
26 Investigating Fragility in Plant–Frugivore Networks: A Case Study of the Atlantic Forest in Brazil

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Introduction

Mutualistic interactions among free-living species, such as in pollination and seed dispersal by animals, have been a major factor in the evolution of flowering plants and animals. The recent disruption of these interactions caused by human activities may bring about a considerable loss of biodiversity (Buchmann and Nabhan, 1996; Jordano, 2000; Herrera, 2002; Fontaine *et al.*, 2006). An important characteristic of mutualistic interactions among free-living species is that exclusive, pairwise interactions are rare (Thompson, 2005). In contrast, in a given ecological community, each species interacts with a few to dozens of mutualistic partners (Jordano, 1987). As a result, at the community level, mutualistic interactions often emerge as web-like systems (Jordano, 1987; Jordano *et al.*, 2003).

Web-like systems such as food webs, the Internet and human social interactions are traditionally described as graphs or networks (reviewed by Albert and Barabási, 2002). Recently, the notion of complex networks has emerged as a key concept for understanding mutualistic interactions among species in a given community (Olesen and Jordano, 2002; Bascompte *et al.*, 2003; Jordano *et al.*, 2003; Vazquez and Aizen, 2004; Guimarães *et al.*, 2006). Indeed, by applying the network approach, several consistent patterns in the structure of mutualistic ecological interactions have been described, including high heterogeneity in the degree of specialization (Jordano *et al.*, 2003), strong asymmetrical specialization among partners (Bascompte *et al.*, 2003; Vazquez and Aizen, 2004; Guimarães *et al.*, 2006) and an allometric relationship between number of interactions and species richness (Bascompte *et al.*, 2003).

The description of structural patterns of plant–animal networks allows inferences to be made about the robustness of ecological interactions to disturbances (e.g. Jordano *et al.*, 2003). In addition, the network approach

also allows theoretical investigation of the vulnerability of networks by means of numerical simulations (reviewed by Albert and Barabási, 2002), an approach recently introduced for mutualistic interactions (Memmott *et al.*, 2004; Fortuna and Bascompte, 2006; Pascual and Dunne, 2006). Here, we define fragility as the vulnerability of ecological systems to disturbances. We investigate the fragility of the largest plant–frugivore network characterized so far (Bascompte *et al.*, 2003): the interactions between vertebrates and fruiting plants in the Parque Estadual Intervalas (hereafter PEI network), a reserve that is part of one of the last remaining forest blocks of the endangered Atlantic forest in south-eastern Brazil.

The remainder of the chapter is divided into four sections:

1. In *Plant–Animal Interactions as Networks* we review how to describe plant–animal mutualisms as networks, and quantify the resulting structure.
2. In *Investigating Fragility* we discuss how to infer the fragility of a network to the two general classes of disturbances: disturbances that propagate through the network and extinction of species.
3. In *A Case Study: PEI Network* we investigate different aspects of fragility of PEI network, including the investigation for the first time of how disturbances may cascade through plant–frugivore networks.
4. In the *Discussion* we discuss our results, with special attention to our findings for the studied Atlantic forest.

Plant–Animal Interactions as Networks

In this section we introduce the description of field data of plant–animal interactions in a given community as a complex network. We focus on three basic aspects of the network description:

1. How to gather the data and potential bias (*Data sampling*);
2. The equivalence of binary matrices and graphs (*Graph and matrix representations*);
3. The basic structural aspects of plant–animal networks and their biological interpretation (*Basic structural features*).

Data sampling

Ideally, the network description should include all interactions between all elements of the system. In the case of plant–frugivore networks, this means that every interaction between species of frugivores and plants should be recorded. **Methods to record these interactions include all the traditional methods used in studies of seed dispersal; for example, direct observation of animals foraging for fruits, focal observations under fruiting plants, inspection of scats of frugivorous species, records from automatic camera traps placed close to fallen fruits and faeces samples from animals captured using mist-nets (see, e.g. Donatti *et al.*, Chapter 5, this volume).**

However, it is very difficult to sample all the interactions in an ecological community. Most plant–frugivore networks are indeed subnets of larger networks, in which a specific taxonomic group (e.g. birds or primates) is sampled (see data set from Jordano *et al.*, 2003). Analyses of subnetworks also occur for other web-like systems, and subnets may not have the same properties as entire networks (Stumpf *et al.*, 2005). Nevertheless, analyses of subnets are helping to shed light on important questions about the organization of ecological communities (Olesen and Jordano, 2002; Jordano *et al.*, 2003; Vazquez and Aizen, 2004; Guimarães *et al.*, 2006; Lewinsohn *et al.*, 2006).

It is important to note that, even studying a subnetwork, it is almost certainly true that we are not able to record every interaction. It is clear that future work is needed to allow a more rigorous statistical characterization of ecological networks. So far, the study of mutualistic networks has been based on the assumption that the sampled network is a good approximation of the complete network. This belief is supported by the use of data from long-term field studies (e.g. Bascompte *et al.*, 2003), by complementary analyses that control for potential sampling bias (Guimarães *et al.*, 2006), and by the assumption that non-recorded interactions are usually rare, ‘weak’ interactions that do not have much importance for the biological processes related to the structure of plant–animal interactions. However, it is worth mentioning that some missed interactions may sometimes reflect the difficulty of recording all possible interactions in fieldwork, especially when sampling forest habitats that may contain species of frugivores with nocturnal and/or secretive behaviour, confined to the understorey or canopy.

Graph and matrix representations

Plant–animal interactions data can be described as a binary, or presence/absence, matrix in which species of fruiting plants are represented by rows and species of frugivores are depicted as columns (the opposite definition is also valid) (Jordano *et al.*, 2003). Quantitative descriptions of plant–animal interactions (number of visits to fruiting trees, number of fruits consumed, etc) are useful for estimating the strength of the interaction, but as this measure is not always available for most of the interactions recorded during the fieldwork, the binary matrix is sufficient as a first approximation. The matrix element, a_{ij} , has a value of 1 if the frugivore species i harvests the fruit of the fruiting plant j and zero if these species do not interact (Jordano *et al.*, 2003). This matrix, depicted in Figure 26.1a, can be interpreted as an adjacency matrix; that is, a matrix that describes a graph or network (Harary, 1969). The basic idea is that rows and columns represent two sets (fruiting plants and frugivores, respectively) of elements called nodes or vertices, and the cells represent the presence or absence of a link (also called edge) connecting two nodes. By definition, in a seed dispersal network there is no direct interaction between two plants or two animals, and for this

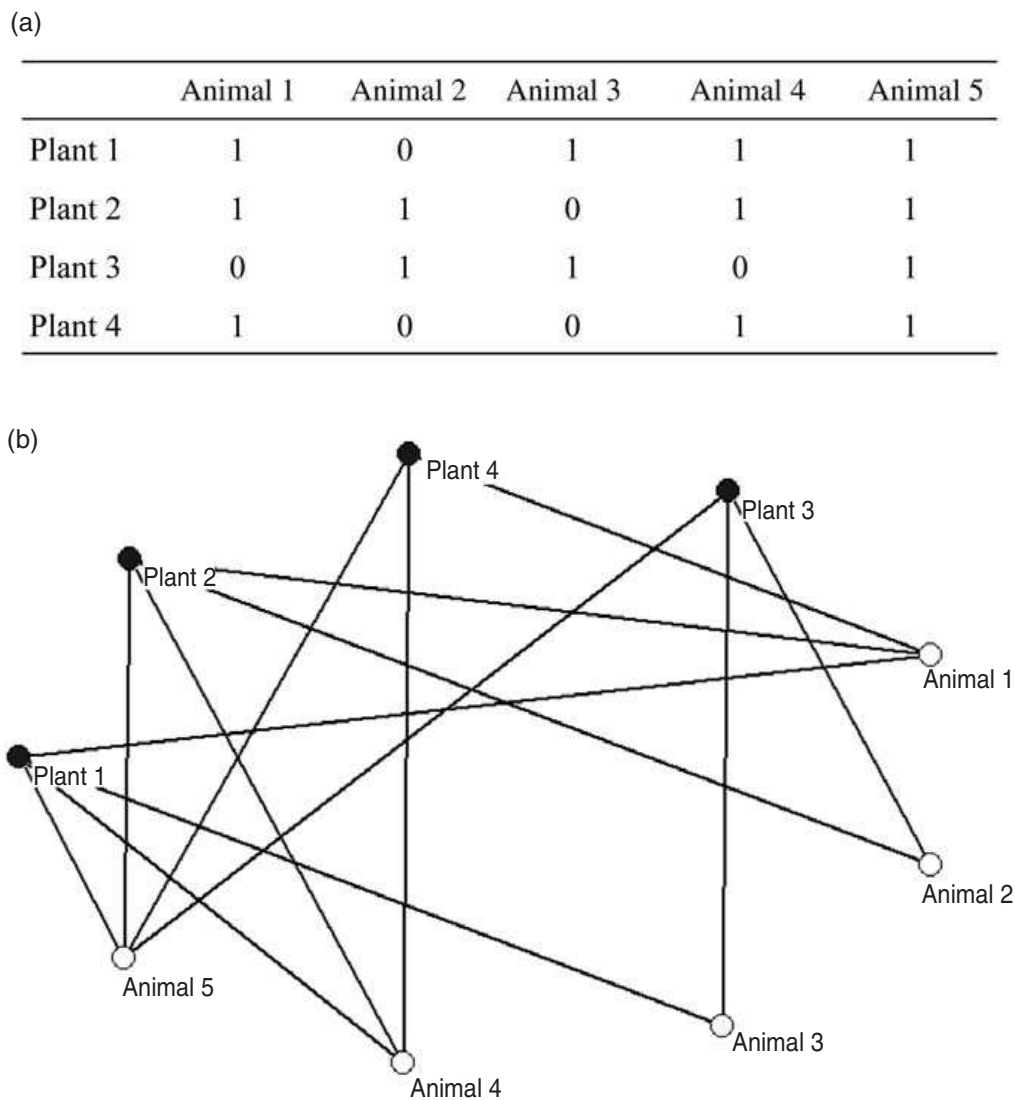


Fig. 26.1. The equivalence between two representations of plant–animal interactions (see text for further details): (a) binary matrix, in which plants are rows, animals are columns and interactions are represented by ‘1’; (b) network, in which plants are black nodes, animals are white nodes and interactions are represented by links.

reason the network is called bipartite (Fig. 26.1b). The network contains all information described in the original, binary matrix and, as a consequence, both representations are equivalent (Harary, 1969; Lewinsohn *et al.*, 2006).

Basic structural features

The network literature is full of examples of network metrics, whose main function is to describe different structural aspects of the network (see Wasserman *et al.*, 1994). Here we focus on some basic aspects of network structure and their classical measurements.

Size

Size is the most fundamental network feature and is defined as the number of nodes in the network. In plant–frugivore networks it is the number of species.

Components

A component is a maximally connected subnetwork. Therefore, if a network has more than one component, its structure is characterized by at least two totally disconnected subnetworks (Fig. 26.2a,b). If the network describing the interactions between assemblages of plants and frugivores shows more than one component, the ecological dynamics may be independent in each component.

Average degree and connectance

The degree of a node is equal to its number of links. In the context of ecological interactions, the degree can be interpreted as the level of ecological specialization (see Olesen and Jordano, 2002): specialists are those species with few mutualistic partners (few links), whereas generalists are species that interact with many species in the network (many links) (Jordano *et al.*, 2003). Regarding frugivory, the terms ‘specialist’ and ‘generalist’ used hereafter are used in a somewhat different sense from that usually found in typical studies dealing with this theme (for comparison see Moermond and Denslow, 1985). The average degree for an ecological network can be interpreted as the average level of ecological specialization (or generalism) of a species in a community. It is important to note that the average degree is a function of network size. An alternative measure for the average level of ecological specialization is connectance, which is the proportion of possible links in the network that are actually established (Fig. 26.2c,d). In fact, connectance is a size-independent measure (Olesen and Jordano, 2002).

Nestedness

A nested network is a bipartite network in which there is a specific pattern of interaction among nodes, in which the nodes with small degrees interact with a proper subset of the nodes that interact with a larger degree node (Fig. 26.2e,f). Bascompte *et al.* (2003) defined the degree of nestedness, N , as $N = (100 - T)/100$, in which T is a standardized measure of how much the binary matrix that describes the network departs from perfect nestedness. To calculate T , the binary matrix is maximally packed (see Atmar and Patterson, 1993, for further details). Then, an isocline of perfect nestedness is calculated and deviations from isocline (i.e. unexpected recorded presences and absences of interactions that deviate from a perfectly nested pattern) are standardized and recorded. The degree of deviation of this isocline is T . In ecological terms, the degree of nestedness

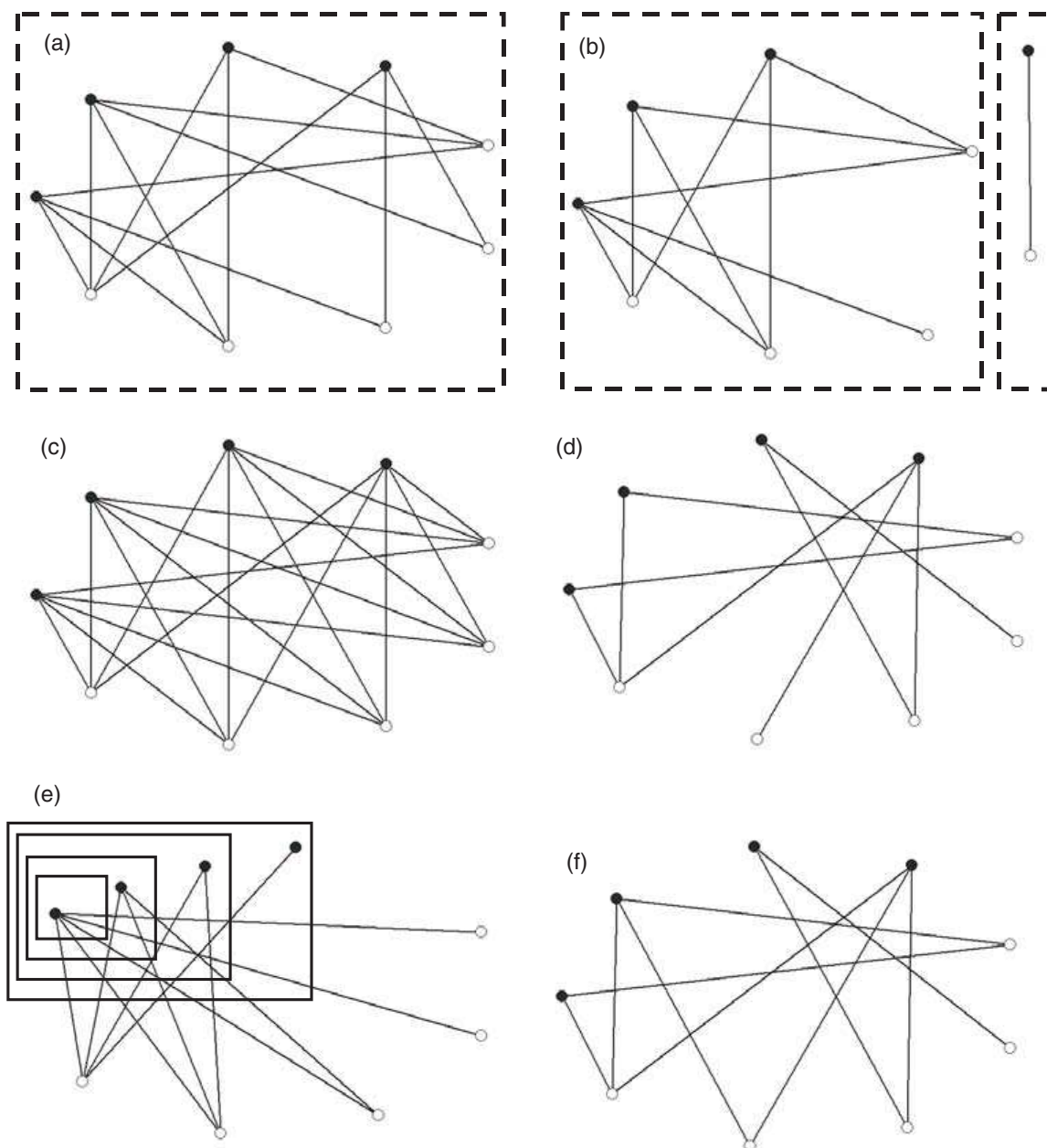


Fig. 26.2. Basic structural aspects of networks: (a) network formed by one component, (b) network formed by two components. Components identified by the dashed rectangles, (c) a network showing high connectance, (d) a network showing low connectance, (e) nested network in which the specialist interacts with a subset (small rectangle) of the partners that also interact with more generalist species (larger rectangles), (f) non-nested network. All networks were drawn using Pajek (see de Nooy *et al.*, 2005).

(N) is a measure of the level of observed asymmetrical specialization: values of N close to 1 therefore indicate strong asymmetrical patterns in specialization (= high degree of nestedness). One of the main discoveries of the network approach to plant–animal mutualisms is that they are often nested (Bascompte *et al.*, 2003; Thompson, 2005; Guimarães *et al.*, 2006).

Investigating Fragility

Ecologists have been concerned about the vulnerability of ecological systems to disturbance for a long time (Pimm, 2002). In network theory, ‘fragility’ can be defined in many distinct ways (see Pascual and Dunne, 2006). Here, we explore two classes of fragility.

First, a network can be considered fragile if the removal of a node or a group of nodes markedly affects its structure, changing the observed values for one or more network metrics (Fig. 26.3a,b). Examples of the disturbances that can be modelled as node removal include death (in social networks), bankruptcy of companies (in economic networks), and errors in protein synthesis (in molecular networks) (reviewed by Albert and Barabási, 2002). In ecology, node removal can be used to simulate the local extinction of frugivores or/and plants (Memmott *et al.*, 2004; Fortuna and Bascompte, 2006).

Second, a network can be considered fragile if any disturbance easily cascades through the entire network. In this case, the disturbance can be modelled as a diffusion process, in which the disturbance flows from the perturbed node to others (Fig. 26.3c,d). Examples of disturbances that propagate in networks are diseases and technological innovations, in social networks (de Nooy *et al.*, 2005). In ecological networks, an example of

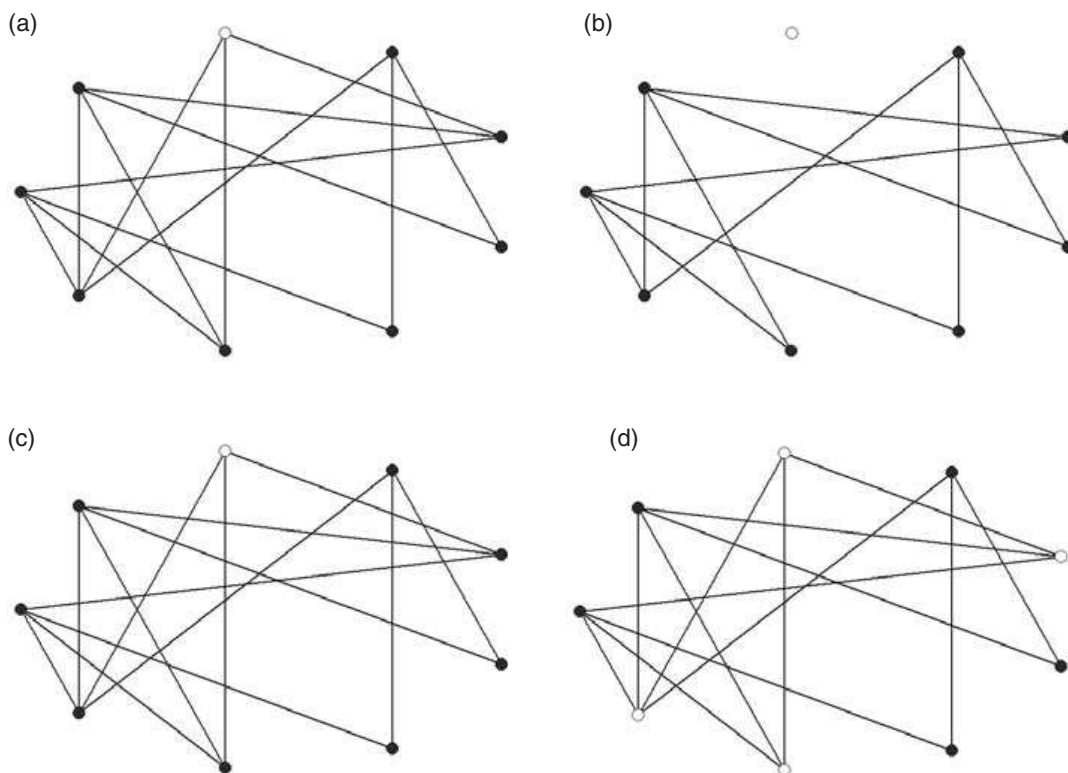


Fig. 26.3. Simulating disturbance in networks: (a) one node is selected (in white) and (b) removed from the network, (c) one node is perturbed (in white) and (d) the disturbance propagates to the nodes that interact with it (in white).

disturbances that can be modelled as diffusion processes are the indirect effects of the increase in abundance of a given species, in which the disturbance (change in abundance) may affect species that directly interact with the perturbed species and may also cascade through the network.

The investigation of fragility in terms of experimental manipulations is very difficult (but see Fontaine *et al.*, 2006) and is certainly limited to species-poor systems. However, the researcher can use at least two broad classes of approach: the inference of fragility based on structural aspects (see *Structure and fragility*) or the simulation of disturbance dynamics (see *Simulating diffusion and extinctions*).

Structure and fragility

Due to simulation and observational studies of complex networks in different scientific areas, we now have many examples of relationships between structural aspects of the network and its vulnerability to disturbances (see Albert and Barabási, 2002). Thus, we can infer aspects of the fragility of a given network by simply calculating and interpreting the values of different network metrics. Below, we describe possible interpretations of the different values for network metrics already introduced in this chapter. It is important to note that much of the interpretation will depend on the particulars of the dynamics of the diffusion or node removal that we assume to occur in the network (see *Simulating diffusion and extinctions*). Here we interpret the values of different metrics by assuming two very simple dynamics: (i) random node removals in which any species has the same probability of going extinct; and (ii) degree-dependent diffusion processes, in which the probability that species i will be affected by a perturbed partner j is inversely proportional to the number of partners of i . In these dynamics, a generalist species is less likely to be affected by changes in the abundance of a partner, whereas extreme specialists will often be affected by changes in the abundance of its partner.

Size

The effects of node removal will probably be weaker in large networks, since the larger the network, the less probable it is that the removal of a single node will change the community-level properties of the network. Thus we can usually assume that large networks are less fragile than smaller networks. Accordingly, the diffusion of disturbances is clearly dependent on the size of a network. In food webs, it is usually assumed that the effects of a disturbance in a given species will only affect species that are connected by a small path of interactions to the perturbed species (Williams *et al.*, 2002). If the network is very large, a disturbance will probably affect a small proportion of the network. In contrast, in smaller networks, some disturbances will easily diffuse through the entire network (but see Pimm, 2002, for a more complete discussion, considering other fragility regimes).

Components

The number of components may not be an important structural aspect for the removal of species, except in extreme situations in which the network is formed by components of few (e.g. two) species. In this case, the extinction of a species may lead to the disconnection of the mutualistic partner. In contrast, the number of components can markedly affect the propagation of disturbances. By definition, there is no path between two components and, as a consequence, a disturbance that affects one component cannot propagate to the other component. In conclusion, networks formed by more than one component are less sensitive to the propagation of disturbances than networks formed by a single component.

Average degree and connectance

In networks with low connectance, the extinction of species may lead to deep structural changes, such as the emergence of a new component (e.g. Fig. 26.3c,d). In contrast, in densely connected networks there are several paths connecting groups of species, and the disconnection of a species or the emergence of new components are less likely. Thus, we can usually assume that densely connected networks are less fragile than sparse networks with regard to disturbances. Accordingly, in networks with low connectance (sparse networks) a randomly selected species will usually have few interactions. As a consequence, species are likely to be more sensitive to the propagation of disturbances. In contrast, in networks that show high connectance, each species will have many interactions and, therefore, it is unlikely that an environmental disturbance that affects only one species will cascade through its ecological partners (but see Pimm, 2002).

Nestedness

The existence of high levels of asymmetrical specialization implies that the fragility of the network markedly depends on the identity of the perturbed species. In a perfectly nested network, all specialists interact with the most generalist species. As a consequence, if the extinct species is a generalist, all the specialists may lose their unique mutualistic partner. In contrast, if a specialist goes extinct, no species loses its mutualistic partners. Similarly, a disturbance that affects a generalist will propagate to all specialists (e.g. Fig. 26.3c,d). In contrast, a disturbance that affects a specialist will rarely propagate to the generalist.

Simulating diffusion and extinctions

The inference of fragility from structural aspects is a powerful tool for predicting the possible consequences of disturbances and extinctions for the network. However, the structure of real networks cannot be completely described using one or a few structural features. Moreover, different metrics

can lead to opposite interpretations. For example, a network can be simultaneously large, implying less sensibility to species removal, and sparse, implying higher sensibility to species removal. Is such a large and sparse network fragile? The answer cannot be derived directly from both measures because we still do not understand the extent to which the effects of one topological pattern balance the effects of other structural patterns. To circumvent the above problems, we can adopt a more direct approach by simulating disturbances propagating through the network, or species removal. By performing numerical simulations of disturbances we are able to investigate how fragile the network is to different disturbance dynamics without being limited to the measured structural metrics.

A Case Study: PEI Network

The Atlantic forest and the Parque Estadual Intervales

The Atlantic forest of south-eastern Brazil is among the top five world hotspots of biodiversity and is also one of the most threatened ecosystems in the world (Myers *et al.*, 2000). This forest has been reduced, since colonial times, to 8% of its original extent of more than 1 million km² along the Brazilian Atlantic coast (Dean, 1995). Today the largest continuous forest tracts are confined to south-eastern Brazil, a region where 70% of the country's population live (Ministério do Meio Ambiente, 2000). Direct threats to this biome include logging, poaching, wildlife trade, urban and industrial development, and deforestation driven by agriculture and expansion of pastureland (see several chapters in Galindo-Leal and Câmara, 2003).

The **Parque Estadual Intervales (PEI)** is a 42,000-ha reserve in south-eastern São Paulo state characterized by a mosaic of pristine forest and second-growth vegetation along an altitudinal gradient ranging from 60 to 1100 m (for a detailed description of PEI, see Carvalho *et al.*, 2002). Different sites inside the park were visited monthly from January 1999 to October 2002, for a 3–4 day census at each site. **During the censuses, interactions between frugivorous vertebrates and plants were recorded,** using several methods: mist netting and searching for seeds in faecal samples (**birds and bats**), collecting scats in forest trails (**large birds and mammals**), trapping with folding Sherman traps (**opossums**) and observation of fruit-eating behaviour (**birds and primates**). Like many other sites in the Brazilian Atlantic forest, the fauna of frugivorous vertebrates at PEI includes several species of threatened birds and mammals (de Vivo and Gregorin, 2001; Vielliard and Silva, 2001) which are liable to experience severe shifts in abundance, leading to extinction in a medium-term future (Brooks *et al.*, 1999; Chiarello, 2000). Thus, we applied the approach introduced in previous sections of this chapter to investigate and predict the consequences of these disturbances to the organization of the biodiversity of PEI.

Basic structural features and inferences of fragility in the PEI network

The PEI network (Fig. 26.4) is the largest plant–frugivore network recorded to date, with 317 species, making it 1.5 times larger in number of species than the second largest plant–frugivore network, and more than six times higher than the average number of species found in recorded networks (49.1 ± 63.8 species, mean \pm SD; data from Bascompte *et al.*, 2003). All the nodes represent individual species: = 207 plant and 110 animal species. As with other typical large plant–frugivore networks (Bascompte *et al.*, 2003), the PEI network is formed by a single but sparse component, showing a small average degree (5.4 ± 6.3 animal partners per plant and 10.2 ± 11.5 plant partners per animal). Consequently, very low connectance was observed (only 4.9%). We also calculated the degree of nestedness, N , of the PEI network using ANINHADO (Guimarães and Guimarães, 2006). The PEI is a highly asymmetrical network, since $N = 0.96$ is very close to perfect nestedness ($N = 1$), indicating that specialists often depend on generalists in the PEI network, corroborating previous analysis with a less complete version of the PEI network (Bascompte *et al.*, 2003).

What can we infer about the fragility of the PEI network based on structural aspects? The large size of the network suggests that it is probably not very sensitive to disturbances, even considering that the network is

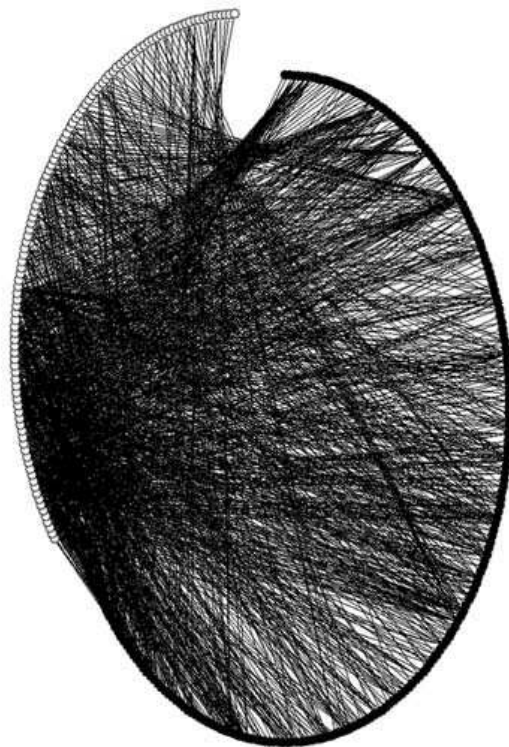


Fig. 26.4. The PEI network, in which plants are represented by black nodes and animals are represented by white nodes. Links represent interactions between frugivores and plants.

formed by a single component. However, the sparse structure and the strong pattern of asymmetrical specialization suggest that the network is potentially vulnerable to disturbances, especially if the perturbed species is a generalist one supporting many species with few interactions. Due to the uncertainties associated with simple analyses of topology, we simulated disturbances in the network and describe our findings in the next two sections. Special attention is given to: (i) the possibility that single-species disturbances propagate through a large proportion of interacting species; and (ii) the consequences of the extinction of already endangered vertebrates.

Simulating disturbances that propagate in the PEI network

We simulated the degree-dependent diffusion processes ($n = 1000$ simulations). The algorithm used was defined as follows:

1. A species is randomly selected in the network and perturbed;
2. The probability that each partner species directly connected with the perturbed species ('target' species) is affected is equal to $1/k$, where k is the number of partners of the target species;
3. The simulation proceeds until all species are affected or until no new species is perturbed.

Although very simple, these propagation dynamics have some interesting properties: generalist species are less susceptible to being affected by disturbances, while specialists will often be affected by changes in the abundance of their partner. Indeed, an extreme specialist interacting with a single partner will always be affected by disturbance of its partner.

In 58.5% of simulations, the disturbance did not propagate to any species in the network. However, the distribution function that describes the probability to find a simulation in which S species are perturbed by the propagation decays slowly, following a power-law (Fig. 26.5). As a consequence, there is a small, but non-negligible, probability that the disturbances will affect nearly half of the species in the network.

Simulating species extinction in the PEI network

In PEI, 11 species of vertebrates (10%) are considered threatened (adapted from São Paulo state, Law No. 42.838, February 1998), eight species of birds *Tinamus solitarius* (Tinamidae), *Aburria jacutinga* and *Penelope obscura* (Cracidae), *Laniisoma elegans*, *Lipaugus lanioides*, *Procnias nudicollis* and *Pyroderus scutatus* (Cotingidae) and *Tangara peruviana* (Thraupidae), and three species of mammals: *Alouatta guariba* and *Brachyteles arachnoides* (Cebidae) and *Tapirus terrestris* (Tapiridae). As the number of interactions of a species is directly related to its abundance (Jordano, 1987) and as a consequence of strong asymmetrical specialization, we should expect that:

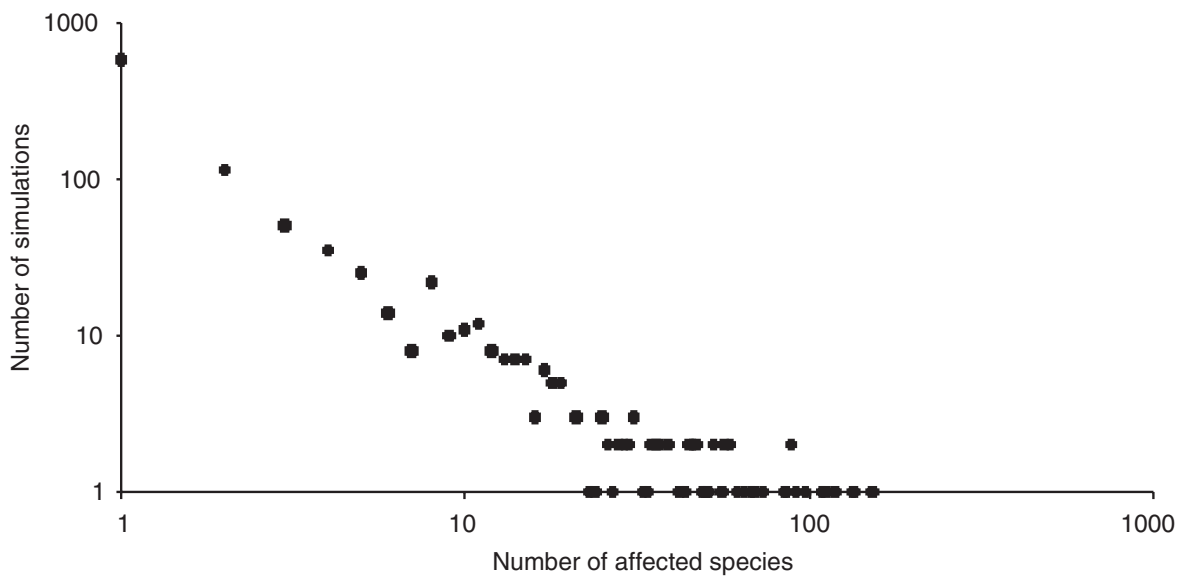


Fig. 26.5. Probability that a disturbance propagates through the PEI network (see text for further details), affecting n species. Note that the probability decays as a power-law, indicating that there is a non-negligible probability of a disturbance cascades to a great part of the network.

1. Many endangered species, often rare, will usually show few interactions;
2. As species with few interactions usually interact with generalists, few plant species will show total seed dispersal collapse (i.e. loss of all seed dispersers) due the extinction of endangered seed dispersers.

The network with and without the endangered species has similar macroscopic structures (Table 26.1). This is a consequence of the relatively small number of endangered animals. The main difference between the networks is that the network without endangered species is formed by two components. However, one component contains only two species (0.7% of the remaining species) and all remaining species are in the other, giant, component.

Only 11 species of plants will lose all their seed dispersers. Although this number represents only 5.3% of the plant richness, we do not know a priori whether this number is too small, too large, or as expected if any set of 11

Table 26.1. Differences in macroscopic properties of the PEI network before and after the extinction of 11 species of endangered vertebrates.

	Size	No. of components	C (%)	$\langle k \rangle$ (plants)	$\langle k \rangle$ (animals)	N
Before the extinction	307	1	4.92	5.4 ± 6.3	10.2 ± 11.5	0.96
After the extinction	295	2	5.25	5.2 ± 5.9	10.3 ± 11.6	0.96
Difference (%)	3.9	100	6.7	3.7	1.1	0.1

C = connectance, $\langle k \rangle$ = average degree, N = degree of nestedness (see text for further details).

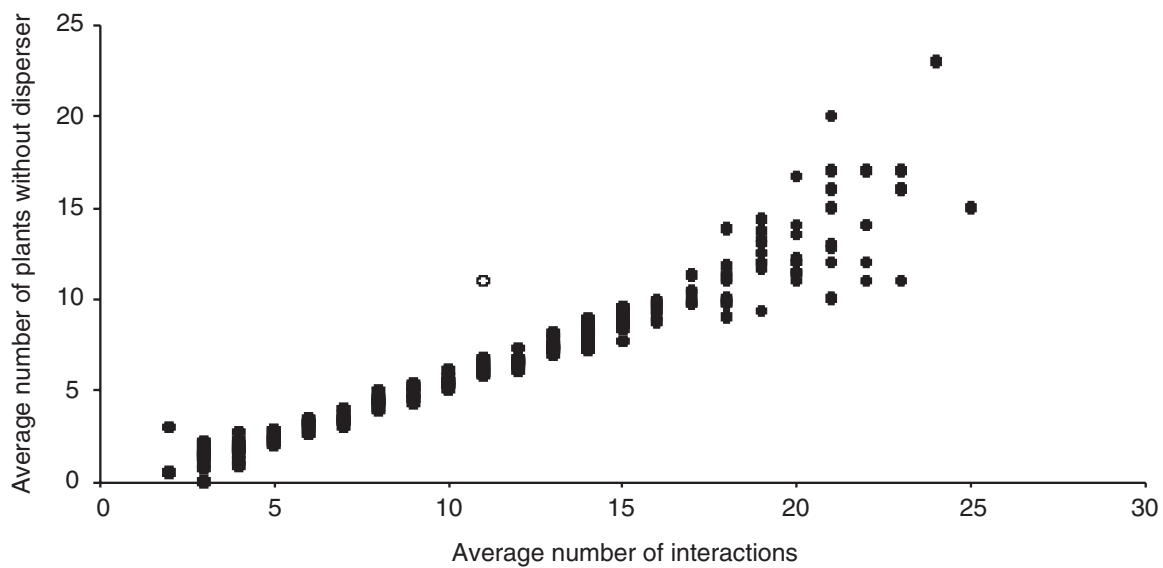


Fig. 26.6. Relationship between the average degree (number of interactions) of 11 animal species and the average number of plants that will lose all seed dispersers with their extinction: random extinction of 11 animal species (black nodes) and the extinction of the endangered animal species (white node).

species of animals goes extinct. We simulated the extinction of random sets of 11 species of animals and recorded the number of plants that lost all their seed dispersers. The results suggest that 11 species of plants without seed dispersers is too high when compared to what is expected by random extinctions ($P = 0.09$). Additionally, we compared the effects of the extinction of endangered species with the extinction of 11 randomly selected seed dispersers but with a similar average number of interactions. In this situation, the seed dispersal collapse of 11 species of plants is twice as high as expected for a random extinction of 11 seed dispersers with a similar average number of interactions (Fig. 26.6), indicating that there is an unexpected set of plants that will be severely affected by the extinction of endangered seed dispersers.

Discussion

In different ecosystems, many plants rely on animals to disperse their seeds (Jordano, 2000). Thus, the disruption of these interactions and other mutualisms may profoundly affect the organization of ecological communities (e.g. Galetti *et al.*, 2006) and indirectly affect the ecological services necessary to sustain humankind (Levin, 1999). We now have a relatively good understanding of how the local extinction of frugivores may affect the regeneration of natural plant populations (e.g. McConkey and Drake, 2002; Galetti *et al.*, 2006). However, we need to develop approaches that allow us to predict, at least in broad terms, the consequences of

disturbance processes to the organization of plant–animal mutualisms. Only by enhancing our predictive success will we be able to optimize our conservation efforts and efficiently protect threatened ecological areas.

Until recently, attempts to predict the fate of plant communities after animal extinctions were based on indirect evidence; for example, morphological traits such as seed size and frugivore gap width (e.g. Cardoso da Silva and Tabarelli, 2000). An alternative to these indirect approaches is the analysis of network fragility. In this chapter, we investigate for the first time how disturbances may propagate across species in a plant–frugivore network. Moreover, we also contribute to an enhancement of our understanding of how disturbances that may lead to local extinction of species may affect the structure of plant–animal mutualisms (see also Fontaine *et al.*, 2006; Fortuna and Bascompte, 2006).

The study of the mutualistic networks is now only just beginning (but see Jordano, 1987). Considerable work will be needed before we are able to apply this approach to management plans. It is possible that only more complete descriptions of quantitative, well-studied networks will provide information at the necessary level of detail needed to guide conservation policies. Nevertheless, the study of binary networks has provided useful and interesting insights into how complex systems respond to disturbances; for example, assisting in understanding and controlling how viruses propagate in digital and sexual networks (Albert and Barabási, 2002).

In this chapter, we corroborate the general view that large networks may be robust to disturbance (Albert and Barabási, 2002; Jordano *et al.*, 2003; Memmott *et al.*, 2004; Fortuna and Bascompte, 2006). Indeed, our simulations suggest that, for example, the effects of changes in the abundance of a single species will seldom propagate throughout the entire Atlantic forest network. This is probably a result of the large number of species with few interactions that interact with a few super-generalists. Moreover, the extinction of the endangered dispersers will not markedly affect the large-scale properties of plant–frugivore interactions in this tropical community, an expected consequence of the few species that are endangered in PEI.

Nevertheless, two of the ways in which the PEI network responds to disturbances suggest that plant–frugivore networks may be severely affected in some situations. First, although disturbances probably will not propagate throughout the network, our results also emphasize that there is a non-negligible probability that a considerable proportion – up to half of the species – will be affected by a single-species disturbance. These drastic events, in which nearly half of the species in the community will be affected, are also a consequence of asymmetrical specialization. If a random disturbance affects a super-generalist, this disturbance may propagate through many species in the network, eventually affecting a large proportion of the interacting species. **Therefore, we suggest that special attention should be devoted to investigating the vulnerability to extinction of the most-connected species in the Atlantic forest such as the already threatened *Penelope obscura* and the palm tree *Euterpe edulis* (Arecaceae), which is threatened by intense harvesting.**

Second, although the extinction of endangered birds and mammals will not lead to dramatic shifts in network structure, an unexpectedly large proportion of plant species will probably show seed dispersal collapse. This result is quite surprising, due to the nested structure of plant–animal mutualisms (Bascompte *et al.*, 2003). However, no plant–frugivore network shows perfect nestedness (asymmetrical specialization) and eventual, unique interactions between species with few interactions will occur. Our results indicate that these unique interactions chiefly involve endangered forest seed dispersers such as large-bodied birds and mammals. Unique interactions are community-level properties that emerge as a result of ecological and evolutionary processes relating plants and large-bodied vertebrates (see Donatti *et al.*, Chapter 5, this volume). Thus, the extinction of endangered animals will not only lead to the reduction of plant richness, but to the simplification of the ecological community and the loss of relevant aspects of biodiversity structure. We suggest that future conservation policies in the Atlantic forest should focus on long-term maintenance of these endangered frugivores and their interacting plants.

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