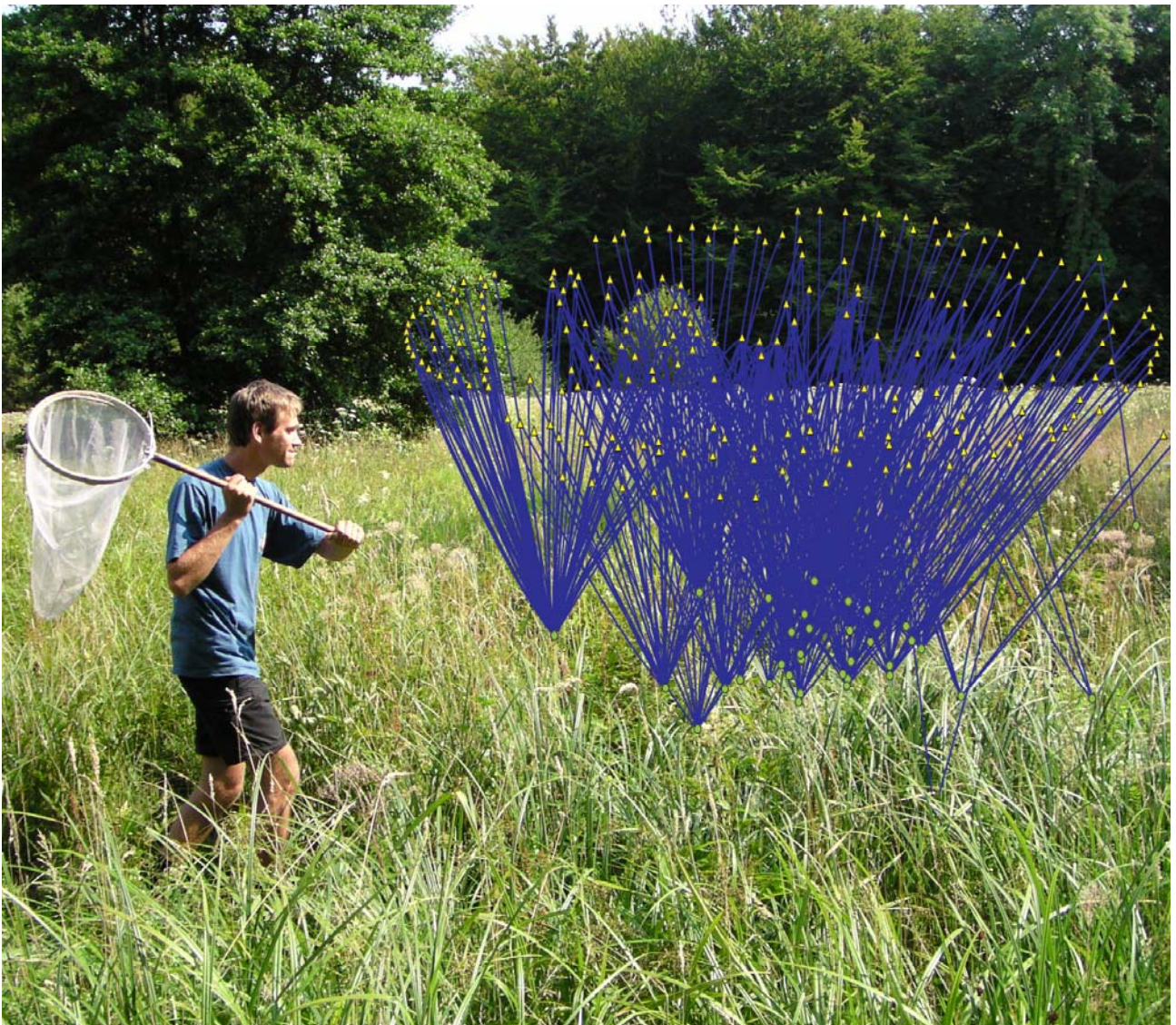


# A pollination network from a Danish forest meadow

Danish title: Et bestøvningsnetværk fra en dansk skoveng

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## General introduction

Joseph Gottlieb Kölreuter (1761) was the first to fully recognise the role insects play in the sexual reproduction of plants, while they are collecting nectar for nourishment. His successor Christian Konrad Sprengel discovered that plants can be generalised or specialised in their pollination, when he observed that some plant species were pollinated by a great variety of species while other were visited by one pollinator species only, he linked these observations to diversity of floral phenotypes. Charles Darwin, influenced by both scientists, placed the science of pollination in an evolutionary framework (Waser 2006). Darwin (1862) found the long-spurred orchid *Angraecum sesquipedale* and predicted that a pollinator existed which had a long tongue in order to match the long spur of the orchid. When the moth *Xanthopan morgani f. praedicta* was found, the most famous example of mutualistic co-evolution was born. Since then pollination interactions have been considered textbook examples of mutualistic interactions (Jordano 2006). As a consequence there has been a shortage of studies considering the ecology of entire pollination communities (Memmott 1999). In recent years an increasing number of studies have collected and analyzed large, highly resolved pollination networks. However most of these studies cumulate the data of the entire study period, thus hiding information of temporal variation in the network structures (Kaiser 2006). In this thesis, I investigate the strength and weaknesses of the cumulative network analytical approach, and used a method of temporal network analysis I call timeslice network analysis. Chapter 1 contains an analysis of the pollination network of the forest meadow Moesgaard Have, using both approaches, and comparing, cumulative and timeslice networks. Chapter 2 is a more detailed study of cumulative network analyses using the data from Moesgaard Have, with special attention to the methods vulnerability to variation in sampling effort. In chapter 3 the temporal variation of the Moesgaard Have data are analyzed and used to investigate aspects of timeslice networks analysis.

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# Chapter 1

## An analysis of the plant-pollinator network of the forest meadow Moesgaard Have



**Foto:** *Helophilus pendulus* visiting *Angelica sylvestris*

by Søren Bek

## Introduction

Network analysis has been used in the social sciences since the 1930s, as a way to process complex data. In 1990 the interest for using network analysis began to grow rapidly and has now spread to many other scientific disciplines (Carrinton 2005).

A network consists of vertices connected by edges. In ecological networks the species are shown as vertices, and the edges illustrate the interactions, or links between species.

In a pollination network there are two kinds of vertices, plants and pollinators, and the edges always run between these two. This is called a two-mode network. A pollination network is usually constructed, by pooling observations found in a study season. This is here termed a cumulative network.

In network analysis it is usually assumed that all vertices are capable of interacting. In a pollination network, this means that all pollinator species are capable of interacting with all plant species. This is rarely the case. Different phenological or morphological characters of the species can make interactions impossible. Such interactions are forbidden, and an example could be that a plant species does not flower, while a pollinator species is present (Jordano, Bascompte et al. 2003; Medan 2006). To eliminate the forbidden interactions, that arise when flowers and pollinators do not overlap in time, a timeslice network can be constructed for each field day, on the basis of the two following premises:

1. A species will be considered present in the study area in the entire period between the first and last observation.
2. An observed interaction between a plant and a pollinator is active in the entire period between the first and the last observation where both species are present.

A timeslice network portrays the ecological network in the moment in time where the observations were made, and series of timeslice networks will reveal the temporal dynamic of the ecosystem. The scope of this chapter is to describe the pollination ecology of the forest meadow Moesgaard Have. This is done using two analytical approaches; the cumulative network and the timeslice networks. The advantage of each approach and the comparison of the two approaches will be evaluated. In the description of the pollination system special emphasis will be laid on the taxonomical composition of the pollinators, and the relationship between plant phenology and generalization.

## Methods

### Study area

I conducted my studies in a 10,000 m<sup>2</sup> large meadow called “Moesgaard Have”, located south of Aarhus, Denmark, (N 56°04'879'' E 10°13'886''). Denmark has a temperate coastal climate.

Moesgaard Have was, at the time of the study, managed by “Aarhus Amt - Natur og Miljø”. The meadow is cut every year in the beginning of August, to prevent the succession of the meadow into forest. Harvested plant matter is removed in order to counteract any eutrophication of the meadow (“Natur- og Miljø Worker pers. com.).

The meadow is surrounded on three sides by mixed deciduous forest, composed mainly of *Fagus sylvatica*. In the spring *Anemone nemorosa* dominates the understory. In the summer the canopy is dense and only a few herbaceous plants are present in the understory. There is some *Galium odoratum*, and a few other sparsely scattered flowering plants. To the west the meadow is bordered by a row of trees dividing it from an intensely cultivated field. From the cultivated field a small stream is running into the meadow flooding the lower parts, probably contributing to the eutrophication of the meadow. In the forest, a few meters south of the meadow the larger stream “Giberå” runs.

In the meadow a few trees are present: *Corylus avellana*, *Fraxinus excelsior*, *Malus* sp., and *Prunus cerasifera*, the latter two have a great influence on the meadow's pollination community in the spring because they have an intense blooming, but they are for practical reasons not included in this study. Along the northern forest edge *Rubus fruticosus* is found, a species that is also excluded from the investigation. In the spring, the meadow is dominated by different species of *Poa* and *Carex*. In the wet parts there also grows *Urtica dioica*. During the summer *Cirsium vulgare*, *C. oleraceum*, *Filipendula ulmaria*, and *Pimpinella major*, and towards the end of the field study, *Angelica sylvestris* become dominant.

All herbaceous insect pollinated plant species, flowering at the time of the investigation were observed (For a complete list of the plant species see table 1).

The studies were conducted in the period from 07-Jun to 04-Aug 2003.

One or more plant individuals were observed for a period of 15 min, all insects that landed on the flowers were collected, with the exception of some butterflies identified in the field. The insects were captured with a plastic beaker with an opening diameter of 3 cm, or by a net. They were transferred to labelled plastic tubes for later identification. The insects were identified to species if

possible, or grouped as morpho-species. Females of the genus *Sphaerophoria* not identifiable with the available literature, were grouped with the identifiable males based on similarities in size.

*Sphaerophoria* females less than 8 mm in length were included into *S. taenata*, females of 8 mm or larger were included into *S. scripta*. A few insects escaped before they could be captured causing a small bias in the data, in favour of the butterflies identified in the field.

Each plant species was observed several times during the field study and at different times of the day.

Juvenile insects and species of Thysanoptera were excluded from the study.

All insects found on a flower were termed pollinators (for a complete list of pollinator species see table 2).

The nomenclature used in this chapter follows the ones used in the identification literature (for the complete list of identification literature, see table 3).

### **Vegetation analyses**

Two vegetation analyses were conducted in the year 2006. One in the first half of the season on June 30, and one in the second half of the season on July 27. These results are believed to be valid for the year 2003 too.

Ten randomly chosen plots of a size of 1\*1 meters were examined and the number of stems with open flowers was counted, and the plant species identified. Species that did not have a distribution sufficiently scattered to become included in the 10 randomly chosen plots, were examined in five (30/06) and six (27/07) non random plots.

For each plant species the following was noted; the average number of inflorescences on the stem, the number of open flowers on the inflorescence and the diameter of the inflorescence. In species with solitary flowers or a loose inflorescence, the number of flowers on the stem and the diameter of the flower were scored. From these data the average flower area per m<sup>2</sup> were calculated for each plant species.

### **Network analysis**

In the following only present-absent data are used. Any abundance data were discarded, so that a rare pollinator species collected only once have the same appearance as an abundant specialist collected several times, on the same plant species. Thus it is not possible to see the difference between rarity and specialization.



The data in a two-mode network can be presented in a “presence absence matrix”, where data on each plant species are presented in a column (i) and each pollinator species in a row (j). If there is an interaction between species (i) and species (j),  $a_{ij}=1$ . If there is no interaction  $a_{ij}=0$ .

A timeslice is constructed not only from the observations of the corresponding field day, but also the previous and coming observations. This has the consequences that the networks in the beginning and near the end of the study season are made from a weaker dataset than the networks in the centre of the study season. Discarding the first four and the last four timeslice networks minimize these errors. In this chapter the average values of the timeslice networks are analysed rather than the individual timeslice networks.

Both the cumulative and the averaged timeslice network are described by the following characteristics:

1. The total number of plant species (P) observed during my survey.
2. The total number of pollinator species (A) found throughout the observation period.
3. The network size (S) = A+P.
4. The number of possible interactions (M) = A\*P.
5. The plant: pollinator ratio (A/P).
6. The observed interactions (I).
7. The percentage of realized Interactions, called the connectance (C) =  $I*100/M$
8. The number of pollinator species visiting a plant species ( $L_n$ ).
9. The number of plants species which a pollinator species visits ( $L_m$ ).
10. The nestedness temperature (Nt).

(Olesen, Bascompte et al. 2006)

The network characteristics of the cumulative network and the average timeslice network are calculated, and the two network types are compared.

### **Connectance**

Connectance is a measure of the density of links in the network (Jordano 2006). Comparison of different networks has shown a negative correlation between network size and connectance (Olesen and Jordano 2002).

## Nestedness

A matrix is nested if it has a structure where the most specialized species is linked to the most generalized species, so that the links of a vertex are a subset of the links of more connected vertices. The nestedness temperature is a measure of the degree of nestedness from 0° for a perfectly nested pattern, to 100° for a complete chessboard pattern (Figur 1). The matrix was tested for nestedness using the freeware program *aninhado* available from the website: <http://aics-research.com/nestedness/tempcalc.html>. The program packs the matrix to optimal nestedness by rearranging rows and columns to minimize the numbers of unexpected absences and presences, using the algorithm developed in an earlier program *nestedness calculator* available from the website: <http://aics-research.com/nestedness/tempcalc.html> (Guimarães Jr. P; Atmar 1995). (For further discussion of the best way of packing a matrix for nestedness analysis see (Rodríguez-Gironés and Santamariá 2006)).

In order to distinguish between real nested networks and random structures, the program also performs 1000 Monte Carlo simulations on the data using four null models: Er, Co, Li and Ce. The null models have the same dimensions, columns, rows and interactions as the matrix tested, and all columns and rows have at least one interaction.

- Er: all cells are randomly assigned the value  $a_{ij}=1$  by the probability found in the network  $p(C)$ .
- Co: is arranged by columns, so  $a_j=1$  by the probability  $p_{(j)} = L_j/A$ , where  $L_j$  are the number of observed interactions in column  $j$ .
- Li: is arranged by rows, so  $a_i=1$  by the probability  $p_{(i)} = L_i/P$ , where  $L_i$  are the number of observed interactions in column  $i$ .
- Ce: all cells have an individual probability that  $a_{ij}=1$ ,  $(p_{(j)} + p_{(i)})/2$ .

(Guimarães Jr. P).

Here, all nestedness temperatures are tested against the null models Er and Ce, and the matrix are accepted as nested, if  $N_t$  differ from the null models by  $p \leq 0.05$ .

## The composition of pollinators

All pollinators were grouped into orders. For each order, number of species, percentage of all species, number of interactions, percentage of all interactions and interactions per species, were calculated.

All Dipterans were grouped into families. For the five largest families, number of species, percentage of all Dipteran species, number of interactions, percentage of all interactions including Diptera and interactions per species, were calculated.

To see the taxonomical composition of the most generalist pollinator species, all species with a  $L_m \geq 10$  were found.

The importance of Dipterans as pollinators increases with latitude. Elberling and Olesen (1999) proposed three formulas to explain the relationship between latitude and pollinator composition. One explain the proportion of Diptera species of all pollinators, the two others explain the proportion of the Diptera families muscidae and empididae respectively. To examine if this network differs from the expected pollinator composition, the proportions found here were compared to the model's prediction of this latitude.

The analyses mentioned in this section were made only on the cumulative network. The Diptera species as percentage of all pollinator species in the cumulative network were compared to the results of the individual timeslice networks, to see if the results were stable throughout the season.

### **Flower phenology and plant generalisation level**

If pollinators choose the plant they pollinate indiscriminately, plants with the longest flowering period and greatest abundance would be expected to receive visits from more pollinator species than others.

To examine the relationship between the flower area of the plant species, and the plants generalisation level, the average flower area from the vegetation analysis was tested against  $L_n$  in a regression analysis.

To examine the relationship between flower period and the plants generalisation level, the length of the period from the first day a plant species was observed in flower, to the last day, were recorded and tested against  $L_n$  in a regression analysis.

## Results

### Vegetation analysis

In the vegetation analysis 25 plant species was observed, thus covering most of the 37 plant species observed in the pollination study. Thirteen of the 25 plant species were found in the random plots. About half of the plants had a uniform distribution covering most of the study site, while the rest had a patchy distribution, being very abundant in small areas and nearly absent from the rest of the study site. In the early (30/06) vegetation analysis of the random plots, the averaged flower area was  $1.93 \cdot 10^4 \pm 4.99 \cdot 10^8 \text{ mm}^2 \text{ per m}^2$ , in the late (27/07)  $2.59 \cdot 10^4 \pm 5.97 \cdot 10^8 \text{ mm}^2 \text{ per m}^2$ . In the 11 non random plots of the two analyses the flower area varied from  $6.46 \cdot 10^3$  to  $1.77 \cdot 10^5 \text{ mm}^2 \text{ per m}^2$ . The plant species found in the vegetation analyses are listed in table 1.

### The properties of the cumulative networks

During the course of the investigation, 226 species of pollinators (A) were caught on 37 different plant species (P). This produces a network size (S) of 263 and a A/P ratio of 6.11 pollinator species per plant species.

I observed 590 interactions (I) between animals and plants, which produce a connectance C of 7.06%. Each plant was visited by an average of  $\langle L_n \rangle = 16.0 \pm 15.2$  pollinators. The minimum and maximum number of pollinator species visiting a plant species was 1 and 80 respectively. Each pollinator visited an average of  $\langle L_m \rangle = 2.6 \pm 3.6$  plant species, the minimum was 1, and the maximum was 24.

The nestedness temperature was 6.62, which was significantly different from the null models ( $p \leq 0.05$ ).

### The properties of the timeslice networks

The average values from the timeslice networks, minus the first and last two days were:

$A = 49.2 \pm 15.8$ ,  $P = 23.1 \pm 1.4$ ,  $S = 72.3 \pm 15.6$ ,  $A/P = 2.1 \pm 0.8$ ,  $I = 206 \pm 64$ ,  $C = 18.2\% \pm 1.32$ ,  $\langle L_n \rangle = 8.97 \pm 2.89$ ,  $\langle L_m \rangle = 4.20 \pm 0.42$ , and  $Nt = 20.5 \pm 4.3$ . All Nt-values were significantly different from values produced by the null models ( $p \leq 0.05$ ).

The maximum number of pollinator species found in any timeslice network was 86, and the maximum number of plant species was 25.

### **The composition of pollinators**

The most dominant order of pollinators was the Diptera, which was represented by 131 species or 58% of all pollinator species. After Diptera in descending order comes Hymenoptera with 38 species (17%), Coleoptera with 27 species (12%), Lepidoptera with 17 species (8%), and Hemiptera with 13 species (6%). The Diptera had an  $\langle L_m \rangle$  of 2.60, which is close to the total  $\langle L_m \rangle$  of 2.6. The most generalized insect order was Lepidoptera, that had an  $\langle L_m \rangle$  of 3.88 (table 4).

The most prominent Diptera family was Syrphidae being represented by 39 species or 30% of all Diptera species, being responsible for 50% of the Dipteran interactions (table 5). The importance of Diptera increased during the season. In the beginning of the season, 40–50% of the species were dipterans, and towards the end of the season as much as 60-70% of the species were dipterans.

Nine pollinator species had an  $L_m \geq 10$ . These represented the orders Diptera, Hymenoptera, Coleoptera and Lepidoptera. The two most connected species, both with an  $L_m$  of 24, were both members of the family Syrphidae (table 6).

The three formulas to explain the relationship between latitude and pollinator composition (Elberling and Olesen 1999), were calculated for the latitudinal value 56. The results are: 58% of all pollinator species should be Dipterans, 15% of all Dipteran species should be Muscidae and 5% Empididae. In this study the results are 58%, 15% and 8%, respectively.

### **Flower phenology vs. plant generalisation**

There were some non significant positive correlational trends found between the averaged flower area for the 13 plant species in the random plots of the vegetation analysis, and the number of visiting pollinator species ( $L_n$ ) (Figur 2). There was no significant correlation between the number of days the plants flowered and  $L_n$  (Figur 3).



## **Discussion**

### **Vegetation analysis**

The vegetation composition is dynamic, both spatially and temporally. The spatial dynamic is due to both biological and physical conditions of the study area, e.g. the shadows of the trees, and the interspecific competition between plant species and the streams running through the area influencing the surrounding vegetation. The temporal dynamics is due to the different flowering seasons of the different plant species, and differences in the way the plants bloom throughout their season. The latter because some have their peak flowering in the beginning of their season, while others have a normally distributed flowering. A through vegetation analysis would have to be conducted in a large proportion of the study area and every day of the study season. However, such a through analysis would disturb the pollination. The vegetation analysis shows a rough picture of a meadow with about half of the plant species included in the study, more or less uniformly distributed throughout the study area, and a number of plant species distributed in one or more, sometime very dense, patches throughout the area.

### **The properties of the networks**

A high A/P ratio of the cumulative network indicates that the plants on average were more generalized than the animals. This is supported by the fact that each plant species was visited by an average of 16.0 pollinator species, while pollinators visited an average of only 2.6 plant species. However, there were substantial deviations from this average, ranging from 1 to 80 pollinator species visiting one plant species, and from 1 to 24 plant species visited by one pollinator species. There were specialists and generalists amongst both plants and pollinator species, and the low nestedness temperature of  $6.62^\circ$  show that both specialists and generalists exhibit preferential attachment towards generalists.

The phenologically forbidden interactions are eliminated in the timeslice network, because they only consist of species that are present at exactly the time the network is constructed.

There were some interesting differences between the cumulative network and the averaged timeslice network. The connectance was on average 18.2% in the timeslice network, which had an average size of  $(S) = 72$ . The connectance in the cumulative network, however, was 7.1% and the size was 263. This reduction in  $C$  was due to the removal of the forbidden interactions, but it could also be a result of the decrease in network size (Olesen and Jordano 2002). The average nestedness

temperature was higher in the timeslice network than in the cumulative network, but the nestedness temperature changes with C and S (Rodríguez-Gironés and Santamaría 2006), so it would not be correct to make direct comparisons, therefore I just note that both the cumulative network and all the timeslice networks considered here, were significantly different from their null models. The timeslice networks had an average  $P = 23.1$ , and  $A = 49.2$  which gave an  $A/P$  ratio of 2.13. In the cumulative network the  $A/P$  ratio were 6.11, which indicates a higher turnover rate of the pollinator species compared to the plant species. This could be the effect of a short time span of the pollinator species adult life stage, migration or by a poor overlap between the presence of the pollinator species in the study area and the study period.

### **The composition of the pollinators**

Dipterans are the most dominant order of pollinator species, this is expected from a pollinator network of this latitude. The predictions of the (Elberling and Olesen 1999) models were surprisingly accurate, which means that the composition of pollinators of the network is normal for an ecosystem of this latitude. The dominance of the Diptera is also confirmed by the fact that four of the nine pollinator species with 10 or more interactions are Dipterans. Not only Dipterans are of importance. All orders except Hemiptera, the smallest order in the network, are amongst the most generalized, and Lepidoptera has the most interactions per species.

### **Flower phenology and plant generalisation level**

There was a tendency towards a positive correlation between flower area per  $m^2$  and the plants generalisation level (Figur 2). The most generalized plant species *Angelica sylvestris* ( $L_n = 80$ ), was the plant with the second highest flower coverage ( $5.5 \cdot 10^3 \text{ mm}^2 \text{ per } m^2$ ), if this is removed from the equation the tendency towards the correlation disappears. So there is no basis, in my data, to conclude that evolving larger flower coverage has any effect on the generalization of a plant species.

The findings that pollinator species has a higher turnover rate than the plant species, could lead you to believe that plants with a long flowering period received visits from more pollinator species, than plants with a short flowering season. In the light of this it is surprising that there is no correlation between the number of days a plant species is flowering and the species generalisation level (Figur 3).

## Conclusions

Both the cumulative and the average timeslice network analysis provide a thorough description of the network. The cumulative approach describes a large network with a low connectance, while the average timeslice network describes a smaller network with higher connectance. Both analyses give a valid description of the pollination system, if the analytical approach is taken into account. More information is yielded when the two network analyses are compared. Thereby the higher turnover rate of pollinators than plants and the presence of phenological forbidden interactions are revealed. The cumulative approach should be used when you want an overview of the season, like the composition of pollinators, and the examination of the plant generalisation. The real strength of the timeslice approach is the description the temporal dynamics of the pollination system, instead of average values. An example of this use is the discovery of the changes of the frequency of Dipterans doing the season. The temporal dynamics of the timeslice networks will be further investigated in chapter 3.

## Tables

**Table 1**

List of plant species. r1 and n1 refers to plant species found in the random and non-random plots, respectively, of the early vegetation analysis. r2 and n2 refer to the late vegetation analysis.

<i>Ajuga reptans</i>				
<i>Angelica sylvestris</i>			r2	n2
<i>Anthriscus sylvestris</i>				
<i>Centaurea Jacea</i>				n2
<i>Cerastium fontanum</i>	r1	n1		n2
<i>Cirsium oleraceum</i>			r2	n2
<i>Cirsium vulgare</i>	r1	n1	r2	
<i>Crepis paludosa</i>	r1	n1		
<i>Filipendula ulmaria</i>		n1		n2
<i>Galium palustre</i>	r1	n1		n2
<i>Geranium robertianum</i>		n1		n2
<i>Geum riviale</i>		n1		
<i>Lathyrus montanus</i>		n1		
<i>Lathyrus pratensis</i>	r1	n1		
<i>Lotus uliginosus</i>		n1	r2	n2
<i>Lychnis flos-cuculi</i>	r1	n1		n2
<i>Lysimachia vulgaris</i>				n2
<i>Lythrum salicaria</i>				n2
<i>Mentha aquatica</i>				
<i>Myosotis palustris</i>		n1		n2
<i>Pimpinella major</i>				n2
<i>Polygonum amphibium</i>			r2	n2
<i>Potentilla erecta</i>		n1		n2
<i>Ranunculus acris</i>	r1	n1		
<i>Ranunculus flammula</i>		n1		
<i>Silene dioica</i>		n1		n2
<i>Stellaria graminea</i>	r1	n1	r2	n2
<i>Stellaria palustris</i>				
<i>Trifolium campestre</i>		n1		n2
<i>Trifolium pratense</i>		n1		
<i>Trifolium repens</i>		n1		n2
<i>Valeriana officinalis</i>	r1	n1		n2
<i>Veronica beccabunga</i>		n1		n2
<i>Veronica chamaedrys</i>		n1		
<i>Veronica serpyllifolia</i>				
<i>Vicia cracca</i>		n1		
<i>Vicia sepium</i>		n1		

**Table 2**

List of pollinator species

Pollinator species	Order	Familiy
<i>Anaspis frontalis</i>	Coleoptera	Anaspidae
<i>Anaspis rufilabris</i>	Coleoptera	Anaspidae
<i>Anthobium minutum</i>	Coleoptera	Staphylinidae
<i>Anthobium ophthalmicum</i>	Coleoptera	Staphylinidae
<i>Anthobium torquatum</i>	Coleoptera	Staphylinidae
<i>Apion apricans</i>	Coleoptera	Curculionidae
<i>Apion flavipes</i>	Coleoptera	Curculionidae
<i>Cateretes pedicularius</i>	Coleoptera	Nitidulidae
<i>Cetonia aurata</i>	Coleoptera	Scarabaeidae
<i>Dasytes plumbeus</i>	Coleoptera	Dasytidae
<i>Gastroidea viridula</i>	Coleoptera	Chrysomelidae
<i>Grammoptera ruficornis</i>	Coleoptera	Cerambycidae
<i>Gymnetron veronicae</i>	Coleoptera	Curculionidae
<i>Hydrothassa marginella</i>	Coleoptera	Chrysomelidae
<i>Judolia cerambyciformis</i>	Coleoptera	Cerambycidae
<i>Laria loti</i>	Coleoptera	Lariidae
<i>Limnobaris T-album</i>	Coleoptera	Curculionidae
<i>Meligethes aeneus</i>	Coleoptera	Nitidulidae
<i>Meligethes coeruleovirens</i>	Coleoptera	Nitidulidae
<i>Phyllobius urticae</i>	Coleoptera	Curculionidae
<i>Rhagonycha fulva</i>	Coleoptera	Cantharidae
<i>Rhinoncus perpendicularis</i>	Coleoptera	Curculionidae
<i>Stenocorus meridianus</i>	Coleoptera	Cerambycidae
<i>Strangalia melanura</i>	Coleoptera	Cerambycidae
<i>Strangalia quadrifasciata</i>	Coleoptera	Cerambycidae
<i>Strophosomus melanogrammus</i>	Coleoptera	Curculionidae
<i>Tachinus fimetarius</i>	Coleoptera	Staphylinidae
<i>Aclonempis longipes</i>	Diptera	Empididae
<i>Agromyzidae</i> sp.	Diptera	Agromyzidae
<i>Alliopsis</i> species 1	Diptera	Anthomyiidae
<i>Alliopsis</i> species 2	Diptera	Anthomyiidae
<i>Alliopsis</i> species 3	Diptera	Anthomyiidae
<i>Alloestylus sudeticus</i>	Diptera	Muscidae
<i>Anthomyzidae</i> sp.	Diptera	Anthomyzidae
<i>Azelia triquetra</i>	Diptera	Muscidae
<i>Bombylius major</i>	Diptera	Bombyliidae
<i>Brachicoma devia</i>	Diptera	Sarcophagidae
<i>Calliphorinae onesia</i>	Diptera	Calliphoridae
<i>Cheilosia nigripes</i>	Diptera	Syrphidae
<i>Cheilosia pagana</i>	Diptera	Syrphidae
<i>Cheilosia proxima</i>	Diptera	Syrphidae



<i>Cheilosia pubera</i>	Diptera	Syrphidae
<i>Cheilosia variabilis</i>	Diptera	Syrphidae
<i>Chloromyia formosa</i>	Diptera	Stratiomyidae
<i>Chloropis</i> species 1	Diptera	Chloropidae
<i>Chloropis</i> species 2	Diptera	Chloropidae
<i>Chrysogaster solstitialis</i>	Diptera	Syrphidae
<i>Chrysops pictus</i>	Diptera	Tabanidae
<i>Chrysotoxum bicinetum</i>	Diptera	Syrphidae
<i>Conioscinella frontella</i>	Diptera	Chloropidae
<i>Craspedochoeata</i> sp.	Diptera	Anthomyiidae
<i>Dasyphora cyanicolor</i>	Diptera	Muscidae
<i>Delia</i> species 1	Diptera	Anthomyiidae
<i>Delia</i> species 2	Diptera	Anthomyiidae
<i>Delia</i> species 3	Diptera	Anthomyiidae
<i>Delia</i> species 4	Diptera	Anthomyiidae
<i>Discocerina obscurella</i>	Diptera	Ephydriidae
<i>Drosophilidae</i> sp.	Diptera	Drosophilidae
<i>Egle</i> sp.	Diptera	Anthomyiidae
<i>Empis aestiva</i>	Diptera	Empididae
<i>Empis albinervis</i>	Diptera	Empididae
<i>Empis nigripes</i>	Diptera	Empididae
<i>Empis nuntia</i>	Diptera	Empididae
<i>Empis pennipes</i>	Diptera	Empididae
<i>Empis rustica</i>	Diptera	Empididae
<i>Ephydriidae</i> species 1	Diptera	Ephydriidae
<i>Ephydriidae</i> species 2	Diptera	Ephydriidae
<i>Ephydriidae</i> species 3	Diptera	Ephydriidae
<i>Episyrphus balteatus</i>	Diptera	Syrphidae
<i>Eristalis interrupta</i>	Diptera	Syrphidae
<i>Eristalis intricaria</i>	Diptera	Syrphidae
<i>Eristalis pertinax</i>	Diptera	Syrphidae
<i>Fannia fuscula</i>	Diptera	Muscidae
<i>Fannia pallitibia</i>	Diptera	Muscidae
<i>Fannia polychaeta</i>	Diptera	Muscidae
<i>Fannia rondanii</i>	Diptera	Muscidae
<i>Fannia</i> sp.	Diptera	Muscidae
<i>Graphomya maculata</i>	Diptera	Muscidae
<i>Graphomya picta</i>	Diptera	Muscidae
<i>Haematopota pluvialis</i>	Diptera	Tabanidae
<i>Helophilus hybridus</i>	Diptera	Syrphidae
<i>Helophilus pendulus</i>	Diptera	Syrphidae
<i>Helophilus trivittatus</i>	Diptera	Syrphidae
<i>Hercostomus germanus</i>	Diptera	Dolichopodidae
<i>Hercostomus nigripennis</i>	Diptera	Dolichopodidae

<i>Heteronychia haemorrhhoa</i>	Diptera	Sarcophagidae
<i>Heteronychia vagens</i>	Diptera	Sarcophagidae
<i>Hilara brevistyla</i>	Diptera	Empididae
<i>Hilarella stictica</i>	Diptera	Sarcophagidae
<i>Holoclera nigripennis</i>	Diptera	Empididae
<i>Hylemya species 1</i>	Diptera	Anthomyiidae
<i>Hylemya species 2</i>	Diptera	Anthomyiidae
<i>Hylemya species 3</i>	Diptera	Anthomyiidae
<i>Ischyrosyrphys laternarius</i>	Diptera	Syrphidae
<i>Limnophora riparia</i>	Diptera	Muscidae
<i>Limnophora triangular</i>	Diptera	Muscidae
<i>Liriomyza</i> sp.	Diptera	Agromyzidae
<i>Lophosceles cinereiventris</i>	Diptera	Muscidae
<i>Lucilia caesar</i>	Diptera	Calliphoridae
<i>Lucilia sericata</i>	Diptera	Calliphoridae
<i>Lucilia silvarum</i>	Diptera	Calliphoridae
<i>Melanostoma mellinum</i>	Diptera	Syrphidae
<i>Melanostoma scalare</i>	Diptera	Syrphidae
<i>Melinda gentilis</i>	Diptera	Calliphoridae
<i>Melinda viridicyanea</i>	Diptera	Calliphoridae
<i>Meliscaeva cinectella</i>	Diptera	Syrphidae
<i>Morellia aenescens</i>	Diptera	Muscidae
<i>Morellis simplex</i>	Diptera	Muscidae
<i>Myathropa florea</i>	Diptera	Syrphidae
Mycetophilidae species 1	Diptera	Mycetophilidae
Mycetophilidae species 2	Diptera	Mycetophilidae
<i>Neoascia obliqua</i>	Diptera	Syrphidae
<i>Neoascia podagrica</i>	Diptera	Syrphidae
<i>Neoascia tenur</i>	Diptera	Syrphidae
<i>Onesia floralis</i>	Diptera	Calliphoridae
<i>Ophiomyia</i> sp.	Diptera	Agromyzidae
<i>Orthelia caesarion</i>	Diptera	Muscidae
<i>Oscinella hortensis</i>	Diptera	Chloropidae
<i>Oscinella vastator</i>	Diptera	Chloropidae
<i>Parasyrphus lineola</i>	Diptera	Syrphidae
<i>Parhelophilus versicolor</i>	Diptera	Syrphidae
<i>Phaonia exoleta</i>	Diptera	Muscidae
<i>Phaonia incana</i>	Diptera	Muscidae
<i>Phorbia species 1</i>	Diptera	Anthomyiidae
<i>Phorbia species 2</i>	Diptera	Anthomyiidae
<i>Phorbia species 3</i>	Diptera	Anthomyiidae
<i>Platycheirus cyaneus</i>	Diptera	Syrphidae
<i>Platycheirus peltatus</i>	Diptera	Syrphidae
<i>Platycheirus scutatus</i>	Diptera	Syrphidae

<i>Platycheirus</i> sp.	Diptera	Syrphidae
<i>Poletes steini</i>	Diptera	Muscidae
<i>Pollenia pediculata</i>	Diptera	Calliphoridae
<i>Pollenia rudis</i>	Diptera	Calliphoridae
<i>Pseudonapomyza</i> sp.	Diptera	Agromyzidae
Psychodidae sp.	Diptera	Psychodidae
<i>Pyrophaena rosarum</i>	Diptera	Syrphidae
<i>Rhamphomyia hirtula</i>	Diptera	Empididae
<i>Rhingia campestris</i>	Diptera	Syrphidae
<i>Rhinophorinae</i> sp.	Diptera	Calliphoridae
<i>Sarcophaga</i> sp.	Diptera	Sarcophagidae
<i>Senotainia conica</i>	Diptera	Sarcophagidae
<i>Sepsis cynipsea</i>	Diptera	Sepsidae
<i>Sepsis flavimana</i>	Diptera	Sepsidae
<i>Sepsis fulgens</i>	Diptera	Sepsidae
<i>Sphaerophoria scripta</i>	Diptera	Syrphidae
<i>Sphaerophoria</i> sp.	Diptera	Syrphidae
<i>Sphaerophoria taenata</i>	Diptera	Syrphidae
<i>Sphegina</i> sp.	Diptera	Syrphidae
<i>Stratiomya potamida</i>	Diptera	Stratiomyidae
<i>Syrpita pipiens</i>	Diptera	Syrphidae
<i>Syrphus ribesii</i>	Diptera	Syrphidae
<i>Syrphus vitripennis</i>	Diptera	Syrphidae
<i>Tetanocera silvatica</i>	Diptera	Sciomyzidae
<i>Thrypticus bellus</i>	Diptera	Dolichopodidae
<i>Tricimba cincta</i>	Diptera	Chloropidae
<i>Tropidia scita</i>	Diptera	Syrphidae
<i>Volucella pellucens</i>	Diptera	Syrphidae
<i>Wahlgrenia magnicornis</i>	Diptera	Muscidae
<i>Xylota abiens</i>	Diptera	Syrphidae
Aphidoidea sp.	Hemiptera	
Cercopidae species 1	Hemiptera	Cercopidae
Cercopidae species 2	Hemiptera	Cercopidae
<i>Calocoris norvegicus</i>	Hemiptera	Miridae
<i>Calocoris sexguttatus</i>	Hemiptera	Miridae
<i>Hadrodemus m-flavum</i>	Hemiptera	Miridae
<i>Leptopterna dolabrata</i>	Hemiptera	Miridae
<i>Lygus lucorum</i>	Hemiptera	Miridae
<i>Nabis ferus</i>	Hemiptera	Nabidae
<i>Orthops kalmi</i>	Hemiptera	Miridae
<i>Picromerus bidens</i>	Hemiptera	Pentatomidae
<i>Saldula</i> sp.	Hemiptera	Miridae
<i>Stenotus binotatus</i>	Hemiptera	Miridae
<i>Apis mellifera</i>	Hymenoptera	Apidae

Apocrita species 1	Hymenoptera	
Apocrita species 10	Hymenoptera	
Apocrita species 11	Hymenoptera	
Apocrita species 12	Hymenoptera	
Apocrita species 13	Hymenoptera	
Apocrita species 2	Hymenoptera	
Apocrita species 3	Hymenoptera	
Apocrita species 4	Hymenoptera	
Apocrita species 5	Hymenoptera	
Apocrita species 6	Hymenoptera	
Apocrita species 7	Hymenoptera	
Apocrita species 8	Hymenoptera	
Apocrita species 9	Hymenoptera	
<i>Athalia lineolata</i>	Hymenoptera	Tenthredinidae
<i>Athalia spinarum</i>	Hymenoptera	Tenthredinidae
<i>Bombus agrorum</i>	Hymenoptera	Apidae
<i>Bombus hortorum</i>	Hymenoptera	Apidae
<i>Bombus hypnorum</i>	Hymenoptera	Apidae
<i>Bombus lucorum</i>	Hymenoptera	Apidae
<i>Bombus pratorum</i>	Hymenoptera	Apidae
<i>Bombus terrestris</i>	Hymenoptera	Apidae
<i>Calameuta filiformis</i>	Hymenoptera	Cepidae
Chalcidoidae species 1	Hymenoptera	Chalcidoidae
Chalcidoidae species 2	Hymenoptera	Chalcidoidae
Chalcidoidae species 3	Hymenoptera	Chalcidoidae
Chalcidoidae species 4	Hymenoptera	Chalcidoidae
Chalcidoidae species 5	Hymenoptera	Chalcidoidae
<i>Crossocerus affinis</i>	Hymenoptera	Sphegidae
<i>Gorytes campestris</i>	Hymenoptera	Sphegidae
<i>Halictus calceatus</i>	Hymenoptera	Apidae
<i>Halictus leucopus</i>	Hymenoptera	Apidae
<i>Halictus quadrinotatus</i>	Hymenoptera	Apidae
<i>Hylotoma ciliaris</i>	Hymenoptera	Tenthredinidae
<i>Macropis labiata</i>	Hymenoptera	Apidae
<i>Myrmicinae</i> sp.	Hymenoptera	Formicidae
<i>Prosopis communis</i>	Hymenoptera	Apidae
<i>Vespa holsatica</i>	Hymenoptera	Vespidae
<i>Aphantopus hyperantus</i>	Lepidoptera	Satyridae
<i>Cynthia cardui</i>	Lepidoptera	Nymphalidae
<i>Inachis io</i>	Lepidoptera	Nymphalidae
Lepidoptera species 1	Lepidoptera	
Lepidoptera species 2	Lepidoptera	
Lepidoptera species 3	Lepidoptera	
Lepidoptera species 4	Lepidoptera	

Lepidoptera species 5	Lepidoptera	
Lepidoptera species 6	Lepidoptera	
Lepidoptera species 7	Lepidoptera	
Lepidoptera species 8	Lepidoptera	
Lepidoptera species 9	Lepidoptera	
<i>Maniola jurtina</i>	Lepidoptera	Satyridae
<i>Ochlodes venata</i>	Lepidoptera	Hesperiidae
<i>Pieris napa</i>	Lepidoptera	Pieridae
<i>Polyommatus icarus</i>	Lepidoptera	Lycaenidae
<i>Thymelicus sylvestris</i>	Lepidoptera	Hesperiidae

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**Table 3**

List of identification literature.

Lepidoptera:

Michael Stoltze; 1997; Dagsommerfugle I Danmark; Nordisk forlag A.S. Copenhagen.

Diptera:

Anthomyzidae, Chloropidae, Drosophilidae, Ephydriidae, Mycetophilidae, Psychodidae and Sciomyzidae to family by: Leif Lyneborg; 1960; Danmarks fauna 66, Tovinger II; G.E.C. Gads forlag, København.

Stratiomyiidae and Tabanidae: Leif Lyneborg; 1960; Danmarks fauna 66, Tovinger II; G.E.C. Gads forlag, København.

Agromyzidae: Ryuén, N. Lyneborg, L & Overgaard Nielsen, B; 1963; Danmarks fauna 68, Tovinger III; G.E.C. Gads forlag, København.

Bombyliidae: Leif Lyneborg; 1965; Danmarks Fauna 70, Tovinger IV; G.E.C. Gads forlag, København.

Syrphidae: Ernst Torp; 1994; Danmarks dyreliv 6, Danmarks Svirrefluer; Apollo Books, Stenstrup.

Empididae: Milan Chvála; 1994; Fauna entomologica scandinavica Vol 29, the Empidoidea (diptera) of Fennoscandia and Denmark. III; E.J. Brill, Leiden- New York- Köln. And: Milan Chvála; 1983; Fauna entomologica scandinavica Vol 12, the Empidoidea (diptera) of Fennoscandia and Denmark. II; Scandinavian Science press Ltd, Klampenborg.

Dolichopodidae: E. C. M. d'Ássis Fonseca; 1978; Handbooks for the identification of british insects Vol. IX part 5; Diptera Orthorrhapha Brachycera Dolichopodidae; Royal entomological society of London.

Muscidae: E. C. M. d'Ássis Fonseca; 1968; Handbooks for the identification of british insects Vol. X part 4(b); Diptera Cyclorrhapha Calyptrata section (b) Muscidae; Royal entomological society of London.

Sepsidae: Pony, A, C. and Meier, R; 2002; Fauna entomologica scandinavica Vol 37, The Sepsidae (Diptera) of Europe; Brill, Leiden - Boston – Köln.

Calliphoridae: Knut Rognes; 1991; Fauna entomologica scandinavica Vol 24, Blowflies (Diptera, Calliphoridae) of Fennoscandia and Denmark; E.J. Brill/Scandinavian Science press Ltd, Leiden - New York - København – Köln.

Sarcophagidae: Thomas Pape; 1987; Fauna entomologica scandinavica Vol 19, The Sarcophagidae (Diptera) of Fennoscandia and Denmark; E.J. Brill/Scandinavian Science press Ltd, Leiden – Copenhagen.

Anthomyiidae: Papp, d & Darvas, B. (eds.) Contributions to a Manual of Palaearctic Diptera. Vols. I-III, Appendix. Science Herald. Budapest. 1998-2000.

#### Hymenoptera:

Vespidæ and Sphegidae: J. C. Nielsen; 1907; Danmæks fauna II, Gravehvepse og gedehamse; G.E.C. Gad, København.

Tenthredinidae and Cephidae: J.C. Nielsen og K. Henriksen; 1915; Danmarks Fauna 18, Træ- og Bladhvepse; G.E.C. Gads forlag, København.

Apida: Lavrids Jørgensen; 1921; Danmarks fauna 25, Bier; G.E.C. Gads forlag, København. Except for the family Bombus: Hammer, K og Nørgaard Holm, Sv; 1970; Danske humlebier og snyltehumler; Natur og Museum 14. årgang nr. 2-3, Naturhistorisk museum, Århus.

#### Coleoptera:

Curculionidae: Victor Hansen; 1918; Danmarks fauna 22, Biller IV; G.E.C. Gads forlag, København.

Lariidae and Chrysomelidae: Victor Hansen; 1927; Danmarks fauna 31, Biller VII; G.E.C. Gads forlag, København.

Cantharidae: Victor Hansen; 1938; Danmarks fauna 44, Biller X; G.E.C. Gads forlag, København.

Nitidulidae: Victor Hansen; 1950; Danmarks fauna 55, Biller XIII; G.E.C. Gads forlag, København.

Scarabaeidae: Victor Hansen; 1925; Danmarks fauna 29, Biller VI; G.E.C. Gads forlag, København.

Cerambycidae: Victor Hansen; 1914; Danmarks fauna 16, Biller III; G.E.C. Gads forlag, København. And Victor Hansen; 1966; Danmarks fauna 73, Biller XXII; G.E.C. Gads forlag, København.

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Heteroptera: T.R.E. Southwood and D. Leston; 1959; Land and water bugs of the british isles; Frederick Warne & Co. LTD, London & New York. Except for the family Miridae: Sven Gaun; 1974; Danmarks fauna 81, Vinderup bogtrykkeri A-S.

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**Table 4**

The distribution of pollinator species within orders.

Order	Number of species		Number of interactions		interactions per species
Hemiptera	13	6%	20	3%	1.54
Lepidoptera	17	8%	66	11%	3.88
Coleoptera	27	12%	73	12%	2.70
Hymenoptera	38	17%	91	15%	2.39
Diptera	131	58%	340	58%	2.60
Total	226	100%	590	100%	2.61

**Table 5**

The distribution of Diptera species within families.

Families	Number of species		Number of interactions		interactions per species
Syrphidae	39	30%	171	50%	4.38
Muscidae	20	15%	33	10%	1.65
Anthomyiidae	15	11%	16	5%	1.07
Calliphoridae	10	8%	22	6%	2.20
Empididae	10	8%	42	12%	4.20
Other	37	28%	56	16%	1.51
total	131	100%	340	100%	2.60

**Table 6**

The nine most connected species.

Species	Order	Family	L <sub>m</sub>
Episyrphus balteatus	Diptera	Syrphidae	24
Platycheirus cyaneus	Diptera	Syrphidae	24
Meligethes aeneus	Coleoptera	Nitidulidae	22
Aphantopus hyperantus	Lepidoptera	Satyridae	18
Eristalis interrupta	Diptera	Syrphidae	13
Pieris napa	Lepidoptera	Pieridae	12
Empis aestiva	Diptera	Empididae	11
Bombus agrorum	Hymenoptera	Apidae	11
Cateretes pedicularius	Coleoptera	Nitidulidae	10

## References

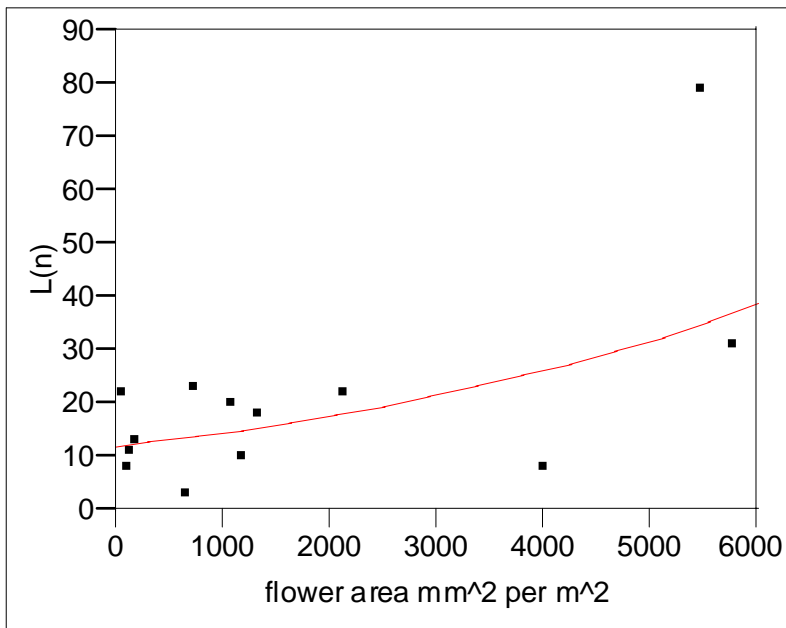
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## List of Figures



**Figure 1**

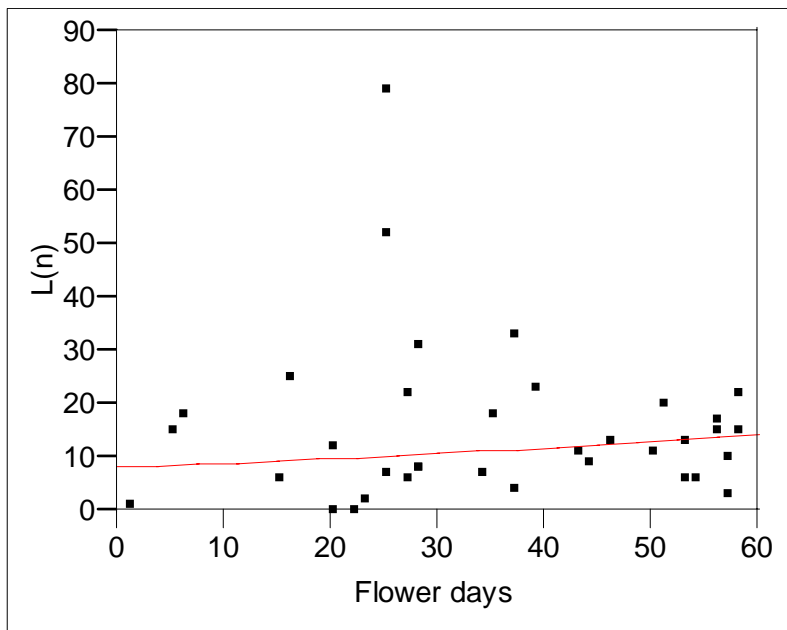
Examples of nestedness: from the left, a matrix with the nestedness temperature  $0^\circ$ , matrix from timeslice network day three temperature  $37^\circ$ , a matrix with the temperature  $100^\circ$ . A black square indicates an interaction, absence of a black square indicates that there is no interaction.



**Figure 2**

Regression analysis of the plant species generalization level vs average flower area per m<sup>2</sup>:  $\text{Log}(L_n) = 2.47 + 0.0002 \text{ flower mm}^2 \text{ per m}^2$ ,  $\text{Rsquare adj.} = 0.23$ ,  $F_{1,11} = 4.66$ ,  $P \leq 0.0537$ .





**Figur 3**

Regression analysis of the plant species generalition level vs. the length of there flowering period,  $\text{Log}(L_n) = 2.08 + 0.0095 \text{ flower-days}$ ,  $\text{Rsquare adj.} = 0.00$ ,  $F_{1,33} = 0.95$ ,  $P \leq 0.3356$

## Chapter 2

### Analysis of the cumulative network



**Foto:** *Bombus terrestris* visiting *Cirsium oleraceum*

by Søren Bek

## Introduction

Pollination networks are the cumulated results of a series of observations, over a given time span, on a number of plant species limited by the researcher, or by geographical parameters defined by the researcher. Network size, and other network parameters that the researcher focus on, are not objectively defining the pollination ecosystem, but are to some extent consequences of the researcher's sampling effort and the decisions taken to limit the investigation in space and time. In order to interpret results found in a network investigation, it is crucial to understand how the different characteristics of the network changes with changing sampling efforts. This is especially true when comparing networks made by different researchers with different purposes in mind. A better understanding of the effect of differences in sampling efforts will also enable researchers to estimate the necessary sampling effort needed to obtain the results in question.

This chapter will focus on how connectance, nestedness temperature, degree distribution, degree centralization, closeness centralization and betweenness centralization, respond to changes in sampling effort. The cumulative network described in chapter 1 will be the basis of the analysis using network size as a measure of sampling effort. Connectance, nestedness temperature and degree distribution are traditionally used to describe pollination networks. The first two were defined in chapter 1, and the latter will be defined below. Degree centralization, closeness centralization and betweenness centralization are traditionally used to describe social networks. Applied to a pollination network these measures give valuable information about the network in addition to the traditionally used network parameters. The three measures of centralization are defined below. All the above mentioned parameters were chosen because they are simple measures describing network topography, and thereby obvious candidates to describe and compare different networks.

The networks were cumulated on a day to day basis, so that, network 1 is based on observations from the first field day, network 2 represents observations from the first and second field day, and so forth. Network 37 represents the combined data from the whole study period.

## Methods

### Network parameters

Ecological networks consist of vertices, the species, connected by edges, the interactions between species pairs (see Figure 1A). In a pollination network there are two kinds of vertices, plants and pollinators, and the edges always run between these two. This is a so-called 2-mode network.

I describe the two-mode networks by the following characteristics:

- The total number of plant species ( $P$ ), observed during the survey.
- The total number of pollinator species ( $A$ ), found throughout the observation period.
- The network size ( $S$ ) =  $A+P$ .
- The number of possible interactions ( $M$ ) =  $A \cdot P$ .
- The plant, pollinator ratio ( $A/P$ )
- The observed number of interactions ( $I$ ).
- The percentage of realized interactions, called the connectance ( $C$ ) =  $I/M \cdot 100\%$ .
- The nestedness temperature ( $Nt$ )

The freeware program Pajek (Vladimir Batagelj 2004) can transform a two-mode network into two one-mode networks, and calculate degree centralization, closeness centralization and betweenness centralization for the networks. In a pollination network, the two one-mode networks are a plant network and a pollinator network. In a one mode plant network  $a_{ij} = 1$ , if plant species  $i$  and  $j$  have one or more pollinator species in common. The one-mode pollinator network is constructed in the same manner. In small loosely connected networks there may be unconnected single species or small networks not connected to the main network. These are called isolates (Olesen, Bascompte et al. 2006). Closeness centralization can only be calculated in networks where all vertices are connected, so isolates were removed from the data.

The one-mode networks are described by the following characteristics:

- The degree ( $k_i$ ), e.g. the number of links species ( $i$ ) has to other species.
- The degree centralization ( $k_{net}$ ).
- The closeness centralization ( $c_{net}$ ).
- The betweenness centralization ( $b_{net}$ ).

## **Connectance**

Connectance (C) is defined in chapter 1. To determine how a shorter study period would affect the connectance, C was plotted against days, and tested by regression analysis for correlation with S. C was log arcsin transformed to obtain normal distribution.

## **Nestedness temperature**

Nestedness temperature (Nt) is defined in chapter 1. Nt were tested against S using regression analysis.

To determine how much of the variation of Nt could be explained by each of the four null models, defined in chapter 1, the four null models were tested against S using regression analysis. The residuals of the Nt vs. S were then tested against the residuals of the null models against S using regression analysis. Nt and the four null models were log transformed to obtain normal distribution.

## **Degree distribution**

The degree distribution is the probability that a species (i) has at least k interactions  $p(\geq k)$ .

Originally it was assumed that the links in a network were formed randomly (Barabási and Albert 1999), but in 1998 a survey of the World Wide Web showed that the links follow a power law distribution. That the links in a network has a power law distribution means that the network is dominated by a relatively small number of vertices that link to a large number of other vertices. Networks that exhibit a power law distribution are called scale-free networks. Scale-free networks have the characteristic feature that they are robust against a random loss of vertices, but vulnerable to the loss of the most linked vertices, called key species. Scale-free networks have in recent years, besides the internet, been found in social networks, the structure of language, transportation, the nerve cells of the brain, metabolic systems of the cells, and in ecological networks (Barabasi and Bonabeau 2003).

In networks that are made through preferential attachment, (new vertices links mainly to the most connected species), the degree distribution usually follows a power law model. Pollination networks, however, often follow a truncated power law, or an exponential model. This means that the most generalistic species have fewer links than expected from a power law function. The truncated power law follows a power law model at small k values, but after reaching a cut-off point, it declines. An explanation of this behaviour is the occurrence of forbidden interactions.

Phenological or morphological characters of a species can make interactions impossible to even the most generalistic species (Jordano, Bascompte et al. 2003). If the truncation results from phenological constraints (e.g. two species do not interact because they have no overlap in time), then the effect of the truncation is expected to increase as the cumulated study period lengthens. If the truncation results from morphological constraints, (e.g. short tongued pollinators can not utilize the resources of long-corollar flowers), then the effect of the truncation is expected to be independent of the length of the study period. Another explanation for a truncated degree distribution is called “finite size artefact” (Keitt and Stanley 1998). According to this theory the network has a power law distribution, and the truncation is an artefact of species and interactions missing from our samples. If this is the case the effect of the truncation is expected to decrease as the cumulated study period lengthens. Networks which show a truncated power law or exponential degree distribution are less vulnerable to the loss of key species.

The degree distributions of this study were fitted to a power law, a truncated power law and an exponential model, to determine to which model it had the best fit.

### **Degree centralization**

Degree centrality is a measure that applies to a single vertex, while degree centralization applies to the whole network. The degree centrality of a vertex is its number of interactions divided by the number of possible interactions (Nooy, Mrvar et al. 2005). In example A (Figure 1), species 2 has one interaction out of five possible, while species 1 has five. This means that their degree centrality is  $1/5 = 0.2$  and  $5/5 = 1.0$  respectively. The degree centralization is the sum of variance of the degree centrality of all vertices, divided by the largest possible sum of variance (Nooy, Mrvar et al. 2005). The network in example A has the largest possible variation, because species 1 links to all other species which in turn only has one link (to species 1). For a network of the size 6 the sum of variance is  $(1-0.2) + (1-0.2) + (1-0.2) + (1-0.2) + (1-0.2) + (1-1) = 4$ . The degree centralization of example A, is thus  $k_{\text{net}} = 4/4 = 1.0$  and in example B, is  $k_{\text{net}} = 0.4/4 = 0.1$  and in example C,  $k_{\text{net}} = 0/4 = 0$  (Figure 2).

A network with high degree centralization, (close to 1), has a core of one or more highly connected species, and a periphery of species loosely connected to the network, while in networks with low degree centralization the species have a homogenous distribution of links.

A network of mutualistic interactions with high degree centralization, is vulnerable to the local extinction of a core species, and robust against removal of the peripheral species.

To see how degree centralization reacts to changes in sampling effort,  $k_{\text{net}}$  were tested against  $S$ .

### **Closeness centralization**

The closeness centrality is a value that refers to a single vertex, and is a measure of how closely the vertex is connected to other vertices, based on its geodesic.

The geodesic of two vertices is the shortest path between them, (i.e. the lowest number of edges you need to go along to get from one to the other). The geodesics are divided by the longest possible geodesic  $S-1$ , to enable comparison of networks of different sizes. The geodesic between species 1 and species 6 in example A (Figure 1) is 1, in example B it is 5. The size-corrected geodesic is 0.2 and 1.0 respectively. The closeness centrality of a vertex is the reciprocal of the sum of the size-corrected geodesics of the vertex and all other vertices in the network. Closeness centralization is the sum of variance of the closeness centrality of all vertices, divided by the largest possible sum of variance (Nooy, Mrvar et al. 2005). The calculation of the closeness centralization is similar to the calculation of the degree centralization (Figure 2).

Closeness centralization can be described as a measure of the structure of a network, which illustrates how tightly the vertices in the network are connected. In the social sciences it is used as a measure of how easily information spreads in a network of people. In pollination networks there is not an obvious interpretation of the closeness centralization. But as removal of a species will not only influence its direct mutualistic partners, but also the partners partners, it makes sense to measure how “information” e.g. the effect of disturbance spreads through a network.

The network in example A, has a maximum closeness centralization of  $c_{\text{net}} = 1.0$ , the closeness centralization of the network in example B, is  $c_{\text{net}} = 0.29$  and in example C,  $c_{\text{net}} = 0.0$ .

Closeness centralization was, as  $k_{\text{net}}$ , tested against  $S$ .

### **Betweenness centralization**

In most networks there will be more than one geodesic between two vertices, most of the geodesic will run through the most centralised vertex. The betweenness centrality is a measure of the proportion of paths between any combinations of two vertices that go through a given vertex.

The betweenness centralization is the sum of variance of the betweenness centrality of all vertices divided by the largest possible sum of variance. The calculation of the betweenness centralization is similar to the calculation of the degree centralization (Figure 2).

In example A (Figure 1) all paths between two species other than species 1, runs through species 1, while no paths runs through other species. The betweenness centralization of the network in example A are  $b_{\text{net}} = 1.0$  in Example B  $b_{\text{net}} = 0.32$  and in example C,  $b_{\text{net}} = 0.0$ .

Compartments can be described as smaller networks with in the network. A species in a compartment has more links to other species in that compartment, than to species in the surrounding network (Dicks, Corbet et al. 2002). Connector species are generalistic species that links different compartments. A connector species has a high betweenness centrality, while species that only link within the compartment has a low betweenness centrality. Networks with high betweenness centralization have few important connector species, while more homologues networks have low betweenness centralization.

### **And finally**

The three measures of centralization were tested for any correlation between each other.

All above mentioned values were calculated for each cumulated network.

It was not possible to calculate all results for the networks of the first days, because these small networks were too fragmented. Therefore they were excluded from parts of the analyses.

The degree distribution as well as the centralization of the one-mode pollinator network was analysed starting from network 2. The centralization of the one-mode plant network was analysed starting from network 3. To test (Nt) the two first networks were discarded because they were not significantly different from the null models Er and Ce.

The data for (C), (nt),  $k(a)_{\text{net}}$ ,  $c(a)_{\text{net}}$ ,  $b(a)_{\text{net}}$ ,  $k(p)_{\text{net}}$ ,  $c(p)_{\text{net}}$  and  $b(p)_{\text{net}}$  were tested for any correlation to network size (S) by a regression analysis. The tests were made using the statistical software package *JMP*, [www.jmp.com](http://www.jmp.com).



## Results

### The descriptive values of the cumulative networks

The descriptive values of the cumulative network are presented in Figure 3.

Network size (S), number of pollinator species (A) and number of interactions (I) raised linearly with number of observation days. Number of plant species (P) stagnated towards the end of the study season, which in turn cause the A/P ratio to increase.

### Connectance

The correlation between (C) and network size (S) was significant, but when the initial behaviour, during the first four days, was discarded there was no correlation (Figure 4). There was very little variation in the connectance when the initial behaviour was discarded,  $C = 7.03\% \pm 0.31$ .

Connectance was arcsin transformed to allow the use of a regression analysis.

### Nestedness

There was no significant correlation between nestedness temperature (Nt) and C when the initial behaviour was excluded (Figure 5). The Nt was significantly negatively correlated with S (Figure 6). Test of the four Nt null models revealed that the random model Er did not correlate with S, whereas the three remaining null models did correlate with S (Figure 7).

A regression analysis of the residuals of Nt against (S), against the residuals of the last three null models against (S), revealed that model Co explained much of the variation in nestedness temperature not, explained by size. Model Ce did less well and model Li showed no significant correlation (Figure 8).

Nestedness temperature, and the four null models were log-transformed to allow the use of a regression analysis.

### Degree distribution

In order to describe the degree distribution of the cumulative one-mode pollinator network for the full period, network 37 was fitted to a power law model, a truncated power law model and an exponential model. It had the best fit to the truncated power law model, as seen by the SSE values (Figure 9). Spot sampling showed a best fit to the truncated power law model for network 2, and throughout the whole season.

The one-mode plant network for the full period, network 37, also had a best fit to the truncated power law model (Figure 10), but the fit was not as good as for the pollinator network. The poor fit was due to a higher frequency than expected of high  $k$  species, (species with many links). As the season progressed the distribution deviated increasingly from a truncated power law model. But spot sampling showed a best fit to the truncated power law model for network 2, and through out the rest of the season.

### **Centralization**

Three measures of centralization were used, degree centralization ( $k_{\text{net}}$ ), closeness centralization ( $c_{\text{net}}$ ) and betweenness centralization ( $b_{\text{net}}$ ). These were calculated for each of the two one-mode networks: the plant network (p) and the pollinator network (a).

#### **Centralization in the one-mode pollinator network**

$k(a)_{\text{net}}$  and  $c(a)_{\text{net}}$  showed a positive correlation with sampling effort (Figure 11).  $b(a)_{\text{net}}$  showed a negative correlation with  $S$  (Figure 12).

$c(a)_{\text{net}}$  correlated positively with  $k(a)_{\text{net}}$ ,  $b(a)_{\text{net}}$  correlated negatively with  $k(a)_{\text{net}}$  and  $b(a)_{\text{net}}$  correlated negatively with  $c(a)_{\text{net}}$  (Figure 13).

#### **Centralization in the one-mode plant network**

$k(p)_{\text{net}}$  and  $c(p)_{\text{net}}$  decreased with  $S$  (Figure 14).

$b(p)_{\text{net}}$  decreased with  $S$ , the first 18 days, where after  $b(p)_{\text{net}}$  was not significantly dependent upon  $S$  (Figure 15).

$c(a)_{\text{net}}$  correlated positively with  $k(a)_{\text{net}}$ ,  $b(a)_{\text{net}}$  correlated positively with  $k(a)_{\text{net}}$  and  $b(a)_{\text{net}}$  correlated positively with  $c(a)_{\text{net}}$  (Figure 16).

## Discussion

### The descriptive values

There was a steady increase in all descriptive values and only the number of plants (P) reached a plateau (Figure 3). The fact that number of pollinator species (A) and number of interactions (I) did not reach a plateau shows that the end of the study season do not correlate with the end of the ecological pollinator season. To minimize the disturbance of the pollination system, the harvest of the meadow should be exposed to later in the fall (see chapter 1).

### Connectance

The connectance (C) decreased rapidly with size (S), and for  $S > 51$ , C is independent of S (Figure 4). This independence contradicts with earlier findings that C decreased exponentially with S (Olesen and Jordano 2002). One explanation of this difference could be that these findings came from a comparison of 29 different pollination networks, while the scale-invariance I found is within one network. The results of this study suggest that connectance is robust against variation in sampling effort, i.e. it is a stable measure defining an ecosystem and thus a good measure when comparing different ecosystems. Of course, more studies are needed to determine if this is true for other networks than this one. If both the results of this study and the study of Olesen and Jordano is general valid for pollination networks, then the finding that C decreases exponentially with S also suggests that the network sizes of the 29 networks of the Olesen and Jordano paper, are not the results of the researchers decisions to limit there study, but rather a representation of a real ecological phenomenon.

### Nestedness

The nestedness temperature is not correlated with connectance (Figure 5), but there is a good fit to a negative correlation with S (Figure 6). If this pattern is found in other cumulative networks as well, it is possible to correlate with networks size. The nestedness of a network will then be given as a function of S rather than as a single measure. Thus the temperature of this network is not  $Nt = 6.62^\circ$  but rather  $Nt = e^{3.117 - 0.005S}$ . It would then be possible to compare the nestedness of different networks by comparing nestedness formulas.

A comparison of the four null models shows that the nestedness of random networks ( the Er null model) is independent of network size (Figure 7 a), and thus will have a tendency to overestimate the nestedness of larger networks.

Tests of the residuals of the null models vs. S, against the residuals of the Nt vs. S (Figure 8), showed that much of the variation not explained by S is explained by model Co. In the Co null model all cells in column, j, were assigned an interaction by the probability of  $P(k_j)$ , and thus the distribution of the plants' generalization levels is preserved. This means that in this network the nestedness temperature mainly depends on network size and the plants' generalisation level. That the plants' and not the pollinators' generalization level influenced the nestedness temperature, must result from the fact that there is a high A/P ratio.

### **Degree distribution**

It was found that the degree distribution of the pollinator-network had a best fit to a truncated power law function from the beginning of the study season and to its end. This correspond to the explanation that morphological forbidden interactions are responsible for the truncation of the distribution. However it can not be excluded that a combination of phenologically forbidden interactions and finite size artefact also are responsible.

The degree distribution of the plant-network also had a best fit to the truncated power law in the full period, but the fit got weaker during the season (Figure 10). Toward the end of the study season, the number of plants stagnated while the number of pollinators kept increasing (Figure 3) thus increasing the k values in the plant network. This produced a higher than expected frequency of highly linked plant species, resulting in the weak fit late in the season.

### **Centralization**

In the one-mode pollinator network the positive correlation between the network size (S) and the centralization measures degree centralization  $k(a)_{net}$ , and closeness centralization  $c(a)_{net}$ . This showed that the difference between the linkage level of core of key species and the linkagelevel of the periphery of looser connected species increased with S (Figure 11). The negative correlation between  $b(a)_{net}$  and S indicated that the importance of the individual key species as an agent of information transmission (to use a metaphor from the social sciences) are reduced (Figure 12). My interpretation of this is that the importance of the individual key species increases, but as a whole the network gets more homogeneous. Thus increasing the structural integrity of the network.

The close positive correlation between  $k(a)_{\text{net}}$  and  $c(a)_{\text{net}}$  showed that in this network there was no great difference between the two measures of centralization. But both correlated negatively to  $b(a)_{\text{net}}$  (Figure 13).

In the one-mode plant network  $k(p)_{\text{net}}$  and  $c(p)_{\text{net}}$  decreases with network size showing that the difference between the linkage level of the core and periphery diminishes. Also  $b(p)_{\text{net}}$  decreases with  $S$  to a point where  $b(p)_{\text{net}}$  becomes independent of  $S$  (Figure 15). The reason for this is the same as the reason for the deviation of the plant networks' degree distribution from the truncated power law model. Toward the end of the study season, the numbers of plants stagnated, while the number of pollinators kept increasing. When most vertices are linked to most other vertices, the betweenness centralization becomes small and independent of sampling effort. The plant network not just has small world properties, (characterized by short path lengths between the vertices), nearly all possible interactions within the one-mode plant network, are realized.

As in the pollinator network there is no great difference between  $k(p)_{\text{net}}$  and  $c(p)_{\text{net}}$ . But contrary to the findings in the pollinator network,  $k(p)_{\text{net}}$  and  $c(p)_{\text{net}}$  correlated positively to  $b(p)_{\text{net}}$  (Figure 16). The reason for this difference is unclear. Investigating the changes of the underlying centrality measures may clear this up, but that is beyond the scope of this paper.

## Conclusion

In order to interpret the data yielded from network analysis, or to compare different networks, it is important to know how the data react to differences in sampling effort.

This analysis shows that connectance is robust to changes in sampling effort. The test of what model best describe the degree distribution also shows to be invariant to difference in sampling effort. The network shows, after a few days of field work, to be nested, and this does not change as the amount of data grows. The three factors mentioned above can thus be obtained with a relatively small sampling effort. They are scale-invariant and therefore usable to compare different networks. Nestedness temperature correlate negative with network size. This has the consequences that the nestedness temperature is dependent on sampling effort, and can not be uniquely defined for a network. This also means that nestedness temperature can not be compared between different networks, as a similar sampling effort can not be ensured.

I propose that nestedness temperature can be described as a function of  $S$ . Thus providing a method to determine which of two networks have a more nested structure, even in networks of different sizes.

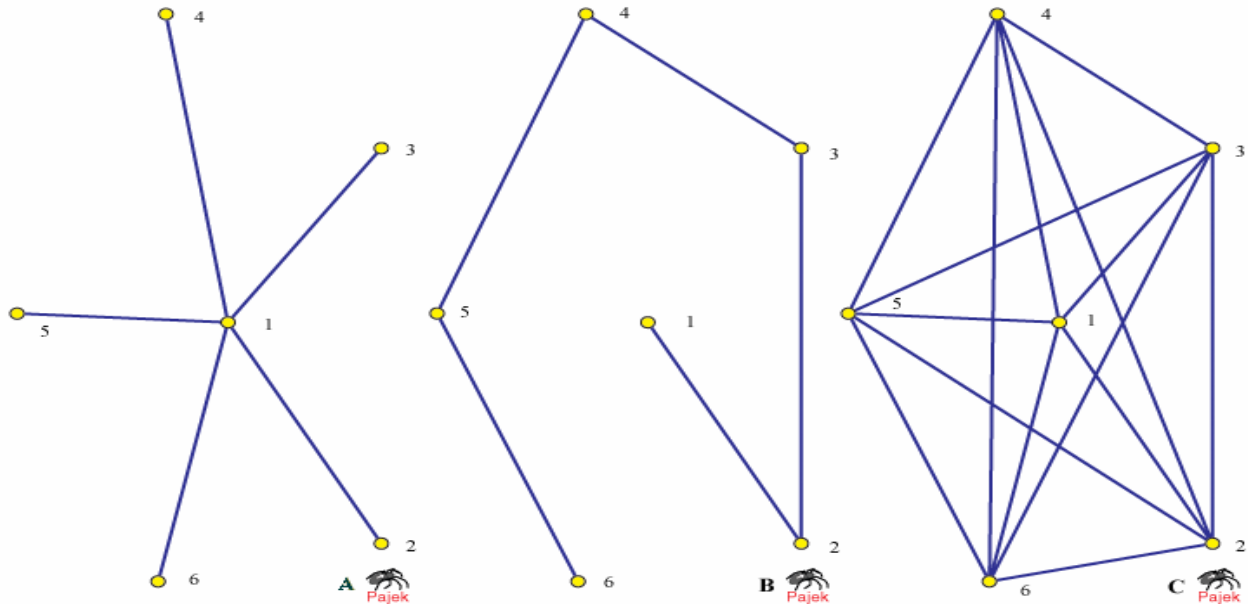
This study suggests that centralization has the potential to provide important information about pollinator networks' structure and stability. Still there is a need for a precise ecological interpretation of centralization, in regards to pollination networks.

Future pollination networks, considering sampling effort, are needed to show if these findings are general.

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## List of Figures



**Figure 1**

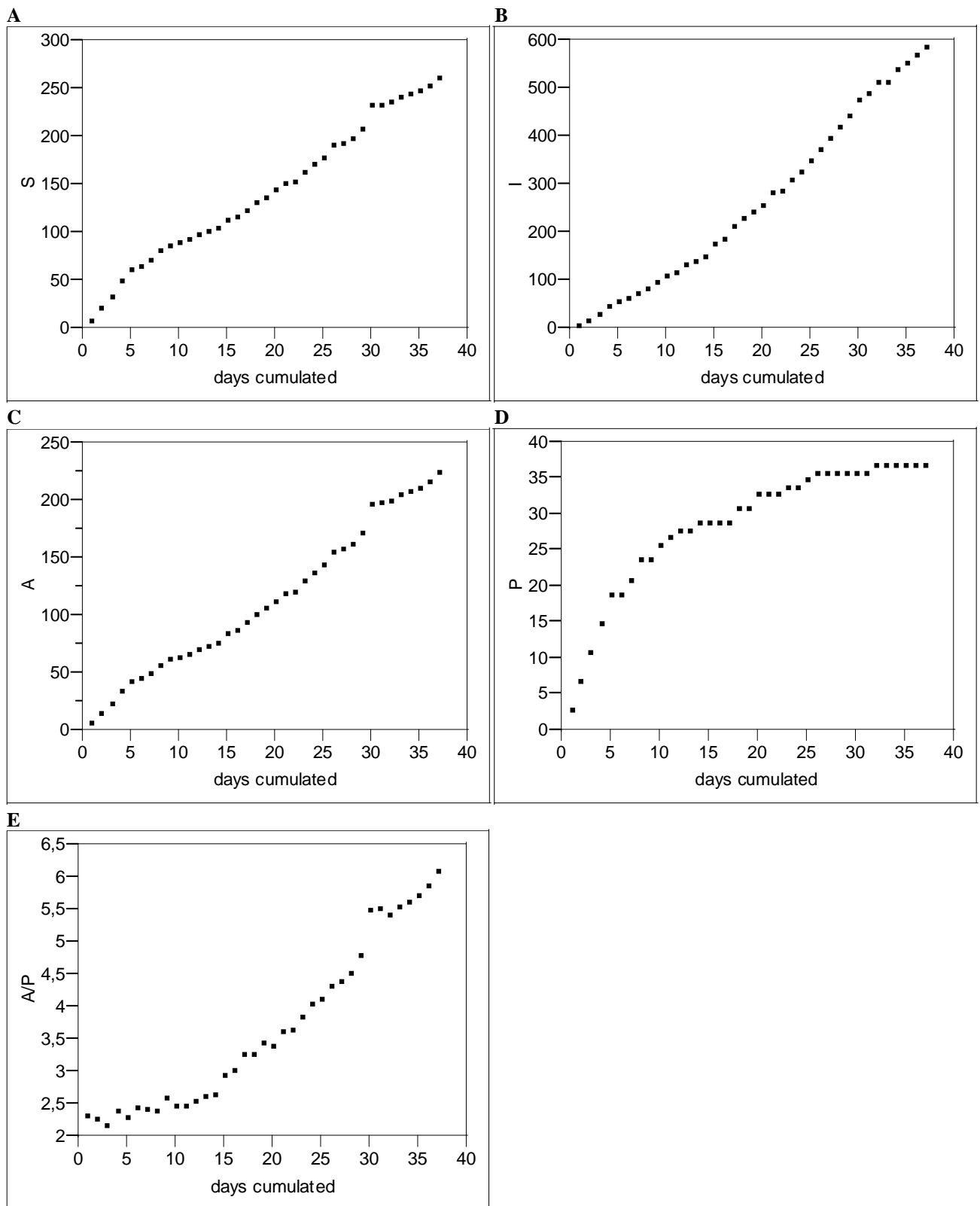
Three examples of one-mode networks, a circle (1-6) represent a species, a line represents an interaction between two species.

$$k_{net} = \frac{\sum_{i=1}^n (k_{max} - k_i)}{\sum_{i=1}^n (k_{max} - k_i)_{ideal}}$$

**Figure 2**

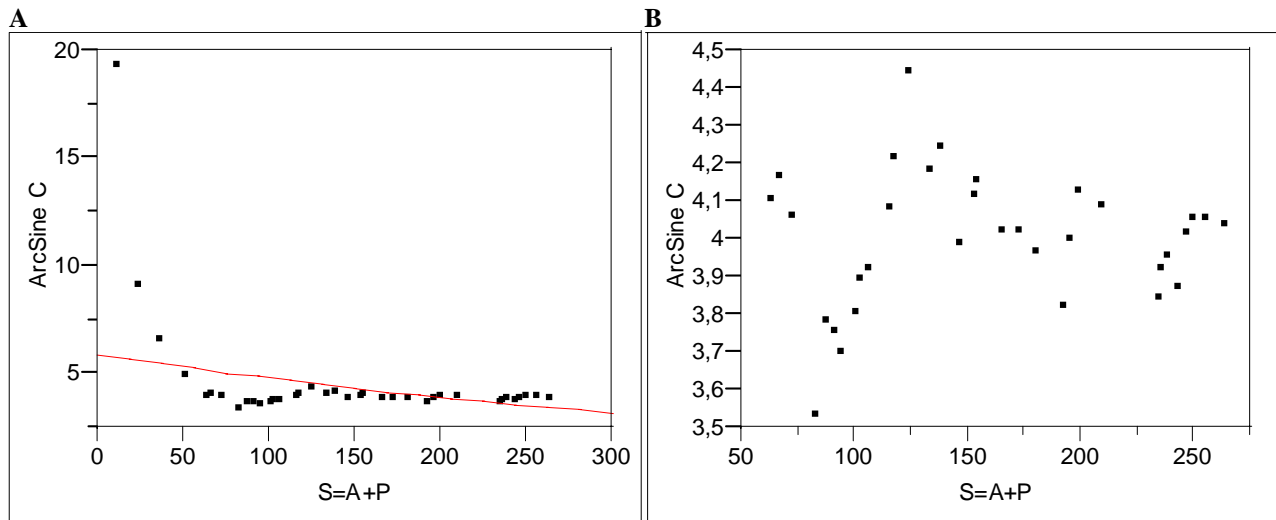
The equation for calculating degree centralization  $k_i$  is the degree centrality for species  $i$ ,  $k_{max}$  is the highest degree centrality in the network. The formula in the denominator is the equivalent value for an idealized network of maximum variation of the same size, like example A in Figure 1.





**Figure 3**

A: network size plottet against each cumulated network from 1 to 37. B: numbers of interactions, C: numbers of pollinator species, D: numbers of plant species and E: pollinator-plant ratio plottet against each cumulated network from 1 to 37.

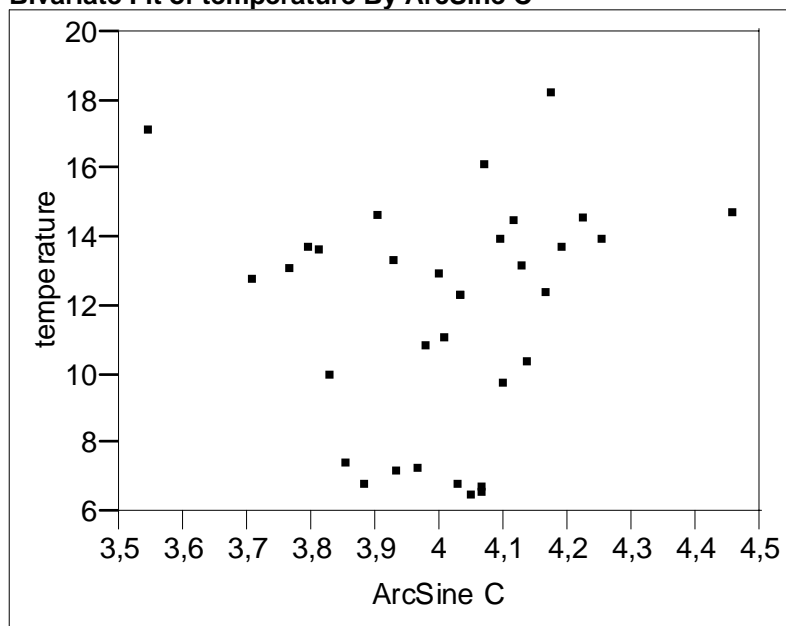


**Figure 4**

A: Regression analysis of connectance vs. network size:  $\text{Log}(\text{Arcsin } C) = 1.768 + 0.002S$ ,  $\text{Rsquare adj.} = 0.22$ ,  $F_{1,35} = 10.89$ ,  $P \leq 0.0022$

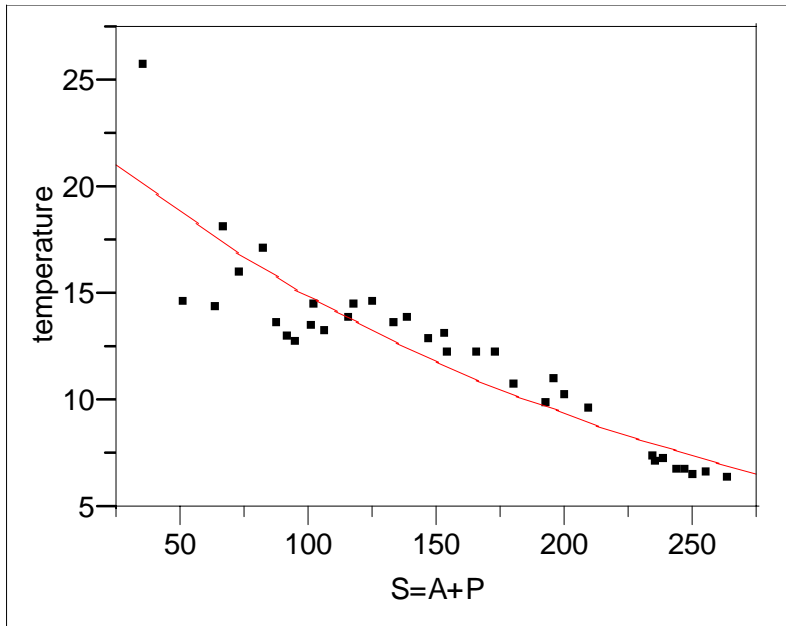
B: The same analysis without the initial behaviour of the first four days:  $\text{Log}(\text{Arcsin } C) = 1.378 + 0.0001S$ ,  $\text{Rsquare adj.} = 0.00$ ,  $F_{1,31} = 0.24$ ,  $P \leq 0.6303$

**Bivariate Fit of temperature By ArcSine C**



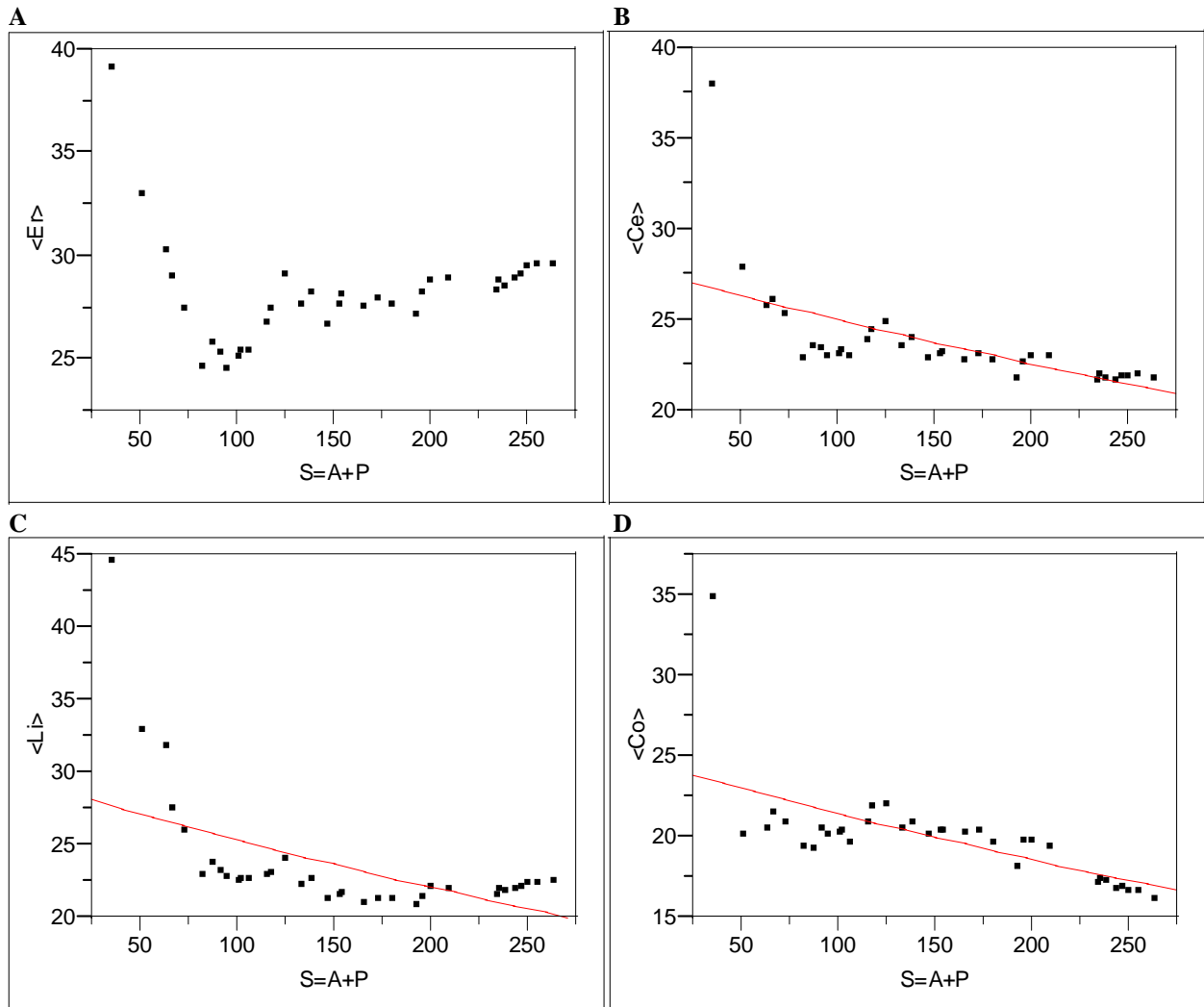
**Figure 5**

Regression analysis of nestedness temperature vs. connectance:  $\text{Log}(nt) = 1.796 + 0.458\text{Log}(\text{ArcSin } C)$ ,  $\text{Rsquare adj.} = 0.00$ ,  $F_{1,31} = 0.14$ ,  $P \leq 0.7142$



**Figure 6**

Regression analysis of nestedness temperature vs. network size:  $\text{Log}(\text{Nt}) = 3.117 - 0.005S$ ,  $\text{Rsquare adj.} = 0.88$ ,  $F_{1,33} = 241.14$ ,  $P \leq 0.0001$



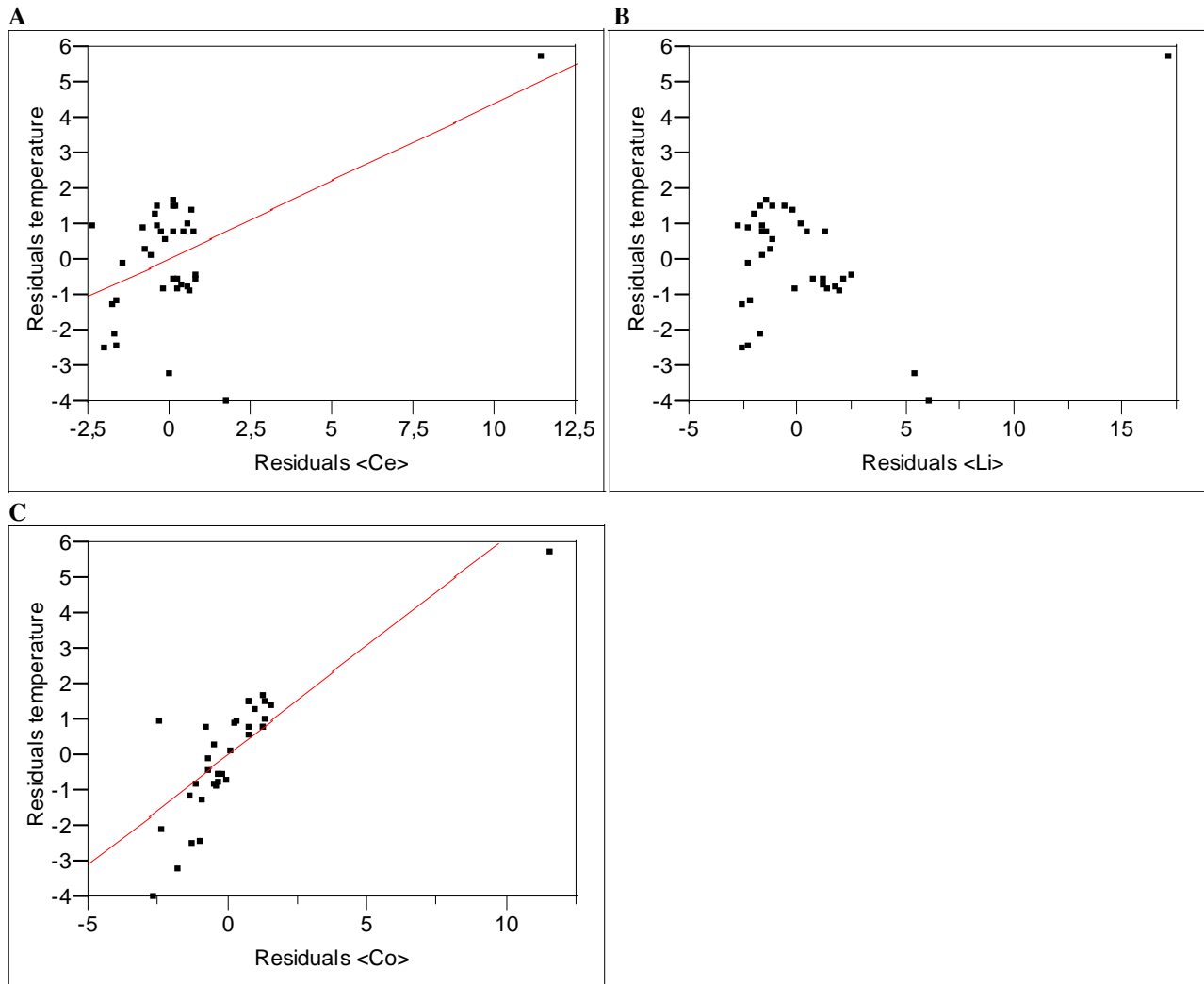
**Figure 7.**

A: A regression analysis of Er vs. network size (S):  $\text{Log(Er)} = 3.328 + 0.0001S$ ,  $\text{Rsquare adj.} = 0.00$ ,  $F_{1,33} = 0.11$ ,  $P \leq 0.7422$

B: A regression analysis of Ce vs. S:  $\text{Log(Ce)} = 3.322 - 0.001S$ ,  $\text{Rsquare adj.} = 0.45$ ,  $F_{1,33} = 29.34$ ,  $P \leq 0.0001$

C: A regression analysis of Li vs. S:  $\text{Log(Li)} = 3.369 - 0.001S$ ,  $\text{Rsquare adj.} = 0.36$ ,  $F_{1,33} = 20.08$ ,  $P \leq 0.0001$

D: A regression analysis of Co vs. S:  $\text{Log(Co)} = 3.206 - 0.001S$ ,  $\text{Rsquare adj.} = 0.52$ ,  $F_{1,33} = 38.52$ ,  $P \leq 0.0001$

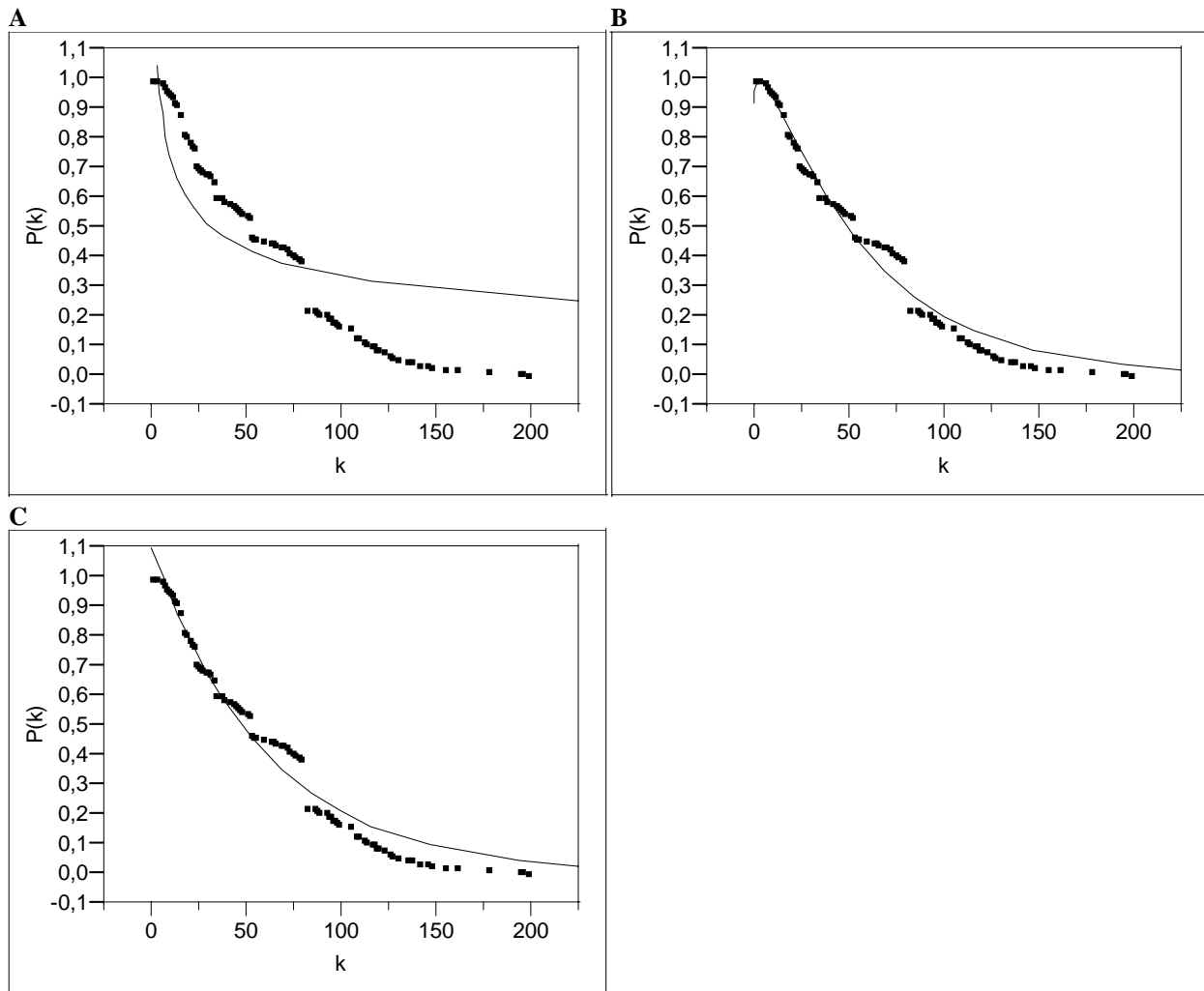


**Figure 8**

A: A regression analysis of the residuals of the analysis in Figure 6 vs.the residuals of analysis B in Figure 7: residuals  $Nt = 0.039 + 0.457 \text{ residuals Ce}$ ,  $R_{\text{square adj.}} = 0.28$ ,  $F_{1,33} = 14.28$ ,  $P \leq 0.0006$ ).

B: A regression analysis of the residuals of the analysis in Figure 6 vs.the residuals of analysis C in Figure 7: residuals  $Nt = 0.048 + 0.113 \text{ residuals Li}$ ,  $R_{\text{square adj.}} = 0.03$ ,  $F_{1,33} = 1.95$ ,  $P \leq 0.1722$

C: A regression analysis of the residuals of the analysis in Figure 6 vs.the residuals of analysis D in Figure 7: residuals  $Nt = 0.014 + 0.620 \text{ residuals Co}$ ,  $R_{\text{square adj.}} = 0.65$ ,  $F_{1,33} = 66.85$ ,  $P \leq 0.0001$



**Figure 9**

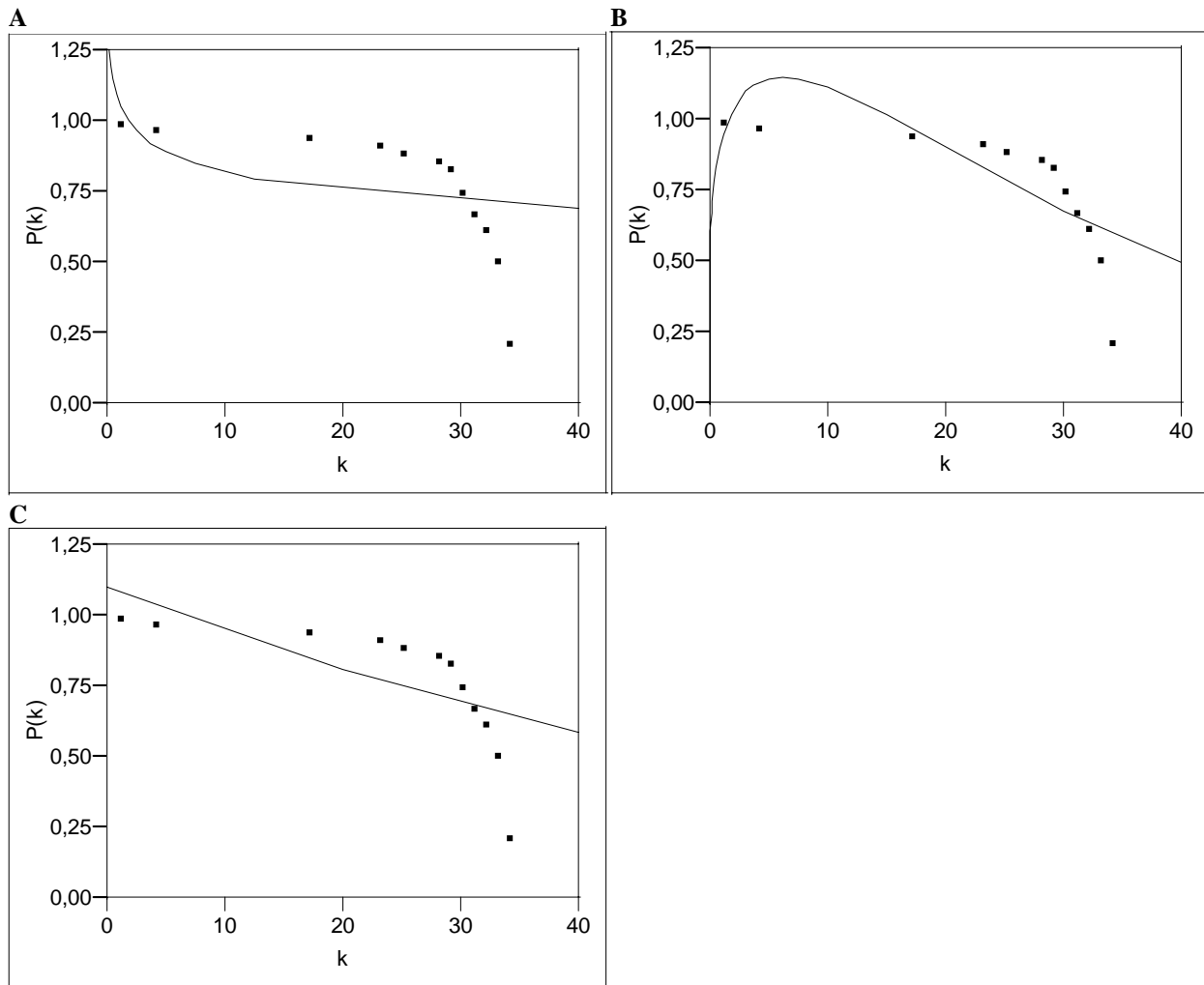
Three models fitted to the degree distribution of the pollinator network. The notation on the Y axis should be  $P(\geq k)$ .

A: The first model is the power law model  $P(\geq k) = 1.69 k^{-0.35}$  SSE = 3.00

B: Is the truncated power law model  $P(\geq k) = 0.98 k^{0.07} \cdot \text{Exp}(-k/52.51)$  SSE = 0.18

C: Is the exponential model  $P(\geq k) = 1.11 \cdot \text{Exp}(-0.02 \cdot k)$  SSE = 0.21

Model B had the lowest SSE value, this shows that the data had the best fit to the truncated model.



**Figure 10**

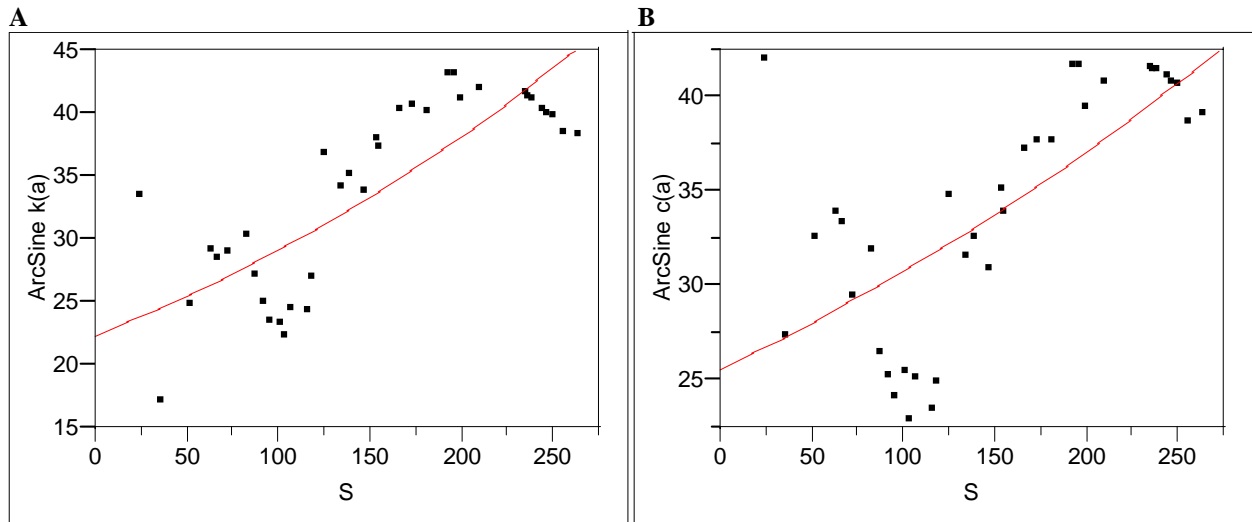
Three models fitted to the degree distribution of the plant network. The notation on the Y axis should be  $P(\geq k)$ .

A: The first model is the power law model  $P(\geq k) = 1.08 k^{-0.12}$  SSE = 0.42

B: Is the truncated power law model  $P(\geq k) = 0.95 k^{0.23} \cdot \text{Exp}(-k/26.66)$  SSE = 0.26

C: Is the exponential model  $P(\geq k) = 1.10 \cdot \text{Exp}(-0.02 \cdot k)$  SSE = 0.32

Model B had the lowest SSE value, this shows that the data had the best fit to the truncated model

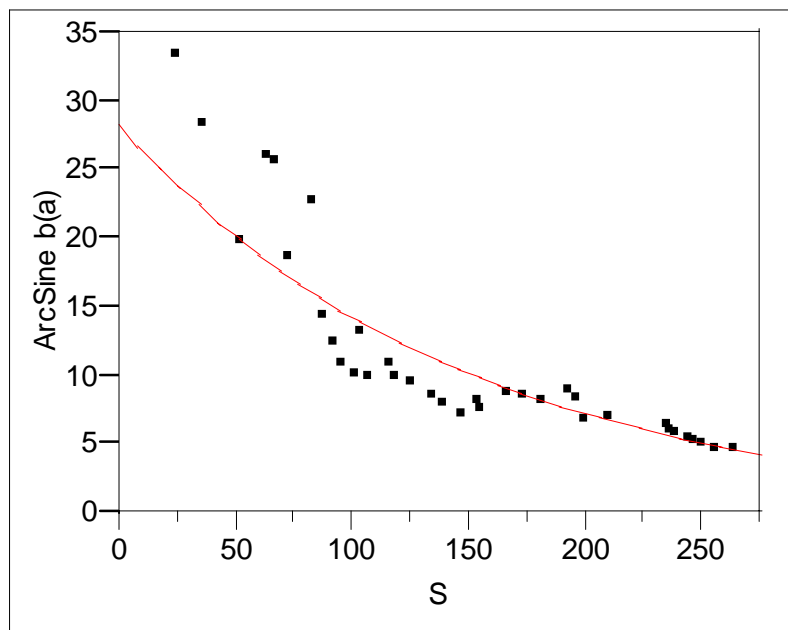


**Figure 11**

Centralization of the one-mode pollinator network.

A: A regression analysis of  $k(a)_{\text{net}}$  vs. network size:  $\text{Log}(\text{Arcsin } k(a)_{\text{net}}) = 3.105 + 0.003S$ ,  $\text{Rsquare adj.} = 0.60$ ,  $F_{1,34} = 53.54$ ,  $P \leq 0.0001$

B: A regression analysis of  $c(a)_{\text{net}}$  vs. network size:  $\text{Log}(\text{Arcsin } c(a)_{\text{net}}) = 3.242 + 0.002S$ ,  $\text{Rsquare adj.} = 0.41$ ,  $F_{1,34} = 25.78$ ,  $P \leq 0.0001$

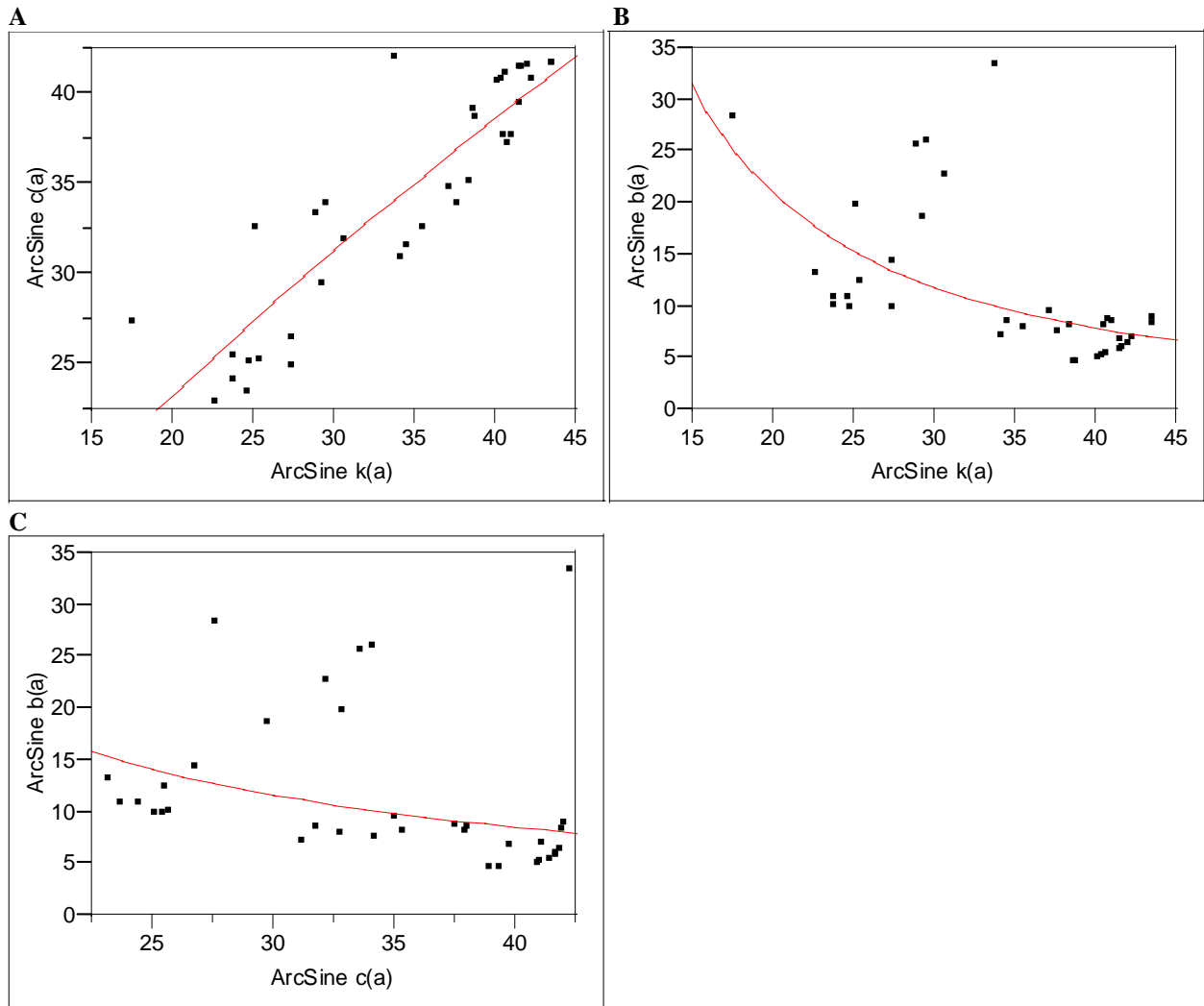


**Figure 12**

Betweenness centralization of the one-mode pollinator network.

Regression analysis of  $b(a)_{\text{net}}$  vs. network size:  $\text{Log}(\text{Arcsin } b(a)_{\text{net}}) = 3.346 - 0.007S$ ,  $\text{Rsquare adj.} = 0.84$ ,  $F_{1,34} = 191.04$ ,  $P \leq 0.0001$





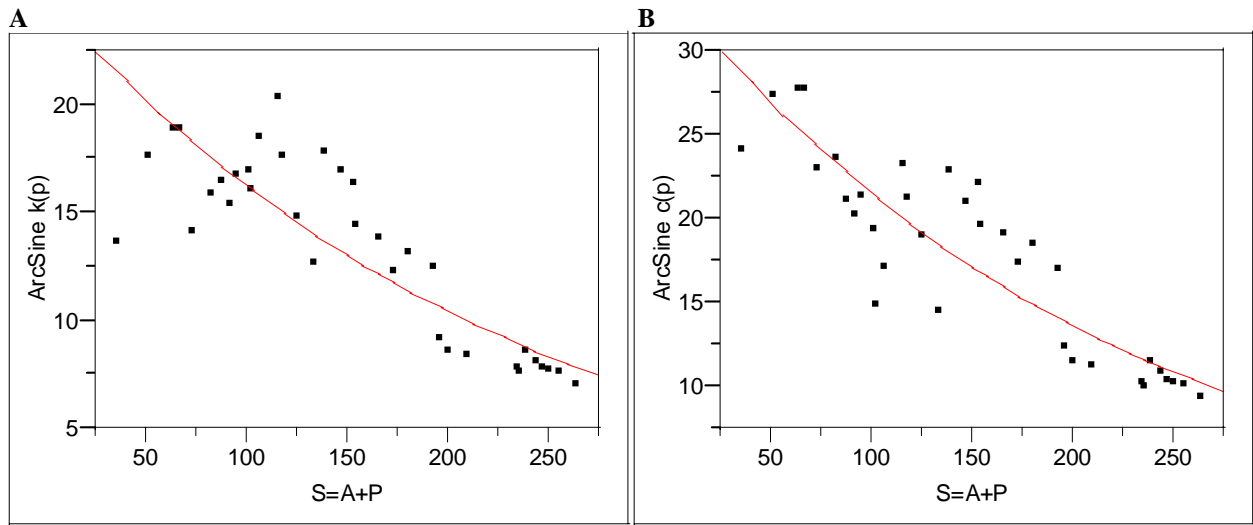
**Figure 13.**

Centralization of the one-mode pollinator network.

A: A regression analysis of  $c(a)_{\text{net}}$  vs.  $k(a)_{\text{net}}$ :  $\text{Log}(\text{Arcsin } c(a)_{\text{net}}) = 0.960 + 0.730\text{Log}(\text{Arcsin } k(a)_{\text{net}})$ ,  $\text{Rsquare adj.} = 0.77$ ,  $F_{1,34} = 119.09$ ,  $P \leq 0.0001$

B: A regression analysis of  $b(a)_{\text{net}}$  vs.  $k(a)_{\text{net}}$ :  $\text{Log}(\text{Arcsin } b(a)_{\text{net}}) = 7.296 - 1.420\text{Log}(\text{Arcsin } k(a)_{\text{net}})$ ,  $\text{Rsquare adj.} = 0.40$ ,  $F_{1,34} = 24.81$ ,  $P \leq 0.0001$

C: A regression analysis of  $b(a)_{\text{net}}$  vs.  $c(a)_{\text{net}}$ :  $\text{Log}(\text{Arcsin } b(a)_{\text{net}}) = 6.110 - 1.076\text{Log}(\text{Arcsin } c(a)_{\text{net}})$ ,  $\text{Rsquare adj.} = 0.14$ ,  $F_{1,34} = 6.78$ ,  $P \leq 0.0136$

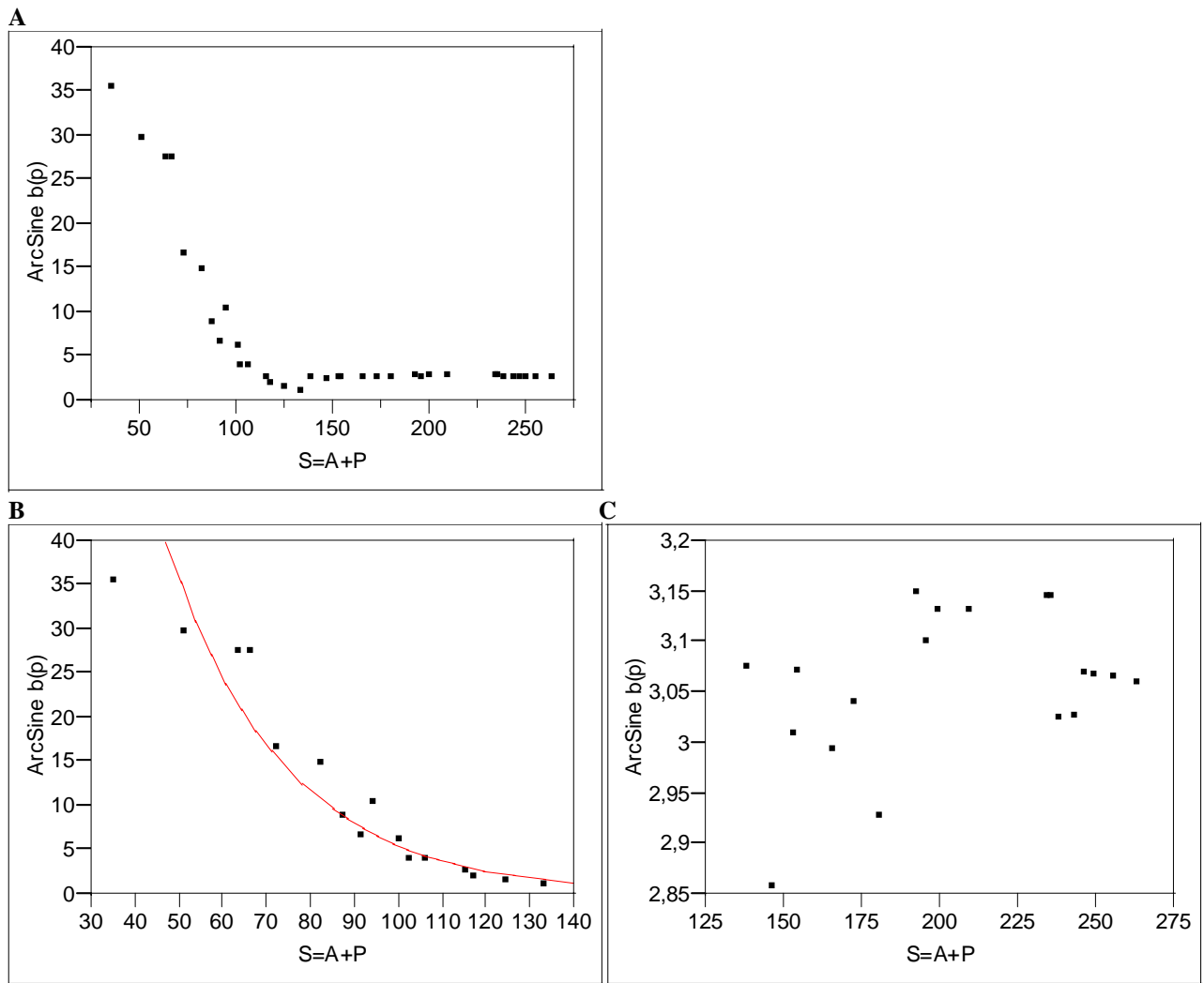


**Figure 14**

Centralization of the one-mode plant network.

A: Regression analysis of  $k(p)_{\text{net}}$  vs. S:  $\text{Log}(\text{Arcsin } k(p)_{\text{net}}) = 3.228 - 0.004S$ ,  $\text{Rsquare adj.} = 0.77$ ,  $F_{1,33} = 112.76$ ,  $P \leq 0.0001$

B: Regression analysis of  $c(p)_{\text{net}}$  vs. S:  $\text{Log}(\text{Arcsin } c(p)_{\text{net}}) = 3.524 - 0.005S$ ,  $\text{Rsquare adj.} = 0.80$ ,  $F_{1,33} = 140.44$ ,  $P \leq 0.0001$



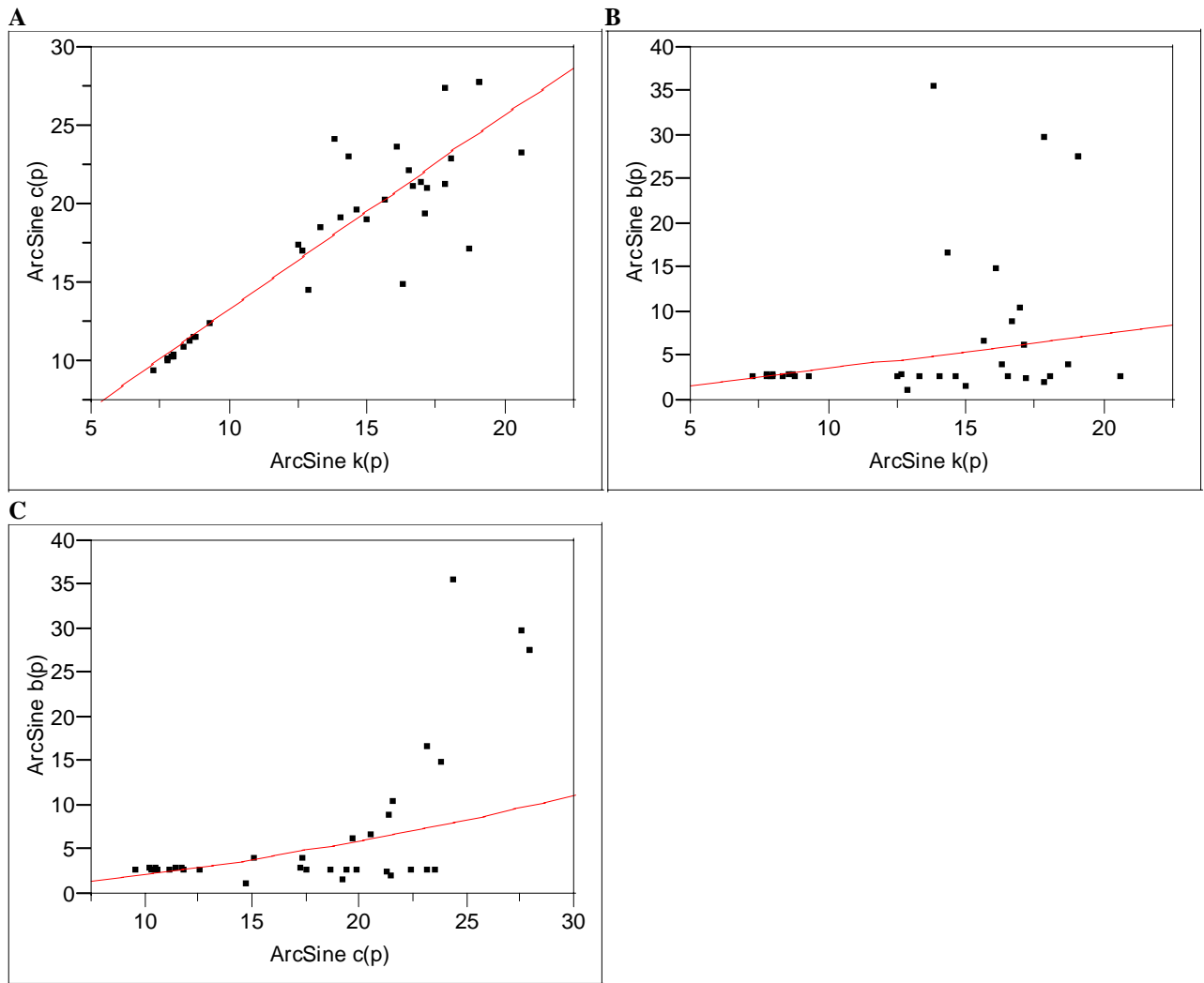
**Figure 15.**

Betweenness centralization of the one-mode plant network.

A:  $b(p)_{\text{net}}$  vs.  $S$  after day 18,  $b(p)_{\text{net}}$  is independent of  $S$ .

B: Day 3 to 18, regression analysis,  $\text{Log}(\text{Arcsin } b(p)_{\text{net}}) = 5.473 - 0.038S$ ,  $\text{Rsquare adj.} = 0.93$ ,  $F_{1,14} = 216.35$ ,  $P \leq 0.0001$

C: Day 19 to 37, regression analysis,  $\text{Log}(\text{Arcsin } b(p)_{\text{net}}) = 1.071 + 0.0002S$ ,  $\text{Rsquare adj.} = 0.10$ ,  $F_{1,17} = 2.93$ ,  $P \leq 0.1053$



**Figure 16**

Centralization of the one-mode plant network.

A: Regression analysis of  $c(p)_{\text{net}}$  vs.  $k(p)_{\text{net}}$ :  $\text{Log}(\text{Arcsin } c(p)_{\text{net}}) = 0.426 + 0.941\text{Log}(\text{Arcsin } k(p)_{\text{net}})$ ,  $\text{Rsquare adj.} = 0.87$ ,  $F_{1,33} = 221.59$ ,  $P \leq 0.0001$

B: Regression analysis of  $b(p)_{\text{net}}$  vs.  $k(p)_{\text{net}}$ :  $\text{Log}(\text{Arcsin } b(p)_{\text{net}}) = -1.121 + 1.048\text{Log}(\text{Arcsin } k(p)_{\text{net}})$ ,  $\text{Rsquare adj.} = 0.15$ ,  $F_{1,33} = 6.83$ ,  $P \leq 0.0134$

C: Regression analysis of  $b(p)_{\text{net}}$  vs.  $c(p)_{\text{net}}$ :  $\text{Log}(\text{Arcsin } b(p)_{\text{net}}) = 02.674 + 1.495\text{Log}(\text{Arcsin } c(p)_{\text{net}})$ ,  $\text{Rsquare adj.} = 0.33$ ,  $F_{1,33} = 18.12$ ,  $P \leq 0.0002$

## Chapter 3

### Analyses of the timeslice networks



**Foto:** *Pieris napa* visiting *Lotus uliginosus*

by Søren Bek

## Introduction

A cumulative network is a static image of all species and interactions observed in a study period. However, the true ecological network is dynamic and changes in the course of the season. To illustrate this a timeslice network was constructed for each field day as described in chapter 1. Timeslice networks have two large advantages compared to cumulative networks: they reveal the temporal dynamics of the ecological network as it changes during the season, and they make it possible to study networks without phenological forbidden interactions.

As described in chapter 1, a timeslice network is constructed not only from the observations of the actual field day, but also from the previous and coming observations. This has the advantage that even if the observations of the individual field day only discover a fraction on the interactions, the corresponding timeslice network will still be a reliable representation of the ecological network of that day.

Only a few studies have tried to describe the temporal dynamics of pollination networks. Two studies have illustrated temporal network dynamics as a continuous series of cumulative networks (Lundgren and Olesen 2005; Kaiser 2006). Each temporal network was made from cumulating the results of three field days (Lundgren and Olesen 2005), or a fortnight of observations (Kaiser 2006). The disadvantages of making a series of cumulative networks instead of timeslice networks are: A long observation period per network will result in a low temporal resolution and the possibility of sampling phenological forbidden interactions. A short observation period per network increases the risk of missing rare interactions.

Chapter 2 is concentrating on one network with variation in the sampling period, this chapter is considering 37 different networks. The aim of this chapter is to describe the temporal dynamics of the pollination network. This is done by observing the changes of the network parameters, described in chapter 2, as they changes during the course of the season.

A consequence of the way in which the timeslice networks are constructed is that the networks in the beginning and near the end of the study season are made from a weaker dataset than the networks in the centre of the study season. To avoid errors that occur because of these weak networks the four first and four last networks were excluded from the investigation.

## **Methods**

### **Temporal dynamics of the descriptive characters**

The changes of the network properties, network size (S), number of Interactions (I), number of pollinators (A), number of plants (P) and pollinator-plant ratio (A/P) during the season were illustrated by plotting network properties against field days.

### **Connectance**

Connectance (C) is defined in chapter 1. C was plotted against days, and tested with a regression analysis for correlation with S. C was log arcsin transformed to obtain normality.

### **Nestedness temperature**

Nestedness temperature (Nt) is defined in chapter 1. Nt was plotted against days. Nestedness temperature change with S and C, therefore networks of different sizes and density can not be directly compared (Rodrigz-Gironés and Santamariá 2006). To enable a valid comparison the Nt was tested with a regression analysis for correlation with S and C. The Nt corrected for correlation with S, was then plotted against days.

### **Degree distribution**

Degree distribution, the power law model, the truncated power law model and the exponential model are defined in chapter 2. The degree distribution of all one-mode pollinator networks were calculated and tested in order to determine which of the three distribution models they had the best fit. The degree distribution of all one-mode plant networks was calculated. The first 15 plant networks and spot samples of the last 22 networks were tested to see to which of the three models they had the best fit. Spot samples of the last 22 networks were sufficient as these networks were very similar.

## Centralization

Three measures of centralization were used: degree centralization ( $k_{\text{net}}$ ), closeness centralization ( $c_{\text{net}}$ ) and betweenness centralization ( $b_{\text{net}}$ ), all being defined in chapter 2. These three measures of centralization were calculated for each of the one-mode plant networks (p) and the one-mode pollinator networks (a). The centralization values were plotted against field days to visualize the changes in centralization over the season.



## Results

### Temporal dynamics of the descriptive characters

There is a steady increase in network size (S) and numbers of pollinators (A), throughout the season (Figure 1a and c). Number of interactions (I) also increased but after day 25 it declined (Figure 1b). The number of plants was close to constant (Figure 1 d). The pollinator-plant ratio (A/P) increased throughout the season: from  $A/P = 1$  at day 5 to  $A/P = 4$  at day 30 (Figure 1e).

### Connectance

Connectance (C) was constant throughout the season, with a large variance (Figure 2a). There was no correlation between C and S (Figure 2b).

### Nestedness temperature

The nestedness temperature (Nt) increased from day 5 to day 14, after which it decreased throughout the rest of the season (Figure 3a). Nt was significantly negatively correlated to (S) but independent of C (Figure 3b and c). Therefore Nt was corrected for S only. The size-corrected Nt showed a steep increase in the beginning of the season, and decreased through the rest of the season (Figure 3d).

### Degree distribution

All pollinator and plant networks had a best fit to the truncated power law model.

The plant networks had a weaker fit than the pollinator networks, because more high k species were present than expected from the model.

### Centralization in the one-mode pollinator network

Degree centralization ( $k(a)_{\text{net}}$ ) and closeness centralization ( $c(a)_{\text{net}}$ ) decreased throughout the season (Figure 4a and b). Betweenness centralization ( $b(a)_{\text{net}}$ ) decreased and reached a plateau at day 20. (Figure 4c).

**Centralization in the one-mode plant network**

$k(p)_{\text{net}}$ ,  $c(p)_{\text{net}}$  and  $b(p)_{\text{net}}$  all declined from the beginning of the season, and finally reached a steady level.  $k(p)_{\text{net}}$  and  $c(p)_{\text{net}}$  reached the steady level at day 15 (Figure 5a and b).  $b(p)_{\text{net}}$  came very close to zero after day 12 (Figure 5c).

## Discussion

### Temporal dynamics of the descriptive characters

The number of plants (P) was virtually unchanged throughout the season, while the number of pollinators (A) increased (Figure 1c and d). This resulted in a four fold increase in the A/P ratio during the season (Figure 1e). The increase in the A/P ratio indicates that many insects emerge late in the season and only have a short overlap with the study season. However another explanation could be that the pattern was an artefact of a phytocentric sampling. Many pollination networks are phytocentrically biased because it is the plant species that are observed and their interactions that are sampled (Jordano 2006). If this is the case, then pollinators that enter in the meadow late in the season, could be migrants from other places, and thus be part of a larger pollination network.

In chapter 2, the increase network parameters were interpreted as evidence that the season had not yet peaked. The increase of S and A gives some support to this view, but the decline in number of interactions (I) towards the end of the season suggests that the activity period peaks at day 25.

A study of the seasonal variation of descriptive network characters in an arctic pollination system (Lundgren and Olesen 2005) showed great variation from one temporal network to the next. The characters fluctuate with two separate periods of peak activity. Compared to the arctic system, the continuity of the network parameters of the Moesgaard Have networks was striking. All changes occurred gradually over the course of the season. Some of the differences between the fluctuating of the arctic network and the continuity of the network parameters in the Moesgaard Have study, can be explained by the different ways the temporal networks were constructed. The timeslice networks are insensitive towards periods of low activity, e.g. a cold period in the middle of the season. The method used to construct the temporal networks of the arctic study, is vulnerable to sampling errors due to an underestimation of the number of rare interactions.

### Connectance

Connectance (C) was independent of network size and there was no large seasonal change (Figure 2). However a study that compared a series of pollination networks sampled in a period of half a year, showed great temporal variation in C, and a trend towards a negative correlation between C and S (Kaiser 2006). In Kaiser's study, each of the temporal networks was made by cumulating observations made over a period of two weeks. The different approaches to show the temporal dynamics of the networks, may account for the different findings. The variation Kaiser found in the

connectance values could be an artefact of a method that does not eliminate phenologically forbidden interactions. Another, maybe more obvious, explanation for the difference in the temporal behaviour of C, is that the field season in the Moesgaard Have network, was not sufficiently long to record the variation in C (two months, opposed to Kaiser's six months).

### **Nestedness temperature**

The networks in the middle of the season were the least nested (Figure 3d). To discover the mechanism behind this, it is necessary to look at the individual nestedness matrices to see how individual interactions emerge and disappear from day to day.

A nested network is built up around a core of closely interlinked generalist species, to which all other species are connected. In the beginning of the field season the plant species *Anthriscus sylvestris* was the most generalistic plant species, whereas at the end of the season *Angelica sylvestris* was the most generalistic plant species. There was neither a temporal overlap between the flowering of these two species, nor were the nine most generalistic pollinator species, mentioned in chapter 1, present throughout the whole study period. One possible explanation of the observed changes in nestedness temperature is that a core of closely interconnected early summer species breaks up and are replaced by a new core of late summer species. This could be tested by a compartment analysis, but that is beyond the scope of this paper.

### **Degree distribution**

The degree distribution of all timeslice networks, both plant and animals were best described by a truncated power law model. No seasonal changes were found. Kaiser (2006) found great variation throughout the season. The degree distribution of the plant networks shifted between having a best fit to a truncated power law model and an exponential model. The degree distribution of the pollinator networks varied between having a best fit to all three models. This difference could be an indication that the Moesgaard Have network is very stable, or it can be an artefact of the difference in the construction of the temporal networks.

## **Centralization**

When looking at seasonal changes, the centralization measures all showed the same tendencies. All centralization levels dropped from the beginning of the season until they reached a steady and low level (Figure 4 and 5). Biologically, such a seasonal change can be explained by the following. In the beginning of the season, there was a core of high  $k$  species, and an array of more loosely connected species. As the season progresses the loosely connected species form additional links creating a more connected network. The network is most vulnerable to the loss of key species in the beginning of the season (for a explanation of the ecological consequences of changes in the centralization, see the method section in chapter 2). This means that pollinator species which are only active in the beginning of the season, and plant species that only flower in the beginning of the season are more vulnerable to disturbances, involving the key species, than species which are active later in the season. These findings would not have turned up in an analysis of a cumulative network, and thus illustrate the importance of adding the analyses timeslice networks, to the traditional cumulative network analyses.

## Conclusion

Analyses of the temporal dynamics of a pollination network reveal patterns that are hidden in a cumulative network. The finding that the number of pollinators increases throughout the season, while the number of interactions peaked at day 25 is interesting. This would not be seen in a cumulative network. Ecologist could use this knowledge to place short studies pollination diversity in a period near the 25'th observation day, while entomologist should wait a while longer to make collections. Another result that would not show in a cumulative network analysis is the changes in centralization throughout the season and the changes in network stability that can be deduced from this. If Moesgaard Have was a protected area special attention could be made to the conservation of generalist pollinator species that are active, and generalist plant species that flower, in the beginning of the season.

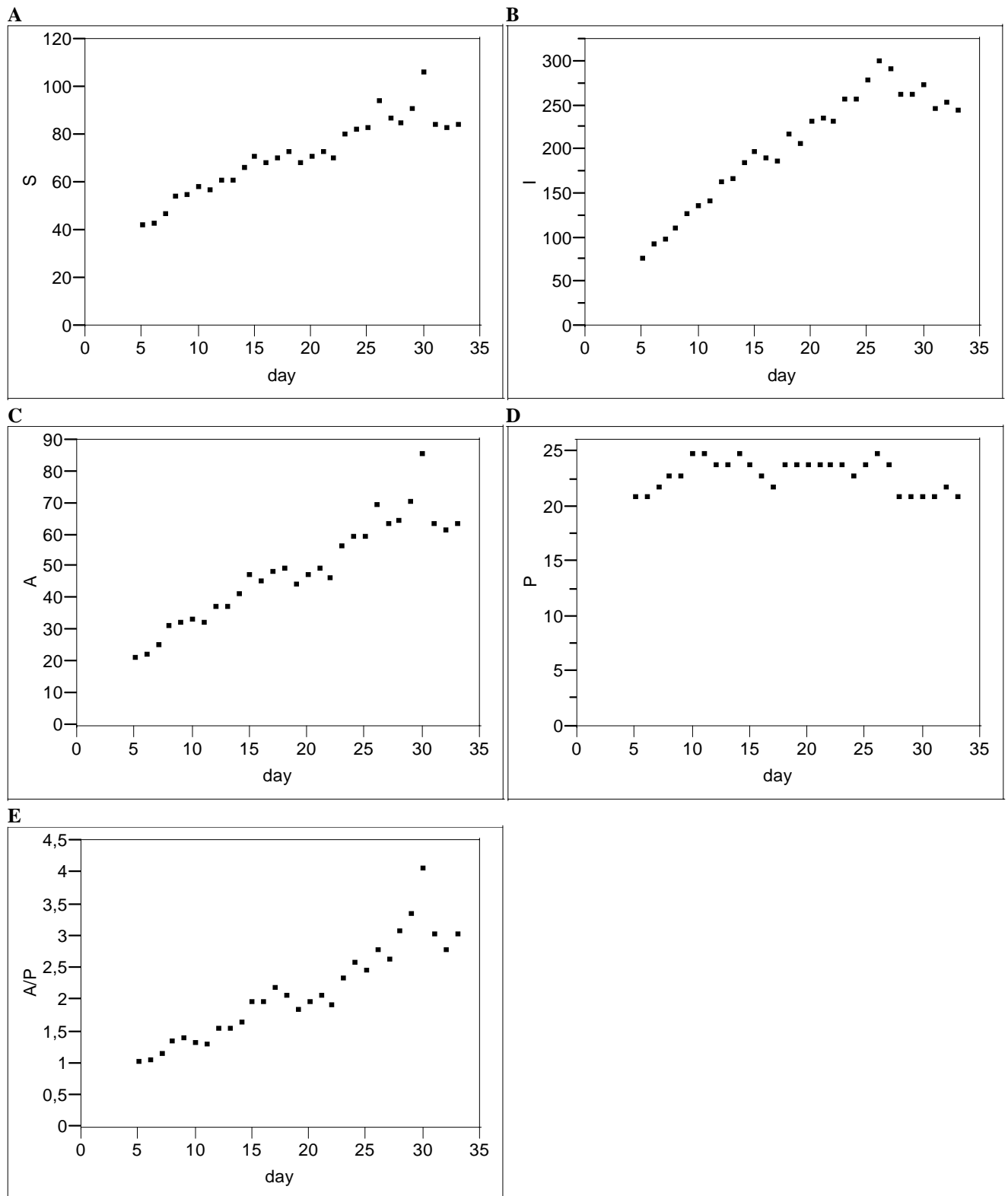
The timeslice approach to the temporal dynamics analysis also has some obvious advantages, compared to studies of continual series of cumulative networks. In timeslice networks there are no phenological forbidden interactions, and timeslice networks have a high temporal resolution, without the errors that occur because of a short sampling time.

Future analyses of timeslice networks will determine if the findings of this study, e.g. the temporal continuity, with gradually changes of the network parameters, and the scale invariance of the connectance, are general properties of timeslice networks, or if they change between different ecosystems or in a different climate.

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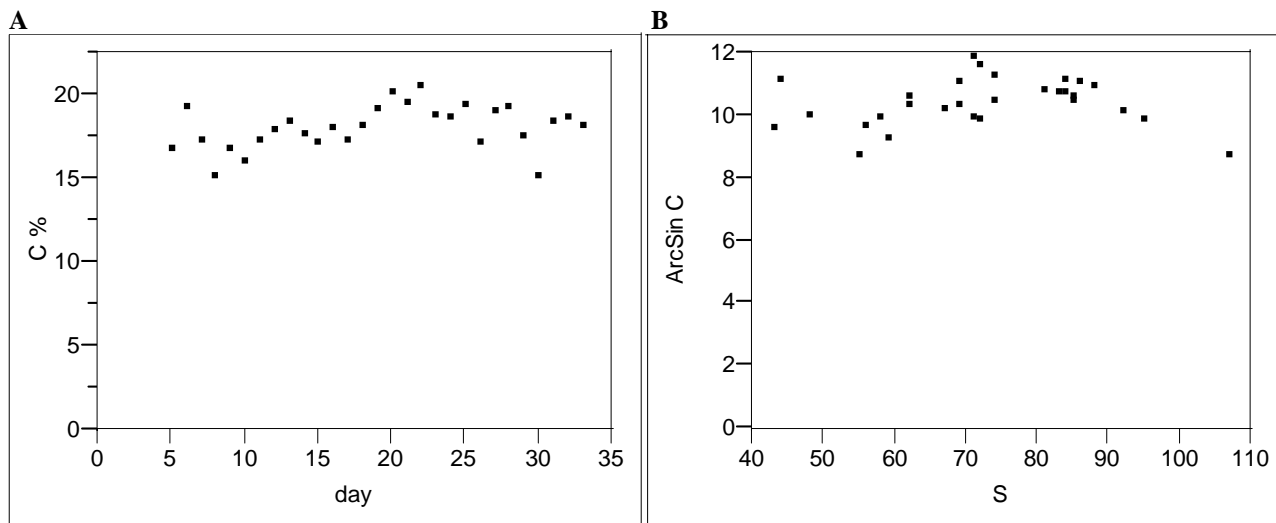
## List of Figures



**Figure 1**

A) The network size of the timeslice networks of field day 5-33. B) Number of interactions per day. C) Number of pollinator species per day. D) Number of plant species per day. E) The pollinator/plant ratio per day.

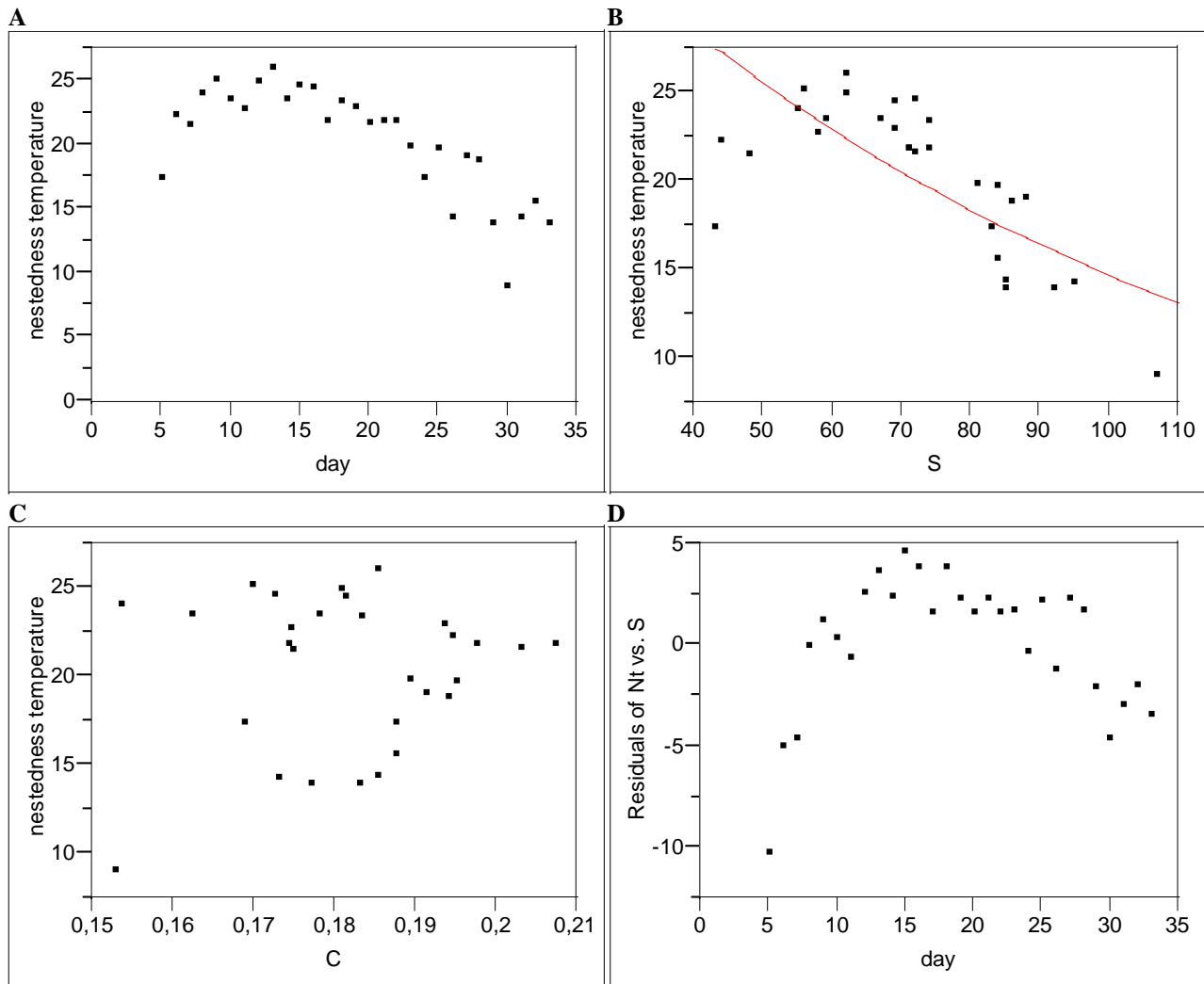




**Figure 2**

A: The connectance of each field day.

B: Regression analysis of conectance vs. network size:  $\text{Log}(\text{Arcsin } C) = 2.310 + 0.0005S$ ,  $\text{Rsquare adj.} = 0.00$ ,  $F_{1,37} = 0.29$ ,  $P \leq 0.5920$



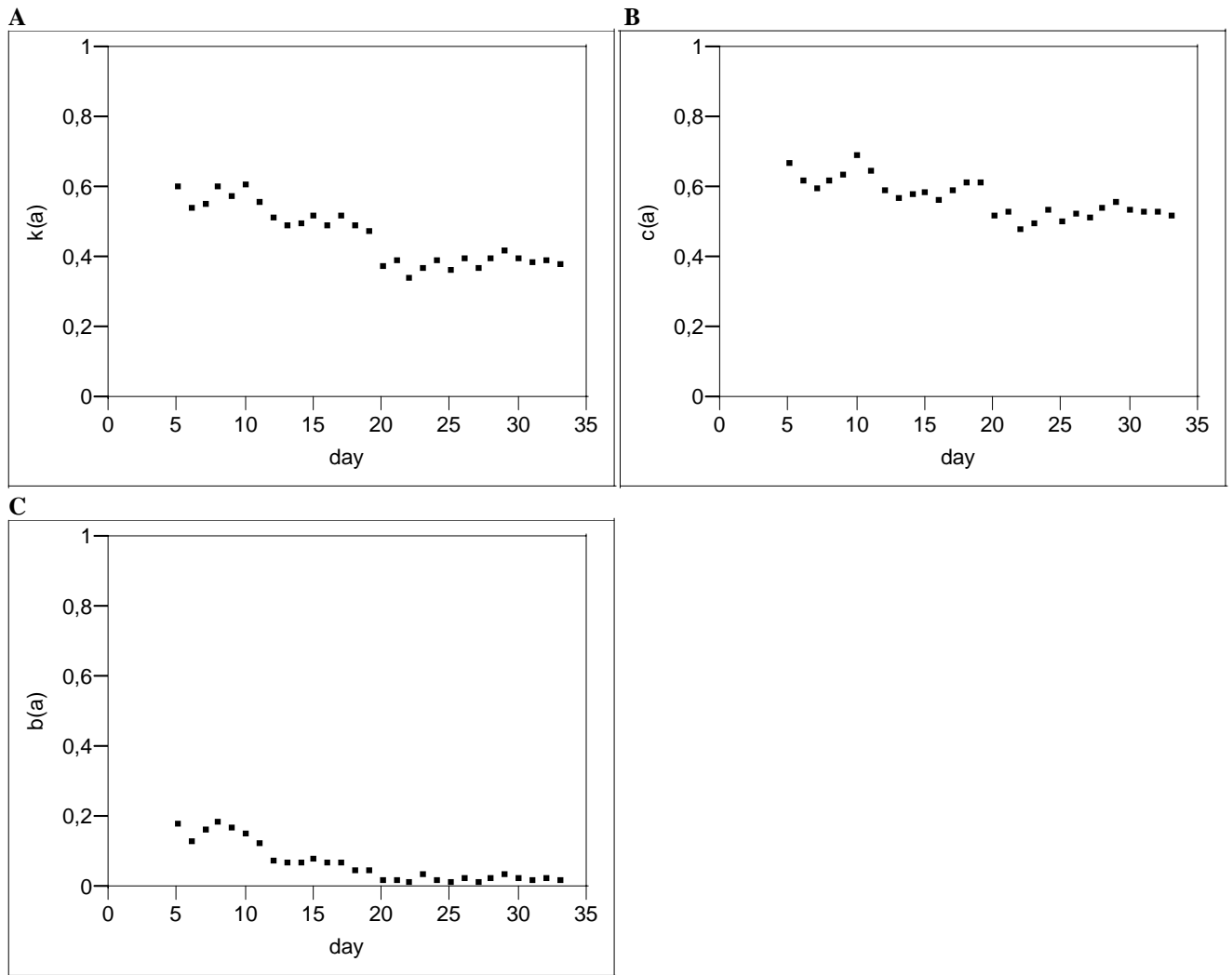
**Figure 3**

A: Nestedness temperature plotted against field days

B: Regression analysis of nestedness temperature vs. network size:  $\text{Log}(\text{Nt}) = 3.795 - 0.011\text{S}$ ,  $\text{Rsquare adj.} = 0.48$ ,  $F_{1,27} = 27.71$ ,  $P \leq 0.0001$

C: Regression analysis of nestedness temperature vs. Connectance:  $\text{Log}(\text{Nt}) = 2.346 + 3.568\text{C}$ ,  $\text{Rsquare adj.} = 0.002$ ,  $F_{1,27} = 1.07$ ,  $P \leq 0.3106$

D: The residuals of Nt vs. S plotted against field days



**Figure 4**  
 Centralization in the one-mode pollinator network  
 A: Degree centralization  $k(a)_{\text{net}}$  plottet against days.  
 B: Closeness centralization  $c(a)_{\text{net}}$  plottet against days.  
 C: Betweenness centralization  $b(a)_{\text{net}}$  plottet against days.

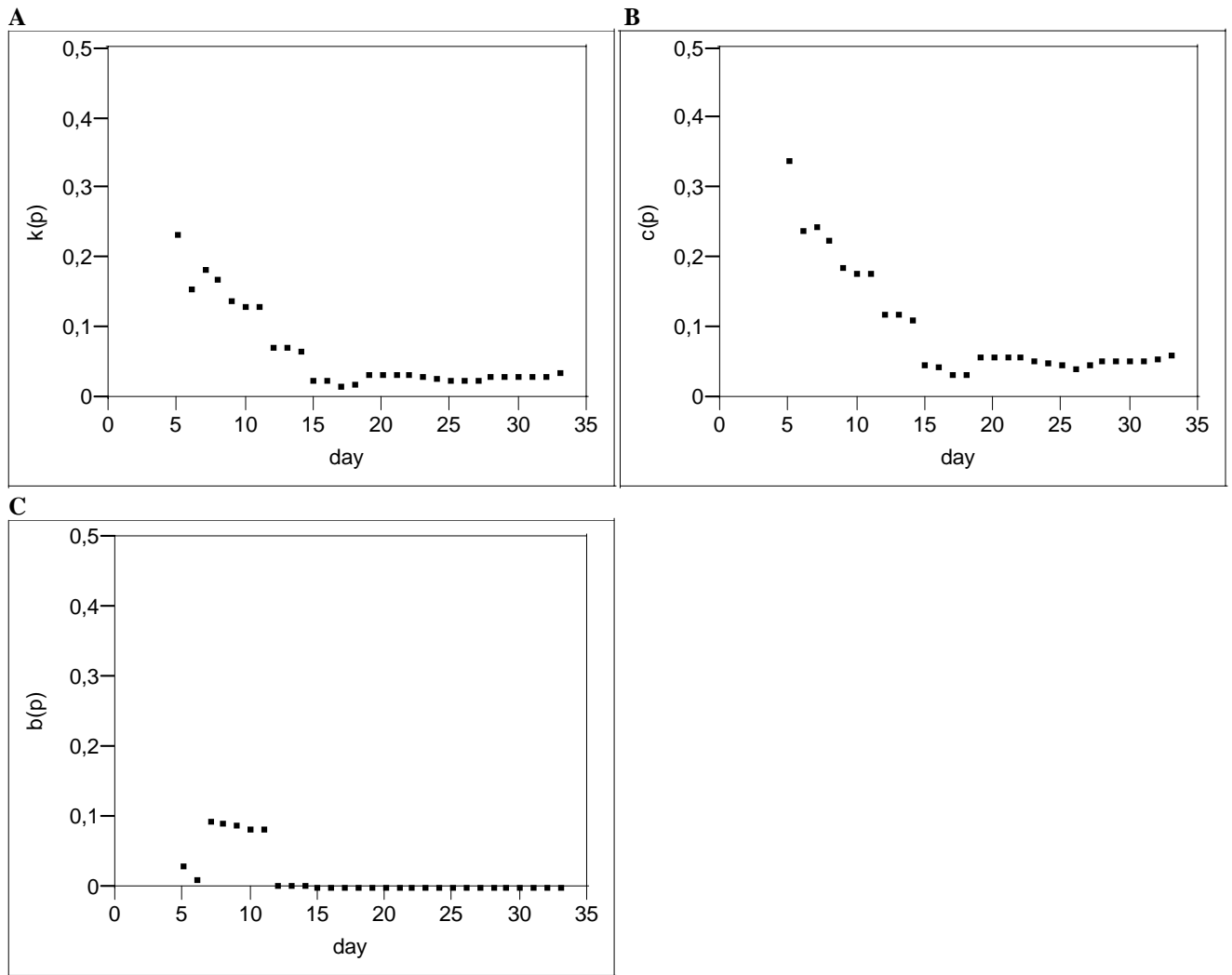


Figure 5  
 Centralization in the one-mode plant network  
 A: Degree centralization  $k(p)_{\text{net}}$  plotted against days.  
 B: Closeness centralization  $c(p)_{\text{net}}$  plotted against days.  
 C: Betweenness centralization  $b(p)_{\text{net}}$  plotted against days.

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**Foto:** *Homo sapiens* with *Pieris napa* in captivity.

by Anita S. Albrektsen