



Spatio-temporal variation in the structure of pollination networks

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Pollination networks are representations of all interactions between co-existing plants and their flower visiting animals at a given site. Although the study of networks has become a distinct sub-discipline in pollination biology, few studies have attempted to quantify spatio-temporal variation in species composition and structure of networks. We here investigate patterns of year-to-year change in pollination networks from six different sites spanning a large latitudinal gradient. We quantified level of species persistence and interactions among years, and examined year-to-year variation of network structural parameters in relation to latitude and sampling effort. In addition, we tested for correlations between annual variation in network parameters and short and long-term climate change variables. Numbers of plant and animal species and interactions were roughly constant from one year to another at all sites. However, composition of species and interactions changed from one year to another. Turnover was particularly high for flower visitors and interactions. On the other hand, network structural parameters (connectance, nestedness, modularity and centralization) remained remarkably constant between years, regardless of network size and latitude. Inter-annual variation of network parameters was not related to short or long term variation in climate variables (mean annual temperature and annual precipitation). We thus conclude that pollination networks are highly dynamic and variable in composition of species and interactions among years. However, general patterns of network structure remain constant, indicating that species may be replaced by topologically similar species. These results suggest that pollination networks are to some extent robust against factors affecting species occurrences.

In the past decade, network studies have become increasingly common in a wide range of ecological disciplines, especially in pollination ecology (Olesen et al. 2007, Ings et al. 2008). A pollination network encompasses all zoophilous plant species and their flower visiting animal species, and all their mutual interactions within a researcher-defined study site. Networks are often treated as static entities (but see Alarcón et al. 2008, Olesen et al. 2008, Petanidou et al. 2008). However, species composition and abundance together with strengths (efficiencies) of interactions changes locally (Traveset and Saez 1997, Dicks et al. 2002, Thompson 2005) and regionally across sites (Devoto et al. 2005, Thompson 2005, Dupont and Olesen 2009). Furthermore, pollination interactions may also change through the season (Herrera 1988, Traveset and Saez 1997, Basilio et al. 2006, Olesen et al. 2008) and from one year to another (Lundgren and Olesen 2005, Sahli and Connor 2007, Olesen et al. 2008, Petanidou et al. 2008). Thus, pollination networks are highly dynamic both spatially and temporally. Little is, however, known about the level of spatio-temporal variation. We here address this question by comparing highly resolved pollination networks for two to four years from six sites representing different habitat types, network sizes and latitudes.

Empirical network studies are time consuming, in particular when networks include a large number of species and an even greater number of interactions. Thus, sampling effort per species usually diminishes in large networks (Waser et al. 1996, Olesen and Jordano 2002). Other studies suffer from low taxonomic resolution, i.e. species are grouped into morpho-types or identified only to higher taxonomic levels (Waser et al. 1996, Dicks et al. 2002, Ings et al. 2008). Network studies often lack replication, and few networks are constructed using the same sampling protocol over several sites or years, thus being directly comparable (exceptions include Devoto et al. 2005, Alarcón et al. 2008, Petanidou et al. 2008, Dupont and Olesen 2009).

In spite of rigorous sampling protocols, networks are, in general, governed by variation in species occurrences and abundance patterns, in addition to phenologies of flowering plants and activity of foraging insects. This strongly affects the structure of the network. Interactions between plants and flower visitors may change because of (1) local extinction and colonization of species, and (2) rewiring, i.e. formation of new interactions among pre-existing species (Olesen et al. 2008). These biotic processes are affected by abiotic factors, e.g. climatic fluctuations (Alarcón et al. 2008). Recent concern about the impact of climate change also applies to

mutualistic networks (Memmott et al. 2007, Tylianakis et al. 2008). In the high arctic, which is exposed to the highest level of global warming, a recent study documented a rapid advancement of phenologies in various taxa (flowering, insect emergence, and egg laying in birds), some by up to 30 days during the last decade (Høye et al. 2007). If plant and flower visitor species respond differently to climate change, phenological shifts may result in flower visitor species suffering shortage of floral reward supplies (i.e. none of its food plants are blooming) during part of its activity period (Memmott et al. 2007, Tylianakis et al. 2008, Hegland et al. 2009). Similarly, plants may experience a shortage of pollinators during part of their flowering period. Hence, phenological shifts may have cascading consequences to species abundances and ultimately survival of species. On the other hand, opportunities for new interactions may arise. Climate change may thus have unforeseen consequences to the structure and dynamics of pollination networks. Moreover, temporal variation of networks may be found across latitudes due to differences in the magnitude and effects of climate change at different latitudes.

Here we investigate patterns of year-to-year variation in pollination networks from different geographical regions representing different latitudes and biomes (arctic, continental, Mediterranean). To avoid shortcomings of comparative networks studies mentioned above, we used well-sampled and highly resolved plant–flower visitor networks, which include all flowering plants above a certain abundance threshold and their flower visitors. We made yearly comparisons in networks having a fixed spatial and seasonal delimitation, similar levels of sampling effort, sampling method and identification of insects by the same taxonomical experts in all years of the study. We specifically attempt to answer the following questions:

1. What is the year-to-year variation among networks in turnover of species and interactions?
2. What is the year-to-year variation in network structural properties, and how do these properties vary with latitude and sampling effort?
3. To what extent can climate (annual precipitation and mean annual temperature) explain the variation observed in (1) and (2) during the study years and in the long term?

Material and methods

Data sets

We used highly resolved entire pollination networks, observed for two to four years. ‘Entire’ means that each network includes all flowering plants (except very rare ones) and all flower visitors observed at a site. Flower visitors were defined as animals probing the flowers in search of pollen and nectar, and thus potentially acted as pollinators. Some networks were temporally delimited within part of a flowering season, while others included the entire flowering season. All networks were sampled intensively during the study period, including most or all days with weather

conditions permitting moderate to high flower visitor activity. All plants were identified to species level, and most animals to species by taxonomic experts (Acknowledgements). All networks, except for one (Moesgaard, DK), were observed in consecutive study years.

To justify comparison between different study years at each site, the studies conformed to the following criteria: (1) data were collected in spatially similar plots of equal size, (2) during similar sampling periods at approximately the same time in the season, (3) using similar sampling effort, (4) by the same people and/or by using the same sampling techniques, and (5) mostly the same experts identified or verified the insect collections for all years within a site.

The sites spanned a large geographical gradient, including both island and mainland (Fig. 1, Table 1):

- Teno Bajo (Teno Natural Park), Tenerife, Spain. The study site was a rocky coastal area, with many endemic plants. Vegetation was a low and sparse shrub, dominated by *Rubia fruticosa*, *Plocama pendula*, *Euphorbia* spp., *Withania aristata*, *Periploca laevigata* and the alien *Opuntia dillenii*. The network was observed for one month (June), encompassing the active flower visiting animal community and visited plants during the flowering season of the alien *O. dillenii*. The network was observed for two years.
- Llimpa (Es Grau Natural Park), Menorca, Spain. The vegetation was Mediterranean scrub mixed with abandoned crop fields. Common plants were *Pistacia lentiscus*, *Olea europaea*, *Phyllirea* spp., and some herbs, in addition to the alien, *Opuntia maxima*. The network was observed for one month (June) during two years, encompassing flowering plants and flower visitors active during the flowering period of *O. maxima*.

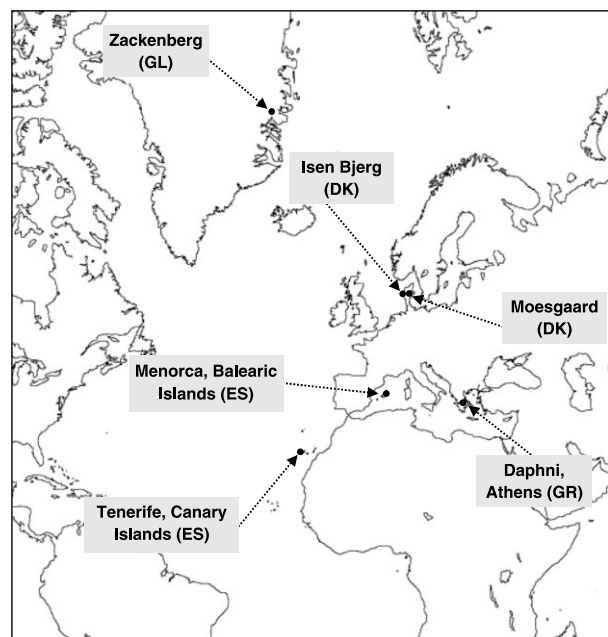


Figure 1. Location of study sites.

Table 1. Locality, site characteristics, sampling effort and methods applied.

Locality	Year	Insularity ¹	Geographical coordinates		Vegetation	Area (ha)	Sampling		
			Latitude, longitude	Altitude (m)			Days	Period	Method ³
Tenerife, ES	2005	I	28°21'19"N	115	coastal desert	0.26	5 ⁴	June	Q
	2006		16°54'19"W				14 ⁵	June	
Daphni, GR	1983	M	38°00'29"N	135–215	Mediterranean low scrub (phrygana)	ca 30	105	Apr–March ²	RCW
	1984		23°38'31"E				117	Apr–March ²	
	1985						147	Apr–March ²	
	1986						134	Apr–March ²	
Menorca, ES	2005	I	39°56'25"N	45	Mediterranean scrub (garrigue)	0.26	6 ⁶	June	Q
	2006		4°15'06"E				13 ⁷	June	
Isenbjerg, DK	2004	M	56°04'21"N	90	temperate dry heath	5	66	Apr–Oct ²	Q, RCW
	2005		9°16'32"E				41	Apr–Sep ²	
Moesgaard, DK	2003	M	56°04'50"N	10	forest meadow	1	19	July	Q
	2007		10°13'52"E				8	July	
Zackenbergl, GL	1996	I	74°30'00"N	50	arctic heath	25	c.45	June–Aug ²	RCW
	1997		21°00'00"W				c.70	June–Aug ²	

¹I = island, M = mainland.

²entire flowering season.

³Q = observation in plots (1 × 1 m), RCW = observation by random census walks.

⁴241 3-min observation periods.

⁵232 3-min observation periods.

⁶209 3-min observation periods.

⁷217 3-min observation periods.

- Daphni, Athens, Greece. The site was part of the Diomedes Botanical Garden of Athens University Nature Reserve, on the slopes of Mt Aegaleo. The dominant vegetation was phrygana, a low-growing, arid Mediterranean scrub. Flowering occurred all year round, although most species flowered during February–June (Petanidou et al. 1995). Flower visitor observations were carried out continuously throughout the year, for four years. Each annual cycle began the 1 April (hereafter, each study year is named after the year in which it began). For details see Petanidou and Ellis (1996) and Petanidou et al. (2008).
- Isenbjerg, Denmark. An area of temperate dry heathland, consisting of a hill and a plain, surrounded mainly by conifer plantation. The heath was dominated by dwarf shrubs, in particular species of Ericaceae and *Empetrum nigrum*. Flower visitor censuses were carried out during the entire flowering season (6–7 months) for two consecutive years. For details see Dupont and Overgaard Nielsen 2006.
- Moesgaard Have, Denmark. A humid forest meadow, bounded on three sides by mixed deciduous forest dominated by *Fagus sylvatica*, and on one side by a cultivated field. The meadow was managed by mowing in late summer. Network observations were done during one month during the main flowering period in mid summer (July) for two years.
- Zackenberg, Greenland. An arctic tundra consisting of several plant communities, particularly fell fields, heathlands dominated by *Dryas octopetala* and *Cassiope tetragona*, dry *Dryas–Kobresia* communities, old riverbed and snow patch habitats. Network data were collected for an entire growing season (< two months) for two consecutive years. For details see Olesen et al. 2008.

Data analysis

We constructed a qualitative plant–flower visitor interaction matrix for each year at each site. In the matrices, columns and rows represent plant and pollinator species, respectively, while cells represent interactions ($x_{ij} = 1$ for presence and 0 for absence of an interaction between pollinator species i , and plant species j).

For each matrix, we calculated a set of network parameters. These included: numbers of plant (P) and animal (A) species, number of interactions (I) between plants and animals; linkage level, i.e. the number of species interactions formed per species, for plants (k_p) and animals (k_a); cumulative degree distributions of plants ($P(k_p)$) and animals ($P(k_a)$), and network structural summary statistics: system size (AP), connectance (C), relative nestedness (N^*), modularity (M) and centralization (CE).

We fitted the cumulative distributions $P(k)$ of the number of links per species, k , to three models using R ver. 2.7.1 (library ‘Brainwaver’, <<http://cran.mirror.org/src/contrib/Descriptions/brainwaver.html>>): (1) exponential, $P(k) = \exp(-\gamma k)$, (2) power-law, $P(k) = k^{-\gamma}$, and (3) truncated power-law, $P(k) = k^{-\gamma} \exp(-k/k_x)$, where γ is a constant and k_x is the truncation value. Cumulative degree

distributions were fitted separately for plant and animal communities, and the Akaike information criterion (AIC) was obtained for each fit. The model with the lowest $\Delta AIC = AIC_i - AIC_{\min}$, where AIC_i are the alternative models and AIC_{\min} is the model with the lowest AIC value, was selected as the best fit (Burnham and Anderson 2002).

We calculated network size as the total number of possible interactions (AP), and connectance (C) as the proportion of realized interactions (I/AP). The connectance C of a network ranges from C_{\min} ($= \max[A, P]/AP$) to one, where C_{\min} is the minimum connectance of a coherent network, i.e. if all species only form one interaction.

Nestedness is a network structural pattern, in which interactions tend to form around a core of generalist species and asymmetrical tails between many specialists and a few generalists. We employed the commonly used nestedness metric N^* , termed relative nestedness N^* . This is based on a matrix nestedness temperature (T), a metric of matrix disorder calculated by the software ANINHADO (Guimarães Jr. and Guimarães 2006). Absolute nestedness $N = (100 - T)/100$, while relative nestedness $N^* = (N - N_R)/N_R$, where N_R is the average nestedness (N) of 1000 randomized matrices using null model 2 proposed by Bascompte et al. (2003).

Modularity M is the degree to which a network consists of sub-groups, each consisting of tightly interacting species (modules) (Olesen et al. 2007, Dupont and Olesen 2009). We used a method developed by Guimerà and Amaral (2005) to calculate and test M. Modularity:

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

where N_M is number of modules in the network, I is number of interactions in the network, I_s is number of interactions between species in module s (‘within-module interactions’) and k_s is number of interactions of species in module s . Thus, M becomes high when many interactions are found inside modules but few between modules. Modularity was assessed relative to 100 randomizations of the network (for details see Olesen et al. 2007).

Centralization (CE) (also termed group centrality efficiency) measures the extent to which a network is centred on particular species (hubs) around which other species connect (Everett and Borgatti 1999), i.e. networks having high CE are star-shaped (Jordano et al. 2006). Centralization (CE) is obtained as the sum of eigenvector centralities of each species in the plant (ec_p) or flower visitor (ec_a) community in the network divided by $(AP)^2$ ($CE = \sum ec_p / (AP)^2$ or $\sum ec_a / (AP)^2$). The eigenvector centrality of species i is a measure of its ‘topological importance’ in the network, a weighted score proportional to the linkage level of i in addition to linkage level of its nearest neighbours. Thus, generalists interacting with other generalist species have a high ec . Eigenvector centrality of a species is calculated as its associated eigenvector of the interaction matrix (Jordano et al. 2006).

At each site, we compared A, P, I and proportions of the five major insect orders between two years using the non-parametric Wilcoxon signed ranks test (in this analysis we only included data from the first two observation years at

Daphni). In addition, we estimated level of turnover of species and interactions at each site. For two consecutive study years, we calculated persistence of plant and animal species and interactions as the proportion of conserved species or interactions out of the total number of species or interactions observed. Finally, we compared network properties (AP, C, N*, M, CE) across sites with respect to latitude, climatic variation, and sampling effort. To correct for temporal autocorrelation between networks from the same site, we used between-year Euclidean distances in network parameters. Thus for each site and variable we got one distance value, except for Daphni, where we had four years and thus three distances between consecutive years. To avoid pseudo-replication, we used the average of the three year-to-year distances. Due to the small sample size, we used the non-parametric Spearman rank correlation coefficient (r_s) to test for correlations.

Climatic variables

Climate data were obtained from weather databases of Agencia Estatal de Meteorología, Spain (<www.aemet.es>), the Hellenic National Meteorological Service (<www.hnms.gr>), and the Danish Meteorological Institute (<www.dmi.dk>). As short-term summary statistics of climate variables, we used average annual temperature (°C) and annual precipitation (mm) for each study year and site. As a measure of long-term climatic variance, we used the coefficient of variation (CV) of annual temperature and annual precipitation for 15–33 years prior to our studies, only including years of complete climate records.

Results

Year-to-year variation within sites

Within site, numbers of plant and animal species, and their interactions were stable among years (Wilcoxon tests: $p > 0.05$; Fig. 2). However, species composition varied inter-annually. Plant communities were more stable between years than the flower visitor communities, often only one third of the animal species being persistent between years. (Fig. 3a–b). However, within-site the proportional representation of animal orders was similar between years (Wilcoxon test: $p > 0.05$; Fig. 4). Moreover, a large proportion of the interactions changed, due to the loss and addition of species, and to rewiring of interactions among species present in both years (Fig. 3c). Often less than one fourth of the interactions were stable between years. If only the core (*sensu* Petanidou et al. 2008, i.e. species found in two consecutive study years) was considered, then 14–48% of interactions were conserved. Hence, networks of interacting plants and flower visiting species are highly dynamic systems, and a pollination network of a specific site is unique in its species and link composition for each year. In spite of this, network properties, such as AP, C, N*, M and CE were very stable between years (Fig. 5). All networks, except Tenerife 2005, were significantly nested. Furthermore, Menorca 2006, and

networks from Isenbjerg, Moesgaard and Daphni were significantly modular.

In general, average linkage level within a site did not differ from year to year (Table 2). The plant community at Tenerife had the strongest annual variation, linkage level being nearly twice as high in the second year compared to the first year. Linkage level distributions were highly skewed. Link distributions of flower visitors mostly had a best fit to a power-law model. On the other hand, link distributions of plant species fitted best to either a power-law or a truncated power-law, although in six of 14 cases, AIC of the best and second best models differed only little (<two points). At four of the six sites, the plants preserved a best fit to a truncated power-law both study years (Table 2).

Among-site comparison

In Fig. 2, 3 and 4, sites are sorted according to increasing latitude (two pairs of sites, Menorca and Daphni, and also Isenbjerg and Moesgaard, were located approximately on the same latitude). No clear latitudinal trends were found (Fig. 5). Networks of the small islands at low latitude, Tenerife and Menorca, contained the smallest number of species and interactions, while the arctic network of Greenland was intermediate, followed by the temperate networks of Denmark (Isenbjerg and Moesgaard), and the Mediterranean mainland network (Daphni).

Correlations of latitude and euclidian distances of the network parameters C, M and CE were non-significant,

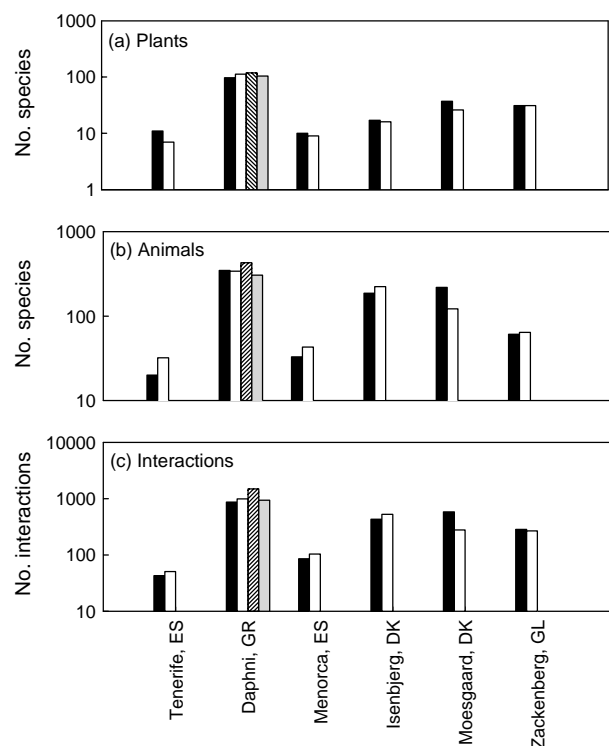


Figure 2. Numbers of (a) plant species, (b) flower visiting animal species and (c) interactions in each network (black bars are first year of observation, white bars second year, hatched bars third year, grey bars fourth year).

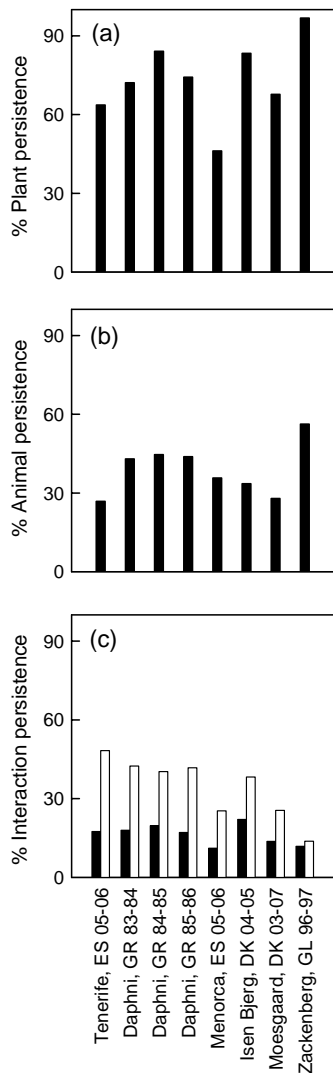


Figure 3. Persistence of (a) plant species, and (b) animal species as percentage of the total number of species recorded at the site during two consecutive years of observation. Between-year persistence of interactions (c) as percentage of total number of interactions observed for two consecutive study years (black) or total number of interactions between species persistent for two consecutive study years (white).

while relative nestedness N^* was significantly and negatively correlated with latitude ($r_s = -0.83$, $p < 0.05$). Between-year distances of C and CE were significantly correlated with differences in network size (AP) (C: $r_s = -0.83$, $p < 0.05$; CE: $r_s = -0.99$, $p < 0.05$), while M and N^* were not associated with differences in AP. Between-year variation in sampling effort (observation days) was not correlated with distances in any of the structural network parameters ($p > 0.05$). Similarly, short and long term climate variables were not related to distances in network structural parameters ($p > 0.05$). Climate variables (differences in annual temperature and precipitation between study years and long-term variation in annual temperature and precipitation) were not significantly correlated ($p > 0.05$), except for differences in temperature between years and CV of annual precipitation ($r_s = 0.94$, $p < 0.05$). Moreover, none of the climate variables were correlated with latitude ($p > 0.05$).

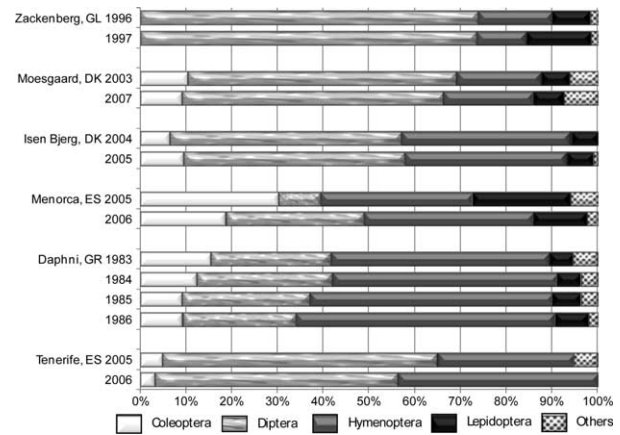


Figure 4. Proportional representation of flower visitor orders (viz Coleoptera, Diptera, Hymenoptera, Lepidoptera and remaining orders) in each network.

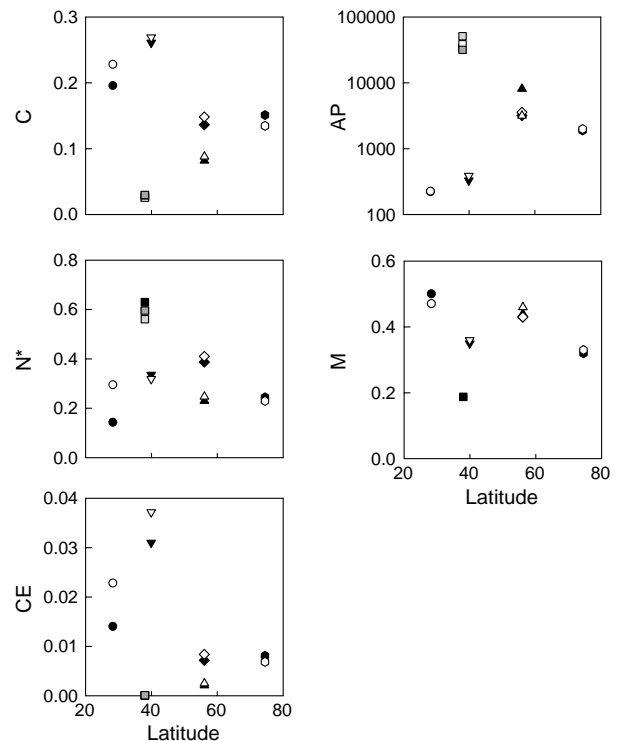


Figure 5. Year-to-year variation in network parameters AP, C, N^* , M and CE plotted against latitude. Each study site is represented as: ● Tenerife (ES), ■ Daphni (GR), ▼ Menorca (ES), ▲ Moesgaard (DK), ◆ Isenbjerg (DK), ● Zackenberg (GL). Black symbols are first year of observation, white symbols second year, light-grey third year, and dark-grey fourth year.

Discussion

Temporal variation of pollination interactions

In general, richness of species and links in the pollination network of a site remained relatively stable from year to year, although many species, especially animals, colonize and others disappear locally. Thus there was a large annual

Table 2. Mean linkage level (\pm SD) and best fitted function for degree distributions of plant and animal communities.

Site	Year	Plants		Animals	
		k_p	$P(k_p)^1$	k_a	$P(k_a)^1$
Tenerife, ES	2005	3.9 \pm 2.63	pow (50.4) ²	2.2 \pm 1.23	pow (46.9)
	2006	7.3 \pm 5.65	tru (42.5) ²	1.6 \pm 0.91	pow (20.8)
Daphni, GR	1983	9.0 \pm 11.48	pow (579.6)	2.5 \pm 2.57	pow (799.4)
	1984	8.8 \pm 8.54	tru (715.5)	2.9 \pm 3.76	pow (875.9)
	1985	12.5 \pm 10.93	tru (839.4)	3.5 \pm 4.50	pow (1383.7)
	1986	9.0 \pm 9.57	pow (653.8)	3.1 \pm 3.96	pow (875.7)
Menorca, ES	2005	8.6 \pm 5.25	tru (62.2)	2.6 \pm 1.64	pow (102.6)
	2006	11.6 \pm 10.31	tru (63.8) ²	2.4 \pm 1.18	tru (124.7)
Isenbjerg, DK	2004	25.5 \pm 20.12	tru (144.2) ²	2.3 \pm 2.34	pow (335.8)
	2005	33.1 \pm 28.05	tru (145.9) ²	2.4 \pm 1.91	pow (505.2)
Moesgaard, DK	2003	13.3 \pm 13.35	tru (221.7)	2.5 \pm 3.27	pow (311.1)
	2007	10.7 \pm 11.63	tru (176.0) ²	2.3 \pm 2.70	pow (198.2)
Zackenbergl, GL	1996	9.2 \pm 5.55	tru (190.7)	4.7 \pm 4.15	pow (272.3)
	1997	8.6 \pm 6.17	tru (193.3)	4.2 \pm 4.06	pow (259.9)

¹pow = power law, tru = truncated power law, exp = exponential. Number in brackets is the AIC for the fitted function.

²less than two points difference in AIC between the best and second best models.

variation in flower visitor species composition and pollination interactions in our study networks. However, most of the remaining network parameters were more or less stable between years.

In investigations of annual variation in flower visitor assemblages of plant species, some studies document little year-to-year variation (Gibson et al. 2006, Sahli and Connor 2007), whereas others show strong temporal variation (Herrera 1988, Horvitz and Schemske 1990, Pettersson 1991, Fishbein and Venable 1996, Mahy et al. 1998, Fenster and Dudash 2001, Ivey et al. 2003). Little is known about the temporal dynamics of entire pollination networks. Very recently a few studies explored the temporal dynamics of entire pollination networks and documented a highly dynamic day-to-day change in an arctic pollination network (Olesen et al. 2008) and a high year-to-year change in composition of species and interactions (Alarcón et al. 2008, Olesen et al. 2008, Petanidou et al. 2008). All these authors agree with the results of the present study. However, we still have very limited knowledge to explain the dynamic character of the plant–pollinator networks through time.

Trends across networks

Our meta-analysis is the first comparison of year-to-year variation in a geographically wide-spread sample of pollination networks, albeit the set of networks was small and heterogeneous. However, certain trends were clearly visible in the data. Network structural parameters (AP, C, N*, M and CE), were stable between years in spite of the large annual variation in composition of species and interactions. This is in accordance with Alarcón et al. (2008), reporting a similar level of nestedness in a pollination network observed for three consecutive years. Furthermore, Nielsen and Bascompte (2007), showed that nestedness (N and N*) remains relatively stable in a pollination network observed from four to 28 days. Similarly, level of modularity is robust to temporal scaling in pollination networks observed from 0.5–7 months (Dupont and Olesen unpubl.).

In our study, no latitudinal trend was observed in most network parameters. The proportions of dipteran and hymenopteran species, however, increased and decreased with latitude, respectively, as shown also in previous studies (Elberling and Olesen 1999, Fig. 4). Any latitudinal gradient in species richness in the present study may be blurred by the species-poor island biotas at low latitudes. The small size of these networks was even more pronounced because the study of these included only part of the flowering season. Network size was an important predictor of network structural properties, including N*, which has been corrected for network size. Thus, future comparative studies should aim at a more rigid methodology.

We did not detect any significant association between annual variation of network parameters and short term (study years) or long term (15–30 years) variation in average annual temperature and annual precipitation. Species composition and interaction patterns of networks may be influenced by other, more subtle climatic factors not included in the current study. Alternatively, lack of associations between inter-annual variation of network parameters and climate variables may be attributed to the relatively small range of climatic variation. Natural pollination networks are robust to moderate perturbations, e.g. tolerance to species extinctions (Mélian and Bascompte 2002). How stability of networks is affected by larger scale changes in abiotic factors is an important issue for future studies.

Turnover and sampling effects

At all sites, between-year persistence of plant species was high (46–97%), lower for animals (27–56%), and very low for interactions (11–22%). A methodological bias may contribute to this pattern. Plants are sessile, and thus easier to detect than mobile animals and these are often small, and difficult to spot from a distance. In addition, insect species often fluctuate immensely in abundance between years (Herrera 1988, Petanidou and Ellis 1996, Cane et al. 2005, Price et al. 2005, Alarcón et al. 2008), and rare species may

remain undetected even when present. If plant and animal communities vary among years, so will all their interactions, leading to a low level of interaction persistence. However, links between the core of persistent species were much more stable (14–48%). Interactions may remain undetected because flower visitors are rare, their visits short-lived and no traces are left on the plant. Thus, turnover rates should be interpreted with some caution because they may be inflated by ‘pseudo-extinctions’ and ‘pseudo-immigrations’, if species or interactions were present but undetected during a census.

Although turnover data are confounded by sampling incompleteness, levels of persistence of plants, animals and interactions, were similar across sites and sampling design. This is surprising, considering that network size (AP) varied 1–2 orders of magnitude. In general, sampling effort per species often diminishes in large networks (Olesen and Jordano 2002), and hence pseudo-turnover due to under-sampling is expected to increase. However, sampling effort was high in all networks included in this study. Accumulation of species and interactions leveled off before sampling ceased. We conclude that annual turnover of pollinator species and links was high, and thus long-term persistence of interactions was rare (Petanidou et al. 2008). In particular, networks observed for short observation periods may experience high year-to-year turnover of species and interactions due to phenological shifts of plants and flower visitors. Constancy of network properties indicates that links shift to other, topologically similar species, i.e. similar in link structure, as species composition of the networks changes from one year to the next (Thompson 2005, Alarcón et al. 2008). Whether these species are functionally and/or taxonomically equivalent needs further investigation.

Conclusions

Since Preston (1960), studies of species diversity have mainly included descriptions of its static structure and to some extent its spatial pattern, particularly species–area relationships. On the other hand, temporal dynamics have been rarely explored (White 2007). In this study, using a set of pollination networks of different size, sampling effort, and provenance (biogeographical region, latitude), we discovered a considerable annual turnover in composition of both plant and animal communities and particularly in their interactions. Despite the high turnover, however, the descriptors of the overall network structure remained relatively stable, indicating that the regional pool of plants and their pollinators may contain many functionally equivalent species. The present study included a limited number of long-term network data, available at this time. More multi-year network studies are needed to increase our understanding of general trends in structure and function of mutualistic networks.

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