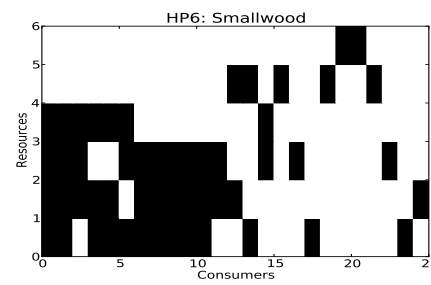
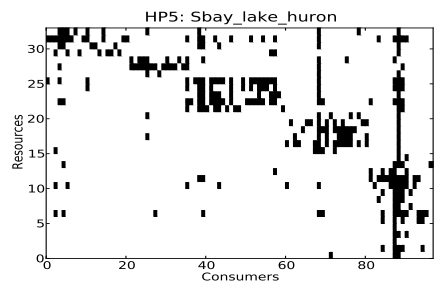
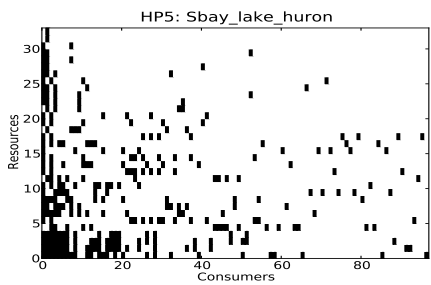
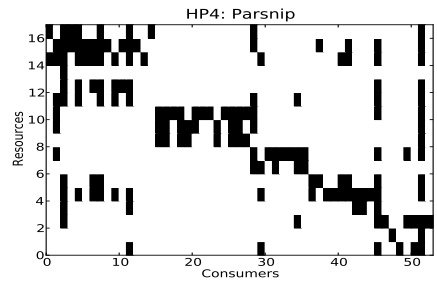
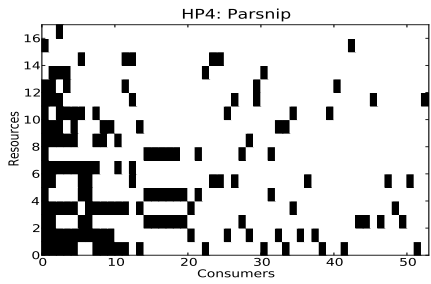
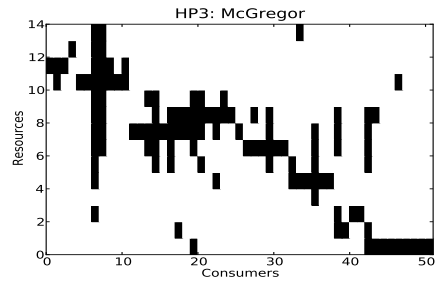
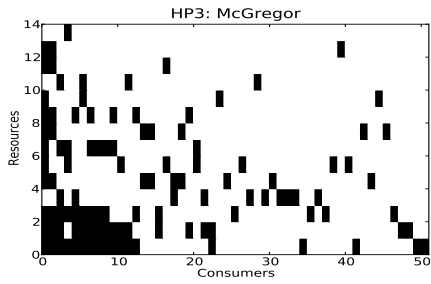
# Appendix A

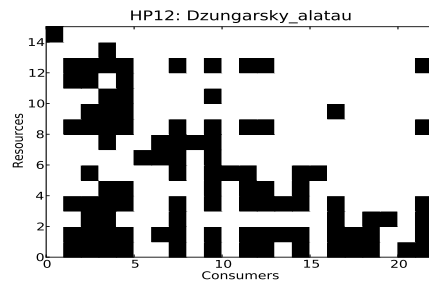
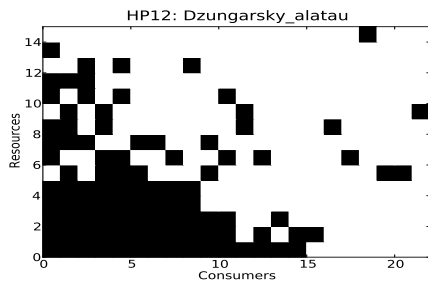
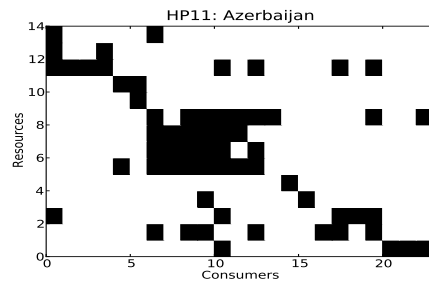
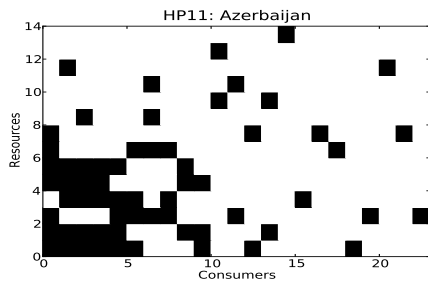
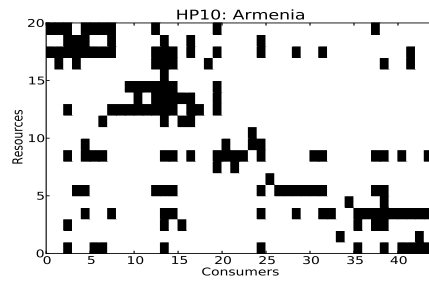
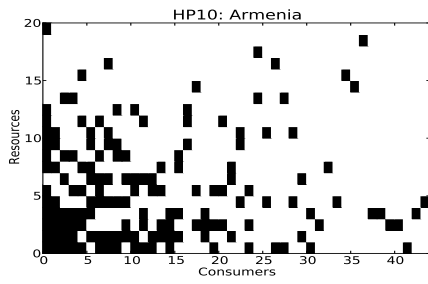
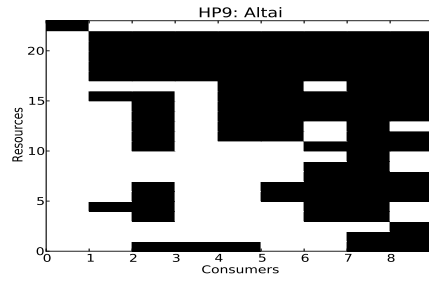
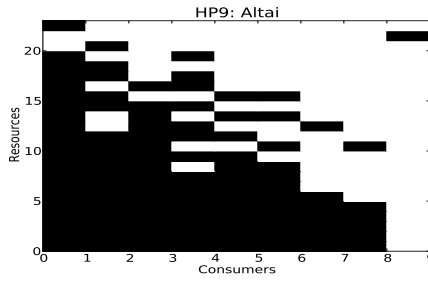
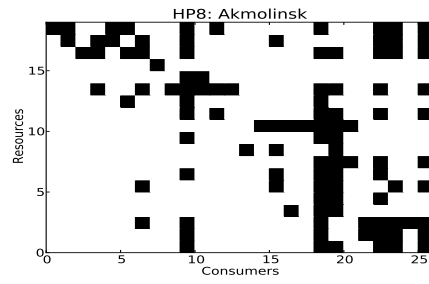
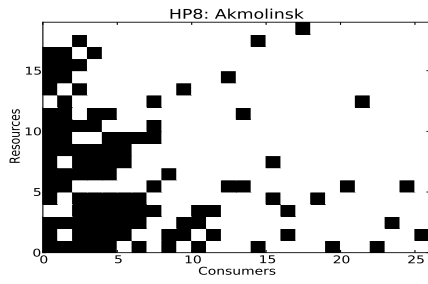
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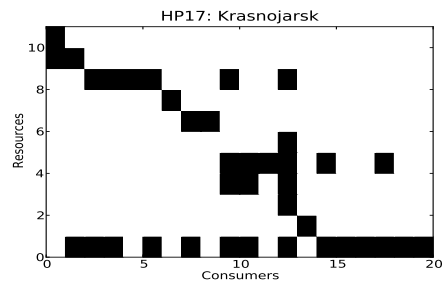
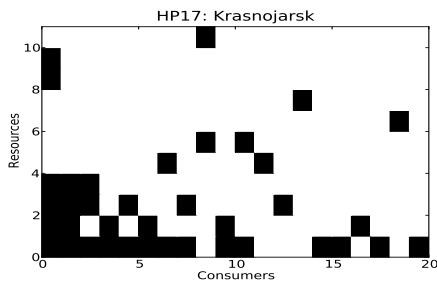
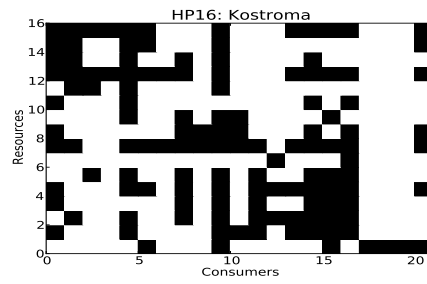
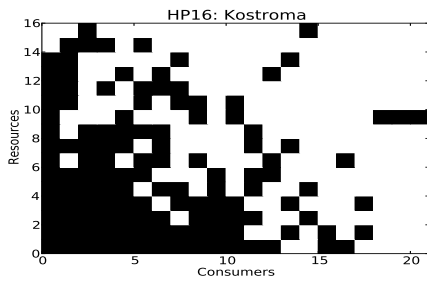
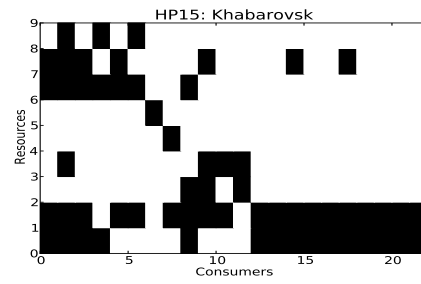
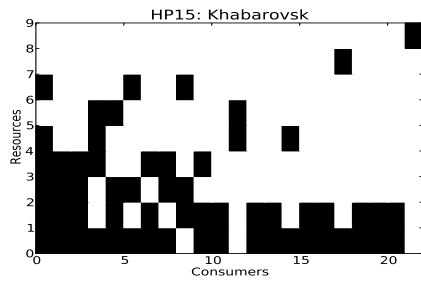
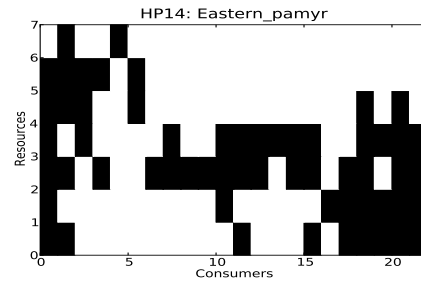
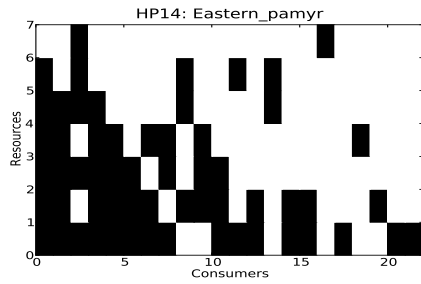
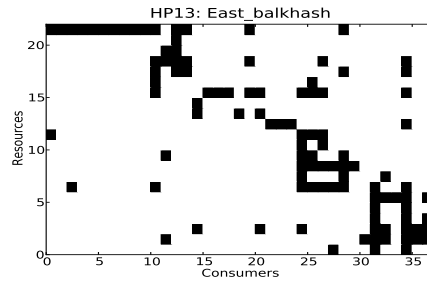
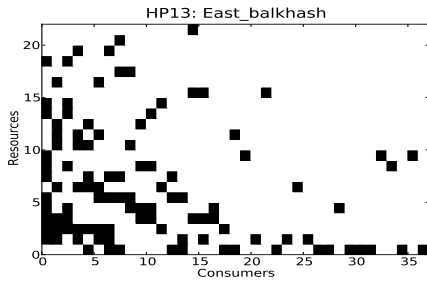
The data used in this thesis was obtained from published materials as mentioned in Chapter 2. We here present the interaction matrix plots for each of the 61 networks. Each of the plotted matrices is arranged in nested (left) and compartmentalised (right) forms. The titles of the plots indicate the network ID as used in the main document and the dataset name from the network source. For instance, the title of the first plot indicates that the network ID used in the thesis is HP1 while the dataset name for that network is Aishihik. Note that for each ID name, HP stands for host-parasite while PH: plant-herbivore. HP1 – 6 were obtained from the interaction web data base ([www.nceas.ucsb/interactionweb/index.html](http://www.nceas.ucsb/interactionweb/index.html)), HP7 – 33: Krasnov *et al.* (2012) and PH1 – 28: interaction web data base ([www.nceas.ucsb/interactionweb/index.html](http://www.nceas.ucsb/interactionweb/index.html)). Specifically, for PH1-24, two adjacent trophic levels were extracted from the predator-prey food webs while PH25 – 28 were directly extracted.



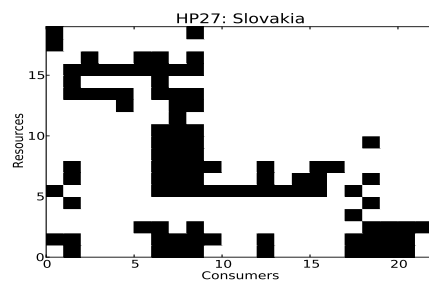
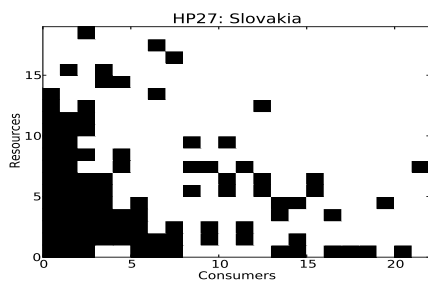
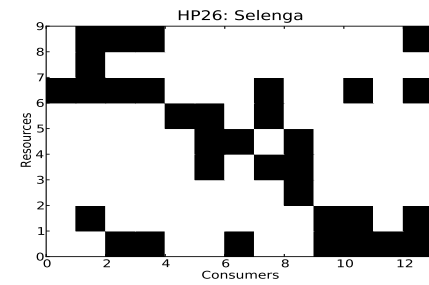
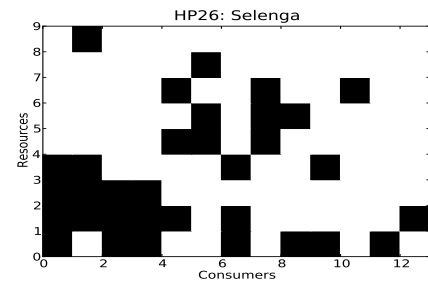
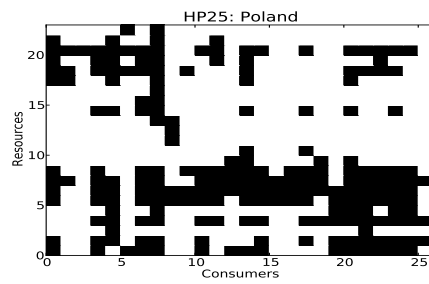
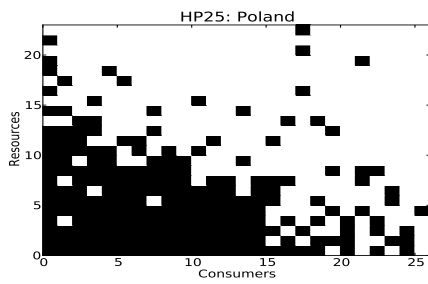
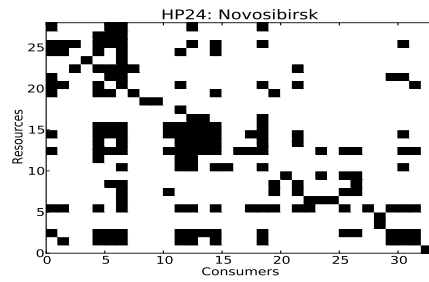
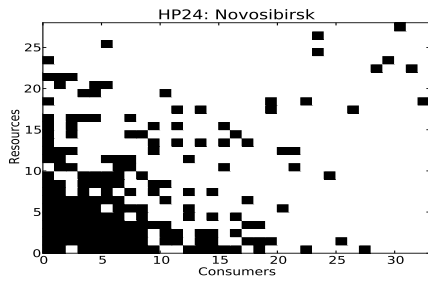
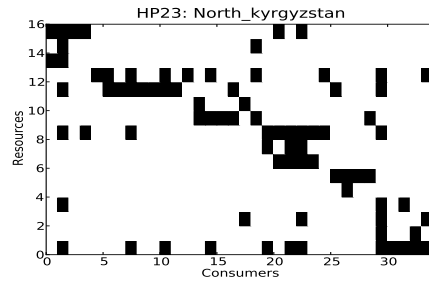
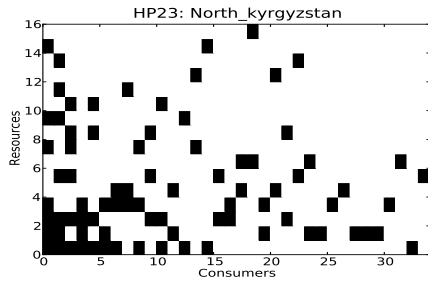


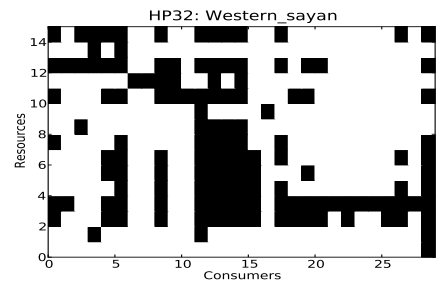
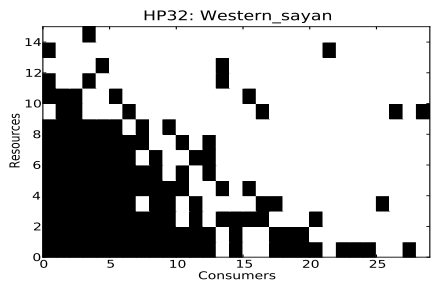
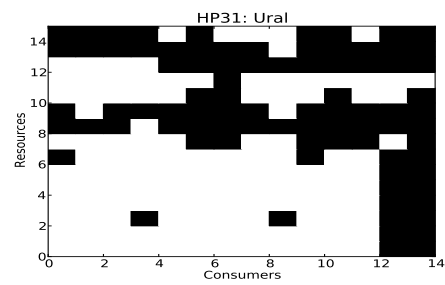
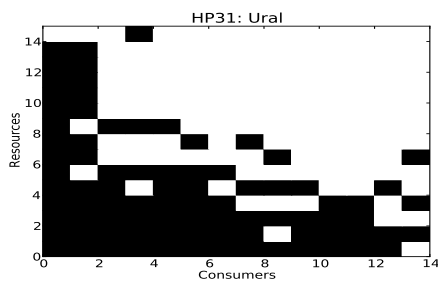
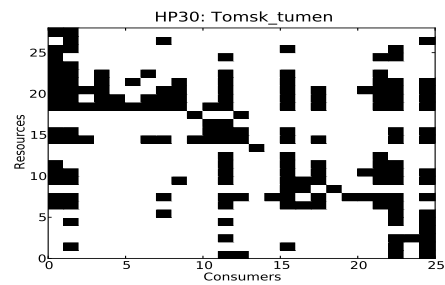
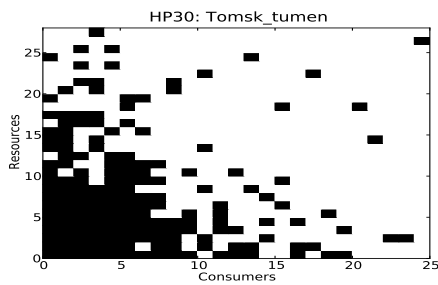
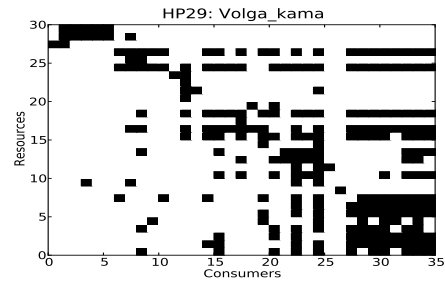
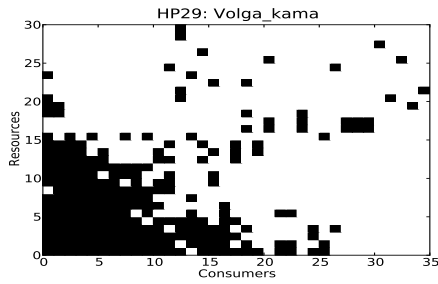
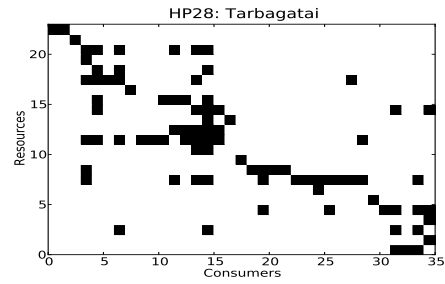
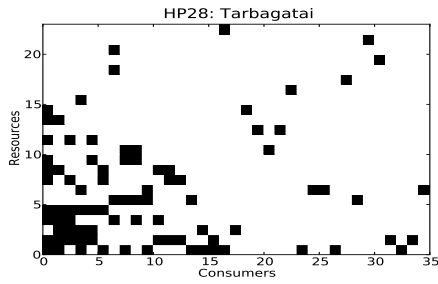


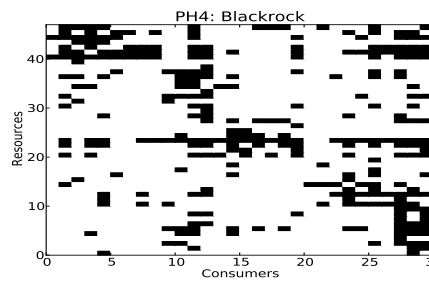
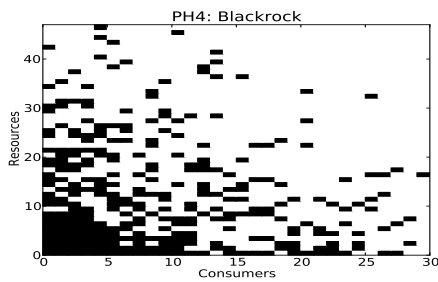
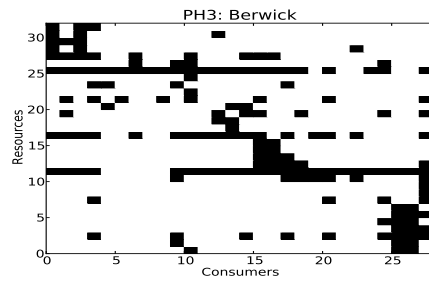
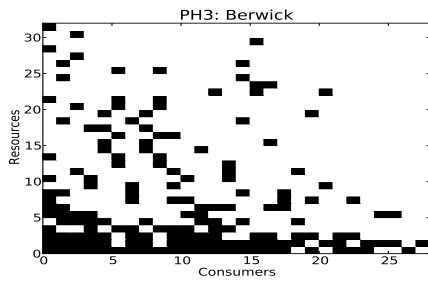
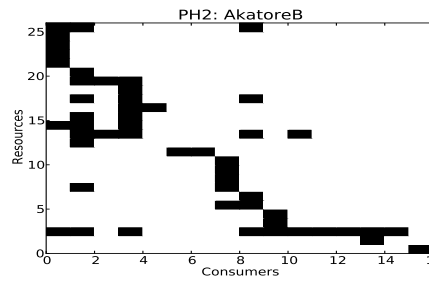
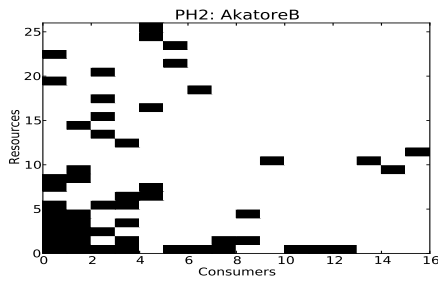
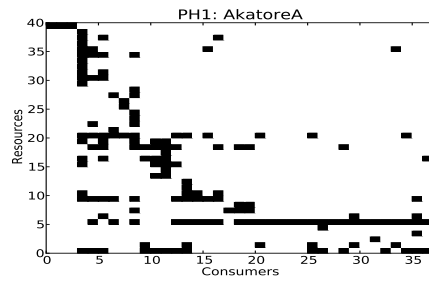
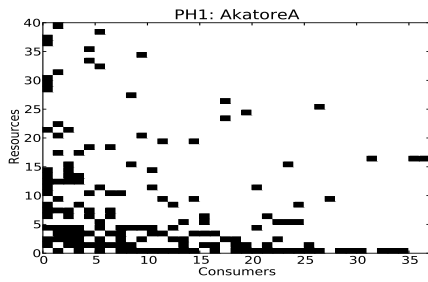
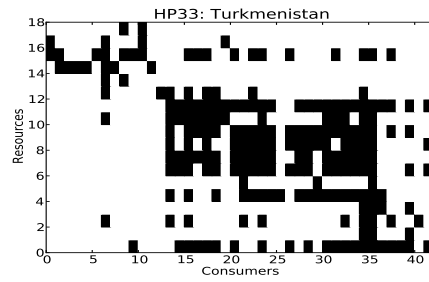
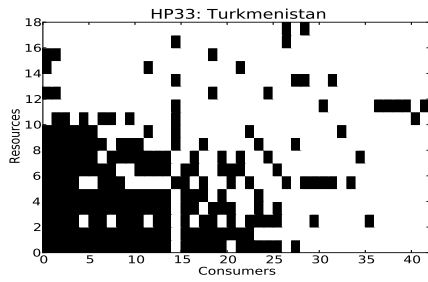


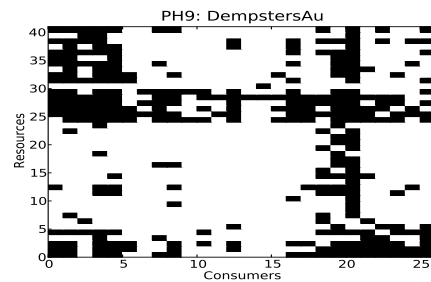
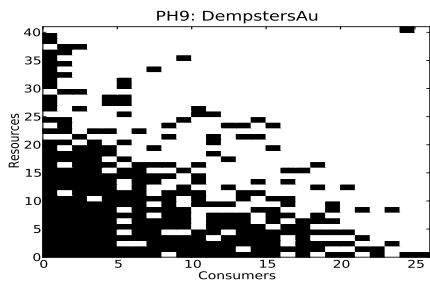
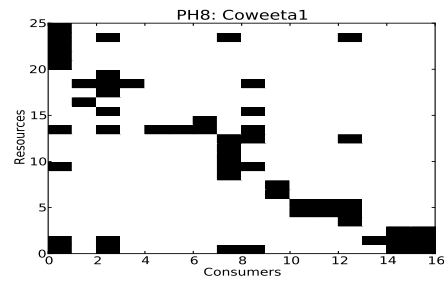
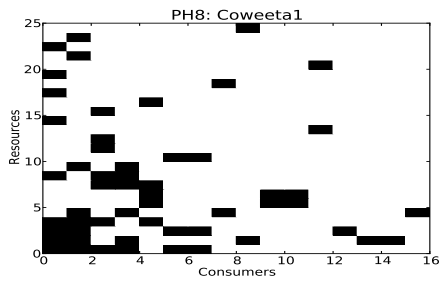
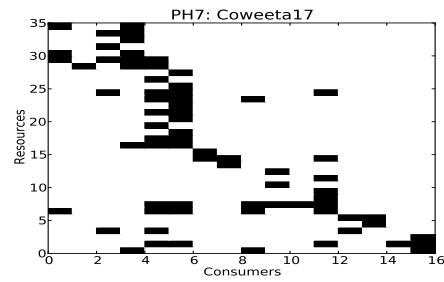
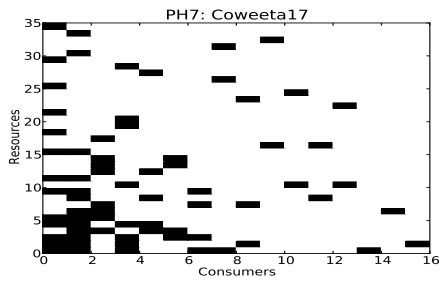
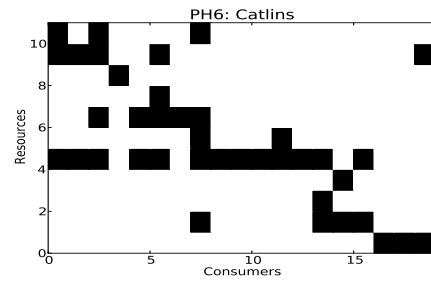
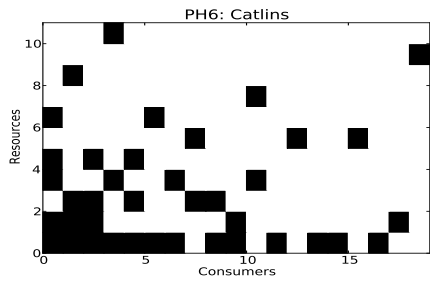
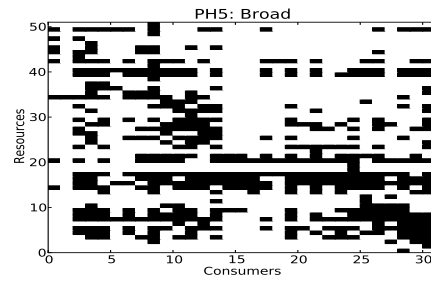
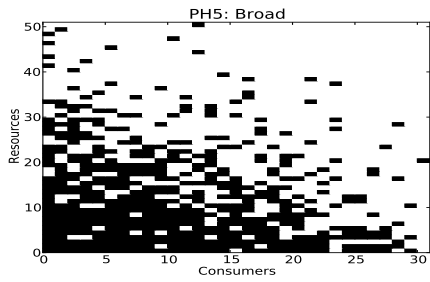




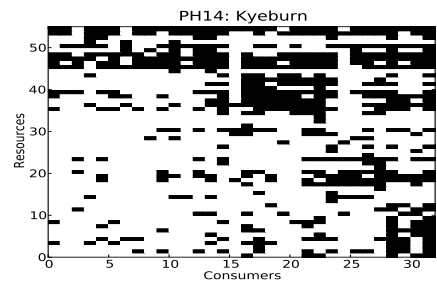
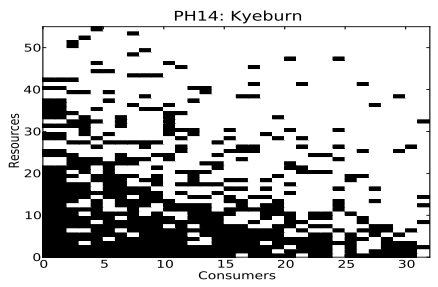
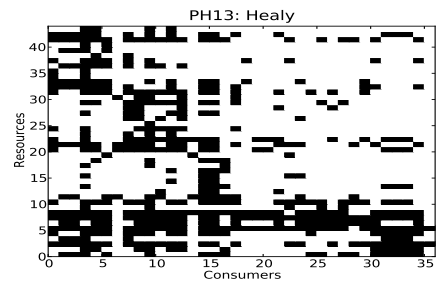
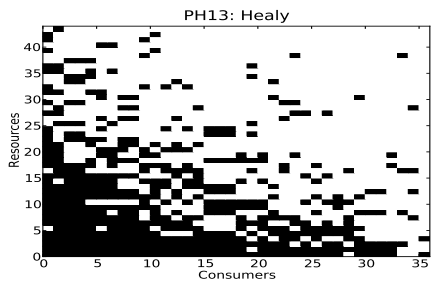
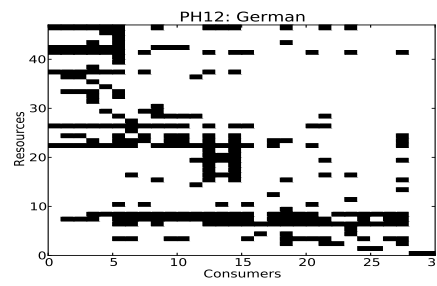
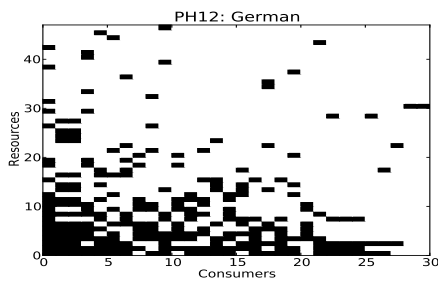
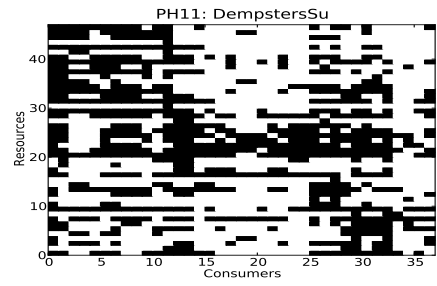
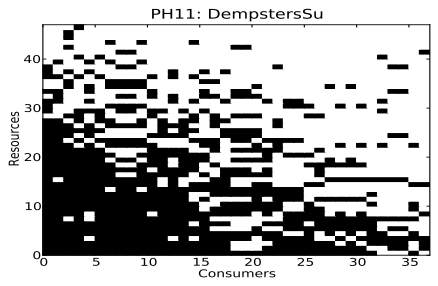
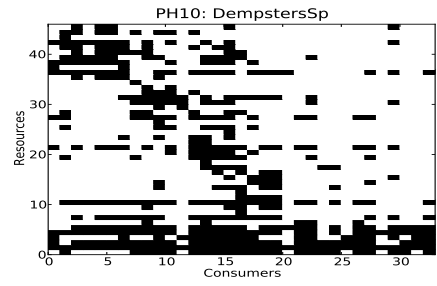
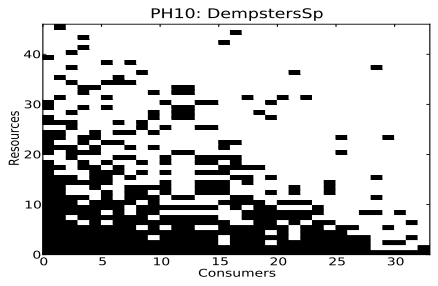


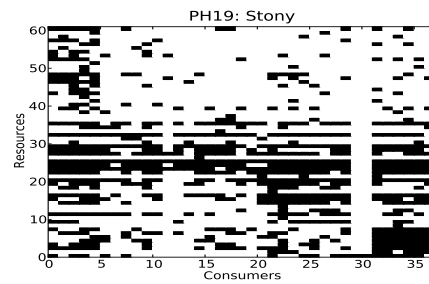
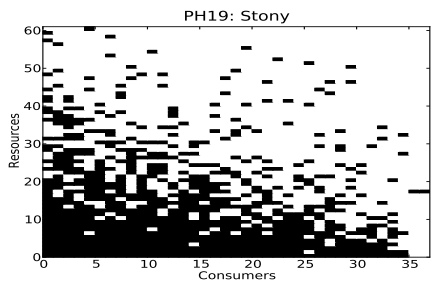
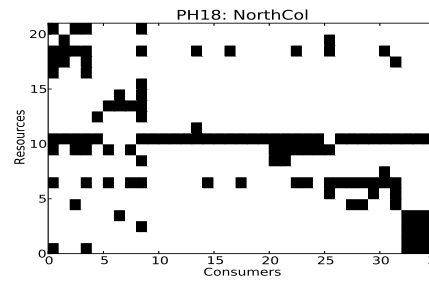
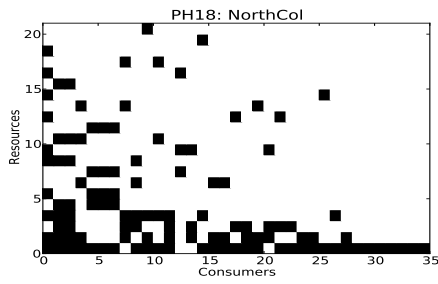
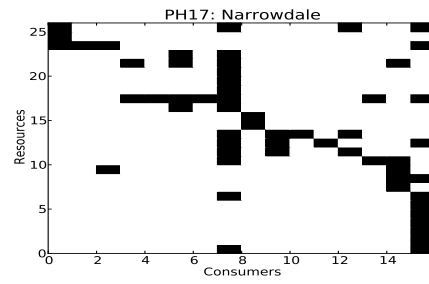
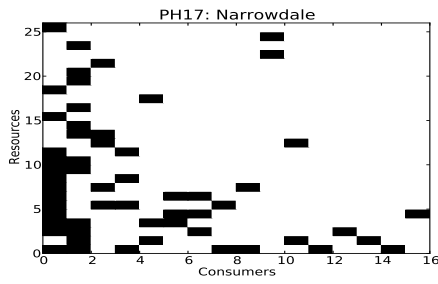
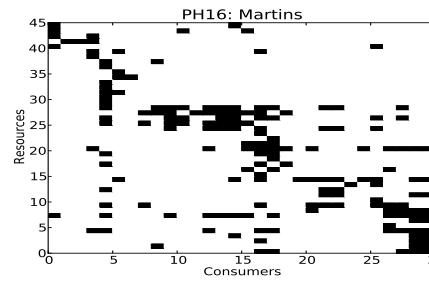
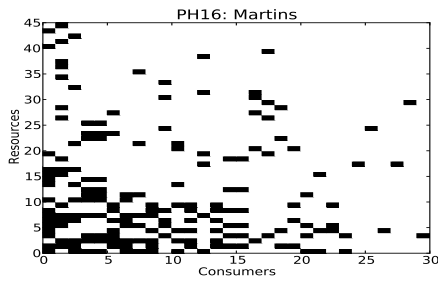
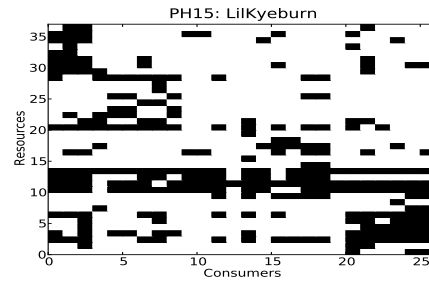
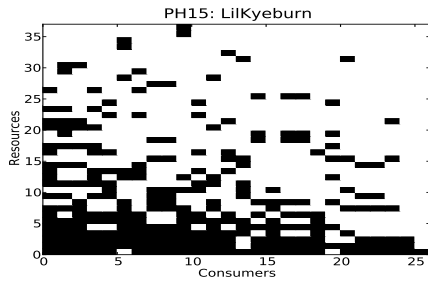


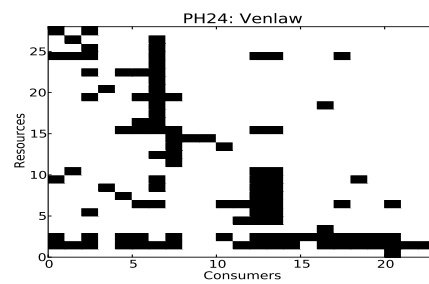
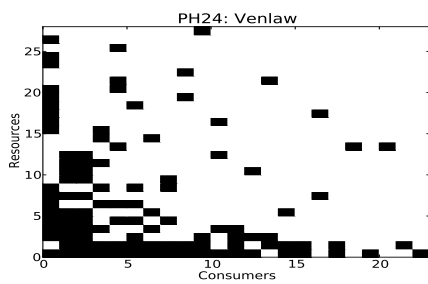
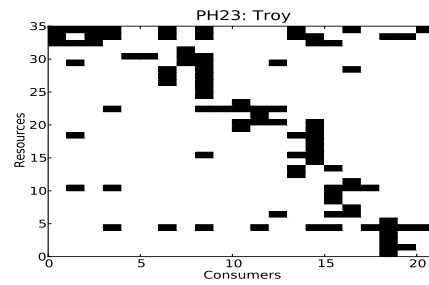
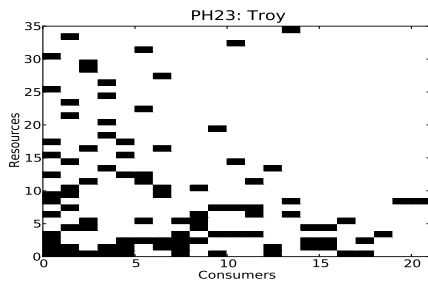
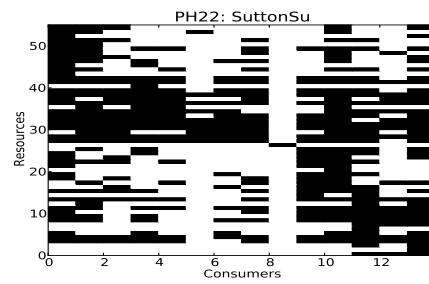
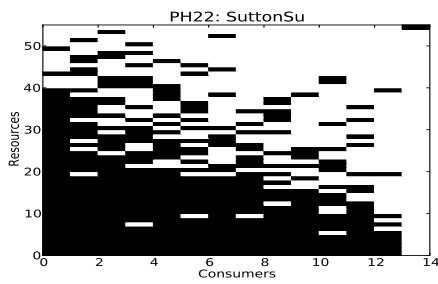
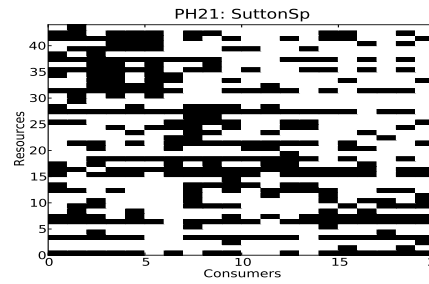
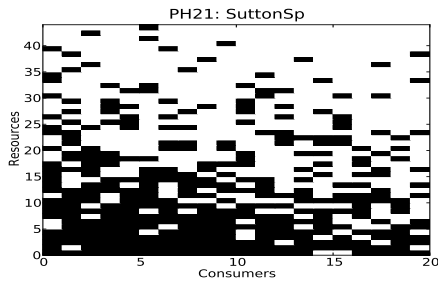
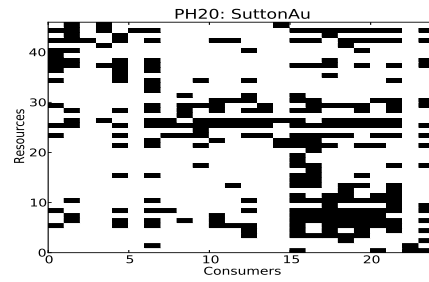
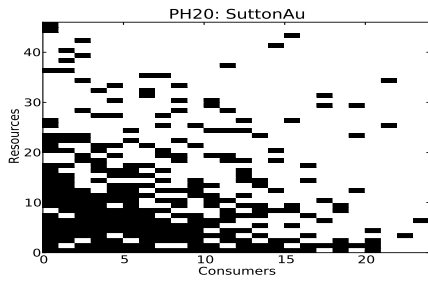


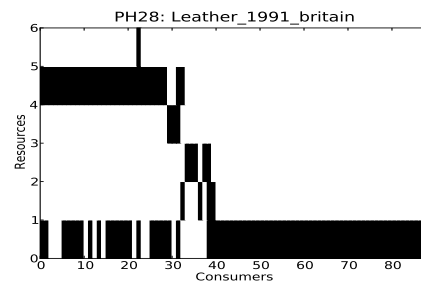
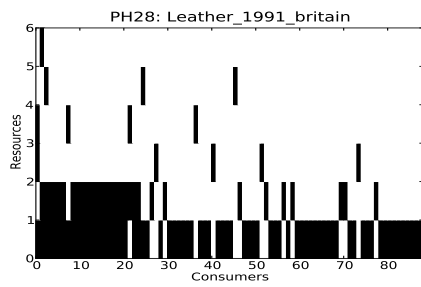
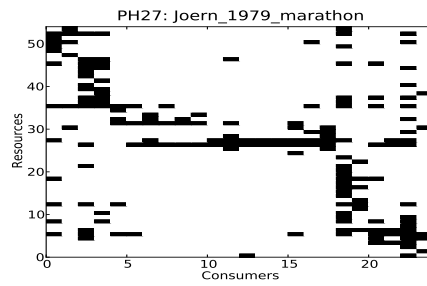
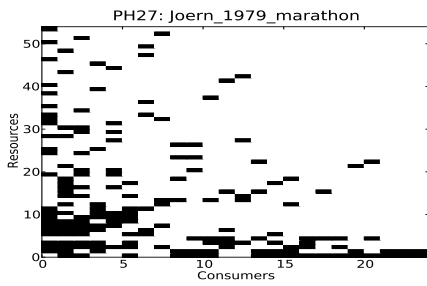
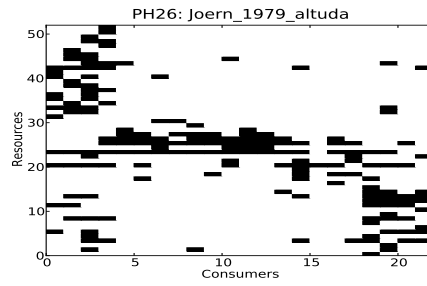
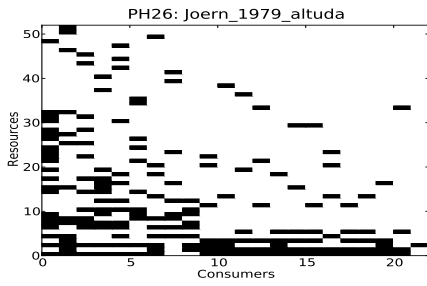
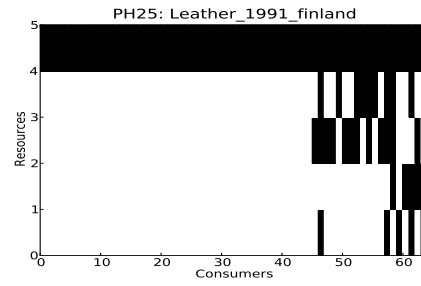
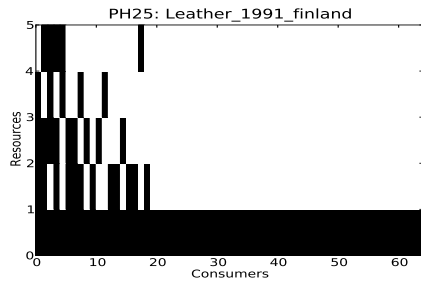












# Bibliography

- Abrams, P. and Matsuda, H. (1993). Effects of adaptive predatory and anti-predator behaviour in a two-prey-one-predator system. *Evolutionary Ecology*, vol. 7, pp. 312–326.
- Alcantara, J.M. and Rey, P.J. (2012). Linking topological structure and dynamics in ecological networks. *American Naturalist*, vol. 180, no. 2, pp. 186–199.
- Allesina, S. and Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, vol. 483, pp. 205–208.
- Almeida-Neto, M., Guimaraes, P., Guimaraes, P., Loyola, R. and Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, vol. 117, pp. 1227–1239.
- Aragón, J., Eberly, D. and Eberly, S. (1992). Existence and uniqueness of the maximum likelihood estimator for the two-parameter negative binomial distribution. *Statistics and Probability Letters*, vol. 15, pp. 375–379.
- Atmar, W. and Patterson, B.D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Ecologia*, vol. 96, pp. 373–382.
- Barabasi, A. and Albert, R. (1999). Emergence of scaling in random networks. *Science*, vol. 286, pp. 509–512.
- Bascompte, J. and Jordano, P. (2007). Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, vol. 38, pp. 567–593.
- Bascompte, J., Jordano, P., Melian, C.J. and Olesen, J.M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the USA*, vol. 100, pp. 9383–9387.
- Baskaran, N., Anbarasan, U. and Agoramoorthy, G. (2012). India's biodiversity hotspot under anthropogenic pressure: A case study of nilgiri biosphere reserve. *Journal for Nature Conservation*, vol. 20, pp. 56–61.
- Bastolla, U., Fortuna, M.A., Pascual-Garcia, A., Ferrera, A., Luque, B. and Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increase biodiversity. *Nature*, vol. 458, pp. 1018–1021.

- Bellay, S., P., L.D., Takemoto, R.M., and Luque, J.L. (2011). A host-endoparasite network of neotropical marine fish: are there organizational patterns? *Parasitology*, vol. 138, pp. 1945–1952.
- Boccaletti, S., Latora, V., Moreno, Y., Chavez, M. and Hwang, D.U. (2006). Complex networks: structure and dynamics. *Physics Reports*, vol. 424, pp. 175–308.
- Brose, U. (2011). Extinctions in complex, size-structured communities. *Basic and Applied Ecology*, vol. 12, pp. 557–561.
- Burgos, E., Ceva, H., Perazzo, R.P.J., Devoto, M., Medan, D., Zimmermann, M. and Delbue, A.M. (2007). Why nestedness in mutualistic networks? *Journal of Theoretical Biology*, pp. 307–313.
- Burnham, K.P. and Anderson, D.R. (1992). Multimodel inference : understanding aic and bic in model selection. *Sociological Methods and Research*, vol. 33, pp. 261–304.
- Cagnolo, L., Salvo, A. and Valladares, G. (2011). Network topology: patterns and mechanisms in plant-herbivore and host-parasitoid food webs. *Journal of Animal Ecology*, vol. 80, pp. 342–351.
- Cai, G.Q. and Lin, Y.K. (2007). Stochastic analysis of predator–prey type ecosystems. *Ecological Complexity*, vol. 4, pp. 242–249.
- Caro-Lopera, F.J., Leiva, V. and Balakrishnan, N. (2012). Connection between the Hadamard and matrix products with an application to matrix-variate Birnbaum-Saunders distributions. *Journal of Multivariate Analysis*, vol. 104, pp. 126–139.
- Chartrand, G. and Zhang, P. (2012). *A first course in graph theory*. Dover Publications, Mineola, New York.
- Clauset, A., Shalizi, C.R. and Newman, M.E.J. (2009). Power-law distributions in empirical data. *Society for Industrial Applied Mathematics Review*, vol. 51, pp. 661–703.
- Davis, M.A., Thompson, K. and Grime, J.P. (2005). Invasibility: the local mechanism driving community assembly and species diversity. *Ecography*, vol. 28, no. 5, pp. 696–704.
- de Visser, S. N. and Freymann, B.P. and Olf, H. (2011). The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. *Journal of Animal Ecology*, vol. 80, pp. 484–494.
- Dobson, A., Lafferty, K.D., Kuris, A.M., Hechinger, R.F. and Jetz, W. (2008). Homage to linnaeus: How many parasites? how many hosts? *Proceedings of the National Academy of Sciences of the USA*, vol. 105, pp. 11482–11489.
- Dunne, J.A., Williams, R.J. and Martinez, N.D. (2002a). Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences of the USA*, vol. 99, pp. 12917–12922.

- Dunne, J.A., Williams, R.J. and Martinez, N.D. (2002b). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, vol. 5, pp. 558–567.
- Eklof, A. and Ebenman, B. (2006). Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology*, vol. 75, pp. 239–246.
- Erdos, P. and Renyi, A. (1960). On the evolution of random graphs. *Magyar Tud. Akad. Mat. Kutato Int. Kozl.*, vol. 5, pp. 17–61.
- Estrada, E. (2007). Food webs robustness to biodiversity loss: The roles of connectance, expansibility and degree distribution. *Journal of Theoretical Biology*, vol. 244, pp. 296–307.
- Fordyce, J.A. (2006). The evolutionary consequences of ecological interactions mediated through phenotypic plasticity. *Journal of Experimental Biology*, vol. 209, pp. 2377–2383.
- Fortuna, M.A. and Bascompte, J. (2006). Habitat loss and the structure of plant-animal mutualistic networks. *Ecology Letters*, vol. 2, pp. 278–283.
- Fortuna, M.A., Stouffer, D.B., Olesen, J.M., Jordano, P., Mouillot, D., Krasnov, B.R., Poulin, R. and Bascompte, J. (2010). Nestedness versus modularity in ecological networks: two sides of the same coin? *Journal of Animal Ecology*, vol. 79, pp. 811–817.
- Fortunato, S. (2010). Community detection in graphs. *Physics Reports*, vol. 486, pp. 75–174.
- Fred, B. and Castillo-Chavez, C. (2000). *Mathematical models in population biology and epidemiology*. Springer-Verlag New York Berlin Heidelberg, London.
- Fryxell, J.M. and Lundberg, P. (1994). Diet choice and predator-prey dynamics. *Evolutionary Ecology*, vol. 8, pp. 407–421.
- Geffeney, S., Brodie Jr, E.D., Ruben, P.C. and Brodie, E.D. (2002). Mechanisms of adaptation in a predator-prey arms race: Ttx-resistant sodium channels. *Science*, vol. 297, pp. 1336–1339.
- Genini, J., Cortes, M.C., Guimaraes, P.R., and Galetti, M. (2012). Mistletoes play different roles in a modular host-parasite network. *Biotropica*, vol. 44, no. 2, pp. 171–178.
- Getz, W.M. (2011). Biomass transformation webs provide a unified approach to consumer-resource modelling. *Ecology Letters*, vol. 14, pp. 113–124.
- Gotelli, N.J. (2000). Null model analysis of species co-occurrence patterns. *Ecology*, vol. 81, pp. 2606–2621.
- Gotelli, N.J. and Graves, G.R. (1996). *Null models in ecology*. Smithsonian Institution Press, Washington, USA.
- Graham, S.P., Hassan, H.K., Burkett-Cadena, N.D., Guyer, C. and Unnasch, T.R. (2009). Nestness of ectoparasite-vertebrate host networks. *PLoS One*, vol. 4, no. e7873.

- Gregson, J.P. (2007). *Compartmentalisation of human immunodeficiency virus type 1 in the secondary lymphoid tissues*. PhD, Brigham Young University.
- Guimera, R. and Amaral, L.A.N. (2005a). Cartography of complex networks: modules and universal roles. *Journal of Statistical Mechanics: Theory and Experiment*, pp. 895–900.
- Guimera, R. and Amaral, L.A.N. (2005b). Functional cartography of complex metabolic networks. *Nature*, vol. 433, pp. 895–900.
- Guimera, R., Sales-Prado, M. and Amaral, L.A.N. (2004). Modularity from fluctuations in random graphs and complex networks. *Physical Review E*, vol. 70, p. 025101.
- Guimera, R., Stouffer, D.B., Sales-Pardo, M., Leicht, E.A., Newman, M.E.J. and Amaral, L.A.N. (2010). Origin of compartmentalisation in food webs. *Ecology*, vol. 91, pp. 2941–2942.
- Harper Jr, G.R. and Pfennig, D.W. (2008). Selection overrides gene flow to break down maladaptive mimicry. *Nature*, vol. 451, pp. 1103–1106.
- Holling, C.S. and Buckingham, S. (1976). Behavioral model of predator-prey responses. *Behavioral Science*, vol. 21, pp. 183–195.
- Jackson, M.O. (2008). *Social and economic networks*. Princeton University Press, Princeton.
- James, A., Pitchford, J.W. and Plank, M.J. (2012). Disentangling nestedness from models of ecological complexity. *Nature*, vol. 487, pp. 227–230.
- Kiers, E.T., Palmer, T.M., Ives, A.R., Bruno, J.F. and Bronstein, J.L. (2010). Mutualisms in a changing world: an evolutionary perspective. *Ecology Letters*, vol. 13, pp. 1459–1474.
- Kimbrell, T. and Holt, R.D. (2005). Individual behaviour, space and predator evolution promote persistence in a two-patch system with predator switching. *Evolutionary Ecology*, vol. 7, pp. 53–71.
- Kirkpatrick, S., Gelatt, C.D. and Vecchi, M.P. (1983). Optimization by simulated annealing. *Science*, vol. 220, pp. 671–680.
- Ko, W. and Ryu, K. (2006). Qualitative analysis of a predator–prey model with holling type ii functional response incorporating a prey refuge. *Journal of Differential Equations*, vol. 231, pp. 534–550.
- Kondoh, M. (2003). Foraging adaptation and the relationship between food-web complexity and stability. *Science*, vol. 299, pp. 1388–1391.
- Kondoh, M. (2006). Does foraging adaptation create the positive complexity-stability relationship in realistic food-web structure? *Journal of Theoretical Biology*, vol. 238, pp. 646–651.
- Kondoh, M., Kato, S. and Sakato, Y. (2010). Food webs are built up with nested subwebs. *Ecology*, vol. 91, no. 11, pp. 3123–3130.



- Krasnov, B.R., Fortuna, M.A., Mouillot, D., Khokhlova, I.S., Shenbrot, G.I. and Poulin, R. (2012). Phylogenetic signal in module composition and species connectivity in compartmentalised host-parasite networks. *American Naturalist*, vol. 174, no. 4, pp. 501–511.
- Krivan, V. and Sikder, A. (1999). Optimal foraging and predator-prey dynamics, ii. *Theoretical Population Biology*, vol. 55, pp. 111–126.
- Liu, B., Teng, Z. and Chen, L. (2006). An analysis of a predator-prey model with Holling ii functional response concerning impulsive control strategy. *Journal of Computational and Applied Mathematics*, vol. 193, pp. 347–362.
- May, R.M. (1973). *Stability and complexity in model ecosystems*. Princeton University Press, Princeton.
- McCann, K.S. (2000). The diversity-stability debate. *Nature*, vol. 405, pp. 228–233.
- Memmott, J., Waser, N.M. and Price, M.V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London B*, vol. 271, pp. 2605–2611.
- Meskens, C., Mckenna, D., Hance, T. and Windsor, D. (2011). Host plant taxonomy and phenotype influence the structure of a neotropical host plant-hispine beetle food web. *Ecological Entomology*, vol. 36, pp. 480–489.
- Morin, P.J. (1999). *Community ecology*. Blackwell Science, Carlton, Australia.
- Murdoch, W.W. (1969). Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs*, vol. 39, pp. 335–354.
- Musser, R.O., Hum-Musser, S.M., Eichenseer, H., Peiffer, M., Ervin, G., Murphy, J.B. and Felton, G.W. (2002). Caterpillar saliva beats plant defences - a new weapon emerges in the evolutionary arms race between plants and herbivores. *Nature*, vol. 416, pp. 599–600.
- Newman, M.E.J. (2003). The structure and function of complex networks. *Society for Industrial and Applied Mathematics*, vol. 45, no. 2, pp. 167–256.
- Newman, M.E.J. and Girvan, M. (2004). Finding and evaluating community structure in networks. *Physical Review E*, vol. 69, p. e26113.
- Nuismer, S.L., Ridenhour, B.J. and Oswald, B.P. (2007). Coevolutionary alternation in antagonistic interactions. *Evolution*, vol. 60, pp. 2207–2217.
- Okuyama, T. and Holland, J.N. (2008). Network structural properties mediate the stability of mutualistic communities. *Ecology Letters*, vol. 11, pp. 208–216.
- Olesen, J.M., Bascompte, J., Dupont, Y.L. and Jordano, P. (2007). The modularity of polination networks. *Proceedings of the National Academy of Sciences of the USA*, pp. 19891–19896.
- Pasteur, G. (1982). A classificatory review of mimicry systems. *Annual Review of Ecology, Evolution, and Systematics*, vol. 13, pp. 169–199.

- Patterson, B.D., Dick, C.W. and Dittmar, K. (2009). Nested distributions of bat flies (diptera: Streblidae) on neotropical bats: artifact and specificity in host-parasite studies. *Ecography*, vol. 32, pp. 481–487.
- Piazzon, M., Larrinaga, A.R. and Santamaria, L. (2011). Are nested networks more robust to disturbance? a test using epiphyte-tree, commensalistic networks. *PLoS One*, vol. 6, no. 5, p. e19637.
- Pires, M.M., Guimaraes, P.R., Araujo, M.S., Giaretta, A.A., Costa, J.C.L. and dos Reis, S.F. (2011). The nested assembly of individual-resource networks. *Journal of Animal Ecology*, vol. 80, pp. 896–903.
- Poisot, T., Thrall, P.H. and Hochberg, M.E. (2012). Trophic network structure emerges through antagonistic coevolution in temporally varying environments. *Proceedings of the Royal Society of London B*, vol. 279, pp. 299–308.
- Prado, P.I. and M., L.T. (2004). Compartments in insect-plant associations and their consequences for community structure. *Journal of animal ecology*, vol. 73, pp. 1168–1178.
- Price, P.W. (1977). General concepts on the evolutionary biology of parasites. *Evolution*, vol. 31, no. 2, pp. 405–420.
- Seal, H.L. (1952). The maximum likelihood fitting of the discrete pareto law. *Journal of the Institute of Actuaries*, vol. 78, pp. 115–121.
- Sever, M. (1987). *Ordinary differential equations*. Boole Press Limited, Ireland.
- Shirley, M.D.F. and Rushton, S.P. (2005). The impacts of network topology on disease spread. *Ecological Complexity*, vol. 2, pp. 287–299.
- Smout, S., Asseburg, C., Matthiopoulos, J., Fernandez, C., Redpath, C., Thirgood, S. and Harwood, J. (2010). The functional response of a generalist predator. *PLoS One*, vol. 5, p. e10761.
- Spottiswoode, C.N. and Stevens, M. (2010). Host-parasite arms races and rapid changes in bird egg appearance. *American Naturalist*, vol. 179, pp. 633–648.
- Staniczenko, P.P.A., Lewis, O.T., Jones, N.S. and Reed-Tsochas, F. (2010). Structural dynamics and robustness of food webs. *Ecology Letters*, vol. 13, pp. 891–899.
- Stephens, D.W. and Krebs, J.R. (1986). *Foraging theory*. Princeton University Press, Princeton.
- Stouffer, D.B. and Bascompte, J. (2011). Compartmentalisation increases food-web persistence. *Proceedings of the National Academy of Sciences of the USA*, vol. 108, no. 9, pp. 3648–3652.
- Thebault, E. and Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, vol. 329, pp. 853–856.

- Thierry, A., Beckerman, A.P., Warren, P.H., Williams, R.J., Cole, A.J. and Petchey, O.L. (2011). Adaptive foraging and the rewiring of size-structured food webs following extinctions. *Basic and Applied Ecology*, vol. 12, pp. 562–570.
- Tilman, D. (1986). A consumer-resource approach to community structure. *American Zoologist*, vol. 26, no. 1, pp. 5–22.
- Timi, J.T. and Poulina, R. (2008). Different methods, different results: temporal trends in the study of nested subset patterns in parasite communities. *Parasitology*, vol. 135, pp. 131–138.
- Vacher, C., Piou, D. and Desprez-Loustau, M. (2008). Architecture of an antagonistic tree/fungus network: the symmetric influence of past evolutionary history. *PLoS One*, vol. 3, p. e1740.
- van Baalen, M., Krivan, V., van Rijn, P.C.J. and Sabelis, M.W. (2001). Alternative food, switching predators, and the persistence of predator-prey systems. *American Naturalist*, vol. 157, no. 5, pp. 512–524.
- Vazquez, D.P., Bluthgen, N., Cagnolo, L. and Chacoff, N.P. (2009). Uniting pattern and process in plant–animal mutualistic networks: a review. *Annals of Botany*, vol. 103, pp. 1445–1457.
- Vincent, T.L.S., Scheel, D., Brown, J.S. and Vincent, T.L. (1996). Trade-offs and coexistence in consumer-resource models: It all depends on what and where you eat. *American Naturalist*, vol. 148, no. 6, pp. 1038–1058.
- Warnke, D., Barreto, J. and Temesgen, Z. (2007). Antiretroviral drugs. *Journal of Clinical Pharmacology*, vol. 47, pp. 1570–1579.
- Watts, D.J. and Strogatz, S.H. (1998). Collective dynamics of ‘small-world’ networks. *Nature*, vol. 393, pp. 440–442.
- Williams, R.J. (2011). Biology, methodology or chance? the degree distributions of bipartite ecological networks. *PLoS One*, vol. 6, p. e17645.
- Zhang, F., Hui, C. and Pauw, A. (2013). Adaptive divergence in Darwin’s race: How coevolution can generate trait diversity in a pollination system. *Evolution*, vol. 67, pp. 548–560.
- Zhang, F., Hui, C. and Terblanche, J.S. (2011). An interaction switch predicts the nested architecture of mutualistic networks. *Ecology Letters*, vol. 29, pp. 47–65.