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Structure in plant–animal interaction assemblages

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We present a comprehensive approach to detect pattern in assemblages of plant and animal species linked by interactions such as pollination, frugivory or herbivory. Simple structural models produce gradient, compartmented or nested patterns of interaction; intermediate patterns between a gradient and compartments are possible, and nesting within compartments produces a combined model. Interaction patterns can be visualized and analyzed either as matrices, as bipartite networks or as multivariate sets through correspondence analysis. We argue that differences among patterns represent outcomes of distinct evolutionary and ecological processes in these highly diversified assemblages. Instead of choosing one model a priori, assemblages should be probed for a suite of patterns. A plant–pollinator assemblage exemplifies a simple nested pattern, whereas a plant–herbivore assemblage illustrates a compound pattern with nested structures within compartments. Compartmentation should reflect coevolutionary histories and constraints, whereas differences in species abundance or dispersal may generate nestedness.

Recognition of pattern in species assemblages counts among the oldest pursuits in ecology. Community ecology to a large extent has focused on two fundamental tasks, developing adequate methods of detecting patterns in species sets, and identifying processes that might generate certain patterns. Biogeographers and community ecologists have put substantial effort into exploring two particular kinds of pattern: nestedness (Atmar and Patterson 1993) and, to a lesser degree, compartmentation (Leibold and Mikkelson 2002). Both kinds of pattern reflect interests in quite different ecological or biogeographical processes, and each one has usually been investigated in itself, without much concern for alternatives. Hence, evidence for one particular pattern, or for its absence, does not rule out other patterns.

Assemblage structure has almost always been examined either on sets of real islands, geographical or ecological (Diamond 1975, Patterson 1987, Lomolino 1996, Weiher and Keddy 1999, Leibold and Mikkelson 2002), or on arbitrary sampling units within a landscape or a continuous habitat. In this paper we turn to a different setting. We examine the interaction structure within species assemblages in which the habitat or resource units are themselves species, or higher-level taxonomic or functional entities. We focus on assemblages of plants and the animals they interact with, be they mutualists (pollinators or seed dispersers), antagonists (herbivores), or undefined (e.g. frugivores or flower visitors). Even though we concentrate on plant-animal associations, the general argument is applicable to other interactive species assemblages (e.g. fish parasites, Poulin 1997). Moreover, though we apply this to sets of different species, similar theory and procedures can be extended to assemblages on conspecific host populations or individuals.

We have two aims for this paper: first, to propose a comprehensive framework for assessing sets of interacting plants and animals, so as to detect patterns linked to ecological and coevolutionary processes that shape and maintain these assemblages. Second, to extend this approach over the gamut of conceivable nonrandom configurations of interactive assemblages. We show that the common procedures of testing an assemblage solely for one particular pattern, be it nestedness or compartmentation, against a null hypothesis of random incidence or interaction, is of limited use, for both theoretical and practical grounds (see Leibold and Mikkelson 2002 for a similar argument regarding biogeographic patterns). If instead assemblage structure can be assessed within a broader framework, we stand to gain in effectiveness in detecting actual pattern in real, complex and species-rich communities. Ultimately, we should be able to predict the ecological circumstances under which certain configurations are to be expected and, conversely, the recognition of such consistent configurations will be indicative of a given set of coevolutionary processes.

Representations of interaction structure

The ecological interactions we address are antagonistic (plant–herbivore) as well as mutualistic (plant–seed disperser or plant–pollinator). Host ranges, the set of plant species which an animal feeds on, are a dimension of insect niches, whereas the number of hosts has been used as a measure of niche breadth (Pielou 1972). Plant faunas, the set of animal species associated with a given plant, especially herbivorous insects, have also been examined for general properties and their determinants, often using models derived from island biogeography (Janzen 1968, Strong et al. 1984, Lewinsohn et al. 2005).

We assume, first, an assemblage with explicit bounds (spatiotemporal and taxonomic); second, a high level of taxonomic resolution, in which most species are reliably separated if not named; third, a set of interaction records among these species obtained by means of a consistent procedure. Although it is hard to record all interactions in species-rich assemblages, and equally hard to prove that records are exhaustive, we will also assume that the data are comprehensive enough to evince interaction patterns if present, and that these patterns will not be substantially modified by additional observations (but see Goldwasser and Roughgarden 1997, Martinez et al. 1999 for food webs; and Jordano 1987, Ollerton et al. 2003, Smith-Ramirez et al. 2005 for plant–animal mutualisms).

Plant–animal interactions are commonly presented in two ways: either as a rectangular matrix or as a bipartite graph (Memmott 1999, Valladares et al. 2001, Jordano et al. 2003). We will employ both representations, as well as the graphical result of ordination by correspondence analysis (Greenacre 1984, ter Braak 1995), in order to show equivalences between these modes and to highlight their particular advantages.

The basic rectangular matrix (Fig. 1A-D) consists of two distinct sets of species: animals (A rows, subscript i) and plants (P columns, subscript j). Interactions are most often represented as binary with $a_{ij} = 1$ for any recorded plant–animal association, but can be quantitative, given any suitable measure of frequency or intensity of each interaction. The interaction matrix has dimension $A \times P$, which is also the maximum number of interactions for the matrix. Note that this dimension is not equivalent to $[(A+P) \times (A+P-1)]/2$, the maximum number of links used in classical food web analysis.

A first step in detecting structure in these assemblages is the rearrangement of rows, columns, or both. These can be moved around freely without altering the original data. Various procedures for reordering rows and columns are suitable to reveal different kinds of structure in interaction matrices (Fig. 1A-D). Such matrices can also be probed for non-randomness, profiting from the extensive experience gained in analyses of species

occurrences in islands (Diamond 1975, Atmar and Patterson 1993, Wright et al. 1998), which depend on the choice of a suitable null model (Gotelli and Graves 1996, Cook and Quinn 1998, Bascompte et al. 2003, Vázquez and Aizen 2003).

The bipartite graph view (analogous to a food web representation, Memmott 1999) of the same sets of interactions (Fig. 1E-H) presents species in columns (or rows) respectively of animals and plants facing each other. Observed interactions are drawn as links that, when not binary, can render their intensity or frequency in graded thicknesses. In the interaction matrix, links are represented as nonzero cells on the intersection of a row and column. Several areas of mathematics have contributed methods to explore such sets: topology, graph theory and, recently, complex networks. These have provided new insights to the analysis of food webs. However, ecologists have directed most of their efforts to analyse entire food webs (Cohen et al. 1990, Dunne et al. 2002, Pimm 2002) so that bimodal webs as those shown by the bipartite graphs are still largely unexplored (Jordano et al. 2003). Bipartite webs do in fact offer several advantages of their own: first, they are often fully resolved, without the problems of uneven resolution which haunt the analysis of complete webs. Second, all links are of a single kind of ecological interaction (e.g. mutualism), which ensures structural integrity as well as similar ecological and evolutionary processes throughout the entire assemblage.

Finally, several multivariate methods can be used to elucidate complex relationships among associated plants and animals, recorded in the interaction matrix (Fig. 1 A-C). Among these, correspondence analysis (CA) is an obvious method of choice because it is designed precisely to bring out reciprocal relationships among two sets of equal interest (Greenacre 1984, ter Braak 1995) – plant and animal species in our case – rather than using one of them solely as an ordination criterion for the other. For similar reasons, Leibold and Mikkelson (2002) chose CA to detect structure in sets of species across different sites. Correspondence analysis can be applied both to binary and to quantitative data.

The results can be presented as a biplot graph showing scores of both species sets on the ordination axes (Fig. lI-L). The score of each species on the first axis provides an objective criterion for reordering the original rectangular matrix. After reordering, the matrix should maximize the match of rows to columns, that is of animals to plants. This is equivalent to bringing each link as close as possible to the main matrix diagonal. A high reciprocal match between the plant and animal sets means that most matrix elements are on or near the main diagonal, whereas many off-diagonal links signify a low level of reciprocal agreement (ter Braak 1995). Likewise, bipartite graphs can be reordered based on the first CA axis, in which case closely linked species
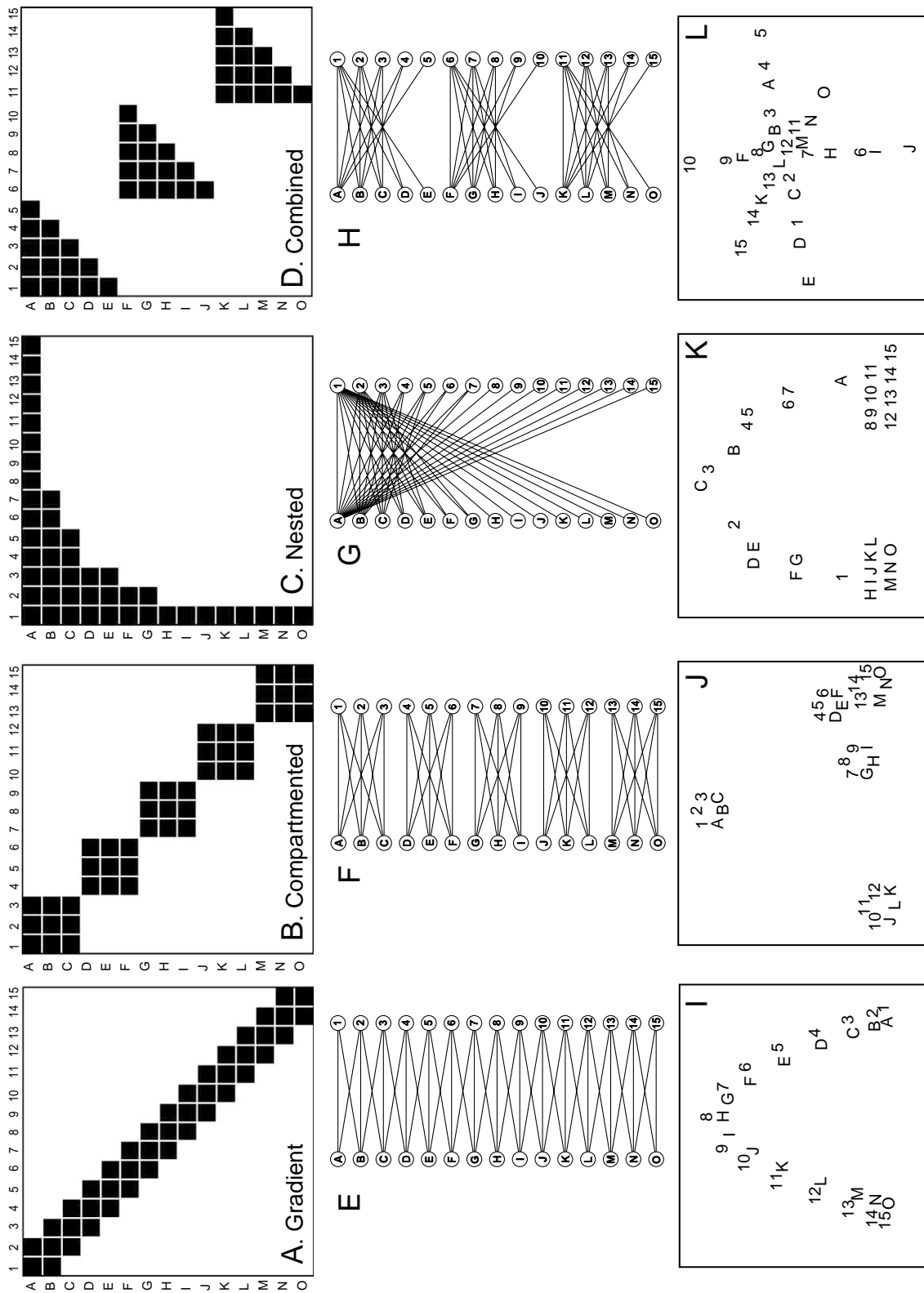
Fig. 1

(Fig. lE) or species subsets (Fig. lF, H) will tend to face each other.

Another convention orders species approximately according to a decreasing number of interactions, either in the bipartite graph or in rows and columns of the interaction matrix; this has been generally adopted to evince nested structures (Atmar and Patterson 1993, Bascompte et al. 2003), which are discussed below.

A plot of the eigenvalues of the axes obtained through CA is a further potential probe for detecting and discriminating among interaction patterns; Jackson (1993) uses such 'scree plots' to ascertain significant axes in principal components analysis (PCA).

Simple structures and their generating processes

A nonrandom interaction matrix can be positioned among three simple configurations: a gradient, a compartmented structure or a nested structure (Fig. 1). These will be considered in turn, before we examine combined patterns. Table 1 summarizes some key features of models for the primary and compound patterns in interactive assemblages, as outlined below.

Gradients

In suitably reordered interaction matrices, a gradient will appear as a band of interactions that stretch along the main diagonal (Fig. lA). Formally, this corresponds to a two-way Petrie matrix, defined by the property that the interactions within each row are adjacent, and within each column as well (ter Braak 1995). In the particular case where the extreme host ranges and faunas overlap in a cyclic pattern, a circular gradient or circumplex will result. The width of the diagonal band is set by the ratio of A to P and by the amount of overlap among adjacent host ranges or faunas.

In a bipartite graph view, the gradient will appear as a uniformly intermeshed series, without noticeable clusters or discontinuities (Fig. lE), whereas in an ordination graph, matching sequences of plants and animals face each other, again without any strong cluster (Fig. 1I). The arch shape of this double sequence is a graphical

distortion inherent to CA and conveys no information (ter Braak 1995).

Gradients are bread and butter to vegetation ecologists, who expect plant communities to reflect gradual changes in the underlying physical environment. In plant–animal assemblages, however, a simple gradient, although conceivable, is less likely than other patterns. It could be produced for instance if, in a strongly seasonal environment, a set of plants gradually replaced themselves in their flowering or fruiting, and their floral visitors or seed dispersers followed suit. But, whereas such a pattern has indeed been found in plants, in these communities the animals tend to switch sequentially among plant species, rather than to be replaced in a matching sequence (Waser and Real 1979). Oligolectic bees visiting flowering plants in stressed environments do fit a gradient pattern reasonably well (Moldenke 1979, Petanidou et al. 1995). In temperate/Mediterranean regions, many plant species are mainly visited by bees, either solitary or social ones. The solitary bee–plant system may resemble a gradient system. Social bee species, on the other hand, link the entire flora together (Westrich 1990).

Even though they may be uncommon in actual plant–animal assemblages, gradients deserve notice as one endpoint in a continuum of patterns which extends to fully compartmented or else to nested structures (Fig. 1A-C).

Compartmented assemblages

An assemblage will be compartmented if there are recognizable subsets of interacting animals and plants, so that species are more linked within than across subsets. If compartments are of equal dimensions, host ranges and faunas may all be of uniform size, as they are in an ideal gradient (Fig. lA), but compartmentation is readily apparent by their blocked structure (Fig. 1B). In analyses of species incidence across sites, Leibold and Mikkelson (2002) call such patterns Clementsian gradients.

Compartments appear in ordered interaction matrices as distinct clusters of cells (Fig. 1B). When species are ordered according to their scores on the first CA axis, such clusters are drawn as close as possible to the main diagonal (ter Braak 1995). In a bipartite graph, compartments are recognizable as distinct subwebs with

Fig. 1. Three simple models and the combined model for structure in highly diversified plant–animal assemblages. All models have same dimensions (15 animal species in rows labeled A-I, 15 plant species in columns, labeled 1-15) and same density or fill: 20% of the 225 potential interactions, except for the combined model (33%, to avoid broken subsets). Each model is shown in three different representations, (A-D) Animal–plant interaction matrices, arranged to show their main structural features. Data are binary, black squares standing for recorded interactions between an animal species in row i and a plant in column j (E-H) Bipartite graphs, animal species to the left and plant species to the right; recorded interactions are shown as links ("edges") connecting pairs of species ("vertices"), (I-L) Ordination graphs by correspondence analysis (CA), showing animal species (letters) and plant species (numbers) conventionally plotted on the first two ordination axes, except for the combined model in which variables are plotted against axes 3 and 4. When necessary, overlapping symbols are displaced for visibility; thus, the small circles of symbols in J are actually overlaid in their centre.

Table 1. Distinguishing features of three basic models of interaction structure in highly-diversified plant–animal assemblages. These features characterize interaction patterns when plant and animal species are arranged in interaction matrices as columns and rows (Fig. 1). A compound model should combine elements from any two of these basic models.

Model	Discrete subsets of species	Variation of links/species (specialists to generalists)	Is a combined model possible?
Gradient	No	Less than in random models	Only in transition to compartmented
Compartmented	Yes, in both sets of species (rows and columns)	Possible, depending on compartment size	As above
Nested	No	Yes, in both sets of species (rows and columns)	Only within compartments

denser links, whereas few or no links connect compartments among them (Fig. 1F). The CA ordination graph shows animals and plants overlaid or tightly clustered in groups for each compartment (Fig. 1J); species that have links to other compartments will be displaced to intermediate positions.

Compartments have been sought for in complete food webs, where they seemed to be absent and indeed were deemed unlikely to occur, except in webs that encompass distinct habitats (Pimm et al. 1991). Although Raffaelli and Hall (1992) found evidence of compartmentation in some webs, there has been little further interest in this subject until fairly recently, apart from some studies of particular mutualistic assemblages (Fonseca and Ganade 1996, Dicks et al. 2002). Indications of compartmentation have been found through reanalysis of several complete food webs (Krause et al. 2003), or by way of new analytical procedures applied to plant–herbivore assemblages (Prado and Lewinsohn 2004). Nonetheless, procedures for detecting compartmentalization are not yet fully established, and most proposed procedures depend on an arbitrary criterion at some stage (Raffaelli and Hall 1992, Leibold and Mikkelson 2002).

In interactive assemblages, host ranges and faunas may vary in size and therefore encompass both generalists and specialists. Nonetheless, any substantially compartmented structure derives from restrictions to both host ranges and faunas, so that most if not all species should be specialized to some degree, especially when there is a phylogenetic basis for specialization.

Nested assemblages

A nested structure is one in which, if rows and columns both are ordered in decreasing totals, the interaction matrix will show a progression of inclusive subsets in either direction (Fig. 1C) (Atmar and Patterson 1993, Bascompte et al. 2003). Note that any non-nested structure can be rearranged in decreasing size of either rows or columns, but not for both simultaneously.

A nested configuration is called a simplex in topological algebra and in the social sciences (Wasserman and

Faust 1994). In an ordered bipartite graph, nested structures will appear as link clusters of decreasing density on each side (Fig. 1G), which need not however be symmetrical in either species number or in link distributions.

Ordination by correspondence analysis (Fig. 1K) shows two arches sliding past each other; at their extremes, species with restricted host ranges or faunas (animals, H-O; plants, 8-15) are clustered close to, but not overlaying, their partners. The order of species along this arch corresponds to the ordering in the nested matrix, in decreasing number of interactions per species (Leibold and Mikkelson 2002). As before, the arch shape itself conveys no important information; the positioning and separation of plants and animals are of main interest.

In nested assemblages, plants with few interactions will only be associated with generalist animals; conversely, specialized animals will only be found associated to plants with many links, that is, with large associated faunas. Moreover, generalists in one species set tend to interact with generalists in the other, forming a dense core of interactions.

Nested structures have been extensively sought for in sets of geographical or ecological islands, and also in habitat units within fragmented landscapes (Atmar and Patterson 1993, Wright et al. 1998). More recently, a large series of mutualistic interaction assemblages have shown a significantly nested structure (Bascompte et al. 2003). Substantial effort has gone into devising and evaluating various measures of nestedness, especially in the choice of a randomization procedure to provide appropriate null models against which to test observed data sets (Wright and Reeves 1992, Atmar and Patterson 1993, Cook and Quinn 1998, Bascompte et al. 2003, Vázquez and Aizen 2003). It is worth noting that a nested pattern can be generated by the random combination of sets of plants and animals solely in proportion to their different abundances or colonization abilities; thus, nestedness in a sense might itself be viewed as a null model for other kinds of pattern, generically called 'anti-nested' by Poulin and Guégan (2000).

Compound structures

As mentioned before, there is a continuum between a strict gradient (Fig. 1A) and a completely compartmented matrix (Fig. 1B). As the gradient starts showing recognizable lumps, compartments will become gradually more distinct and any intermediate level between the patterns in Fig. 1A and 1B is feasible. It is easy to envisage such intermediate states in different forms of representation. In the interaction matrix and the bipartite graphs, extra links bridge the compartments. In the CA ordination graph, compartments are not represented by tight clusters of points (Fig. 1J) anymore, but become fuzzier as some species spread out from them.

There is only one strictly combined model (Fig. 1D): a compartmented model in which the species within each block are themselves nested, thus forming nested compartments. Its reverse, a compartmented substructure within a fully nested model, is unfeasible. In our simple example, both the interaction matrix (Fig. 1D) and its bipartite graph (Fig. 1H) show an obvious combination of compartmented and nested structures. The ordination graph (Fig. 1L), however, deserves comment. A graph for axes 1 and 2 (not shown) reveals only the clustered structure due to the compartments and is thus similar to Fig. 1J except for the number of compartments. Further dimensions show the nested substructures as reverse series of species at different angles for each compartment (Fig. 1L).

This combined model is potentially quite important in actual communities. Processes that generate a nested structure – for instance, if animals link preferentially to plants according to their abundance, and abundant animals tend to have a larger host range – will operate within a framework of boundaries set by morphological, functional or phylogenetic constraints. If this is so, most species, but not necessarily all, will preferentially establish links in a given compartment and, within that compartment, their host range or fauna will be conditioned by more proximate factors.

Examples

We illustrate the application of this approach with two examples drawn from our own work. This offers the advantage of our familiarity with the biological systems studied, and also of ensuring that the data stem from consistent sampling schemes and taxonomic treatments. Thus, these cases are comprehensive for the interactions of interest and they are taxonomically highly resolved.

Plants and flower visitors in Zackenberg, Greenland

During two seasons at Zackenberg, NE-Greenland (74°N, 21°W), all plant–pollinator interactions were scored (1st season 286; 2nd season 270) between all flowering plant species (31 species) and their pollinators (1st season 61 species; 2nd season 64 species) were scored. The length of the pollination season is brief (45-70 days). As in other arctic pollination studies Diptera were by far the most dominant pollinator group, both in species number (72%) and in individuals (85%). Compared to similar-sized assemblages the Zackenberg system had a high connectance (19%, seasons pooled).

This assemblage was probed for a nested structure as part of an extensive comparative analysis (Bascompte et al. 2003). Fig. 2A shows the interaction matrix rearranged to evince nestedness, which is easily perceived. Indeed, assessment against a fairly conservative null model yields a $p < 0.01$ of obtaining this degree of nestedness in a randomly interacting assemblage (details in Bascompte et al. 2003).

To examine this assemblage for indications of other structural patterns, it was subjected to correspondence analysis. Fig. 2B shows the result of reordering the same interaction matrix according to plant and animal scores on the first ordination axis. Even after recorded interactions are drawn as close as possible to the main diagonal, there is substantial scatter and thus no indication of a gradient or compartmentation is apparent. Thus the Zackenberg plant–pollinator assemblage indeed presents a distinctly nested structure with no evidence for any other pattern. This is fairly representative for the 52 mutualistic webs examined in Bascompte et al. (2003), of which 75% showed significant nestedness.

Asteraceae and herbivores in the Espinhaço range, Brazil

The upper parts of the Espinhaço range in Southeast Brazil are occupied by a complex of highland savannas and grasslands. We surveyed five localities in an approximately North-South direction in the state of Minas Gerais (16°34′ to 20°30′ S) five times at different seasons for two years. The study focused on flowerhead-feeding insects on Asteraceae, one of the most diverse and abundant plant families in the region. Interactions were established from rearing records from extensive field samples of each plant population (details in Prado and Lewinsohn 2004).

Fig. 3 shows interactions of Vernonieae, one of the major tribes in the neotropical Asteraceae, with the main group of their flowerhead feeders, fruit flies in the family Tephritidae (arranged for nestedness in Fig. 3A and for compartmentation in Fig. 3B). Species and their interactions are shown pooled for the five localities, hence this is a regional interaction matrix. In all, 162 interactions were recorded between 35 insect species and their
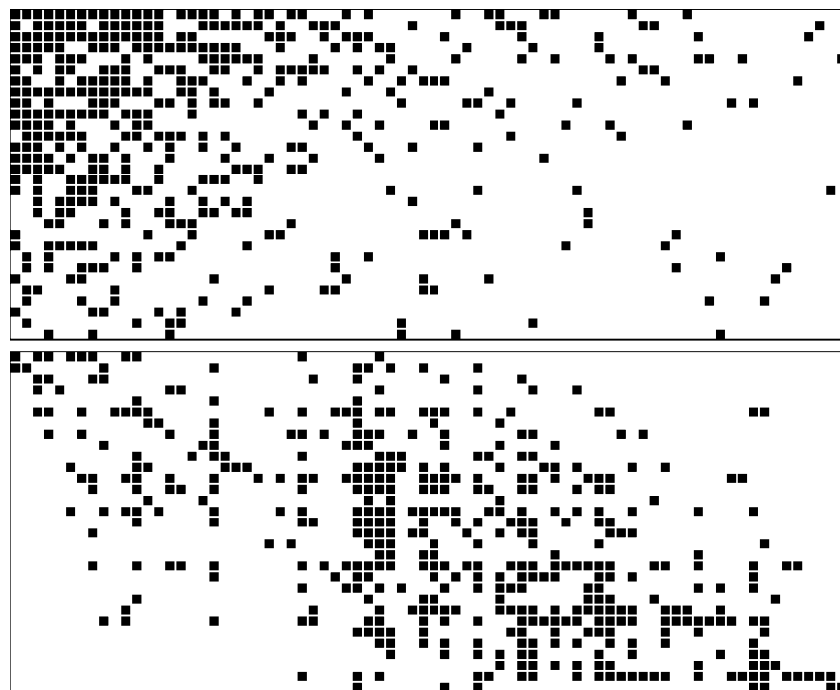
Fig. 2. An arctic plant–pollinator assemblage in Zackenberg, Greenland, recorded by J.M. Olesen and H. Elberling (unpubl.); 31 plant species in rows, 76 animal species in columns; plants and animals are transposed with regard to Fig. 1 for better placement. Black squares show observed interactions. In (A), rows and columns are arranged to maximize nestedness according to the Atmar and Patterson (1993) algorithm; in general, decreasing totals both for rows and for columns. In (B) rows and columns are rearranged according to ordination by correspondence analysis, to maximize reciprocal agreement between rows and columns, i.e. grouping together species with similar interaction patterns.

81 host plants, or about 6% of all possible plant-insect combinations.

Contrary to the Zackenberg plant–pollinator system, this plant assemblage was originally analyzed solely for compartmentation. Correspondence analysis was used to order insects and plants for reciprocal links and to examine them for potential subsets. Four main compartments were detected as shown in Fig. 3B, and their departure from a random assembly was confirmed by a randomization test (Prado and Lewinsohn 2004, where the two larger compartments were further subdivided into two weaker but still significant subsets; linkage similarities within versus among compartments were higher in the observed network than in 10 000 randomized ones). To probe this assemblage further, it was rearranged for nestedness. As Fig. 3A shows, a weakly nested structure is apparent, and randomization tests confirm this (Atmar and Patterson temperature $T = 8.9$; $p < 0.01$; the observed pattern exceeded the nestedness values of 50 randomizations with Bascompte et al's (2003) more conservative null model 2). Each of the two larger compartments was also rearranged separately for nestedness; the resulting subsets in Fig. 3C and 3D both reiterate the nested character that is confirmed by randomization (respectively $T = 13.5$ and 14.4, $p < 0.01$ for either). Thus, this plant–herbivore assemblage turns out to contain a more complex pattern than seemed to be the case at first: even though as a whole it is manifestly compartmented, nesting is recognizable within the larger compartments. Positive tests both for nesting and for compartmentation indicate a combina-

tion of these patterns, rather than a shortcoming of the analytical procedures. Interaction in this assemblage thus fit a combined model, with compartments and nested interactions within them.

Discussion

Detecting pattern in interaction assemblages

Plant–animal interaction assemblages present a striking diversity of patterns, becoming even more baffling when various researchers portray them with quite distinct representations. The visual glossary in Fig. 1 should be helpful to recognize equivalences among three representation modes (bipartite networks, matrix representation, and ordination plots) in common use. We do not advocate the exclusive adoption of one of these, since each one has its advantages and will be more convenient for researchers used to investigate assemblages as matrices, networks, or multivariate sets. Furthermore, they are all worth considering for alternative and presumably complementary analytical and exploratory tools.

The statistical procedures usually employed to test for each of the simple patterns in Fig. 1 are meant to detect a single kind of structure and their results allow no inference on the presence or absence of other patterns in the same assemblage. This is aggravated because they are commonly deployed on the entire assemblage, even when it is demonstrably heterogeneous in structure. As in other areas of ecology, the main difficulty often lies not in showing an acceptable fit to a particular model, but in ruling out alternative models at the same time.
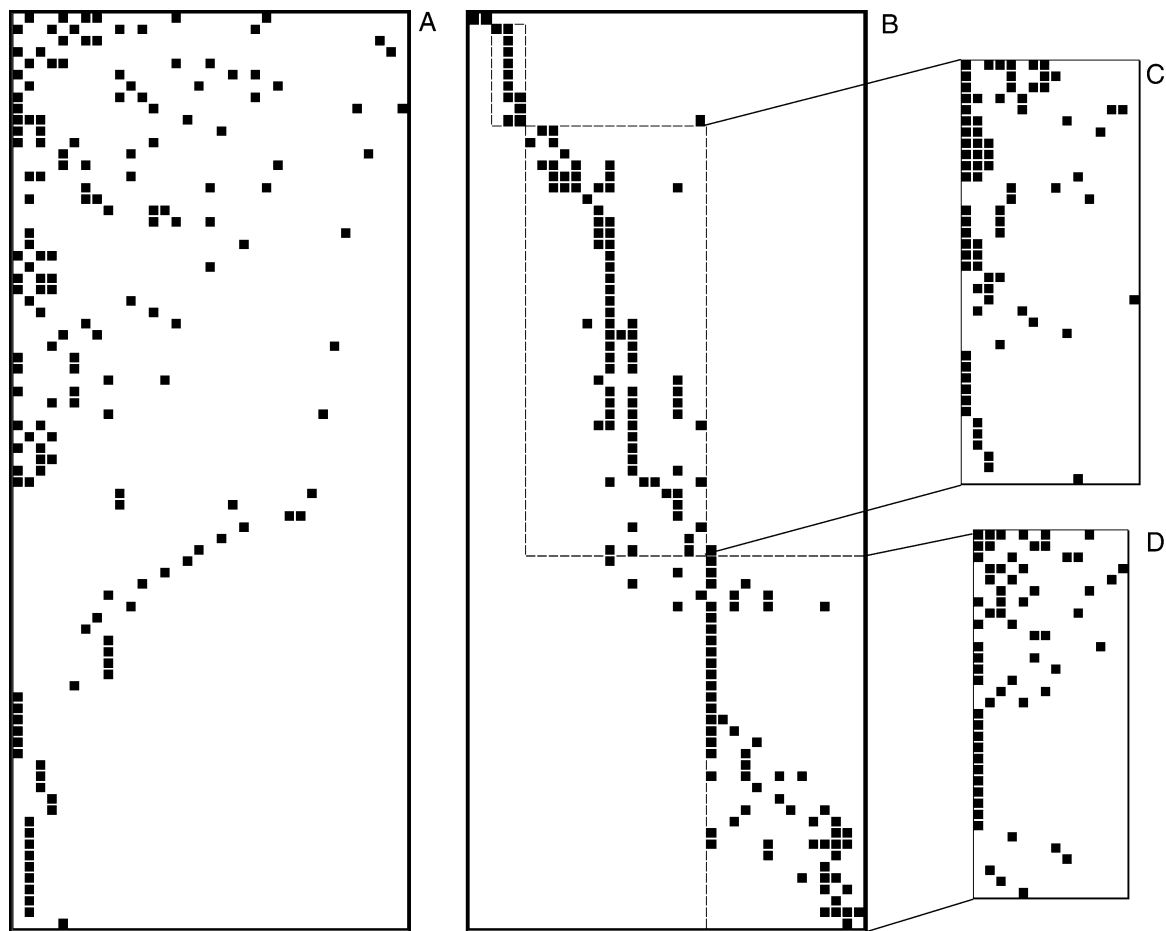
Fig. 3. A plant-herbivore assemblage in the Espinhaço mountain range, Brazil; 81 plant species in rows, 35 animal species in columns (B) modified from Prado and Lewinsohn 2004). (A) ordered for nestedness; (B) ordered for maximum agreement of rows and columns. Dashed lines outline four compartments recognized from correspondence analysis and confirmed a posteriori through a multiple permutation procedure; (C) and (D) show the two larger compartments in (B), rearranged for nestedness.

Rather than set out to inspect the entire observed assemblage against one given expected pattern, we submit that assemblage structure should be examined to detect whether, and how, it fits which kind of pattern. This point was previously raised by Poulin and Guégan (2000) for parasite infracommunities in fishes and by Leibold and Mikkelson (2002) for species occurrences across sites. A variety of null models can then be used to elucidate processes generating the pattern. Many assemblages clearly fit one simple pattern, but even in these cases some portions or components can signal a different substructure. The most comprehensive series of analyses achieved so far on plant-animal assemblages has proved that, as expected, nested patterns are common in mutualistic sets of plants and their pollinators or frugivorous dispersers (Bascompte et al. 2003); however, these analyses at the time were undertaken to test solely for nesting or connectivity distributions (Jordano et al. 2003). Thus, they are amenable to further exploration (Jordano et al. 2006).

A potentially contentious issue is whether a compartmented assemblage should be still considered a single entity. Strictly speaking, an assemblage that contains disconnected sets would not fit the usual definition of a food web or an interaction web. There are several reasons, however, to pursue their analysis as a single assemblage. First, unless one has chosen an absurd delimitation of the study system, all plants and animals a priori are capable of wide-ranging if not universal interactions; compartments therefore are an empirical result rather than a preordained structural feature of which one has advance knowledge. Second, in several cases (as in the Espinhaço example above) interactions not recorded in one locality have actually been observed elsewhere, proving that they are achievable – the same logic by which vacant niches were posited in comparative studies of bracken-feeding insects (Lawton et al. 1993). Thus, disqualifying compartmented assemblages from further analysis would eliminate some of the potentially most interesting ecological systems. Moreover, compart-

ments in actual assemblages are commonly bridged by few but structurally important interactions, rather than being fully isolated.

In order to encompass a wider range of structural alternatives in plant–animal assemblages, both in field and in theoretical studies, the analytical and statistical procedures used to assess these various patterns need to be reconsidered. Ultimately, this will require a comprehensive procedure to address the full range of possible patterns. Meanwhile, we suggest parallel tests for nesting (using Atmar and Patterson's 1993 test or subsequent modifications) and for compartmentation or gradients (using correspondence analysis to reorder both species sets, followed by randomization procedures to test candidate compartments). If nesting is the only significant pattern, no further tests are needed. Interactive networks that are intermediate in our pattern continuum may give significant results both for compartments and for nesting. According to the rationale presented above, compartments take functional precedence, hence in this case we ascribe the significant nesting found in the entire network to the pattern within compartments; this can be ascertained by testing each compartment separately, as we showed in the Espinhaço example. Finally, when only compartmentation is detected in the entire network, we would still proceed with further inspection of each compartment, be it for inbuilt nesting structure or for subcompartments that otherwise may not be apparent.

Following current usage, we have till now analyzed these interaction assemblages in binary form. However, preliminary explorations of quantitative data sets show that patterns are enhanced and statistical inferences can shift when interactions are weighted for interaction strength or frequency (J. Bascompte, P. Jordano and J. Olesen unpubl.).

Processes underlying interaction structures

In highly diversified interaction assemblages of varying specificity, such as many mutualistic (e.g. plant–pollinator and plant-frugivore) and antagonistic (e.g. plant–herbivore, host–parasite, host–pathogen) networks, evolutionary processes and dynamics yielding complex patterns can be extremely difficult to decipher. Nonetheless, recent analyses of complex interaction networks have shed some light on the various ways coevolutionary interactions are shaped in species-rich communities. The stringent assumptions of coevolution – symmetry, mutual strength, and specificity (Janzen 1980, Wheelwright and Orians 1982) – are not held in these assemblages, and their structure cannot be accounted for either by one-to-one, or by entirely diffuse, evolutionary processes (Memmott 1999, Bascompte et al. 2003, Jordano et al. 2003, Vázquez and Aizen 2003, Memmott et al. 2004, Olesen et al. 2006).

Coevolutionary processes can be expected to diverge between mutualistic and antagonistic assemblages, and hence ensuing structural patterns should diverge as well. However, this is complicated by the average level of specificity and asymmetry of reciprocal links in different assemblages. We can expect strongly compartmented interaction networks when dealing with low-diversity and/or high specificity interactions, such as host–parasite interactions (Poulin 1997, but see Rohde et al. 1998) where mutual extreme specificity is common, as is the case for some highly coevolved pollinator mutualisms (e.g. figs and fig-wasps, Jousselin et al. 2003). Conversely, in extreme mutualistic assemblages of low specificity and high diversity we can expect a single compartment with a nested structure, where the system 'pivots' on a core of highly interconnected species (Bascompte et al. 2003).

Compartments should reflect phylogenetic splits and high historical stability or inertia. Thus, they are structural expressions of constraints that establish bounds to possible or to favoured interactions among sets of species. Likewise, one could expect these bounds to be clearer to perceive at a large-scale or regional level. Compartmentation has been shown in a highly-resolved plant–herbivore assemblage (Prado and Lewinsohn 2004) and can be found in other such assemblages (T. M. Lewinsohn, unpubl.). Compartmentation is also conspicuous in some coevolved mutualistic assemblages of plants and their insect flower visitors (Dicks et al. 2002), or of tropical plants and their resident patrolling ants (Fonseca and Ganade 1996). Nestedness can occur within these more specialized compartments or assemblage modules (Prado and Lewinsohn 2004) in the form of nested coevolutionary vortexes of more specialized interactions (Thompson 2005), yielding compound interaction outcomes such as in Fig. 1D.

Nestedness may be generated by differential dispersal, abundance, spatial distribution and similar ecological processes that can be expressed across a wide gamut of temporal and spatial scales. If this is so, we can predict two consequences: first, nested structures will appear within compartments whenever these are of sufficient dimension (both in animal and in plant richness), and local assemblages are sufficiently long-lasting to embody the results of these processes. Second, in studies across sites or time-periods we should expect to find species shifting in position within a nested set far more often than they should shift compartments.

The dichotomy of mutualistic and antagonistic networks needs further investigation, and so does the substructure that we also expect to find in many antagonistic networks. Our analyses emphasize a continuum gradient among the attendant patterns. Compartments, once established, are partly independent co-evolutionary arenas, in each of which ecological and

evolutionary processes can produce further patterns. Coevolution may proceed to further fragmentation and set novel compartments within existing ones. Alternatively, several ecological processes (e.g. 'passive sampling' of each species set by the other, see Connor and McCoy 1979) can concur to establish asymmetric link distributions (specialized animals to generalistic plants and vice-versa) and thus generate nested patterns within compartments.

Mutualists should tend to encompass the maximum of counterpart species from whose services they benefit; at the same time, if each species set converges in functional traits, a core set of strongly interacting plants and animals will be established, and other species may in time be drawn into this core (Thompson 2005). Though some hyperspecialized associations may break away from the main core, many if not most specialists will associate with core generalists, reinforcing the linkage asymmetry and the pervasive nested pattern of the entire interactive network. On the other hand, in antagonistic systems coevolutionary processes will tend to reinforce constraints against grand generalists. Thus, given that only a small proportion of herbivorous animals are true generalists, an upper limit will be set to the maximum fraction of all herbivores linked to any given plant, and compartments should often be apparent in such networks.

To conclude, we propose that most interactions between given sets of animals and plants can be depicted as ordinations of the interacting entities that position them on a continuum of patterns. Such a continuum may reflect coevolutionary dynamics varying from sequential specialization, by way of coevolutionary vortexes within diverse assemblages (Thompson 2005), up to highly diversified mutualisms evolving around a core of species in a nested assemblage (Jordano et al. 2006). We expect this comprehensive approach to open the way to improved hypotheses, some of which are suggested above. Among them, we emphasize the comparative analysis of mutualistic and antagonistic plant–animal assemblages. A broader view should assist the production of theoretical predictions about the ways highly diversified plant–animal assemblages are structured and how to ascertain their signature in already existing data sets.

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