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Journal Article

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Publication date:
2018-03

Permanent link:
https://doi.org/10.3929/ethz-b-000253158

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Originally published in:
Nature Communications 9, https://doi.org/10.1038/s41467-018-03448-w
Disentangling the role of floral sensory stimuli in pollination networks

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Despite progress in understanding pollination network structure, the functional roles of floral sensory stimuli (visual, olfactory) have never been addressed comprehensively in a community context, even though such traits are known to mediate plant-pollinator interactions. Here, we use a comprehensive dataset of floral traits and a novel dynamic data-pooling methodology to explore the impacts of floral sensory diversity on the structure of a pollination network in a Mediterranean scrubland. Our approach tracks transitions in the network behaviour of each plant species throughout its flowering period and, despite dynamism in visitor composition, reveals significant links to floral scent, and/or colour as perceived by pollinators. Having accounted for floral phenology, abundance and phylogeny, the persistent association between floral sensory traits and visitor guilds supports a deeper role for sensory bias and diffuse coevolution in structuring plant-pollinator networks. This knowledge of floral sensory diversity, by identifying the most influential phenotypes, could help prioritize efforts for plant-pollinator community restoration.
early in the twentieth century, biologists adopted network theory in order to investigate complex systems such as food webs. Networks now constitute a powerful analytical tool used in the study of mutualistic interactions, such as pollination, seed dispersal, plant–mycorrhiza associations and cleaner–client reef fish relationships. In particular, network analysis has transformed the conceptualization of pollination from a biological function traditionally studied in isolated pairs or small groups of species, to a key ecosystem function that sustains primary productivity and the stability of communities. At present, given that all the major worldwide threats to biodiversity affect plant–pollinator (p–p) interactions as well, intensive global research efforts focus on understanding the structure and dynamics of p–p networks, so that conservation and restoration strategies can be effectively employed.

During the last twenty years, there has been a lively debate regarding the interplay of ecological and evolutionary specialization in p–p interactions. The assessment of large interaction datasets revealed that symmetrical specialization in communities is rarer than expected from the pollination ‘syndrome’ paradigm, the applicability and influence of which remain contentious subjects. Tight pairwise or 1:1 species relationships strictly matching the ‘syndrome’ concept (according to which specific sets of plant traits provide some predictive power in the identification of evolutionarily important pollinator groups) are indeed rare in natural communities. Thus, studies of p–p networks have tended to de-emphasize specialization and, as a consequence, the importance of floral phenotypes as adaptations in ordering network structure. Long-term observations of p–p networks indicate that they are characterized by a great temporal plasticity of interactions. Furthermore, the opportunistic foraging behaviour of flower-visiting insects has been attributed to extreme seasonality in certain biomes, whereas theoretical models have inferred that, in mutualistic networks, linkage rules may largely be explained by phenology and/or species’ abundance.

However, we know that, in pollination networks, nearly half of the visitor species interact with only one or very few plant species. Moreover, mutualistic interactions entail at least some degree of phenotypic complementarity, exemplified by the simple matching between proboscis length and corolla depth, to the more sophisticated interplay of floral stimuli (e.g. scent, colour) and the sensory systems of pollinators. The shared evolutionary history of plants and pollinators is linked to their interaction patterns, is considered a major driver of floral diversification and, although it may not act alone, has been shown to operate within the almost generic asymmetrical structure of mutualistic networks. Recently, our study revealed a phenotypic integration between floral colour (as perceived by pollinators) and scent at a community level among the flowering plants; this finding suggests a coordinated adaptation of plants to the sensory systems of pollinating insects. We build upon this finding by asking whether floral phenotypes that match visitors’ physical and sensory biases in a community context represent evolutionary vestigial traits or relics with no extant function, or alternatively, whether they are correlated with the realized pollinator-niches of the plants.

Distinct sensory biases and cognitive abilities of pollinators are expected to filter the information available in floral landscapes, and to shape foraging behaviours. In this context, insect responses to natural floral volatile blends were found to correlate with visitation patterns, and experimental manipulation of those blends was shown to reversibly affect visitation patterns in two keystone plant species studied simultaneously in a community. Similarly, floral reflectance has been connected to visitation patterns, and recently, the phenotypic matching between the flower colour of temporally overlapping plants and the visual systems of pollinators was shown to influence insect attraction and the plants’ ecological specialization in one community. However, pollinators likely experience floral traits as multimodal sensory information, rather than solely visual or olfactory cues. Pollination network studies have not yet considered the full complement of floral stimuli; hence, it remains unclear whether community visitation patterns have a sensory basis or, as inferred in most studies to date, they represent a function of floral density and/or phenological matching. Answering this question requires a comprehensive dataset on the sensory ecology of an entire floral community, including human-unbiased parameterizations of floral scent and colour, and an evaluation of specialization through a balanced design that directly compares the relative impacts of phylogeny, floral traits, phenology and density.

Species must co-occur in time in order to interact; therefore, flowering phenology is the first factor filtering p–p interactions in a community. Yet, by assessing the overall (static) p–p network of the entire flowering/sampling season one considers putative interactions that are not possible in time, thereby inflating the calculated measures of specialization. The resulting inflation can be considerable, given that most species in many communities, including the Mediterranean ones, tend to have short flowering phenophases. Recent studies have addressed this issue by partitioning the total network into smaller regular time-sequential networks. However, even network studies with a day-scale resolution inevitably employ the static version of plants’ ecological specialization and centrality (i.e. the degree of the influence that a given species has on the network’s structure), simply because this type of data aggregation provides the total number of links among the nodes, against which the realized interactions will be compared.

To overcome this methodological bias, we introduce a dynamic approach to data pooling in bipartite ecological networks, the ‘phenonet’ structure, which partitions the total cumulative network into a set of networks equal in number to the interacting species in the community. Here, a phenonet becomes a snapshot of the entire p–p network of the community, encompassing the interaction spectrum occurring within each species’ phenophase. Our method is based on the simple facts that (i) not all species interact directly with each other, but only with the temporally co-occurring species and (ii) species interact directly with other trophic levels only during their phenophase. Thus, the actual ecological or evolutionary specialization may vary according to time and depending on the ecological context, i.e. the antagonistic or facilitative interactions with co-occurring species.

The second key element known to determine interaction patterns and the structure of networks is floral density. In general, floral abundance is used in p–p network studies as an independent factor; however, from a functional ecological standpoint, the number of flowers represents the relative abundance of specific (e.g. visual and olfactory) phenotypic traits that constitute the floral sensory landscape in a community of blooming plants. We thus adopt the concept of ‘apparent’ in chemical ecology of herbivory, to describe the multiple ways that a plant can present olfactorily or visually distinguishable (and thus more apparent) flowers across the community.

Here we investigate the role of floral sensory stimuli on the structure of a p–p network in the phrygana, a natural Mediterranean scrubland, by employing the above-mentioned dynamic data pooling, and by accounting for species’ functional abundance and phylogeny. We specifically ask (i) whether plant centrality and generalization are significantly associated with floral phenotype, (ii) whether floral phenotype predicts visitation rates by the different pollinator groups and (iii) which phenotypic elements are important for the structure of the p–p network. Our findings
Bipartite networks disentangles the signals. Overall, our approach, which can be applied in different pollinator groups are correlated with different type in the interacting community, and helps to define the most influential plant species.

**Results**

The static p–p network of the community. The total p–p network (Supplementary Data 1) sampled in two consecutive flowering periods (see Methods) consisted of 41 plant species (18 families) and 168 insect species (44 families), including 403 plant–insect species links and 7955 interaction events, i.e. insect visits to individual flower units. Most of these events were made by bees (57.9%), followed by beetles (Coleoptera; 33.8%), flies (Diptera; 5.2%), butterflies (Lepidoptera; 2.2%) and wasps (0.7%) (Supplementary Data 1). The bees were also the most species-rich group (66 taxa), followed by flies (37), beetles (26), wasps (19) and butterflies (17) (Supplementary Table 1). Connectance (i.e. the number of realized interactions as a proportion of all possible interactions) was 5.9%, which is an intermediate value for Mediterranean scrubland networks. Nestedness (i.e. the asymmetrical pattern in which interactions of specialist species are subsets of the interactions of the generalist ones, with the latter representing the core of interacting species in a community) was 95.5%, a value typical for mutualistic networks.

The coupled evolutionary history of plants and insects was associated with the structure of the pollination network in the community. The cophylogenetic signal of the binary network (including only the presence/absence of p–p interactions) was significant (Procrustes sum of squares, \( m^2 = 0.97, P = 0.001 \)), indicating that the backbone of interactions was correlated with the shared evolutionary history of plants and pollinators. For example, interactions between the sunflower family (Asteraceae) and beetles (Coleoptera) showed the lowest Procrustean residuals, implying particularly strong cophylogenetic signal between these clades compared with the rest of the network (Fig. 1c). Given that the Procrustean analysis employs the binary version of the network (i.e. not including the number of visits for each link), we could suggest that it actually measures the cophylogenetic signal of the initial attraction between plants and insect, exactly because it equally values all links: some p–p links occurred repeatedly (i.e. many visitation events), yet some others only occurred once because although the insect was attracted, it decided not to visit another flower of the same plant species. Thus, this approach revealed that the “first contacts” between plants and pollinators are related to p–p coevolution.

Moreover, we found that the modular structure of the network (consisting of nine modules, Supplementary Table 2) is significantly associated with the insect phylogeny (Rezende’s algorithm, \( P < 0.001 \)), and not with that of the plants (\( P = 0.355 \)). The fact that the insect (instead of the plant) phylogeny shapes module composition could imply convergence of floral traits of unrelated plant lineages as a response to selection pressure by specific clades of pollinators, or the exploitation of specific floral resources by the different taxonomic groups of pollinators from randomly selected plant species (refs. 24,44 and refs. therein).

Finally, the phylogenetic relatedness of plants was a source of variation for the prevailing group of visitors. When visitation by each major pollinator group was treated as a categorical plant variable, we found that for each plant species in the community, the predominant group (as to no. of visits), showed a significant phylogenetic signal, i.e. phylogenetically related plant species were mainly visited by the same pollinator group (Rezende’s algorithm, \( P = 0.008 \); Fig. 1a, b). Furthermore, significant phylogenetic signals were found for the visitation rates by flies, beetles, and wasps (Supplementary Fig. 1). These associations align with the view that the phylogenetic congruence of interacting plants and pollinators occurs at high taxonomic levels (orders, rather than species), and suggest that grouping the flower visitors of the Mediterranean scrubland studied according to their taxonomic order was ecologically meaningful.

**Phenonets reveal the temporal plasticity of interactions.** A phenonet is the interaction network covering each plant species’
flowering period. The plant phenonets in the study community (Supplementary Table 3) had various sizes depending on the phenophase length of each plant species. The smallest phenonet consisted of 42 insect and 15 plant species (phenonet of Centaurea pulchellum), whereas the largest phenonet contained 165 insect and 36 plant species (Anthemis auriculata). One caveat is that this data-pooling method generates binary networks, and hence the metrics and algorithms used in the analysis should be appropriately selected (see Methods).

Nestedness was negatively correlated with plants’ phenonet size (Pearson’s \( r = -0.82, P < 0.001, N = 40 \) (Fig. 2), and ranged from 78.7% (Ornithogalum sp.) to 95.8% (Echium plantagineum, Linum trigrum)). For plant species that flowered at the temporal extremes of the flowering season, phenonets became smaller in size, more connected and more nested compared with the mid-season ones, when the interaction patterns were more random (Fig. 2). Nestedness in mutualistic systems is directly linked to season ones, when the interaction patterns were more random compared with the mid-season extremes of the flowering season, phenonets became smaller in size, more connected and more nested compared with the mid-season ones, when the interaction patterns were more random.

In the phenonets, the functional roles of the plant species in the community. Plant phenonets are shown in the top row (shaded in black) and are sorted temporally, so that plants with Earlier start and shorter duration are ordered first, from left to right. Months correspond to the start of flowering only. For each phenonet, the values of three network properties are provided in a gradient colour scale: Connectance (C), Nestedness (N), and Network size (\( P \times A \)). For each plant species (rows), the pollinator group with the highest number of species visiting the plant in each phenonet is also provided: Bees (B), Coleoptera (C), Diptera (D), Lepidoptera (L) and Wasps (W). White cells denote absence from the respective phenonet. For the phenonet name abbreviations, see Supplementary Table 6.

**Fig. 2** The functional roles of the plant species in the phenonets of the community. Plant phenonets are shown in the top row (shaded in black) and are sorted temporally, so that plants with earlier start and shorter duration are ordered first, from left to right. Months correspond to the start of flowering only. For each phenonet, the values of three network properties are provided in a gradient colour scale: Connectance (C), Nestedness (N), and Network size (\( P \times A \)). For each plant species (rows), the pollinator group with the highest number of species visiting the plant in each phenonet is also provided: Bees (B), Coleoptera (C), Diptera (D), Lepidoptera (L) and Wasps (W). White cells denote absence from the respective phenonet. For the phenonet name abbreviations, see Supplementary Table 6. The series of phenonets allowed for a detailed observation of the p-p network’s temporal dynamics. During the entire sampling season, the aforementioned functional roles of plants were generally far from static: species considered peripheral (i.e. extreme specialists) in the static network temporarily became generalists (e.g. Anemone pavonina, Ranunculus paludosus; Fig. 2), in the phenonets of other species. Apart from Cistus creticus, which was the only network hub in the static network (Supplementary Table 4), other species also served as network hubs for shorter periods, e.g. Cistus salviifolius, Crepis neglecta, Onopordum taureicum and Taraxacum sp. (Fig. 2). On the other hand, there were specific plants that maintained their role as...
module hubs, thus their pollinator “clientele” persisted in the community over a long time, across several plant phenonets (e.g. \textit{Anthyllis hermanniae}, \textit{Crepis neglecta}, \textit{Lavandula stoechas} and \textit{Scandix} sp.). Interestingly, the above-mentioned hubs mainly attract bee species (Fig. 2). ‘Connectors’ (i.e. species that connect different modules) show also a general constancy regarding the most species-rich order of visitors they receive. Thus, even generalist plants or those with shifting roles during the flowering season are mainly associated with species of specific insect orders. In sum, our approach reveals (i) the multidimensional temporal mosaic of the functional diversity of insect-pollinated plants, (ii) species that are highly influential in the community during their phenophases and (iii) those plants that maintain in time certain modules of the p–p network, being thus potentially important for the conservation of their module partners, both plants and animals.

**The role of floral phenotype.** After evaluating the analytical adequacy of the phenonets, and revealing the temporal dynamics of the interactions, we tested the three network node properties that describe the plant species’ behaviour within them (ND, BC and CC) against the components of floral phenotype. For this, we applied generalized least-squares models corrected for statistical dependence due to phylogenetic proximity (PGLS in Table 1). Apart from the standard floral traits (viz. scent variables, colorimetric properties, symmetry, nectar presence and corolla depth—see Methods), we calculated the chemical and the physical floral apparency for each plant species (Fig. 4). These values describe the degree to which a plant species has more or less noticeable flowers compared to its co-flowering species, regarding its inflorescence emissions or its physical appearance, given its floral abundance in the community (Supplementary Fig. 2). We found that the behaviour of the plant species in their phenonets was significantly associated with floral sensory stimuli (Table 1).

The level of generalization (ND) was significantly related to visual (viz. trichromatic floral colour, horizontal and vertical apparency) and chemical floral traits (viz. apparency of sesquiterpene and aliphatic volatiles). BC was significantly related to trichromatic colour, sesquiterpene apparency, proportion of aliphatics in the emissions and surface apparency. Thus, the trichromatic floral colour, scent and surface apparency predicted the importance of plant species for the cohesion or, inversely, the fragmented nature of the p–p network. Interestingly, CC, the rate of shared pollinator species with other plants in the community, was correlated only with floral scent properties (Table 1). CC values increased with the number of pollinator species that a plant species shared with other plants, i.e. with the pollinator niche overlap\(^{48}\). Thus, pollinator niche similarity was significantly associated with floral scent in our focal community. This result expands upon recent findings about the importance of floral scent as a key partitioning factor for two major plant nodes within a p–p network\(^{31}\). Since high values of BC and CC identify species with the greatest influence on network topology\(^{48}\), we may conclude that the diversity of floral sensory stimuli, i.e. the relative variability of colour descriptors and scent properties of the flowers, was a driver of plant functional complexity in the assembly.

Then, we tested the relationship between the different components of floral phenotype and the overall structure of the static p–p network. For this, we applied a multivariate-response generalized linear model designed for compositional data (MGLMs in Table 2), using the weighted (quantitative) static network interaction matrix as a multidimensional response variable (see Methods). We found that visual and olfactory floral stimuli (viz. trichromatic colour, emissions of sesquiterpene volatiles and horizontal apparency) contributed significantly to the network link structure, implying that interactions were not randomly assembled (Table 2). Repeating the same analysis for every subset of the p–p network including a major pollinator taxonomic group (viz. bees, wasps, Coleoptera, Diptera and
Table 1 Floral traits associated with the three node properties of plants in the network studied

| Node property       | AICnull | AICbest | Predictor                                | d.f. | F    | P-value | Slope |
|---------------------|---------|---------|------------------------------------------|------|------|---------|-------|
| Normalized Degree   | −4.1    | −48.1   | Trichromatic colour ($r_{chi} \times \theta_{pi}$) | 6,30 | 8.11 | 0.008   | +     |
|                     |         |         | %Aliphatics                              | 41.35| <0.001| -       |       |
|                     |         |         | Sesquiterpene apparency                  | 16.10| <0.001| +       |       |
|                     |         |         | Height apparency                         | 23.02| <0.001| +       |       |
|                     |         |         | Surface apparency                        | 12.93| 0.001 | +       |       |
|                     |         |         | Normal boiling point of scent blend       | 4.06 | 0.053| +       |       |
| Betweenness Centrality | −5.0 | −36.3   | Trichromatic colour ($r_{chi} \times \theta_{pi}$) | 4,32 | 6.70 | 0.014   | +     |
|                     |         |         | %Aliphatics                              | 17.02| <0.001| -       |       |
|                     |         |         | Sesquiterpene apparency                  | 24.66| <0.001| +       |       |
|                     |         |         | Surface apparency                        | 12.33| 0.001 | +       |       |
| Closeness Centrality | −119.7 | −123.6 | %Aliphatics                              | 2,34 | 5.52 | 0.025   | -     |
|                     |         |         | Al_{app} × Be_{app} × Mo_{app} × Se_{app} | 2.62 | 0.115| +       |       |

The best phylogenetically informed generalized least-squares models according to AIC are presented. The AIC value of the null model (~1) is provided for comparison. Significant P-values (>0.050) are indicated in bold. Positive or negative relationships are given (slope > 0, < 0). For details on the predictors, see Methods and the Supplementary Information.

Al aliphatics, Be benzenoids, Mo monoterpenes, Se sesquiterpenes, app apparency.

Discussion

In this study, we conducted a trait-based analysis to investigate the roles of sensory phenotypic characteristics of insect-pollinated flowers in structuring the C–C network of a natural community, and in shaping plant behaviour in the network. In order to achieve the latter, we (i) removed the effects of phenology by applying a new dynamic data-pooling methodology, (ii) we used a functional approach that incorporated floral abundance into the phenotypic apperance of the species and (iii) we accounted for the effects of phylogenetic affinity between plant species. Thus, what remained to be tested was merely the functional relationship between floral phenotypic traits and species’ centrality or specialization. This work represents a step toward the unbiased assessment of multimodal floral stimuli and the role of sensory landscapes in community-wide pollination studies. Despite the limited knowledge of the enormous phenotypic diversity of flowers, and of the innate preferences and sensory systems of insect pollinators, this study has shed light on the roles of sensory phenotypic characteristics of insect-pollinated flowers in structuring the C–C network of a natural community, and in shaping plant behaviour in the network.
their visitors, we found significant relationships within a single network, suggesting that our approach could be fruitfully applied to p-p networks elsewhere.

The plant phenonet structure introduced here is centred on the temporally experienced ‘flowering lifetime’ of each community member with the subset of species that co-flower or are active during that lifetime. Consequently, it is possible to track down every species’ behaviour during the active lifetime of every other species in the community. The static pooling would instead only describe species’ behaviour during the entire flower season of the area studied or during (biologically) arbitrary time intervals, resulting, inevitably, in inflated specialization or underestimated centrality for the nodes. Different types of mutualistic networks have been shown to exhibit invariant properties, leading to a predictable community structure\(^6\). At the same time, the extent of spatio-temporal scale dependency of mutualistic networks and their analysis is still largely unresolved, although this is crucial to our comprehension of natural complexity in general (e.g. ref. \(^59\)). Thus, any approach that disentangles the drivers that shape network topology and dynamics may be applicable to a variety of ecological systems. Phenological constraints may operate in any interaction network: e.g. fruiting phenology is a known constraint in plant–disperser networks\(^14\). The phenonet methodology offered here (i) is fully compatible with the temporally dynamic nature of any interaction network, (ii) allows a phenology-unbiased approach and (iii) can be used to more accurately describe the species’ roles, specialization and centrality in any network dataset that has been sampled with regular intervals during their periods of activity. In this manner, trait-based analyses may focus on the actual role of phenotypes in shaping interaction patterns, beyond phenology.

Our phenonet results highlight an interesting, and perhaps nuanced and less typological concept of floral syndromes\(^29\). The plant phenonet structure introduced here is centred on the temporally experienced ‘flowering lifetime’ of each community member with the subset of species that co-flower or are active during that lifetime. Consequently, it is possible to track down every species’ behaviour during the active lifetime of every other species in the community. The static pooling would instead only describe species’ behaviour during the entire flower season of the area studied or during (biologically) arbitrary time intervals, resulting, inevitably, in inflated specialization or underestimated centrality for the nodes. Different types of mutualistic networks have been shown to exhibit invariant properties, leading to a predictable community structure\(^6\). At the same time, the extent of spatio-temporal scale dependency of mutualistic networks and their analysis is still largely unresolved, although this is crucial to our comprehension of natural complexity in general (e.g. ref. \(^59\)). Thus, any approach that disentangles the drivers that shape network topology and dynamics may be applicable to a variety of ecological systems. Phenological constraints may operate in any interaction network: e.g. fruiting phenology is a known constraint in plant–disperser networks\(^14\). The phenonet methodology offered here (i) is fully compatible with the temporally dynamic nature of any interaction network, (ii) allows a pheno-

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colour to the topologically important plants in the network (Table 1) corroborates the fundamental role of bees as important pollinators and selective agents in this habitat type. Accordingly, the PGLS models showed that the variation in bee visitation rates relates to the trichromatic floral hue and increases with sesquiterpene emissions (Table 3). Hence, beyond the signal efficacy hypothesis, it is possible that some groups of bees may have sensory biases to C15 compounds deserving further exploration.

Interestingly, semi-volatile sesquiterpenes have been shown to mediate positive plant–plant associations in natural communities, through diverse mechanisms of conspecific eavesdropping67, as well as adsorption and re-emission by (heterospecific) neighbouring plants, to defend against herbivores68. Given the profusion of sesquiterpenes in Mediterranean scrublands and the association of native plants’ emissions with the sensory systems of bees, future research should focus on their broader functional roles across the spectrum of plant–plant interactions, from allelopathy and associational herbivore resistance to facilitation of shared bee pollinators. Specifically, it is worth exploring whether floral scent mediates facilitative interactions in p−p assemblies, as compared with floral morphological traits28.

Rapid progress has been made towards the development of tools for the functional restoration of pollination networks7,8, and the identification of plant species with high conservation priority69. Given that floral traits relate to plant population vulnerability70, our approach indicates that sensory-targeted functional restoration and conservation schemes would increase our understanding of and ability to maintain network dynamics and possibly facilitative effects in natural communities. For example, it has been shown that selecting plants for restoration only according to the amount of rewards they offer may undermine facilitative effects and result in undesirable effects due to elevated competition (e.g. ref. 7). We provide evidence that influential plants in the community may exhibit visual and/or olfactory traits associated with specific pollinator groups, such as bees. Perspectives expand if we consider that floral traits are also involved in antagonistic interactions71, and the spread of pathogens72. Overall, the numerous well-resolved p−p datasets collected across the world are invaluable ecological resources; yet their predictive capacity will remain incomplete as long as floral trait assessments, focusing on sensory stimuli perceived by floral visitors, remain overlooked or omitted from such studies. Despite the methodological challenges, trait-based analyses of interaction webs improve our understanding of the complexity of natural communities.

Methods

Flower visitation. Visitation censuses were conducted during the spring flowering periods (April–July) in two successive years (2011–2012). The repetition of observations was important in order to account, to the fullest possible extent, for the above-mentioned high temporal plasticity of species and interactions. We haphazardly established six permanent observation plots with dimensions 3 × 25 = 75 m² in the study area. During both years of sampling, the same observer (AK) visited the study site in 10 day-intervals and recorded all plant–insect interactions during three 15 min diurnal sessions (quarters), distributed from 9 am to 3 pm. During each quarter of an hour, the observer moved at a steady pace within the plot, recording interactions, and collecting insect specimens with a hand net, in case the instant taxonomic identification was not possible at the site. Plant and insect specimens were identified to species or to the lowest taxonomic level possible. An interaction was recorded only when an insect touched the reproductive organs of a flowering plant for more than two seconds. Following a convention in this type of studies45,46,47, these visitors have been used as a proxy for pollinators. In total, 46,712 were spent observing floral visitation (23,2 h in 2011 and 23,5 h in 2012). To evaluate sampling completeness, we used the approach of Chacoff et al. (based on the Chao 2 estimator)48, which showed that we detected 73.0% of the total visitor species richness in the community (Supplementary Fig. 3), which is typical in similar studies of p−p networks50,51.

During every sampling day, all open flower units were counted in the observation plots. As flower units we defined (i) all inflorescences (e.g. compact spikes in Lavandula, heads in Asteraceae, dense umbels in Apiaceae), where the distance between individual flowers was so short as to allow small insects to walk on the surface of the inflorescence rather than fly in search of the next source of reward or (ii) the individual flowers that either were solitary or placed in less compact inflorescences than in (i). Flower density was calculated as flower units per m², by dividing the total number of units counted in all censuses by the total area observed (250 m²). None of the plants in this community has an exclusively

| (Sub-)network | AICsum null | AICsum best | Predictor | Deviance | P-value |
|---------------|-------------|-------------|-----------|----------|---------|
| Total         | 5166        | 4843        | Trichromatic colour (τ_{vis} × θ_{vis}) | 343.60 | 0.027   |
|               |             |             | %Sesquiterpenes | 352.80 | 0.038   |
|               |             |             | Phenology (start × duration) | 343.60 | 0.030   |
|               |             |             | Surface apparency | 551.10 | 0.004   |
|               |             |             | Phenology (start × duration) | 79.94  | 0.009   |
|               |             |             | Symmetry | 90.78  | 0.003   |
| Coleoptera    | 1188        | 1015        | Trichromatic colour (τ_{vis} × θ_{vis} × ψ_{vis}) | 76.78  | 0.069   |
|               |             |             | Phenology (start × duration) | 88.31  | 0.024   |
|               |             |             | Surface apparency | 158.75 | 0.001   |
| Diptera       | 1054        | 1021        | Trichromatic colour (τ_{vis} × θ_{vis} × ψ_{vis}) | 90.09  | 0.025   |
|               |             |             | Phenology (start × duration) | 103.80 | 0.143   |
| Hymenoptera—Bees | 2035      | 1897        | Sesquiterpene apparency | 163.60 | 0.011   |
|               |             |             | Height apparency | 192.70 | 0.005   |
|               |             |             | Surface apparency | 206.00 | 0.055   |
| Hymenoptera—Wasps | 353        | 310         | Trichromatic colour (τ_{vis} × θ_{vis}) | 25.87  | 0.128   |
|               |             |             | Surface apparency | 63.17  | 0.012   |
| Lepidoptera   | 462         | 374         | Phenology (start × duration) | 68.16  | 0.001   |
|               |             |             | Surface apparency | 63.09  | 0.005   |
|               |             |             | Phenology (start × duration) | 93.36  | 0.001   |

Each subnetwork includes one of the major pollinator groups in the study community. The best multivariate-response generalized linear models (family: negative binomial) according to AIC are presented. The AIC value of the null model (~1) is provided for comparison. Significant P-values (>0.050) are indicated in bold. % Sesquiterpenes: the percentage of sesquiterpene compounds in the total floral emissions. For details on the predictors, see Methods, and the Supplementary Information.
Table 3: Floral traits associated with visitation rates by the major pollinator groups in the community

| Insect group | AIC_Cnull | AIC_Cbest | Predictor | d.f. | F    | P-value | Slope |
|--------------|-----------|-----------|-----------|------|------|---------|-------|
| Coleoptera   | 53.5      | 45.0      | Nectar    | 3,34 | 6.98 | 0.012   | -     |
|              |           |           | AL_app × Be_app × Mo_app × Se_app | 7.92 | 0.004 | +       |       |
| Diptera      | 9.0       | 2.4       | Symmetry  | 4.33 | 3.38 | 0.075   | -     |
| Hymenoptera—Bees | 121.5 | 97.6 | Height apparent | 3.77 | 0.061 | +       |       |
|              |           |           | %Aliphatics | 8.34 | 0.007 | +       |       |
| Hymenoptera—Wasp | −13.9 | −14.3 | Phenology (start × duration) | 7.30 | 0.00 | 0.928   | -     |
| Lepidoptera  | 11.9      | 90.4      | Trichromatic colour (r_t × θ_t) | 4.35 | 0.045 | +       |       |
|              |           |           | Sesquiterpene apparent | 4.92 | 0.034 | +       |       |
|              |           |           | %Aliphatics | 8.92 | 0.006 | +       |       |
|              |           |           | Surface apparent | 9.34 | 0.005 | +       |       |
|              |           |           | Tetrachromatic saturation (r_tu) | 15.29 | <0.001 | +       |       |
|              |           |           | %Aliphatics | 18.14 | <0.001 | +       |       |

Note: The best phylogenetically informed generalized least-squares models according to AIC are presented. The AIC value of the null model (+1) is provided for comparison. %Compound class: the percentage of compounds of this class in the total floral emissions. Significant P-values (p > 0.050) are indicated in bold. Positive or negative relationships are given (slope: +: > 0, −: < 0). For details on the predictors, see Methods and the Supplementary Information.

Insect group AICc null AICc best Predictor d.f. F P-value Slope

The floral traits recorded in each one of the 41 insect-pollinated plant species of the community are:

1. Inflorescence scent composition sampled in vivo and in situ, expressed as the relative proportions of each chemical class (viz. aliphatics, benzenoids and phenylpropanoids, monoterpens, and sesquiterpens) in the total species blend.
2. Colorimetric properties (viz. key descriptors of saturation and hue) as perceived by either the trichromatic visual system of bees or the potentially higher dimension tetrachromatic visual system of swallowtail butterflies.
3. Presence/absence of nectar.
4. Floral symmetry.
5. Flower height.
6. Frontal surface area of the flower unit.
7. Corolla depth.
8. Flowering phenology.
9. Floral density.

Scent collections were carried out in vivo and in situ with dynamic headspace sampling, except for Blackstonia perfoliata, which was sampled in vivo in the lab 1 h after the test plant was collected in the field and transferred to the lab in a pot along with the original soil. All collections were performed once during the peak of the flowering period of a species, on days with clear and calm weather, and at the peak of the pollinators’ activity (9 am–1 pm). Scents (Supplementary Data 2) were collected from April to July 2012, except for Cistus creticus and Teucrium.
divaricatum from which scents were collected in May–June 2011. On average, we collected four replicate samples of floral headspace for each plant species in the community. During volatile collection sessions, the mean ambient temperature (±SD) was 25.7 ± 1.4 °C, and the mean ambient humidity (±SD) was 55.5 ± 2.8%, measured on the spot. For the dynamic headspace sampling we used a PAS-500 personal air sampler (Supelco, Bellefonte, PA, USA) set at a 200 mL min⁻¹ flow rate. Once we arrived at a healthy-looking, flowering plant of each species and up to 20 individuals for common taxa. Measurements were carried out in the field at the peak of each plant’s flowering period using a tape measure.

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For floral surface area, we estimated the area of the floral unit as observed from a frontal view. For actinomorphic or globose flowers and flower units (e.g. *Lagurus camouindes, Sandi sp.*), we measured the diameter of the circular contour and calculated the frontal area using the formula *A = πr² radius*². For zygomorphic flowers and dense spike-like flower units (e.g. *Lavandula stoechas, Prasium majus, Teucrium divaricatum*), we calculated the rectangular area using the formula *A = length × width*. All measurements were performed on 5 (for rare taxa) to 20 flowers per taxon, using a digital calliper (Supplementary Table 6).

**Floral apparency.** We used the term ‘apparency’ in order to describe the degree to which a plant species in the community has noticeable scents compared to its co-flowering insect-pollinated species (see analogy in ref. 80), and we distinguish between visual and chemical floral apparency (Supplementary Fig. 2). For the first one, we used two metrics based on *(i)* floral height (vertical apparency) and *(ii)* flower display area (horizontal apparency). We must underline that floral apparency is irrelevant to plant growth form, i.e. species larger in size or perennials are not necessarily more apparent than the other ones in all dimensions examined here (Supplementary Table 6).

The flowers of a plant are apparent unless the co-flowering species have more highly-positioned flowers (compare to ref. 81): therefore, we calculated flower height apparency as the difference of the median floral height of a plant from the median floral height of the co-flowering species in the community, during its flowering period. Vertical apparency for a focal plant *(ΔH)* is defined as the difference of its floral height from the median floral height of its co-flowering plants in the community:

\[
ΔH = H_f - H_i
\]

For the calculation of the median, only the co-flowering plants of the focal species were taken into consideration, in accordance to the phenon concept (Supplementary Table 3). The values are negative in case the focal plant’s flowers are lower-positioned and therefore less apparent than the co-flowering plants. To estimate horizontal apparency, we first weighted floral surface values for each plant by its mean floral density (flower units per m²) measured in 2011 and 2012. In this way, we obtained the total floral area of each plant species per m² of flower cover. Floral surface apparency of a focal plant *(ΔA)* was calculated in accordance with height apparency *(ΔH)*, and it represents the difference of the weighted floral area of the focal plant *(A)* and the median weighted floral area of the co-flowering plants in the community:

\[
ΔA = A_i - A_f
\]

Again, for the calculation of the median, only the co-flowering plants of the focal one were taken into consideration, in accordance to the phenon concept. Negative values indicate lower horizontal apparency compared with the other co-flowering plants.

Chemical apparency is defined as the difference of the ER of scent per m² occupied by a given plant *(ΔER)* from the median ER of the co-flowering plant taxa. The median was used as a measure of central tendency because of the right-skewed distribution of the ER data owing to the large differences of scent among the plants in the community:

\[
ΔER = ER_i - ER_f
\]

Chemical apparency was calculated for the sum of ER in each plant, as well as for the ER of each one of the four main VOC classes (viz. aliphatics, benzenoids, monoterpenes and sesquiterpenes) (Supplementary Table 5).

Floral apparency is a function of the maximal floral density of each entomophilous plant species in the community. This approach does not intend to
capture the dynamics of floral density exhibited by species during the entire flowering period, but it is used as a measure of the highest possible influence of a given species during its own phenophas. *Heliotropium lasiocarpum* was the last insect-pollinated plant that was in flower alone in the community (Supplementary Table 6). Therefore, for this species, apparency could not be calculated in relation to the co-flowering plants.

**Phylogenies and phylogenetic signal of interactions and traits.** Plant phylogeny was built with the online software Phylomatic v.3 (tree R20120829). We used the ‘Slad’ algorithm in the software Phylocom v.4.2 (Ref. 83) in order to adjust branch lengths of the phylogeny so as to correspond to evolutionary divergence time between clades, using the most recently updated node age.48 The phylogram of the plants of the community is presented in detail in Kantza et al.28 Animal phylogeny (Supplementary Fig. 4) was constructed using the online tool Open Tree of Life84. Clade divergence times were retrieved up to the next taxonomic level (when possible, we used the family ages) from the online database TimeTree.86 Pairwise phylogenetic distance matrices for the two trophic levels were calculated using the function ‘cohenst phylo’ in the R package ape v.3.5.

With the ‘PACo’ function in the R package paco v.0.3.2, in order to calculate the phylogenetic congruence of the binary interaction matrix of plants and pollinators in the community. According to this method, plant–pollinator interactions are projected into module composition. We conducted Principal Coordinate Analysis, underpinning Procrustean superimposition, where the level of cophenetic signal is taken as the global sum of squared residuals (m2) in the best-fit superimposition of the two phylogenies.49 For each trophic level of the weighted network, we applied separate Mantel tests in the R package vegan v.2.4.0 to calculate the correlation of the interaction binary matrix of plants and insects (Bray-Curtis index) with their phylogenetic distance matrices.46

For measuring phylogenetic signal in continuous and in arcsine-transformed proportional independent variables (Supplementary Tables 7 and 8) as well as in the visitation rates by the five major pollinator groups (viz. bees, butterflies, flies, butterflies, flies allowing the λ value), we used a model-based method for compositional data developed by Rezende,89 which tests the phylogenetic signal in discrete variables assuming a Brownian motion model of evolution, with the R function phylo.signal disc in the R package mvabund v.3.12. The statistical significance of the fitted models was assessed with ANOVA (likelihood ratio tests) using 999 bootstrap iterations via PIT-trap residual resampling, a method which shows low rates of type I errors, and in our case yielded the most conservative results. Unless stated otherwise, statistical analyses were performed in R v. 3.3.1 (R Development Core Team; http://www.R-project.org).

**Data availability.** Data on phenophases, floral appearance, floral measurements, network module composition, interaction phylogeny and the phylogenetic signal of the tested variables are provided in the Supplementary Information. Plant phylogeny and the flower reflectance spectra are included in ref. 28. The plant–pollinator network (Supplementary Dataset 1) and the volatile emission rates of the plant species (Supplementary Dataset 2) are available in the online repository Figshare (https://doi.org/10.6084/m9.ﬁgshare.5663457).

Received: 5 July 2017 Accepted: 14 February 2018
Published online: 12 March 2018

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**Statistical modelling.** We used two modelling approaches in order to explore the role of the above-mentioned elements of floral phenotype into shaping visitation patterns of insects in the community. First, focusing on the plants of the community, we tested which phenotypic traits relate to (i) the visitation rates by the major pollinator groups and to (ii) node properties (BC, CC and ND) of plants. For this, and in order to correct for statistical dependence due to phylogenetic proximity of the plants, we applied phylogenetically informed generalized least-squares models25 assuming a Brownian motion model of evolution, with the R function glm of package nlme v.3.1.128 that included the phylogenetic correlation matrix of the plants of the community, generated by the R function corPagel in package ape v.4.0. The response variables (ND, BC and CC) as well as the proportion predictor variables (Supplementary Table 8) were arcsine-transformed, whereas height/surface/chemical apparency values were log−2 transformed before analysis. Best-fitting models were selected according to AICc, following a forward selection of variables. Predictors were not strongly correlated with each other (mean absolute value of Pearson’s r = 0.22, maximum value = −0.62).

Second, we tested for the role of floral phenotypic traits (Supplementary Table 4) in shaping the link structure of the overall quantitative (weighted) p–p network. For this, we used a model-based method for compositional data, i.e. Multivariate-response Generalized Linear Models (MGLMs). This approach fits a separate generalized linear model to the visitation matrix of each insect of the network, using a common n-dimensional set of explanatory variables and a resampling-based hypothesis testing21. The multidimensional response variable is either the entire (static) weighted p–p network or one of its subsets including the insects belonging to the five major groups: Coleoptera, Diptera, Hymenoptera—bees, Hymenoptera—wasps and Lepidoptera. It should be stressed that (i) the residuals of the MGLM model of the p–p network (Manhattan distance matrix) correlate neither with the phylogenetic distance matrix of the plants nor with the insect matrix (Mantel rplanes = −0.13, P = 0.915; rmainecct = 0.06, P = 0.173), showing that there is no phylogenetic signal in this analysis and (ii) no phylogenetic signal is detected in the weighted interaction matrix (Mantel tests with Bray-Curtis distance in Supplementary Table 7), allowing us to use a non-phylogenetic modelling approach for this question.92 For each network, we found the best MGLM model (family: negative binomial) based on the sum of the AIC over all variables following a forward selection of variables. Models were built using the function ‘manylm’ in the R package ‘lme4’, version 1.1.2. The statistical significance of the fitted models was assessed with ANOVA (likelihood ratio tests) using 999 bootstrap iterations via PIT-trap residual resampling, a method which shows low rates of type I errors, and in our case yielded the most conservative results. Unless stated otherwise, statistical analyses were performed in R v. 3.3.1 (R Development Core Team; http://www.R-project.org).
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Acknowledgements
This research was co-financed by EU (European Social Fund) and Greek national funds through the Operational Program “Education and Lifelong Learning” of the National Strategic Reference Framework—Research Funding Program: Heraclitus II (2324-1/77/0340). Chemical analyses were carried out at the Laboratory of Water and Air Quality, Department of Environment, University of the Aegean. We are grateful to insect taxonomists: Ante Vujic (Syrphidae), Jelle Devalez and Marino Quaranta (Hymenoptera), and Jos Dils (Bombyliidae). Stefanos Sgardelis and Thanasis Kallimanis provided valuable advice on statistical analysis. A.K. and T.P. thank particularly Theostokles Lekkas, Peter Davies, Maria Aloupi and Olga-Ioanna Kalantzis for support and involvement throughout the research. A.G.D. acknowledges Australian Research Council Discovery Project DP160100161 for support.

Author contributions
A.K. and T.P. designed the study. A.K. collected the data. A.K., A.G.D., R.A.R. and T.S. analysed the data. The manuscript was written primarily by A.K. with major contributions by A.G.D., R.A.R., T.P., J.M.O. and T.T.

Additional information
Supplementary Information accompanies this paper at https://doi.org/10.1038/s41467-018-03448-w.

Competing interests: The authors declare no competing interests.

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