The Dense and Highly Connected World of Greenland's Plants and Their Pollinators

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Abstract

A pollination network of 26 pollinator species interacting with 17 plant species from the small Greenlandic island Uummannaq was analyzed for multiple parameters values. Of the insects collected, 77% of all individuals and 77% of all species belonged to Diptera. The ratio of pollinators to plant species was 1.5, which is lower than in other Arctic pollination networks. This might be a double-island effect as Uummannaq is a small island next to Greenland. Connectance was 14.3%, and linkage level of pollinator and plant species averaged 2.4 and 3.7 species links, respectively. The characteristic path length and average clustering coefficient of the 1-mode networks were 1.4 and 0.83, respectively, for the pollinator species and 1.3 and 0.79, respectively, for the plant species. For both pollinator species and plant species, the tail of the degree distribution had the best fit to an exponential model, indicating that the most connected species was constrained in their linking. However, the extremely short path length and high clustering indicated that the networks had small-world behavior, meaning that any disturbance is spread very fast to the entire network and that the networks are error tolerant but vulnerable to attack on the most linked species.

Introduction

Networks link related objects or nodes and show similar properties but also unique differences across vastly different research fields, such as social sciences, World-Wide Web studies, economics, neurobiology, traffic planning, film analysis, methodological studies of scientific citation and co-authorship, planning for electrical power supply, biochemistry, and food-web ecology (e.g., Memmott, 1999; Albert and Barabási, 2000; Williams and Martinez, 2000; Strogatz, 2001; Barabási, 2002; Buchanan, 2002; Solé et al., 2003). Recently, a similar kind of network analysis has been applied to the field of plant and animal mutualisms (Jordano et al., 2003, 2005).

The functional implications of these broad similarities in network topology have been discussed by a number of workers (Watts and Strogatz, 1998; Albert and Barabási, 2000; Albert et al., 2000; Jeong et al., 2000, 2001; Strogatz, 2001; Barabási, 2002; Bascompte et al., 2003; Jordano et al., 2003, 2005; Solé et al., 2003; Watts, 2003). Signals spread throughout a network in a way and at a rate that depend upon the size and link topology of the network, affecting how robust and stable the network is (Albert et al., 2000). The possibility of deducing level of robustness from network structure makes this approach appealing to studies of Arctic ecosystems, which generally are regarded as very sensitive to disturbance because of their poor resilience. No Arctic pollination network has ever been analyzed from this strict network approach, which is an extension of the methodology used in older pollination community studies (Mosquin and Martin, 1967; Hocking, 1968; Kevan, 1970; Elberling and Olesen, 1999).

Here we present an analysis of a pollination network from northwest Greenland. We estimate a set of values of important network parameters and make predictions about the robustness of the network against disturbance.

Materials and Methods

FIELD WORK

Field work took place from 1 July to 4 August 2002 in northwest Greenland on Uummannaq Island (71°N, 52°W). The study site was a 100×100 m plot covered by a mosaic of *Betula*-dominated heath and bare rock. The plot was situated on an east-facing slope 180 m a.s.l. Observations of flower-visiting animals, here indiscriminately termed pollinators, were done daily by regular walks in the plot, observing the same plant individuals of each species during its entire flowering season. Observations were done from 10:00 a.m. to 4:00 p.m., and on every observation day we spent 20 min per plant species. In total, each plant species was observed for ~4 h. In order to minimize effects of variable weather conditions, visitation observations were not made during periods of rain and high wind. This stipulation reduced the number of observation days from 35 to 21. We divided these into seven periods of three successive "good" observation days. In general, identification of pollinators was not possible in the field, and most animals were caught for later identification. Jens Böcher and Verner Michelsen of the Zoological Museum, Copenhagen, kindly identified the insects, and vouchers were deposited here. A total of 40 flower pollinators escaped before capture, but 19 of these (mainly mosquitoes, and therefore a slight bias exists toward more mosquitoes and fewer other dipterans in the data set) could be identified, and these observations were included in the data set.

NETWORK ANALYSIS

Total number of pollinator species, A, and plant species, P, and total number of interactions, I, between A and P were counted. Connectance, $C = 100 \, I/(AP)$, was calculated (Olesen and Jordano, 2002). Thus, C is the percentage of all possible interactions within the network that were realized. Whereas C is a measure of the generalization level of the network, linkage level is the generalization level of species. Average linkage levels of pollinator species, $\langle L_m \rangle = I/A$, and of plant species, $\langle L_n \rangle = I/P$, were calculated (Olesen and Jordano, 2002). Temporal turnover of A, P, and I was calculated as the fraction, which was exchanged every third day. In order to examine longitudinal variation, parameter values from this study were compared to those from other Arctic and sub-Arctic studies.

The network was also analyzed as a graph consisting of a set of nodes and links between nodes (Wasserman et al., 1994). The 2-mode network with links between pollinator and plant species was

TABLE 1

Total-season, bipartite pollination matrix, Uummannaq Island (71°N, 51°W), North-West Greenland. Matrix entries are total number of animal species visitors observed in the flowers of an individual of a given plant species during ~4 h.

	Dryas integrifolia	*Campanula gieseckiana*	*Ledum palustre*	*Saxifraga tricuspidata*	*Silene acaulis*	*Polygonum viviparum*	*Salix*	*Cerastium alpinum*	*Rhododendron lapponicum*	*Vaccinium uliginosum*	*Chamaenerion latifolium*	*Viscaria alpina*	*Saxifraga caespitosa*	*Cassiope tetragona*	*Pedicularis flammea*	*Potentilla rubricaulis*	*Pyrola grandiflora*	No. visitors	L_m
Chironomidae sp.	6		5	45	1	1	1	1		1								61	8
Culicidae sp.	1		1	1		1			3	1			1		1			10	8
Nysius groenlandicus	2					5					2	2				1		12	5
Thysanoptera sp.	3		1	3				1	1									9	5
Eupeodes curtus	2	1			1			1									1	6	5
Ephydridae sp.	4	1		1	2													8	4
Spilogona sp.	1			2			1											4	3
Ceratopogonidae sp.		1				1												2	2
Pegomya sp.	1				1													2	2
Platycheirus lundbecki	2		1															3	2
Dolichopus sp.		1	3															4	2
Sphaerophoria scripta	1							1										2	2
Platycheirus hyperboreus	2				1													3	2
Delia sp.		2																2	1
Acarina sp.		10																10	1
Mycetophilidae sp.			1															1	1
Coccinella transversoguttata							1											1	1
Cecidomyiidae sp.														1				1	1
Ichneumonidae sp.				1														1	1
Sympsitis zetterstedtii						1												1	1
Heleomyzidae sp.		1																1	1
Platycheirus groenlandicus		1																1	1
Protophormia terranovae		1																1	1
Empididae sp.	1																	1	1
Lasiomma sp.	1																	1	1
Eupeodes luniger	1																	1	1
No. visitors	28	19	12	53	6	9	4	3	4	2	2	2	1	1	1	1	1	149	
L_n	14	9	6	6	5	5	4	3	2	2	1	1	1	1	1	1	1		63

TABLE 2

Characteristics of 2-mode sub-Arctic pollination networks. A = no. of pollinator species, P = no. of plant species, AP = network size, I = no. of interactions, $C = I/(AP)$ = connectance, $\langle L_m \rangle$ = average pollinator linkage level, and $\langle L_n \rangle$ = average plant linkage level.

Source	Locality	Habitat	Latitude	A	P	AP	I	C	A:P	$\langle L_m \rangle$	$\langle L_n \rangle$
Kevan (1970)	Hazen Camp, Ellesmere Island	tundra	82°N	91	20	1820	190	10.4%	4.6	2.1	9.5
Hocking (1968)	Hazen Camp, Ellesmere Island	tundra	82°N	81	29	2349	179	7.6%	2.8	2.2	6.2
J. M. Olesen and H. Elberling (unpublished data)	Zackenberg, Greenland	tundra	75°N	61	31	1891	286	15.1%	2	4.7	9.2
J. M. Olesen and H. Elberling (unpublished data)	Zackenberg, Greenland	tundra	75°N	65	31	2015	270	13.4%	2.1	4.2	8.7
P. Witt (unpublished data)	Kangerlussuaq, Greenland	dwarf shrubs	66°N	39	15	585	92	15.7%	2.6	2.4	6.1
Elberling and Olesen (1999)	Abisko, Sweden	rocky slope	68°N	118	24	2832	242	8.5%	4.9	2.1	10.1
This study	Uummannaq, Greenland	dwarf shrubs	71°N	26	17	442	63	14.3%	1.5	2.4	3.7

transformed into two 1-mode networks: one for the pollinator species and one for the plant species. In a 2-mode network, a link is an icon of visitation by a pollinator species to a plant species. If two pollinator species share at least one plant species, they are linked in the 1-mode pollinator network and likewise among the plant species in the 1-mode plant network. Thus, a 2-mode pollination network is a map of mutualistic interactions between a community of plant species and a community of pollinator species. A 1-mode network, on the other hand, is a map of competitive and facilitative interactions within a species community of either plants or pollinators. The 1-mode networks were used to calculate three parameter values:

1. The characteristic path length, $\langle l \rangle$ is the average of all shortest distances between any pair of species. For example, if two pollinator species share a plant species, they are one link apart. As a second example, if animal species f only visits plant species 1, animal species g visits both plant species 1 and 2, and animal species h visits only plant species 2, then species f is two links from species h, etc.

2. The average clustering coefficient, $\langle c \rangle$, is the second parameter. The neighborhood of species i constitutes all species linked to i, excluding i itself. Then c_i is the proportion of realized links in the neighborhood of i (a sociology analogue is "how many of your friends are friends"). If species f, g, and h constitute the neighborhood of i (i.e., they are all three linked to i) then these three species may be connected by a maximum of three links. If only one of these links is realized, then $c_i = 1/3$. If the links in a 1-mode network are randomly distributed, then $\langle c \rangle$ is equal to the density, d, of links in the network, e.g., in the pollinator network $d = 2m/[A(A-1)]$, where m is total number of links in the 1-mode network.

3. The third parameter, $p(\geq k)$, is the fraction of all species that have $\geq k$ links to other species; k is termed the degree of a species. By plotting $p(\geq k)$ against k, we get the cumulative degree distribution. A small world, also called a scale-free network, has short $\langle l \rangle$, high $\langle c \rangle$, and a distribution with a tail best described by a power-law, i.e.,

$$p(\geq k) \propto k^{-\gamma},$$

where γ is a fitted exponent. In some networks, the tail of $p(\geq k)$ fits better to a power law with an exponential cutoff,

$$p(\geq k) \propto k^{-\gamma} \exp(-k/k_x),$$

where k_x is the cutoff point of the distribution, i.e., it follows a kind of truncated power law. In other cases, Albert et al. (2000), Amaral et al. (2000), and Jordano et al., (2003, 2005) have demonstrated that $p(\geq k)$ best fits an exponential distribution,

$$p(\geq k) \propto \exp(-\gamma k).$$

In the latter two cases of $p(\geq k)$, we speak about small-world-like networks, because these topologies have some of the properties

of real small worlds. However, in both the latter models, the degree of the most connected nodes is constrained, i.e., the degree is lower than one should expect in a true small world. In ecological networks, the degree of the most connected nodes, the so-called hubs, may be constrained by saturation, aging, resource limitation, morphology, physiology, etc.

Networks were analyzed by using the software Pajek. This package is available at http://vlado.fmf.uni.lj.si/pub/networks/pajek.

Results

TOTAL FIELD-SEASON NETWORK

During the total field season, 149 pollinator individuals belonging to $A = 26$ taxa were observed on $P = 17$ plant species, resulting in $I = 63$ pollination interactions (Table 1). Of all pollinator individuals and species, 77% were dipterans. Chironomidae was the most species-rich dipteran family; it was involved in 41% of all species interactions in the network. The pollinator taxon that visited the most plant species was Chironomidae sp. (eight plant species). *Dryas integrifolia* was the most visited plant species (14 pollinator taxa). The strongest interaction measured in number of visitor individuals (45 of the 149 interactions) was the visitation of *Saxifraga tricuspidata* by Chironomidae sp. (Table 1). The *A:P* ratio was 1.5, which is the lowest *A:P* ratio recorded for any Arctic or sub-Arctic pollination network (Table 2). The mean linkage level of pollinator and plant species was $\langle L_m \rangle = 2.4$, and $\langle L_n \rangle = 3.7$, respectively. In this study, L_m was similar to the L_m determined in other Arctic and sub-Arctic studies, whereas our estimate of L_n was the lowest found in any Arctic or sub-Arctic study (Table 2). This discrepancy was probably due to the few pollinator species observed. Only one 1:1 interaction was observed (*Cassiope tetragona*–Cecidomyiidae sp.). Connectance $C = 14.3\%$.

SEASONAL VARIATION IN NETWORK STRUCTURE

In addition to the total field-season network study, parameter values were also estimated continuously during the field season. The study site had two bursts of flowering and pollinator activity (in periods 2 and 5), i.e., nine "good" days apart (Figs. 1a, 1d–1g). The early- and late-season networks were "bridged" by a few species with an all-season phenology, e.g., *Dryas integrifolia*, *Silene acaulis*, and *Saxifraga tricuspidata* flowered the entire field season. Bridge species got high linkage levels. At the two bursts, connectance went down (Fig. 1b). Average linkage levels for plants and pollinators also had strong seasonal dynamics (Fig. 1c). Thus, a total field-season network hides a lot of the dynamics.

ONE-MODE NETWORKS

By using the Pajek software, we transformed the 2-mode pollinator-plant network into a 1-mode pollinator network and a 1-mode plant
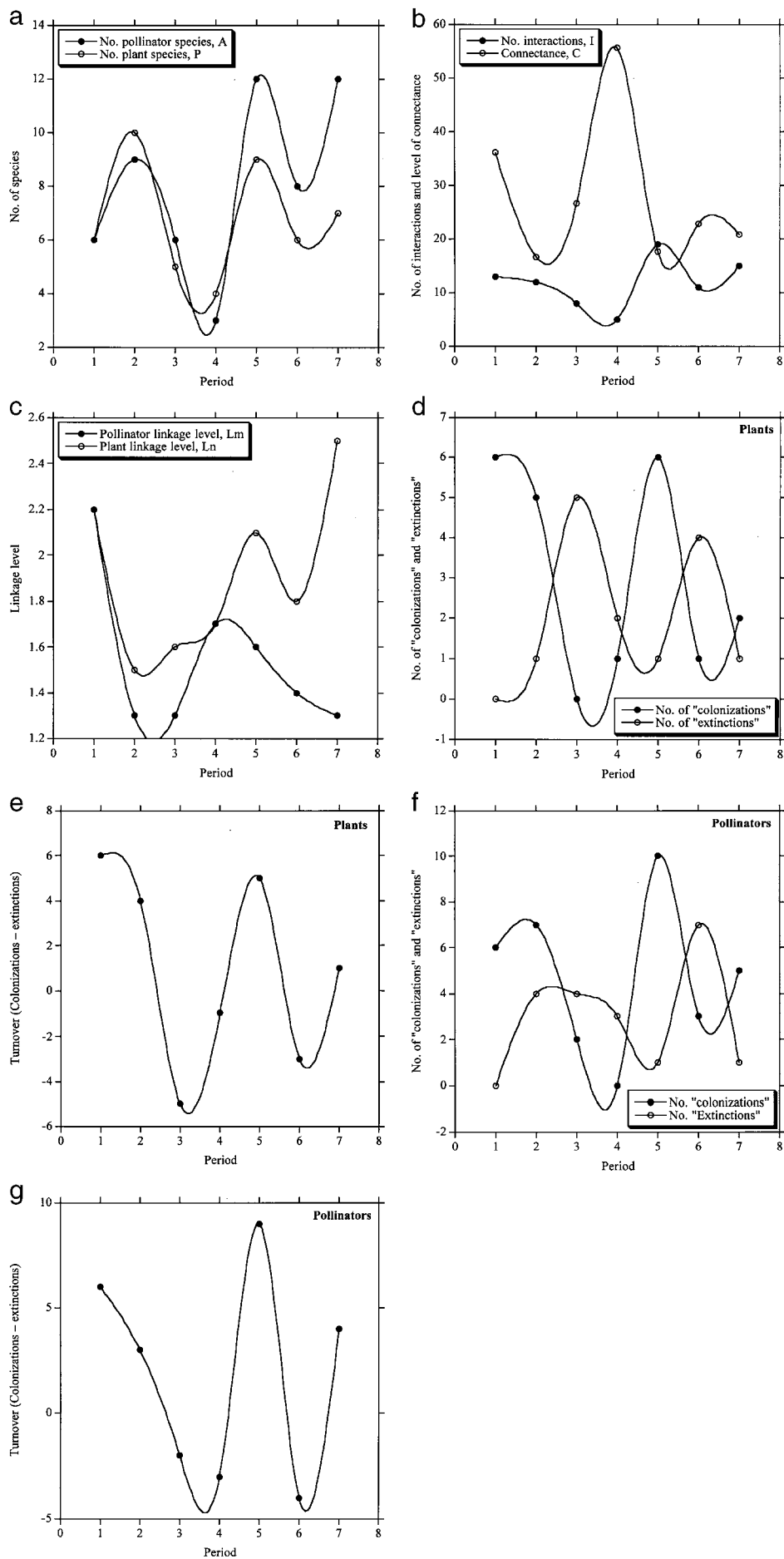
FIGURE 1. Seasonal variations, Uummannaq Island, Greenland. (a) Numbers of plant and pollinator species. (b) Total number of interactions and connectance. (c) Generalization level for pollinators and plants. (d) "Colonizations" (plant species that are flowering and that did not flower in the previous period) and "extinctions" (plant species that are not flowering but that did flower in the previous period). (e) Plant-species turnover (= colonizations minus extinctions). (f) Colonizations (pollinator species that are foraging and that did not forage in the previous period) and extinctions (pollinator species that are not foraging but that did forage in the previous period). (g) Pollinator species turnover.
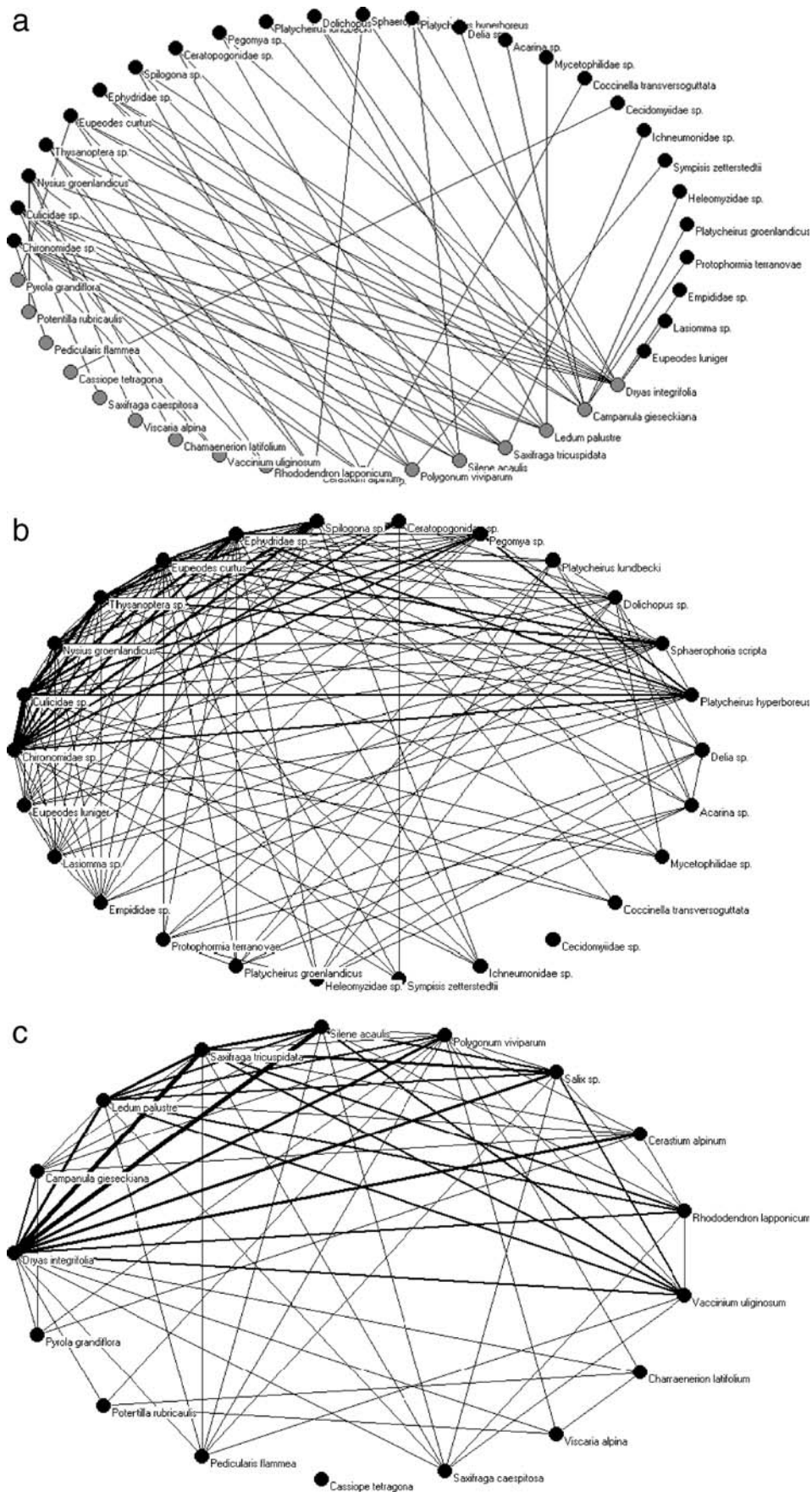
FIGURE 2. Species networks, Uummannaq Island, Greenland: (a) the 2-mode pollination network and the 1-mode networks for (b) pollinators and (c) plants. Line thickness indicates the interaction strength between a species pair. Interaction strength is given as number of species shared, i.e., the interaction strength between two pollinator species is strong if they both visit the same high number of plant species.

TABLE 3

Characteristic path length, $\langle l \rangle$, and average clustering coefficient, $\langle c \rangle$, of real and random 1-mode pollination networks, Uummannaq Island, North-West Greenland.

	Plant		Pollinator	
	real	random	real	random
$\langle l \rangle$	1.3	2.1	1.4	2.1
$\langle c \rangle$	0.18	0.79	0.83	0.18

network (Figs. 2a and 2b). An option in the software makes it possible to construct random networks with a given number of nodes and links. Both 1-mode networks appeared dense and highly connected. Characteristic path length, $\langle l \rangle$, was similar in plant and pollinator networks and much shorter than in random networks (Table 3). Clustering coefficient, $\langle c \rangle$, was similar in plant and pollinator networks and much larger than in random networks (Table 3). In both 1-mode networks, the tail of the cumulative distribution of k values, $p(\geq k)$, had the best fit to an exponential model ($R^2 = 0.98$ in both pollinator and plant networks) (Fig. 3).

Discussion

A DOUBLE-ISLAND EFFECT

Greenlandic pollination networks have a lower species number than other Arctic or sub-Arctic networks (Table 2). The present study had the lowest number of species and interactions of any of these studies with the exception of one (P. Witt, personal communication, Table 2), which had a slightly lower plant species number. In the present study, the A:P ratio was the lowest of all Arctic or sub-Arctic studies (Table 2). Olesen and Jordano (2002) analyzed 29 total field-season pollination networks worldwide and found that the A:P ratio, generally, was lower on islands than on the mainland. In general, species density is often lower on islands than on the adjacent mainland (Carlquist, 1970), so if one assumes similar sampling effort in all studies, the explanation for the low species number in this study could be a double-island effect due to the presence of the small island Uummannaq adjacent to the large island Greenland.

A DOMINANCE OF DIPTERANS

The dominance of dipterans as pollinators in the Arctic was stressed by Elberling and Olesen (1999). The proportion of dipteran species in studies compared by these authors had a range of 67–77% and was thus in accordance with the results of this study (77%). One explanation for the dominance of Diptera as flower visitors is their general dominance in the Arctic insect fauna. Approximately half of all insect species in Greenland belong to Diptera (Böcher, 2001).

SMALL-WORLD BEHAVIOR

Both the plant and the pollinator 1-mode network had high clustering and small path-length values, indicating that they both behaved as small worlds (Watts and Strogatz, 1998), i.e., all species are closely linked. Compared to food webs in general (Dunne et al., 2002; Montoya and Solé, 2002), this particular Arctic pollination network was more clustered and had shorter path lengths between species. In a pollination system, "information" can be an external signal like a species invasion or extinction or changes in the behavioral or population ecology of species already present. The small-world topology means that information (e.g., disturbance) spreads rapidly through the network (Watts and Strogatz, 1998). Whether it spreads faster or slower than in low-latitude pollination networks we do not
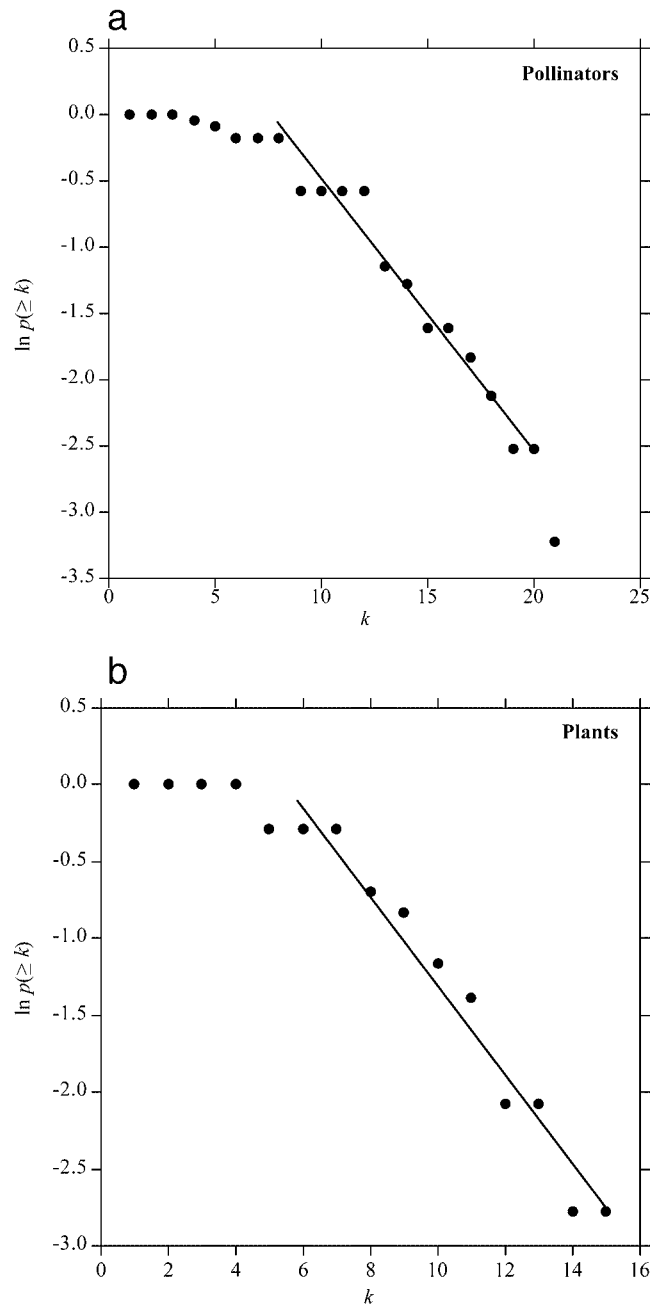
FIGURE 3. Cumulative degree distributions of $p(\geq k)$ for (a) pollinators and (b) plants. The line is fitted to the tail of the distribution.

know yet, because this study is the first in which 1-mode pollination networks were analyzed.

If species linkage is unconstrained the tail of the degree distribution has the best fit to a power law. However, in this study we found that the tail of the degree distribution had the best fit to an exponential model; this result tells us that the most connected species are constrained in their linkage to other species (Albert et al., 2000; Jordano et al., 2003, 2005). The reason for this is unknown. However, the high clustering and short path length mean that the Uummannaq network is error tolerant but vulnerable against attacks on the most connected species (Albert et al., 2000).

We conclude that the Uummannaq networks seem to show a double-island effect in their low pollinator:plant species ratio and in the low linkage level of the plants. The 1-mode networks had small-world

properties indicating a high tolerance against errors but vulnerable if the most connected species are attacked.

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