

# The modularity of pollination networks

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In natural communities, species and their interactions are often organized as nonrandom networks, showing distinct and repeated complex patterns. A prevalent, but poorly explored pattern is ecological modularity, with weakly interlinked subsets of species (modules), which, however, internally consist of strongly connected species. The importance of modularity has been discussed for a long time, but no consensus on its prevalence in ecological networks has yet been reached. Progress is hampered by inadequate methods and a lack of large datasets. We analyzed 51 pollination networks including almost 10,000 species and 20,000 links and tested for modularity by using a recently developed simulated annealing algorithm. All networks with >150 plant and pollinator species were modular, whereas networks with <50 species were never modular. Both module number and size increased with species number. Each module includes one or a few species groups with convergent trait sets that may be considered as coevolutionary units. Species played different roles with respect to modularity. However, only 15% of all species were structurally important to their network. They were either hubs (i.e., highly linked species within their own module), connectors linking different modules, or both. If these key species go extinct, modules and networks may break apart and initiate cascades of extinction. Thus, species serving as hubs and connectors should receive high conservation priorities.

coevolution | compartment | module | nestedness | species role

Biodiversity encompasses not just species but also interactions among species. Within habitats, species and their interactions assemble into large, complex ecological networks. Such networks are rich in structural heterogeneity (1). Understanding network structure and its underlying causes are essential parts of any study of biodiversity and its responses to disturbances, yet it is a conceptual and methodological challenge to address these problems in highly diversified communities with thousands of interactions.

Moving through an ecological network of species and their connecting links, one traverses a heterogeneous universe of link-dense and -sparse areas. Link-dense regions are termed compartments (2) or, here, modules (3), whereas link-sparse regions demarcate their boundaries. Species within a module are linked more tightly together than they are to species in other modules. The extent to which species interactions are organized into modules is termed the modularity of the network. Modularity may reflect habitat heterogeneity, divergent selection regimes, and phylogenetic clustering of closely related species (4, 5), leading to nonrandom patterns of interaction and ultimately contributing to the complexity of ecological networks. Modules with their tightly linked species may even be the long-sought key units of coevolution, in which reciprocal selection leads to trait convergence in unrelated species (6). However, modularity has been notoriously difficult to demonstrate either because of its rarity or because of a lack of sufficiently strong module-detecting algorithms (1).

In ecology, Pimm and Lawton (4) presaged recent methodological developments by constructing a modularity statistic, which they compared with a distribution of randomly generated webs. Later, Raffaelli and Hall (7) used the distribution of a trophic similarity index between species pairs to look for mod-

ules in an estuary web. Dicks *et al.* (8), adopting the latter method (7), analyzed two pollination networks and found that they were modular. Today, strong modularity-detecting algorithms are used outside ecology, e.g., in social sciences (9), information theory (10), and network studies of airlines and biochemistry (11–13). Recently, one of these algorithms (14) was used to detect modularity in five food webs (15). We used an algorithm, here termed SA (11–13), which is based on simulated annealing [see supporting information (SI) *Materials and Methods* for a review of different methods] in a search for modules in pollination networks. Together with other properties of such mutualistic networks, e.g., nestedness and asymmetry (16–20), modularity is expected to be an essential ingredient of network complexity. Thus, modularity may play a critical role in both the functioning of these networks, e.g., to their stability (21, 22) and in the potential for coevolution of plant and animal species (6). An identification of modules can tell us what highly connected groups of species look like and perhaps also at what scale coevolution is taking place. This may ultimately assist us in the maintenance of biodiversity by preserving key groups of taxa playing a fundamental role to network persistence.

A long-lasting tenet in mutualistic plant–animal interaction studies is the concept of syndromes (23, 24), i.e., that species converge on correlated suites of traits shaped by similar interaction patterns. Such a process may result in a heterogeneous web of interactions, with taxonomically or functionally related taxa packed into distinct modules. Understanding how species interact and evolve at the modular level may thus be a key to an understanding of trait evolution. Many pollination studies implicitly assume modularity by focusing on subwebs of interacting species sharing a syndrome (e.g., hummingbirds and their flowers; ref. 25). Thus, a stronger, more explicit focus on modules in mutualistic networks as study objects may open up routes to a broader study of functional diversity and coevolutionary units.

Here, we focus on the modularity of entire pollination networks, i.e., all interacting species within an area are included. Our aims are (i) to estimate the level of modularity in pollination networks, (ii) to identify different types of modules in networks, and (iii) to classify species into different functional roles with respect to their position within and among modules.

## Results

For each pollination network in the dataset, we ran the modularity-detecting algorithm SA (see *Materials and Methods*). It produced a modularity index  $M$ , which was a measure of the degree to which the network was organized into clearly delimited modules. The algorithm also provided (i) the significance level of  $M$  of the real network by comparing its value to that of similar-sized random networks, (ii) the number of modules per

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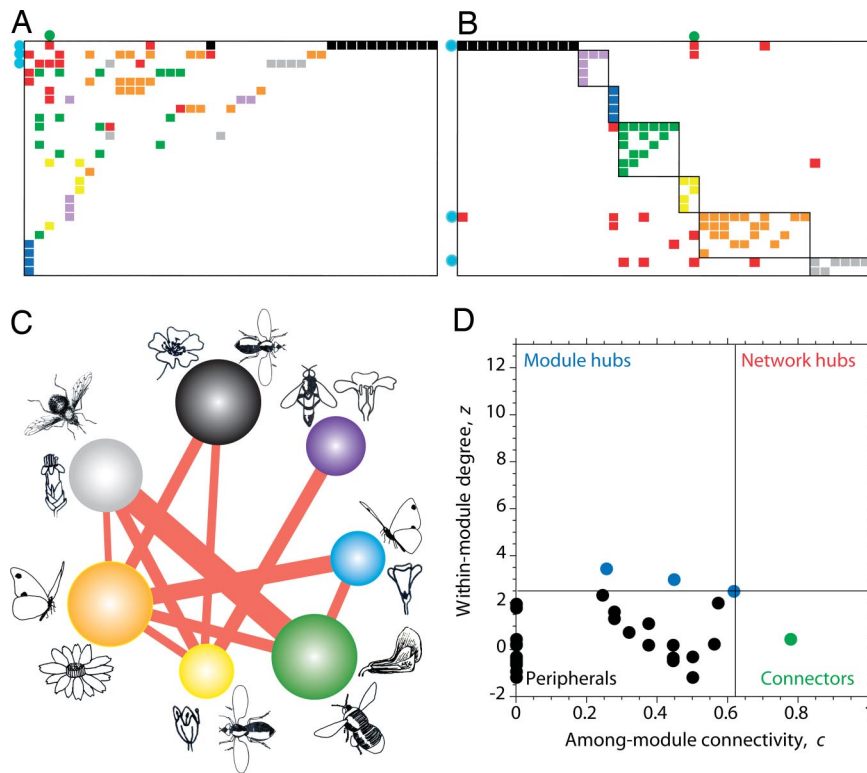
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**Fig. 1.** Pollination network structure and species roles. The example is from the Andes (28). (A) Nested matrix version of the network, with plant species in columns and pollinator species in rows sorted from the upper left corner according to descending species degree. (B) Modular matrix version of the same network as in A; species are now sorted according to their modular affinity (order of modules is arbitrary). Red cells are species links gluing the seven modules together into a coherent network, and nonred cells are links within modules (links of the different modules can be identified in A by their color). (C) Graph of modules. Module links are weighted by both the number of species links between modules and number of species within modules; vignettes show dominant pollinator and flower type: black module: Diptera species and mainly white flowers; purple module: small-to-medium-sized beetles, flies, an ant, and small, white/yellow flowers; blue module: butterflies and one plant species, *Oxalis* species; green module: bees, birds, and large, mainly yellow flowers with a closed morphology; yellow module: large flies and small, yellow umbellifer flowers; orange module: butterflies, a large fly, and white/yellow/pink/purple flowers; and gray module: large flies and mainly small, white flowers. (D) zc-plot of species roles with three module hubs and one connector, but no network hub. In A and B, species acting as module hubs and connectors are shown as blue and green dots, respectively, just outside the matrix border. Notice that the connector species in B (green dot) has >50% of its links outside its own module.

network, and (iii) the content of species of each module (see *Materials and Methods*). In total, 51 networks were analyzed, and 29, or 57%, were significantly modular, i.e., they had a modularity index  $M$  significantly higher than that of random networks (see *SI Table 1*). Mean  $\bar{M} \pm \text{SD}$  was  $0.52 \pm 0.071$  ( $n = 29$  networks). All networks of >150 species were modular and all <50 species were nonmodular. Thus, modular networks encompassed by far most of the species and links in our sample (8,233 species and 16,799 links, or 85%).

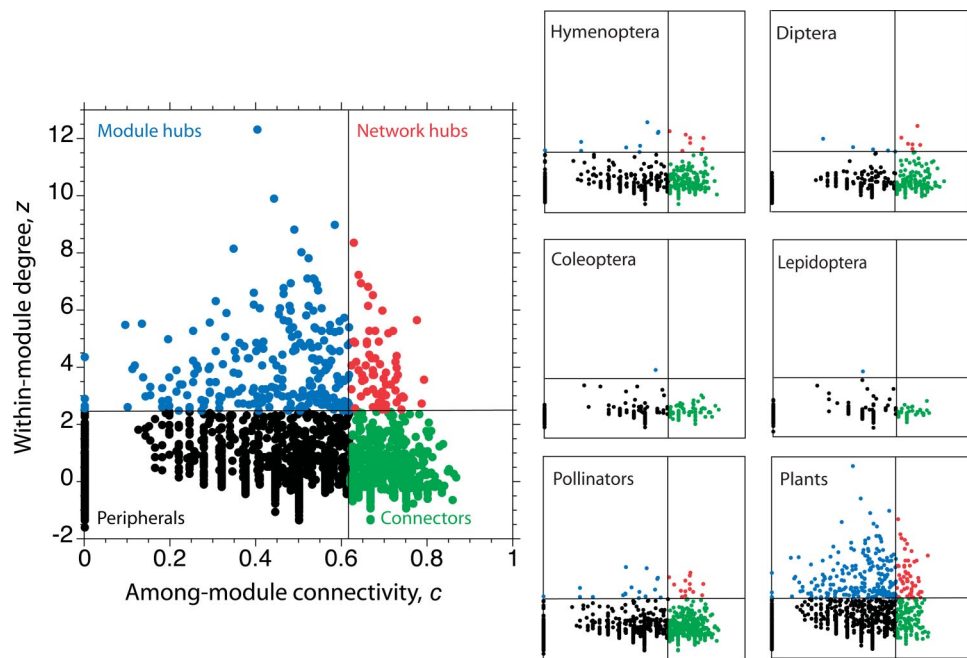
Our subsequent analysis included only the 29 significantly modular networks. These networks had, on average,  $8.8 \pm 3.7$  modules—with a maximum of 19 modules for the Amami Islands (26) and a minimum of five for a temperate forest meadow (27) and heathland (Y.L.D., unpublished work). Modularity  $M$  was independent of network size  $S$ , i.e., total number of species of pollinators  $A$ , and plants  $P$  ( $n = 29$  networks:  $F_{1,27} = 0.0003$ ,  $P \geq 0.99$ ), whereas, number of modules in a network  $N_M$ , and mean module size  $S_M$ , i.e., number of species per module, both increased with  $S$  ( $n = 29$ :  $F_{1,27} = 9.9$ ,  $P \leq 0.004$ ; and  $F_{1,27} = 45.5$ ,  $P \leq 0.0001$ , respectively).

Most links in a network were among species within the same module (on average 60% of all links  $I$  in a network). Thus, mean connectance  $C_M$ , within a module (number of observed links/number of possible links in the module, excluding links to other modules), became very high ( $42 \pm 28\%$ ), whereas mean con-

nectance  $C$  ( $=100I/(AP)$ ), for the total networks was much lower ( $7 \pm 4\%$ ).

All 51 networks were also tested for nestedness, i.e., a widespread pattern where specialists interact with a subset of the species that the more generalized species interact with (16). All networks, except five small ones, were significantly nested (see *SI Table 1*). Levels of nestedness  $N$  and modularity  $M$  were uncorrelated [ $n = 29$  networks:  $F_{1,27} = 2.96$ ,  $P \leq 0.10$ , negative trend; in this analysis, we corrected for among-network variation in  $S$  and  $I$  by using relative nestedness  $(N - \bar{N}_{\text{random}})/\bar{N}_{\text{random}}$  and relative modularity  $(M - \bar{M}_{\text{random}})/\bar{M}_{\text{random}}$ , where  $\bar{N}_{\text{random}}$  and  $\bar{M}_{\text{random}}$  were average nestedness and average modularity, respectively, of the random runs]. A nested matrix thus appeared to be built on modules assembled by interactions that connected them; largely generalist species (Fig. 1A) were involved in these interactions. In Fig. 1A and B, an example of a real network is shown in both its nested and modular matrix version, and in Fig. 1C, its modular structure is depicted as a graph. The nested pattern in Fig. 1A resulted from the assembly of distinct modules (nonred colors in Fig. 1B) “glued” together by interactions among modules (red cells).

The 29 modular networks consisted of 254 modules. Individual modules differed in size and shape because of variation in species number  $S_M$  ( $= A_M + P_M$ , i.e., the sum of pollinator and plant species in a module) and species ratio  $A_M/P_M$ . On average,  $\pm \text{SD}$ , a module contained  $32 \pm 34$  species, namely, 26 pollinator species and six plant species, i.e.,  $A_M/P_M = 4.2$ . Thirty-six (14%)



**Fig. 2.** Distribution of pollinator and plant species according to their network role. Each dot represents a species; large pane includes all 8,233 species from the 29 modular networks. Small panes show role distribution of selected groups of species.

of all modules were isolated species groups without any links to the remaining network. Twenty-one of these isolates were small 1:1 modules, consisting of only one pollinator species interacting with one plant species. Twenty-nine (11%) of all modules were structurally very asymmetrical or star-shaped, consisting of one generalist hub species, most often a plant species, linked to a swarm of peripheral pollinator species (range 3–51) linked only to the hub. The hub, however, had links to other modules. The remaining 189 (74%) of the modules varied a lot in size and shape (for examples of module types, see Fig. 1*B*). Individual modules might be dominated by a few species, taxonomically or functionally delimited; for example, in the subandine scrub (28), there was an 8:18-module (i.e., a module of eight pollinators interacting with 18 plants), which was dominated by three or more floral oil-collecting bees, namely, *Centris* spp. and *Tapi-notaspis* species, together with five or more floral oil-producing plants, namely, *Sisyrinchium* species and *Calceolaria* species. In a Jamaican network (29), one of the seven modules was a 5:3 module consisting of four birds (Streamertail Hummingbird, Bananaquit, Orangequit, and Jamaican Blackbird), one *Anolis* lizard, and three plant species with red/purple-colored flowers.

Topologically, species played different roles in the networks. The algorithm SA described the role of each species by its within-module degree  $z$ , i.e., its standardized number of links to other species in the same module, and its among-module connectivity  $c$ , i.e., the level to which the species was linked to other modules (see *Materials and Methods*). For each species in a network, SA calculated these parameter values (11–13). Species with both a low  $z$  and a low  $c$  were peripheral species or specialists, i.e., they had only a few links and almost always only to species within their module. Species with either a high value of  $z$  or  $c$  were generalists. These included module hubs, i.e., highly connected species linked to many species within their own module (high  $z$ , low  $c$ ), and connectors linking several modules (low  $z$ , high  $c$ ). Species with both a high  $z$  and a high  $c$  were network hubs or super generalists, acting as both connectors and module hubs. An example of this mapping of species roles is given for a single network in Fig. 1*D*. The scatter of  $zc$ -roles of all species from all modular networks is shown in Fig. 2.

Eighty-five percent of all species were peripherals with most of their links inside their module (72% of these even had a  $c = 0$ , i.e., they had no links at all outside their own module) and 15% were generalists, i.e., 3% were module hubs, 11% connectors, and only 1% network hubs. The strongest module hubs were plants, like umbellifers (e.g., refs. 26, 30, and 31). Connectors were mainly beetles, flies, and small-to-medium-sized bees (e.g., refs. 32–34). Most network hub pollinators were social bees, especially *Apis* spp. (31, 35) and *Bombus* spp. (27) or large solitary bees, e.g., *Xylocopa* sp. (34) and a few Diptera species (Fig. 2).

### Discussion

Above a size of 50 species, all pollination networks got significantly nested (16) and some also became modular, and passing 150 species, they were always both significantly nested and modular (see *SI Table 1*). Thus, within the observed size range of pollination networks ( $S = 16$ –952 species), testing solely for one kind of network pattern is too simplified (5); both sides of the coin are needed. This lack of correlation between nestedness and modularity suggests that modularity dictates the basic building blocks of networks. These building blocks or their species can then be combined in different contrasting ways, e.g., maximizing either nestedness or modularity. The nested and modular matrix versions are two complementary, yet uncorrelated, analytical steps toward a more profound understanding of network complexity and its causes. In the nested matrix version, species are ranked according to their number of links, whereas in the modular version, they become grouped according to their linkage affinity to other species. This insight, however, could only be gained with the recent appearance of strong algorithms (e.g., 11, 14, 36), allowing a robust identification of modules and a testing of modularity and nestedness. The presence of nestedness in pollination networks tells us that their structure is more than just a string of distinct modules. The link-dense core in the nested version (upper left matrix corner in Fig. 1*A*) is partly composed of between-module links (red cells in Fig. 1*A* and *B*), i.e., links connecting generalist species. The SA

algorithm identifies these generalists (15% of our species sample) by their high  $z$ - and/or  $c$ -scores. Generalists “glue” peripheral species together into modules, but also modules together into networks and, in this way, blur module boundaries. The key innovative insight obtained from our analysis is that all larger pollination networks are modular and that modularity is complementary to nestedness.

The smallest networks were nonmodular. The reason for this may be a lack of module-detecting power of the algorithm SA when network size decreases. However, the reason may also be related to the connectance of the networks. In general, if connectance in pollination networks increases, then network size decreases (37). If connectance increases, the size of the core of links between generalized species also increases, which may reduce the level of modularity.

Modularity is expected to increase with link specificity (5). It may, for example, be stronger in insect herbivory networks than in pollination and seed-dispersal networks, characterized by low interaction specificity, and in traditional food webs. In an analysis of a herbivory network, flower head-breeding Tephritidae flies and their Asteraceae host species were sorted into six modules (38). Using SA on this network, we detected seven modules and a high modularity (116 species,  $M = 0.63$ ), higher than in most pollination networks ( $\bar{M} = 0.52$ ; see [SI Table 1](#)). In this herbivory network, generalists, especially connectors, played a more inferior role as network “glue” (6% of all species) than in pollination networks (15% of all species). Trophic specialization was suggested to cause modularity (38). If so, modularity may be driven by evolution among plant species in various key traits, e.g., chemicals and flower head morphology that “filters out” subsets of species from the overall pattern of species interactions. Reanalyzing a tropical host–parasitoid network also with an expected high link specificity (39), we found an even stronger modularity (104 species,  $M = 0.67$ , 12 modules). Networks of domatia-living ants and their plants are also expected to show high link specificity. Fonseca and Ganade (40) identified seven modules and strong modularity in a South American plant–ant network. Three modules were even isolated from the main network. Using SA, we confirmed their results (41 species,  $M = 0.58$ ). These “long-term intimate mutualisms” (41) strengthen modularity (38, 40, 42), but are rarely seen in networks of interactions among free-living species such as plants and their pollinators or seed dispersers (6).

Many argue for a synthesis of community ecology and evolutionary biology (e.g., refs. 43 and 44). Modularity and nestedness may be the stepping-stone, bridging evolutionary biology and not just community ecology, but also network ecology (45). This may intensify cross-disciplinary work in a research area poor in synthetic field studies (ref. 43; however, see ref. 46). Identification of modules and their component species may be the missing protocol bullets making such studies feasible. If trait evolution within a focal species has only one-to-one species links as its drivers, the network context becomes redundant. However, because such pairwise one-to-one links are extremely rare among free-living mutualists (6, 41) and extremely rare in pollination networks (this study, ref. 47), reciprocal selection is believed to be multispecific, i.e., involving a module, a couple of tightly linked modules, or maybe even an entire small, (non)modular network (6, 44). Within individual modules, connectance was 42%, i.e., almost half of all pollinators and plants were likely to interact directly (Fig. 1B). Thus, the multispecies selection regime in a module must be intense.

Small groups of strongly interacting species are favorite study objects in pollination biology, but without authors explicitly stating that these are modules, e.g., bumblebees and their plants (48) and hummingbirds and heliconias (25, 49). Convergence toward syndromes, e.g., the bird–flower pollination syndrome, in a pollination network may promote modularity (6, 50). Thus, an

identification of modules may bring us closer to an understanding of the basic coevolutionary units that structure complex webs of interaction. This conclusion is strongly supported by the “biological content” of modules. Some of those identified in this study contained a set of species with convergent traits related to their pollination biology, e.g., corolla color or reward type, or they were closely related taxonomically (Fig. 1C). Thus, our study provides a straightforward relationship between a network property and its ecological equivalence expressed as life-history attributes of the component species. The study of modularity may serve to bridge two major coevolutionary research agendas, namely that focusing on small groups of strongly interacting species (6) and that focusing on entire networks (16, 17, 19). In this way, modularity may shed light on how small groups of species scale up to form complex networks of interactions.

The demonstration of modularity in pollination networks has far-reaching conservational implications. Disturbances are expected to spread more slowly through a modular than a non-modular structure. The identification of the role of species in modular networks may also have valuable bearings to conservation. The network consequences of species extinctions depend on species role, e.g., an extinction of a module hub may cause its module to fragment with no or minor cascading impact on other modules (38), whereas the extinction of connectors may cause the entire network to fragment into isolated modules but with minor impact on the internal structure of individual modules. Conversely, alien invaders of a network, often being highly generalized (51), may cause fusion of modules with profound, long-term effects on network functioning and selection regime.

The omnipresence of modularity and other structural properties, e.g., nestedness, in large pollination networks may change our view on the structuring of biodiversity. Our study shows that modules are small blocks of species, candidating as manageable study objects, and that their study may bridge evolutionary and functional ecology.

## Materials and Methods

**Database.** Pollination networks are a well studied type of networks (e.g., refs. 8, 16–20, and 52–54). We analyzed 51 total pollination networks encompassing almost 10,000 species of plants and flower-visiting animals and 20,000 links, using our own data and data extracted from the literature (see [SI Table 1](#)). “Total” does not mean a complete sampling of species and links but only that all plants and flower-visitors observed were included (37). All flower-visiting animals were regarded as pollinators, which, of course, was not necessarily true. Thus, a link is a record of an animal species visiting the flowers of a plant species. The number of links a species has to other species is its degree  $k$ . A pollination network is two-modal, i.e., it includes only links connecting plant and animal communities, and it is represented as an adjacency matrix (Fig. 1A and B; ref. 52), whose elements consist of presence and absence of links (colored and uncolored cells, respectively). Most data are sampled over an extensive period, most often one season, and the sample of study sites covers a wide geographical range and many habitat types (see [Table 1](#)). We are aware of the methodological heterogeneity of our database. However, it is more homogeneous than most earlier databases in ecology; for example, almost all taxa were resolved to species level, and links were scored in a similar way, albeit, by many researchers. Data on link strength was not included because such information was lacking in approximately half of the networks and because the module-detecting algorithm (SA) operates only with binary (presence/absence) data (see [SI Appendix](#)).

**Modularity Analysis.** A modular network consists of interconnected modules. Each module is a group of species, which are more closely connected to each other than to species in other



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