Ecological modules and roles of species in heathland plant–insect flower visitor networks

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Summary

1. Co-existing plants and flower-visiting animals often form complex interaction networks. A long-standing question in ecology and evolutionary biology is how to detect nonrandom subsets (compartments, blocks, modules) of strongly interacting species within such networks. Here we use a network analytical approach to (i) detect modularity in pollination networks, (ii) investigate species composition of modules, and (iii) assess the stability of modules across sites.

2. Interactions between entomophilous plants and their flower-visitors were recorded throughout the flowering season at three heathland sites in Denmark, separated by ≥ 10 km. Among sites, plant communities were similar, but composition of flower-visiting insect faunas differed. Visitation frequencies of visitor species were recorded as a measure of insect abundance.

3. Qualitative (presence–absence) interaction networks were tested for modularity. Modules were identified, and species classified into topological roles (peripherals, connectors, or hubs) using 'functional cartography by simulated annealing', a method recently developed by Guimerà & Amaral (2005a).

4. All networks were significantly modular. Each module consisted of 1–6 plant species and 18–54 insect species. Interactions aggregated around one or two hub plant species, which were largely identical at the three study sites.

5. Insect species were categorized in taxonomic groups, mostly at the level of orders. When weighted by visitation frequency, each module was dominated by one or few insect groups. This pattern was consistent across sites.

6. Our study adds support to the conclusion that certain plant species and flower-visitor groups are nonrandomly and repeatedly associated. Within a network, these strongly interacting subgroups of species may exert reciprocal selection pressures on each other. Thus, modules may be candidates for the long-sought key units of co-evolution.

Key-words: coevolutionary units, community structure, compartmentalization, mutualistic webs, network topology

Introduction

Angiosperm flowers exhibit an immense diversity in size, structure, colour, scent, nectar, and pollen traits, and the vast majority is pollinated by animals (Ricklefs & Renner 1994). Animal-pollinated flowers and flower-visiting animals are expected to exert reciprocal selective pressures on each other, and thus may co-evolve complementary traits (Darwin 1859; Faegri & van der Pijl 1966; Thompson 2005). Furthermore, groups of unrelated plant species may converge in traits of importance to pollinator attraction (Fenster *et al.* 2004). The highly debated pollination syndromes (Faegri & van der Pijl 1966; Waser *et al.* 1996; Fenster *et al.* 2004) are classic

examples of such convergence. For instance, hummingbird-pollinated flowers have evolved in a range of plant families. Although hummingbird flowers have various appearances, they often share a suite of floral traits, which are associated with the attraction and utilization of hummingbirds as pollinators and exclusion of insects, e.g. vivid colours, copious nectar, long tubular corollas and weak or no scent (Faegri & van der Pijl 1966; Proctor, Yeo & Lack 1996). Similarly, individual species or species-groups of pollinators may evolve complementary traits, e.g. in their beak morphology, as adaptations to flower visitation (Fenster *et al.* 2004). Complementarity of mutualistic traits and convergence of unrelated species on these traits may structure biological communities (Thompson 2005). However, it is debated how fine-tuned and taxonomically fine-grained co-evolutionary

complementarity and convergence actually are (Herrera 1996; Waser *et al.* 1996; Johnson & Steiner 2000; Fenster *et al.* 2004; Thompson 2005). An important issue is to pin down the units of ecological and co-evolutionary interaction (Thompson 2005).

Plants and flower-visitors range from specialists, having few interaction partners, to generalists forming many inter-actions (e.g. Waser *et al.* 1996). Pollination interactions are mostly asymmetric, i.e. specialist plant and pollinator species tend to interact with generalists, rather than specialists (Vázquez & Aizen 2004; Bascompte, Jordano & Olesen 2006). Thus, most species are integrated in a complex interaction network. In recent years, a new line of research has appeared in interaction biology, *viz.* network analysis (Ings *et al.* 2008). This follows a strong development in the analysis of complex networks in physics, social science, computer science, biochemistry and biology (Strogatz 2001; Barabasi 2002; Proulx, Promislow & Phillips 2005). In ecology, network thinking has provided insight into the structure and dynamics of food webs, host-parasitoid webs and mutualistic networks (Bascompte *et al.* 2006; Ings *et al.* 2008). In pollination networks, every link represents an animal species visiting the flowers of a plant species. Often, the link structure of networks is heterogeneous, indicating nonrandom association of plant and flower-visitor species. Some species may interact more strongly and for longer than others, exerting a signifi-cant selection regime upon each other (Olesen *et al.* 2007). These subgroups may thus reflect co-evolutionary units.

Groups of tightly linked species have long attracted the interest of researchers in ecology and evolutionary biology (e.g. Thompson 2005). Such species groups are labelled compartments, blocks, clusters, components, guilds, cohesive subgroups, communities, modules etc. (e.g. Pimm & Lawton 1980; Corbet 2000; Girvan & Newman 2002; Krause *et al.* 2003; Guimerà & Amaral 2005a,b). Here we use 'modules' defined as subsets of highly linked species, whereas between-module links are sparse. Many workers have searched for modules in ecological networks (e.g. Pimm & Lawton 1980; Raffaelli & Hall 1992; Dicks, Corbet & Pywell 2002; Girvan & Newman 2002; Krause *et al.* 2003; Prado & Lewinsohn 2004; Olesen *et al.* 2007), although this enterprise has been hampered by lack of a powerful method. Modules may be common in plant–ant networks (Fonseca & Ganada 1996), food webs (Krause *et al.* 2003), herbivory networks (Prado & Lewinsohn 2004), and pollination networks (Corbet 2000; Dicks *et al.* 2002). In a meta-analysis of 51 pollination networks, Olesen *et al.* (2007) used a strong modularity-detecting algorithm to demonstrate that pollination networks larger than 150 species are always modular, but less so than plant–ant, plant–herbivore and host–parasitoid networks. However, nearly nothing is known about the species composition of modules, and the stability of modules in space and time.

Here we investigate composition and stability of the mod-ular organization of pollination networks across three different sites of a similar heathland type. The networks were large (> 150 spp.), and thus expected to contain modules. All networks were well sampled and taxonomically highly resolved. The sites were separated by ≥ 10 km, i.e. beyond the foraging range of most flower-visiting insects (Dupont & Overgaard Nielsen 2006), and flower-visitor assemblages of the sites were hence assumed independent. Specifically, we asked: (i) do the heathland networks have a modular struc-ture? (ii) if so, what is the species composition of the modules? and finally, (iii) how stable is the modular structure geograph-ically? A prerequisite to our study is an access to a strong module-detecting algorithm. We used an algorithm recently developed by Guimerà & Amaral (2005a,b), which is one of the most accurate module-detecting algorithms to date (Danon *et al.* 2005). We found that all three networks were significantly modular. Modules were always organized around one or two plant species (hubs), which link to a large number of insect species, although often few taxonomic groups of insects dominated each module. Finally, very similar modules were found at the geographical scale of our study. These pat-terns strongly indicate a substructure of pollination networks, with repeated association of at least some of the flowering plant species and insect groups.

Materials and methods

STUDY SITES

At three heathland sites, we observed interactions between plants and their flower-visiting insects in plots of equal size (100 × 500 m): (i) Isen Bjerg (hereafter IB) (56°04′21″N, 9°16′32″E), a large contin-uous tract of heathland (122 ha) surrounded mainly by conifer plantation; (ii) Skov Olesen plantation (hereafter SO) (56°6′15″N, 9°6′28″E), a mosaic area consisting of heath fragments (12 ha), conifer plantation and deciduous forest (33 ha), grassland and bog (10 ha), embedded in an agricultural landscape (for a detailed description of SO and IB, see Dupont & Overgaard Nielsen 2006); and (iii) Hoer-bylunde (hereafter HL) (56°08′30″N, 9°23′24″E), a small continuous tract of heathland (21 ha) surrounded mainly by conifer plantation and grassland. The sites were separated by 10–17 km.

DATA SET

Plant–insect flower-visitor interactions were observed during an entire flowering season in each plot (1 April to 1 November 2004 at IB and SO, and 1 April to 1 October 2005 at HL). This resulted in a total of 66 observation days at IB, 72 days at SO, and 41 days at HL. Only plant species represented by ≥ 5 individuals per plot or having coverage large enough to be represented in ≥ 5 different 1 × 1-m quadrates per plot were observed for flower visitors (Table 1). All plant species were observed regularly throughout their flowering period. In the dioecious species *Salix repens*, male and female plants were treated as separate species, due to sex-specific differences in floral display and phenology. Only male plants of *Empetrum nigrum* were included in the analysis, because females did not attract any insects. *Vaccin-ium vitis-idaea* and *Genista anglica* had a main, primary flowering period in early season, and a late-summer secondary flowering period (notated as *V. vitis-idaea1* and *2*, and *G. anglica1* and *2*, respectively). The two flowering periods were treated separately, except for *G. anglica* at IB, in which the two periods were pooled due to small sample sizes.

Flower-visitor observations were made between 8 h and 17 h, on calm and dry days with a moderate-high insect activity. Census followed two protocols: (i) 1 × 1-m quadrates were placed where

Table 1. Floral traits and local abundance of plant species

Family	Species	Colour	Morphology	Nectar[a]	Local abundance[b]		
					IB	SO	HL
Asteraceae	*Arnica montana* L.	Yellow	Composite	1	–	a	–
	Hieracium pilosella L.	Yellow	Composite	0	vr	r	vr
	Hieracium umbellatum L.	Yellow	Composite	0	r	a	–
	Hypochoeris radicata L.	Yellow	Composite	0	a	r	r
	Scorzonera humilis L.	Yellow	Composite	?	r	vr	–
	Solidago virgaurea L.	Yellow	Composite	1	a	a	r
Campanulaceae	*Campanula rotundifolia* L.	Blue	Campanulate	2	vr	r	–
Dipsacaceae	*Succisa pratensis* Moench	Blue	Composite	1	–	r	–
Empetraceae	*Empetrum nigrum* L. ♂	Crimson	Brush	0	a	a	a
Ericaceae	*Calluna vulgaris* (L.) Hull	Pink	Dish/bowl	2	a	a	a
	Erica tetralix L.	Pink	Urceolate	2	r	a	a
	Vaccinium myrtillus L.	Pink	Urceolate	2	a	a	a
	Vaccinium uliginosum L.	White	Urceolate	2	r	a	a
	Vaccinium vitis-idaea L.	White	Urceolate	2	a	a	a
Fabaceae	*Genista anglica* L.	Yellow	Flag	0	r	a	–
	Genista pilosa L.	Yellow	Flag	0	–	r	vr
Onagraceae	*Epilobium angustifolium* L.	Pink	Dish/bowl	2	vr	r	vr
Primulaceae	*Trientalis europaea* L.	White	Dish/bowl	0	a	r	a
Rosaceae	*Potentilla erecta* (L.) Raeusch.	Yellow	Dish/bowl	1	a	a	–
Rubiaceae	*Galium saxatile* L.	White	Dish/bowl	0	a	a	r
Salicaceae	*Salix repens* L. ♀	Yellow	Brush	2	a	a	a
	Salix repens L. ♂	Yellow	Brush	2	a	a	a
Scrophulariaceae	*Melampyrum pratense* L.	Yellow	Gullet	2	–	–	a

[a]Nectar: 0 = no nectar, 1 = nectar poor, 2 = nectar rich (Christensen 1999, Y. L. Dupont & V. González-Álvaro, personal observations).
[b]Local abundance: vr = very rare (< 5 individuals or different 1 × 1 m quadrates in the plot, thus not included in network), r = rare, a = abundant.

blooming plants had high densities. Flowering plants were observed in 15-min trials, and the visitation frequency of each flower-visitor species was recorded. (ii) Plot observation, i.e. walks inside the plot, scoring presence or absence of interactions between flowering plants and flower visitors. Only flower-visiting insects touching reproductive flower parts, or being large enough to be potential pollinators, were regarded as pollinators. Insects were collected for identification, unless field identification was possible. Sample specimens of field-identified species were collected for verification by experts. The majority of insects were identified to species by taxonomists (see acknowledgments). Individuals of the complex *Bombus lucorum* (L.), *B. terrestris* (L.), *B. magnus* Vogt and *B. cryptarum* (F.) were common, but difficult to distinguish in the field, and therefore pooled as a *Bombus lucorum/terrestris* morphotype. Similarly, *B. pratorum* (L.) and *B. lapidarius* (L.) were lumped as a *B. pratorum/lapidarius* morphotype.

DATA ANALYSIS

For each site, we constructed an interaction network consisting of all pairs of interacting plant and insect species, pooling data from both observation protocols. We used the method of functional cartography by simulated annealing to test for modularity (see Guimerà & Amaral 2005a,b; Olesen *et al.* 2007 for further details). This technique identifies modules by maximizing a measure of modularity *M* of the network using simulated annealing (hereafter SA). The method of SA is a stochastic optimization technique, which combines multivariate optimization and statistical mechanics to maximize *M* (Kirkpatrick, Gelatt & Vecchi 1983). In contrast to previous heuristic methods, SA makes an exhaustive search to minimize the problem of finding sub-optimal partitions. Configurations are explored initially at a high computational temperature *T*, then the temperature is decreased stepwise by a cooling factor *q* ($T' = qT$), until a final temperature (T_f) is reached. The procedure is initiated by randomly selecting a partition. At each step (*T*) of the algorithm, a species is displaced from its module, and the resulting configuration assessed with respect to *M*. If *M* is increased the displacement is accepted, and the new configuration used as a starting point of the next step. If *M* is unchanged or decreased, the displacement is accepted or discarded according to a probability. Nearly all nodes are placed unambiguously in modules. The results of this algorithm are robust, yielding nearly the same partitions in different runs, and is one of the most accurate module-identifying algorithms to date (Danon *et al.* 2005; Guimerà & Amaral 2005a).

The modularity index *M* produced by SA, is a measure of the degree to which the network is organized into clearly delimited modules.

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

where N_M is number of modules, *I* is number of links in the network, I_s is number of links between species in module *s* ('within module links') and k_s is number of links of species in module *s*. Thus, *M* is high if link density is high inside modules, and between-module connectedness is low, when compared to randomly assembled networks. Modularity of the three heathland networks in the current study was assessed relative to 100 randomizations of the network, using an iteration factor of 0·9, cooling factor *q* = 0·999, and final temperature T_f = 0 (values recommended by R. Guimerà).
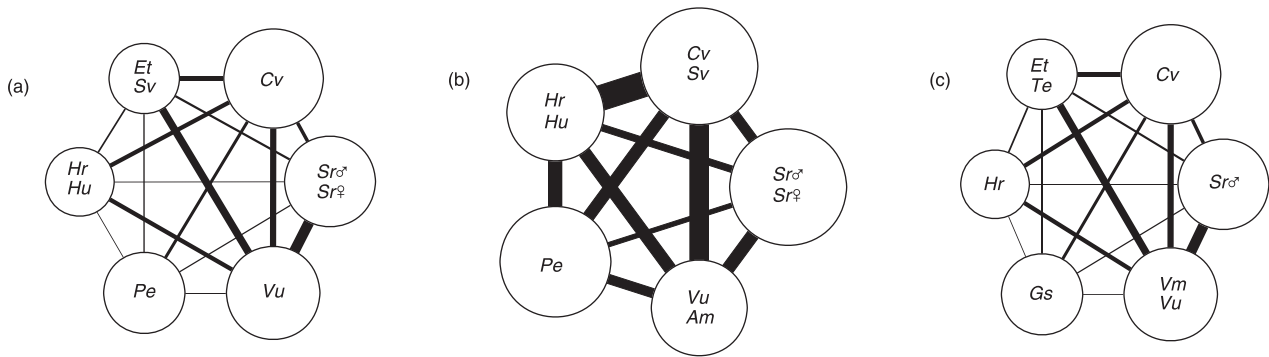
Fig. 1. Cartography of heathland pollination networks for (a) IB, (b) SO and (c) HL. Size of modules (depicted as circles) is proportional to their number of species, while line thickness is proportional to number of links between the modules. Hub plant species in each module is indicated, abbreviated as follows: *Salix repens* ♂ (*Sr*♂), *Salix repens* ♀ (*Sr*♀), *Vaccinium myrtillus* (*Vm*), *Vaccinium uliginosum* (*Vu*), *Arnica montana* (*Am*), *Potentilla erecta* (*Pe*), *Galium saxatile* (*Gs*), *Hypochoeris radicata* (*Hr*), *Hieracium umbellatum* (*Hu*), *Trientalis europaea* (*Te*), *Erica tetralix* (*Et*), *Solidago virgaurea* (*Sv*), and *Calluna vulgaris* (*Cv*).

The number of modules is not defined a priori, but is an outcome of the algorithm. N_M represents the optimal number of partitions when M is maximized for the network. For each module, we calculated the within-module connectance, defined as $C_m = I_m/(A_m*P_m)$, where A_m and P_m are numbers of animal and plant species in module m and I_m is the number of within-module links in m. Connectance of the entire network was calculated as $C = I/(A*P)$, where I, A and P are the total numbers of interactions, animal and plant species in the network.

In modular networks, species take different topological roles, defined by the two parameters, z and c (Guimerà & Amaral 2005a,b; Olesen *et al*. 2007). The within-module degree z_i is the standardized number of links of a species i to other species in the module,

$$z_i = \frac{k_{is} - \bar{k}_s}{\sigma_{ks}} \qquad \text{eqn 2}$$

where k_{is} is number of links of species i to other species in the same module s_i, while $\bar{k}_s$ and σ_{ks} are average and standard deviation of within-module links (k) for all species in s_i. Species are divided in highly linked hubs ($z \geq 2·5$), and sparsely linked nonhubs ($z < 2·5$).

The among-module connectivity c_i is a measure of how connected species i is to all modules:

$$c_i = 1 - \sum_{s=1}^{N_M} \left(\frac{k_{is}}{k_i}\right)^2, \quad c \in [0;1[\qquad \text{eqn 3}$$

k_i is number of links of species i. If all links of i are within its own module, $c = 0$, while if links are distributed evenly among modules, c approaches 1. Nonhubs ($z < 2·5$) are sub-divided into peripherals ($c_i \leq 0·62$), which have all or most links inside their own module; and connectors ($c_i > 0·62$), which have links across several modules.

TAXONOMIC GROUPS OF POLLINATORS

Insects species were grouped according to higher-level taxonomic classes, and differences in structure and behaviour important to pollination (Proctor *et al*. 1996). These included the four main flower-visiting orders (Coleoptera, Diptera, Hymenoptera, Lepidoptera), in addition to Dictyoptera. Diptera was further sub-divided into syrphids (Diptera, Syrphidae) and nonsyrphids (Diptera, non-Syrphidae). Hymenoptera was sub-divided into bees (Hymenoptera, Apoidea) and wasps/ants (Hymenoptera, non-Apoidea). For complete lists of species, see Tables S1–S3 in Supporting information. Singletons, i.e. species recorded by only one visit, were excluded to minimize influence of accidental visitation. The remaining species were weighted by visitation frequency. For each site, differences in visitation by different groups were tested for by a *G*-test. Rare groups (Coleoptera, Dictyoptera and Lepidoptera) were pooled in the analysis.

Results

All three networks were significantly modular. At IB, six modules were found, and level of modularity was $M = 0·43$ ($P < 0·01$); at SO, five modules were found, and $M = 0·38$ ($P < 0·01$); and at HL, six modules were found, and $M = 0·45$ ($P < 0·01$).

Modules contained one to six plant species at IB, three to six at SO and one to four at HL. All modules were organized around one to two hub plant species, which were linked to many pollinator species. Nonhub plant species were peripherals, except for the connectors *V. vitis-idaea2* at IB and *Hieracium pilosella* at SO (Fig. 1). Almost identical modules were found at the three study sites (Fig. 1, Tables S1–S3) (hub plant species in bold):

1. ***Salix repens*** ♂ ♀ module (hereafter SALIX), including *Vaccinium myrtillus* at IB and SO.

2. ***Vaccinium uliginosum***, *V. vitis-idaea1* and *E. nigrum* were associated at all sites, together with a few other species (***Arnica montana*** and *Erica tetralix* at SO, *Genista anglica* and *Trientalis europaea* at IB and ***V. myrtillus*** and *Melampyrum pratense* at HL) (hereafter VACCINIUM).

3. ***Potentilla erecta*** was the hub of a POTENTILLA-module at SO (also including *Galium saxatile* and *Trientalis europaea*) and IB. An analogous module was centred on ***G. saxatile*** at HL (hereafter GALIUM), where *P. erecta* was missing.

4. One module consistently formed around ***Hypochoeris radicata***, in association with another yellow composite ***Hieracium umbellatum*** at IB and SO (hereafter HYPOCHOERIS).

5. At all sites, ***Calluna vulgaris*** was the hub of a module, which in addition included other late-flowering species at SO (hereafter CALLUNA).

Table 2. Insect species repeatedly found in the same modules at the three sites, IB, SO and HL

Module	Insect species	Order	Total no. of interactions (total no. of visits)		
			IB	SO	HL
SALIX	*Andrena haemorrhoa* (F.)	Hymenoptera	4 (31)	4 (26)	3 (1)
VACCINIUM	*Bombus pratorum* (L.)/*lapidarius* (L) type	Hymenoptera	12 (93)	15 (99)	7 (19)
	Bombus pascuorum (Scop.)	Hymenoptera	8 (38)	16 (106)	8 (18)
	Bombus terrestris (L.)/*lucorum* (L.) type	Hymenoptera	11 (140)	15 (60)	9 (55)
	Callophrys rubi (L.)	Lepidoptera	4 (10)	4 (4)	1 (1)
POTENTILLA/GALIUM	None	–	–	–	–
HYPOCHOERIS/(HIERACIUM)	*Episyrphus balteatus* (DeG.)	Diptera	9 (519)	14 (341)	4 (382)
	Eupeodes corollae (F.)	Diptera	9 (106)	11 (62)	2 (77)
	Lasioglossum leucozonium (Sch.)	Hymenoptera	3 (6)	4 (4)	1 (3)
	Lasioglossum villosulum (K.)	Hymenoptera	3 (4)	1 (5)	1 (1)
ERICA/SOLIDAGO[a]	None	–	–	–	–
CALLUNA	*Pollenia rudis* (F.)	Diptera	1 (4)	6 (11)	1 (1)
	Tachina grossa (L.)	Diptera	1 (1)	2 (2)	1 (8)
	Andrena fuscipes (K.)	Hymenoptera	1 (9)	1 (2)	1 (11)
	Colletes succinctus (L.)	Hymenoptera	1 (4)	1 (1)	1 (2)
	Autographa bractea (D&S.)	Lepidoptera	1 (2)	1 (1)	1 (2)

[a]Species in the CALLUNA/SOLIDAGO and ERICA/SOLIDAGO modules were considered as members of the same module.

6. *Solidago virgaurea* was part of CALLUNA at SO, but formed a separate module together with *E. tetralix* at IB (hereafter ERICA/SOLIDAGO). At HL, *Solidago virgaurea* was rare (Table 1), and *E. tetralix* formed a module together with *T. europaea* (ERICA/TRIENTALIS).

Modules were highly linked groups of species, and module connectance C_m was $66·2 ± 27·8\%$ ($N = 6$) at IB, $39·6 ± 5·1\%$ ($N = 5$) at SO and $63·5 ± 18·8\%$ ($N = 6$) at HL. Connectance of the entire network C was much lower: $19·0\%$ at IB, $15·0\%$ at SO and $23·7\%$ at HL.

We collected 1068 flower-visiting insect individuals, representing a total of 301 species. Of these, 65 spp. (22%) were found at all sites, 60 spp. (20%) at two sites, and 176 spp. (58%) at one site. Only 14 insect species (5%), mainly bees, were repeatedly found in the same module at all three sites (Table 2). These included some of the most common generalist flower-visitors (e.g. *Bombus* spp. and migrant syrphids), in addition to insects with a preference or specialization for certain host plants (e.g. oligolectic bees). On the other hand, the dominant generalist *Apis mellifera* was associated with VACCINIUM at IB and SO, but ERICA/TRIENTALIS at HL.

Several orders of insects were represented in all modules (Tables S1–S3). Each module contained 19–49 insect species at IB, 33–54 at SO, and 18–41 at HL. However, when singletons were excluded and insect groups weighted by frequency, representation of taxonomic insect groups differed significantly among modules within a site (IB: $N = 2118$, d.f. $= 20$, $G^2 = 2860$, $P < 0·05$; SO: $N = 2004$, d.f. $= 16$, $G^2 = 1791$, $P < 0·05$; HL: $N = 1854$, d.f. $= 20$, $G^2 = 2255$ $P < 0·05$). Only one or a few insect groups dominated each module (Fig. 2). With a few exceptions, corresponding modules at the three sites contained similar insect groups (Fig. 2). SALIX mostly contained flies, and at SO and IB also solitary bees. Bees, mainly *A. mellifera* and *Bombus* spp. dominated VACCINIUM. At HL, this module also included syrphids. In the 'dish-flowered'

POTENTILLA, nonsyrphid flies were the most common visitors, in addition to syrphids at IB and beetles at SO. At HL, where *P. erecta* was missing, these visitor guilds were included into GALIUM. Pollinators of HYPOCHOERIS were mostly syrphid flies, and at SO to a lesser extent also ants. The pollinator fauna of CALLUNA was always highly diverse, but species content varied somewhat among sites. At IB, it was characterized by many butterflies, some nonsyrphid flies, bees and wasps, whereas at SO and HL, flies were the most common visitors. At all localities, some specialist insects were associated with *C. vulgaris*: the oligolectic solitary bees *Andrena fuscipes* (K.) (Andrenidae) and *Colletes succinctus* (L.) (Colletidae). In addition, *Nomada rufipes* (F.) (Apidae), *viz.* the nest parasite of *A. fuscipes,* was found in CALLUNA at SO and IB. ERICA/SOLIDAGO contained a large number of bees, in particular *Bombus* spp.

Discussion

Using a newly developed method 'functional cartography by simulated annealing' (Guimerà & Amaral 2005a,b), we detected tightly linked subgroups of species in all three heath pollination networks. These modules showed a high constancy in composition across sites. Modules were centred on one to two hub plant species, which attract a large number of flower-visitor species. When visitors were weighted by frequency, few taxonomic groups dominated each module. We thus conclude that plant and flower-visitor species of heathland networks are substructured in more or less distinct units of interactions.

MODULE SPECIES COMPOSITION

Neither individual plant species nor individual modules were visited exclusively by a single flower-visitor group. However, when we included visitation frequency data, more distinct
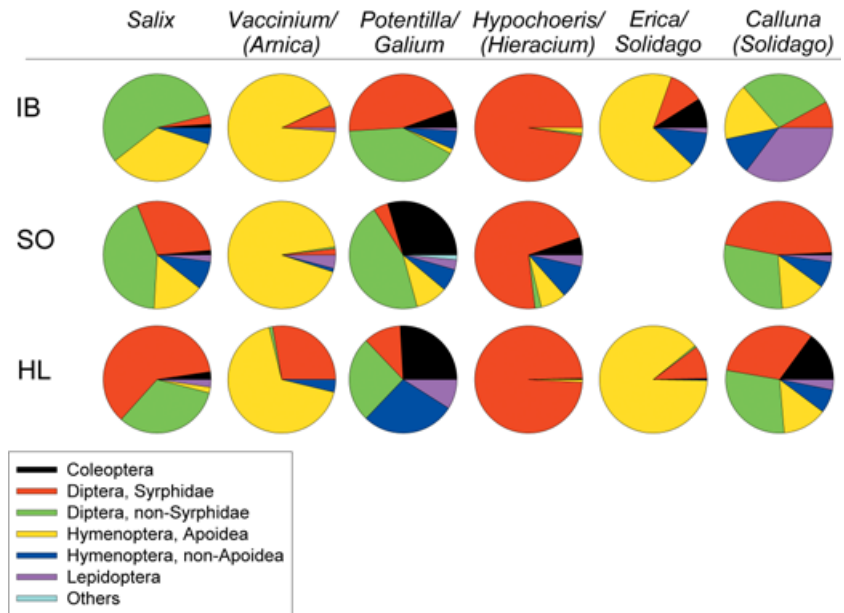
Fig. 2. Insect groups (in percentage) weighted by visitation frequency. Each row represents one study site, and pie charts in the same column represent comparable modules (hub plant species indicated in top row). For affiliation of insect species to modules, see Tables S1–S3.

groups of pollinators emerged. Despite large compositional differences in the insect faunas of the three study sites, these patterns were found repeatedly. In this study, we did not consider differences in pollination effectiveness of visitors. If this had been carried out, the pollinator fauna of each module might have been even more distinct, considering that most plants are effectively pollinated by only a subset of their visitors (Stebbins 1970; Spears 1983; Fenster *et al*. 2004). In future analyses of modularity in pollination networks, it is highly desirable to incorporate data on interaction strength. However, this has to await the development of new algorithms.

The modules recognized in the current study were largely concordant with the main pollinator groups reported from single-species studies: bees, in particular *Bombus* spp., were common visitors of the white-pinkish, nectar-rich, urceolate flowers of *Vaccinium* spp. in spring (Ritchie 1955, 1956; Jacquemart 1996) and *E. tetralix* in summer (Bannister 1958). Open, yellow and white, nectar-poor flowers (in POTENTILLA, GALIUM and HYPOCHOERIS) were visited mostly by a variety of syrphids and other flies, which were attracted to the pollen resource. SALIX contained flies and small bees, typical to willows (Vroege & Stelleman 1990; Karrenberg, Kollmann & Edwards 2002). Only CALLUNA had a highly diverse assemblage of flower visitors. *Calluna vulgaris* is a widespread generalist-pollinated species, which attract a diverse array of potential pollinators across sites and years, and the plant may even be wind-pollinated (Hagerup 1950; Gimingham 1960; Mahy, De Sloover & Jacquemart 1998).

In two grassland pollination networks, Dicks *et al*. (2002) detected modules of plant species with closed, nectar-rich flowers associated with bees (and butterflies) and modules of open, pollen-rich flowers associated with flies. These patterns are consistent with the VACCINIUM and ERICA modules vs. POTENTILLA, GALIUM and HYPOCHOERIS modules in the present study. Thus, modules of the heathland networks may correspond to those of other habitats.

CO-EVOLUTIONARY UNITS

Co-evolution in pollination networks involves complementarity in a core set of mutualistic traits of plants and pollinators, and convergence of traits in unrelated species (Thompson 2005; Bascompte *et al*. 2006). Thus, species are expected to attach preferentially to certain interaction cores in the network. Because the ecological and functional basis of pollination mutualisms and the traits under convergent selection are often similar geographically, interactions may shift to other, functionally equivalent species as species composition of networks changes (Thompson 2005). The modules detected in the present study consisted of similar hub plant species across sites. Although this applied only to the most abundant generalist insect species, dominant insect groups were remarkably similar among corresponding modules at different sites (Fig. 2). Moreover, species within modules were highly connected, thus possibly exerting strong reciprocal selection on mutualistic traits. We suggest that these stable groups of tightly interacting species are candidates for co-evolutionary units.

Recently, it was demonstrated that adaptive phenotypic evolution may take place on an ecological time-scale, bridging community ecology and evolutionary biology (Strauss & Irwin 2004; Johnson & Stinchcombe 2007). If so, evolution may affect demographic and community processes, and thus ecosystem functioning. If, on the other hand, modules reflect deeper phylogenetic splits, they may be regarded as conservative units of species within networks, bounded by certain constraints imposed by the plant or animal partners, e.g. morphology or phenology. In fact, niche segregation of plant species (in terms of soil-hydrological requirements) appears to arise at different taxonomic levels, and accumulate through the evolutionary history of species (Silvertown, Dodd & Gowling 2001). Phylogenetic relatedness is an important factor determining interaction patterns in at least

some mutualistic networks (Rezende *et al.* 2007). Whether phylogeny is an important structuring factor of modules in pollination networks is in need of further investigation.

MODULAR STRUCTURE AND CONSERVATION

The heathland networks of this study are typical of pollination networks in terms of descriptive parameters (Olesen *et al.* 2007). Thus, our key finding of spatial stability of modules and their species content may have general implications.

A stable modular pattern may influence network robustness. In theoretical networks, modularity enhanced stability (May 1972; Krause *et al.* 2003). Sinha (2005), on the other hand, found that the transition point from stability to instability did not differ between modular and random networks, but the transition was more gradual in the former. Modular networks avoid abrupt deterioration leading to extinctions, and thus modularity may slow down the rate of biodiversity loss (Wilmers 2007).

Modules were mostly organized around one or a few hub plant species, while no insect species acted as hubs. This appears to be a general trend in pollination networks (J.M. Olesen & Y.L. Dupont, unpublished data). Thus, hub plants, similar to cornucopian species (Ellis & Ellis-Adam 1993), are keystone floral resources supporting a high diversity of flower-visiting insects. If these plant species go extinct, their modules may fragment causing cascading loss of insect visitors (Memmott, Waser & Price 2004; Jordano, Bascompte & Olesen 2006). Structurally, pollination networks are expected to be unaffected by extinction of specialists or peripherals (Memmott *et al.* 2004), analogous to the removal of peripheral metabolites in biochemical networks (Guimerà & Amaral 2005a). Connectors, on the other hand, play an indispensable role in metabolic networks (Guimerà & Amaral 2005a), whereas their importance in pollination networks is less obvious. In pollination networks, the majority of connectors are insect species (Olesen *et al.* 2007). If these are lost, modules become decoupled and modularity of the network becomes more pronounced. How this will affect ecosystem functioning is in need of further exploration.

Conclusions

Our analysis shows that pollination networks from habitat patches separated in space by small geographical distances have a stable modular structure, modules consisting of similar hub plant species and insect groups. Within a network, species play different topological roles (hubs, connectors and peripherals), which may have implications for network functioning and conservation. Future studies should be aimed at understanding the importance of phenological pattern, floral biology, phylogeny, and differential interaction strength to the formation of modules. Furthermore, an important task is to identify characteristics of hub plant species, which act as network keystones.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. Plant and insect species in modules at IB

Table S2. Plant and insect species in modules at SO

Table S3. Plant and insect species in modules at HL

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