Ecological interaction networks: prospects and pitfalls

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Abstract. Interaction networks are a tool to visualize and to study the relationships between interacting species across and within trophic levels. Recent research uncovered many properties of such networks that remained undetected in previous food web studies. These patterns could be related to evolutionary and ecological processes. The study of interaction networks promises therefore progress in the study of constraints that act on the coevolution of interacting species and on food webs. However, there are still many pitfalls associated with the statistical analysis, the properties of the metrics involved and the appropriate null model choice. Here I review the mechanisms that shape interaction matrices, the possible internal structures and their ecological interpretation, and the analytical tools to identify matrix structure. Progress in the field needs critical meta-analytical and comparative studies that indentify the best suited null models (low type I and II error probabilities and high power to disentangle statistical from ecological processes) and clarify the interdependence of different concepts and metrics associated with network approaches. It is not improbable that many patterns recently associated with ecological and evolutionary processes might turn out to be simple side effects of the sampling from the underlying metacommunity distributions.

Key words: presence – absence matrix, nestedness, coherence, idiosyncrasy, co-occurrence, asymmetric interactions, marginal distribution, food webs, phylogeny, null models.

1. Ecological networks

Within true ecological communities species interact in different ways. Vertical interactions (herbivory, predation, parasitism etc.) are traditionally described as a food chain with a food web approach. Food webs, however, have also a horizontal dimension: species of the same or adjacent trophic levels interact in various ways. These interactions are rarely random but constraint in various ways by the ecology and evolutionary history of the interacting species (Bascompte et al. 2003; Bascompte & Jordano 2007; Ollerton et al. 2007). Interaction (often termed mutualistic) networks are a tool to visualize and to study the relationships between interacting species across and within trophic levels (Bascompte et al. 2003). These are commonly given as ordered bipartite *m*x*n* matrices where the *m* rows and *n*

columns denote species of two communities that potentially interact (Fig. 1). Typical examples are plant-pollinator or plant seed-disperser networks (Bascompte et al. 2003; Dupont et al. 2003; Ollerton et al. 2003), host – client networks (Guimarães Jr. et al. 2007), host-parasite networks (Valtonen et al. 2001), or plant-herbivore networks (Lewinsohn & Prado 2006).

Typically, interaction matrices are nested (reviewed in Bascompte & Jordano 2007; Ulrich et al. 2009) that means the species that interact with specialist species form an ordered subset (a true sample) of the species that interact with generalist species. Such a pattern implies that specialists from both sets of species interact preferentially with generalists of the other set (Bascompte & Jordano 2007). Contrary generalists of both sets interact mainly with themselves (Fig. 1). Thus a typical interaction matrix is composed of two more or less distinct subwebs, one that

| | Species | | | | | | | | Row total |
	1	2	3	4	5	6	7	8	
Species									
A	1	1	1	1	1	1	1	1	8
B	1	1	1	1	1	1	0	0	6
C	1	1	1	1	0	1	0	0	5
D	1	1	1	0	1	0	0	0	4
E	0	1	1	1	1	0	0	0	4
F	1	1	0	0	1	0	1	0	4
G	1	1	1	1	0	0	0	0	4
H	1	0	0	0	0	1	0	0	2
I	1	0	1	0	0	0	0	0	2
J	1	1	0	0	0	0	0	0	2
Column total	9	8	7	5	5	4	2	1	41

Figure 1. A typical bipartite interaction network can be represented by a matrix where interactions (incidences) are denoted with ones and absences with zeros. Typically we can identify a group of generalist species (species with numbers of interactions) that interact with themselves and with specialist species (species with low numbers of interactions). The generalist species of both communities often form a submatrix of high matrix fill. A second submatrix of not realized interactions is frequently interpreted as to mark forbidden interactions (Bascompte et al. 2003; Bascompte & Jordan 2007; Ulrich et al. 2009)

contains generalist species of both sets and one containing specialist species only (Bascompte et al. 2003).

An understanding of the structure of interaction networks needs knowledge about local and regional as well as ecological and evolutionary processes that constrain the numbers of interactions of each species in the network (Bascompte et al. 2006). The present paper is intended as a short review of the mechanisms that shape interaction matrices, of the possible internal structures and their ecological interpretation, and the analytical tools to identify matrix structure.

2. Quantifying matrix properties

2.1. Basic concepts

The food web literature is full of metrics that have been applied to quantify web properties (review in Berlow et al. 2004). However, despite their common use many of them are still weakly defined and have unknown statistical properties. Examples are diversity and evenness metrics, distributions of marginal totals (abundance distributions), or interaction strength (Berlow et al. 2004). Even half a century after their introduction there is still no consensus about their usage and statistical properties (Magurran 2004; Olszewski 2004; McGill 2006; Jost 2008). In this respect, the matrix approach to interaction networks promises progress while many of the food web metrics

can be translated into metrics on matrices that have been applied in other fields and of which the statistical properties are better understood. Table 1 gives an overview over different concepts and metrics and shows their relationships. Simple matrix wide metrics of species interactions within an interaction network are the matrix size (the product nm but not the sum $n+m$ as sometimes used in food web analysis), matrix fill (connectivity), and mean marginal totals (linkage density). Note that diversity, evenness, connectivity, and degree distributions directly follow from matrix size and fill (Tab. 1). The interplay of size and fill is therefore a basic property of any network and needs explanation. The above derived properties are then logical consequences.

Other derived metrics are nestedness (Ulrich et al. 2009), togetherness (overdispersion, species aggregation) (Stone & Roberts 1992) and turnover (underdispersion, segregation) (Stone & Roberts 1990). Niche overlap had been defined in various ways (Hurlbert 1978; Sohn 2001) but the matrix definition of average togetherness seems intuitively clear.

In 2002 Leibold and Mikkelson identified three important elements of biogeographic metacommunity structure: coherence, species turnover, and boundary clumping. Although so far only applied to biogeographic matrices these concepts apply to interaction networks as well (Fig. 2). Further, many properties of food webs seem to be determined by these three concepts and can be understood as

Table 1. Important metrics to describe properties of interaction networks. N: Number of ones in the matrix; m, n: numbers of rows and columns, respectively; a_{ij}: number of interactions of species i and j; A_i: total number of interactions of species i. BR, T, and NODF are measures of nestedness (Almeida-Neto et al. 2008); NODFc and NODFr are the respective metrics for matrix wide column and row species aggregation (Almeida-Neto et al. 2008); max (1...1) denotes the maximum number of adjacent incidences per row or column

Food web terminology	Matrix terminology	Metric
Links	number of incidences	N
Connectivity	matrix fill	$$F = \frac{N}{mn}$$
Linkage density	mean marginal total	$$D_i = \frac{N}{m}$$
Web asymmetry	matrix shape	$$WA = n - \frac{m}{n+m}$$
Compartments	boundary clumping	Morisita, Fractal dimension
	coherence	$$C = \frac{1}{m} \sum \max(1 \cdots 1)$$
Diversity	matrix size	Nm
Evenness	degree distribution	$d(N_i)/dI$
Shared links	togetherness	$$T = \frac{4}{mn(m-1)(n-1)} \sum_{i=1}^{n} \sum_{k=1}^{m} \begin{pmatrix} 1 & 0 \\ 1 & 0 \end{pmatrix} ; \begin{pmatrix} 1 & 1 \\ 0 & 0 \end{pmatrix}$$
Underdispersion	aggregation	NODFc, NODFr
	nestedness	BR, T, NODF
Overdispersion	turnover	$$CS = \frac{4}{mn(m-1)(n-1)} \sum_{k=1}^{n} \sum_{k=1}^{m} \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} ; \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$$
Dependence	interaction asymmetry	$$AS = \frac{\dfrac{a_{ij}}{A_i} - \dfrac{a_{ij}}{A_j}}{\dfrac{a_{ij}}{A_i} + \dfrac{a_{ij}}{A_j}}$$
Niche overlap	mean togetherness	Bray-Curtis distance, coefficient of correlation

inevitable consequences of their interplay. Hence, at least in part they appear to be derived features or even sample artefacts (Krishna et al. 2008).

A completely coherent range of species interactions is an array of columns or rows all of which contain the species (Fig. 2A). Hence, the sequence of occurrences within the rows or columns of this array is not interrupted by absences (Leibold & Mikkelson 2002). Of course any row or column can be ordered in that way that the occurrences are completely coherent. However, it is unlikely that the whole matrix can be ordered in such a way. The degree to which this is possible is an important feature of any bio-

Table 2. Important metrics to describe interaction networks and associated ecological hypotheses. Note that such a table can only point to some important hypotheses that might emerge from a certain concept and the associated metric

Metric	High or significant	Low or insignificant	Source
Numbers of incidences	equal relative abundances, phenotypic constraints	no constraints	Stang et al. (2006)
Matrix fill	generalist dominated	specialist dominated	Ulrich (unpubl.)
Mean marginal total	–	–	–
Matrix shape	bottom up control	top down control	Ulrich (unpubl.)
Boundary clumping	evolution of generalist subcommunities	no divergent evolution	Guimarães et al. (2007)
Degree distribution	scale invariance of matrix properties	–	Vázquez (2005)
Togetherness	similar traits dominate over competition	competitive driven community	Stone & Roberts (1992)
Aggregation	similar ecological constraints	few constraints	Ulrich (unpubl.)
Nestedness	forbidden species interactions, gradient driven	competitive driven community	Rezende et al. (2007a, b)
Turnover	competitive driven community	random associations	Diamond (1975)
Interaction asymmetry	gradient in abundance/specialization	equal abundances/degree of specialization	Vázquez et al. (2007)
Mean togetherness	–	–	–

geographic and interaction matrix. A simple measure of coherence is the maximum number of adjacent incidences (ones) summed over all rows and columns and normalized for matrix dimension (Tab. 2). However, this needs an appropriate ordering of the matrix so that a maximum number of adjacent incidences can appear. This is not a trivial task. Leibold & Mikkelson (2002) proposed ordination, particularly reciprocal averaging due to its ease in use. However, different ordination techniques give different orderings and probably no single solution exists as has been shown by Rodríguez-Gironés and Santamaría (2006) in the similar case of matrix disorder.

Species turnover (species segregation or underdispersion) refers to a pattern where two species replace each other within columns or rows (Fig. 2B). This so called checkerboard pattern has long been discussed within the framework of community assembly rules (Diamond 1975; Gotelli & Graves 1996; Ulrich 2004). Note that if two species form a complete checkerboard one of them forms with any third species necessarily an aggregated pattern. Hence turnover is always associated with some degree of species aggregation. Thus, turnover must be seen as a matrix wide pattern. Note also that turnover is connected to the degree of nestedness of a matrix (Leibold & Mikkelson 2002; Ulrich et al. 2009). In a nested pattern, the species compositions of small assemblages are nested subsets

(true samples) of the species compositions of large assemblages (Patterson & Atmar 1986). Ranges of species with lower numbers of occurrences are nested within the range of species with higher numbers of occurrences. Thus in a completely nested matrix species occurrences in rows and columns are maximally aggregated. Nestedness and turnover (disorder in the nestedness terminology) are therefore to a certain degree opposite patterns although matrices might be significantly nested and significantly segregated (Ulrich & Gotelli 2007a, b; Ulrich et al. 2009). Species disorder is easy to measure and metrics like the C-score (Stone & Roberts 1990) and the checkerboard score (Gotelli 2000) are implemented in standard software (Gotelli & Entsminger 2004; Ulrich 2007). Respectively, nestedness is best measured by the *NODF*, the *BR* and the temperature metric (Ulrich et al. 2009). In both cases recent work clarified the statistical properties and type I and II error probabilities (Ulrich & Gotelli 2007a, b).

Boundary clumping is the degree to which the boundaries of the ranges of different species within a matrix are clustered or compartmented (Leibold & Mikkelson 2002). This refers to two common views about ecological communities. Dating back to Clements (1916) communities were seen a distinct entities, that share few species (the traditional phytosociological approach). Within a food web this view refers to subwebs of interacting species with few or

A   Coherence

Species	1	2	3	4	5	6	7	8	Row total
A	1	1	1	1	0	0	0	0	4
B	0	1	1	1	1	0	0	0	4
C	0	1	1	1	1	0	0	0	4
D	0	0	1	1	1	1	0	0	4
E	0	0	1	1	**0**	1	0	0	3
F	0	0	0	1	**0**	1	1	0	3
G	0	0	0	0	1	**0**	1	1	3
H	0	0	0	0	0	1	1	1	3
I	0	0	0	0	0	0	1	1	2
J	0	0	0	0	0	0	0	1	1
Column total	1	3	5	6	4	4	4	4	31

B   Turnover

Species	1	3	8	4	5	6	7	2	Row total
A	1	1	1	0	1	0	1	0	5
B	1	0	1	1	0	1	0	1	5
C	0	1	1	0	1	0	1	1	5
D	0	1	0	1	0	1	1	1	5
E	1	1	1	0	1	0	0	0	4
F	1	1	0	1	0	1	0	0	4
G	0	1	0	0	1	0	1	1	4
H	1	0	1	1	0	1	0	0	4
I	1	0	1	0	1	0	1	0	4
J	1	0	0	1	0	1	0	0	3
Column total	7	6	6	5	5	5	5	4	43

C   Boundary clumping

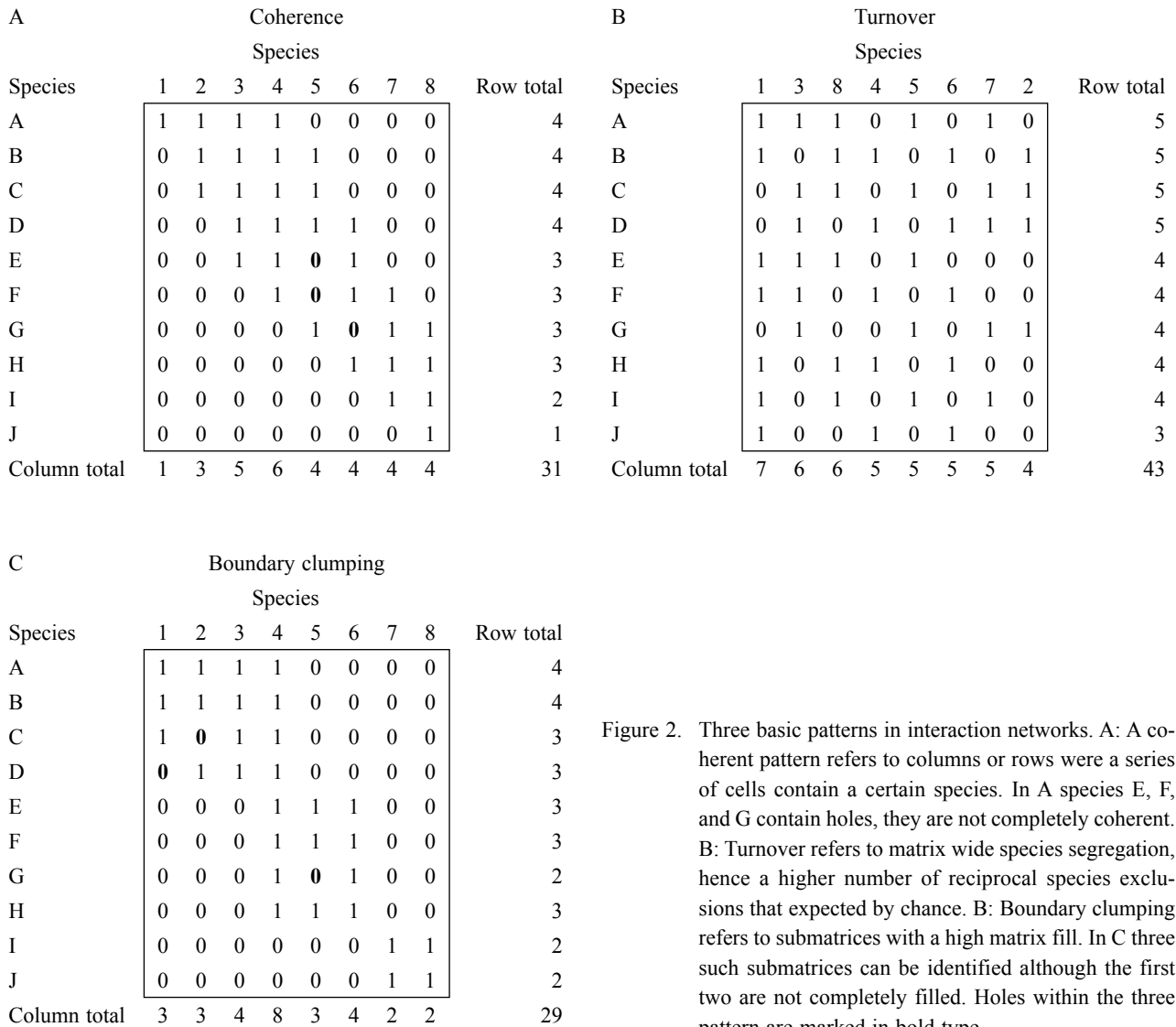| Species	1	2	3	4	5	6	7	8	Row total
A	1	1	1	1	0	0	0	0	4
B	1	1	1	1	0	0	0	0	4
C	1	**0**	1	1	0	0	0	0	3
D	**0**	1	1	1	0	0	0	0	3
E	0	0	0	1	1	1	0	0	3
F	0	0	0	1	1	1	0	0	3
G	0	0	0	1	**0**	1	0	0	2
H	0	0	0	1	1	1	0	0	3
I	0	0	0	0	0	0	1	1	2
J	0	0	0	0	0	0	1	1	2
Column total	3	3	4	8	3	4	2	2	29

Figure 2. Three basic patterns in interaction networks. A: A coherent pattern refers to columns or rows were a series of cells contain a certain species. In A species E, F, and G contain holes, they are not completely coherent. B: Turnover refers to matrix wide species segregation, hence a higher number of reciprocal species exclusions that expected by chance. B: Boundary clumping refers to submatrices with a high matrix fill. In C three such submatrices can be identified although the first two are not completely filled. Holes within the three pattern are marked in bold type

no connections with other subwebs. However, the individualistic view of Gleason (1926) might also result in compartments if species are distributed along an environmental gradient (Leibold & Mikkelson 2002). In interaction matrices this would refer to a situation where the availability of potentially interacting species gradually decreases or increases with phylogenetic and ecological distance. Hence the existence of distinct compartments does not necessarily need the existence of closed ecological communities that coevolved.

Boundary clumping (numbers and sizes of compartments) has traditionally been measured by the incidence based Morisita index (Morisita 1971; Leibold & Mikkelson 2002), although metrics based on fractal dimensionality (Bloom 1981) seem better suited. Note that aggregation, compartmentization, and niche overlap are not clearly separated concepts within the food web approach, a fact that has lead to much confusion about their measurement (Plotkin & Muller-Landau 2002). In this respect the matrix approach performs better and provides associated metrics (Tab. 1). However, much work is still needed to clarify their interdependence.

2.2. Ecological significance

A critical point of all metrics is that they should estimate something meaningful. Many studies applied a certain metric simply to measure something. For instance, if we

measure a high diversity or evenness what does this mean for the processes and pattern in a community? Diversity itself does not point to any mechanism that generates it. However, any metric to be meaningful should be associated with a precise hypothesis about pattern or processes in ecological communities. Table 2 provides for important metrics of bipartite networks associated hypotheses about underlying ecological processes. Of course, such a table cannot be exhaustive. It should be rather read as a starting point for further research.

Clearly, the majority of derived concepts and the associated metrics tell something about the evolutionary history of a network. Particularly important are generalist – specialist gradients (Bascompte et al. 2003). Different gradients for the species in rows and columns determine to a large extent the shape and internal structure of the network. Hence a gradient analysis should be the first step in the analysis of interaction networks (Jordano & Bascompte 2006; Ulrich et al. 2009). Evolutionary and ecological gradients determine the matrix size and number of realized links in the network. This gives immediately the matrix fill (connectivity). A high matrix fill is associated with a generalist dominated web while low fill points either to strong competition among potentially interacting species or to the evolution of many ecologically separated lineages (the ghost of competition past; Connell 1980).

Matrix shape and asymmetry measure differences in row and column dimensions. For instance in host – parasite networks asymmetry tells whether a net is dominated by host or parasite species, hence whether interactions predominantly act from the higher to the lower trophic level (top down) or from the lower to the higher level (bottom up). Bascompte et al. (2006) studied 26 mutualist networks and found them to be highly asymmetric. By a comparison to randomly constructed symmetric networks they showed that the latter were temporarily less stable and species rich. Hence, asymmetry might have strong influence on the stability of a net and on the maintenance of biodiversity.

Macroecological research showed that the species richness of most local ecosystems is under top down control, hence regional species richness determines local richness (Srivastava 1999; Cornell et al. 2007). Recent theoretical work on interaction networks point to a similar situation in foods webs (Krishna et al. 2008). These convergent results again corroborate the view that space and time are ecologically equivalent (interchangeable) with respect to models of community structure (Preston 1960; Adler & Lauenroth 2003; Ulrich 2006).

A significant boundary clumping indicates the evolution of generalist subcommunities within the network. In turn, the regions outside these compartments evolve forbidden links, that means ecological, morphological, or behavioural mismatches that prevent interaction (Bascompte et al. 2003).

Species turnover, togetherness, niche overlap, and nestedness have often been confused in the ecological literature (reviewed in Gotelli 2000; Jordano et al. 2006; Ulrich et al. 2009). All these concepts are related to the interplay of competition and joint habitat and resource requirements but focus on different aspects of this interplay. Turnover and nestedness mark the end of a gradient shaped by differential species specific traits (Leibold & Mikkelson 2002). These might be competition (Diamond 1975), evolutionary constraints (Rezende et al. 2007a), or ecological drift (Krishna et al. 2008). Strong competition should cause high species turnover, and low niche overlap (Weiher & Keddy 1999). A high degree of togetherness indicates common resource or habitat requirements (Stone & Roberts 1992). Nestedness points to the simultaneous influence of two gradients acting on the ordering of incidences of rows and columns (Lomolino 1996; Ulrich et al. 2009), while aggregation refers to one gradient only that acts on either the rows or the columns. Particularly nestedness and aggregation have often been confused (Ulrich et al. 2009). There is still no critical comparative study that reveals the interdependence between aggregation, nestedness and niche overlap. Particularly, niche overlap and aggregation might turn out to refer to the same pattern.

2.3. Statistical inference

The study of interaction networks requires the same inference techniques as had been applied to the analysis of species co-occurrence, nestedness, or spatial pattern seeking (Gotelli 2000; Gotelli & McGill 2006; Ulrich & Gotelli 2007a, b). Any statistical inference needs two contrasting hypothesis (Ulrich 2009). While our metrics provide H_1, the hypothesis about a certain pattern within the matrix the question about H_0, the null hypothesis, has been discussed highly controversial (Connor & Simberloff 1979; Diamond & Gilpin 1982; Gotelli & Graves 1996). However, it becomes more and more clear that standard statistical tests that require equiprobable null distributions do not fit to an ecological definition of randomness (Gotelli & McGill 2006). We need ecologically realistic null models that are able to disentangle ecological and evolutionary mechanisms from pure statistical and sampling artefacts (Ulrich et al. 2008). A step into this direction is the recent work of Krishna et al. (2008). They showed that ecological drift (Hubbell 2001) is able to generate bipartite networks that have similar degrees of nestedness, coherence, and forbidden interactions as observed in many real networks. Because their neutral approach used the abundance distributions of the associated metacommunity (Etienne & Olff 2004) their results explain basic observed network properties from differential dispersal abilities at the specie level. However, species interactions are the result of evolutionary processes not covered by ecological drift. A proper

modelling would therefore require a joint model of genetic (Kimura 1983) and ecological drift (Hubbell 2001). Nevertheless, the work of Krishna et al. (2008) raises the question whether observed network and therefore food web properties might be explained from marginal abundance distributions alone.

Any statistical analysis in ecological matrices needs appropriate null models that retain basic biological constraints independent of the pattern under study. In this respect, null models can be ordered to the number and strength of the constraints they put upon the matrix (Gotelli 2000; Ulrich & Gotelli 2007a, b). In biogeographic matrices null models that do not constrain marginal totals too often point to non-randomness due to the effect of passive sampling because occupancy probabilities (incidences) differ among species (Ulrich et al. 2009). Whether this result also holds for interaction matrices is questionable (Vázquez & Aizen 2006; Vázquez 2007; Stang et al. 2007). In biogeographic matrices the major players are individuals that disperse and die. In interaction matrices the basic unit are species of which all members interact in a similar way. Hence more liberal null models might be appropriate. If the incidence probabilities are equal among species (no evolutionary constraints) even an equiprobable null model might be appropriate. On the other hand, the unseen species problem might be for interaction networks even more severe (McKenzie et al. 2004; Nielsen & Bascompte 2007, Ulrich unpubl.). Networks are generally based on samples from multispecies communities of which the total species richness is often unknown. To account for unseen species at least in larger networks a model that constraints total column and row richness to observed values seems best suited (Ulrich et al. 2009).

4. Conclusion

The study of interaction networks promises progress in the study of constraints that act on the coevolution of interacting species and on food webs (Bascompte et al. 2006; Bascompte & Jordano 2007; Rezende et al. 2007). However, there are still many pitfall associated with the statistical analysis, the properties of the metrics involved and the appropriate null model choice (Gotelli 2000; Ulrich et al. 2009). Many studies used inappropriate null models that did not clearly control for undesired sampling effects (Ulrich & Gotelli 2007a, b; Ulrich et al. 2009). Progress in the field needs critical meta-analytical and comparative studies that indentify the best suited null models (low type I and II error probabilities and high power to disentangle statistical from ecological processes) and clarify the interdependence of different concepts and metrics associated with network approaches. It is not improbable that many patterns recently associated with ecological and evolutionary processes might turn out to be simple side effects of the sampling from the underlying metacommunity distributions.

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