Computational Ecology and Software, 2015, 5(4): 317-327

Article

The architecture of antagonistic networks: Node degree distribution, compartmentalization and nestedness

Savannah Nuwagaba[1], **Cang Hui**[1,2]

[1]Centre for Invasion Biology, Department of Mathematical Sciences, Stellenbosch University, Matieland 7602, South Africa

[2]Mathematical and Physical Biosciences, African Institute for Mathematical Sciences, Cape Town 7945, South Africa

E-mail: chui@sun.ac.za

Received 25 July 2015; Accepted 3 August 2015; Published online 1 December 2015

Abstract

Describing complex ecosystems as networks of interacting components has proved fruitful – revealing many distinctive patterns and dynamics of ecological systems. Of these patterns, three have often been brought up in literature, including species degree distribution, compartmentalization and nestedness, due largely to their implications for the functionality and stability of communities. Here, using 61 empirical antagonistic networks, we aim to settle the inconsistency in literature by (i) fitting their node degree distributions to five different parametric models and identifying the one fits the best, (ii) measuring the levels of nestedness and compartmentalization of these 61 networks and testing their significance using different null models, and (iii) exploring how network connectance affects these three network architecture metrics. This research showed that most antagonistic networks do not display power law degree distributions and that resource species are generally uniformly distributed. We also clearly showed that the conclusion of whether a network is significantly compartmentalized or nested depends largely on the null model used.

Keywords ecological network; modularity; null model; connectance.

Computational Ecology and Software
ISSN 2220-721X
URL: http://www.iaees.org/publications/journals/ces/online-version.asp
RSS: http://www.iaees.org/publications/journals/ces/rss.xml
E-mail: ces@iaees.org
Editor-in-Chief: WenJun Zhang
Publisher: International Academy of Ecology and Environmental Sciences

1 Introduction

Complex ecosystems can be depicted either as co-occurrence patterns of species distributions (Gaston and Blackburn, 2000; Hui and McGeoch, 2007a, 2008, 2014), or networks of interacting components, known as ecological networks (Zhang, 2011, 2012a,b). Of the most widely reported network structures, three have often been emphasized: species degree distribution, compartmentalization and nestedness, as these network structures could potentially signal 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; Minoarivelo et al., 2014). While in antagonistic networks, it is usually uniform (Boccaletti et al., 2006; Dunne et al., 2002a; but see, Hui and McGeoch, 2006).

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. In fact, most studies on network properties are centered on 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). In these studies especially on social, biological or even ecological networks, there has been a tendency of investigating whether the network degree distribution fits to a power law, thereby exhibiting the scale-free property. This is indeed an important network property due to its implications for community structure (such as its influence on network robustness). However, as observed from literature, many ecological networks do not possess this property. A general assessment of whether the degree distribution of antagonistic networks follows any other parametric functions of node degree distribution is needed.

Compartmentalization is characterized through organizing species into clusters so that interactions are more likely to happen between species within the same cluster than across clusters (Guimera et al., 2010; Newman and Girvan, 2004) while nestedness depicts that species interacting with specialists form only a subset of those interacting with generalists (Bascompte et al., 2003). The two patterns (compartmentalization 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; Dormann, 2011; Zhang et al., 2011), antagonistic networks of parasitism and predation (Krasnov et al., 2012; Vacher et al., 2008; Thebault and Fontaine, 2010), species co-distributions (Hui et al., 2013) 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). However, for the same networks, different metrics so far have yielded inconsistent results based on comparisons with networks generated from null models.

Here, using 61 empirical antagonistic networks, we aim to settle the inconsistency in literature by (i) fitting their node degree distributions to five different parametric models and identifying the one fits the best, (ii) measuring the levels of nestedness and compartmentalization of these 61 networks and testing their significance using different null models, and (iii) exploring how network connectance affects these three network architecture metrics.

2 Materials and Methods

The data sources are listed in Nuwagaba et al. (2015) and also below, with most of the data being used for analyses in recent publications (Krasnov et al., 2012; Fortuna et al., 2010). The data used here represent both terrestrial and aquatic systems and include networks with species richness (also known as network size) ranging from 18 to 130, the number of interactions ranging from 33 to 736, and network connectance (Co, defined for bipartite networks, the ratio of the number of realized interactions to the number of all possible interactions) ranging from 9.87 to 55.56% (i.e. Co ranges from 9.87 to 55.56). These ranges lie within those commonly used in ecological analyses, suggesting that the data are reliable and representative.

For each network, we fit the following parametric models to the degree distribution of these empirical networks, and also separately for degree distributions of the resource species only and the consumer species only. These models have been widely used for fitting monotonic rank curves in ecology (Hui, 2012; Hui and McGeoch, 2007b). The power law distribution is given by: $p(k) = Ck^{-\alpha}$, where C is the normalising constant, k ($> k_{\min}$) a specified node degree, and α the scaling constant (Seal, 1952). The truncated power law distribution is given by, $p(k) = Ck^{-\alpha}e^{-k/\lambda}$, where λ is the truncation parameter (Seal, 1952). The exponential distribution is defined as, $p(k) = Ce^{-\lambda k}$, where λ is the rate parameter. The negative binomial distribution is of the form: $p(k)$ = binomial $(k - r - 1, r - 1)p^r(1\text{-}p)^k$, where $r > 0$ is a positive discrete parameter. Given that the minimum value of k for the data is 1, we consider a zero-truncated negative binomial distribution. The uniform distribution is given by, $p(k) = 1/(b - 1)$ for $a \le k < b$ and $p(k) = 0$ otherwise. For convenience, the continuous form of these parametric functions was used; however, discrete values were used for model fitting.

All the above distributions were fitted to data numerically and the best-fitting distribution was selected as its degree distribution. This model selection was determined by comparing the corrected Akaike Information Criterion (AICc) score for each of the model distributions (Burnham and Anderson, 1992):

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

where L is the maximum value of the likelihood function for a specific model, β 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 AICc score is not used for rejecting or accepting a model but rather to compare the performance of different models. In other words, it only provides a relative goodness of the fit. AICc scores were computed for the node degrees of the general network, consumer species alone and resource species alone.

Although a number of measures have been proposed to quantify the level of compartmentalization in a network, the measure proposed by Newman and Girvan (2004) has been 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

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

where $A_{ij} = 1$ if i and j have a link between them and 0 otherwise, l is the total number of links in the network, $k_i k_j/(2l)$ is the expected number of links between nodes i and j, 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 although their optimisation techniques are quite different. In this study, we use the software NETCARTO, which uses the simulated annealing as the modularity optimisation technique (Guimera and Amaral, 2005a,b). The modularity can also be measured using the R package *modMax* (Schelling and Hui, 2015) which has implemented 38 algorithms for maximizing the above modularity measure.

Like with the modularity measures, scientists have also proposed various measures of nestedness, among which the matrix temperature (Atmar and Patterson, 1993) has been used the most (Almeida-Neto et al., 2008). However, the recent measure of nestedness which relaxes the weaknesses of the matrix temperature has been proposed by Almeida-Neto et al. (2008) and has quickly become the most popular measure of nestedness (Boyero et al., 2015). This new measure, known as the NODF, is based on two fundamental properties as per the meaning of nestedness: the decreasing fill and the paired overlap (for details, see Almeida-Neto et al, 2008).

We chose to use this measure due to its consistence in quantifying the level of nestedness as reported by Almeida-Neto et al. (2008). Here, we calculate the level of nestedness using the software package ANINHADO 3.0 (Guimera and Amaral, 2005a) that has implemented the NODF metric.

A null model is defined as “a pattern generating model that is based on randomization of ecological data or random sampling from a known or imagined distribution” (Gotelli and Graves, 1996). As mathematical models often include assumed mechanisms to capture reality, null models deliberately exclude these potential mechanisms in order to test the importance of these mechanisms on system behavior. To reach an affirmative conclusion from analyzing these network structures, we need to compare the observed structures with those random ones generated from null models for statistical significance (Guimera et al., 2004; Gotelli, 2000). As such, we investigated the significance of nestedness and modularity for these networks using the following null models where applicable.

The Erdos-Renyi random graph (Er or R) 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 the testing network. Probabilistic model (CE or P) assumes that the probability of having an interaction is proportional to the degree of both nodes of 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 connected with in the null model. Fixed null model (F) can be implemented in three different ways hence three different models. It can generate networks which have: (i) the same column sums (Fc), (ii) the same row sums (Fr), or (iii) the same row and column sums simultaneously (F) as the testing network (Gotelli, 2000). The three varieties of the fixed null model imply, respectively, that the number of resources per consumer, the number of consumers per resource and the number of interacting partners per species do not change. All the null models maintain the connectance of the network, and the third variety of the fixed null model (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).

3 Results

3.1 Degree distribution

Most of the antagonistic networks in this study did not display power law degree distributions regardless of whether the network was considered as a whole or the consumer or resource species only (Fig. 1). In total, 8.2% of the networks showed power law degree distribution, 15.3% truncated power law, 31.15% exponential, 12.02% negative binomial and 33.33% uniform degree distribution.

To understand the details of these distributions, we divided these networks into three groups depending on their connectance ($Co < 19$, $19 \leq Co < 30$ and $Co \geq 30$) and found that different forms of node degree distributions were dominant in specific ranges of connectance. The truncated power law distribution dominated the node degree distribution in the networks with lower connectance $Co < 19$; the exponential distribution dominated the networks with the middle range of connectance $19 \leq Co < 30$, and the uniform distribution dominated the networks with the upper range of connectence ($Co \geq 30$). We also investigated the connectance ranges for specific parametric forms. The power law was equally concentrated in the ranges $Co < 19$ and $19 \leq Co < 30$, the exponential distribution in the ranges $19 \leq Co < 30$, the truncated power law in the range $Co < 19$, and the negative binomial and the uniform distributions were concentrated in the range $Co \geq 30$ (Table 1).

When we investigated the degree distributions for the resource and consumer species separately, the degree distributions for resource species were different in most cases from these for the consumer species. The resource species had an exponential degree distribution in networks with low connectance (Co < 19) and changed to the uniform form in networks with moderate and high connectance (19 ≤ Co < 30 and Co ≥ 30; Table 1). All parametric forms were concentrated in the range Co < 19 except for the uniform distribution which dominated the high connectance range Co ≥ 30 (Table 1). The consumer species in networks with low and moderate connectance (Co < 19 and 19 ≤ Co < 30) were dominated by the exponential distribution, while the uniform distribution dominated networks with high connectance (Table 1). The power laws and truncated power law were concentrated in consumer species of networks with low connectance (Co < 19), the exponential in networks with moderate connectance (19 ≤ Co < 30) and the negative binomial and uniform distributions in networks with high connectance (Co ≥ 30; Table 1). In general, high connectance implied uniform or negative binomial degree distribution, low connectance implied power law or truncated power law degree distribution, and moderate connectance implied exponential degree distribution.

Table 1 Parametric forms of node degree distributions in 61 antagonistic networks. Five forms are included: power law (pl), truncated power law (tpl), uniform (un), negative binomial (nb) and exponential (exp). Network connectance (Co) is divided into three groups. Section 1: percentage of networks belonging to different parametric forms in each connectance group; section 2: percentage of best-fitting forms belonging to different connectance groups; section 3: percentage of resource species of networks belonging to different parametric forms in each connectance group; section 4: percentage of best-fitting forms of resource species in different connectance groups; section 5: percentage of consumer species of networks belonging to different parametric forms in each connectance group; section 6: percentage of best-fitting forms of consumer species in different connectance groups.

Range	pl	tpl	un	nb	exp
Co < 19	8.7	60.87	13.04	17.39	0
19 ≤ Co < 30	11.11	5.56	61.11	16.67	5.56
Co ≥ 30	0	10	20	25	45
Co < 19	50	82.35	16.67	33.3 3	0
19 ≤ Co < 30	50	5.88	61.11	25	10
Co ≥ 30	0	11.76	22.22	41.67	90
Co < 19	17.37	13.04	52.17	13.04	4.35
19 ≤ Co < 30	5.56	11.11	27.78	5.56	50.0
Co ≥ 30	0	0	5	10	85
Co < 19	80	60	66.67	50	3.7
19 ≤ Co < 30	20	40	27.78	16.67	33.33
Co ≥ 30	0	0	5.56	33.33	62.96
Co < 19	21.74	26.09	34.78	4.35	13.04
19 ≤ Co < 30	5.56	0	55.56	5.56	33.33
Co ≥ 30	0	0	15	10	75
Co < 19	83.33	100	38.1	25.0	12.5
19 ≤ Co < 30	16.67	0	47.62	25	25
Co ≥ 30	0	0	14.29	50	62.5

3.2 Modularity

The modularity of networks ranged from 0.140 to 0.547. Although the average modularity of the networks was quite high (M = 0.327), the networks were not significantly modular compared to random networks from null models. 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. Regardless of the insignificance, we observed a pronounced relationship between the modularity and connectance in these networks (Fig. 2a), suggesting that generally, less connected networks are modular or more compartmentalized.

3.3 Nestedness

The level of nestedness (measured as NODF) ranged from 13.07 to 74.31, with an average of NODF=42.97. Most of the networks were significantly nested regardless of the null model used. In fact, the fixed and probabilistic null models identified 55 and 49 networks, respectively, as significantly nested. There is an obvious negative correlation between the NODF and modularity (Fig.2b), suggesting that there should also be a pronounced relationship between nestedness and connectance: highly connected networks are less compartmentalized but more nested.

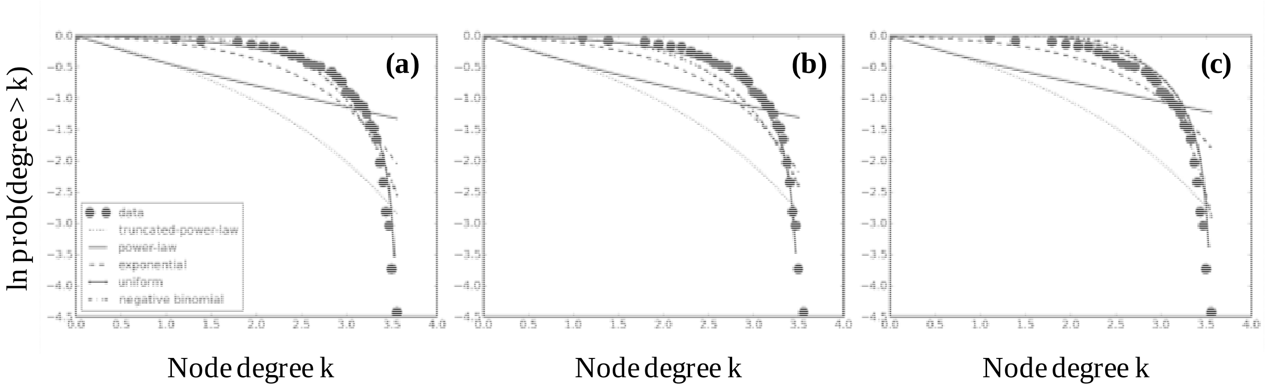

Fig. 1 An example of a network fitted with the five degree distribution forms. Panels (a), (b), and (c) are the degree distribution for the entire network, the consumers only and the resources only, respectively, for network PH11 (Nuwagaba et al., 2015).

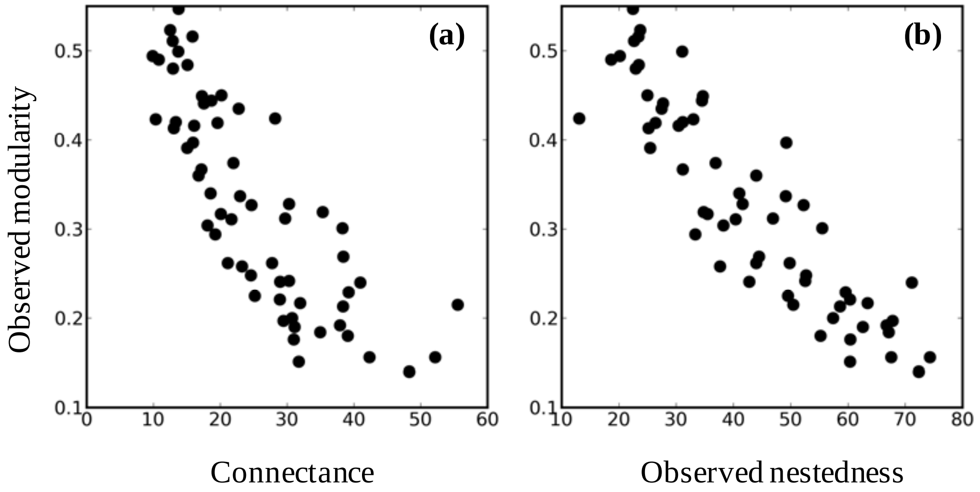

Fig. 2 Relationships (a) between modularity (the level of compartmentalization) and connectance and (b) between modularity and nestedness for 61 real networks.

4 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.

Table 2 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, individualresource; 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 probably 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(R_d,8), Q_d(R_d,15)	-	Modularity was significant but only slightly higher than null model expectation	16

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.

Antagonistic interactions are ubiquitous in nature (Ouyang et al., 2014; Shi et al., 2014; Soufbaf et al., 2012; Su and Hui, 2011; Su et al., 2015; Landi et al., 2015; Zhao et al., 2012, 2013, 2015), and the networks formed by these kind of interactions have often been regarded as being compartmentalized (Genini et al., 2012;

Krasnov et al., 2012; Alcantara and Rey, 2012), we had a rather surprising result when comparing the structures of the 61 real networks 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)]. 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 3.1.7), 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).

Acknowledgements

We acknowledge funding received from the South African National Research Foundation (No. 76912, 81825 and 89967) to CH and the PhD Scholarship from the Deutscher Akademischer Austausch Dienst (DAAD; German Academic Exchange Service) to SN.

References

Alcantara JM, Rey PJ. 2012. Linking topological structure and dynamics in ecological networks. American Naturalist, 180: 186-199

Allesina S, Tang S. 2012. Stability criteria for complex ecosystems. Nature, 483: 205-208

Almeida-Neto M, Guimaraes P, Guimaraes P, Loyola R, Ulrich W. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos, 117:1227-1239

Atmar W, Patterson B.D. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia, 96: 373-382

Bastolla U, Fortuna MA, Pascual-Garcia A, Ferrera A, Luque B, Bascompte J. 2009. The architecture of mutualistic networks minimizes competition and increase biodiversity. Nature, 458: 1018-1021

Bellay SP, Takemoto LD, Luque JL. 2011. A host-endoparasite network of neotropical marine fish: are there organizational patterns? Parasitology, 138:1945-1952

Boccaletti S, Latora V, Moreno Y, Chavez M, Hwang DU. 2006. Complex networks: structure and dynamics. Phys. Rep., 424:175-308

Boyero L, Pearson RG, Swan CM, Hui C, Albariño RJ, Arunachalam M, Callisto M, Chará J, et al. 2015. Latitudinal gradient of nestedness and its potential drivers in stream detritivores. Ecography (in press) doi:10.1111/ecog.00982

Burgos E, Ceva H, Perazzo RPJ, Devoto M, Medan D, Zimmermann M, Delbue AM. 2007. Why nestedness in mutualistic networks? Journal of Theoretical Biology, 249: 307–313

Burnham KP, Anderson DR. 1992. Multimodel inference : understanding aic and bic in model selection. Sociol. Method. Res., 33: 261-304

Cagnolo L, Salvo A, Valladares G. 2011. Network topology: patterns and mechanisms in plant-herbivore and host-parasitoid food webs. Journal of Animal Ecology, 80: 342–351

Dormann CF. 2011. How to be a specialist? Quantifying specialisation in pollination networks. Network Biology, 1(1): 1-20

Dunne JA, Williams RJ. Martinez ND. 2002a. Food-web structure and network theory: The role of connectance and size. Proceedings of the National Academy of Sciences USA, 99: 12917-12922

Dunne JA, Williams, R.J. and Martinez, N.D. 2002b. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecology Letters, 5:558–567.

Erdos P, Renyi A. 1960. On the evolution of random graphs. 343-347, Institute of Mathematics, Hungarian Academy of Sciences, Hungary

Estrada E. 2007. Food webs robustness to biodiversity loss: The roles of connectance, expansibility and degree distribution. Journal of Theoretical Biology, 244: 296-307

Fortuna MA, Bascompte J. 2006. Habitat loss and the structure of plant-animal mutualistic networks. Ecology Letters, 2: 278-283

Fortuna MA, Stouffer DB, Olesen JM, Jordano P, Mouillot D, Krasnov BR, Poulin R, Bascompte J. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? Journal of Animal Ecology, 79: 811-817

Fortunato S. 2010. Community detection in graphs. Phys. Rep., 486: 75-174

Gaston KJ, Blackburn TM. 2000. Pattern and Process in Macroecology. Blackwell Science, Oxford, UK

Genini J, Cortes MC, Guimaraes PR, Galetti M. 2012. Mistletoes play different roles in a modular host-parasite network. Biotropica, 44: 171-178

Gotelli NJ. 2000. Null model analysis of species co-occurrence patterns. Ecology, 81: 2606-2621

Gotelli NJ, Graves GR. 1996. Null models in ecology. Smithsonian Institution Press, Washington, USA

Graham SP, Hassan HK, Burkett-Cadena ND, Guyer C, Unnasch TR. 2009. Nestedness of ectoparasite-vertebrate host networks. Plos One, 4: e7873

Guimera R, Amaral LAN. 2005a. Cartography of complex networks: modules and universal roles. Journal of Statistical Mechanics, P02001.

Guimera R, Amaral LAN. 2005b. Functional cartography of complex metabolic networks. Nature, 433: 895-900

Guimera R, Sales-Prado M, Amaral LAN. (2004). Modularity from fluctuations in random graphs and complex networks. Physical Review E, 70: 025101

Guimera R, Stouffer DB, Sales-Pardo M, Leicht EA, Newman MEJ, Amaral LAN. 2010. Origin of compartmetalisation in food webs. Ecology, 91: 2941–2942

Hui C. 2012. Scale effect and bimodality in the frequency distribution of species occupancy. Community Ecology, 13: 30-35

Hui C, McGeoch MA. 2006. Evolution of body size, range size and food composition in a predator-prey metapopulation. Ecological Complexity, 3: 148-159

Hui C, McGeoch MA. 2007a. Modeling species distributions by breaking the assumption of self-similarity. Oikos, 116: 2097-2107

Hui C, McGeoch MA. 2007b. Capturing the ‘droopy tail’ in the occupancy-abundance relationship. ÉcoScience, 14:103-108

Hui C, McGeoch MA. 2008. Does the self-similar species distribution model lead to unrealistic predictions? Ecology, 89: 2946-2952

Hui C, McGeoch MA. 2014. Zeta diversity as a concept and metric that unifies incidence-based biodiversity patterns. American Naturalist, 184: 684-694

Hui C, Richardson DM, Pyšek P, Le Roux JJ, Kučera T, Jarošík V. 2013. Increasing functional modularity with residence time in the co-distribution of native and introduced vascular plants. Nature Communications, 4: 2454

Jackson MO. 2008. Social and economic networks. Princeton University Press, Princeton, USA

James A, Pitchford JW, Plank MJ. 2012. Disentangling nestedness from models of ecological complexity. Nature, 487: 227-230

Kirkpatrick S, Gelatt CD,Vecchi MP. 1983. Optimization by simulated annealing. Science, 220: 671-680

Kondoh M, Kato S, Sakato Y. 2010. Food webs are built up with nested subwebs. Ecology, 91: 3123-3130

Krasnov BR, Fortuna MA, Mouillot D, Khokhlova IS, Shenbrot GI, Poulin R.2012. Phylogenetic signal in module composition and species connectivity in compartmentalised host-parasite networks. American Naturalist, 174: 501-511

Landi P, Hui, C, Dieckmann U. 2015. Fisheries-induced disruptive selection. Journal of Theoretical Biology, 365: 204-216

Memmott J, Waser NM, Price MV. 2004. Tolerance of pollination networks to species extinctions. Proceedings of the Royal Society B, 271: 2605-2611

Meskens C, Mckenna D, Hance T, Windsor D. 2011. Host plant taxonomy and phenotype influence the structure of a neotropical host plant-hispine beetle food web. Ecological Entomology, 36: 480-489

Minoarivelo HO, Hui C, Terblanche JS, Kosakovsky Pond SL, Scheffler K. 2014. Detecting phylogenetic signal in mutualistic interaction networks using a Markov process model. Oikos, 123: 1250-1260

Newman MEJ, Girvan M. 2004. Finding and evaluating community structure in networks. Physical Review E, 69: 26113

Nuwagaba S, Zhang F, Hui C. 2015. A hybrid behavioural rule of adaptation and drift explains the emergent architecture of antagonistic networks. Proceedings of the Royal Society B, 282: 20150320

Olesen JM, Bascompte J, Dupont YL, Jordano P. 2007. The modularity of polination networks. Proceedings of the National Academy of Sciences USA, 104: 9891-9896

Ouyang F, Hui C, Ge S, Men XY, Zhao ZH, Shi PJ, Zhang YS, Li BL. 2014. Weakening density dependence from climate change and agricultural intensification triggers pest outbreaks: a 37-year observation of cotton bollworms. Ecology and Evolution, 4: 3362-3374

Patterson BD, Dick CW, Dittmar K. 2009. Nested distributions of bat flies (diptera: Streblidae) on neotropical bats: artifact and specificity in host-parasite studies. Ecography, 32: 481-487

Piazzon M, Larrinaga AR, Santamaria L. 2011. Are nested networks more robust to disturbance? a testusing epiphyte-tree, cosmensalistic networks. PLoS One, 6: e19637

Pires MM, Guimaraes PR, Araujo MS, Giaretta AA, Costa JCL, dos Reis SF. 2011. The nested assembly of individual-resource networks. Journal of Animal Ecology, 80: 896-903

Price PW. 1977. General concepts on the evolutionary biology of parasites. Evolution, 31: 405-420

Seal HL. 1952. The maximim likelihood fitting of the discrete pareto law. Institute and Faculty of Actuaries, 78: 115-121

Schelling M., Hui C. 2015. modMax: Community structure detection via modularity maximization. R package version 1.0. USA

Shi PJ, Hui C, Men XY, Ge F, Zhao ZH, Ou-Yang F, Cao HF, Li BL. 2014. Cascade effects of crop species richness on the diversity of pest insects and their natural enemies. Science China Life Sciences, 57: 718-725

Soufbaf M, Fathipour Y, Zalucki MP, Hui C. 2012. Importance of primary metabolites in canola in mediating interactions between a specialist leaf-feeding insect and its specialist solitary endoparasitoid. Arthropod-Plant Interactions, 6: 241-250

Stouffer DB, Bascompte J. 2011. Compartimentalisation increases food-web persistence. Proceedings of the National Academy of Sciences USA, 108: 3648-3652

Su M, Hui C. 2011. The effect of predation on the prevalence and aggregation of pathogens in prey. BioSystems, 105: 300-306

Su M, Hui C, Lin ZS. 2015. Effects of the transmissibility and virulence of pathogens on intraguild predation in fragmented landscapes. BioSystems, 129: 44-49

Thebault E, Fontaine C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. Science, 329: 853-856

Timi JT, Poulina R. 2008. Different methods, different results: temporal trends in the study of nested subset patterns in parasite communities. Parasitology, 135: 131-138

Vacher C, Piou D, Desprez-Loustau M. 2008. Architecture of an antagonistic tree/fungus network: the symmetric influence of past evolutionary history. PLoS One, 3: e1740

Williams RJ. 2011. Biology, methodology or chance? the degree distributions of bipartite ecological networks. PLoS One, 6: e17645

Zhang F, Hui C, Terblanche JS. 2011. An interaction switch predicts the nested architecture of mutualistic networks. Ecological Letters, 14: 797-803

Zhang WJ. 2011. Constructing ecological interaction networks by correlation analysis: hints from community sampling. Network Biology, 1(2): 81-98

Zhang WJ. 2012a. Computational Ecology: Graphs, Networks and Agent-based Modeling. World Scientific, Singapore

Zhang WJ. 2012b. How to construct the statistic network? An association network of herbaceous plants constructed from field sampling. Network Biology, 2(2): 57-68

Zhao ZH, He DH, Hui C. 2012. From the inverse density-area relationship to the minimum patch size of a host-parasitoid system. Ecological Research, 27: 303-309

Zhao ZH, Hui C, He DH, Ge F. 2013. Effects of position within wheat field and adjacent habitats on the density and diversity of cereal aphids and their natural enemies. BioControl, 58: 765-776

Zhao ZH, Hui C, He DH, Li BL. 2015. Effects of agricultural intensification on ability of natural enemies to control aphids. Scientific Report, 5: 8024