



## Scaling down from species to individuals: a flower–visitation network between individual honeybees and thistle plants

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Studies of ecological networks usually focus upon interaction patterns among species. However, linkage among species is mediated by their constituting individuals. Thus, every linked species pair in a network encapsulates a new network of interacting individuals. Very few studies outside the sociology of larger animals have investigated networks at the level of the individual. Here, we analyse the structure of a flower–visitation network of individual thistles *Cirsium arvense* and honeybees *Apis mellifera* in a small meadow patch in Denmark. We marked and numbered 62 honeybees and 32 thistle stems and monitored all floral visits. The constructed bipartite network of individual plants and bees had a high connectance and low nestedness, but it was not significantly modular. Frequency distributions of number of links per species (i.e. linkage level) had their best fit to a truncated power law, and interactions were asymmetrical. Unipartite networks of either plants or bees had exceedingly short average path length and high clustering. Linkage level of plants increased with their number of flower heads and height of inflorescence (floral display parameters). Overall, the individual network of honeybees and thistles was denser linked than what is known from species pollination networks. Characteristics of both plants (e.g. floral display) and animals (e.g. foraging behaviour) are likely to generate this intra-specific, inter-individual link pattern. Such features of individual–individual networks may scale up and become important drivers of the structure and dynamics of species–species networks.

Networks are complex interactive systems of nodes and links, and in theoretical statistics and social sciences their study has a history of more than 50 years. In 1998–1999, a set of paradigmatic papers about large, real networks appeared, especially Watts and Strogatz (1998), Barabási and Albert (1999) and Albert et al. (1999). With a total of more than 10 000 citations (ISI: April 2010), these three publications have had and still have an enormous impact upon the development of empirical network analysis. In ecology, network analysis started off in Strogatz (2001), Solé and Montoya (2001), Montoya and Solé (2002), Williams et al. (2002), and Dunne et al. (2002a, 2002b). Subsequently, the interest in ecological networks, especially food webs, host–parasitoid webs, and mutualism networks, has increased dramatically (Ings et al. 2009).

Networks have a hierarchical organization, if each node, so to speak, both is a part of a whole and a whole of parts. In nature, species are assemblages of individuals and are themselves parts of larger assemblages, viz. communities and networks (Ravasz and Barabási 2003). Ecological network analysis has mostly operated at species level or actually population level, i.e. where nodes are species, and links may be any kinds of antagonistic or mutualistic interaction. However, such species–species or here *S–S* networks are rarely scaled down or up. In ecology, individual–individual or here *I–I* networks are known from studies of social interactions among larger animals (Krause et al. 2007, Lusseau et al.

2008), gene flow in plant populations (Fortuna et al. 2008), animal–disease dynamics (Perkins et al. 2009), bat–roosting tree interactions (Fortuna et al. 2009), and foraging–niche width relationships (Araújo et al. 2008).

Comparisons of organizational levels is on the agenda of the so-called hierarchy theory, which examines macro-patterns in hierarchies and makes predictions about phenomena and processes on a hierarchical level based on information from adjacent levels (Waltho and Kolasa 1994). Thus given our knowledge about *S–S* networks, how would we predict the characteristics of *I–I* networks? No specific knowledge or ready-made hypotheses are at hand. However, a line of arguments may lead to testable predictions: species and individuals vary in linkage-important traits and linkage probability depends on the variation of these, e.g. a certain tongue length for nectar extraction or a specific set of digestive enzymes for fruit consumption are needed to establish a link. In general, the variation of such traits will be larger among the different species in a community than among individuals in a population. Thus if one bee can extract nectar from a flower most of its conspecifics may also be capable of doing it. Thus linkage may be less constrained in *I–I* networks than in *S–S* networks. Consequently, linkage probability will be higher, and number of observed links and connectance *C* of the *I–I* network will also be higher than in a similar-size *S–S* network. *C* is the proportion of realized links in a network. Higher *C* means lower nestedness (Fortuna et al. 2010)

and disappearance of modularity (Olesen et al. 2007; see Material and methods for definitions of nestedness and modularity). In addition, a denser network (i.e. higher  $C$ ) means, *cetera paribus*, a shorter distance and higher clustering among species. Here, we tested this idea about hierarchical scale–variance for these most used parameters in network analysis. As our study system we constructed an  $I$ – $I$  pollination network and compared it to a sample of  $S$ – $S$  networks (data from Jordano et al. 2003, Olesen et al. 2006, 2007).

With more than 100 publications, pollination networks are a very intensely studied class of networks. All studied pollination networks are bipartite  $S$ – $S$  networks, i.e. networks of two interacting sets of flowering plant species and their pollinator species. However, any interacting pair of plant and pollinator species can be dissolved and analyzed as a bipartite  $I$ – $I$  network of two interacting populations of individuals. Of course, if our resources allowed, all interactions between all individuals of all species could be studied simultaneously. Here, we analysed a network between individuals of one plant and one pollinator species, and asked, (1) if this bipartite  $I$ – $I$  network differed topologically from bipartite  $S$ – $S$  pollination networks in general? (2) How do ecological characteristics of nodes (here plant and pollinator individuals) influence network topology, and (3) do these structural features of  $I$ – $I$  networks affect the way empirical  $S$ – $S$  networks are composed and interpreted?

## Material and methods

### Study site

The field site was at Hørhaven, Moesgaard Skov, Denmark (56°6'34"N, 10°13'46"E), a mosaic of deciduous forest dominated by *Fagus sylvatica*, mown and non-mown grassland, gardens and camping sites. The experiment was carried out in a small patch (0.6 ha) of meadow dominated by tall grasses and *Cirsium arvense*. A total of ca 1100 flowering *C. arvense* stems (here 'individuals') were found in the entire patch. Within the patch, only few individuals of other insect-pollinated plants were found.

*Cirsium arvense* attracted many species of flower visitors, including several species of bumblebees, vespine wasps, butterflies, syrphid flies and other small and large dipterans, and the beetles *Rhagonycha fulva* and *Meligethes aeneus*. On the days of the experiment, however, *Apis mellifera* was, by far, the most dominant visitor. The majority of honeybees observed in the area were attracted to the flower heads of *C. arvense*. We selected an experimental patch of tall grass and *C. arvense*, which was surrounded on one side by newly mown grass, and on the other sides by *Fagus sylvatica* forest.

### *Cirsium arvense*

*Cirsium arvense* is a perennial herb with stems bearing several pink-purple, sweetly scented flower heads. The plant is usually dioecious, and spreads horizontally from rhizomes, forming clones of erect stems (Lloyd and Myall 1976, Heimann and Cussans 1996). Flowers are insect pollinated,

but the species reproduces both vegetatively and sexually (Lalonde and Roitberg 1994, Heimann and Cussans 1996). Seeds are 3 mm long, slightly tapered, have a pappus, and are dispersed by wind. The plant is native to Europe and temperate Asia, and invasive throughout the temperate zone (<www.issg.org>, Heimann and Cussans 1996). It is common and often dominant in pastures, roadsides, fences, and grass meadows, and is a noxious weed in e.g. cereal fields. In the latter case, *C. arvense* is often the only dominant insect-pollinated weed, and hence may act as nectar 'oasis' for bees in a 'desert' of grasses or cereals.

Within our study patch, nearly all stems were female (1060 female and 31 male stems), possibly representing only a few clones. A small patch of male stems was found, within an area of  $4 \times 4$  m, confined to one corner of the patch. These males were not included in the experiment.

### Experimental set-up

The experiment was carried out on the 6–8 of July 2009, in the early to mid flowering stage of *C. arvense*. Prior to the recording of plant–bee interactions, 62 honeybee individuals were marked in two trials (22 bees in the afternoon and 40 bees on the next morning, and then observation began the following day). Furthermore, 32 female plants were tagged within the study patch. For each plant, its height, number of flower heads and number of neighbouring plants within 40 cm were registered.

All flower–visitor observations were done during daytime (9 to 16 h) under favourable weather conditions (no rain, no strong wind,  $>20^\circ\text{C}$ ). An interaction between a plant and a bee individual was recorded as present, if the bee visited a flower head of the plant. Observations on flower visitation were carried out simultaneously by four observers, who each observed eight marked plants. One observer was placed in the middle and the other three at the periphery of the patch. Each observer registered all visits by marked bees to marked plants in 10 observation trials of 20 min each. Observation trials were separated by at least 15 min.

### Data analysis

#### Network parameters

We constructed a bipartite network of interacting individuals of plants and honeybees (an  $I$ – $I$  network). A bipartite network has two sets of nodes, which here are individuals of thistle plants and honeybees. Such a network may be represented as a qualitative or quantitative matrix, listing all observed links between plants and animals. If qualitative, each possible link between a plant and an animal is just scored as present or absent, i.e. all observed links get the same strength. If quantitative, the strength of each observed link is estimated, e.g. as the number of floral visits made by a given animal to a given plant during a given time span.

The frequency distribution of number of links (linkage level,  $k$ ) per individual reflects variation in level of generalization, i.e. individuals having few interaction partners are 'specialists', while individuals having many interaction partners are 'generalists'. Using the qualitative bipartite  $I$ – $I$

network, we made the cumulative distributions  $P(\geq k)$  of linkage level  $k$  per individual for both the plant and the bee assemblage. These distributions were fitted to three models using the statistical software JMP ver. 8.01: (1) exponential:  $P(\geq k) = \exp(-\gamma k)$ , (2) power-law:  $P(\geq k) = k^{-\gamma}$ , and (3) truncated power-law:  $P(\geq k) = k^{-\gamma} \exp(-k/k_x)$ , where  $\gamma$  is a constant and  $k_x$  is the truncation value (Jordano et al. 2003). The model with lowest SSE (error sum of squares) value was chosen as the best fit.

Estimates of link strength were obtained from the quantitative bipartite matrix: link strength  $d_{ij}$  of plant individual  $i$  on bee individual  $j$ , i.e. the fraction of visits by a particular bee  $j$  out of all visits received by a given plant  $i$ , and link strength  $d_{ji}$  of bee individual  $j$  on plant individual  $i$ , i.e. the fraction of visits paid to a particular plant  $i$  out of all visits paid to plants by a given bee  $j$  (Jordano 1987). Asymmetry among interacting pairs of individuals was calculated according to Bascompte et al. (2006):

$$AS(i, j) = \frac{d_{ij} - d_{ji}}{\max(d_{ij}, d_{ji})}$$

Thus  $AS = 0$  indicates no asymmetry, and  $AS = 1$  strong asymmetry.

#### Nestedness

Nestedness is a non-random pattern of links in a qualitative bipartite network, in which links of specialists are subsets of links of generalists (Bascompte et al. 2003, Dupont et al. 2003). Thus, in a nested network, the bulk of links are organized as a core among generalist nodes (Bascompte et al. 2003). In an  $I-I$  network, generalists are plants attracting many bee individuals, or bees visiting many plant individuals. We calculated and assessed level of nestedness of the  $I-I$  bipartite network using ANINHADO ver. 3 (Guimarães Jr. and Guimarães 2006). As a nestedness metric, we calculated both the commonly used matrix temperature ( $T$ ) (Atmar and Patterson 1993), and the newly developed  $NODF$  index, which is a more conservative measure of nestedness (Almeida-Neto et al. 2008). Significance of  $T$  and  $NODF$  were assessed against 10 000 randomizations using the null model proposed by Bascompte et al. 2003.

Furthermore, we obtained the idiosyncratic temperatures for all plant individuals using ANINHADO. Idiosyncratic temperature ( $it$ ) is the contribution of each plant (or bee) individual to the matrix nestedness temperature ( $T$ ), or its deviation from expectation if the matrix was perfectly nested. Hence, individuals with a low  $it$  have a high contribution to nestedness of their network. Average idiosyncratic temperature of all plant or bee individuals is equal to the matrix temperature  $T$ .

#### Modularity

Ecological modularity  $M$  is the degree to which a network is organized into sub-groups of highly inter-connected nodes that are less connected to nodes in other sub-groups, i.e. modules (Olesen et al. 2007, Dupont and Olesen 2009). We used the method of Guimerà and Amaral (2005), which is

based on simulated annealing, to test for modularity. Level of modularity

$$M = \sum_{s=1}^{N_M} \left( \frac{I_s}{I} - \left( \frac{k_s}{2I} \right)^2 \right), M \in \left[ 0; \left( 1 - \frac{1}{N_M} \right) \right]$$

where  $N_M$  is number of modules in the network,  $I$  is number of links in the network,  $I_s$  is number of links between species in modules ('within-module links') and  $k_s$  is the sum of the number of links of the species in module  $s$ . Significance of  $M$  was assessed relative to 100 randomizations of the network (for more details see Olesen et al. 2007).

#### Path length and clustering

To investigate pattern and importance of links between individuals of the same species, we analysed the link structure of unipartite networks. In unipartite networks, nodes consist of either plant or animal individuals, and a link connects a pair of conspecific individuals sharing at least one interaction partner, i.e. two plant individuals receiving visits by the same bee individual are linked to each other and so are two bees visiting the same plant individual. Unipartite networks are constructed using the software Pajek ver. 1.24 (Batagelj and Mrvar 2009).

Shortest path length  $l$  between two individuals in a unipartite network, is defined as the smallest number of steps (links) connecting the two. Clustering coefficient  $c$  for a bee or a plant in a unipartite network, is defined as the proportion of realized links between all the individuals to which the bee or plant are linked. Average shortest path length  $\langle l \rangle$  between all pairs of individuals and average clustering coefficient  $\langle c \rangle$  for all individuals were obtained using the software Pajek. The smaller  $\langle l \rangle$  and the higher  $\langle c \rangle$  are, the denser is the network (a "small world", Watts and Strogatz 1998), i.e. a disturbance will spread very fast through the entire network.

#### Plant characteristics

Effects of plant characteristics on linkage level ( $k$ ), average link strength  $\langle d \rangle$  and idiosyncratic temperature ( $it$ ) of plant individuals were investigated using regression analysis (R Cran ver. 2.10.0). The characteristics plant height, number of flower heads, number of neighbours within a circle of 40 cm radius, and total number of visits were used.

## Results

Of the 62 marked bees, 35 bees were later observed visiting the study plants. All marked plants received visits from at least one marked honeybee. Thus, our  $I-I$  network of honeybees visiting *Cirsium arvense* plants consisted of 32 plants, 35 bees and 317 interactions documented by 681 visits (Fig. 1). In general, about half of the bees observed to visit the thistles were marked.

Observed connectance (Table 1) was significantly higher than expected for a similar-sized  $S-S$  network ( $p < 0.05$ , i.e. outside the 95% confidence band for the regression of  $C$  on species number for  $S-S$  networks, using data from Olesen et al. 2007).

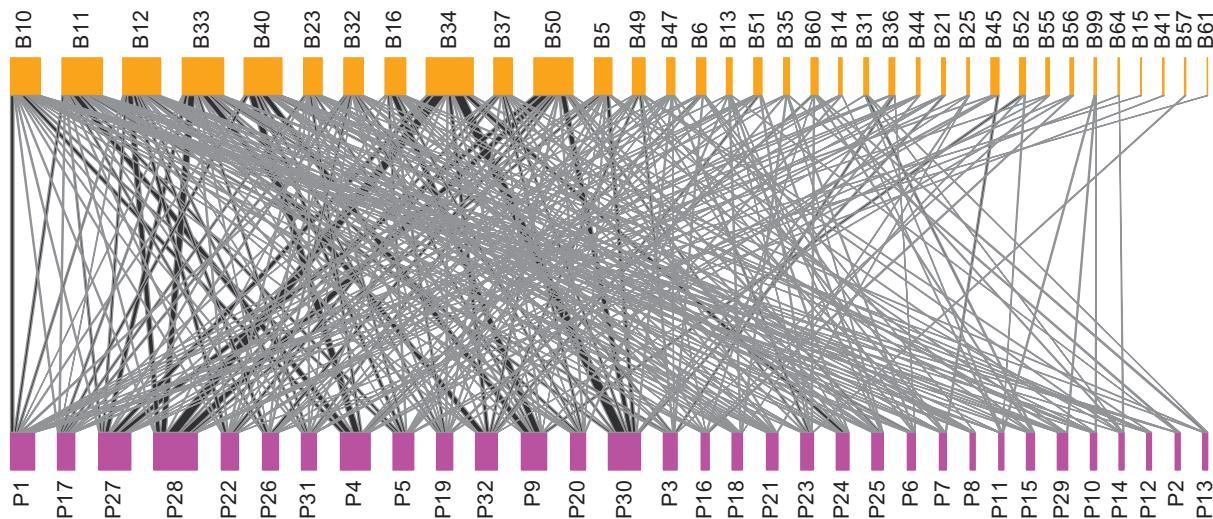


Figure 1. Bipartite network of plant (marked P) and honeybee (marked B) individuals. Individuals are sorted (left to right) according to decreasing linkage level. Width of box is proportional to the total number of visits observed for that individual. Lines connecting plants and bees denote links, and thickness of lines is proportional to the number of visits observed by a bee to a plant.

Average linkage level did not differ statistically significantly between plants and honeybees (average  $k_i = 9.9 \pm 3.1$  vs average  $k_j = 9.1 \pm 6.9$ ;  $F_{1,65} = 3.27$ ,  $p = 0.08$ ), whereas link strength was the same ( $d_{ij} = 0.11 \pm 0.14$  vs  $d_{ji} = 0.10 \pm 0.07$ ;  $F_{1,65} = 0.54$ ,  $p = 0.46$ ) (Table 1). Linkage level distributions of plants and bees had the best fit to a truncated power-law model (SSE = 0.0417 for plants, SSE = 0.018531 for bees), although the linkage level distribution of plants had an almost equally good fit to an exponential model (SSE = 0.018532). This is in accordance with S–S pollination networks, where 2/3 of a sample followed a truncated model, and 1/3 a pure power-law model (Jordano et al. 2003).

Frequency distributions of link strength were skewed to the right (skewness  $g_1 = 3.94$ ,  $t = 14.0$ ,  $p < 0.001$  for plants, and  $g_1 = 1.36$ ,  $t = 25.1$ ,  $p < 0.001$  for animals), i.e. low dependencies dominated (Fig. 2). Asymmetry values ( $AS$ ) ranged from 0 to 1 (average  $AS = 0.57 \pm 0.26$ , Fig. 2), thus many plant–animal interactions were asymmetrical. This is a general pattern, also observed in most mutualistic S–S networks (Vázquez and Aizen 2004, Bascompte et al. 2006, Vázquez et al. 2007). The matrix was highly significantly nested ( $T = 34.3$ ,  $p > 0.0001$ ;  $NODF = 43.2$ ,  $p > 0.0001$ ). Observed nestedness was highly significantly lower than expected for similar-sized S–S networks ( $p < 0.01$ , using data from Olesen et al. (2007) as a comparative statistical population). However, the network was not significantly modular ( $M = 0.243$ ;  $M_{rand} = 0.249 \pm 0.0062$ ,  $p > 0.05$ ).

The unipartite versions of the network were densely connected (Fig. 3), i.e. with a very high link density ( $q$ ), short average path length ( $\langle l \rangle$ ) and high average clustering coefficient ( $\langle c \rangle$ ) (Table 1).  $d$  for both the plant and the animal unipartite networks was significantly higher than similar-sized S–S network ( $p < 0.05$ ), whereas  $\langle l \rangle$  and  $\langle c \rangle$  were within the confidence bands of the regression lines of  $\langle l \rangle$  or  $\langle c \rangle$  on species number (using data on S–S networks from Olesen et al. (2006), as comparative statistical populations). In particular, the plant unipartite network was almost fully connected (Table 1).

### Plant attributes

In multiple regressions using the predictors plant height, number of flower heads and nearest neighbours, only number of flower heads was retained as a significant predictor of plant link number (AIC = 153.65) and idiosyncratic temperature (AIC = 298.86, Table 2). Average plant interaction strength was significantly associated only with plant height (AIC = −109.79).

Inflorescence height, number of flowers, and nearest neighbours were not significantly correlated ( $p > 0.05$ , although tall plants tended towards more flower heads ( $p = 0.06$ )). Total number of visits per plant was significantly associated with number of flower heads (linear regression:  $b = 1.71$ ,  $F = 26.34$ ,  $p < 0.0001$ ,  $R^2 = 46.8\%$ ),

Table 1. Properties of a thistle individual–honeybee individual network.

Network mode	Network property	Parameter	Plants	Animals
Unipartite	Link density	$q$	0.97	0.70
	Average path length	$\langle l \rangle$	$1.03 \pm 0.32$	$1.30 \pm 0.48$
	Average clustering coefficient	$\langle c \rangle$	$0.97 \pm 0.023$	$0.85 \pm 0.11$
Bipartite	Connectance	$C$	0.28	
	Average linkage level	$\langle k \rangle$	$9.1 \pm 6.9$	$9.9 \pm 3.1$
	Average link strength	$\langle d \rangle$	$0.11 \pm 0.14$	$0.10 \pm 0.07$



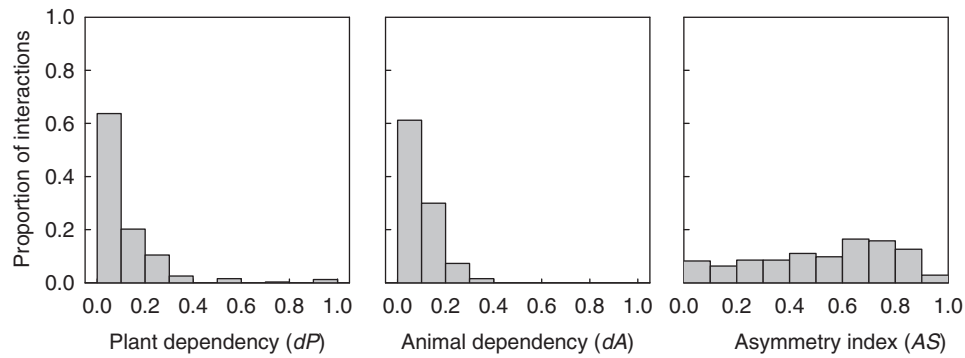


Figure 2. Dependencies of plants on bees ( $dP$ ) and bees on plants ( $dA$ ), and asymmetry index ( $AS$ ).

inflorescence height (linear regression:  $b = 0.78$ ,  $F = 14.02$ ,  $p < 0.0008$ ,  $R^2 = 31.9\%$ ), and nearest neighbours (linear regression:  $b = 2.96$ ,  $F = 6.53$ ,  $p < 0.01$ ,  $R^2 = 18.0\%$ ). Spatial configuration of plants within the patch appeared to have an influence on interaction structure. The plant stems having most flower heads, and which were also the most attractive to honeybees, were mostly found in the upper/central part of the patch.

## Discussion

### Properties of individual–individual (I–I) and species–species (S–S) networks

S–S pollination networks are small worlds because of their short average path length and high average clustering

coefficient, i.e. all species are in close mutual contact (Strogatz 2001, Olesen et al. 2006). Some of the parameters (average linkage level, average path length, average clustering coefficient, modularity, asymmetry distribution) of the thistle–honeybee *I–I* network had values within the range of similar-sized S–S pollination networks, others were smaller (nestedness) and others again larger (connectance  $C$  in bipartite and link density in unipartites). This indicates that *I–I* networks may be denser and more connected than S–S networks, i.e. *I–I* networks are even smaller small worlds than S–S networks (Olesen et al. 2006). This result supports our hypothesis. Thus network patterns change at lower hierarchical levels, mainly because of a higher  $C$ . The *I–I* network was non-modular, as expected because of its small size (67 individuals). In a study encompassing 51 S–S networks, networks smaller than 50 species were never significantly modular or rephrased – they were indeed

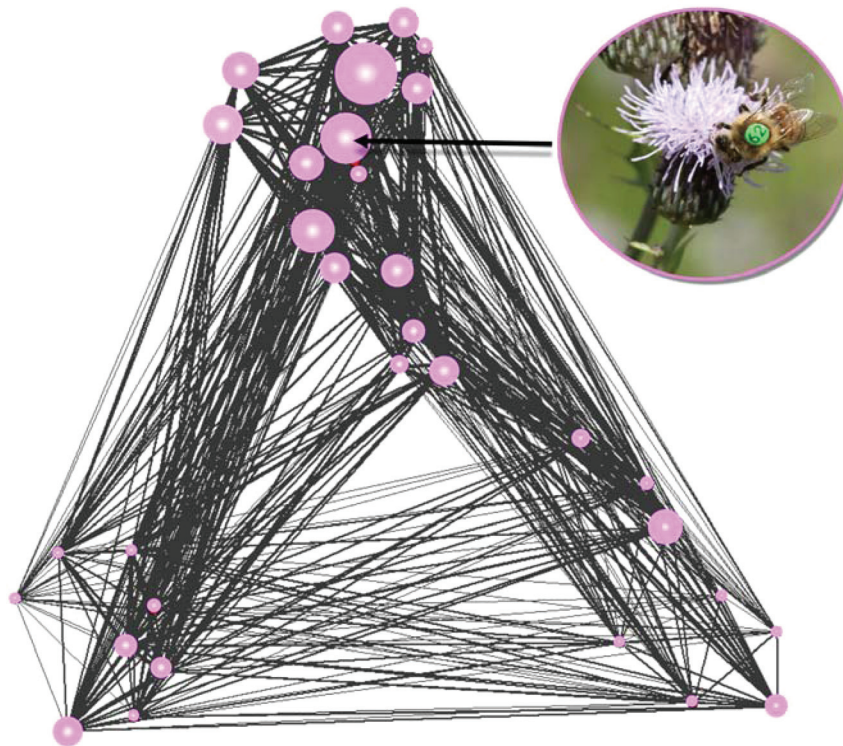


Figure 3. Unipartite network of plants (circles) with their spatial location in the study patch. Size of circles is proportional to their number flower heads, and thickness of links is proportional to the number of visiting bees shared by a pair of plants.

Table 2. Stepwise regressions (p to enter = 0.1 and to leave = 0.05). Slope only for significant predictors.

Dependent variable (transformation)	Plant height (slope)	No. flower heads (slope)	No. neighbours (slope)	SS	F	p	R <sup>2</sup> (%)
Plant linkage level (none)		0.34		113.67	18.04	0.0002	37.6
Plant idiosyncratic temperature (ln)		-0.062		3.83	5.76	0.03	16.1
Plant link strength (ln)	0.021			1.48	10.48	0.0003	25.9

modular, but they only consisted of one module or part of one module (Olesen et al. 2007). Skewed frequency distributions of link strength and asymmetry are common features of *S-S* pollination networks, which to some extent is a derived property of nestedness (Jordano 1987, Vázquez and Aizen 2004, Bascompte et al. 2006). Thus, not surprisingly, our nested *I-I* network also showed skewed frequency distributions of link strength. However, in contrast to *S-S* networks, where link strength of animals is more skewed than that of plants (Jordano 1987), skewness of plant individuals were stronger than that of animals. This is, without doubt, partly caused by a lower ratio of interacting animals and plants (~1, compared to 3–6 in *S-S* networks, Olesen et al. 2006). In at least some *S-S* networks, the distribution of abundance among species contributes to generate an asymmetric structure, if abundant species form more links and have stronger effects on their interaction partners (i.e. the partners have higher link strength) than less abundant species (Vázquez et al. 2007). Asymmetry in the *I-I* network may be associated with a skewed distribution of floral display size (i.e. number of flower heads and inflorescence height).

### Plant-mating networks

*I-I* pollination networks may be regarded as detailed road maps of pollen flow in plant populations (Fortuna et al. 2008). However, the efficient pollen flow pattern in *Cirsium arvense* must be very complicated, because of its strong clonality and female-biased dioecy (Lalonde and Roitberg 1994, Heimann and Cussans 1996). Our study of the *Cirsium*-honeybee *I-I* network shows that all plants in the patch were highly connected, and that nearly all flowering stems were linked to at least one visiting bee. Thus, even a small number of male stems are likely to be included into the network, securing pollen to females, assuming that male flower heads are equally attractive to honeybees. Generally, reported minimum distances for unlimited seed set in *C. arvense*, i.e. no pollen limitation, range from 16.5 to several hundred meters (Heimann and Cussans 1996). In our study patch, the most distant, yet linked plant stems were only approximately 13 m apart. On the other hand, we only very rarely observed marked bee individuals visiting flowers outside the experimental patch, suggesting an effect of isolation and that all stems and their bees constituted one single module (Olesen et al. 2008).

### Individual foraging behaviour and *S-S* network

The honeybee is probably the world's most generalized flower-visitor species, e.g. at a Greek phrygana it visits more than one hundred plant species (Petanidou 1991). Colonies regularly

exploit floral resources up to 10 km from their nest (Visser and Seeley 1982) and can rapidly locate resource-rich patches because of their advanced communicating waggle dance, in which recruits are guided to resources of food found by scouts (Frisch 1967). However, generalist species may consist of individuals varying in their level of specialization (Araújo et al. 2008). Exactly how individuals in a population of a species partition resources is poorly known. Araújo et al. (2010) studied this for an opossum species and showed that individual diet width was nested, i.e. choosy individuals consumed food items also explored by more omnivorous individuals. However, the linkage pattern may be analyzed in different ways: species-species, species-individuals, individuals-species and individuals-individuals. Araújo et al. (2010) looked at individual opossums foraging on different prey taxa, whereas we here are looking at individual thistles-individual bees. These hierarchical link patterns need much more study. We observed a nested link pattern indicating that a few bees visited many thistles, whereas most bees only visited a few. A few scout bees and many workers, and a few large thistles and many small ones may contribute significantly to this pattern. Scouts are highly generalized individuals, exploring many flower resources, while their recruits are guided to the most rewarding flower individuals or patches, and hence are expected to behave as patch specialists, at least during a shorter time-span (Seeley 1983, Wells and Wells 1983). Sixty-two bees were tagged and 35 of these were sighted again the following days. Thus, maybe the 27 'lost' bees visited other thistle plants or different plant species outside the study area, whereas the 35 re-sighted ones might be regarded as thistle and patch specialists, and among these, a large proportion might be sub-patch or even single-thistle stem constant. Variation in pollination specialization at the individual level is much less known than at the species level. Trap-lining animals repeat specific foraging paths, e.g. hummingbirds and tropical bees (Janzen 1971). Bumblebees, too, may learn the location of individual plants and follow specific foraging paths (Manning 1956). Honeybees can be patch specific, and has been observed to re-visit rewarding inflorescences on several foraging trips (McGregor et al. 1959).

Our description of an *I-I* pollination network has important implications for the understanding of *S-S* pollination networks and ecological networks in general. For example, in an Arctic network (Olesen et al. 2008), 23% of all flower-visitor species were only observed once, i.e. only one individual was observed to visit one plant individual. Thus ¼ of this *S-S* pollination network is, in fact, based on insect individual-plant individual data. This figure is probably representative for many other networks as well, both mutualism networks and food webs.

The current *I-I* network of *Cirsium* and honeybees were densely connected. However, links of more sparsely visited/visiting individuals may be missed, if e.g. individuals of a particular plant species in the sampling area of a network study do not possess attractive traits, resulting in a high rate of visitation (e.g. large floral display as in *C. arvense*). As a consequence, attributes of nodes can affect the entire topology of the network (Bianconi et al. 2009). Thus, characteristics of individuals of both plants and animals participating in the network at a given site will to some extent cascade up and affect the *I-I* and *S-S* network structure. This may also account for some of the spatial and/or temporal variation of empirical pollination networks, which have been observed repeatedly (Olesen et al. 2008, Dupont et al. 2009).

Thus we need much more research at this interface between foraging theory of individuals and ecological network theory.

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## References

- Albert, R. et al. 1999. The diameter of the world-wide web. – *Nature* 401: 130–131.
- Almeida-Neto, M. et al. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. – *Oikos* 117: 1227–1239.
- Araújo, M. S. et al. 2008. Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. – *Ecology* 89: 1981–1993.
- Araújo, M. S. et al. 2010. Nested diets: a novel pattern of individual-level resource use. – *Oikos* 119: 81–88.
- Atmar, W. and Patterson, B. D. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. – *Oecologia* 96: 373–382.
- Barabási, A.-L. and Albert, R. 1999. Emergence of scaling in random networks. – *Science* 286: 509–512.
- Bascompte, J. et al. 2003. The nested assembly of plant-animal mutualistic networks. – *Proc. Natl Acad. Sci. USA* 100: 9383–9387.
- Bascompte, J. et al. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. – *Science* 312: 431–433.
- Batagelj, V. and Mrvar, A. 2009. Pajek – program for large network analysis. – <http://vlado.fmf.uni-lj.si/pub/networks/pajek/>.
- Bianconi, G. et al. 2009. Assessing the relevance of node features for network structure. – *Proc. Natl Acad. Sci. USA* 106: 11433–11438.
- Dunne, J. A. et al. 2002a. Food-web structure and network theory: the role of connectance and size. – *Proc. Natl Acad. Sci. USA* 99: 12917–12922.
- Dunne, J. A. et al. 2002b. Network structure and biodiversity loss in food webs: robustness increases with connectance. – *Ecol. Lett.* 5: 558–567.
- Dupont, Y. L. and Olesen, J. M. 2009. Ecological modules and roles of species in heathland plant-insect flower visitor networks. – *J. Anim. Ecol.* 78: 346–353.
- Dupont, Y. L. et al. 2003. Structure of a plant-flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. – *Ecography* 26: 301–310.
- Dupont, Y. L. et al. 2009. Spatio-temporal variation in the structure of pollination networks. – *Oikos* 118: 1261–1269.
- Fortuna, M. A. et al. 2008. Spatial mating networks in insect-pollinated plants. – *Ecol. Lett.* 11: 490–498.
- Fortuna, M. A. et al. 2009. The roosting spatial network of a bird-predator bat. – *Ecology* 90: 934–944.
- Fortuna, M. A. et al. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? – *J. Anim. Ecol.* 79: 811–817.
- Frisch, K. v. 1967. The dance language and orientation of bees. – Belknap Press of Harvard Univ. Press.
- Guimarães Jr., P. R. and Guimarães, P. R. 2006. Improving the analyses of nestedness for large sets of matrices. – *Environ. Modell. Softw.* 21: 1512–1513.
- Guimerà, R. and Amaral, L. A. N. 2005. Functional cartography of complex metabolic networks. – *Nature* 433: 895–900.
- Heimann, B. and Cussans, G. W. 1996. The importance of seeds and sexual reproduction in the population biology of *Cirsium arvense* – a literature review. – *Weed Res.* 36: 493–503.
- Ings, T. C. et al. 2009. Ecological networks – beyond food webs. – *J. Anim. Ecol.* 78: 253–269.
- Janzen, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. – *Science* 171: 203–205.
- Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. – *Am. Nat.* 129: 657–677.
- Jordano, P. et al. 2003. Invariant properties in coevolutionary networks of plant-animal interactions. – *Ecol. Lett.* 6: 69–81.
- Krause, J. et al. 2007. Social network theory in the behavioural sciences: potential applications. – *Behav. Ecol. Sociobiol.* 62: 15–27.
- Lalonde, R. G. and Roitberg, B. D. 1994. Mating system, life-history, and reproduction in Canada thistle (*Cirsium arvense*; Asteraceae). – *Am. J. Bot.* 81: 21–28.
- Lloyd, D. G. and Myall, A. J. 1976. Sexual dimorphism in *Cirsium arvense* (L.) Scop. – *Ann. Bot.* 40: 115–123.
- Lusseau, D. et al. 2008. Incorporating uncertainty into the study of animal social networks. – *Anim. Behav.* 75: 1809–1815.
- Manning, A. 1956. Some aspects of the foraging behaviour of bumblebees. – *Behav.* 9: 73.
- McGregor, S. E. et al. 1959. Bee visitors to *Saguaro* flowers. – *J. Econ. Entomol.* 52: 1002–1004.
- Montoya, J. M. and Solé, R. V. 2002. Small world patterns in food webs. – *J. Theor. Biol.* 214: 405–412.
- Olesen, J. M. et al. 2006. The smallest of all worlds: pollination networks. – *J. Theor. Biol.* 240: 270–276.
- Olesen, J. M. et al. 2007. The modularity of pollination networks. – *Proc. Natl Acad. Sci. USA* 104: 19891–19896.
- Olesen, J. M. et al. 2008. Temporal dynamics in a pollination network. – *Ecology* 89: 1573–1582.
- Perkins, S. E. et al. 2009. Comparison of social networks derived from ecological data: implications for inferring infectious disease dynamics. – *J. Anim. Ecol.* 78: 1015–1022.
- Petanidou, T. 1991. Pollination ecology in a Phryganean ecosystem. – PhD thesis, Aristotelian Univ., Thessaloniki.
- Ravasz, E. and Barabási, A. L. 2003. Hierarchical organization of complex networks. – *Phys. Rev. E* 67: 026112.
- Seeley, T. D. 1983. Division of labor between scouts and recruits in honeybee foraging. – *Behav. Ecol. Sociobiol.* 12: 253–259.
- Solé, R. V. and Montoya, J. M. 2001. Complexity and fragility in ecological networks. – *Proc. R. Soc. Lond. B* 268: 2039–2045.

- Strogatz, S. D. 2001. Exploring complex networks. – *Nature* 410: 268–276.
- Vázquez, D. P. and Aizen, M. A. 2004. Asymmetric specialization: a pervasive feature of plant–pollinator interactions. – *Ecology* 85: 1251–1257.
- Vázquez, D. P. et al. 2007. Species abundance and asymmetric interaction strength in ecological networks. – *Oikos* 116: 1120–1127.
- Visser, P. K. and Seeley, T. D. 1982. Foraging strategy of honeybee colonies in a temperate deciduous forest. – *Ecology* 63: 1790–1801.
- Waltho, N. and Kolasa, J. 1994. Organization of instabilities in multispecies systems, a test of hierarchy theory. – *Proc. Natl Acad. Sci. USA* 91: 1682–1685.
- Watts, D. J. and Strogatz, S. H. 1998. Collective dynamics of ‘small-world’ network. – *Nature* 393: 440–442.
- Wells, H. and Wells, P. H. 1983. Honey bee foraging ecology: optimal diet, minimal uncertainty or individual constancy? – *J. Anim. Ecol.* 52: 829–836.
- Williams, R. J. et al. 2002. Two degrees of separation in complex food webs. – *Proc. Natl Acad. Sci. USA* 99: 12913–12916.