It takes a flower and a bee to make a meadow:* mutualistic plant-pollinator interactions are crucial for plant biodiversity conservation

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*title inspired by Ellis & Ellis-Adam's (1993) study

Abstract

Mutualistic plant-pollinator interactions play one of the crucial roles in generating and sustaining biodiversity of terrestrial ecosystems. They are even regarded as 'architecture of biodiversity'. Usually they connect dozens or even hundreds of species, forming complex networks of reciprocally beneficial interactions. The structure of such networks is highly heterogeneous and asymmetric: most of the species are rather weakly connected, while some of the taxa develop much stronger relationships than would be expected by chance. New mathematical tools allow us to analyse the network structure via designation of species playing structural roles in the studied ecosystem: *hubs* – organisms highly connected within their own module of the network, and *connectors* – species connecting several modules. This theoretical approach can be applied to indicate 'keystone' species which determine stability of the studied networks.

Key Words

biodiversity, conservation, ecological interactions, graph, network, pollination

How important is pollination?

In an encyclopaedic definition the process of pollination is quite simple and straightforward: it involves the transfer of a pollen grain from anthers to conspecific stigma. In nature this is usually done by wind, water and, most often, by animals. In zoogamous pollination the most important players from the animal side are insects (Proctor *et al*., 1996).

It is very difficult to say how many out of approximately 260,000 flowering plant species are animal-pollinated. The estimates based on suitably structured flowers indicate that up to 90 per cent of all flowering plants may depend upon animals (mostly insects) for their sexual reproduction (Buchmann & Nabhan, 1996). If we consider the ubiquity of this process, which takes place in all terrestrial ecosystems on all continents (excluding polar regions) we may regard pollination as a critical service, crucial for maintaining the stability of all terrestrial ecosystems where flowering plants are involved (Kearns *et al.,* 1998). It is also important for humans if we think of commercial plants that are animal-pollinated (Buchmann & Nabhan, 1996).

The value of pollinators

There are some 2,000 crop species cultivated around the world, but only about 120 are globally important (Klein *et al*., 2007). As shown by Klein and co-authors (2007) this number includes about 70 species for which animal pollination is crucial or important for a good crop; however, when we consider production volume this means about one third of global production comes from animal-pollinated plants. This voluntary service has quite substantial monetary value – according to various authors it fluctuated at around 120–200 billion US dollars a year in the 1990s (Richards, 1993; Constanza *et al.,* 1997). New estimates calculated solely for crop plants give the sum of 150 billion US dollars in the year 2005 (Gallai *et al*., 2009)! But the economic value of the process of pollination is not the most important aspect of these mutualistic plant-pollinator interactions: its biological significance is far greater. This is because of its crucial role in generating and sustaining biodiversity in terrestrial ecosystems (Kearns *et al.,* 1998).

Pollination networks

Plant-pollinator interactions form complex networks (Fig. 1) connecting dozens or even hundreds of species (Bascompte & Jordano, 2007). These kinds of networks can even be found in highly urbanized habitats and their properties are alike: for instance scientists from Warsaw University Botanic Garden studied two pollination networks from ruderal habitats in Warsaw city centre and, on the study sites that did not exceed 500 sq m, found complete networks built by over 50 species of plants and animals (Fig. 2).

To describe properties of a network ecologists use random graph theory developed in the late 1950s by the great Hungarian mathematicians Paul Erdös and Alfred Renyi. In the simplest network a random graph is defined by a set of nodes and a probability *p* that two such random nodes are connected by a link (Fig. 3). If we apply that to a biological system, nodes may represent species and the links are ecological interactions such as pollination (Bascompte & Jordano, 2007). However their structure may differ: Figure 1 shows a graphic representation of a pollination network in a lowland meadow in north-east Poland. Green dots represent plant species, empty dots are flower visitors. Connecting lines indicate a connection between a given pair of nodes (an insect visiting a flower). This network has the same number of nodes and mean node degree (i.e. the mean number of links) as the one from Figure 3. The architecture of interaction in these two graphs is however different, partly because the second one is a bipartite network with two different subclasses of nodes (i.e. plants and animals) that have no links within a subclass. This network's structure, similar to other mutualistic networks, resembles that of the Internet rather than the random Erdös-Renyi graph. Such biological networks are much more heterogeneous and asymmetric: most nodes (species in this case) are rather weakly connected, while a number develop much stronger links than would be expected by chance (Bascompte & Jordano, 2007). This is similar to the worldwide web, where we have many weakly linked web pages and highly linked portals such as Google or Wikipedia.

This is different to a random graph, where probability of node degree distribution fits the Poisson law (or exponential when the number of nodes keeps growing) and when we look at the Internet it seems to fit with power-law distribution. This kind of network is usually called scale-free as the relationship between number of links (k) and their probability cannot be defined on a particular scale. Biological networks usually fit in between these two kinds of degree distribution (Bascompte & Jordano, 2007).

There are few more interesting characteristics of mutualistic networks. One of the obvious things to be observed is that they contain link-dense and link-sparse regions. This creates compartments or modules, where species are more tightly connected together within their specific module than to other species in different modules. When we further look at specific nodes we can designate several classes of species: ones that have only one or very few connections usually within their own module – they are called peripherals. In biological terms these are usually specialists interacting with very few species. Species that are either highly connected within their module or with other modules are hubs or, biologically speaking, generalists. There may be module hubs – highly connected species linked to many species within their own module, connectors linking several modules, or species with many links both within a module and with other modules. They can be termed network hubs or super generalists, acting as both connectors and module hubs (Olesen *et al*., 2007).

What happens if we extract some nodes from a system? In real life this may happen, for example in species extinctions or if they shift their biogeographic ranges due to climate change. How does it affect the network? The answer depends on the topological role a particular node plays. If it is a peripheral the network structure does not change much, but if it happen to be module or network hub or connector, the whole system may be affected. In other words if we lose one of the structural species, be it plant or animal, other taxa which are linked to this node may be endangered. For highly connected species it usually results only in a decrease in node degree, but for peripherals it may mean exclusion from the network. And as a rule most of our endangered plants are specialists, which means peripherals. Therefore this kind of network approach may be very important in our conservation procedures, as the knowledge of a system structure may greatly enhance our chances of successful preservation or restoration of particular taxa. Thus, in any conservation efforts we must not forget that species are not separate entities and networks are everywhere – and some of them also include us humans.

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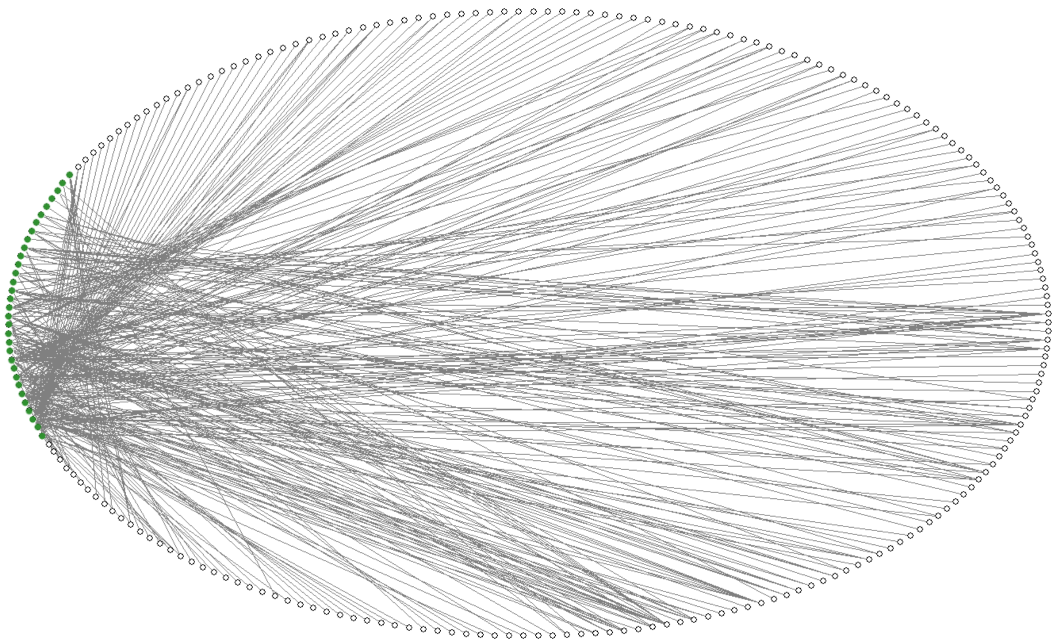

Fig. 1 Graphic representation of a pollination network in a lowland meadow in NE Poland (Zych et al., unpubl.). Green dots represent plant species, empty dots – flower visitors. Connecting lines indicate a connection between a given pair of nodes (an insect visiting a flower)

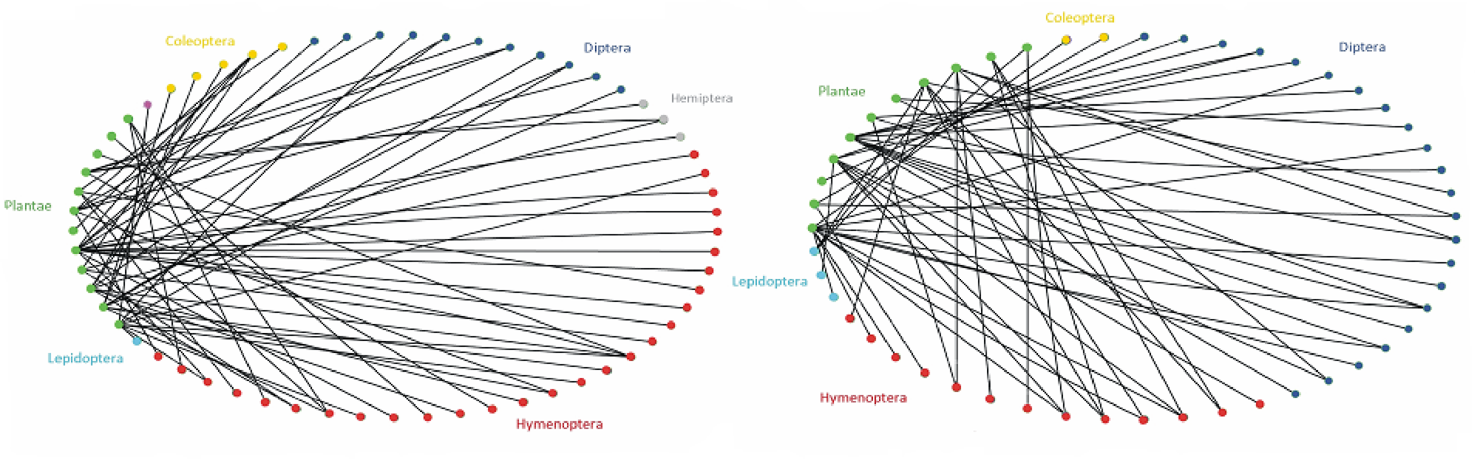

Fig. 2 Complete pollination networks from ruderal habitats in Warsaw city centre built by over 50 species of plants and animals. Green dots represent plants and other color dots insects from various taxonomic orders (Jędrzejewska-Szmek & Zych, unpubl.)

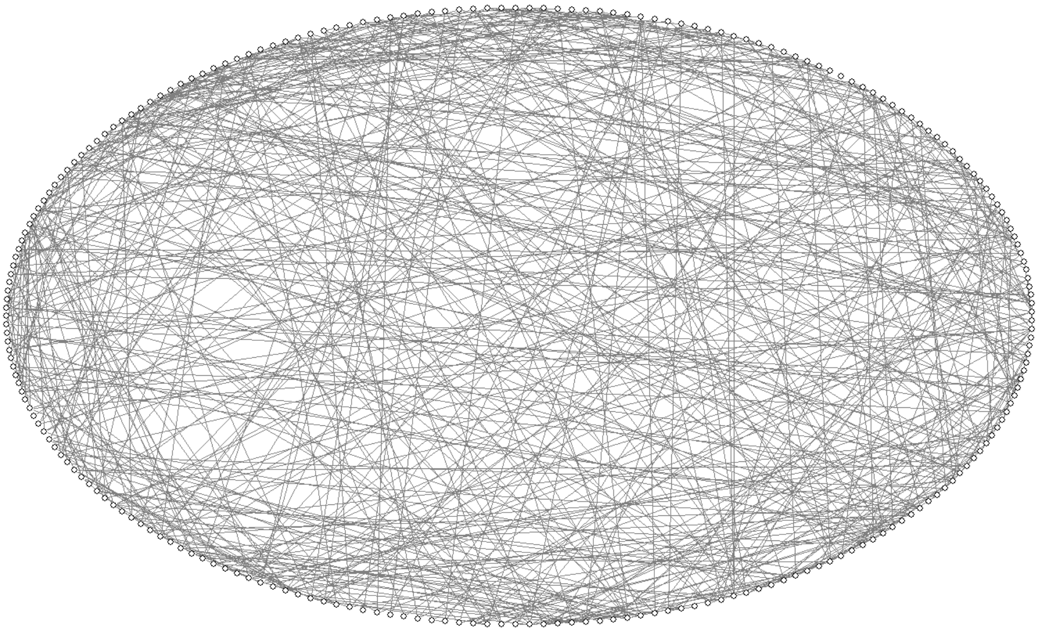

Fig. 3 A random network created by the Erdös-Rényi model. It has the same number of nodes and mean node degree as the graph in Fig. 1