TEMPORAL DYNAMICS IN A POLLINATION NETWORK

JENS M. OLESEN,[1,4] JORDI BASCOMPTE,[2] HEIDI ELBERLING,[3] AND PEDRO JORDANO[2]

[1]*Department of Biological Sciences, University of Aarhus, Ny Munkegade Building 1540, DK-8000 Aarhus C, Denmark*
[2]*Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Avda. M. Luisa, E-41013 Sevilla, Spain*
[3]*Danish Plant Directorate, Skovbrynet 20, DK-2800 Kgs. Lyngby, Denmark*

Abstract. Despite a strong current interest in ecological networks, the bulk of studies are static descriptions of the structure of networks, and very few analyze their temporal dynamics. Yet, understanding network dynamics is important in order to relate network patterns to ecological processes. We studied the day-to-day dynamics of an arctic pollination interaction network over two consecutive seasons. First, we found that new species entering the network tend to interact with already well-connected species, although there are deviations from this trend due, for example, to morphological mismatching between plant and pollinator traits and nonoverlapping phenophases of plant and pollinator species. Thus, temporal dynamics provides a mechanistic explanation for previously reported network patterns such as the heterogeneous distribution of number of interactions across species. Second, we looked for the ecological properties most likely to be mediating this dynamical process and found that both abundance and phenophase length were important determinants of the number of links per species.

Key words: abundance; arctic; constraint; ecological network; linkages between species; mutualistic network; phenology; pollination; preferential attachment.

INTRODUCTION

During the last couple of decades, pollination ecology at community level has attracted a lot of attention (Jordano 1987, Waser et al. 1996, Waser and Ollerton 2006). More recently, general network theory has provided a new framework to describe and quantify interactions in species-rich pollination networks (Olesen and Jordano 2002, Bascompte et al. 2003, 2006, Jordano et al. 2003, 2006, Vázquez and Aizen 2004, Thompson 2005, Olesen et al. 2006, Rezende et al. 2007). In a pollination network, an animal species is linked to a plant species if the animal visits the flowers of the plant. These and other studies point toward invariant network patterns across network size, habitat, and geography. However, barely anything is known about the temporal dynamics of pollination networks. Earlier, food-web ecology experienced similar shortcomings regarding temporal resolution, and the methodology of this research field received serious critique (e.g., Polis 1991).

A few studies explore the temporal dynamics of pollination networks (e.g., Petanidou 1991 [and later analyses of her data set], Medan et al. 2002, 2006, Lundgren and Olesen 2005, Basilio et al. 2006, Kaiser 2006), and all conclude that several variables have strong temporal dynamics, e.g., species number, species linkage level (number of links of a species to other species), total number of links in the network, network

connectance, and nestedness. Connectance is the number of observed links divided by the total number of potential links between all species of plants and animals. Nestedness is a nonrandom link pattern describing the degree to which links of specialized species are proper subsets of those of more generalized species. However, these studies only show the variability of single variables; none describes the temporal dynamics of the entire network structure (however, see Nielsen and Bascompte 2007).

Here we studied a taxonomically, fully resolved arctic pollination network, characterized by a strong seasonality. We analyzed daily over two seasons (of two years) the mechanism of assembly or attachment of new species (i.e., species that initiated flowering or began active foraging) to old species already established in the network. To understand the formation of network patterns, theoreticians have developed a family of models of network buildup (Cohen and Newman 1985, Barabási et al. 1999, Williams and Martinez 2000, Sugihara et al. 2003, Cattin et al. 2004). One of these models is preferential attachment (Barabási et al. 1999). According to this model, a new species is more likely to link to a species that already has many links in the network ("the rich-get-richer" principle). It is one of several ways of generating a scale-free network (for other mechanisms, see e.g., the two-level model by Dangalchev [2004]). Some of the main ecological factors behind preferential attachment, leading to scale-free networks, are expected to be species abundance and phenology, and we analyze how they correlate with

species linkage level. Finally, we discuss a set of factors constraining preferential attachment.

MATERIALS AND METHODS

The pollination network

We studied an arctic pollination network in which a strong component of temporal dynamics was expected, i.e., with a marked species turnover during the short arctic season. The turnover was caused by the temporal sequence of phenophases of plant flowering and pollinator activity. All flower visitors were termed pollinators. The phenophase of a plant species is the time period since the first individual of the species initiates flowering and until the last individual ceases to flower. In the same way, the phenophase of a pollinator species is the time since the first individual of the species is observed in a flower and until the last individual is seen visiting a flower.

The study site was a 500×500 m plot of heathland, old riverbanks, and snow beds near the Zackenberg Research Station, northeastern Greenland ($74°30'$ N, $21°00'$ W); and the study period included two full seasons, i.e., from the last snow melted to the first snowfall (43 and 69 days in 1996 and 1997, respectively). However, bad weather reduced the number of observation days to 25 for each year. Flowering abundance of a species was scored as the number of 0.1-m² plots, out of 30 random plots, containing flowering individuals of the species (Fredskild and Mogensen 1997). Observations of insect visitation to flowers were made at all flowering plant species (≤ 24 simultaneously flowering species) on every day offering suitable activity conditions for insects, i.e., on all sunny and calm days, from 09:00 to 17:00 hours. Each daily observation census per plant species lasted a total of 40 min, i.e., a 20-min period at each of two flowering individuals.

Because we estimated species linkage level daily, i.e., the number of pollinator species visiting a plant species and vice versa (the number of plant species visited by a pollinator), we did not use rarefaction curves to show how the number of pollinator species changed with sampling effort (e.g., Woodward et al. 2005b). Instead we used the Jaccard similarity index (J) to show how the two individuals of a species differed in the composition of their pollinator fauna (Krebs 1999). J was regressed against plant species abundance and found to be independent of abundance (first year: $F_{1, 309} = 0.96$, $P < 0.33$). We then concluded that no artefactual sampling results could be alleged because of variation in abundance, because rare and abundant plant species showed similar differences among sampled pairs of individuals. The choice of diurnal time of observation census of individual plant species and observer was random. Most Diptera and some Hymenoptera species (especially within the Braconidae, Eulophidae, Ichneumonidae, and Megaspilidae) could not be identified in the field and members of these two orders were sampled

for later identification. In total, 1245 or 21% of all observed flower-visiting insect individuals were sampled.

Analysis of attachment of new species to the network

Regardless of their specific nature, all networks consist of nodes interconnected by links. An important characteristic of a node i is its linkage level L_i, i.e., its number of links to other nodes in the network. Conventionally in network analysis (e.g., Barabási and Albert 1999), the frequency distribution of L for all nodes in the network is presented as the cumulative probability $P(\geq L)$ that a given node has L or more links. Often, $P(\geq L)$ follows a power law ($\sim L^{-\gamma}$), i.e., it is scale-free, which means that most nodes in the network have a few links and a few nodes have many more links than expected by chance. Being scale-free, properties of the network are independent of its number of nodes. Some ecological networks are reported to have $P(\geq L)$ with a flat tail leading to an exponential decay or a truncation (e.g., $P(\geq L) \sim e^{-\gamma L}$ or $\sim L^{-\gamma} e^{-(L/L_x)}$, with L_x being a cut-off point). This means that beyond a certain number of links, L_x, the decay is faster than that described by a power law (Dunne et al. 2002, Jordano et al. 2003).

We fitted power law, exponential, and truncated power-law distributions to $P(\geq L)$ using the R package (R Development Core Team 2005; library brainwaver, *available online*).[5] We obtained the Akaike Information Criterion (AIC) for each fit (R Development Core Team 2005). The model with lowest AIC was chosen as the best fit to the observed $P(\geq L)$. A scale-free network may owe its origin to two simultaneous dynamic processes (Barabási and Albert 1999): (1) continuous growth of number of nodes and links (but see Dangalchev 2004), and (2) preferential attachment of new nodes to already well-connected nodes. However, other processes may lead to scale-free networks as well (e.g., gene duplication in genetic networks; Teichmann and Babu [2004]). Let us call $\Pi(L_i)$ the attachment probability of a new node to an existing node with linkage level L_i. Theoretical studies show that the shape of the $P(\geq L)$ distribution depends on $\Pi(L_i)$; that is, structure depends on dynamics. A scale-free distribution seems only to appear if $\Pi(L_i)$ is a linear function of L (Barabási and Albert 1999, Krapivsky et al. 2000, Albert and Barabási 2002, Dorogovtsev and Mendes 2004). Previous studies show that preferential attachment takes place in both social and technological networks (Redner 1998, Newman 2001, Jeong et al. 2003). However, as far as we know, no study has investigated whether this is also the case for ecological networks.

At every observation day t, we produced a network of all links, i.e., observed flower visits, between its nodes, i.e., plant and pollinator species, at least present at day t ("a time-slice network") and recorded linkage level L for

TABLE 1. An example showing how to calculate α (a scaling component determining attachment dynamics and linkage-level distribution) for one time step, from the end of day 9 to the end of day 11 in the first year for new plant species linking to old pollinator species (L_i is the number of links to pollinator species).

Pollinator species, i	L_i, end day 9	New flowering plant species		L_i, end day 11	$\Pi(L_i)$	$\kappa(L_i)$
		Pot. rub.	*Ped. flam.*			
Bombus hyperboreus, B. polaris	1	0	0	1	0.00	0.00
Nysius groenlandicus	1	1	0	2	0.11	0.11
Parasyrphus tarsatus	2	0	0	2	0.00	0.11
Phaonia bidentata	2	0	0	2	0.00	0.11
Rhamphomyia filicauda	2	1	0	3	0.11	0.22
Aedes impiger	3	1	0	4	0.11	0.33
Colias hecla	3	0	0	3	0.00	0.33
Platycheirus lundbecki	3	1	0	4	0.11	0.44
Smittia spp.	4	0	0	4	0.00	0.44
Aedes nigripes	5	1	0	6	0.11	0.56
Limnophyes brachytomus	5	1	1	7	0.22	0.78
Paraphaenocladius sp.	5	1	0	6	0.11	0.89
Clossiana chariclea	6	0	0	6	0.00	0.89
Spilogona sanctipauli	6	1	0	7	0.11	1.00
Total		8	1		1.00	

Notes: On day 10, no observations were made because of bad weather. "Old" means the pollinator species entered the network at day 9 or earlier. During this time step, *Potentilla rubricaulis* (*Pot. rub.*) and *Pedicularis flammea* (*Ped. flam.*) began flowering and became linked, respectively, to eight and to one old pollinator species, for a total of nine new links. An old pollinator species might get 0, 1, or 2 new links or a proportion of 0.00, 0.11, or 0.22 of all links. We call these proportions observed attachment probabilities, $\Pi(L)$. $\kappa(L_i)$'s are cumulative values of $\Pi(L_i)$ (see *Materials and methods: Analysis of attachment of new species to the network*); $\ln(\kappa(\leq L_i))$ was linearly regressed against $\ln(L_i(\text{day } 9))$, the slope being $\alpha + 1$ (here $\alpha = 0.42$) (Fig. 4b). Zero values of $\kappa(L_i)$ were excluded from the regression analysis (here, for *Bombus hyperboreus*, $\kappa(L_{\text{B.h.}}) = 0$). In our analysis, data points were species and not linkage-level classes. Using the latter instead did not significantly change the average α value.

all species. Then we scored the number of new links that each old pollinator species present at time t established to new plant species recruited to the network from day t to day $t + 1$, and vice versa for links between old plant species and new pollinator species. For every day during the two seasons (of two years) this procedure was repeated. We excluded the last days of each year when the network stopped growing and also all time steps when no new attachment took place. A total of 58 discrete time steps were left for our analysis of attachment. Then for each time step and each old species, we calculated the probability $\Pi(L_i)$ (for a calculation example, see Table 1). A link was assumed to be constantly present from the first to the last day of its observation, although it might only be observed on some days during this time span. To reduce variation in the data and to avoid zero bins, the cumulative attachment probability $\kappa(\leq L)$ of an old species of linkage level $\leq L$ being linked to a new species was used (Table 1; Jeong et al. 2003). We analyzed $\kappa(\leq L)$ as a function of L using a procedure from general network analysis (Albert and Barabási 2002, Jeong et al. 2003):

$$\Pi(L_i) \propto L_i^{\alpha}$$

$$\kappa(\leq L_i) \propto \int L_i^{\alpha} dL \propto L_i^{\alpha+1}$$

where α is a scaling exponent determining the type of attachment dynamics and the subsequent linkage-level distribution. If $\alpha = 0$, the attachment probability is constant, i.e., independent of L, and this uniform attachment leads to an exponential linkage-level distribution $P(\geq L)$ (Barabási et al. 1999). If $\alpha < 1$, $P(\geq L)$ is either exponential or follows a truncated power law. If $\alpha = 1$, $P(\geq L)$ becomes scale-free, and if $\alpha > 1$, we get a network in which one or a few super generalists connect to almost all other species in the network, i.e., a star-shaped network (Krapivsky et al. 2000).

RESULTS

Network structure

A matrix depicting links between all plant and pollinator species over the two studied years is shown in Fig. 1 (see also Plate 1). Most species had only a few links, but a few generalists had many more links than expected by chance, e.g., the fly *Spilogona sanctipauli* (Muscidae) and the plant *Dryas octopetala* (Rosaceae). Indeed, the bulk of all links in the network only involved a small group of generalists. Table 2 presents network parameter values for each year separately and for the two years pooled. Most parameters were stable between years in spite of the different length of the seasons. The linkage-level distribution (two-year data combined) for pollinators, $P(\geq L_i)$, had the best fit to a power-law distribution ($\gamma = 1.72$), whereas $P(\geq L_j)$ for plants had the best fit to a truncated power law ($\gamma = 1.39$, $L_x = 13.9$) (Fig. 2). For the first year, the best fits were to a power law for pollinators and to a truncated power law for plants. In the second year, the best fits were to a

Two-year cumulative
network

Column headers (plants):

Dryas octopetala, *Saxifraga oppositifolia*, *Salix arctica*, *Potentilla rubricaulis*, *Saxifraga caespitosa*, *Polygonum viviparum*, *Silene acaulis*, *Cerastium arcticum*, *Papaver radicatum*, *Potentilla hyparctica*, *Cassiope tetragona*, *Saxifraga nivalis*, *Arnica angustifolia*, *Arenaria pseudofrigida*, *Melandrium triflorum*, *Saxifraga cernua*, *Ranunculus sulphureus*, *Cochlearia groenlandica*, *Stellaria longipes*, *Taraxacum phymatocarpum*, *Chamaenerion latifolium*, *Rhododendron lapponicum*, *Armeria scabra*, *Pedicularis hirsuta*, *Vaccinium uliginosum*, *Saxifraga hirculus*, *Draba lactea*, *Draba arctica*, *Erigeron compositus*, *Lesquerella arctica*, *Pedicularis flammea*

Row (pollinator)	L_i
Spilogona sanctipauli	20
Limnophyes brachytomus	19
Spilogona dorsata	18
Paraphaenocladius sp.	16
Platycheirus lundbecki	16
Spilogona almqvistii	16
Spilogona extensa	16
Aedes nigripes	15
Clossiana chariclea	15
Bradysia spp.	14
Pseudosmittia sp.	14
Limnophyes sp.	13
Rhamphomyia nigrita	12
Nysius groenlandicus	12
Smittia spp.	12
Aedes impiger	11
Drymeia segnis	11
Spilogona denudata	11
Rhamphomyia filicauda	10
Spilogona micans	9
Platycheirus carinatus	8
Stenomacrus sp. A	8
Limnophora sinuata	7
Culicoides sp.	6
Parasyrphus tarsatus	6
Sympistis zetterstedti	6
Peleteria aenea	6
Chironomidae sp.	5
Brachypogon sp.	5
Zaphne frontata	5
Spilogona tornensis	5
Colias hecla	5
Cricotopus sp.	4
Rheocricotopus sp.	4
Orthocladiinae sp.	4
Scathophaga furcata	4
Phaonia bidentata	4
Polia richardsoni	4
Cryptinae sp.	4
Bombus hyperboreus/polaris	4
Scatopsciara sp.	4
Eupeodes curtus	3
Eupeodes nigroventris	3
Lasiopiophila pilosa	3
Drymeia groenlandica	3
Lophosceles minimus	3
Spilogona tundrae	2
Procladius sp.	2
Eukiefferiella sp.	2
Orthocladius sp.	2
Forcipomyia sp.	2
Megaselia sp.	2
Phytomyza fuscula	2
Neoleria prominens	2
Delia echinata	2
Spilogona melanosoma	2
Protophormia terraenovae	2
Olethreutes inquitana	2
Plebeius glandon	2
Entephria puncticeps	2
Sympistis lapponica	2
Stenomacrus sp. B	2
Diplazontinae sp.	2
Microgasterinae sp.	2
Megaspilidae sp.	2
Chironomus sp.	1
Gonarcticus arcticus	1
Spilogona arcticola	1
Spilogona deflorata	1
Spilogona malaisei	1
Spilogona obsoleta	1
Olethreutes mengelana	1
Syngrapha parilis	1
Stenomacrus sp. C	1
Aphidius? sp.	1
Eulophidae sp.	1

L_j: 30 29 28 26 25 23 23 20 19 17 16 16 15 14 14 13 11 11 10 10 10 9 9 8 7 6 6 6 6 6 3 452

TABLE 2. Cumulative network properties for each year and for both years pooled.

Network parameter	First year	Second year	Both years
Start of season	21 June	17 June	
End of season	2 August	24 August	
Length of season (days)	43	69	
A, no. pollinator species	61	64	76
N, no. flowering plant species	31	31	31
$M = A \times N$, network size	1891	1984	2356
I, total no. links in network	286	268	452
$C = I/M$, network connectance	0.15	0.14	0.19
$\langle L_i \rangle = I/A$, mean linkage level of pollinators	4.7	4.2	5.9
$\langle L_j \rangle = I/N$, mean linkage level of plants	9.2	8.6	14.6

truncated power law for both pollinators and plants. To understand which ecological processes might explain these network patterns, we next looked at the dynamics of the network and the ecological factors that were expected to correlate best with these dynamics, namely, phenophase length and local abundance.

Network dynamics

The parameter stability seen in Table 2 hid much between-year dynamics. Thus 20% of the pollinator species seen during the first year were not observed in the second year, whereas 23% of the second-year pollinator species were not observed in the first year. Link dynamics were even more dramatic: 66% of the links observed in the first year were not observed in the second year, whereas 63% of the links present in the second year were not seen in the previous year. However, species number and composition of the plant community were the same for the two years. Thus, while network structure seemed stable at a "global" scale, the identity and composition of links and species were quite dynamic.

The frequency distributions of phenophase length had a lognormal shape, except for plants in the second year, where the distribution was normal. A cartoon of daily interaction matrices from six days in the first season (Fig. 3) illustrates the marked seasonality of the interaction dynamics, i.e., the increase in network complexity through time over a maximum peak to the abrupt collapse at the end of the season. This temporal variation in interaction complexity was generated from the temporal turnover of phenophases, varying considerably in their extent.

The linkage level of a species was positively correlated (linear regression) with the length of its phenophase (first-year pollinators, $R^2 = 0.69$, $F_{1,59} = 133.2$, $P < 0.001$; second-year pollinators, $R^2 = 0.52$, $F_{1,62} = 68.4$, P

< 0.001; first-year plants, $R^2 = 0.55$, $F_{1,29} = 38.2$, $P < 0.001$; second-year plants, $R^2 = 0.51$, $F_{1,29} = 33.1$, $P < 0.001$). The linkage level of a plant species was also positively correlated with its abundance (first-year plant, $R^2 = 0.12$, $F_{1,29} = 4.9$, $P < 0.05$; second-year plant, $R^2 = 0.13$, $F_{1,29} = 5.6$, $P < 0.05$). Note that pollinator abundance was not estimated independently of visitation record data. However, plant abundance and phenophase were positively correlated (first year, $R^2 = 0.17$, $F_{1,29} = 6.9$, $P < 0.05$; second year, $R^2 = 0.20$, $F_{1,29} = 8.6$, $P < 0.01$).

Total numbers of species and links in the networks accumulated linearly throughout most of the seasons (network growth phase was 81–85% of the season). At the end of the season, numbers reached a short phase of stasis (Fig. 4a). Thus, for most of the season, the first requirement for a power-law fit of $P(\geq L)$ was fulfilled. However, the actual $P(\geq L)$ was truncated (except for first-year pollinators; Fig. 2).

The average α value for attachment of new plants to old pollinators was $\alpha = 0.64$ ($N = 28$ time steps, standard deviation SD = 0.72); for attachment of new pollinators to old plants, $\alpha = 0.83$ ($N = 30$, SD = 0.85). These values did not differ significantly ($t = 1.06$, $P \leq 0.07$). Thus species attachment probability, $\Pi(L)$, was sub-linear, i.e., intermediate between preferential attachment ($\alpha = 1$) and independent of L ($\alpha = 0$) (Fig. 4b). α was significantly higher than 0 and significantly lower than 1, but it did not differ from 0.5 ($P < 0.36$). This dynamical pattern was fully compatible with the observed truncated power-law linkage-level distribution.

DISCUSSION

Temporal variation in network structure

In the Zackenberg network, properties calculated for an entire season, namely, connectance, average linkage

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FIG. 1. Two-year cumulative pollination matrix, Zackenberg, Greenland. Plant species are listed in columns, and pollinator species in rows. A black square indicates the presence of a link, i.e., one or more visits made by a given pollinator species to a given plant species during one or both study years. L_i (numbers on the right) and L_j (numbers at the bottom) represent the linkage level or number of links between pollinator species i and plant species j to other species, respectively. The total number of links is $I = 452$. The matrix is sorted in a nested way, i.e., pollinator species are sorted downward according to descending L_i, and plant species are sorted from left to right according to descending L_j. Thus the lower nestedness tail is made up of links between plant generalists and pollinator specialists, and the upper right tail is made up of links between pollinator generalists and plant specialists.
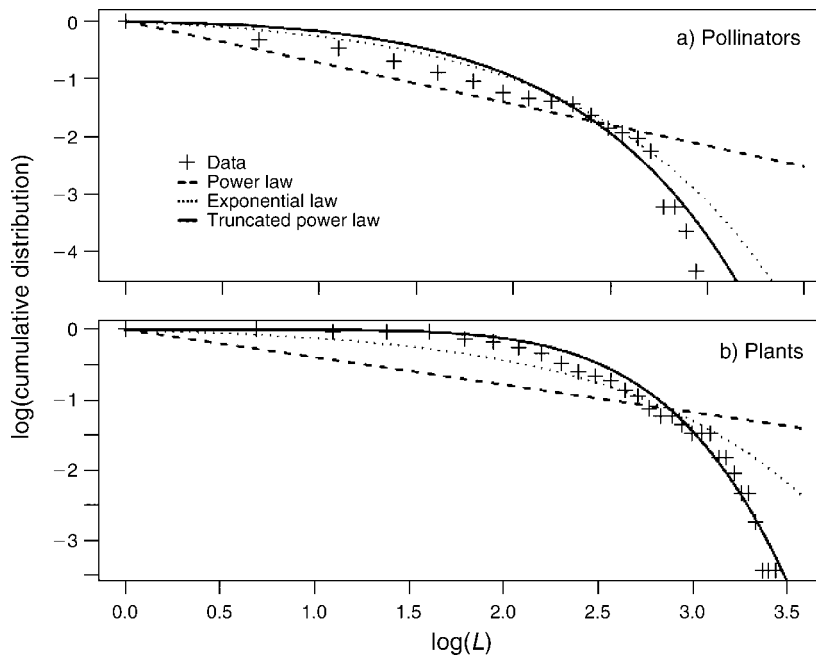
FIG. 2. Cumulative probability distributions of (a) pollinator and (b) plant linkage level (L) in log–log plots for the two years combined. Using the R package (R Development Core Team 2005), a power law (pow), an exponential (exp), and a truncated power-law (tru) distribution were fitted to $P(\geq L)$, the probability that a given node has L or more links. Pollinators had the best fit (in boldface) to a power-law distribution ($AIC_{exp} = 426$, $\mathbf{AIC_{pow} = 415}$, $AIC_{tru} = 422$) and plants to a truncated power-law distribution ($AIC_{exp} = 231$, $AIC_{pow} = 280$, $\mathbf{AIC_{tru} = 210}$). Separate analyses were also done for the first year (for pollinators, $AIC_{exp} = 313$, $\mathbf{AIC_{pow} = 272}$, $AIC_{tru} = 310$; for plants, $AIC_{exp} = 202$, $AIC_{pow} = 231$, $\mathbf{AIC_{tru} = 191}$) and for the second year (for pollinators, $AIC_{exp} = 364$, $AIC_{pow} = 374$, $\mathbf{AIC_{tru} = 356}$; for plants, $AIC_{exp} = 222$, $AIC_{pow} = 266$, $\mathbf{AIC_{tru} = 206}$).

Notes: Different L values have different numbers of points, i.e., they are overlapping in the figure. This is visually confusing in panel (a), where the the truncated power law appears to fit the data better than the power law. However, the more numerous low-L data points result in a better fit to the power law, as indicated above.

level, linkage-level frequency distribution, and so forth, were stable between years (Table 2). However, our highly resolved data set revealed considerable dynamics within and between seasons. One-fifth of the pollinator species and two-thirds of all links were only observed in one of the two years. These species are specialized and often rare and their links make up the lower and the right tails of the link pattern in the nested-matrix version (Fig. 1). Thus matrix dynamics were mainly confined to the nestedness tails. In a Greek pollination network, Petanidou and Potts (2006) noticed a similar, very dramatic turnover in pollinator species number throughout the season, indicating that strong temporal dynamics may be a general property of pollination networks. Other studies have also suggested this (Lundgren and Olesen 2005, Basilio et al. 2006, Medan et al. 2006).

As in many other pollination networks (Jordano et al. 2003), the plant community of the Zackenberg network showed a truncated linkage-level distribution. The pollinator community also showed truncation of its linkage-level distribution in the second year. We believe this deviation from a power-law distribution and the $\alpha < 1$ to be due to various constraints operating in the network, limiting high-linkage-level species in attaching preferentially to new species. Constraints are defined as factors limiting choice decision by a "forager" (Stephens

and Krebs 1986). Our temporally resolved data set allowed us specifically to go a step further and look for candidate factors correlated with this truncation.

Abundance and phenophase

If attachment of one individual of a new species to an individual of an old species i is random, only the abundance of i determines the attachment probability of i. This rationale is, in essence, MacArthur's (1972) "principle of equal opportunity," i.e., if resources are limiting they should be utilized in proportion to their abundance. Thus attachment among individuals is unconstrained, whereas attachment at the species level is constrained by abundance. Because abundance frequency distributions generally are lognormal (e.g., Grey et al. 2006), a few common species get a high attachment probability, whereas most species are rare and consequently get a low attachment probability. Significant, positive mutualistic abundance–linkage-level relationships are well known (e.g., Elberling and Olesen 1999). In seed-dispersal networks, linkage level is correlated with abundance both for plants and animals (Jordano 1987). However, in Zackenberg, Greenland, plant abundance explained only 12% of plant linkage level. The use of a more pollinator-relevant abundance measure such as floral reward amount would most

a) Time-slice networks
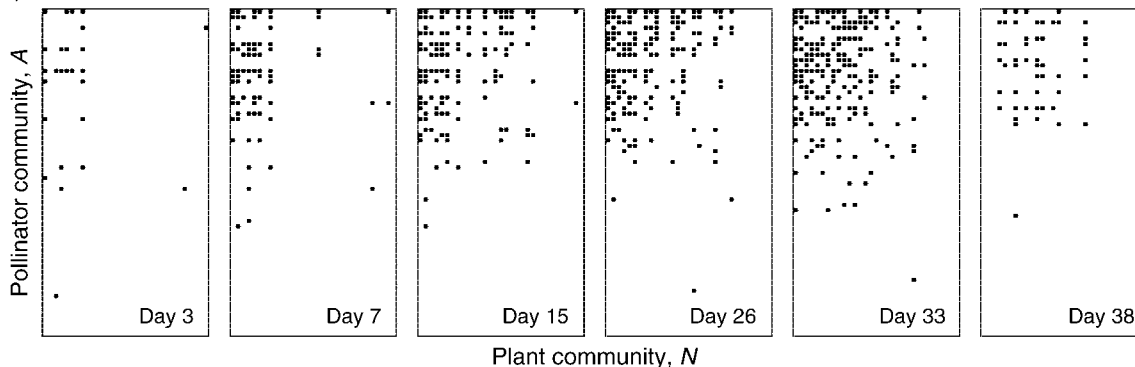
b) Insect visitation phenology
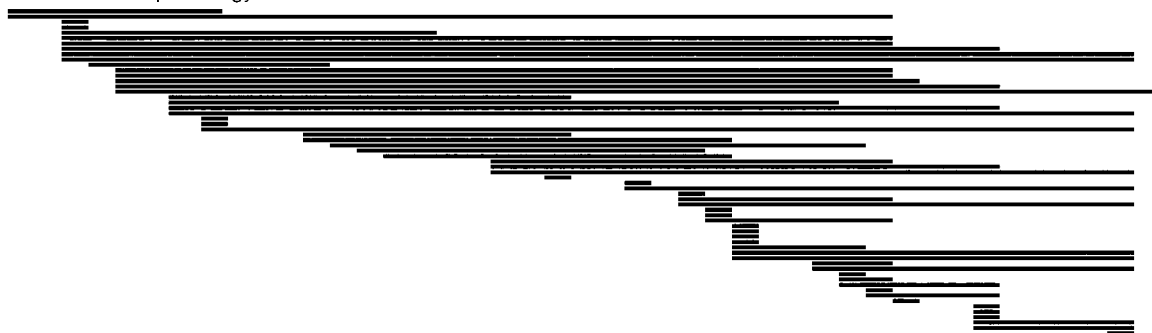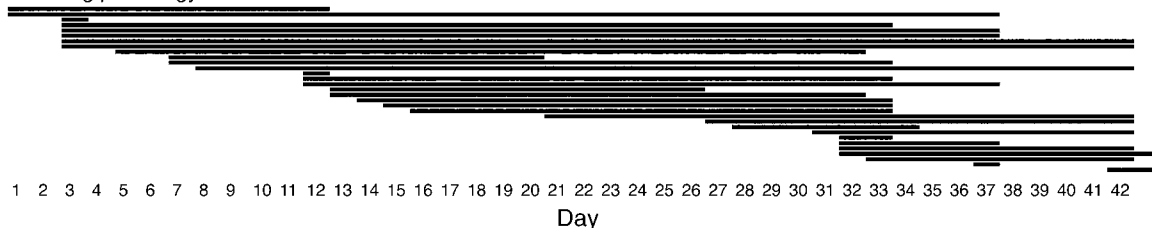
c) Flowering phenology

Day

FIG. 3. Matrix dynamics and pollinator and plant phenophase distributions from the first study season of the Zackenberg pollination network (day 1 is 21 June; see Table 2). (a) A cartoon of six time-slice matrices from different days during the season. All species present during the season are included (A and N are the pollinator and plant communities, respectively). For each time-slice t, only links observed at least on day t are shown as black squares. These links may also be present earlier and/or later. (b, c) The phenophase length diagrams show the minimum temporal extent of insect flower visitation and flowering of each species ("minimum" because an insect or a plant species might have foraged or flowered earlier or later than observed). Each bar represents a species. Species are sorted according to their date of commencement of flowering or foraging, and then according to the date when flowering and foraging came to an end.

certainly increase R^2. This is paralleled by food-web analyses using very elaborated measures of resource quality, e.g., C:N ratios. A robust estimation of the correlation strength between abundance and linkage level of pollinators has to await studies including abundance data produced independently of observations of flower visitation.

For both plants and pollinators at Zackenberg, phenophase length and linkage level were correlated. A longer phenophase of a species translated into more days of potential attachment to new species and an increased linkage level. Thus the shape of the pheno-phase frequency distribution influenced linkage-level distribution. At Zackenberg, the shape of the pheno-phase distribution was lognormal. In an analysis of

phenophase distributions (J. M. Olesen, *unpublished data*), two-thirds of a sample of 32 species communities had a lognormal phenophase distribution. A few species had a very long phenophase, whereas most species had only a short burst of activity. If the number of species in a habitat was higher than 36, the distribution was always lognormal. At Zackenberg, phenophase length ex-plained 51–69% of the variation in linkage level. Thus phenology contributed to the skewed frequency distri-bution of linkage level.

Constraints to species attachment

The cumulative linkage level of species i at day t, $L_i(t)$, summarizes the influence of all factors on the attach-ment of new species to species i during the first t days of
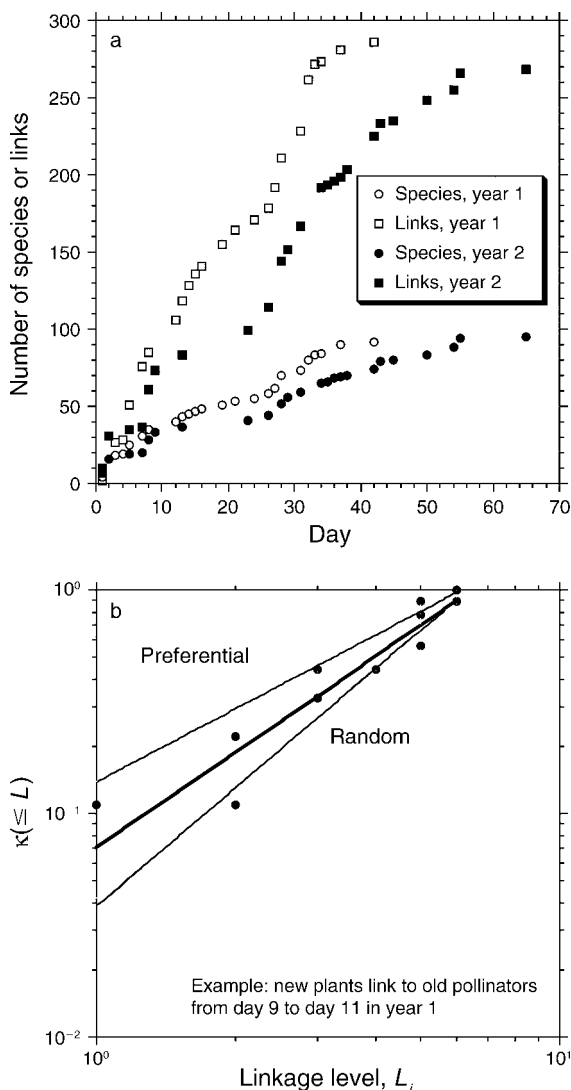
FIG. 4. (a) Seasonal growth and stasis in numbers of species (plants and pollinators pooled) and links recorded during the two study years; day 1 is 21 June in year 1 and 17 June in year 2. (b) Cumulative probability $\kappa(\leq L)$ of new plant species becoming attached to old pollinator species with L_i links, using the time step from day 9 to day 11 in the first study season as an example (see Table 1 for details). Each circle is a species; note the log–log scale. The upper thin "preferential" line is based on a preferential attachment model, the lower thin "random" line is based on random attachment, and the heavy line is the regression of $\kappa(\leq L)$ on L_i.

is large (Mitchell 1989). Instead the pollinator tends to search among close floral resources, i.e., it perceives only local, not global, information about the full range of floral resources available in the network (a mechanism termed "information filtering," e.g., Mossa et al. 2002). Thus information filtering is based on behavioral factors. Attachment becomes a function of the linkage level of the flowering plant species in the vicinity of the new pollinator. This informational constraint upon attachment reduces the value of α and lowers the tail of $P(\geq L)$. The same scenario may operate for a new flowering plant species entering the "pollinator market."

Another constraint is the length of the phenophase or the "age" of a species. At Zackenberg, we noted that linkage level of the most linked species seemed to level off before network growth reached stasis at the end of the season (Fig. 4a). Thus these species may experience "senescence," with old flowers being less attractive and long-lived pollinators ceasing to forage late in life. Thus age constraints will reduce attachment of new species to species with a long phenophase (which often are also the most linked ones), and thus will lower α and truncate $P(\geq L)$.

Morphological and phenological factors make certain links "forbidden" through morphological mismatching and phenological uncoupling, respectively (Jordano 1987, Jordano et al. 2003, 2006, Stang et al. 2006). Pollinator body size–flower size mismatching is an example of a morphological constraint (e.g., Woodward et al. 2005a; however, see Stang et al. 2006). Links between early-flowering plant species and late-seasonal pollinator species, for example, are phenologically constrained because their phenophases do not overlap. Thus only a fraction of all potential interactions in the network are actually observed, independently of sampling effort, i.e., they represent structural zeroes in the link matrix. Phenological uncoupling was already noted by Elton (1927), who devoted an entire chapter to "Time and animal communities," and it receives increasing interest in relation to global climate change (e.g., Høye et al. 2007, Memmott et al. 2007). Thus these constraints also push the mode of attachment away from being preferential. Other constraints are resource related, such as a mismatch between type of floral reward presented by a plant and type of resource searched for by a pollinator. At Zackenberg, *Papaver radicatum* offers only pollen. Thus the butterflies, which do not consume pollen, avoid this species. Overall, this battery of factors or constraints may explain the mode of species attachment and the truncation of the power-law linkage-level distributions observed at Zackenberg.

CONCLUSION

Higher abundance and longer phenophase increased the likelihood that a species would become attached to new species. However, our analysis demonstrated that this attachment of new species preferentially to the most linked old species was constrained. Such a pattern of

its phenophase. Thus we expect $L_i(t)$ to be a strong predictor of the attachment success, $\Pi(L_i)$, of any new species to i during the subsequent time step from t to $t + 1$. Because α values were lower than predicted according to a preferential attachment model ($\alpha = 0.63$–0.84), we suggest that some species-specific constraints, besides abundance and phenology, limited the attachment probability. We will discuss some of these constraints.

For cost reasons, a new pollinator entering a habitat cannot scan the entire "floral market," especially if this

PLATE 1. Some of the plant species in the Zackenberg pollination network. Uppermost row from left: *Dryas octopetala*, *Melandrium triflorum* with its pollinator *Nysius groenlandicus*, and *Saliz arctica*. Second row: *Silene acaulis*, *Taraxacum* sp., and *Armeria scabra*. Lowermost row: *Cassiope tetragona*, *Saxifraga hirculus*, and *Vaccinium uliginosum*. Photos courtesy of Marianne Philipp and Jens Böcher.

network dynamics is fully compatible with previously reported network patterns, e.g., the truncated power-law linkage-level distribution. Our analysis represents a first step in linking network structure to dynamics, and in understanding the ecological processes behind network dynamical processes. Future studies may focus upon the temporal dynamics of small groups in networks of strongly linked species, such as modules (Olesen et al. 2007), and the quantification of the relative importance of constraints in various kinds of ecological networks. The latter type of research may help to explain the relative contribution of different mechanisms to the formation of network patterns by going beyond purely static descriptions, which only give us correlations. Thus a dynamic approach brings us closer to causality, also in relation to studies of network robustness against external perturbations.

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