MEDITERRANEAN ODORSCAPES:

THE ROLE OF PLANTS' VOLATILE ORGANIC COMPOUNDS IN POLLINATION NETWORKS

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ΜΕΣΟΓΕΙΑΚΑ ΟΣΜΟΤΟΠΙΑ:
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Στον πατέρα μου.

[...] *Γύρω απ' την ολοπράσινη επιτυχία των φύλλων*

Οι πεταλούδες ζουν μεγάλες περιπέτειες

Ενώ η αθωότητα

Ξεντύνεται το τελευταίο της ψέμα

Γλυκιά περιπέτεια Γλυκιά

Η Ζωή.

Οδυσσέας Ελύτης, *Δεύτερη Φύση, ΙΙ*

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"…a very little thief of occasion will rob you of a great deal of patience…"

A well-respected scientist once said to me, in a joking manner, that you spend all these years doing research in order to finally write a prologue. Back then I laughed, but I'm afraid that I now have to acknowledge the overwhelming satisfaction of this very moment. Another well-respected scientist I know, stoically (or perhaps Socratically) concluded that although when you get your first degree you think that you know everything, when you get your PhD, you confirm that you actually know nothing. Being fully conscious of these two conditions, I feel like thanking all those people who patiently helped me through this intellectual achievement ☺.

It all started with Prof. Theodora Petanidou. She first introduced me to the floral sensory ecology by suggesting measuring the odorscape created by the insect-pollinated flowers in an entire community, and study its effects on the local pollination network. I was easily fascinated by the idea. I would have probably thought about it a bit more, if I knew the amount of work required, nevertheless my decision would not have been any different. If I ever become a decent ecologist, it will be largely due to her 'demonic' instinct and profound knowledge on the Mediterranean nature, to the tough fieldwork training (no joke), to the endless conversations and the arguments we've had (hardcore as well), and to the education she's constantly providing. She is probably the most cultured person I've ever met, and although I often feel perplexed by this, she is a precious mentor and friend.

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<div align="right">A.K.

Mytilene, November 2016.</div>

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General Introduction & Thesis Outline

General Introduction & Thesis Outline

'I am tempted to give one more instance showing how plants and animals,
most remote in the scale of nature, are bound together by a web of complex relations'.
Charles Darwin, 1859 (*1*)

Plant–pollinator interactions: the invaluable mutualism

Nine out of ten flowering plants on earth need animals in order to produce seeds (*2*). This number alone shows clearly that biotic pollination is one of the key-ecosystem services sustaining global primary production (*3*). The mutualistic relationship between plants and pollinators is thought to have been a major driver of diversification of plants and animals ever since the first higher plants colonized the land, and especially after the great angiosperm radiation in the Cretaceous, i.e. for the last ca. 65 Myr; Indeed, insects and flowering plants are currently the most diverse groups of living beings (*4-12*). The parallel declines of bees and wild insect-pollinated plants in Northern Europe during the 20th c. (*13*) imply a high degree of interdependence between these organisms. It is evident that the preservation and the evolution of terrestrial biodiversity on earth depend to a great extent on the outcome of plant–pollination (p–p) interactions.

Human life is also directly dependent on pollination. More than 1,500 species of crops rely on biotic pollination, which has also been shown to improve the production of ca. 70% of the leading food crops in a global scale (*14*). It should be stressed that, especially in temperate non-tropical regions, the yields of crops depend to a great extent on wild insect pollinators and not to managed honeybees (*15*). In 2005 alone, the monetary value of pollination services was estimated at €153 billion, i.e. 9.5% of the value of the total agricultural production of that year (*16*), rendering pollination services a significant resource for the world's economy. Apart from supporting the nutrition of the human population on the planet, pollination is the basic biotic function behind the exquisite floral diversity that has affected human cultures across the world and eras, and may or may not have a market price: aesthetic enjoyment, art, architecture, pigments, and aromas (*17-19*). Finally, it is the mere philosophical significance of mutualism, which as a term was not easily adopted by biology both for technical and for political reasons (*12, 20*), that could state nature's sound paradigm to the ongoing global issues.

At present, overexploitation of species, aggressive agricultural practices, land-use changes, biological invasions, pollution, and climate change represent, in descending order of magnitude, the main global-scale threats to biodiversity (*21*). Given that the majority of these phenomena represent threats also to p–p interactions worldwide (e.g. *22*), intensive research efforts across the world are focusing on disentangling the dynamics and structure of the p–p interactions, so that prevention, conservation, and restoration strategies can be effectively designed and implemented (*23-27*).

The colorful and fragrant floral landscape

Plants are sedentary organisms and their only channels of communication are signals, visual and olfactory. The outstanding diversity of palettes, shapes and fragrances in flowers is there in order to allure pollinators to its reproductive parts, in a legitimate or in a deceptive way (*28*). Visual and olfactory floral signals are known to interact additively or synergistically (*29, 30*) in order to affect

foraging behaviors (*31*), and promote flower constancy of pollinators (*32*), which are known to be important selective agents for both suites of traits (*33-35*).

Floral color is formed by blends of pigments that belong to three groups of compounds: (i) anthocyanins, a class of flavonoids, that are widely distributed among plant species and produce a variety of colorations from orange to blue; (ii) carotenoids, isoprenoid lipophilic compounds that are distributed in higher plants, algae, fungi, and bacteria, producing yellow-to-red hues; and (iii) betalains, yellow and purple pigments that occur exclusively in the order Caryophyllales instead of anthocyanins (*36-38*). Floral color's main ecological role is the attraction of pollinators (*39-41*), although it has also been connected to thermoregulation (*42*), and to herbivory (*43, 44*). Although the significance of floral color in interspecific interactions has been a long-held hypothesis, floral color in ecological studies had been mostly parameterized qualitatively, as perceived by the human eye. Employment of unbiased measurements of color, i.e. either the concentration of pigments in petal tissue or the reflectance spectrum of the floral surface, only very recently started to be widely employed. Stimulatingly, this has been accompanied by advances in understanding the sensory systems of pollinators, a combination that revealed novel insights into visually-mediated interspecific interactions, as well as into regional floral color diversity patterns (*45-52*).
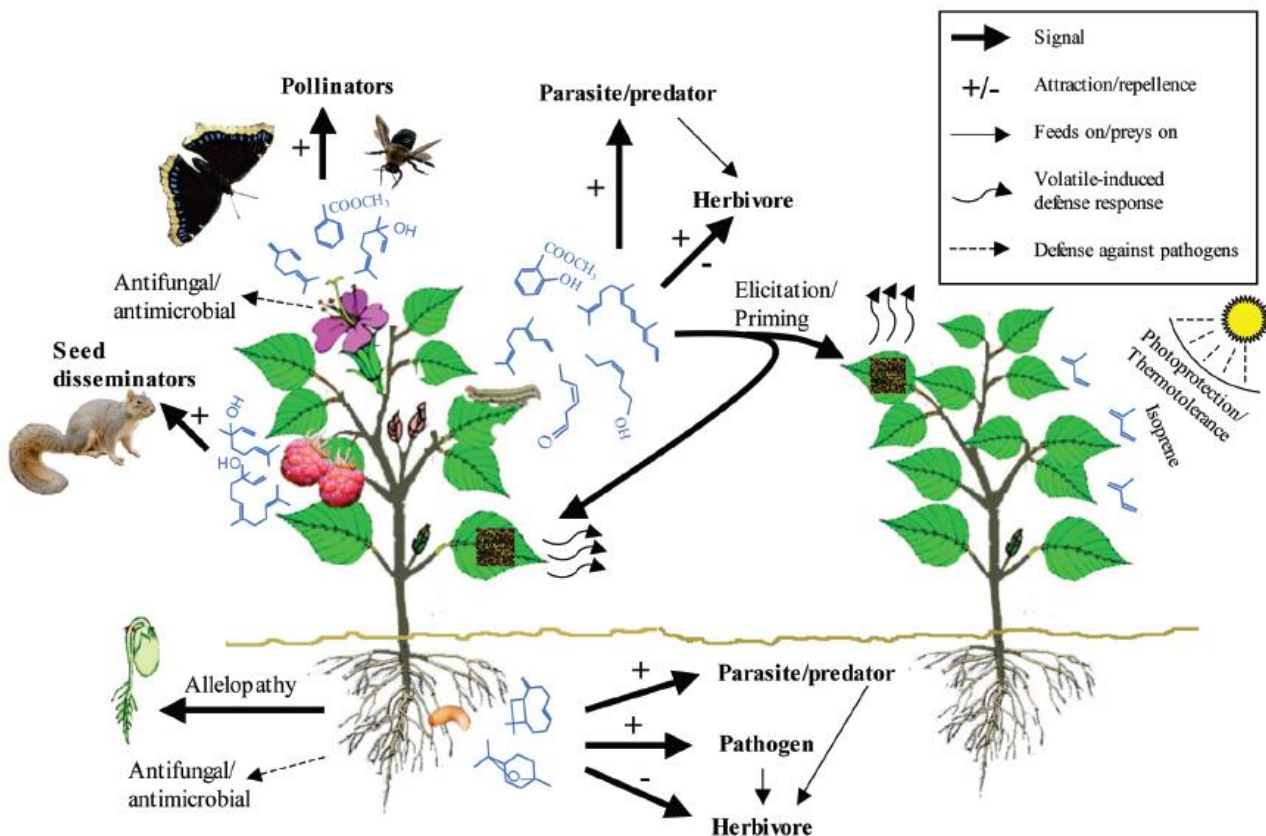
Fig. 1.1. The multiple ecological roles of plants' volatilome. From Dudareva *et al.* (*59*).

Plant scents are mixtures of volatile organic compounds (VOCs) with low molecular weight (usually <300 Da) and low normal boiling point, synthesized and emitted by all plant organs: flowers, green parts, roots, fruits, and seeds (*53-56*). They are products of plants' secondary metabolism, their majority being classified into three major categories according to their biosynthetic origin: terpenoids, benzenoids/phenylpropanoids, and fatty acid derivatives (aliphatics) (*54*). Mosses are known to emit complex blends of VOCs involved in mutualistic interactions (*57*) and only *Selaginella moellendorffii*'s genome (lycophyte), having emerged 400 Myr before angiosperms, includes 18 terpene synthase genes (*58*), implying that volatile emissions are tightly associated with plant's terrestrial lifestyle ever since land colonization. Indeed, scents represent a key phenotypic element that variously involves into ecosystem functioning by mediating intra- and interspecific biotic interactions such as pollination, herbivory, seed dispersal, plant–plant communication, allelopathy, and bacterial colonization of plant parts, contributing to community dynamics (Fig. 1.1) (*59*). Moreover, volatile emissions may represent adaptations to abiotic factors, e.g. providing photoprotection to plant tissues (*60*). So far, more than 1,700 floral VOCs have been recorded in 90 families of angiosperms (*53*). Compounds emitted by the different floral parts (including pollen and nectar), apart from directly or indirectly attracting pollinators, they may also: (i) attract herbivores (*61*); (ii) repel facultative floral visitors (*62*); (iii) repel herbivores (*63, 64*); (iv) participate in tritrophic interactions (*65, 66*); (v) interact with flower-dwelling microbes (*67*); (vi) exhibit antimicrobial activity against phytopathogens (*63, 64, 68*).

Beyond the ecological significance of floral emissions (Fig. 1.1), in the context of this thesis I am furthermore interested in plants' scents as natural products. The immense chemical diversity revealed so far (*69, 70*) reflects the amplitude of biological functions and applications yet to be explored, such as agricultural practices, pharmaceuticals, food processing, and cosmetics. Indeed, these secondary metabolites encompass some of most economically important medicinal compounds (*71, 72*). Thus the conservation and sustainable exploitation of the plant sources may be beneficial both for the conservation of interspecific interactions and for the primary sector of the economy, especially in the countries of the Mediterranean. Large-scale assessments taking into account the spatial distribution of chemodiversity are very rare (*73*), even though plant volatile blends as well as single compounds are natural resources that may show geographically patterned intra-specific variability in well-defined areas(*74, 75*). Furthermore, volatile emissions as floral signals may actually be susceptible to pollution and climate change (*76, 77*). Thus revisiting published data systematically is essential for the understanding and preserving plant volatilome and its functions.

Pollination networks and floral traits

Systems and processes representing webs or networks, i.e. entities interconnected by links (Box 1.1), are all around us and constantly affect our life in various aspects, as do the Internet, media of social connection, transportation networks, metabolic networks, and food webs. As a fundamental clade of mathematics, network theory (known as 'graph theory' in the mathematical terminology) originated in the 18th c. and was largely developed during the 20th c. (*78*). It was in the early 20th c. that biology adopted network theory in order to study complex systems of interspecific interactions, such as the trophic webs (see *79*). Currently, ecological networks are grouped into three main categories: (i) food webs, (ii) host–parasitoid webs, and (iii) mutualistic webs (*80*).

Network analysis of mutualistic interactions is a multi-tool for studying the diversity of interspecific interactions both in micro- and in macro-ecological scales (*81-83*). It has revolutionized the study of pollination that was traditionally viewed in isolated pairwise cases, and allowed a broader perspective that helped define pollination as a key functional ecosystem service that sustains primary production and community structure and stability (*12*). Network analysis of pollination interactions (i) describes the functional structure of communities (*84*), (ii) offers a pragmatic view on the plasticity of visitation patterns (*85*), (iii) indicates conservation priorities in prospect of global change phenomena and biological invasions (*27, 86*), and (iv) can be used for designing the ecological restoration of functional diversity (*87*). Pollination networks have been described in numerous communities from the tropics to the arctic regions (*51, 82, 85, 88-90*), yet the role of floral traits in configuring visitation patterns in community assemblies has been addressed in only very few studies so far (Table 1.1).

Box 1.1. Networks: Basic terms used in the thesis

Bipartite (or two-mode) network: The representation of the interactions between two sets of nodes, e.g. two trophic levels, plants – animals. It is usually depicted either as a graph (i, iii) or as an incidence matrix (ii).

Binary network: A network that includes only the presence or absence of interactions (qualitative) (iii).

Weighted network: A network where each interaction (link/vertex) has a measured strength (quantitative) (i, ii).

Module (compartment): A link-dense area, where nodes are more strongly connected together than with the rest of the network (shaded region in iii).

Node degree: The number of interaction partners of one node, i.e. the number of links a node has to other nodes. It is a simple measure of the specialization of nodes.

Connectance: The number of interactions realized as a proportion of all possible interactions. For example, in (ii) C=0.36.

Node properties: Metrics describing the behavior or the influence of each node in the network.

Centrality indices: Node properties denoting the positional importance of a node in the network. If central nodes are removed, networks collapse more easily compared with randomly selected nodes.

Figure (iii) is from Newman (*110*) with modifications.

Here I am interested particularly in exploring the relationship of floral traits and the visitation patterns recorded in a natural community-context. During the last twenty years, there has been a vivid debate regarding the interplay of floral phenotype and the type of pollinator, greatly triggered by the development of network analysis (*91*). Employing big datasets (*92, 93*), as well as theoretical models (*94, 95*) revealed that generalization is far more frequent than expected by tight coevolution between pollinators and plants and by pollination syndromes (*4, 96, 97*), and that plant–pollinator interactions show great temporal plasticity (*85, 98-100*). These findings are quite challenging, given that plant–pollinator (p–p) coevolution is considered a major driver of floral diversification since the great angiosperm radiation in the Cretaceous (*5, 101*). And although it may not be the only driver (see *102*), pollinator-mediated selection of floral color and scent traits is actually happening (*33, 103*).

Table 1.1. The floral traits found to be related to flower visitation by the main four insect pollinator orders, in five community studies. For each case, type of vegetation and geographic location is given. We distinguish between floral color and reflectance because the latter implies measurement with a spectrophotometer, whereas the former is a human-biased qualitative parameterization (e.g. red, yellow, etc.). See respective references for the statistical methods used in each case, and for the exact trend of each relationship.

Study community	Floral trait	Coleoptera	Diptera	Hymenoptera	Lepidoptera
Daphni/Athens, Greece	Type of reward[1]	+	+	+	
Phrygana	Symmetry	+	+	+	+
(*92*)	Color	+	+	+	+
	Size[2]	+	+	+	
	Height[2]	+	+	+	+
	Phenology[2]	+	+	+	+
	Corolla depth[2]	+	+	+	
	Abundance[2]		+	+	
Rudsviki, Norway	Size			+	
Lowland grassland	Phenology			+	
(*111-113*)	Symmetry	+	+	+	+
	Shape	+	+	+	+
	Abundance	+			
	Color	+	+	+	+
Finse, Norway	Color		+	+	+
Alpine vegetation	Shape		+	+	+
(*113*)	Symmetry		+	+	+
Ryghsestra, Norway	Color	+	+	+	+
Semi-natural meadow	Shape	+	+	+	
(*113*)	Symmetry	+	+	+	
Würzburg, Germany	Reflectance	+	+	+	
Fallow land	Size	+	+		
(*114*)	Height	+	+	+	+
	Corolla depth	+	+	+	
	Phenology	+	+	+	+
	Abundance	+			
	Phylogeny	+	+	+	+

[1]Qualitative description (nectar/pollen/no); [2]Ordinal variable

In the context of a network, pollinators are expected to filter information received in the floral landscape they encounter based on what their sophisticated sensory systems perceive, their cognitive abilities and their innate preferences are (*52, 104-107*). Recently, floral color has been shown to relate

to plant generalization in a community (*51*). Similarly, insect responses to natural floral blends were found to correlate with visitation patterns (*108*), and floral scent manipulation has been shown to affect visitation patterns in two plant species studied simultaneously in a community (*109*). However, to date no study has considered the sensory floral stimuli holistically (i.e. visual and olfactory together) in a comprehensive, natural p–p assembly. This thesis aims at addressing the lack of such empirical information, in particular whether floral visitation patterns by insects have a sensorial basis or it is all about opportunism, relatively unaffected by coevolutionary forces.

Thesis Outline

In *Chapter 2*, published in *Chemistry & Biodiversity* (*115*), I conducted a review focusing on the volatile chemodiversity and geographical distribution of aromatic plants in Greece. Specifically, I combined the published data on plant volatile chemodiversity in the country for the last 25 years into a geodatabase. This allowed the assessment of the VOC richness and distribution within the 178 plant taxa studied. Additionally, I explored the chemical properties of the volatilome, evaluated the acquisition methods frequently used, introduced the chemodiversity maps as a special case of natural resource maps and discussed their applications in ecological research and in productive activities.

In the research described in *Chapter 3*, I directed my attention to the floral sensory stimuli of 41 insect-pollinated plants in a natural phryganic community, and investigated the hypothesis of floral phenotypic integration between scent and color. This question is based on the existing knowledge that pigments and VOCs share metabolic pathways, implying possible adaptive advantages by the covariation of multiple traits; moreover, this question has been further enhanced by the evidence provided by sporadic intraspecific investigations on color–scent covariation, although by employing mostly human-biased qualitative parameterization of floral color. Having measured floral reflectance using a spectrometer, and having collected floral scent with dynamic-headspace sampling *in vivo* and *in situ*, I claim this study to be the first assessment of floral color and scent at a community level.

After exploring the floral phenotype in the community, I assess the role of floral sensory diversity in structuring the plant–pollinator (p–p) network, in *Chapter 4*. Specifically, I focus on the plants in the community, and explore the hypothesis that floral sensory stimuli (i.e. color and scent), which are known to mediate pairwise interspecific interactions, associate with the plants' influence in the p–p network of the community. This research is based on the long-standing debate between the ecological and the evolutionary specialization of pollination mutualisms and their significance for the structure and stability of pollination networks. Moreover, it represents the first community-wide assessment of floral traits and p–p visitation patterns. Finally, I introduce a novel approach for network data compilation in order to calculate species' specialization, and reinvent the concept of plant apparency applied in this Chapter analysis.

Lastly, in *Chapter 5*, I construct and analyze the bipartite network of insects and volatile organic compounds compiled by the plant–pollinator visitation data and the plants' floral scent blends collected in the study community. The scope of this research is to introduce a network-based approach in the investigation of the fundamental relationship of plant chemical signals and arthropod behavior, focusing directly on chemical compounds. By employing simple metrics and calculating the modularity of the insect–VOC network, I describe and discuss interesting association patterns between insect groups and VOC classes.

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CHAPTER TWO

Plant volatilome in Greece: a review on the properties, prospects, and chemogeography

Abstract. – Knowing plant volatile chemodiversity and its distribution is essential in order to study biological processes, to estimate plants' value in use, and to establish sustainable exploitation practices. Yet, attempts to collect and assess data on scent diversity and properties in well-defined geographical areas are rare. Here, we developed a geo-referenced database of the plant volatilome in Greece by consolidating the results included in 116 research papers published in the last 25 years. The dataset compiled includes 999 volatile organic compounds distributed into 178 plant taxa, 59 genera and 19 families. Distillation is the acquisition method almost exclusively used, whereas headspace techniques that would allow the study of subtle ecological processes are generally lacking. Sesquiterpenes show the greatest richness of compounds, followed by monoterpenes and aliphatics. We assess the volatility of the compounds using the normal boiling point (nBP) as its reverse indicator, and we present the volatility spectra of the blends of the genera studied. Mean nBPs vary among genera, with maximal differences as wide as 118.4 ºC. Finally, we feature basic chemodiversity maps for three aromatic plants, and discuss their importance and prospects as a special case of natural resources maps.

Plant volatilome in Greece: a review on the properties, prospects, and chemogeography

Introduction

The volatilome i.e. the volatile chemodiversity (*1*) is one of the plants' outstanding traits that has influenced modern civilization: throughout the world and ever since the prehistoric times, plant scents have been widely used to flavor, cure, charm, and sanctify (*2-4*). Yet, beyond the human perspective, scents have always shaped ecosystem functioning by mediating intra- and interspecific biotic interactions as semiochemicals (i.e. pollination, herbivory, plant communication, bacterial colonization of plant parts) and by contributing to community dynamics by regulating the behavior of plants, animals, and microbes (*5-8*).

By the mid-19th century advances in chemistry enabled the investigation and isolation of the first VOCs (*4, 9*). Ever since, the progress in analytical technology and genomics has established various methods (*10-12*) and boosted research on volatile secondary metabolites. The immense chemical diversity revealed so far (*13-14*) reflects the amplitude of biological functions and applications yet to be explored, such as ecological interactions, agricultural practices, pharmaceuticals, food processing, and cosmetics. Plant VOCs bioprospecting supports both the primary production and the industrial sector of many countries; some of the most economically important medicinal compounds or their precursors are included among these secondary metabolites (*1, 15*). Recently, the EU exports of essential oils (i.e. the complex mixtures of volatiles acquired with distillation of plant parts) have experienced growth that reached €840 million in 2012 (*16*).

During the last 20 years, databases of volatile secondary metabolites have been developed, providing a great amount of information on the chemistry of the compounds and their scent qualities (*14, 17-20*). Yet, large-scale assessments taking into account the spatial distribution of scent chemodiversity are very rare (*18*), even though plant volatile blends as well as single compounds can be considered natural resources that may show geographically patterned intra-specific variability in well-defined areas (see *21, 22-25*). Therefore, revisiting published data systematically may provide a tool for better exploring the geography of the volatilome and its chemical properties, both for the study of biological processes and for primary production.

Since the time of Hippocrates (c. 460-375 BC) and Pedanius Dioscorides (c. 40-90 AD) to the wandering folk physicians of Epirus (*26*), Greece conveys a long ethnopharmacological tradition, which is largely based upon the use of aromatic plants that thrive across the country in a wide range of habitats. This tradition has been naturally sustained by the high local plant diversity (viz. 6,600 species and subspecies) (*27*), which in its turn is associated with a complex landscape consisting of numerous mountainous and insular systems –viz. 109 out of the 255 habitat types encountered in the European Union according to the Habitats Directive 92/43/EEC (*28*). This combination of a rich aromatic flora and a wide variety of habitats remains largely unexplored and represents a promising potential for both ecological and natural product research, rendering Greece a fine case study to start from. Despite the fact that the country stands among the exporting countries of essential oil in the EU (*16*), cultivation of medicinal and aromatic plants represents still a developing sector: in 2013, it

occupied ca. 2,200ha (Ministry of Rural Development, pers. comm.) corresponding to 0.04% of the total cultivated land in the country.

In this Chapter we review the body of the volatilome research literature in Greece published during the last three decades, which we transform into a geo-referenced database (geodatabase hereafter) that we use as a tool in order to address the following: (i) assess the compositions of the blends of the plant species sampled, (ii) record and discuss the methods used for plant samplings and the extraction of the scents, and revisit their role in supporting current research trends, (iii) explore, for the first time, the volatility of the compounds as a physicochemical property of the blends among the plant studied, (iv) display the geographical distribution of the aroma-research in the country, as well as (v) introduce the basic concept of chemodiversity maps that reveal the geographical distribution and variation of the blends. To our knowledge, this is the first attempt to explore the distribution of plant volatilome on a country-wide scale.

Materials and Methods

Literature review and data compilation
Our research has been restricted to those studies including plant material that was collected in Greece, either from the wild or from cultivations. A detailed search in the peer-reviewed literature for the years 1970-2013 was carried out using the online bibliographic sources SCOPUS® and Web of Knowledge®. The information tracked in each publication is shown in Fig. 2.S3. Geographical information was obtained with the highest possible accuracy. When the researchers did not provide coordinates for the sampling sites, we used points in the center of the minimal possible defined area described in the text. In cases where the exact locality was not available, we did not assign geographical coordinates. The Latin names of the plant taxa have been kept as in the original published papers, whereas plant family nomenclature follows the classification of the Angiosperm Phylogeny Group (*75*). We also recorded the methods of sampling and chemical analysis, which vary according to different research approaches (*10-12*). Because the chemical composition of the scent varies between different plant parts and tissues, we refined our results by distinguishing the volatile blends of different plant parts acquired from the same species, whenever this information was available. The technical details of the database development is described in Fig. 2.S3.

Chemical synonyms
In order to ensure that the variability in chemical names used among the publications inserted does not result in duplicate records, the final checklist of VOCs was corrected for synonyms using the NIST Chemistry WebBook database (http://webbook.nist.gov/chemistry/). Nomenclature follows IUPAC, nevertheless, trivial compound names that are widely used both in research and commercially are primarily featured. Isomers have been kept as originally identified in the source papers.

Measure of volatility
The boiling point of a substance varies inversely to its volatility, thus we introduce the normal boiling point (nBP), i.e. the boiling point at an atmospheric pressure of 760 mmHg, as a 'reverse indicator' of a VOC's volatility. Data on the normal boiling points of the VOCs correspond to the predicted values of the PhysChem module of the ACD/Labs Percepta Predictors, available in the ChemSpider database of the Royal Society of Chemistry (http://www.chemspider.com/).

Results and Discussion

Statistics

Presence/absence matrices of the VOCs in each collection site were used for the non-metric multidimensional scaling (NMDS), in order to depict variation in VOC composition among collection sites. Contours of elevation and latitude were fitted on the NMDS plots by using the function 'ordisurf' of the *vegan* package in R. This function fits a smooth response surface of the explanatory variable on the ordination plot using a generalized additive model and is advantageous because it is not restricted to linear variation of the explanatory variables across the ordination space (*76*). All analyses were performed in R version 3.0.2 (*77*).

Study plants

In total, 116 papers published during the period 1988-2013 have been extracted from the bibliographic search. The volatile profiles, acquired almost exclusively with distillation, were recovered for 178 plant taxa (species and subspecies) classified into 59 genera and 19 families (Table 2.S1). All cases represent native taxa that may grow spontaneously in Greece, except of (i) *Citrus aurantium* subsp. *bergamia*, *Pinus attenuata, P. canariensis, P. pinaster,* and *P. radiata,* which represent cultivated plants, and (ii) *Conyza* spp., a genus of American origin with spontaneous occurrences throughout the country (*27*). More than half of the plant taxa studied belong to Lamiaceae as well as the majority of the Greek endemics included in the dataset, viz. 26 out of 38 taxa. Plants of this family thrive in the spring and summer landscapes of the Mediterranean Basin, and comprise some of the most popular aromatic plant genera for food, pharmacy and cosmetic research worldwide. The most popular plants for volatile research in Greece are spearmint (*Mentha spicata*) and oregano (*Origanum vulgare* subsp. *hirtum*), each of them studied in six different research papers (Table 2.S1).

Plant parts sampled

Data compilation showed that the wide majority of the researchers used the terms "aerial parts" or "stems" in order to describe the material used for analysis, without differentiating plant parts (Table 2.S1). Volatiles from inflorescences were isolated and analyzed independently from the green parts only in 13 taxa. Seeds were sampled only for *Ocimum basilicum,* roots for the three *Paeonia* spp., *Centaurea orphanidea* subsp. *thessala,* and *Valeriana dioscoridis,* and fruits for *Ferula communis* subsp. *communis, Citrus aurantium* subsp. *bergamia,* and *Pistacia vera.* The consistent distinction among plant parts would be advantageous in order to focus on the functional/ecological roles of plant volatilome, and is strongly recommended for future research. For example, floral volatiles are important for the reproduction of insect-pollinated plants, among which some of the most widely consumed crops in a global scale (*29, 30*); fruit volatiles have implications to crop quality (*31*), they mediate interspecific interactions (*32, 33*), as do root volatiles too (*34, 35*) and become critical factors for pest management approaches. The scarcity of plant part/organ distinctions in sampling methodologies has been expected since the majority of researches in Greece are ultimately interested in the bulk processing of plant material on industrial scale (mostly for essential oil production): Thus far, the majority of research on plant volatiles in the country concerns agronomic and pharmaceutical questions and hypotheses mainly about (i) the discovery of new compounds, (ii) the identification of plants as new resources of natural compounds, and (iii) the testing of antimicrobial properties of VOCs (e.g. *36-38*). Among the research that is not directly related to industrial applications, chemotaxonomy

is the major topic (e.g. ref. *39*), whereas ecological research with focus to the functional roles of VOCs (*40-41*) is much less frequent (for an overview, browse publications in Table 2.S1).

Chemodiversity

In total, 999 VOCs have been identified in the blends of the 178 taxa studied, i.e. 58.1% of the known scent compounds of flowers acquired by headspace techniques (*14*). We should highlight the fact that the dataset has been corrected for compound synonyms, in order to facilitate comparisons. The per species chemodiversity ranges from eight to 162 VOCs (mean ± SD: 48.4±29.0, N=174) (Fig. 2.1), trace compounds included. Plants with complex blends consisting of more than 100 VOCs in total, in descending order, are: *Cistus salviifolius, Achillea millefolium, Stachys swainsonii* subsp. *swainsonii, Anthemis chia, Stachys swainsonii* subsp. *argolica, Achillea abrotanoides,* and *Cistus parviflorus*. The families Cistaceae, Asteraceae, and Hypericaceae show the highest mean per taxon VOC richness. Among the main chemical classes of the volatilome, sesquiterpenes show the highest diversity of VOCs (29.1% of the total), followed by monoterpenes (25.0%), aliphatics (21.8%), benzenoids (10.4%), diterpenes (7.2%), and other terpenoids (2.9%).
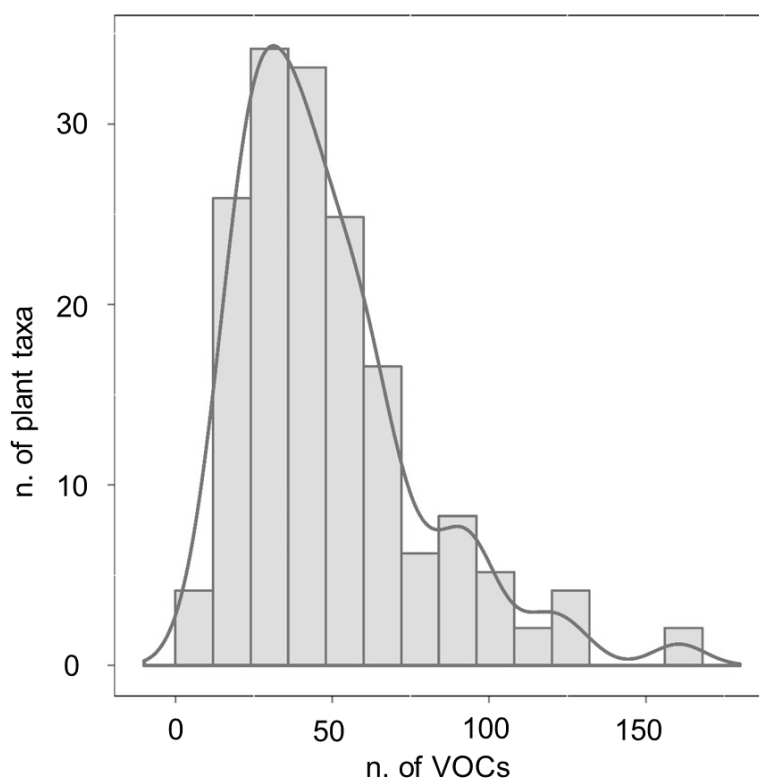
Fig. 2.1. Distribution of the number of VOCs identified per plant taxon in Greece. Trace compounds as originally identified are included in the sums.

Compound classes

Terpenoids (monoterpenes, sesquiterpenes, diterpenes, and other terpenoids) are known to be the most ubiquitous volatile secondary metabolites in plants (*14, 42*). Indeed, in our dataset terpenoids are among the most frequently encountered VOCs among the different plant genera and families (Table 2.1), and they prevail in the blends of the majority of the families as well (Fig. 2.2). Terpenoids in our

dataset include also 76 diterpenoids and three triterpenoids. Diterpenoids have been reported as very rare in floral scent profiles acquired exclusively with headspace techniques, due to their low volatility that challenges their adsorption and further detection (*14*). Triterpenoids are not considered among VOCs, although they are detectable with GC/MS; instead, they are well known constituents of plants' cuticle waxes (*43*). In our dataset, diterpenoids appear in eight families and seven orders and are particularly abundant in the blends of Cistaceae (Fig. 2.2). It should be noticed that the majority of terpenoids in our dataset represent oxygenated compounds (N=445), among which 146 are oxygenated sesquiterpenes; the latter appear with very low frequency in floral scents acquired with headspace methods, mainly due to their low volatility (*42*). Terpenoids have numerous and versatile pharmaceutical, agronomic and ecological properties: they exhibit anti-inflammatory properties (*1*), they are used as food additives for flavor and preservation (1, 4); they induce resistance against fungal and bacterial pathogens (*1, 44*); they mediate interspecific interactions (*1, 44*); they are involved in allelopathy and the regulation of soil properties in the Mediterranean shrublands, and they affect the flammability of the vegetation (*44-46*).

Table 2.1. VOCs detected in more than half of the plant taxa studied. For each VOC, number of occurrences in families is also given.

VOC	n. of taxa	n. of families	Chemical properties
caryophyllene	121	15	Sesquiterpene hydrocarbon
α-terpineol	105	15	Monoterpene alcohol
α-pinene	101	12	Monoterpene hydrocarbon
γ-terpinene	101	13	Monoterpene hydrocarbon
4-terpineol	100	13	Monoterpene alcohol
humulene	99	13	Sesquiterpene hydrocarbon
limonene	98	12	Monoterpene hydrocarbon
δ-cadinene	98	12	Sesquiterpene hydrocarbon
β-pinene	97	11	Monoterpene hydrocarbon
myrcene	92	11	Monoterpene hydrocarbon
linalool	90	16	Monoterpene alcohol
α-terpinolene	90	11	Monoterpene hydrocarbon

Aliphatics make the second most abundant chemical class, prevailing in six families (Fig. 2.2). This class includes some ecologically most important compounds, both for pollination and for herbivory. A good example are the orchids, which are known to emit almost exclusively alkanes and alkenes as key signaling compounds for scent mimicry and specialized pollination systems (see ref. *47*). Furthermore, aliphatics comprise the six-carbon green-leaf VOCs, which play important roles in the regulation of herbivory and parasites, and all the subsequent agronomic applications (*6, 48, 49*). Aliphatics contain numerous VOCs of high boiling point and molecular weight (Fig. 2.S1). Benzenoids prevail only in the blends of the roots of three *Paeonia* spp. (*50*). These compounds comprise known attractants to visitors when emitted by flowers (e.g. *51*), but as root VOCs, they are mainly known to be involved in allelopathy (*52*). Nitrogen- and sulfur-containing compounds are very rare in our dataset (0.4% of the VOC list) and occur only in Asteraceae. Due to their high volatility, these compounds can be missed from chemical analysis but we are confident for their actual rarity because the families

are known to emit them in abundance (*14*) are underrepresented in our dataset; their scarcity also makes sense both ecologically and biogeographically, as these compounds are tightly linked to particular interspecific interactions that are relatively infrequent or even absent in the NE Mediterranean region studied (e.g. pollination by nocturnal hawk moths or bats) and therefore are not readily expected here (*53, 54*).

To our knowledge, volatility has not been systematically assessed as a plant scent's property. The size and extent of our dataset allow for the exploration of volatility in the scents of the Greek flora. The lowest mean normal boiling point (nBP hereafter) is reported for Scrophulariaceae (197.5 ℃) where low-nBP aliphatics prevail, and the highest mean nBP has been found in Euphorbiaceae (315.9 ℃) and Cistaceae (294.5 ℃) where high-nBP aliphatics and high-nBP terpenoids prevail correspondingly. We introduce the volatility spectra of the plant genera of the dataset, as the distributions of the nBPs of the VOCs of the blends, in *Supplementary Material 2*. Among the volatility spectra of the genera, *Pistacia* (175 ℃), *Verbascum* (197.5 ℃), and *Coridothymus* (202.4 ℃) show the lowest mean nBPs, whereas *Herniaria* (294 ℃), *Cistus* (294.9 ℃), and *Euphorbia* (315.9 ℃) show the highest mean nBPs (Fig. 2.S1). It has been recently shown that warming alters plant emissions, a phenomenon that apart from physiology and transcriptional regulation processes could be explained by the fact that changes of the environmental conditions directly affect the physicochemical properties of the emitted compounds (see *55-57*).
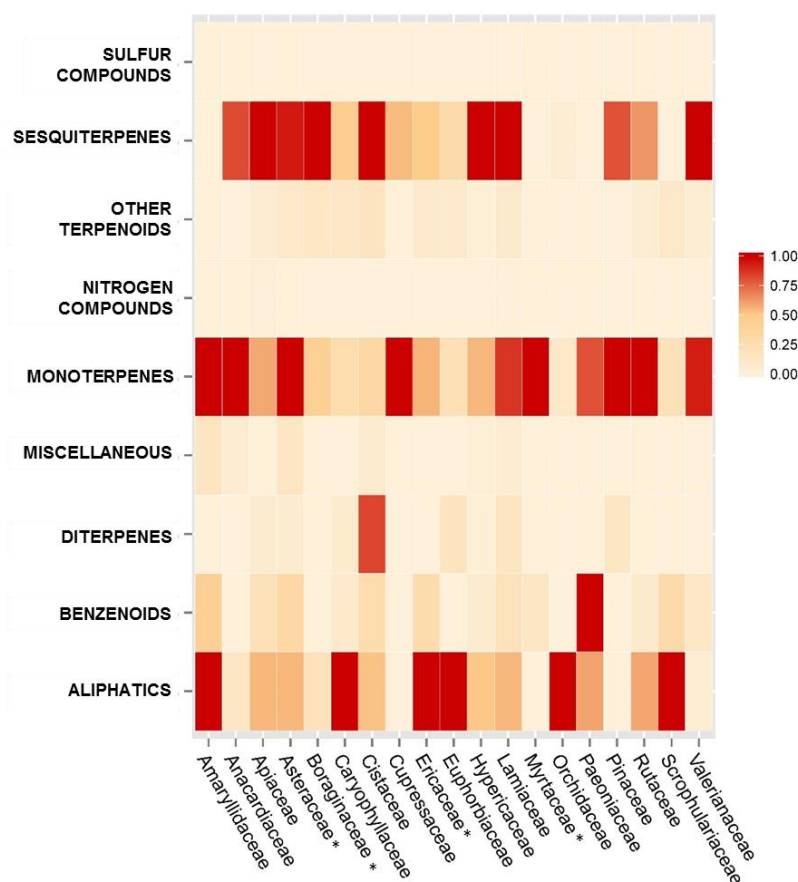
Fig. 2.2. Heat map of the distribution of the chemical classes of the VOCs among the families studied (*: family represented in the dataset by one taxon). Abundance of classes is scaled for easier comparison.

Further investigation of the volatility of scent bouquets as an adaptation of plant species to the ambient conditions of their natural habitats, could offer novel implications on plant ecophysiology, especially in prospect of the global change phenomena affecting interspecific interactions and the crop production worldwide (*58*). Getting to know the volatility of the VOCs in the blends of plant species may be used in order to explore and determine: (i) the optimal cultivation conditions in terms of temperature and humidity, (ii) the most efficient extraction method for large-scale industrial applications when maximum yields of particular compounds are required, and (iii) the correct schemes when transferring or establishing cultivations in areas of various climatic conditions and atmospheric pressures (e.g. altitudinal changes), so as to ensure both high emissions and sustainable agricultural practices. Future research approaches may address the abovementioned issues, and investigate the contributions of the physicochemical and the genetic regulation processes of the scent compounds in response to different ambient conditions.

Methods for future needs
Research questions and hypotheses indicate the adequate extraction methodology to be followed. Our results show that essential oils may contain amounts of the abovementioned 'heavy' compounds (>280-300Da) of low volatility (i.e. oxygenated sesquiterpenes, long-chained fatty acid derivatives, diterpenoids), which apparently remain even '*post-mortem*' in the osmophores, the glandular trichomes and their secretions, and can be detected with chemical analysis. At the same time, distillation, in contrast to headspace sampling, is a drastic process most often applied on dried (dead) plant tissues, hence what has been produced and emitted *in vivo* and *in situ* by the intact plant will not be included in its distillate unless it has survived in the dried material. The raised number of VOCs of high molecular weight and low volatility acquired with distillation methods, and their abundance in certain families in our dataset are meaningful for exploring the less-volatile borders of the plant volatilome. However, the study of VOC-mediated ecological processes undoubtedly requires data acquired *in vivo* (preferably also *in situ*), so as to capture even the low and subtle plant emissions of the highly volatile small molecules, which may represent biotic signals for inter- (or intra-)specific interactions, such as the abovementioned 6-C green leaf VOCs. *In vivo* sampling is also advantageous in order to capture in full range the real-time emission rates of a plant's scent when the circadian rhythms of the volatile emissions (*59*) are to be taken into consideration. Apart from the ecological processes, chemotaxonomic approaches may consider all the above in order to detect meaningful differences among plants and proceed to taxonomic inferences. In Greece and the Mediterranean countries in general, headspace sampling has only been sporadically applied thus far compared to the high rates of essential oil analyses (see refs. *47, 55, 60*).

The geography of aroma-research in Greece
The geodataset compiled includes 245 collection sites located all over Greece within a latitudinal range from 35° 0' to 41° 15'N and a longitudinal range from 19° 50' to 27° 50' (Fig. 2.S2). Mainland sites comprise 35 mountains, among which Mt. Parnassus (central Greece) is the most investigated in terms of analyzed plant species number. Data also cover a wide altitudinal range, with plant collections extending from the sea level up to 2,114 m.a.s.l. (Mt. Oeta, central Greece). Apart from the mainland, collection sites are located on 21 islands, most of them on Crete. In terms of plant taxa studied, Crete and the area around Athens are the research hotspots of the country (Fig. 2.S2). Central and southern Greece have been more preferred by researchers, as the majority of plant taxa have been collected

there, while the NE and western parts of the country still remain largely unexplored. It should be noted that the wide majority of samplings that participate in our database refer to wild populations. Researchers do not usually provide information on the habitat they collected the plant material from, although this information could be useful for large-scale comparisons (see ref. *21*). The majority of the taxa studied in multiple localities belong to Lamiaceae and include one Greek endemic (*Nepeta argolica* subsp. *argolica*) (Table 2.2). In general, Lamiaceae prevail in the volatilome research across the Mediterranean region, almost exclusively regarding the multiple properties and applications of their essential oils in agriculture, food chemistry and pharmacy (*61-63*). However, we should highlight that again there is a pronounced lack of headspace data sampled *in vivo* (see ref. *14*), and ecological research on scent mediated interspecific interactions involving these plants is rare (*64*), although (i) in terms of volatile emissions they can be characterized as 'cornucopias' and (ii) they are known to interact with a particularly high number of pollinating insects, especially bees, sustaining the functional diversity of the Mediterranean ecosystems (*65*).

Table 2.2. The most widely studied plants for aroma research in Greece. We show taxa that have been sampled from at least four sites.

Family	Plant name	n. of sites
Lamiaceae	*Origanum vulgare* subsp. *hirtum*	31
Cistaceae	*Cistus salviifolius*	15
Lamiaceae	*Mentha spicata*	9
Cistaceae	*Cistus parviflorus*	9
Lamiaceae	*Origanum onites*	9
Lamiaceae	*Nepeta argolica* subsp. *argolica*	8
Lamiaceae	*Salvia pomifera* subsp. *pomifera*	6
Lamiaceae	*Melissa officinalis*	5
Asteraceae	*Achillea millefolium*	4
Asteraceae	*Anthemis chia*	4
Lamiaceae	*Mentha × villoso-nervata*	4

Chemodiversity maps: case studies and prospects

Oregano (*Origanum vulgare* subsp. *hirtum*) is a plant with a wide geographical and altitudinal range of study sites, sampled in 35 localities across the country (Table 2.2) and in numerous altitudinal intervals from the sea level up to 1,500 m.a.s.l. The high frequency of samplings reflects the popularity of *O. vulgare*, which has been recently shown as the most preferred for herbal beverages across Europe (*66*); in addition, it is one of the two single *Origanum* taxa included in the European Pharmacopoeia (*67*). The plant contains big amounts of VOCs involved in pharmaceutical discoveries (e.g. carvacrol) (*1, 4*), representing a significant commercial value. In the context of the analyses in the present Thesis, we use oregano as a model case. The compilation of the literature data offers the possibility of constructing chemodiversity maps, where spatial distribution of the chemical properties of the volatilome can be visualized, and geographical patterns of variability can be assessed. A chemodiversity map of oregano's volatilome in Greece based on the proportion of each chemical class in the blends is presented in Fig. 2.3. Geo-referenced material was compiled from five research papers for which complete datasets of the VOC composition of the plant are provided. Collection sites expand all over the country, including seven islands of the Aegean archipelago. For scent acquisition,

distillation was used apart from one case where the plant's oil glands on the leaves were sampled with solid-phase micro-extraction (SPME), a static headspace technique (*68*). Monoterpenes are most abundant, while sesquiterpenes are present in all but one blends. Benzenoids are very rare and were detected only in three cases, whereas their presence cannot be related to sampling method, as they occur both in distillation and SPME samplings.

Aliphatics (mainly 1-octen-3-ol and 3-octanol) are absent only from four collection sites. In the case of oregano, elevation is not a predictor (deviance explained: 2.7%), while latitude explains better the variation of VOC chemodiversity in the sites studied in Greece (deviance explained: 51.1%). Thus, this first large-scale attempt to evaluate chemodiversity of the oregano blend is constant in terms of presence/absence of VOCs along the elevation, but shows some degree of variation from the north to the south of the country. These results should not neglect the fact that chemical analyses were performed in five different experiments; yet, they represent a tool for orientation to productive activities and research plans.

Two chemodiversity maps are presented for the genera *Hypericum* (St. John's worts) and *Mentha* (mints) (Fig. 2.4). A wide array of biological activities have been attributed to essential oils obtained from these two genera and still there seems to be a long distance for pharmacological research to cover; European Pharmacopoeia contains only two mint (*M. × piperita* and *M. canadensis*) and only one *Hypericum* species (*H. perforatum*) (*67*). Four out of the 43 *Hypericum* taxa of Greece are presented herewith. Regardless the number of samples, this case is an example of minimal bias considering sampling and chemical analysis because all VOC data, apart those from the southernmost site (Fig. 2.4), have been obtained in the same experiment (*69*). Terpenoids (mainly sesquiterpenes) are most abundant in the blends followed by aliphatics (e.g. nonane, 3-methyl-nonane), as expected (*70*). The graphic representation of the proportions of the chemical classes in the blends suggests that one population of *H. perfoliatum* in N Greece displays a high number of aliphatic compounds, varying from the chemodiversity pattern observed among the species analyzed. Data for the mints show that monoterpenes is the most compound-rich and proportionally abundant chemical class; *M. spicata* (spearmint) and *M. piperita* (peppermint) show consistently higher numbers of sesquiterpenes than the other taxa studied, in almost all collection sites. Benzenoids have only been detected in one population of spearmint in N Greece, with eugenol and *E*-methyl-cinnamate being most abundant. Given the fact that the genus *Mentha* has been the subject of chemotaxonomic studies for the identification of inter- and intra-specific chemotypes (see ref. *71*), we suggest that spatial analysis may prove useful in order to elucidate the geographical distribution of these chemotypes and their potential biogeographic significance. The above highlight the need to conduct comparable analyses, preferably over large geographical areas, in order to account for the equilibrium between phenotypic plasticity and genetic variability of the plant volatile chemodiversity, and its ecological implications. A number of studies already satisfy this and provide important data on the volatilome of some plant genera in Greece (*37, 72-74*), acquired with distillation of dry plant parts.
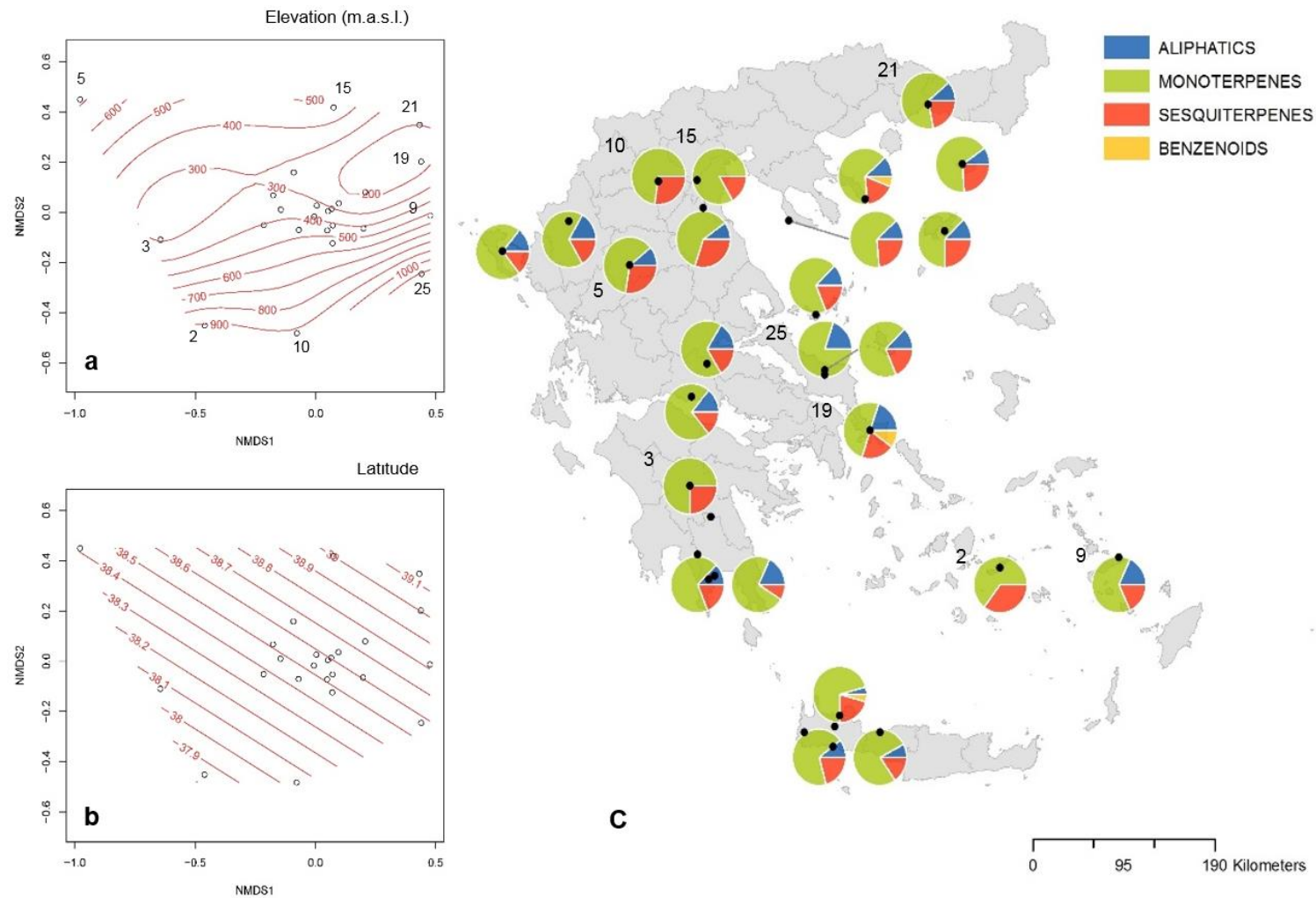
Fig. 2.3. On the right: Non-metric multidimensional scaling (NMDS) plots of the samples' VOC composition matrices with fitted (a) elevation and (b) latitude contours (stress factor: 0.115). On the left: The most divergent populations on the NMDS plot are numbered and shown on the map. (c) Compound class chemodiversity map of the volatilome of *Origanum vulgare* subsp. *hirtum* in Greece. For each collection site the proportions of the chemical classes in the blends is shown.
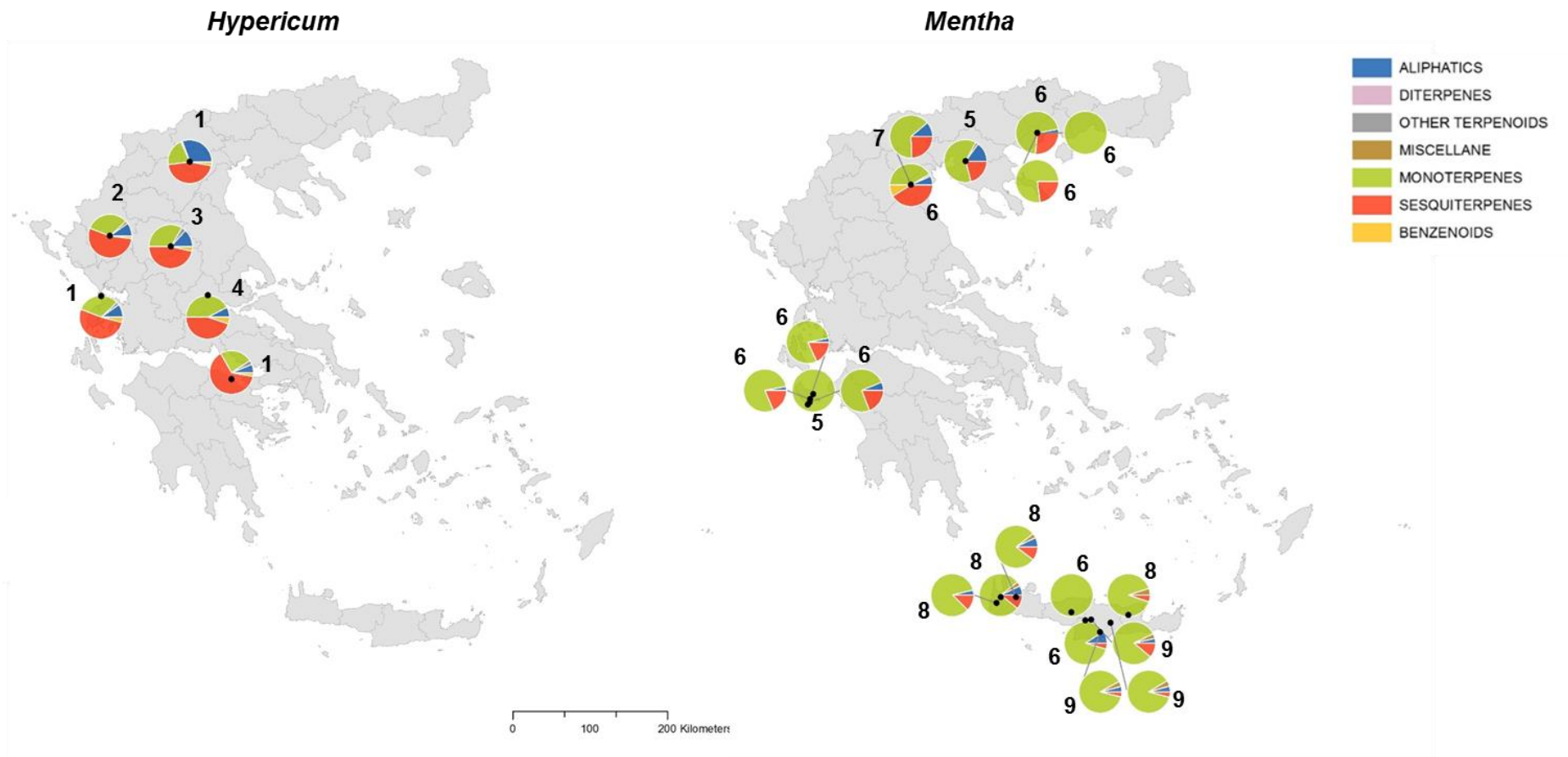
Fig. 2.4. Compound class chemodiversity maps for the genera *Hypericum* and *Mentha* studied in Greece. For each collection site the proportions of the chemical classes in the blends is shown. Numbers correspond to species studied, as follows: (1) *H. perfoliatum;* (2) *H. perforatum;* (3) *H. tetrapterum*; (4) *H. olympicum*; (5) *M. pulegium*; (6) *M. spicata*; (7) *M. piperita*; (8) *M. longifolia*; (9) *M. × villoso-nervata*.

In this Chapter, we have combined the published data on plant volatile chemodiversity in Greece for the last 25 years into a geodatabase. We present and assess the VOC richness and distribution within the 178 plant taxa (59 genera) studied, and we explore the chemical properties of the volatilome. Given that distillation techniques are most widely used by researchers in Greece and the Mediterranean region, we strongly encourage the use of *in vivo* applicable headspace scent sampling techniques in the Mediterranean in order to boost ecological research as well; thus far, industrial production purposes seem to have driven the exclusive application of distillation for the extraction of essential oils. For the first time, the volatility spectra of the blends of the 59 genera studied are presented; in this context, we suggest that the systematic record of this physicochemical property of the scent should have useful applications, especially in prospect of global change phenomena. Chemodiversity maps should be regarded as a special case of natural resources maps with multiple implications: mapping and monitoring is a first step towards chemotaxonomy, sustainable utilization, and cultivation designs of the local plant diversity, and towards the limitation of dubious bioprospecting practices. The extension of the current geodataset in other areas of the Mediterranean Basin and beyond by collecting and assessing the volatilome richness and properties over large geographical areas is certainly challenging. Nevertheless, the prospect of chemodiversity geodatabases as tools not only for basic research and the study of metabolomics on a large spatial scale, but also to support different sustainable productive activities, is promising.

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CHAPTER THREE

Smells like purple: floral color and scent are integrated in a community context

Abstract. – The reproduction of flowering plants comes at the price of synthesizing sophisticated blends of volatile compounds and pigments, principally serving to attract pollinators. The shared biosynthetic pathways and the evolutionary history of these compounds imply a potential phenotypic integration between floral color and scent, sustained by ecological advantages. In a natural Mediterranean scrubland community, we sampled the floral volatile profiles and reflectance spectra of 41 insect-pollinated plants. We find that scent covaries with color according to the visual systems of bees and swallowtail butterflies, and that both traits vary with the presence of nectar. Similar volatile composition may even predict the reflectance spectra. We suggest that this coordinated exploitation of insects' sensory abilities by plants represents the modern expression of ancient relationships between plant metabolism and ancestral insect visual and olfactory physiology. An integrated assessment of floral color and scent is important in community studies of pollination ecology.

Smells like purple: floral color and scent are integrated in a community context

Introduction

The angiosperms have evolved both a dazzling palette of floral colors and a rich bouquet of floral scents which, collectively, mediate pollinator attraction by directly stimulating animals' sensory systems. The basic metabolism behind this phenotypic eclecticism originated long before insect-pollinated flowers, both for pigments (*1-2*) and for volatile organic compounds (VOCs) (*3-4*). Natural selection linked these routes in flowering plants, resulting in the multimodal signals of modern flowers (*5-6*). Indeed, floral pigments and volatiles share pleiotropic networks of genes via complex biosynthetic pathways (*7*).

Ecologically, interactions between types of floral signal shape foraging behaviors (*6*), promote flower constancy (*8-9*), and render pollinators important selective agents for both suites of traits (*10-11*). Given the leading role of floral phenotype to plant fitness and the maintenance of species boundaries, it is reasonable to assume that selection favors phenotypic integration between visual and olfactory channels. We see two main advantages in color–scent covariation vs. a random variation of the two traits: first, reducing the risk of behavioral maladaptation (*12*), and second, mitigating the unpredictable ecophysiological costs of producing the relevant secondary metabolites. Although intraspecific studies show that color–scent covariation does occur (*9, 13-14*), this has never been explored concurrently in more than two plant species (*15*).

Here we conduct the first community-wide interspecific investigation of the association between floral color and scent. In a low scrubland (phrygana) on Lesvos Island, Greece (Fig. 3.S1) we: sampled the floral VOCs and reflectance spectra of 41 spring-flowering insect-pollinated plants (Fig. 3.1 and Table 3.S1), constructed the plant–volatilome bipartite network for the community, and tested (i) the effect of floral reflectance on the composition of the VOC blends using multivariate generalized linear models, (ii) the relationship between colorimetric and chemical properties in each plant (Table 3.S2) using phylogenetically informed generalized least squares models (pGLS), and (iii) the relationship of chemical and spectral pattern similarity. For these analyses, apart from employing independent spectral properties (viz. *brightness*, *chroma*, and *hue*), we calculated the colorimetric properties of the spectra as perceived by bees (viz. saturation: r_{hex}, and hue: θ_{hex}) (*16*) (Fig. 3.S2 and Table 3.S2), and by swallowtail butterflies (viz. saturation: r_{tet}, and hue: θ_{tet}, φ_{tet}) (*17*) (Fig. 3.S3 and Table 3.S2). Bees are highly diverse and abundant pollinators in the Mediterranean (*18*) and floral color in angiosperms strongly matches their trichromatic visual system worldwide (*19-20*); yet, we additionally aimed at testing our hypothesis with reference to a tetrachromatic visual system occurring in alternative pollinators. Moreover, we used the scores of a two-axis NMDS ordination of the raw spectral data, which were interpreted according to the spectral and colorimetric properties (Fig. 3.S4). Finally, we investigated how color or scent relate to the presence of nectar, the main reward offered to pollinators, using the above-mentioned methodology.

Materials and Methods

Study site and plants

Sampling took place in a coastal thermo-Mediterranean sclerophyllous community (East Mediterranean low scrub, a.k.a. *phrygana*) in Aghios Stefanos, Lesvos Island, Greece (39º 18'.00N, 26º 23'.40E; what3words geocode *reviewers.gladness.hesitantly*). The most dominant flowering plants of the community are *Erica manipuliflora* (heath), *Lavandula stoechas* (French lavender), and *Cistus creticus* (pink rock-rose) *Sarcopoterium spinosum* (thorny burnet)*,* with sporadic presence of *Quercus coccifera* (kermes oak), *Pistacia lentiscus* (lentisc), and *Olea europaea* (wild olive tree) (Fig. 3.S1). The climate is Mediterranean (Köppen–Geiger classification: Csa) with hot dry summers and mild winters (January–July mean temperature difference: 17.1 ºC).

The 41 insect-pollinated plants in the study community (Table 3.S1) belong to 14 families and are all native, comprising 16 steno-Mediterranean taxa and 25 of wider Mediterranean or Eurasiatic origin (*39-40*). None of the plants has an exclusively nocturnal anthesis. All plants were scored for nectar presence/absence with field observations and by using published data (*41-42*).

Floral scent sampling and analysis

Scent collections were carried out *in vivo* and *in situ*, except for *Blackstonia perfoliata*, which was sampled *in vivo* in the lab one hour after the plant was collected in the field, and transferred in a pot. 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 pollinator's activity (9am-1pm). Scents were collected from April to July 2012, except for *Cistus creticus* and *Teucrium divaricatum* from which scents were collected in May-June 2011. During the sessions, the mean ambient temperature (±SD) was 25.7 ± 1.4 ºC, and the mean ambient humidity (±SD) was 55.5 ± 2.8 %, measured on the spot.

We performed dynamic headspace sampling (*43-44*) using a PAS-500 personal air sampler (Supelco, Bellefonte, PA, USA) set at 200 mL min^{-1} flow rate. Only apparently herbivore-free, healthy-looking fresh inflorescences were selected and enclosed in PET oven roasting bags with thickness of 12 μm (SANITAS, Sarantis Group, Maroussi, Greece) 10 min prior to sampling. The bagged inflorescences were lightly covered with aluminum foil for shading against sunlight.

Adsorbent traps contained 10 mg of Porapak® Q (80/100 mesh, Supelco), packed between two plugs of silane-treated glass wool (Supelco) in a borosilicate glass Pasteur pipette (ø 7 mm). Collection period was 90 min for the strongly-scented plants (e.g. *Lavandula stoechas, Prasium majus, Teucrium divaricatum*), and 300 min for the remaining, as shorter samplings were found insufficient for capturing the volatile profiles of the less-aromatic plants. During each sampling session two ambient samples were additionally collected. Samples from green plant parts were collected when possible, in order to detect compounds of vegetative origin. However, this was not always feasible due to the small size of some plants (e.g. *Anagallis arvensis, Sedum confertiflorum*), that would require damaging the plant. Besides, we fundamentally aimed at trapping all the compounds emitted naturally by the inflorescence that includes green parts (bracts, calyx), which significantly contribute (especially in Lamiaceae, Apiaceae etc.) to the strong chemosensory environment of pollinators in the Mediterranean shrublands (*45*).

Right after scent collection and yet on the spot, the adsorbent traps were eluted with 300 μL of a 10:1 solution of hexane (puriss. p.a. – Merck, Hohenbrunn, Germany) and acetone (CHROMASOLV® for HPLC – Sigma-Aldrich, Bellefonte, PA, USA), recommended by Kaiser (*46*) to optimize elution of a full spectrum of polar to non-polar volatiles. The eluates were stored in a freezer (-20 °C) until chemical analysis. Before analysis, the scent samples were concentrated down to 50 mL with gaseous N_2, and 1 ng of toluene (Fluka, Bellefonte, PA, USA) was added as an internal standard in order to estimate emission rates (ER) in toluene equivalents per fresh mass of plant tissue. For the ER calculation we used the formula in Svensson *et al.* (*47*), modified for the plant mass, as follows (VOC: volatile organic compound):

$$Emission\ rate = \frac{(\Sigma \frac{peak\ area\ of\ VOC_i}{peak\ area\ of\ toluene}) \times amount\ of\ toluene\ (ng)}{\frac{fresh\ biomass\ sampled\ (g)}{hours\ of\ sampling}} \times concentrated\ volume\ (\mu L)$$

ER of a compound is expressed in ng (compound, in toluene equivalents) g^{-1} (biomass) h^{-1}. For each plant sampled, the average ER for each compound from the different samples (table S1) was calculated.

All analyses were performed on an Agilent 7890A/5975C GC/MS system (Agilent Technologies, Palo Alto, CA, USA) using splitless injections at 240 °C on a polar GC column (Agilent J&W DB-WAX, length 30 m, ø 0.25 mm, film thickness 0.25 μm) and He as a carrier gas with a flow rate of 1 mL min^{-1}. The GC oven was held initially at 40 °C for 3 min and the temperature was increased at 10 °C min^{-1} to 250 °C for 5 min. The two eluents (hexane and acetone) were tested for contaminants using the same method; apart from some other traces, diacetone alcohol (CAS: 123-42-2) was the only abundant contaminant.

We used Agilent MSD Productivity ChemStation software v.E.02.01 (Agilent Technologies) to retrieve the GC/MS data and AMDIS v.2.62 software for peak deconvolution combined with NIST 05 Mass Spectral Library v.2.0d (NIST Mass Spectrometry Data Center, Gaithersburg, MD, USA) to identify VOCs. Kovats retention index was calculated for all the VOCs after analysis of an authentic alkane mix (C10-C40; Sigma-Aldrich) in the abovementioned chromatographic conditions. Published data on mass spectra and retention times were additionally used. Whenever possible, (Table 3.S8) we compared VOC retention times and mass spectra to those of authentic standards.

Floral reflectance sampling
To acquire the reflectance spectra of the insect-pollinated flowers of the community we used a portable Jaz spectrometer equipped with a Premium 600 μm reflectance probe (Ocean Optics Inc., Dunedin, FL, USA). Measurements were taken from the petals or floral units (e.g. umbels) collected from different individuals; in the case of rare plants we collected as many floral units as available (Table 3.S1). We separately measured each of the differently colored areas present on a floral unit (e.g. the yellow tubular and white ligulate florets in *Anthemis* heads), but we included in the analysis only the spectrum of the color of the largest area (Table 3.S1). For *Prasium majus* we used spectra extracted from the Floral Reflectance Database (FReD) (*48*). All spectral measurements were performed in 2014. Spectral data were processed with the R package *pavo* v.0.5-1 (*49*).

Calculation of colorimetric and spectral properties

We aimed at testing for the covariation of scent and color by parameterizing the latter in three different ways. The first two sets of parameters include the colorimetric properties that match the visual systems of pollinating insects, whereas the third one includes the spectral properties that are independent of the vision of any animal (Table 3.S2). More specifically:

1. Because bees are the major pollinators in the Mediterranean communities (including Lesvos Island) in terms of efficiency and/or abundance (*18*, *50-52*), we calculated the loci of the plants in the hexagonal color space of Hymenoptera (*16*) using standard photoreceptor, illumination and adaptation parameters previously used for international comparison of flower spectral data (*19-20*). The polar expression of these coordinates (r_{hex} and θ_{hex}) represent two important and biologically relevant colorimetric properties of the spectra as perceived by bees: The radiant (r_{hex}) is the saturation of the color and the angle (θ_{hex}) is the hue (see ref. *20*). The topography of the hexagon loci of the plants in our community, which is presented in Fig. 3.S2, shows a similar pattern with several plant assemblies across the world (*19-20*). We wish to emphasize here that the trichromatic vision of the Hymenoptera (in UV, blue, and green) is directly derived from an ancient basal visual system in insects that originates long before the emergence of flowering plants and of pollinators (*30*, *53*).

2. We also employed a model according to a tetrachromatic visual system (sensitive in UV, blue, green, and red) that corresponds to the vision of the swallowtail butterfly *Papilio xuthus* (Papilionidae) (*17*). The genus *Papilio* is present in the study community (See Table 4.S2). The great variability of visual systems in butterflies (*21*, *54*) has not yet allowed for the development of an accurate generalized visual model, like in bees. However, we use this model to test for floral–scent covariation according to an alternative visual system occurring in pollinating insects. The polar expression of the loci in the tetrahedral color space representing saturation (r_{tet}), and the two angles of hue (φ_{tet}, θ_{tet}) (*55*) in the swallowtail vision, were calculated using function 'tcs' in the the R package *pavo* v.0.5-1 (*49*). Figure 3.S3 displays the 3D topography of the tetrahedron loci of the plants in the study community.

3. Finally, we calculated three spectral properties independent of any pollinator's vision, viz. *brightness*, *hue*, and *chroma* by applying the function 'summary.rspec' of the R package *pavo* v.0.5-1 (*49*). In the function's output encoding, *brightness* corresponds to variable B2, *hue* to H4, and *chroma* to S5. *Brightness* (achromatic property) is the average reflectance over all wavelengths and represents the amount of light reflected by the floral surface. *Hue* and *chroma* (chromatic properties) were calculated according to the segment classification method (*56*). *Chroma* (aka saturation) corresponds to spectral purity and it is defined as *"a measure of how much grey and white light is mixed in with the 'pure' focal colour"* (*57*). *Hue* represents the primary color, as expressed by the clockwise angle measured in the color space between the focal spectrum and a spectrum with reflectance only in the red segment (*56*).

Modeling visual systems of animals is a challenging task owing to the great variability in photoreceptor sensitivity across animal species (*34*). In the present study, we chose to apply only visual models supported by robust empirical data and realistic assumptions on the psychophysics of obligatory flower foraging insects, in order to avoid inflation of type I errors and the risk of dubious generalizations.

Furthermore, in order to summarize the information contained in the raw spectral data and simplify their dimensionality, we performed a NMDS ordination in two axes (Manhattan distance, stress = 0.119). We then interpreted each NMDS axis by applying Pearson correlation tests of the axes scores and the above-mentioned colorimetric or spectral properties. In total, we found nine significant correlations, among which we considered effective only those with the highest coefficients (r > 0.70) (fig. S4). Thus, NMDS1 axis is negatively correlated with *chroma* (r = -0.91, $p<0.0001$, two-tailed) (fig. S4A), and with r_{tet} (r = -0.80, $p<0.0001$, two-tailed) (Fig. 3.S4I), whereas NMDS2 is negatively correlated with r_{hex} (r = -0.78, $p<0.0001$, two-tailed) (Fig. 3.S4D). Moreover, we found that saturation as calculated for the swallowtails (r_{tet}) and saturation calculated with the segment classification method (*chroma*) are highly correlated (r = 0.93, $p<0.0001$, two-tailed).

Plant phylogeny and phylogenetic signal of traits
Plant phylogeny follows APG III (*58*) and it was built with the online software *Phylomatic* v.3 (tree R20120829) (*59*). We used the 'bladj' algorithm in the software *Phylocom* v.4.2 (*60*) 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 ages (*61*). The pairwise phylogenetic distance matrix of the plant assembly was calculated using the function 'cophenetic.phylo' in the R package *ape* v.3.5 (*62*).

In order to account for phylogenetic non-independence and its statistical implications (*63*), we first calculated the phylogenetic signal of all traits involved in the analysis, following four approaches according to the type of the focal variable (Table 3.S9): (i) For multidimensional data we calculated dissimilarity matrices and tested them for correlation with the phylogenetic distance matrix of the community using Mantel tests in the R package *vegan* v.2.4.0 (*64*). Manhattan distance was used for the raw spectral data, for hexagon loci, and for the NMDS axes scores. Jaccard distance was used for presence/absence data. (ii) For continuous variables we calculated Blomberg's K^* (*65*) as one of the currently most efficient metrics for detecting phylogenetic signal in continuous traits (*66*). Blomberg's K^* was computed with function 'phyloSignal' in the R package *phylosignal* v.1.1 (*67*). (iii) For nectar, we computed the *D* statistic for binary traits, which is based on the sum of the sister-clade differences of the trait in the phylogeny (*68*), with the function 'phylo.D' in the R package *caper* v.0.5.2 (*69*). (iv) For module ID we used the algorithm 'phylo.signal.disc' for discrete traits implemented in R, developed by Enrico Rezende (see ref. *70* for detailed description and example).

Statistics
Multispecies volatilome datasets require special statistical handling owing to the interdependence of VOCs, which is naturally expected due to shared metabolic processes leading to their production (see ref. *71*). Therefore, in order to test the effect of color or nectar to the distribution of the VOCs among the plants of the community, we selected a model-based method designed for compositional data. We employed Multivariate Generalized Linear Models (MGLMs), used for the first time in a bipartite network of plants and metabolites. In practice, MGLMs fit a separate generalized linear model to each VOC of the network, using a common *n*-dimensional set of explanatory variables and a resampling-based hypothesis testing (*72*).

In order to test the relationship between floral color or nectar and the qualitative composition of the scents in the community, i.e. the binary network of VOCs, we built a series of MGLMs with a binomial family (link "cloglog") using the function 'manyglm' in the R package *mvabund* (*72*). 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 (*73*) and in our case yielded the most conservative results. Univariate tests were then performed in order to determine which response variables (VOCs) showed significant effects. The multidimensional response variable was either the binary matrix of the full VOC network (41×351) or one of its subsets that included the VOCs belonging to one of the four major VOC classes, which represent different pathways of plant metabolism (*76*): Aliphatics (95 VOCs); benzenoids and phenylpropanoids (51 VOCs); monoterpenes (68 VOCs); and sesquiterpenes (56 VOCs). This discrimination would allow us to test if the distribution of the VOCs of a specific metabolic route would be associated with the floral color at a community level.

For each of the above-mentioned response variables, we built five sets of MGLMs, each set with the following explanatory variables:

1. The presence/absence of nectar in the flowers.
2. The floral color loci of the plants in the hexagon space of bee vision, expressed as polar coordinates (r_{hex}, θ_{hex}). These two variables represent two different colorimetric properties (saturation and hue), but they are both needed in order to describe the exact color as perceived by Hymenoptera (*20*). Therefore, it is biologically meaningful to test their effects both separately and in combination. Based on the Akaike Information Criterion (AIC), we selected the following three separate formulae: $y \sim r_{hex}$, $y \sim \theta_{hex}$, and $y \sim r_{hex}{:}\theta_{hex}$, for the five response variables (total binary network and its four subsets).
3. The floral color loci of the plants in the tetrahedron space of the swallowtail vision, expressed as polar coordinates (r_{tet}, φ_{tet}, θ_{tet}). Again, these three variables represent hue and saturation for swallowtails, however they are all needed in order to describe the exact color as perceived in this visual system. Thus we applied four separate formulae: $y \sim r_{tet}$, $y \sim \varphi_{tet}$, $y \sim r_{tet}$, $y \sim \theta_{tet}$, and $y \sim \theta_{tet}{:}\varphi_{tet}{:}r_{tet}$.
4. The two NMDS axes of the raw spectral data. The two axes were tested separately ($y \sim$ NMDS1 and $y \sim$ NMDS2). Based on AIC we did include models of the additive effect ($y \sim$ NMDS1+NMDS2). The interaction term of the two axes, apart from the fact that it would be biologically uninterpretable, did not show any significant effect to scent composition when tested in bivariate MGLMs ($y \sim$ NMDS1:NMDS2).
5. The independent spectral properties (*brightness*, *chroma* and *hue*). For each property, we tested both the separate effects and their interaction term against the response variables.

All the above-mentioned floral colorimetric and spectral variables were also tested for association with the chemical properties of the blends (Table 3.S2), i.e. (i) the proportional representation of each VOC class in the total emission rates, (ii) the proportional representation of each VOC class in the sum of VOCs of each plant, and (iii) the specialization of the plants in the volatilome network of the community, as described by three species-level metrics: The d' specialization index (*75*) calculated in the R package *bipartite* v. 2.06 (*76*), the among-module connectivity c, and the within-module connectivity z (*77*). The latter two represent coordinates in the network topography and their combination is used for assigning roles to the nodes, which reflect their generalist/specialist behavior (*77*). For their calculation, we used *NetCarto* software, which implements a Simulated Annealing (SA) algorithm in order to assess the modularity of a binary bipartite network (*78*). Note that the plant–VOC

network of the study community is significantly modular (modularity $M = 0.44$). For testing all these associations we applied phylogenetically corrected generalized least squares models (*79*) with λ branch length transformations, using the 'pgls' function in the R package *caper* v.0.5.2 (*69*). Proportional response variables were arcsine-transformed before fitting the models. For all models, we compared the AIC values with those of the null model (y~1) in order to avoid inflation of type I errors.

To detect the spectral patterns associated with different VOC classes among the plants of the community, we followed two approaches. First, we explored the spectral similarity of the plants included in the modules of the plant–volatilome network. In order to chemically characterize the modules yielded by the SA algorithm (Fig. 3.S6), we applied a Pearson χ^2 conditional independence test (Fig. 3.S7) with the function 'mosaic' in the R package *vcd* v.1.4-1 (*80-81*). This process revealed the statistically significant positive and negative associations of the four main VOC classes with the modules. High proportional participation in one module in respect to the others (block width in Fig. 3.S7) combined with statistical significance, allowed us to identify the positive associations for aliphatics (Module 6), benzenoids/phenylpropanoids (Module 2), and sesquiterpenes (Modules 3 and 4) (fig. S6-S7). Monoterpenes are almost uniformly distributed among the modules, suggesting no clear relationship with any module, so we excluded them from the spectral similarity analysis.

The second approach regards the exploration of the relationship between the realized chemical phenotype of the flowers and their reflectance spectra. To explore this, we distinguished four groups of plants according to the VOC class prevailing in the sum of the floral ER, we calculated the mean pairwise Manhattan distance of the floral spectra in each group and compared them with a Kruskal–Wallis rank sum test. The groups of plants with significantly lower dissimilarities than the other groups would indicate spectral patterns associated with high emissions in the respective chemical groups.

In order to chromatically characterize the modules of the plant–VOC network, i.e. to test if any floral colorimetric or spectral property explain the distribution of plants among the modules, we applied phylogenetically informed ANOVA (*82*) of the each colorimetric or spectral property against the trait 'Module ID' by using function 'aov.phylo' in the R package *geiger* v.2.0.6 (*83*).

Unless stated otherwise, statistics were performed in R v. 3.3.0 (*84*).

Table 3.1 The effect of floral color or nectar on the distribution of VOCs within the community. Effects are tested in the total plant–volatilome network and its four subsets containing the VOCs of each one of the major chemical classes. The results of 70 separate multivariate generalized linear models are shown. Significance was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling.

	Total network			Aliphatics			Benzenoids			Monoterpenes			Sesquiterpenes		
	Df	Dev.	p-value	Df	Dev.	p-value	Df	Dev.	p-value	Df	Dev.	p-value	Df	Dev.	p-value
r_hex	1	604.1	**0.029**	1	262.4	**0.006**	1	31.0	0.614	1	71.8	0.295	1	85.7	0.145
θ_hex	1	416.1	0.239	1	87.0	0.519	1	55.8	0.372	1	59.6	0.550	1	103.8	0.118
$r_\text{hex}{:}\theta_\text{hex}$	1	679.0	**0.007**	1	112.2	0.187	1	62.4	0.314	1	63.8	0.390	1	250.1	**0.001**
NMDS1	1	851.9	**0.003**	1	153.3	0.094	1	43.2	0.458	1	107.0	0.074	1	282.4	**0.001**
NMDS2	1	540.1	**0.040**	1	211.6	**0.024**	1	34.2	0.593	1	78.4	0.250	1	61.3	0.317
r_tet	1	466.6	0.062	1	157.6	0.068	1	16.9	0.810	1	118.5	**0.024**	1	61.5	0.217
φ_tet	1	574.6	**0.023**	1	163.3	0.078	1	58.6	0.293	1	119.9	**0.038**	1	92.8	0.154
θ_tet	1	475.4	0.110	1	85.9	0.479	1	62.2	0.218	1	100.7	0.112	1	112.9	0.073
$r_\text{tet}{:}\varphi_\text{tet}{:}\theta_\text{tet}$	1	361.0	0.137	1	79.0	0.280	1	65.5	0.120	1	74.4	0.188	1	53.2	0.232
Chroma	1	461.0	0.092	1	81.8	0.462	1	121.9	**0.042**	1	76.2	0.136	1	70.7	0.215
Brightness	1	561.1	**0.045**	1	231.2	**0.015**	1	47.0	0.472	1	114.9	0.058	1	66.5	0.329
Hue	1	416.1	0.239	1	87.0	0.519	1	55.8	0.372	1	51.5	0.376	1	103.8	0.118
Chr:Bri:Hue	1	543.0	**0.031**	1	129.6	0.158	1	83.9	0.122	1	66.4	0.378	1	93.0	0.131
Nectar	1	467.2	**0.032**	1	211.8	**0.003**	1	37.3	0.588	1	74.0	0.211	1	52.8	0.389

Results and Discussion

Bee vision explains the substantial structure in the plant–volatilome network (Tables 3.1 and 3.S4-3.S5). Specifically, VOC distribution is associated with saturation as perceived by bees, (r_{hex} and NMDS2) and with the interaction term r_{hex}:θ_{hex}. Swallowtail vision also relates to VOC distribution among the plants through φ_{tet}, and NMDS1. In the four sub-networks including the major VOC classes (Table 3.1), bee vision relates to the distributions of aliphatics and sesquiterpenes, and swallowtail vision is associated with the distributions of monoterpenes and sesquiterpenes (the latter via NMDS1, Fig. 3.S4). The spectral properties are mainly linked to benzenoids and aliphatics. Overall, 171 VOCs (out of the 351) show significant effects against at least one colorimetric or spectral property (Tables 3.S3-3.S4).

Bee and swallowtail colorimetric properties interact variously with the chemical properties in the floral phenotype (Fig. 3.2 and Table 3.S6). Swallowtail vision relates to the percentage of benzenoids in the total emissions, and to the percentages of aliphatics and monoterpenes in the sum of VOCs. Terpenoid emissions show the strongest association with bee vision (Fig. 3.2, Table 3.S6). Hue for bees (θ_{hex}) is a source of variation both for monoterpenes and sesquiterpenes. The latter are also positively associated with color saturation for bees (r_{hex}), and negatively associated with color saturation for swallowtails (via NMDS1), i.e. flowers with higher sesquiterpene emissions exhibit higher color purity for bees and lower color purity for swallowtail butterflies. Sesquiterpenes, a highly diverse class in Mediterranean plants (*21*), are considered among the most attractive terpenoids to obligate floral visitors and least repellent to facultative ones (*22-23*), as well as pheromones both for bees (*24*) and swallowtails (*25*). Thus their connection to both visual systems may imply a diverse inter-signal functionality.

The species–volatilome network was composed of seven link-dense areas (modules), each including plants that share emitted VOCs and, presumably, biosynthetic processes responsible for floral display. Plants in modules vary chromatically only according to *hue* (phylogenetic ANOVA, $F_{6,34} = 2.67$*; Table 3.S7). Furthermore, the spectra of the plants included in the "aliphatics" module (#6 in Figs. 3.S6-3.S7) are significantly more similar in comparison to the other two chemically characterized modules (Kruskal–Wallis, $\chi^2(2)=6.26$*; Figs. 3.3A-B and 3.S8B). This module includes all community members whose flowers are reddish to the human eye and offer only pollen (*Papaver argemone*, *Anemone coronaria*) or nothing edible (*Serapias cordigera, S. vomeracea*) to pollinators. Analogously, grouping plants according to the predominant VOC class in their realized emissions reveals that the reflectance spectra in the group where sesquiterpenes predominate (*Cistus creticus, Centaurium pulchellum,* and *Teucrium divaricatum*) are almost identical (Fig. 3.3C), perceived as pink-purple by the human eye. These spectra show significantly lower interspecific dissimilarity compared with the other three groups (Kruskal–Wallis, $\chi^2(3)=15.41$***; Figs. 3.3D, Fig. 3.S8A).
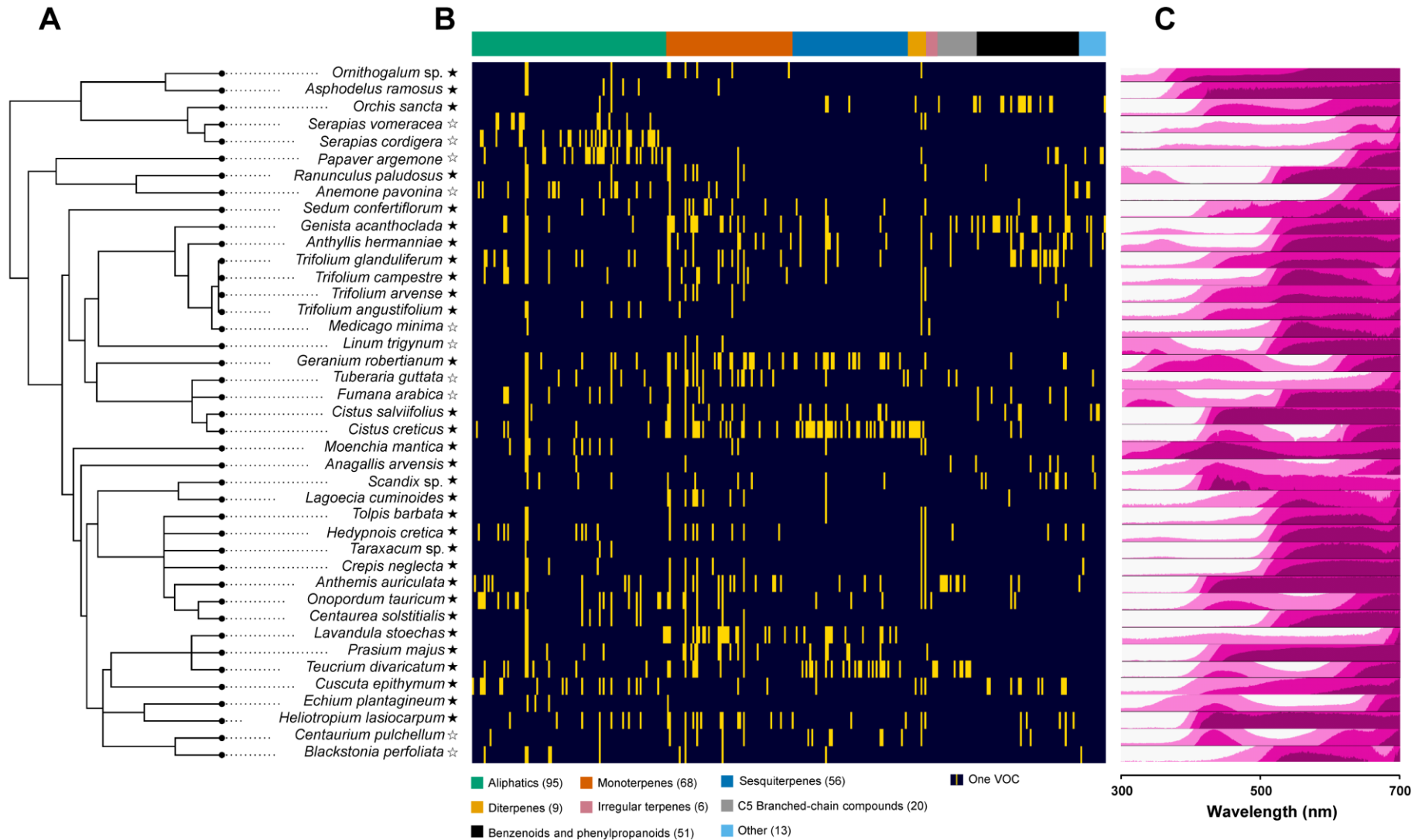
Fig. 3.1. The chemical and visual floral phenotype of the insect-pollinated plants in the study community. (A) Plant phylogenetic relationships. (B) The plant–volatilome network. Compounds are arranged according to the major chemical class. Filled stars denote presence of nectar. Unidentified compounds are not shown. (C) Floral reflectance spectra for each plant displayed in horizon plots, where overlaid darker bands represent higher reflectance rate in the specific wavelength range.

In the study community, nectar presence relates to floral color as perceived by pollinators, implying a coordinated sensory exploitation by plants based on the pollinator's visual abilities (*26-28*). Nectar-producing plants display significantly different hue as perceived by swallowtails (φ_{tet}) ($F_{1,39}$=8.75**; Table 3.S6), and significantly higher color saturation as perceived by bees (r_{hex}: $F_{1,39}$=13.10***; NMDS2: $F_{1,39}$=16.63***; Table 3.S6). This result explains innate preferences of bees for stimuli of higher spectral purity (*26*). In the hexagonal bee color space, almost all non-nectariferous plants cluster near the achromatic center (Fig. 3.S2), suggesting low apparency to bees. In this context, the above-mentioned red nectarless flowers associated with aliphatics (Module #6) offer an interesting insight: all are almost achromatic, i.e. visually non-attractive to bees (Fig. 3.S2; *26*). Aliphatic compounds, instead, are the most frequent VOCs in our community (Fig. 3.1), and their distribution among the plants is linked to bee vision (Table 3.1). At the same time, they are a vital part of bees' life history, e.g. as sex pheromones (*29*). Thus some red flowers may compensate for their visual inconspicuousness by exploiting bees' olfaction in a quasi-deceptive way.

Nectar relates to the qualitative VOC distribution among the plants in the community (Tables 3.1 and 3.S4), specifically that of aliphatic compounds (Tables 3.1 and 3.S5). Also, nectariferous plants are more chemically generalist, showing higher among-module connectivity in the volatilome network (pGLS, $F_{1,39}$=7.85**; Fig. 3.S5). However, no VOC class was found to quantitatively associate with nectar presence. The weaker relationship of nectar with floral scent in the community, as compared with color, could be attributed to a trade-off of display functions between visual and olfactory display functions, given the highly dynamic and multimodal nature of the volatile emissions, counter to the fairly constant chromatic signals.

Overall, our data provide evidence for phenotypic integration between floral scent and color that substantiates our initial hypothesis. Importantly, we find that floral volatile emissions are tuned to the visual systems of pollinators, which is directly linked to the evolution of sensory exploitation of insects by plants. Trichromatic vision in bees is phylogenetically conserved and existed before the great angiosperm radiation in the Cretaceous (*30*). Likewise, both pigment and VOC metabolism preceded insect pollination (*1-4*). Therefore, given the evolutionarily opportune availability of the basic sensory and metabolic requirements, the covariation of floral scent and color as perceived by bees represents, in fact, the current expression of ancient relationships between plant secondary metabolism and the ancestral insect sensory systems, first hypothesized by Pellmyr and Thien in 1986 (*31*).

Although butterflies are less abundant than bees as floral visitors in phrygana (*32*), we find that the tetrachromatic vision of swallowtails relates to floral scent, suggesting that this more recent visual system may also be a driver of floral diversity. Temperate Old World butterflies are strongly associated with floral benzenoids and aliphatics (*33*), the latter also serving as pheromones for some Papilionidae (*25*). Our results support this relationship, but the variability of visual systems in Lepidoptera (*34*) probably constrains a reliable generalization at a taxonomic level higher than the genus *Papilio*.

Interestingly, we find that monoterpenes are almost uniformly distributed among the volatilome network modules (Fig. 3.S7), such that they do not characterize any module. Their ubiquity maybe suggests a more general role of these compounds in the community. Although monoterpenes have been linked to pollinator attraction (*22, 33*) and relate to bee vision (Fig. 3.2, Table 3.S6), they are generally
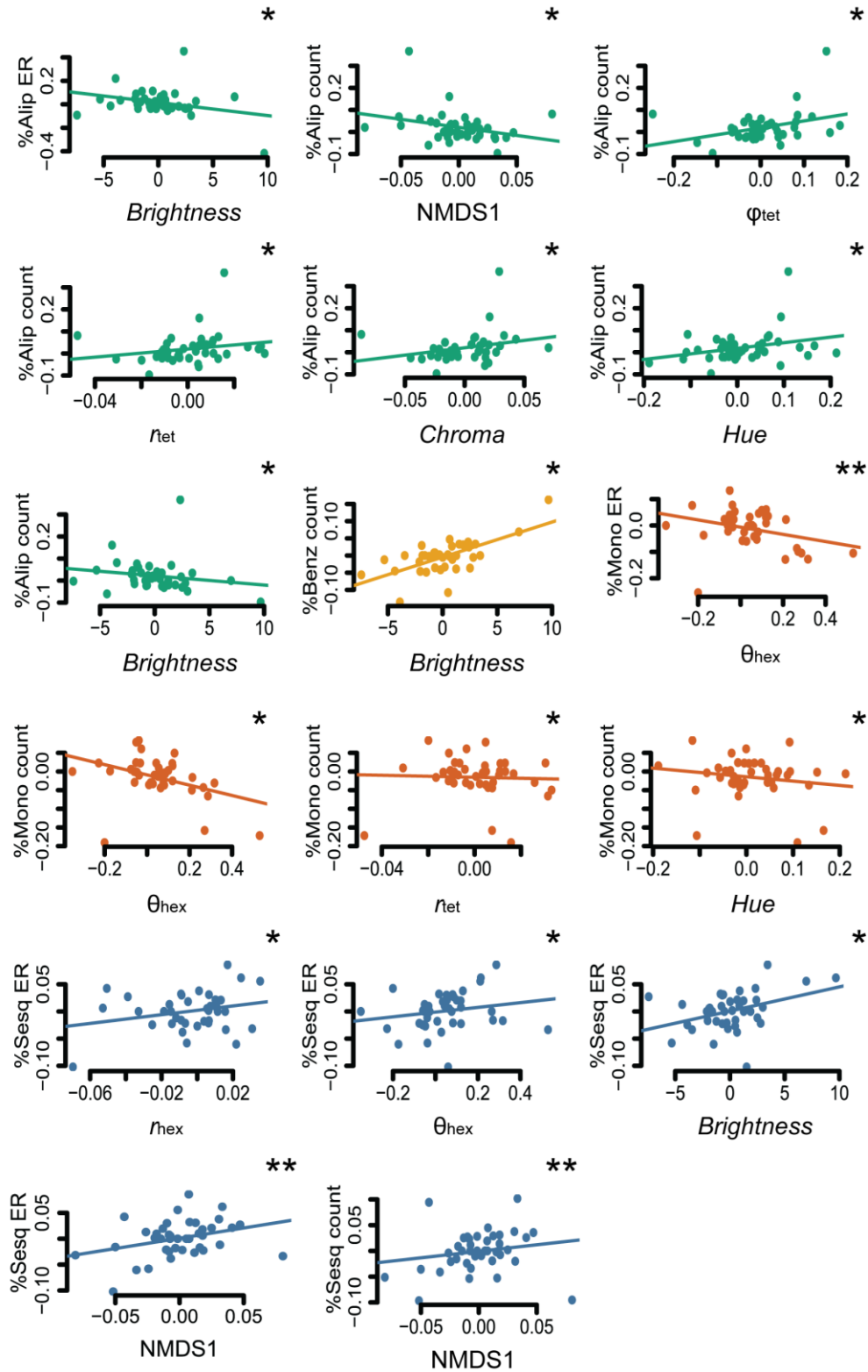
Fig. 3.2. Significant relationships between chemical and colorimetric or spectral properties in the floral phenotypes of the study community. Results were acquired with phylogenetically informed GLS. Plots show the phylogenetically independent contrasts of the traits examined. Colors in plots denote different VOC classes. Alip: Aliphatics; Benz: Benzenoids; Mono: Monoterpenes; Sesq: Sesquiterpenes. %Class ER: proportion of the class in the sum of emission rates. %Class count: proportion of the class in the sum of VOC (*≤0.050; **≤0.010).
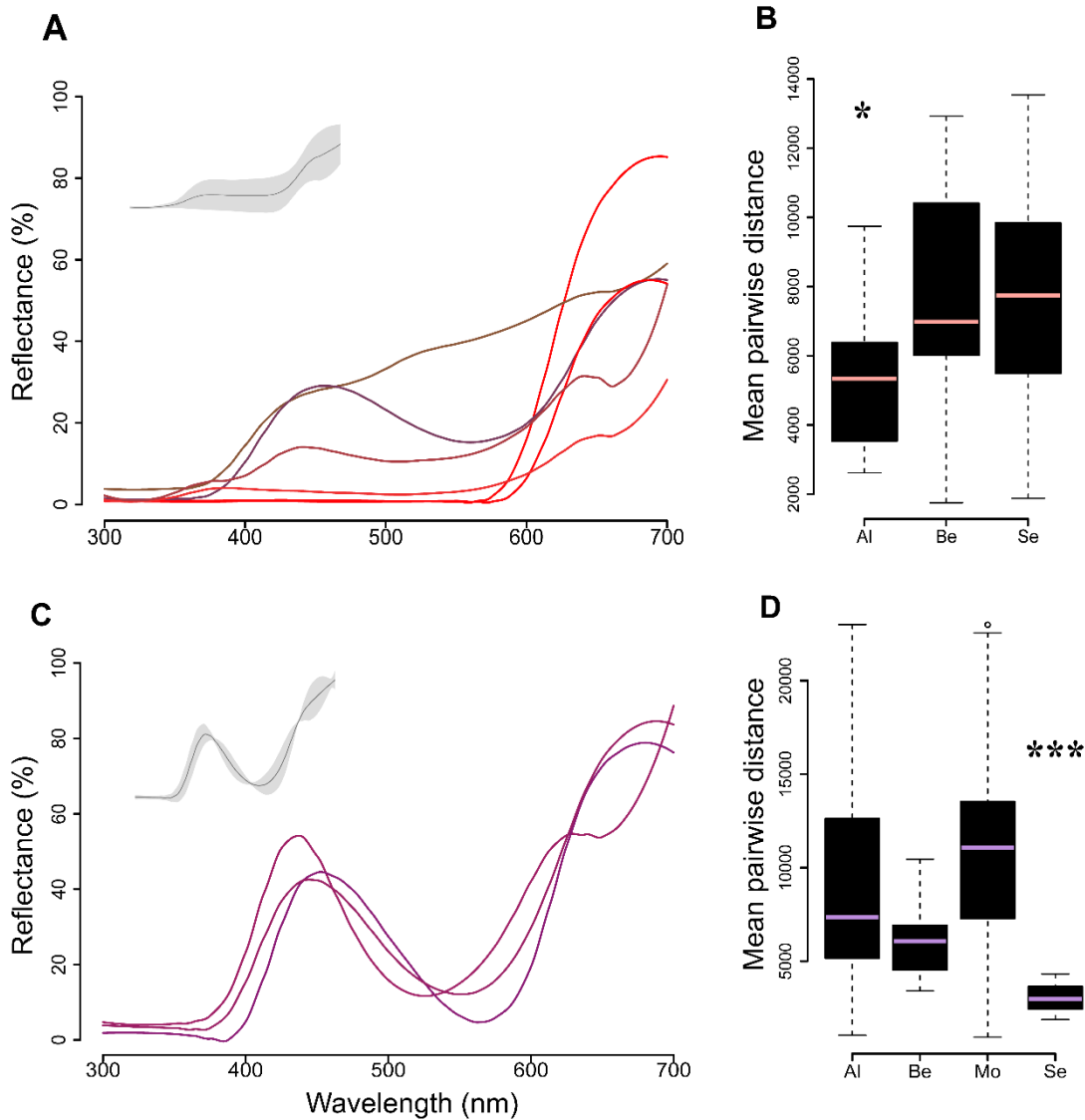
Fig. 3.3. Floral spectral patterns associated with VOC classes. (A) Spectra of the plants included in Module #6 of the plant−volatilome network, which has been characterized as the "aliphatics module" (Fig. 3.S6-3.S7) (B) Mean pairwise Manhattan distance of the spectra in each of the chemically characterized modules (Aliphatics: Module #6; Benzenoids/phenylpropanoids: Module #2; Sesquiterpenes: Modules #3-4, Fig. 3.S6-3.S7). (C) Spectra of the plants in the emissions of which sesquiterpenes prevail. (D) Mean pairwise Manhattan distance of the spectra in each group of plants distinguished according to the chemical class prevailing in their emissions. Insets display the average spectrum of the module/group ± SD. Line colors encoded according to the RGB model. Al: Aliphatics, Be: Benzenoids/phenylpropanoids, Mo: Monoterpenes, Se: Sesquiterpenes (*p≤0.05, ***p≤0.001, Kruskal–Wallis rank sum test).

considered deterrent compounds, both in plants and in animals (*35-36*), thus their primary functional role in floral scent may, on average, be defensive (*23*).

Further findings, still challenging to evaluate, include the association of floral *brightness, hue* or *chroma* with scent (Tables 3.1 and 3.S6, Fig. 3.2). The role of these spectral properties in plant reproductive fitness has rarely been explored (*37-38*), largely in the absence of data on the respective psychophysical responses of pollinators and other floral visitors.

Floral complexity certainly entails more than color and scent. However, their integration as adapted to pollinators' visual systems (i) reveals a plant community-context finely tuned to insect sensory systems, (ii) underscores the fundamental relationship between bees and flowering plants in the Mediterranean, (iii) may serve as a primer for future investigations of the evolution of interspecific interactions, and (iv) indicates that both visual and olfactory floral signals should be considered together to better understand the assembly rules of communities.

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CHAPTER FOUR

Floral sensory landscapes and the structure of pollination networks

Abstract. – Pollination networks represent a most comprehensive method currently used to describe plant–pollinator interactions, to predict community resilience in case of disturbance, and to design restoration schemes. Although immense progress has been made in order to understand network structure and linkage rules, the role of floral sensory stimuli has never been holistically assessed in a community context. Yet, a sophisticated interplay of visual and olfactory signals of the sessile plants and the complex sensory systems of pollinators is anticipated. Here, we analyze the pollination network of a phryganic community by using methodological innovations, and we ask whether floral sensory stimuli associate with the substantial structure of the network, the centrality of plants, and the visitation patterns exhibited by the different pollinator groups. We find that both network cohesiveness and plant niche overlap relate to sensory stimuli. We also attempt a functional hypothesis of long-distance attraction of pollinators in Mediterranean scrublands, and we corroborate the fundamental functional connection of bees and floral cues in this ecosystem. Sensory diversity emerges as an important component of functional diversity that could help designate influential plants in the community and be used in targeted restoration practices for maintaining network dynamics.

Floral sensory landscapes and the structure of pollination networks

Introduction

Network analysis of mutualistic interactions constitutes a multi-tool for the study of biodiversity both at micro- and macro-ecological scales (*1-3*). This mathematical method greatly helped upgrade pollination from a phenomenon traditionally studied in isolated species pairs, substantiating the Darwinian paradigm (*4-6*), to a key functional ecosystem service that sustains primary production and the stability of communities (see ref. *7*, for an excellent historical overview). By constituting a data-intensive method, network analysis of pollination interactions (i) describes the functional structure of communities (*8*), (ii) offers a pragmatic view on the plasticity of visitation patterns (*9*), (iii) indicates conservation priorities in prospect of global change phenomena and biological invasions (*10, 11*), and (iv) can be used for designing schemes for the ecological restoration of functional diversity (*12, 13*).

Even though the structure of pollination networks has been described in numerous communities from the tropics to the Arctic Circle (*2, 9, 14-17*), the role of floral trait suites in configuring visitation patterns has been thus far addressed in very few studies (*Chapter 1,* Table 1.1). On the other hand, during the last twenty years, there has been a vivid debate regarding the interplay of floral phenotype and the suiting pollinator types, greatly triggered by the development of network analysis (*18*): the assessment of big datasets revealed that generalization is more frequent than expected by tight coevolution between pollinators and plants, and by pollination syndromes (*19, 20*); long-term observations of pollination networks showed that they are characterized by a great temporal plasticity of plant–pollinator (p–p) interactions (*9, 21-23*), implying that short-term sampling (which is generally the rule) should lead to a false estimation of species' ecological specialization (*24*); pollination syndromes (*5*) failed to be verified in a global-scale meta-analysis (*25*); theoretical models have inferred that linkage rules in mutualistic networks may be explained mostly by phenology and/or abundance of species (*26, 27*); opportunistic foraging behaviors of insects have been justified under particular environmental conditions of extreme seasonality, as for example in the Mediterranean, where the short-living solitary bees, the most abundant and diverse pollinators in the region (*28, 29*), are too limited in time to complete life cycle and provide for their brood (*9, 30*).

This crescendo of indications against the expected tight pairwise, phenotypically complementary relationships, largely contributed towards a pragmatic assessment of community interactions. Nonetheless, we know that some degree of phenotypic complementarity is essential in order for mutualistic interactions to exist, exemplified by the simple matching between tongue size and corolla depth (*31*), to the more sophisticated interplay of sensory stimuli involving innate preferences and cognitive abilities of pollinators (*32-35*). Coevolutionary forces have also been shown to be compatible with the asymmetric structure of mutualistic networks, i.e. nestedness (occurring when the interactions of specialist species are a subset of the interactions of more generalist ones, ref. *36*). Besides, p–p coevolution is considered a major driver of floral diversification since the great angiosperm radiation in the Cretaceous (*37, 38*); and although it may not be the only driver (see ref. *39*), pollinator-mediated selection of floral color and scent traits is actually happening (*40-43*). In *Chapter 3*, we show that floral color and scent of the insect-pollinated plants in the community covary, implying as sensory exploitation of pollinators originating in ancient interspecific interactions; so we may inevitably ask the question if this community-wide phenotypic integration exists in vain, as a coevolutionary relic, or if it actually relates to visitation patterns.

In the context of a network, pollinators are expected to filter information received in the floral landscape they encounter ('information filtering', cf. ref. *44*) based on what their sensory systems perceive, their cognitive abilities, and their innate preferences (*45*). For example, we know that in pollination networks, the "rich-get-richer" phenomenon occurs when new incoming nodes (e.g. insects) choose highly-connected existing nodes (e.g. plants) to interact with (*21*), enhancing the nested pattern of interactions (*46*). Recently, color matching of temporally overlapping flowers and insect vision was shown to relate to plant generalization in one community (*17*). Similarly, insect responses to natural floral blends were found to correlate with visitation patterns (*47*), and floral scent manipulation was shown to affect visitation patterns in two plant species studied simultaneously in a community (*48*). However to date, since no study has considered the sensory floral stimuli holistically (i.e. visual and olfactory together) in a comprehensive natural p–p assemblage, the questions remain: Does preferential attachment of nodes in the network (*49, 50*) (and, by extension, nestedness) have a sensorial basis, implying the function of coevolutionary forces? Is it because the most generalist plants mostly show high floral abundances (*51, 52*) thus are easily available and noticeable to foraging insects? Or maybe is it a combination of both? For answering these questions, two things are required: (i) a comprehensive dataset on the natural history of the plants of the community, including unbiased parameterizations of floral scent (collected *in vivo*) and color, and (ii) disentangling plants' specialization in the p–p network co-considering flowering phenology and abundance.

Species' flowering phenology is the first factor filtering interactions, thus affecting the structure of pollination networks (*9, 18, 21, 50, 53-55*). The reason is obvious: if two species are not simultaneously present in a community, their interaction is simply impossible. Consequently, by using a pollination network of the entire flowering/sampling season (in fact, the 'static' network) to estimate specialization or centrality of species (see Box 1.1 in *Chapter 1*), we consider putative interactions that are actually not possible in time, therefore we inflate species' specialization rates (*56*). Given that most species in a community tend to have short flowering phenophases (*9, 21*), this overestimation could seriously affect the results. Recent studies have addressed this issue and suggested the partition of the total network into smaller regular time-sequential networks (*14, 15*). However, even daily resolved network studies that finely describe the fluctuating behavior of species throughout the flowering/sampling season, inevitably make use of the 'static' version of plants' specialization and centrality (*14*), because this data aggregation provides the total number of links for each species.

In order to overcome the specialization bias caused by temporal data aggregation, we introduce a new approach in network data pooling, the 'phenonet', which expresses the dynamic nature of p–p networks by partitioning the total cumulative network into (smaller) networks, as many as the interacting species in the community. A phenonet is a snapshot of the entire community p–p network, encompassing only the interaction spectrum occurring within each species' phenophase. The approach is based on the simple facts that (i) plants do not compete with the sum of species occurring in an entire flowering period (the version of the 'static' network), but only with their co-flowering plants, as much as (ii) they cannot interact with all pollinators encountered during the entire flowering/sampling period but, *mutatis mutandi*, only with those with overlapping phenophases. Thus, the actual ecological specialization and network centrality of plants may vary according to time and depending on the qualities/behavior of the available co-existing species.

Here, we employ the plants' phenonets, assembled in order to study the role of floral sensory landscapes in the structural roles of plants in the p–p network. In practice, we retrieve all p–p interactions recorded in the community during the flowering phenophase of each focal plant, including all interactions recorded between its co-flowering plants with the available insects. So, for each plant, node properties correspond to the network operating only during this plant's phenophase. The main advantage of this approach is that it respects and reflects the dynamic nature of the interactions history in a community; thus it allows to account for phenology, which is the major factor that renders interactions possible, and to assign most pragmatic, time-corrected values to all node properties of the species.

Next, we attempt to resolve the role of floral abundance that also has been shown a principal factor determining interaction patterns and the structure of networks (*16, 17, 53, 57, 58*) (and Table 4.1). By adopting a functional approach, we consider floral abundance not as a distinct plant trait, but as the abundance of phenotypic traits, either visual or olfactory that jointly form the floral sensory landscape in the study area. For this, we adopt the term 'apparency' from chemical defense ecology. Apparency was first introduced in the context of the "Plant Apparency Hypothesis" (PAH) by Feeny (*59, 60*), according to which, apparent and unapparent plants display different chemical defense patterns against herbivores, exactly because they differ in their detectability by the latter. Here, we have adapted the term in order to describe the multiple ways that a plant can have noticeable flowers in the community during its flowering phenophase. We distinguish between physical (further discerned as to height and surface area) and olfactory floral apparency. In practice, floral apparency expresses how much a floral trait of a given species is above or below the median value of the trait in the community snapshot which concurs with its flowering phenophase.

Given all the above, in this Chapter we attempt to disentangle the relative importance of the factors related to floral visitation in a natural Mediterranean scrub community. We present the first analysis of the role of floral sensory landscape as shaped by the olfactory and visual floral stimuli, in the structure of the p–p network, focusing on the functional properties of plants. We employ the above-mentioned new methodological approaches, and we ask (i) whether plants' centrality and generalization associate with their floral phenotype, (ii) whether floral phenotype in plants predicts visitation rate by the different insect groups, and (iii) which phenotypic elements shape the structure of the entire p–p network.

Materials and Methods

Study area

Sampling was carried out in a coastal thermo-Mediterranean sclerophyllous community (East Mediterranean low scrub, a.k.a. *phrygana*) in Aghios Stefanos, Lesvos Island, Greece (39º 18'.00N, 26º 23'.40E; what3words geocode *reviewers.gladness.hesitantly*). The most dominant flowering plants of the community are *Lavandula stoechas* (French lavender), *Cistus creticus* (pink rock-rose) *Sarcopoterium spinosum* (thorny burnet), and the autumn-flowering *Erica manipuliflora* (heath) with sporadic presence of *Quercus coccifera* (kermes oak), *Pistacia lentiscus* (lentisc), and *Olea europaea* (wild olive tree) (cf. *Chapter 3,* Fig. 3.S1). The climate is Mediterranean with hot dry summers and mild winters (January–July mean temperature difference: 17.1 ºC).

Floral visitation observations

Samplings 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 (see *23*). We haphazardly established six permanent observation plots with dimensions 3×25=75 m² in the study area. During every sampling period, one observer (Aphrodite Kantsa) visited the study site in 10 day-intervals and recorded all plant–insect interactions in each plot during three 15 min diurnal sessions (quarters), from 9am to 3pm. During each quarter, the observer moved at a steady pace within the plot, recorded interactions, and collected insect specimens with a hand net when taxonomic identification was not possible on site. The latter has been mainly the case because of the high pollinator diversity in the wider area that only recently has been systematically assessed (*61, 62*); consequently, and in order to reduce undersampling of interactions, unknown insects were collected only after they completed their foraging activity within the limits of the plot. An interaction was recorded only when the insect touched the reproductive organs of the flower visited for more than two seconds. In both sampling seasons, 46.7 h were spent in visitation observations and samplings (23.2 h in 2011 and 23.5 h in 2012). Time spent for handling the collected insect specimens was not included in the observation quarter. Following a convention in this type of studies, hereafter, we use the terms 'pollinator' and 'floral visitor' interchangeably for insects, as do we with 'pollination' and 'visitation' network.

On every sampling day, all open flower units of the insect-pollinate plants were counted in the observation plots. We defined as flower units (i) all inflorescences (e.g. compact spikes, heads, dense umbels), where the distance between individual flowers was so short as to allow small insects to walk on the surface of the inflorescence instead of flying for moving to the next source of reward (see *63*) or (ii) the individual flowers that either grow solitarily or in inflorescences less compact than described above. 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).

Phenonets of plants and node properties

The phenophase of a given plant species is defined as the time period between the observation days of the first and the last flowering individuals in the community (Julian day numbers; Table 4.S1). Because we have two years of observations, phenophases consist of the average first and the average last days of flowering for every plant, except for *Geranium robertianum* and *Heliotropium europaeum* that were present in the community only the second year. Accordingly, the phenophase of an insect is defined as the time period between the first and the last day it was recorded in the community irrespective whether its activity went beyond the time limits of the study. For those insects occurring only in one year, we used the original Julian day numbers (Table 4.S2).

In order to construct the phenonet for a given plant species in the community, we extracted all other taxa that were present in the community ('in flower' for plants, and 'active' for insects) during its flowering phenophase. Next, we assembled the realized interactions within the phenophase (accumulated for the two years of sampling) into 41 new networks (Table 4.S3). In this way, all node properties attributed to each focal plant correspond to the values obtained from the analysis performed for this plant's phenonet. This rationale makes use of the dynamic nature of the interaction networks, and it assigns pragmatic roles to the members of the community by taking into account the phenology

of each species and the facts that (i) not all insects are active during the flowering period of a plant, and (ii) not all plants are flowering during an insect's activity. Phenonet data aggregation inevitably assumes that species, even though not observed in one year, may be present in both years. This compromise is necessary in order to acquire the widest possible floral niches of foraging insects; besides, it sorts the phenologically overlapping, thus possibly interacting species within the flowering season.

Currently, there are numerous species-level network properties that describe node behavior. We did not intend to perform an exhaustive analysis of comparisons. Instead, we have selected three major node properties that describe the centrality and generalization of plants in the phenonets, all calculated with the R package *bipartite* v. 2.06 (*64*):

1. *Normalized degree*, i.e. the number of interacting partners of a species as a proportion of the maximum possible number of partners in the phenonet. This is the simplest index for the nodes in one network that indicates their level of generalization (*65*).
2. *Betweenness centrality* (BC). It is a direct measure of the connectivity of a node, proportional to the number of all possible paths connecting all pairs of nodes passing through the focal node. It is computed using the binary unipartite networks of the two trophic levels. High BC values indicate species that are important for the cohesiveness of the network (*65-67*).
3. *Closeness centrality* (CC). It is considered the most 'natural' measure of centrality that reflects the mean distance of a node to other nodes (*66*). It is computed using the binary unipartite networks of the two trophic levels. Higher CC values indicate plants having more pollinators shared with other plants. It thus reflects how close one plant is to the other co-flowering plants via shared pollinators (*68*).

In addition to the above, we calculated the functional role of every plant in the phenonets it participates (i.e. network hub, module hub, connector, or peripheral; cf. ref. *8*), by computing the among-module connectivity c, and the within-module connectivity z, which are the coordinates in the functional network topography. For their calculation, we used the *NetCarto* software, which implements a Simulated Annealing algorithm in order to assess the modularity of a binary bipartite network (*69*). Note that three plants that received no insect visits (*Centaurium pulchellum, Geranium robertianum,* and *Papaver argemone*) and *Heliotropium lasiocarpum*, which had no co-flowering species, were not assigned phenonet node properties.

We compared the mean value of each node property calculated in the entire static network vs. the phenonet node properties for all plants (Table 4S.4), by employing one-sample Wilcoxon signed-rank tests with the function 'wilcox.test' in the R package *MASS*. Most of the plant node properties studied are significantly different between the static network and the phenonets (viz. *normalized degree*: V=0, $p<0.0001$; *betweenness*: V=74, $p=0.002$; *closeness*: V=0, $p<0.0001$). This also applies to the functional roles of the plants in the cumulative network vs. the phenonets (Table 4.S4) tested with a Fisher's exact test for count data ($p<0.001$). Specifically, nine plants (out of the 37) exhibit different functional role, mostly a more generalist one. Thus, the phenonet approach corrects for the overestimated specialization/isolation of plants with short phenophases when evaluated in the 'static' network of the entire flowering season.

Floral traits

Floral morphology, nectar, and dimensions

For each insect-pollinated plant in the community, we assessed floral symmetry by distinguishing actinomorphic from zygomorphic flowers, and corolla depth, by distinguishing shallow (< 3 mm) from deep corollas (≥ 3 mm) (Table 4.S1). The latter assessment was based on measuring the length of the actual depth after inserting Drummond microcaps® in the flower (*70*).

All plants were scored for nectar presence/absence with field observations and by using published data (*70, 71*) (Fig. 3.1).

For flower height, i.e. the average distance of the flower unit from the ground for a given plant species, we took the distance from the ground of the highest and the lowest flower unit per individual (measured five individuals for rare taxa, to 20 individuals). Measurements were carried out in the field at the peak of each plant's flowering period using a tape measure (Table 4.S1).

To assess floral surface area, we estimated the area of the flower unit as observed from a frontal view. For actinomorphic or globose flowers and flower units (*Lagoecia cuminoides, Scandix* sp.), we measured the diameter of the circular contour and calculated the frontal area using $A_c = \pi r^2$ (r = radius). For zygomorphic flowers and dense spike-like flower units (*Lavandula stoechas*) we measured the two dimensions of the frontal view and calculated the rectangular area using $A_r = L \cdot W$ (L = length, W = width). All measurements were performed on five (for rare taxa) to 20 individuals per taxon, using a digital caliper (Table 4.S1).

Floral scent

Scent collections were carried out *in vivo* and *in situ*, except for *Blackstonia perfoliata*, which was sampled *in vivo* in the lab one hour after the plant was collected in the field and transferred in a pot. 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 pollinator's activity (9am-1pm).

We performed dynamic headspace sampling (*72*) as a method of collection, and Gas-Chromatography combined with Mass-Spectrometry for the analysis of the floral scents. The detailed description of the methods employed are part of *Chapter 3, Materials and Methods*.

We should note that when the size of the plant permitted it, green plant parts were separately sampled for tracking VOCs of vegetative origin. Nevertheless, we fundamentally aimed at trapping all the compounds emitted naturally by the inflorescence that includes green parts (bracts, calyx), which significantly contribute (especially in Lamiaceae, Apiaceae etc.) to the strong chemosensory environment of pollinators in Mediterranean shrublands (*73*).

Additionally, we estimated the mean normal boiling point (nBP), i.e. the boiling point at an atmospheric pressure of 760 mmHg, as a 'reverse indicator' of a VOC's volatility (cf. *Chapter 2, Materials and Methods*). Data on the normal boiling points of the VOCs correspond to the predicted values of the PhysChem module of the ACD/Labs Percepta Predictors, available in the ChemSpider database of the Royal Society of Chemistry (http://www.chemspider.com/).

Floral reflectance

To obtain reflectance spectra of the insect-pollinated flowers of the study community we used a portable Jaz spectrometer equipped with a Premium 600 μm reflectance probe (Ocean Optics Inc., Dunedin, FL, USA). More details on reflectance sampling, are available in *Chapter 3, Materials and Methods.*

Modeling visual systems of animals is a challenging task owing to the great variability in photoreceptor sensitivity across animal species (*74*). In the present study, we chose to apply only visual models supported by robust empirical data and realistic assumptions on the psychophysics of obligatory flower foraging insects, in order to avoid inflation of type I errors and the risk of dubious generalizations.

Because bees are the major pollinators in the Mediterranean communities in terms of efficiency and/or abundance (*28, 61, 75*), we calculated the polar loci of the plants in the hexagonal color space of Hymenoptera (*76*). The radiant (r_{hex}) is the saturation of the color, and the angle (θ_{hex}) is hue (*77*). We wish to emphasize here that the trichromatic vision of the Hymenoptera (in UV, blue, and green) is directly derived from an ancient basal visual system in insects that originates long before the emergence of flowering plants and of pollinators (*78, 79*).

Apart from the trichromatic vision, we employed a model according to a tetrachromatic visual system (sensitive in UV, blue, green, and red) that corresponds to the vision of the swallowtail butterfly *Papilio xuthus* (Papilionidae) (*80*). The genus *Papilio* is present in the study community (Table 4.S2). The polar expression of the loci in the tetrahedral color space representing saturation (r_{tet}), and the two angles of hue (φ_{tet}, θ_{tet}) (*81*) in the swallowtail vision, were calculated using function 'tcs' in the the R package *pavo* v.0.5-1 (*82*).

Finally, we calculated three spectral properties independent of any pollinator's vision, viz. *brightness*, *hue*, and *chroma* by applying the function 'summary.rspec' of the R package *pavo* v.0.5-1 (*82*). In the function's output encoding, *brightness* corresponds to variable B2, *hue* to H4, and *chroma* to S5. *Brightness* (achromatic property) is the average reflectance over all wavelengths and represents the amount of light reflected by the floral surface. *Hue* and *chroma* (chromatic properties) were calculated according to the segment classification method (*83*). *Chroma* (a.k.a. saturation) corresponds to spectral purity, and *hue* represents the primary color.

Floral apparency

In this Chapter, we use the term 'apparency' in order to describe the degree a plant has noticeable flowers within the community, and we distinguish between visual and chemical flower apparency. For the first one, we used two metrics based on (i) floral height (vertical apparency) and (ii) flower display area (horizontal apparency). The nature of the above-mentioned colorimetric and spectral variables used here, does not permit us so far to assess the chromatic apparency of the flowers of the plant species. We must underline that flower apparency is irrelevant to plant growth form (see *84*).

Vertical apparency
The flowers of a plant are apparent unless this is surrounded by plants with higher-positioned flowers (see analogy in (*85*)); therefore, we calculated flower height apparency as the difference of the median floral height of a plant from the median flower height of the co-flowering species in the community, during its flowering period. Vertical apparency for a focal plant (ΔH_f) is defined as the difference of its floral height from the median floral height of its co-flowering plants in the community:

$$\Delta H_f = H_f - \widetilde{H}$$

For the calculation of the median, only the co-flowering plants of the focal one were taken into consideration, in accordance to the phenonet concept (Table 4.S5). The values are negative in case the focal plant's flowers are lower-positioned and therefore less apparent than the co-flowering plants.

Horizontal apparency

To estimate horizontal apparency, we first weighted floral surface values for each plant by its mean floral density (flower units per m^2) measured in 2011 and 2012. In this way, we obtained the total floral area of each plant species per m^2 of flower cover. Floral surface apparency of a focal plant (ΔA_f) was calculated in accordance with height apparency (cf. above), and it represents the difference of the weighted flower area of the focal plant (A_f) and the median weighted floral area of the co-flowering plants in the community:

$$\Delta A_f = A_f - \tilde{A}$$

Again, for the calculation of the median, only the co-flowering plants of the focal one were taken into consideration, in accordance with the phenonet concept (Table 4.S5). Negative values indicate lower horizontal apparency compared with the other co-flowering plants.

Chemical apparency

Chemical apparency is defined as the difference of the emission rate (ER) of scent per m^2 occupied by a given plant (ΔER_f) 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:

$$\Delta ER_f = ER_f - \widetilde{ER}$$

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 (i.e. aliphatics, benzenoids, monoterpenes, and sesquiterpenes) based on the convention in the literature on floral volatiles (*86*) (Table 4.S5).

In order to calculate apparency for *Heliotropium lasiocarpum,* the last plant flowering alone in the community (Table 4.S1), we took into account the median values of each trait (height, surface, ER) corresponding to the entire plant community (41 plant taxa).

Phylogeny and phylogenetic signal

In order to account for phylogenetic non-independence and its statistical implications (*87*), we first calculated the phylogenetic signal of all variables relevant to floral visitation, floral morphology and floral apparency, following four approaches according to the type of the focal variable (Table 4.S6): (i) For multidimensional data we calculated dissimilarity matrices and tested them for correlation with the phylogenetic distance matrix of the community using Mantel tests in the R package *vegan* v.2.4.0 (*88*). Bray-Curtis distance was used for the weighted visitation matrices. (ii) For continuous variables we calculated Blomberg's *K** (*89*) as one of the currently most efficient metrics for detecting phylogenetic signal in continuous traits (*90*). Blomberg's *K** was computed with function 'phyloSignal' in the R package *phylosignal* v.1.1 (*91*). (iii) For floral symmetry and floral depth, we computed the *D* statistic for binary traits, which is based on the sum of the sister-clade differences of

the trait in the phylogeny (*92*), with the function 'phylo.D' in the R package *caper* v.0.5.2 (*93*). (iv) For module ID and the functional role in the network we used the algorithm 'phylo.signal.disc' for discrete traits implemented in R, developed by Enrico Rezende (pers. comm.; see (*94*) for detailed description and example).

The phylogenetic signals of variables describing floral scent, color and nectar, are analyzed in *Chapter 3,* Table 3.S9. For plant phylogeny and the calculation of the pairwise phylogenetic distance matrix, see *Chapter 3, Materials and Methods.* For pollinators, we constructed an approximated phylogeny and a rectangular cladogram (with no branch lengths) using the online tool Open Tree of Life (*95*) (Fig 4.S1).

Statistics

We adopted a multi-angle approach in order to explore as thoroughly as possible the role of floral phenotype into shaping visitation patterns in the community.

First, focusing on the quantitative matrix of p–p interactions, we employed the same model-based method for compositional data used in *Chapter 3,* i.e. Multivariate Generalized Linear Models (MGLMs), which fit a separate generalized linear model to each insect of the network, using a common n-dimensional set of explanatory variables and a resampling-based hypothesis testing (*96, 97*). This approach allows us to examine the behavior of each insect species in the community. We thus built a series of single-predictor MGLMs with a negative binomial family, using the function 'manyglm' in the R package *mvabund* (*97*). 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 (*96*) and in our case yielded the most conservative results. Univariate tests were then performed in order to determine which response variables (insects) showed significant effects against the independent variables (phenotypic traits). The multidimensional response variable was either the total weighted p–p network or one of its subsets that included the insects belonging to one of the five major groups: Coleoptera, Diptera, Hymenoptera–Bees, Hymenoptera–Wasps, and Lepidoptera. Moreover, we retrieved the interaction networks for the major anthophilous families in the community, which also showed the most abundant interactions, in order to detect possible relationships. These families are Apidae, Halictidae, and Megachilidae in Hymenoptera; Syrphidae and Bombyliidae in Diptera. We should note that predictors regarding trichromatic and tetrachromatic color included only the interaction terms of the corresponding saturation and hue variables (i.e. $r_{hex}{:}\theta_{hex}$, and $r_{tet}{:}\varphi_{tet}{:}\theta_{tet}$).

Second, focusing on the plants of the community, we examined which phenotypic traits relate to (i) rates of visitation by the different pollinator groups, and to (ii) plant node properties (centrality and specialization), by correcting for phylogenetic similarity. For this, we applied phylogenetically informed generalized least squares models (*98*) with λ branch length transformations, using the 'pgls' function in the R package *caper* v.0.5.2 (*93*). Proportional response variables were arcsine-transformed before fitting the models. We first applied single predictor models, selected the predictors showing significant effects and included them simultaneously in a final model. For all models, we compared the AIC values with those of the null model (y~1) in order to avoid inflation of type I errors.

We computed the modules in the total network using *NetCarto* software (*69*). The total network was found significantly modular (modularity $M = 0.47$). In order to find out the significant associations of

pollinator groups with the p–p network modules, we applied a Pearson χ^2 conditional independence test (Fig. 4.S2) with the function 'mosaic' in the R package *vcd* v.1.4-1 (*99, 100*). This process revealed the statistically significant positive and negative associations of the insect groups with the modules. High proportional participation in one module in respect to the others (block width in Fig. 4.S2) combined with statistical significance, allowed us to identify the positive associations for Diptera (Module #5), Coleoptera (Module #8), Wasps (Modules #1 and #4), and Lepidoptera (Module #7). Bees are almost uniformly distributed among the modules, suggesting no clear relationship with any module, so we excluded them from the spectral similarity analysis.

Finally, to test if any chemical, colorimetric or spectral floral properties explain the distribution of plants among the modules in the total network and among the functional roles in the phenonets (i.e. network hub, module hub, connector, peripheral) (*8*), we applied phylogenetically-informed ANOVA (*101*) of the each colorimetric or spectral property against the trait 'Module ID' of 'functional role' by using function 'aov.phylo' in the R package *geiger* v.2.0.6 (*102*). Proportional variables were arcsine-transformed, whereas chemical apparency variables were $\log_e$-transformed. For categorical predictors (i.e. nectar presence, floral symmetry, and corolla depth) we applied Pearson χ^2 conditional independence tests (see above).

Unless stated otherwise, statistics were performed in R v. 3.3.0 (*103*).

Results and Discussion

'Improbable as it may appear, they [bees] *seem, at least sometimes, to recognize plants even from a distance by their general aspect, in the same manner as we should do. On three occasions I observed bumble-bees flying in a perfectly straight line from a* <u>*tall larkspur*</u> [Delphinium] *which was in full flower to another plant of the same species* <u>*at the distance of fifteen yards*</u> *which had not as yet a single flower open, and on which the buds showed* <u>*only a faint tinge of blue*</u>. *Here neither odour nor the memory of former visits could have come into play, and the tinge of blue was so faint that it could hardly have served as a guide'*.

Charles Darwin, 1876 (*104*)

*'A mint (*Salvia leucophylla*) and a sage-brush (*Artemisia californica*) dominate the community where it* [allelopathy] *was studied by Muller. Both are aromatic, and on a still day the air is redolent with the fragrance of terpenes from these plants. The soft chapparal invades grasslands in this area* [South California].

Robert H. Whittaker, 1970 (*105*)

The total p–p network of the study community compiled from the two consecutive spring samplings consists of 38 plants and 168 insects, and includes 403 links (plant–insect pairs) and 7,934 interaction events (visits). We found no insects visiting *Geranium robertianum, Papaver argemone,* and *Centaurium pulchellum*. Pollinators (Table 4.S2, Fig 4.S1) belong to 44 families; bees are the most species-rich group (39.3%), followed by Diptera (22%), Coleoptera (15.5%), wasps (11.3%), Lepidoptera (10.1%), and Hemiptera (1.8%). For a comparison with other Mediterranean sclerophyllous communities see Petanidou and Ellis (*28*). Plant species turnover between the two years of sampling was very low (4.9%), whereas for insects, species turnover is much higher: only 60 species (out of the 168) are present in both years, resulting in 35.7% species persistence (64.3% turnover) between the two years (see *23* for a comparison).
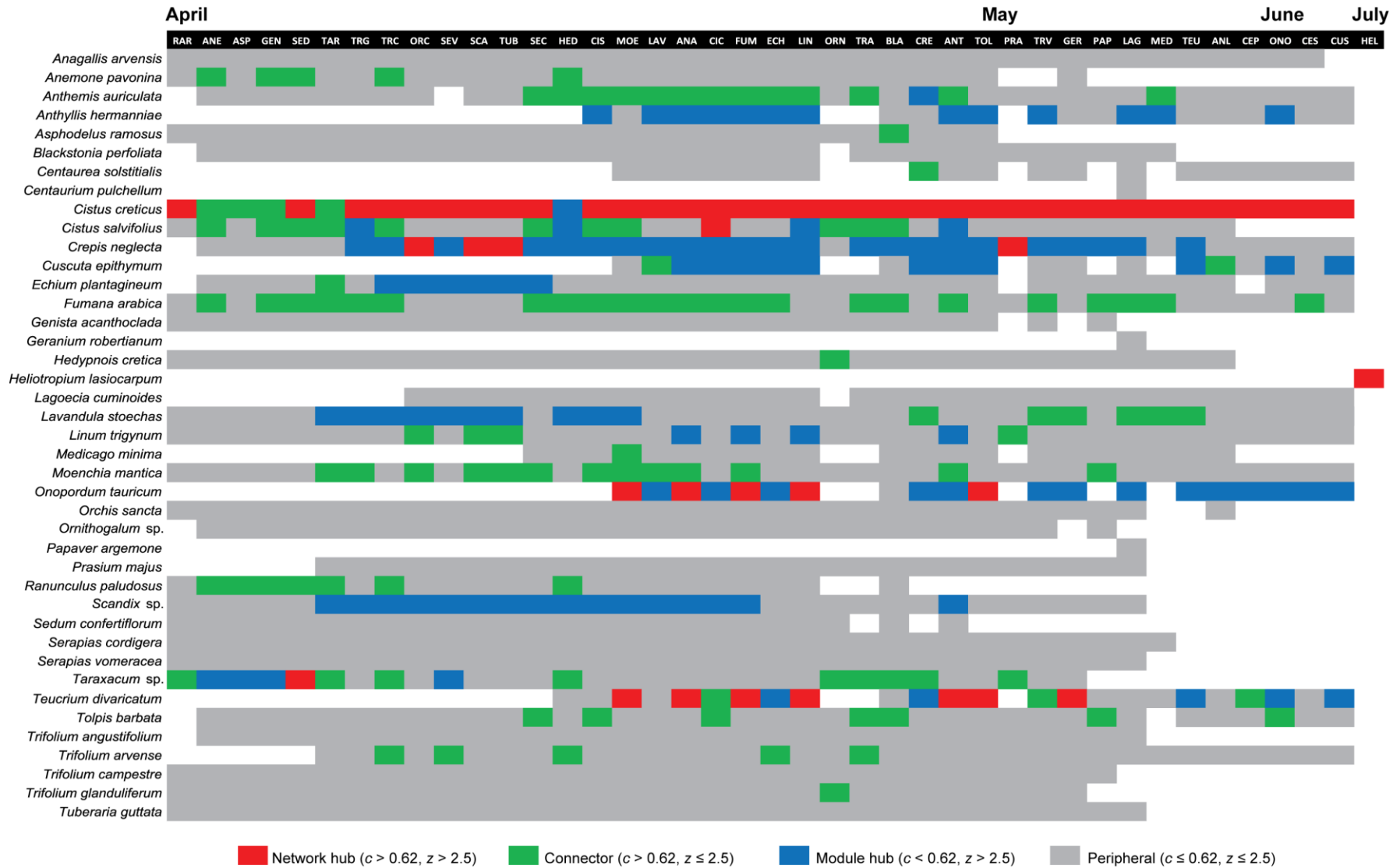
Fig. 4.1. The functional role of each plant in the phenonets of the other plants of the community (see (*8*) and Materials and Methods). Phenonets are shown in the first row (shaded in black) and are arranged temporally, according to (i) the first day of flowering, and (ii) the duration of the flowering period of the focal plant, so that plants with earlier start and shorter duration are order first, from left to right. Months correspond to the start of flowering only.

Phenonets (Table 4.S3) allow to observe the network in multiple time slots, which are meaningful for each one of the species in the community. Figure 4.1 shows the fluctuation of the functional roles of plants in the interaction networks operating during each species' flowering period. Functional roles are far from static: species considered peripheral in the cumulative network (i.e. pure specialists), may have generalist roles in the phenonets of other species (e.g. *Anemone pavonina, Ranunculus paludosus*). Moreover, species may become even network hubs depending on the composition of the community at a particular time period. For example, apart from *Cistus creticus,* which is the major network hub (and the only one in the community according to the analysis of the static network, see Table 4.S4), it appears that species *Cistus salviifolius, Crepis neglecta*, *Onopordum tauricum*, and *Taraxacum* sp. can also sustain the network in other plants' phenonets. We find that plant functional roles in their phenonets are associated only with visual cues, viz. tetrachromatic hue (phylogenetic ANOVA, $F_{3,33}=5.5$**), floral surface ($F_{3,33}=4.0$*), and floral surface apparency ($F_{3,33}=8.8$***). Specifically, the chief network hub (*C. creticus*) occupies the largest floral area in the community (Fig. 4.2).
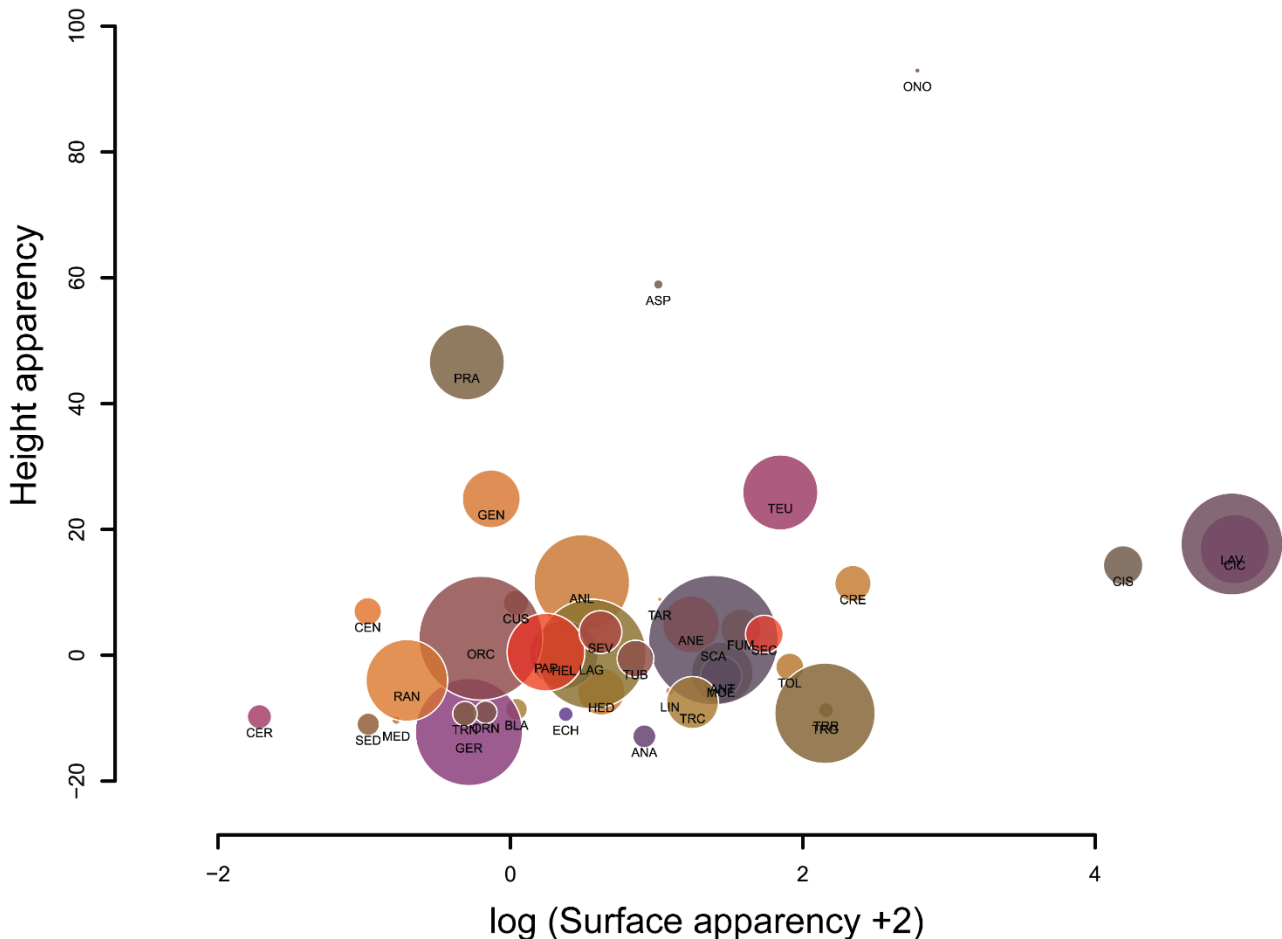
Fig. 4.2. Floral apparency in the plants of the community. Circle diameter is proportional to the apparency of total volatile emissions. Circle colors represent floral color encoded according to the RGB model.

Plant centrality in the network is associated with flowers' sensory stimuli (Table 4.1; Fig. 4.3). To our knowledge, this is the first study that shows the direct connection of the floral sensory landscape and the topology of pollination interactions at a community level. Phylogenetic GLS (PGLS) models show that normalized degree, and by extension the pollinator-niche of the plants in the community, is associated with visual cues (with floral color and physical apparency) and with the presence of nectar. Betweenness centrality (BC) relates to sesquiterpene apparency and physical apparency, whereas closeness centrality (CC) relates to floral scent composition and to floral spectral properties. BC represents the degree to which a node (here a plant species) connects parts of the network that could be otherwise isolated (*66*). Thus, we find that floral color and physical apparency (i.e. the degree to which the flowers of a species visually "stand out from the crowd") predict its importance as an intermediate in the spread of information across the network. In other words, the cohesiveness (or the fragmented nature) of the pollination network relates to visual floral stimuli. On the other hand, CC is correlated mainly with floral scent properties (Table 4.1; Fig. 4.3). The value of CC increases with the number of pollinators shared with other plants, implying that it is a measure of niche overlap (*65, 68*). Thus, in our community, niche similarity of plants, regarding pollinators, associates with the composition of floral scent (interaction term of VOC class proportions in the total emissions: Table 4.1), and with floral spectral properties. Given that BC and CC indicate the "keystone" species in the community (*65*), we may suggest that floral "sensory diversity" is an important component of the functional diversity in the community.

Table 4.1. Floral traits that are correlated with at least one of the four node properties of plants, calculated in the phenonets. The results of 14 single-predictor phylogenetically corrected GLS models are shown. Only the significant relationships are shown ($p \leq 0.050$), with the exception of trichromatic color. Groups of independent variables (viz. color, scent, dimensions, nectar) are separated by alternately shaded bands. Blue font denotes positive relationships (slope estimate > 0).

	Normalized degree		Betweenness centrality		Closeness centrality	
	F	*p*-value	*F*	*p*-value	*F*	*p*-value
Trichromatic color (r_{hex}:θ_{hex})	3.16	0.084				
Tetrachromatic color (r_{tet}:φ_{tet}:θ_{tet})	6.46	**0.016**				
Brightness:Hue:Chroma					4.27	**0.046**
Sesquiterpene apparency			7.72	**0.009**		
Interaction term of VOC class proportions					8.12	**0.007**
Floral height	18.82	**0.000**				
Floral surface	23.69	**0.000**				
Height:Surface	11.17	**0.002**				
Height apparency	17.49	**0.000**				
Surface apparency	9.49	**0.004**	11.27	**0.002**		
Height:Surface apparencies	15.25	**0.000**	11.06	**0.002**		
Nectar	4.31	**0.045**				
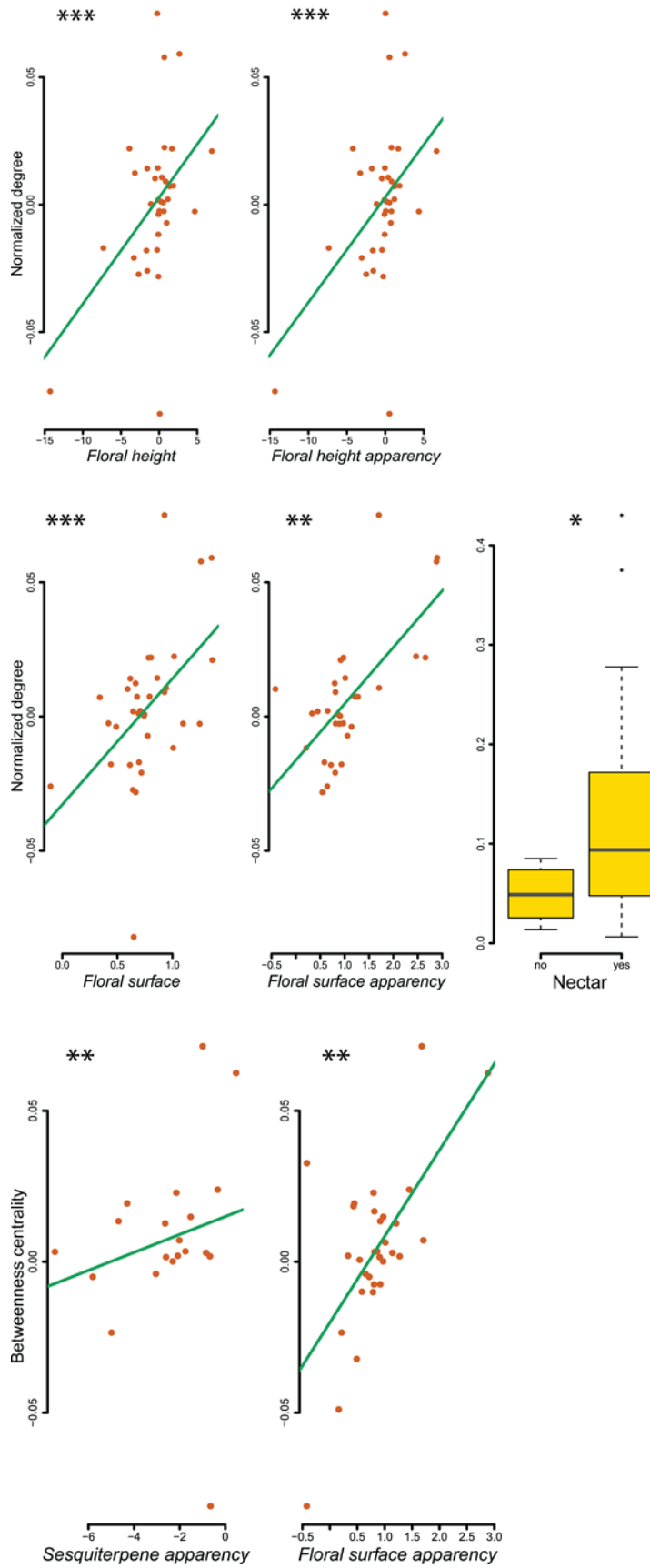
Fig. 4.3. The significant relationships between the different elements of the floral phenotype, normalized degree and betweenness centrality in the study community. Scatter plots show phylogenetically independent contrasts corresponding to the PGLS models in Table 4.1.

It has been a long-standing notion that visual cues are important for long-distance attraction of pollinators (*104, 106-108*). Visual cues, especially in an open, well lit, low vegetation like phrygana, are constant as long as flowers have not senesced. In *Chapter 3,* we show that nectar presence is correlated with floral colorimetric properties, a fact that could be attributed precisely to this constancy. Given the above, we can hypothesize that there are plants with high visual attractiveness that "manage" the incoming links between pollinators and the other co-flowering plants, and perhaps they are important for the preferential attachment of new nodes in p–p networks causing the "rich-get-richer" phenomenon described above (*21*). Pollinating insects have the visual acuity needed for flying close to vegetation and for foraging, as well as for identifying small targets (*109*). Honeybees, in particular, use variable odometric cues and salient landmarks and they are able to discriminate among complex natural scenes (*110*). Their long-distance vision uses achromatic signals (green contrasts), whereas they cannot discriminate the colors of an object at a distance greater than 3.8 times its diameter (*111*). So, for instance, a dense patch of *Cistus creticus* (ø 2 m) can be perceived in color by a honeybee at a maximal distance of ca. 7.5 m and by a bumblebee at ca. 42.5 m (see *112*). These numbers suggest that floral patches formed by visually apparent plants, can become attraction units at a distance (*113*).

Floral scent, on the other hand, may exhibit a dynamic pattern of emissions due to its multi-functionality and/or because of energy-saving strategies of plants (*114-119*); in addition, it is directly subjected to a variety of environmental factors such as ambient temperature and wind (*120, 121*). Floral odor plumes (*122*) do not show smooth VOC concentration gradients that could direct insects to the precise source of scent, because of turbulence forces that dilute the initial odor and blend it with the (differently scented) air (*123, 124*). So, in exposed habitats such as the low Mediterranean scrublands, it is not safe to assume that specific attractive mixtures of compounds would travel intact through long distances and reach the sensory organs of pollinators, indicating accurately the emitting flowers. To the contrary, floral scent has been clearly regarded a long-distance attractant in tropical understory communities, where light is are poor, weather conditions are rather stable, and floral color becomes hard to discriminate unless the pollinator approaches at a very close distance (e.g. *125*).

The story becomes more interesting when aromatic plants come into play. It is well-known that phryganic communities offer a strong diurnal chemosensory environment to pollinators, because of the abundance of aromatic plants, which emit large amounts of VOCs from glandular trichomes on the surface of their green parts (*73, 126, 127*). The role of these terpenoid vegetative emissions in interspecific interactions has remained largely unexplored with the exception of the phenomenon of allelopathy (*105, 128*). In our community, *Lavandula stoechas, Teucrium divaricatum,* and *Cistus creticus* emit in bulk vegetative terpenes and represent very abundant plants with high floral densities and high apparency, both chemical and visual (Fig. 4.2; Table 4S.5). Moreover, these plants are central in the p–p network (Fig 4.1, Tables 4.S4, 4.S7). For example, *L. stoechas* holds a relationship with honeybees that is the strongest than any other p–p pair recorded in the community (2,329 visits out of the 2,451 received by the plant). Here we find that sesquiterpenes positively correlate with BC, which means that plants with higher sesquiterpene emissions in their blends maintain the cohesiveness of the network. All the above suggest an intriguing scenario, which may in part explain the plethora of terpenoids in phrygana: Given the high exposure of scrublands to weather conditions, especially in the islands (*129, 130*), aromatic plants may collectively create a relatively compact, heavily-scented environment sufficiently resistant to dilution by wind forces, acting indeed as a unique long-distance attractant. We already know that isoprenoid emissions from green parts may exert a photoprotective

Table 4.2. The significant effects of floral traits on the quantitative distribution of links in the pollination network of the study community. Effects are tested in the total plant–pollinator network and its five subsets containing the interactions of each one of the major insect orders. The results of 55 separate single-predictor multivariate generalized linear models (family: negative binomial) are shown. Significance was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling. Groups of independent variables (viz. color, scent, dimensions, morphology, and phenology) are separated by alternately shaded bands.

Floral traits	Total network		Coleoptera		Diptera		Bees		Wasps		Lepidoptera	
	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value
Trichromatic color (r_{hex}:θ_{hex})	483.1	**0.004**			80.1	**0.039**	149.0	**0.017**	60.1	**0.020**	52.0	**0.027**
Tetrachromatic color (r_{tet}:φ_{tet}:θ_{tet})	356.6	**0.028**			79.3	**0.029**	150.8	**0.005**			44.8	**0.041**
Hue:Brightness:Chroma												
% Sesquiterpenes	351.2	**0.033**									52.7	**0.019**
Benzenoids apparency					53.8	**0.033**						
Sesquiterpenes apparency	301.2	**0.035**					123.0	**0.026**			41.6	**0.028**
Total emissions apparency					65.9	**0.043**						
Floral height	403.9	**0.020**									65.4	**0.007**
Floral surface	450.9	**0.012**							51.3	**0.032**	72.6	**0.001**
Height:Surface	332.8	**0.020**							38.1	**0.044**	60.1	**0.015**
Height apparency	396.5	**0.018**	80.2	**0.028**			178.8	**0.004**			64.6	**0.006**
Surface apparency	456.9	**0.002**	127.0	**0.002**	83.2	**0.033**	136.2	**0.026**	66.3	**0.005**	43.0	**0.039**
Height:Surface apparencies	519.5	**0.001**	125.7	**0.008**	80.4	**0.029**	192.8	**0.002**	60.1	**0.010**	59.8	**0.008**
Floral symmetry			69.2	**0.042**								
Corolla depth							124.1	**0.016**				
First day of flowering	334.6	**0.041**	75.6	**0.028**	74.4	**0.040**					39.0	**0.046**
Flowering duration	413.8	**0.009**	109.7	**0.011**	95.2	**0.022**	128.0	**0.045**				
Phenology (Start:Duration of flowering)	450.8	**0.006**	107.9	**0.009**	100.4	**0.013**	151.6	**0.019**				

antioxidant-like activity (*131*). By considering terpenoid emissions as an extra adaptation to the abiotic environment, this hypothesis implies a novel type of facilitative effect in pollination (*132*), and remains to be tested. Moreover, sesquiterpenes may be important for specific effective, thus desirable, pollinators for the plants in the community, with indications pointing at bees: we have already shown (*Chapter* 3) that sesquiterpene emissions are tuned with floral color as perceived by the trichromatic visual system of Hymenoptera, thus a special relationship is anticipated. Interestingly, sesquiterpenes are the only VOC class exhibiting a seasonal pattern: emissions are negatively correlated with the start date of flowering in plants (PGLS, $F_{1,37}=5.52^*$), i.e. insect-pollinated plants flowering early in spring emit bigger amounts of sesquiterpenes in their blends compared with late-flowering ones. According to Filella *et al.* (*133*), early terpenoid emissions in a Mediterranean community may be related to high floral competition because of the scarcity of bees during that time.

At this point, we should highlight that the most frequent insect group (viz. Coleoptera, Diptera, bees, wasps, Lepidoptera) as to the total number of visits paid to each plant species is a trait exhibiting phylogenetic signal (*p*=0.008), i.e. phylogenetically-relative plant species are mainly visited by the same order of pollinators (Fig. 4.S3, Table 4.S7). This result alone challenges the assumed stochastic linkage rules in the network and the merely opportunistic nature of interactions (see above), and implies that coevolutionary forces may, indeed, operate.

The MGLM results reveal that the substantial structure of the pollination network in the study community relates to the floral sensory landscape (color, scent), to the vertical and horizontal physical floral apparency (height, surface), and to flowering phenology of the insect-pollinated plants (Tables 4.2, 4.3). In total, 95 insects (out of the 168) show significant effects against at least one floral trait examined here (Tables 4.S8-4.S13; Figs. 4.S4-S34). Specifically, both visual systems examined here (viz. trichromatic and tetrachromatic) are important for the quantitative distribution of links in the network. Moreover, among the chemical properties of the scent, sesquiterpenes seem to be the most important VOC class for flower visitation at the community level. In *Chapter 3*, we show their strong association to floral color, so their functional importance has been expected. In addition, phenology and physical apparency (vertical and horizontal) are very important for the distribution of insect visits among the plants (Tables 4.2 -4.3). The first confirms the paramount importance of phenological coupling of species for the structure of networks. The second reflects opportunistic trends of species, probably related (i) to the great need for time- and effort-effective foraging strategies (e.g. honeybees), or (ii) to limited abilities for flight and long-distance travel (e.g. beetles).

Indeed, the quantitative distribution of visits of the different bee families among the plants (Tables 4.3, 4.S11) relates with floral color and physical apparency in Apidae, Halictidae, and Megachilidae. Phenology is important for Apidae, and corolla depth for Megachilidae and Apidae. The strongest chemical associations are found for Apidae (monoterpenes and sesquiterpenes). Specifically for *Apis mellifera,* we find that the distribution of its visits correlates with flowering duration, corolla depth, and sesquiterpene emissions (Figs. 4.S5, 4.S9, 4.S11, 4.S21, 4.S23, and 4.S25; Tables 4.S8-S11). Accordingly, PGLS models show that in the plants of the study community, visitation rate by Megachilidae is positively associated with benzenoids, whereas visitation rate by Apidae correlates positively with aliphatics and sesquiterpenes. These results complete the jigsaw: Plants with higher floral color saturation as perceived by bees emit higher relative amounts of sesquiterpenes (*Chapter 3*); flowers with higher

Table 4.3. The significant effects of floral traits on the quantitative distribution of links in the interaction sub-networks including each one of the most species-rich anthophilous families in the study community. The results of 38 separate single predictor multivariate generalized linear models (family: negative binomial) are shown. Significance was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling. Groups of independent variables (viz. color, scent, dimensions, morphology, and phenology) are separated by alternately shaded bands.

	Apidae		Halictidae		Megachilidae		Bombyliidae		Syrphidae	
	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value
Trichromatic color (r_{hex}:θ_{hex})			33.7	**0.047**	58.4	**0.022**			36.1	**0.020**
Tetrachromatic color (r_{tet}:φ_{tet}:θ_{tet})	46.8	**0.020**			52.1	**0.028**	25.3	**0.030**		
% Sesquiterpenes					47.2	**0.039**	26.7	**0.030**		
Monoterpenes apparency	37.7	**0.027**								
Sesquiterpenes apparency	65.8	**0.004**					29.6	**0.006**		
Interaction term of VOC class apparencies	32.0	**0.047**								
Total emissions apparency	39.4	**0.041**								
Floral height	59.9	**0.007**	40.2	**0.014**	79.8	**0.004**				
Floral surface			38.6	**0.028**	61.4	**0.019**				
Height:Surface			32.1	**0.032**	61.8	**0.011**				
Height apparency	59.7	**0.012**	39.5	**0.018**	78.0	**0.004**				
Surface apparency	66.1	**0.006**	34.2	**0.042**					35.6	**0.018**
Height:Surface apparencies	85.7	**0.001**	37.9	**0.019**	66.0	**0.003**				
Corolla depth	40.0	**0.037**			49.8	**0.009**				
Flowering duration	58.3	**0.007**					31.7	**0.017**	33.1	**0.033**
Phenology (Start:Duration of flowering)	68.6	**0.007**					38.3	**0.006**	34.1	**0.026**

color saturation are more attractive to bees (*134*); flowers with higher amounts of sesquiterpenes receive more visits by bees. Thus, the fundamental relationship of bees and the plants in Mediterranean communities is once again corroborated in terms of floral phenotype.

In general, bee-pollinated plants show variable volatile profiles with no particular chemical patterns, apart from a general abundance of terpenoids (*135*), implying a chemical generalization of bee–flower interactions. Yet, there are exceptions: (i) the fragrance-collecting male neotropical euglossine bees (Apidae) (*136, 137*), and (ii) male bees involved in sexually deceptive pollination systems, such as the interactions between male *Andrena* (Andrenidae) or *Colletes* (Colletidae) bees with the *Ophrys* orchids in the Mediterranean (*138, 139*). In the first case, benzenoids and monoterpenes are usually preferred by males for enfleurage (*135*), whereas in the second, flowers emit blends of aliphatic compounds mimicking virgin female sex pheromones (*139*). Here we find that floral blends with low volatility (high normal boiling point) are positively associated with visits by mining bees (*Andrena* spp.). Behavioral experiments have shown that a variety of VOCs from all classes can elicit positive behavioral responses to bees (*140, 141*), whereas aliphatics and terpenoids can act as behavior-regulating pheromones (*139, 142, 143*); moreover, bees can learn odors faster than colors and associate them with rewards ((*144*) and references therein). A recent study by Schiestl (*145*) showed that there is an overlap in floral scent compounds and volatiles emitted by pollinating insects, so perhaps insect visitation may be affected by similarity patterns to a greater extent than previously thought. Nevertheless, we should never overlook the facts that VOC functionality is context-dependent and may vary according to the receiver and the environmental conditions (*146*); for example, the same attractive compound can be part of a collectively repellent blend and vice versa.

Additionally, we find that the distribution of visits by the different bee families associates with both trichromatic and tetrachromatic floral color (Table 4.3). For the plants in the community, PGLS models indicate that floral colorimetric properties do not predict visitation rates by bees (Table 4.4). Eusocial bees are known to have innate preferences for different color hues (*147*) and for high color saturation (*134*); bumblebees, for example, show a geographically invariant innate preference for violet/blue flowers (*34*). However, apart from innate biases, honeybees can easily learn to associate different hues with nectar (*147*) as well as with warmth (*148*), displaying an *'enormous richness of experience-dependent behavior'* (*149*). They are also known to use achromatic signals for setting landmarks (*110*). The degree of floral constancy of bees is probably mainly a function of their short-term (working) memory (*150*), and of the apparency (or salience) of the floral stimuli (*151, 152*). Regarding other visual stimuli, bumblebees are known to prefer bilaterally symmetrical flowers (*153*), a trend implied for Apidae and Megachilidae in the study community as well (Table 4.4; Fig. 4.S35). Finally, plants with deep corollae show higher visitation rates by Apidae and Megachilidae, the typically long-tongued bee families (Table 4.4, Fig. 4.S36).

We should emphasize that in spite of the great amount of information on honeybees and bumblebees, we know very little about the preferences and psychophysical responses of solitary bees, which are the most species-rich group of pollinators in many parts of the world (*29, 154*), as well as in Greece (*62, 71*), and in the study community (Tables 4.S2, 4.S7). Moreover, they are the most temporally constant visitors. Phylogenetically corrected ANOVA showed that the modules of the network are not related to any floral trait, apart from the start date of flowering ($F_{8,28}=4.81**$), a trend showed in another Mediterranean community as well (*155*). Bees represent the only group of pollinators that are almost

Table 4.4. Floral traits that are correlated with visitation by the major groups of pollinators in the community. Results of 32 single-predictor phylogenetically corrected GLS models are shown. Only the significant relationships are shown ($p\leq0.050$). Groups of independent variables (viz. color, scent, dimensions, morphology, and phenology) are separated by alternately shaded bands. Blue font denotes positive relationships (slope estimate > 0), red font denotes negative relationships (slope estimate < 0). Visitation by wasps is not correlated with any floral trait, thus it is not included here.

Trait	BEES												DIPTERA						COLEOPTERA		LEPIDOPTERA	
	% Bees		% Andrenidae		% Apidae		% Colletidae		% Halictidae		% Megachilidae		% Diptera		% Bombyliidae		% Syrphidae		% Oedemeridae		% Lepidoptera	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
φ_{tet} Tetrachromatic hue (φ_{tet}:θ_{tet})													4.71	0.036			5.24	0.028				
Brightness													7.48	0.009								
Hue													15.74	0.000	4.99	0.031	6.17	0.029				
Hue:Brightness:Chroma											4.38	0.043										
% Aliphatics													6.47	0.015								
% Benzenoids											5.67	0.022										
% Monoterpenes															9.87	0.003			5.18	0.028		
Interaction term of VOC proportions					5.41	0.026																
Alip apparency					6.51	0.015																
Benz apparency													6.83	0.013								
Sesq apparency					5.07	0.030																
Mean nBP			11.40	0.002																		
Floral height	4.86	0.033							7.61	0.009												
Floral surface															4.58	0.040						
Height:Surface									4.40	0.043												
Height apparency	5.26	0.027							6.71	0.013												
Floral symmetry	24.44	0.000			10.00	0.003					7.55	0.009										
Corolla depth	9.60	0.004									17.41	0.000					5.03	0.031				
First day of flowering							5.63	0.023													4.70	0.036
Flowering duration																			4.10	0.050		
Phenology (start:duration)																			4.92	0.032		

uniformly distributed among the modules (Fig. 4.S2). It has been shown that naïve pollen-seeking solitary bees in Colletidae can easily identify and pick their mother's feeding plants because while still in the larval state, they experienced olfactory conditioning from the odors of the natal provision mass (*156*). Finally, some degree of (color) constancy for solitary bees has been suggested, yet knowledge is very limited (*157, 158*).

Wasps, the closest ancestors of bees, are generally considered non-reliable pollinators, mainly connected with dull-colored flowers (*5, 135*) and, since recently, with florally emitted green-leaf volatiles and specific alarm pheromones otherwise involved in tritrophic interactions (*159, 160*). Here, MGLMs showed that visit distribution of wasps relates to trichromatic floral color and to physical apparency (Tables 4.2, 4.S8, 4.S12; Figs. 4.S26-S27). In contrast, PGLS models show that wasp visitation to the plants of the community is not predicted by any of the examined floral traits, implying a generalist, perhaps opportunistic behavior. However, visitation rate by wasps shows a strong phylogenetic signal (Table 4S.6). We observed especially strong relationships of wasps with *Cuscuta epithymum* (Convolvulaceae) and *Sedum confertiflorum* (Crassulaceae) (Table 4.S7); the latter was exclusively visited in both years by cuckoo wasps (Chrysididae).

The distribution of visits by Diptera is associated with floral sensory stimuli in various ways (Tables 4.3, 4.S8, 4.S10; Figs. 4.S17-S20). Interestingly, there is a significant relationship with benzenoids, which is most probably due to *Scandix* sp. (Apiaceae) which emits huge amounts of such compounds (e.g. estragole, anisaldehyde) and attracts numerous flies (Table 4.S7). We found no significant associations of Diptera and benzenoid compounds in the literature, however there is evidence that Apiaceae plants with similar volatile emissions, such as *Foeniculum* sp. (fennel) and *Scandix australis* are largely visited by flies (*71, 161, 162*). Whether the actual attractants to flies are, indeed, benzenoids or the umbel-shaped flowers constitute simply a convenient floral unit for the flies to land and feed, remains to be tested. PGLS models show that high aliphatic emissions in plants are negatively related with visitation by flies in general (Table 4.5). Floral color and corolla depth are two major predictor traits for hoverfly (Syrphidae) visitation to the plants of the study community (Table 4.5; Fig. 4.S36). On the other hand, the distribution of visits of bee-flies (Bombyliidae) is related not only to color (hue), but also to sesquiterpene and monoterpene emissions (Tables 4.4; 4.5).

Even though the pollination syndrome approach inferred that *myophily* (*5*) consists of no strict floral phenotypic patterns, inter-signal associations are known to relate to fly attraction to rewards (*163*) (Kugler 1956 in ref. *164*). Fly responses to color are highly diverse (*164*), and knowledge on their visual systems is very limited: the only accepted color space in flies is that of *Lucilia* (Calliphoridae), which has a tetrachromatic vision (*165, 166*) but is only an occasional floral visitor (*108, 167*). Anthophilous flies like *Eristalis tenax* (Syrphidae) and *Bombylius fuliginosus* (Bombyliidae) have been shown to use color vision, although large part of the information is retrieved from studies conducted in the early- to mid-20th century (Knoll 1921 and Ilse 1949 in ref. *168*). Empirically, we know that syrphids, which exhibit learning abilities (*164, 169*), innately prefer yellow flowers (*164*), while bee-flies prefer bluish flowers (*170* and refs. therein), although for the latter there are no spectral data. Typically fly-pollinated plants are rare, and (excluding sapromyophily) show no specific volatile emission patterns (*135*).

The quantitative distribution of visits by butterflies is associated with floral color, sesquiterpenes, physical apparency, and phenology (Table 4.4, 4.S8, 4.S13; Figs. 4.S28-S34). Sesquiterpenes have

been expected to relate somehow with butterfly behavior (cf. *Chapter* 3 where shown that sesquiterpene proportions in the total emissions are associated with the color saturation of the tetrachromatic visual system of swallowtail butterflies *Papilio* spp.). However, only plant phenology can predict visitation rates by butterflies in the plants of the community (Tables 4.4). Butterflies are not among the major pollinating insects in Mediterranean scrublands (*28, 171*) and here they emerge mostly towards the end of the flowering season. Factors limiting the activity of these insects in phrygana are well discussed by Petanidou and Ellis (*28*). On the other hand, we know that foraging in butterflies can associate with both visual and olfactory floral stimuli (*172, 173*), and that adult butterflies have well developed, although highly variable and largely unexplored visual systems (*74, 80*). When tested in field conditions, butterflies show various preferences in floral traits (*173*); high visitation by temperate butterfly species has been positively connected in plants with benzenoid, aliphatic and monoterpene emissions (*172*), compound classes that also include important pheromones (*145, 174*).

Beetles' behavior appears least associated with the subtle sensorial floral signals. However, the proportion of beetles in the total visits of the plants in the community exhibits phylogenetic signal (Fig. 4.S37; Table 4.S6), probably implying a trend beyond pure opportunism. Beetles are considered the most primitive pollinating insects, which conveyed the transition from phytophagy to pollination (*5, 175, 176*). This primitiveness is reflected upon their behavior and their morphology. They still use flowers largely as rendezvous spots (Fig. 4.4) like the first pollinators are believed to have done (*177*), they are mediocre fliers, and their mouthparts are primarily adapted to chew (*5, 176*). The so called 'beetle syndrome' (aka *cantharophily*) is one of the most rarely predicted globally (*25*). Beetles in temperate regions of the world have mainly been associated with open shallow floral units with easily accessible rewards (*5, 176*). Moreover, associations with floral scents are highly variable and they mainly exist in tropical regions (*135*). Here, we only find a negative correlation between visitation rates by the fully anthophilous *Oedemera* beetles (Oedemeridae) and monoterpene floral emissions (Table 4.4). The only strong phenotypic association reported in literature is described in Eastern Mediterranean, where the hairy anthophilous beetles of the genus *Pygopleurus* (Glaphyridae) show preference for the 'painted bowl' flowers (e.g. *Ranunculus, Papaver, Anemone, Adonis*) (Fig. 4.4) (*178, 179*). This relationship has recently been supported by the finding of red photoreceptors in their visual systems (*180*). Here, only two beetles are significantly associated with actinomorphic flowers (*Anomala* sp. and *Epicometis hirta*), although the percentage of Coleoptera visits is generally higher in actinomorphic flowers, although not statistically supported (Tables 4.S7, 4.S1). So, we find some evidence for actinomorphic preferences in the beetles of the study community, although it cannot be further associated with more phenotypic traits regarding color or scent.

In this study, the presence of nectar implies higher number of pollinator species for the plants (via normalized degree), however is not associated neither with their centrality nor with visitation rates by different groups of pollinators. On one hand, this can be attributed to the binary type of the variable; if standing crop yields or sugar concentrations were available for the plants, perhaps patterns would emerge (as e.g. *54, 71*). Alternatively, this may be due to the fact that visitors, on average, indeed seek nectar and pollen at a similar rate. Besides, in Mediterranean scrublands, pollen is the main floral reward offered to pollinators as nectar production is limited compared with other habitat types (*71, 181, 182*).

Fig. 4.4. Beetles on the flowers of the study community. 'Mess and soil' pollination *sensu* Faegri and van der Pijl (*5*) is evident. Flowers are extensively used as mating sites. (A) *Dasytes* sp. (Melyridae) on *Cistus creticus.* (B) *Clytra atraphaxidis* (Chrysomelidae) on *Crepis neglecta.* (C) *Eulasia nitidicollis* on *Cistus salviifolius* (D) *Pygopleurus* sp. (Glaphyridae) on *Anemone coronaria.* (E) *Epicometis hirta* (Scarabaeidae) on *Asphodelus ramosus.* (F) *Oxythyrea funesta* (Scarabaeidae) on *Onopordum tauricum.* (G) *Oedemera* sp. (Oedemeridae) on *Tolpis barbata.* (H) *Trichodes alvearius* (Cleridae) on *C. creticus.* (I) *Chrysolina americana* (Chrysomelidae) on *Lavandula stoechas.* Photos: Aphrodite Kantsa.

It is certainly extremely challenging to disentangle the sophisticated interplay of the visual and olfactory elements of the floral sensory landscape that act synergistically or complementarily triggering pollinators' decision tools (*183-185*). This is only the beginning of the assessment of multimodal floral stimuli and the role of sensory landscapes in community-wide pollination studies. In this Chapter, we formulate the idea of sensory plant diversity and outline its significance to the functional stability of the pollination network in a phryganic community. It appears that the most influential plants in the pollination network of the community are either visually or olfactorily apparent at the time of their flowering. Even physical floral apparency alone (height and surface) is quite important for the cohesiveness and structure of the network, and for the visitation by specific pollinator groups (e.g. Halictidae bees: Tables 4.3-4.4, 4.S8, 4.S11; Figs. 4.S6-S9, 4.S22-S23).

Floral traits have been shown to relate to plant population vulnerability (*186, 187*). Our results can help towards conservation and restoration ecology of p–p interactions. During the last years, immense progress has been made towards the development of tools for the effective functional restoration of pollination networks (*11-13, 188, 189*), and the identification of plant species of conservation priority (*190*). We show here that floral sensory diversity of insect-pollinated plants is a key-component of functional diversity, which should be taken into account when setting up restoration practices for maintaining network dynamics and facilitative effects. For example, it has been shown that selecting restoration plants only according to the amount or rewards they offer may undermine facilitation and result in undesirable effects due to elevated competition (*12* and references therein). We provide evidence that influential plants ("magnet" or "keystone"[1] species) in the community (*2, 191-193*) may exhibit specific visual and olfactory traits associated with specific pollinator groups (e.g. bees in phrygana). Perspectives expand if we consider that floral traits are also involved in antagonistic interactions, such as herbivory (*114, 194, 195*), hence the interconnected study of mutualistic and antagonistic networks may offer more insights (*196*). Thus, according to the natural history of a given habitat, the abiotic environment, the local biodiversity, and the functional traits of the target plants, holistic approaches may be adopted, which will take into consideration the suites of floral stimuli that are meaningful to animals, configuring additional sensory-targeted functional restoration schemes.

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[1] 'Keystone' species as defined by Power *et al.* (1996) are those *'whose effect is large, and disproportionately large relative to their abundance'* (*191*). The term 'magnet' species was first used by Thomson (1978) and refers to species that massively attract pollinators in a community (*192*).

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CHAPTER FIVE

Insect– plant metabolite networks: the case of pollinators and floral volatiles

Abstract. – Chemosensory communication between plants and insects is a major ecological research topic with various applications due to the multimodal functionality of plants' volatile chemodiversity. In this Chapter, we present the first insect–VOC network compiled by the plant–pollinator visitation data and the plants' floral scent blends collected in the study community. By employing simple metrics and calculating the modularity of the insect–VOC network, we detect interesting association patterns between insect groups and VOC classes. We finally corroborate that sesquiterpenes are the most influential compounds in the phryganic insect–VOC network, a fact worth investigating in other mediterranean-type ecosystems around the world.

Insects – plant metabolite networks: the case of pollinators and floral volatiles

« Τά τε γὰρ ἔντομα ὄντα πόρρω συναισθάνεται,
καὶ τὰ πτερωτὰ καὶ τὰ ἄπτερα,
οἷον αἱ μέλιτται καὶ οἱ κνῖπες τοῦ μέλιτος·
ἐκ πολλοῦ γὰρ αἰσθάνονται ὡς τῇ ὀσμῇ γινώσκοντα».

Thus Insects perceive objects that have smell a long way off,
both winged and wingless insects,
e.g., bees and knipes perceive honey at a great distance,
no doubt recognizing it by its smell.

Aristotle, *Historia Animalium,* 4th c. BC
transl. A. L. Peck (*1*)

Introduction

It is beyond any doubt that the different components of the outstanding diversity of sensory stimuli in flowering plants may operate additively or synergistically in order to attract pollinators and achieve reproductive fitness (*2, 3*). Nevertheless, the fundamental relationship between the diverse chemical signals (semiochemicals) emitted by plants and the behavior of arthropods has a prominent position in ecological research and offers a variety of applications (*4, 5*). Scent compounds emitted by the different floral parts (petals, pollen, nectar) apart from directly or indirectly attracting pollinators may also: (i) attract herbivores (*6*); (ii) repel facultative floral visitors (*7*); (iii) repel herbivores (*8, 9*); (iv) participate in tritrophic interactions (*10, 11*); (v) interact with flower-dwelling microbes (*12*); (vi) exhibit antimicrobial activity against phytopathogens (*8, 9, 13*). It has been recently suggested that a most effective adaptation of flowering plants would be to produce floral signals that are already part of the insects' life history as for instance pheromones; indeed, in his review, Schiestl found that ca. 90% of the emitted floral VOCs overlap with insects' semiochemicals (*14*). Thus, the compilation of empirical data on pollinator–VOC interactions can help investigate the above-mentioned phenomena, and reveal general trends regarding the insects' own semiochemical diversity.

In this Chapter, we present the first insect–VOC network assembled at a community scale, and based on empirical data on insects' activity and floral emissions acquired *in situ* in a natural Mediterranean scrubland. This by no means intends to describe innate chemical preferences of pollinators, a task that would require special methodology in order to be assessed (see ref. *15*) and is beyond the scope of the present thesis. Besides, as emphasized in *Chapter 4*, VOC functionality is context-dependent and may vary according to the receiver (and its innate preferences combined with its cognitive abilities) and the environmental conditions (*16*). However, our data allow us to construct a novel type of bipartite ecological network, the insect – host-metabolite network that can contribute to the investigation of associations of insects and floral scents both in the study community and in other contexts.

Materials and Methods

In order to construct the insect–VOC network in the study community, we used the pollination network of the already described community in Aghios Stefanos, Lesvos Island, Greece. For details on the visitation sampling methodology, see *Chapter 4,* Materials and Methods.
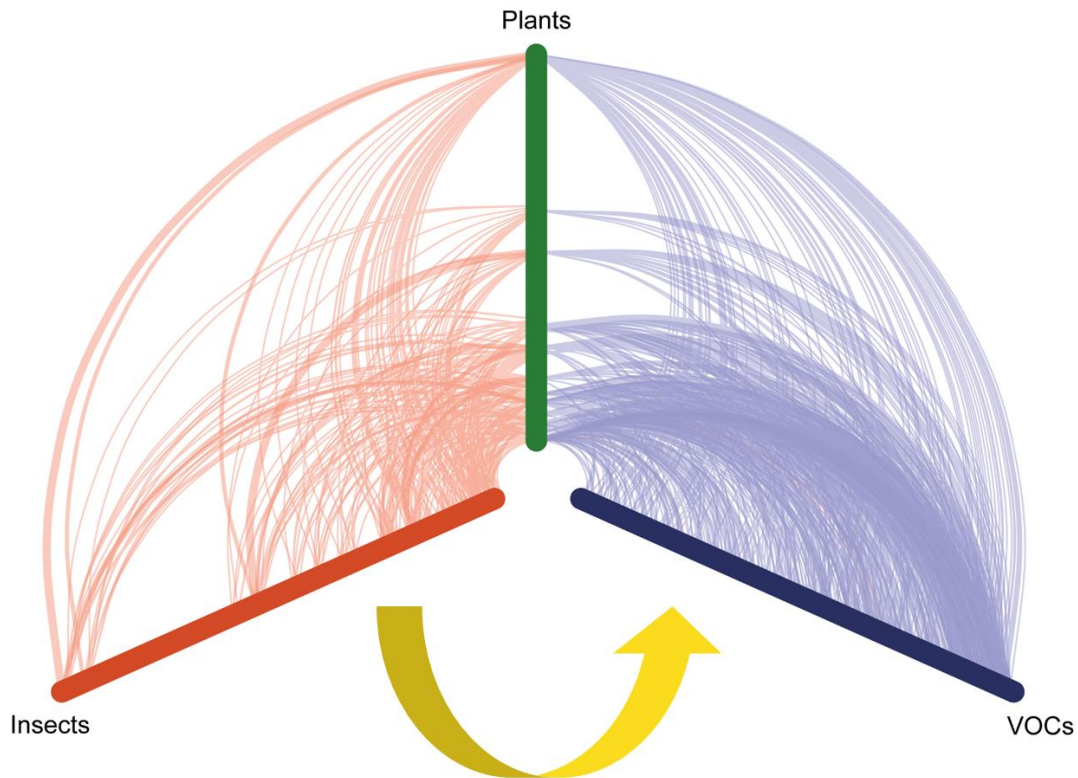
Fig. 5.1. The conceptual framework of the assemblage of the insect–VOC network in the study community. The two networks, plant–pollinator (left) and plant–VOC (right), are visualized in a hive plot (*35*), where each axis represents the linearly arranged nodes of the respective trophic level. Pollinators are linked to VOCs through their visitation to the flowering plants, so the insect–VOC network was constructed by replacing each plant with its emitting VOCs.

The data structure of scent compositions (incidence matrix of plants and VOCs) is particularly fitting to a network analysis (analogously in ref. *17*). This approach would be challenging or impossible with floral reflectance spectral data: the response of a particular receptor depends on the amount of photons of a certain wavelength that hit the receptor, and the spectral line's shape determines the likelihood that photons of each wavelength can be perceived by the receptors. Once quanta are absorbed, this information is represented as a signal that no longer carries wavelength information ('Principle of univariance', ref. *18*). So, dividing the spectrum to multiple components (variables) in order to form a network would be problematic.

In the p–p network, we substituted each plant with the list of VOCs contained in the volatile blends of their floral units (Fig. 5.1). For details on the scent sampling and analysis, see *Chapter 3,* Materials and Methods. A first large network was assembled (168×333) including 10,400 pairwise links. In order to reduce the size of the network, as well as the noise due to randomly assembled interactions, we removed singletons, i.e. we kept only the insect–VOC interactions that occurred at least twice.

We ran modularity analysis in order to explore if there are link-dense areas in the network (*19*), containing nodes (insects and VOCs) that are connected more tightly among them than with the others. For this analysis, we used the *NetCarto* software, which implements the Simulated Annealing (SA) algorithm (*20*). More details are available in the Materials and Methods of *Chapters 3* and *4*.
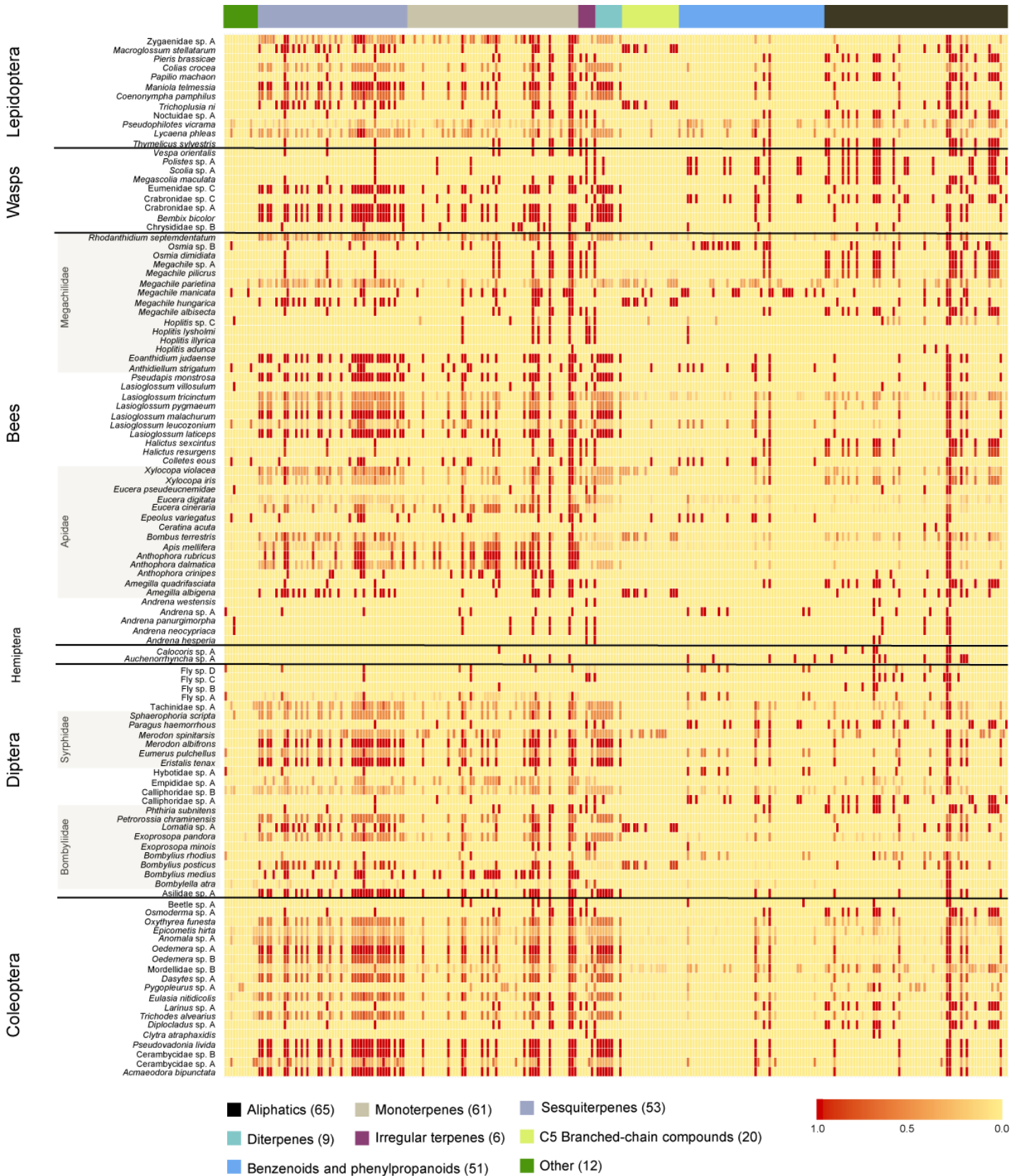
Fig. 5.2. The insect–VOC network of the study community illustrated as an incidence matrix. Only the 111 insects that performed ≥2 interactions involving each VOC are included. VOCs (columns) are ordered according to their chemical class. The weight of the interactions has been standardized (0 to 1).
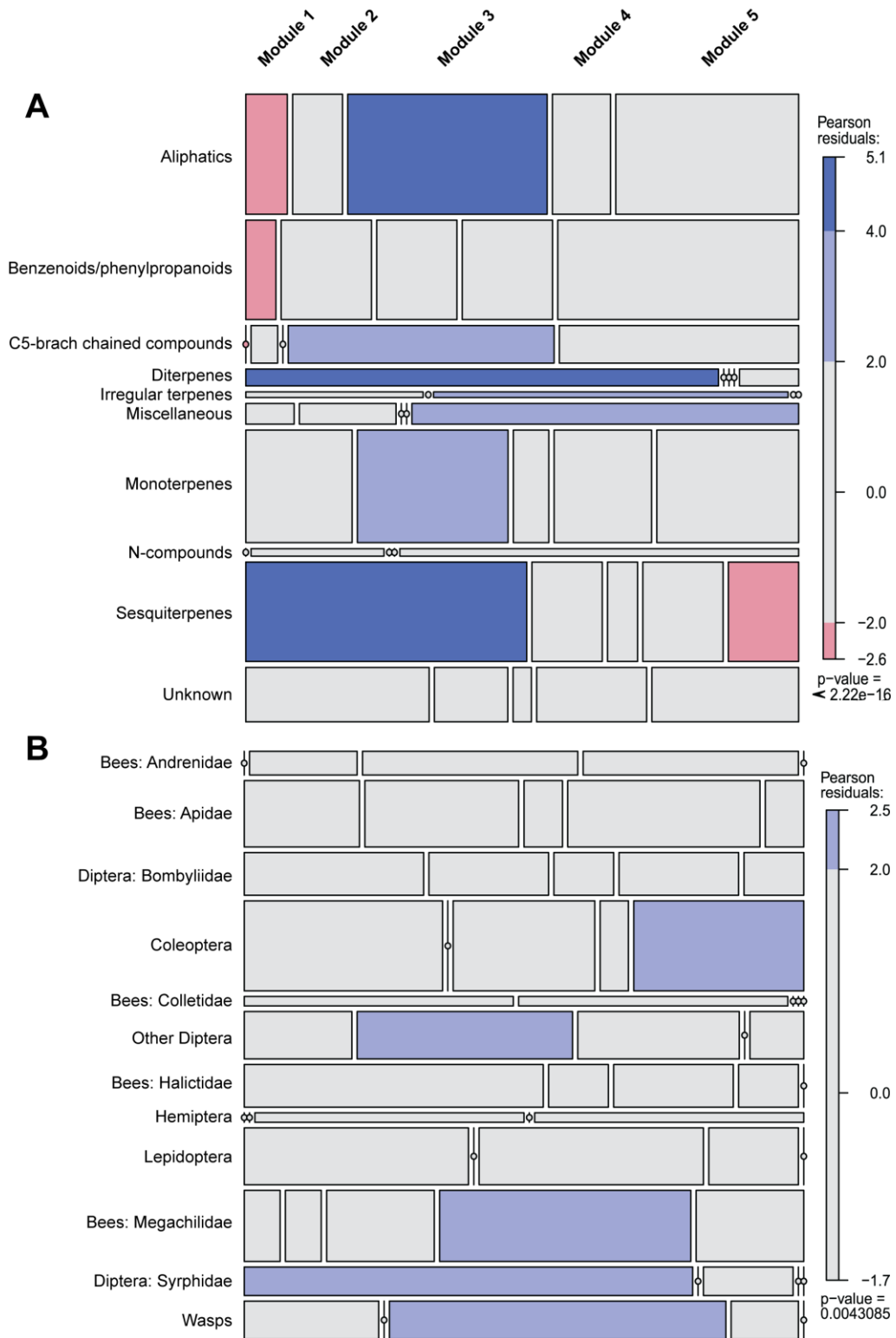
Fig. 5.3. Characterization of the five modules of the insect–VOC network yielded by the SA algorithm according to VOC classes (A) and insect groups (B). Shading shows the module–class or module–group combinations that are more (blue) or less (red) probable corresponding to the magnitude of the standardized residuals of the Pearson χ^2 test. Shaded cells with residual values $>|2|$ and $>|4|$ correspond to residuals that are individually significant at 0.05 and (A) <0.0001, or (B) 0.004, respectively.

In order to detect the significant positive and negative associations of (i) VOC classes (*21*) or (ii) pollinator groups, with the p–p network modules, we applied a Pearson χ^2 conditional independence test with the function 'mosaic' in the R package *vcd* v.1.4-1 (*22, 23*). High proportional participation in one module in respect to the others (block width) combined with statistical significance, allowed us to identify the positive associations. Besides grouping insect according to their order, we distinguished the important anthophilous families of the community that also showed high species-richness and visitation.

We calculated the normalized degree of the insect species (Table 5.S1) and VOCs as a simple metric to identify the nodes with the most generalized behavior. This was computed with the R package *bipartite* v. 2.06 (*24*).

Fig. 5.4. Mammoth wasps (*Megascolia maculata*, Scoliidae) feeding on cottonthistle (*Onopordum tauricum*, left) and on *Anthyllis hermanniae* (right) in the study community. Photos: Aphrodite Kantsa.

Results and Discussion

The final insect–VOC network includes 111 insects and 306 VOCs that altogether establish 6,701 pairwise links and 352,651 interaction events, with number of visits representing the weights of the links (Fig. 5.2). The connectance of the network is 0.197, i.e. ca. 20% of all possible interactions are realized. The network is significantly but not highly modular (*M*=0.13), comprising five modules.

Modularity analysis shows that the insects participating in the network compartment that is positively related with sesquiterpenes and diterpenes are, at the same time, negatively associated with aliphatics and benzenoids (Module #1 in Fig. 5.3A). Module #1 is also positively associated with hoverflies (Syrphidae) (Fig 5.3B). In the previous Chapter, we found no specific association between hoverfly visitation and the VOC classes in the floral blends. However, our finding here may have a sound basis, as hoverflies and terpenes have been shown to associate in two cases: (i) in certain hoverfly-pollinated palms that show high monoterpene and sesquiterpene emissions, and (ii) in orchids attracting aphidophagous hoverflies mimicking aphid alarm kairomones (terpenoid) (*25, 26*). Module #3 is positively associated with aliphatics and irregular terpenes, as well as with wasps (Fig. 5.3A-B). As mentioned in *Chapter 3*, wasps are known to be attracted by (aliphatic) bee alarm pheromones emitted

by the orchid *Dendrobium sinense* (*27*), as well as by the aliphatic green-leaf volatiles (*28*) emitted by the flowers of the orchid *Epipactis helleborine* (*29*). Furthermore, among the irregular terpenes of Module #3, there is (*E*)-4,8-dimethyl-1,3,7-nonatriene, an enigmatic herbivore-induced exclusively floral volatile compound involved in tritrophic interactions (*10* and references therein). In the study community, this compound is emitted by *Anthyllis hermanniae* (Fabaceae) and *Onopordum tauricum* (Asteraceae) (Fig. 5.4). Thus, perhaps the associations in Module #3 suggest that the special attraction mechanism of social pollinating wasps employed by the above-mentioned plants may be a broader phenomenon occurring as well in a community-context. Finally, Module #4 indicates a significant positive relationship with leafcutter bees (Megachilidae) and C5 branch-chained compounds.
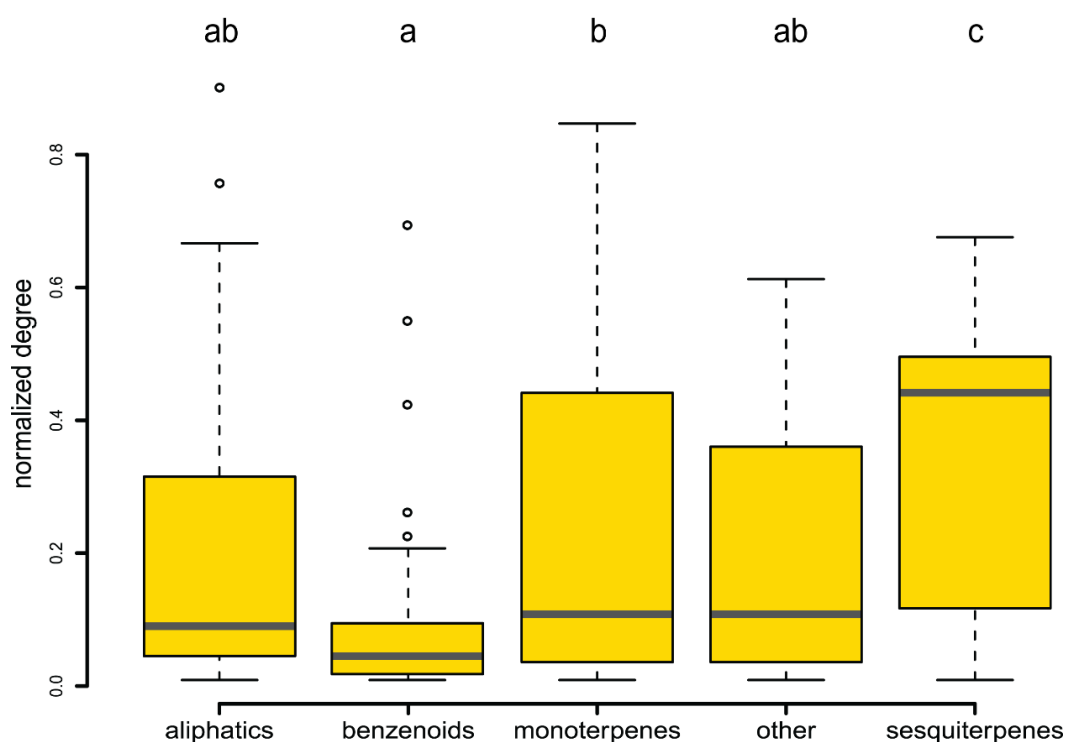
Fig. 5.5. Mean normalized degree of the major VOC classes in the insect–VOC network. Among-class differences were acquired with a Nemenyi post-hoc test with Tukey-Dist. approximation.

There is no significant difference in the mean normalized degree (ND) among the different insect orders (Kruskall–Wallis test, *p*>0.050), implying that insects' chemical generalization does not vary according to their classification into taxonomic groups. To the contrary, VOC classes show significantly different mean ND (Kruskall–Wallis test, $\chi^2(4)=47.91^{***}$) with sesquiterpenes being the most generalized chemical class showing the highest mean ND (Fig. 5.5). Evidently, they represent key-components of the floral phenotype in the phryganic community studied (see also *Chapters 3* and *4*). Even if the various insects of the community have no innate preferences for these VOCs, it is obvious that they spend their adult life in a sesquiterpene-saturated sensory landscape, and the majority of them come into direct contact with large amounts of these compounds during foraging or mating. This floral phenotypic peculiarity could also hold for other mediterranean scrublands beyond the

Basin, as for example in the equally fragrant Californian chaparrals, where studies of plant volatile diversity focus mainly on allelopathy ever since the seminal work of Cornelius Muller in the 1960s (*30, 31*). The spectrum of the functional significance of sesquiterpenes' profusion in Mediterranean-type habitats becomes an intriguing research topic, if we consider possible physiological phenomena involved, such as addiction (*32*) or habituation (*33, 34*), that may affect pollinator's decision-making, foraging behavior, and ultimately the interaction patterns in a community-context.

This *Chapter* represents a relatively simple although data-intensive approach in order to introduce network analysis into the investigation of the fundamental relationship of plant semiochemicals and arthropod behavior, focusing directly on the chemical compounds. Also, in our case, it contributes to the description of the chemosensory environment of the community.

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SUPPLEMENTARY MATERIALS

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SM Chapter 2

Fig. 2.S1. (**A**) Chemical class composition and volatility spectra of the blends of the 59 plant genera studied in Greece. Distributions of the normal boiling points (nBP) of the main chemical classes are distinguished according to their metabolic pathway (*: list of VOCs incomplete). LOX: Lipoxygenase pathway; MVA: Mevalonic acid pathway; MEP: Methylerythritol phosphate pathway.

A
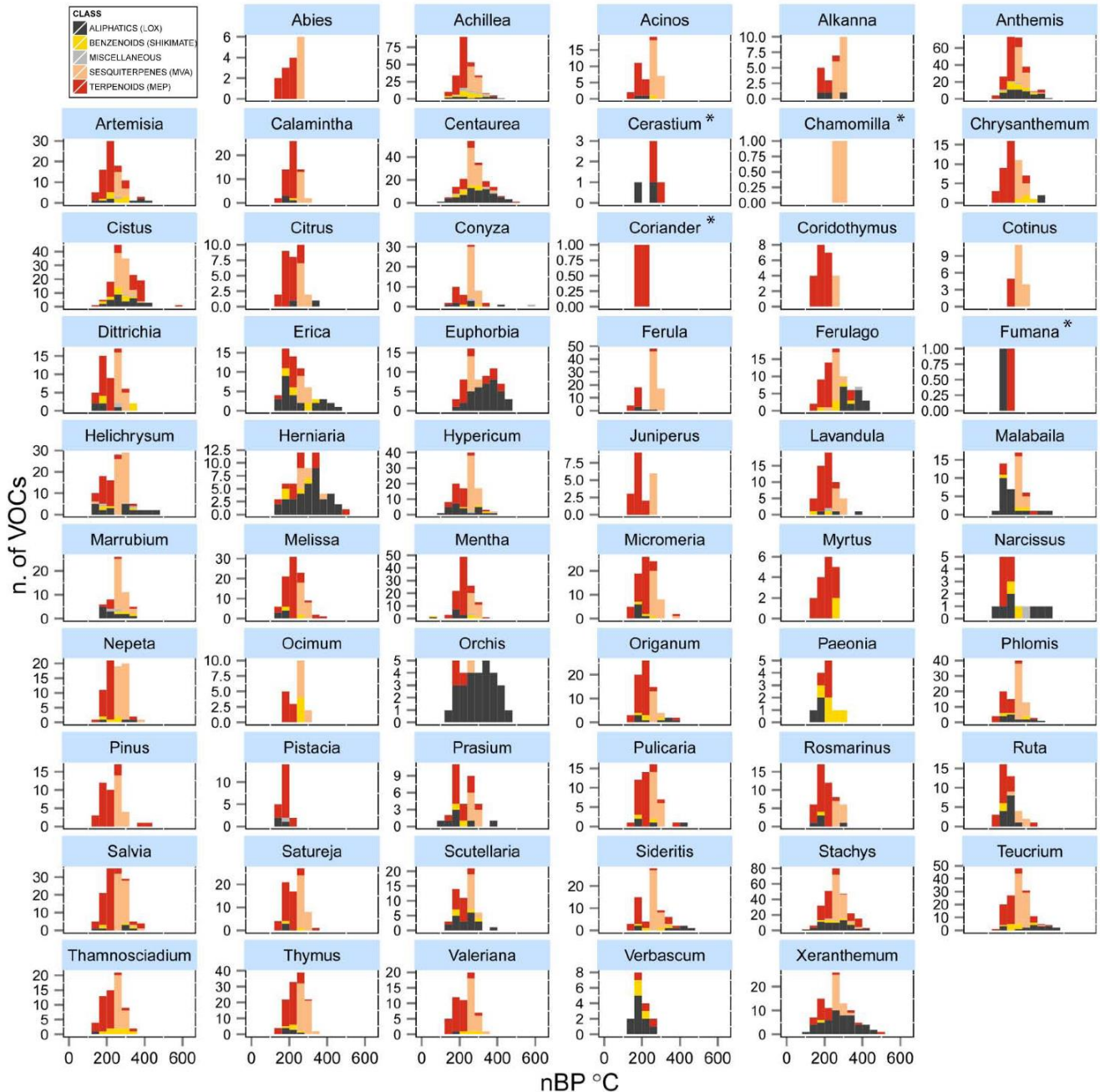
(B) Volatility as expressed with the normal boiling point (nBP) (± SE) of the blends of the genera studied in Greece. Scents have been acquired with distillation in all genera, apart from *Paeonia*. (*: list of VOCs incomplete).

B

cont.

Genus	Mean nBP (ºC)	±	SE	Genus	Mean nBP (ºC)	±	SE
Abies	222.6	±	12.0	*Melissa*	229.3	±	5.2
Achillea	241.4	±	3.4	*Mentha*	227.6	±	4.3
Acinos	236.6	±	6.9	*Micromeria*	229.9	±	5.4
Alkanna	255.4	±	9.7	*Myrtus*	214.1	±	8.5
Anthemis	253.1	±	3.4	*Narcissus*	240.9	±	19.9
Artemisia	236.7	±	6.2	*Nepeta*	248.3	±	5.6
Calamintha	221.5	±	5.0	*Ocimum*	239.3	±	9.8
Centaurea	282.0	±	5.3	*Orchis*	291.2	±	14.7
*Cerastium**	256.7	±	20.0	*Origanum*	227.0	±	6.2
*Chamomilla**	283.1	±	10.6	*Paeonia*	212.7	±	11.0
Chrysanthemum	236.3	±	7.8	*Phlomis*	243.1	±	5.1
Cistus	294.9	±	5.0	*Pinus*	233.5	±	7.9
Citrus	226.1	±	8.6	*Pistacia*	175.0	±	3.5
Conyza	258.0	±	8.6	*Prasium*	225.0	±	10.5
*Coriander**	203.0	±	4.5	*Pulicaria*	242.9	±	7.4
Coridothymus	202.4	±	8.7	*Rosmarinus*	212.8	±	7.0
Cotinus	266.0	±	5.9	*Ruta*	209.0	±	6.6
Dittrichia	229.8	±	7.2	*Salvia*	248.5	±	4.7
Erica	245.8	±	9.5	*Satureja*	230.4	±	5.3
Euphorbia	315.9	±	9.2	*Scutellaria*	236.2	±	6.8
Ferula	248.1	±	4.9	*Sideritis*	259.8	±	8.0
Ferulago	269.7	±	8.6	*Stachys*	262.7	±	3.8
*Fumana**	207.4	±	16.6	*Teucrium*	267.1	±	5.0
Helichrysum	255.0	±	6.4	*Thamnosciadium*	237.5	±	6.0
Herniaria	294.0	±	10.6	*Thymus*	240.1	±	4.2
Hypericum	241.5	±	5.4	*Valeriana*	232.4	±	6.6
Juniperus	204.6	±	10.5	*Verbascum*	197.5	±	8.6
Lavandula	219.1	±	6.7	*Xeranthemum*	266.9	±	8.3
Malabaila	241.8	±	8.1				
Marrubium	263.1	±	5.7				

Fig. 2.S2. The hotspots of volatile research in Greece. **(A)** Distribution of collection sites in the country. **(B)** Distribution of the plant taxa studied among the regional units. Shading is in proportion to the number of plant taxa sampled in each area.
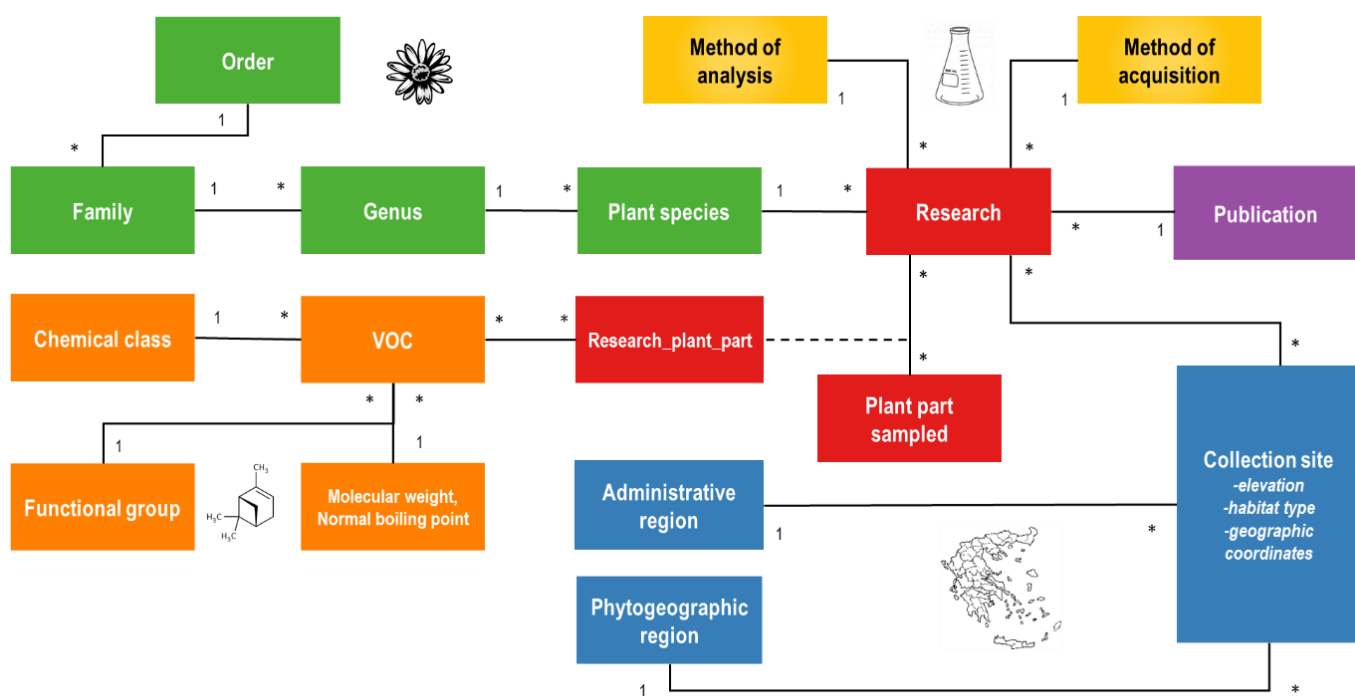
Fig. 2.S3. Database development. The conceptual design of the geodatabase was based on the class diagram of the Unified Modeling Language (UML) and consists of 17 classes and 15 binary relationship types among them. The development of the database took place on top of the MS Access relational DBMS using the ESRI ArcCatalog geospatial data management software. This resulted in a geodatabase of 20 tables. The alphanumerical data were managed through an MS Access form, while the maps were implemented using the ESRI ArcMap GIS software (ArcGIS™ 10.0).

Table 2.S1. The chemical composition of the volatile blends of the plant taxa that have been sampled in Greece during the years 1988-2013.

For this material, please refer to the CD-ROM attached to the Thesis.

SM CHAPTER 3

Fig. 3.S1. Northeastern view of the study community at Aghios Stefanos, Lesvos Island, Greece (Photo: Aphrodite Kantsa).
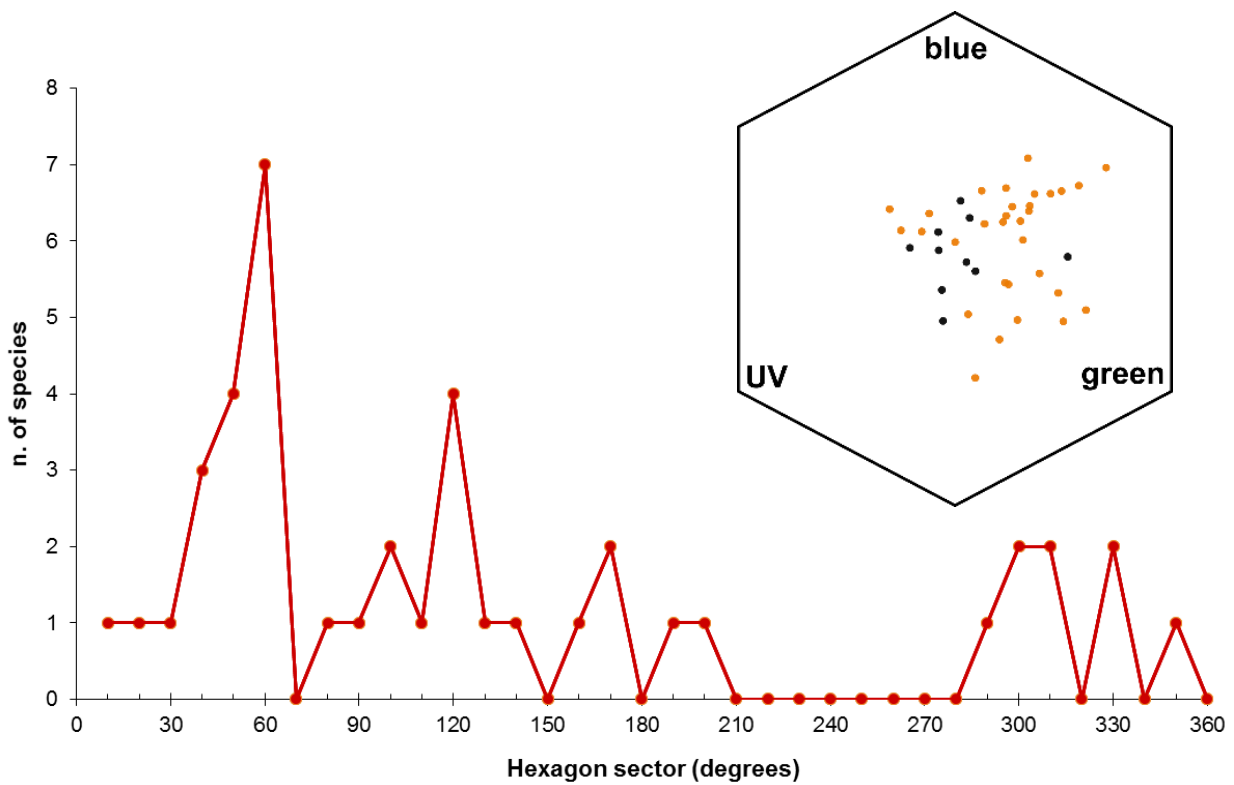
Fig. 3.S2. Color loci of the flowers in the study community in the hexagonal color space of the bee trichromatic visual system (inset), and their absolute frequency in the 36 sectors (10° each) of the color space. See *19* and *20* for comparison with plant datasets in other parts of the world. Orange dots: nectariferous plants; black dots: non-nectariferous plants.
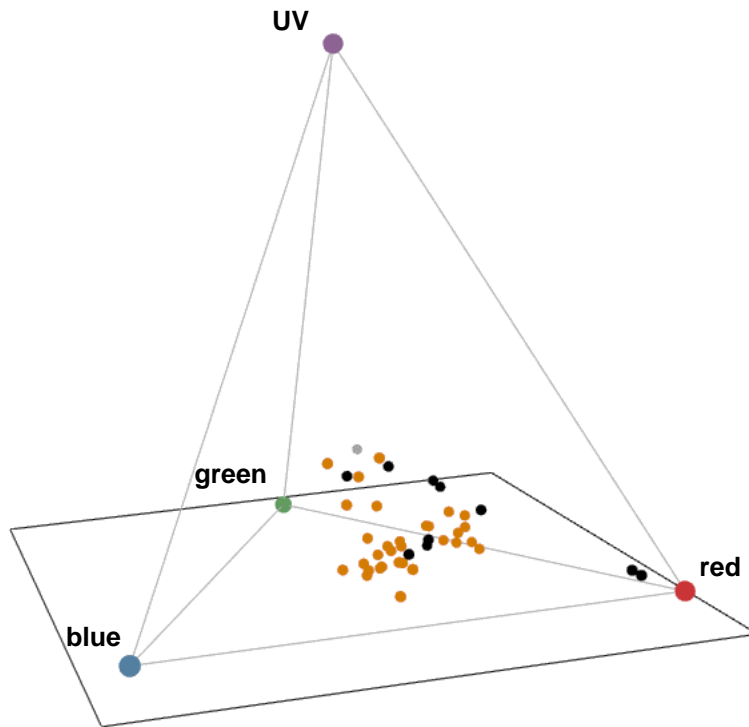
Fig. 3.S3. The loci of the flowers in the study community in the tetrahedral color space of the tetrachromatic visual system of the swallowtail butterfly *Papilio xuthus* (Lepidoptera, Papilionidae). Orange dots: nectariferous plants; black dots: non-nectariferous plants. The grey dot represents the position of an achromatic object.
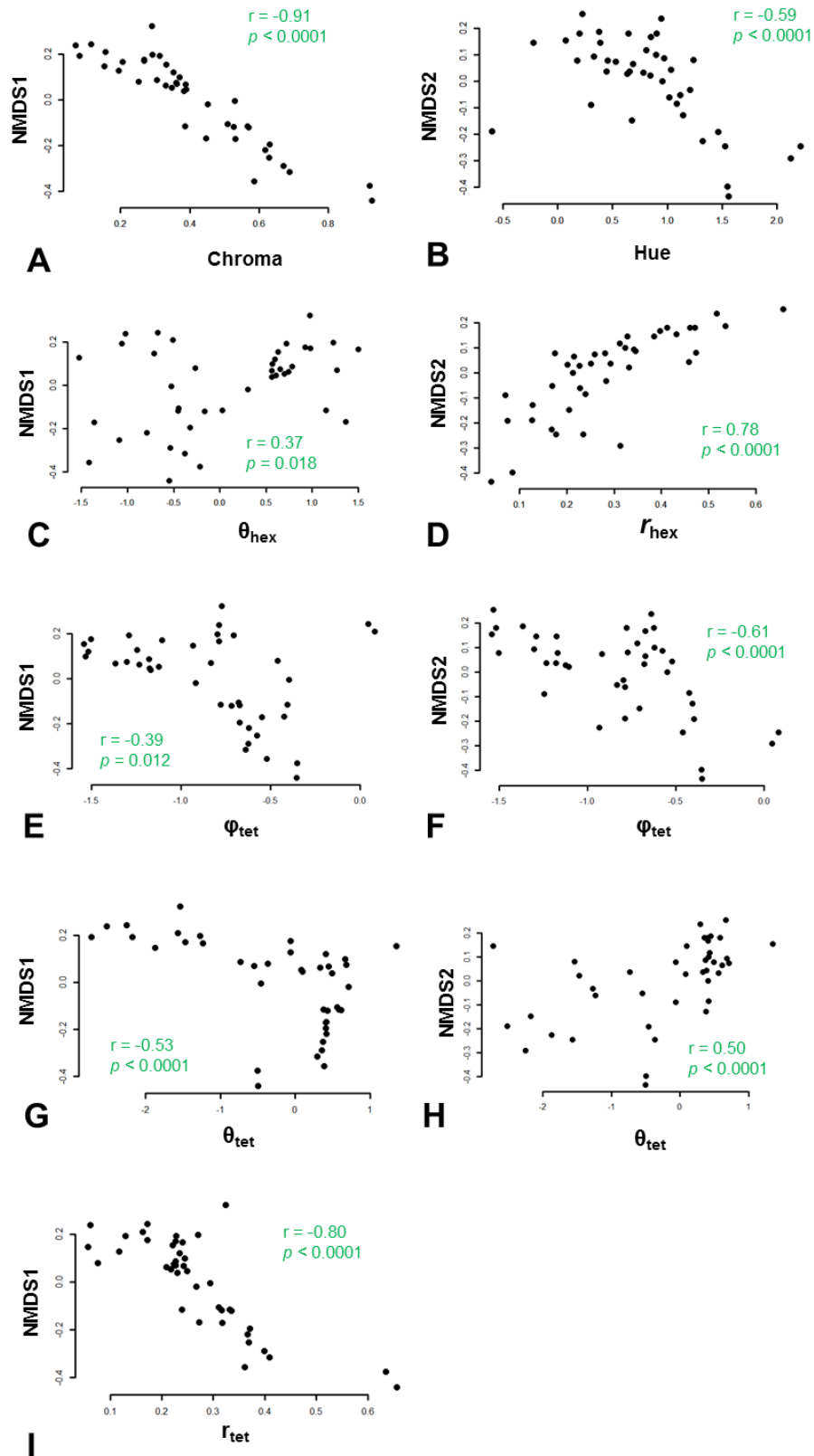
Fig. 3.S4. The statistically significant Pearson correlations between spectral or colorimetric properties of the plants in the community and the two NMDS axes calculated from the raw spectral data. For details on the spectral or colorimetric properties, see *Chapter 3, Materials and Methods.*
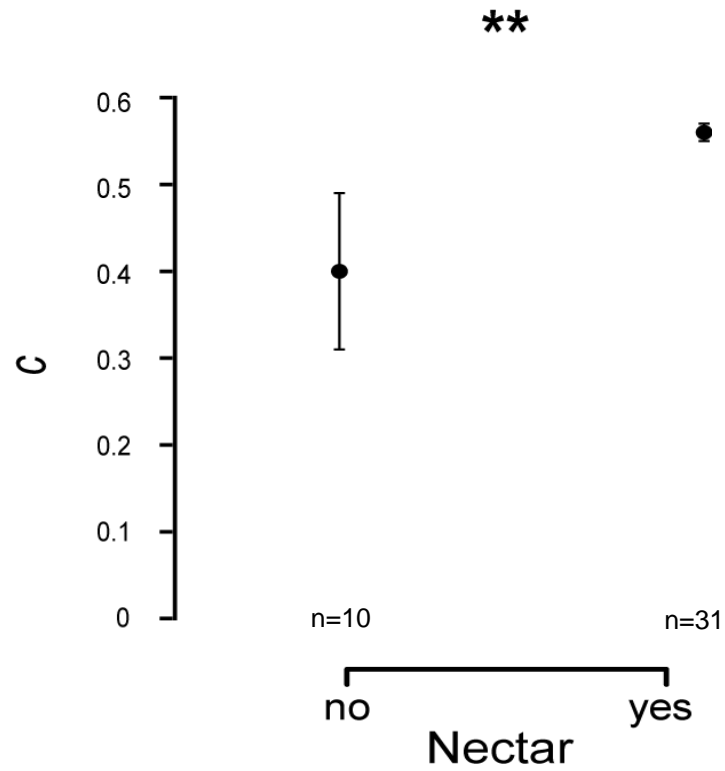
Fig. 3.S5. The mean among-module connectivity (c) of the plants in the plant–volatilome network according to the presence/absence of nectar. Relationship tested with phylogenetically informed GLS ($F_{1,39}=7.85$, $p=0.008$). Mean values ± SE are shown.
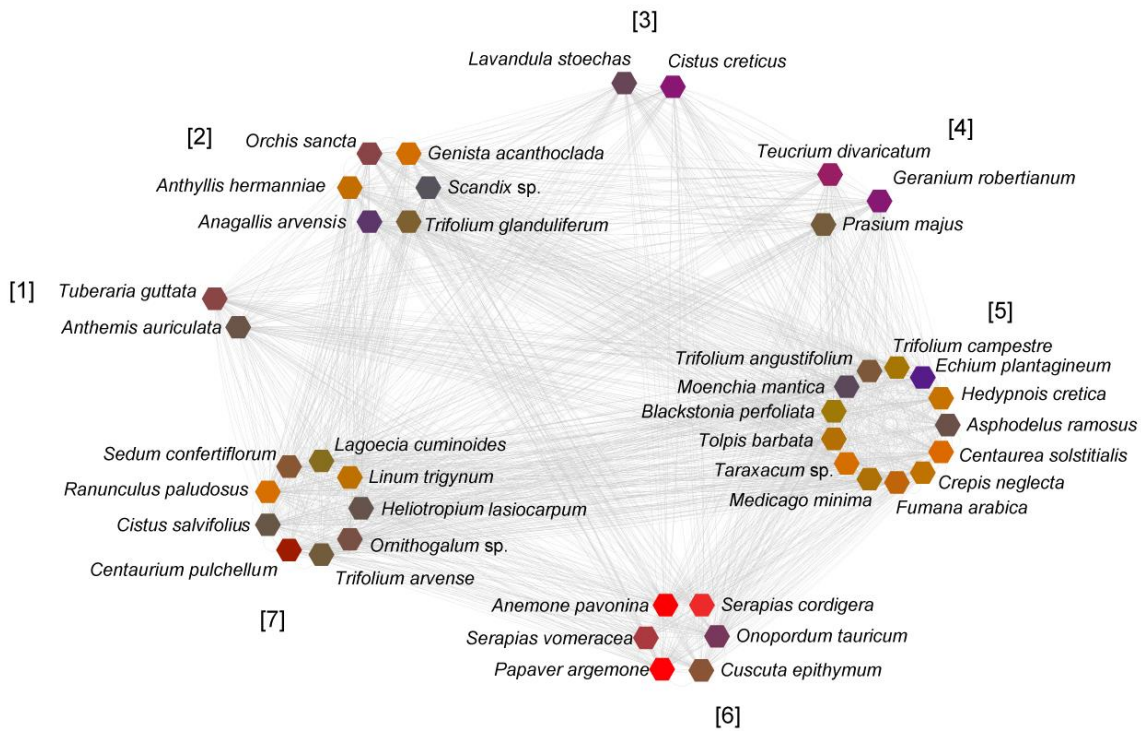
Fig. 3.S6. The seven modules of the plant–volatilome network yielded by the SA algorithm (*77-78*). Network displayed as one-mode including only the plants. Numbers match those given in Fig. 3.S7. Colors of nodes represent floral colors of each species, determined after the raw spectra were encoded according to the RGB model.
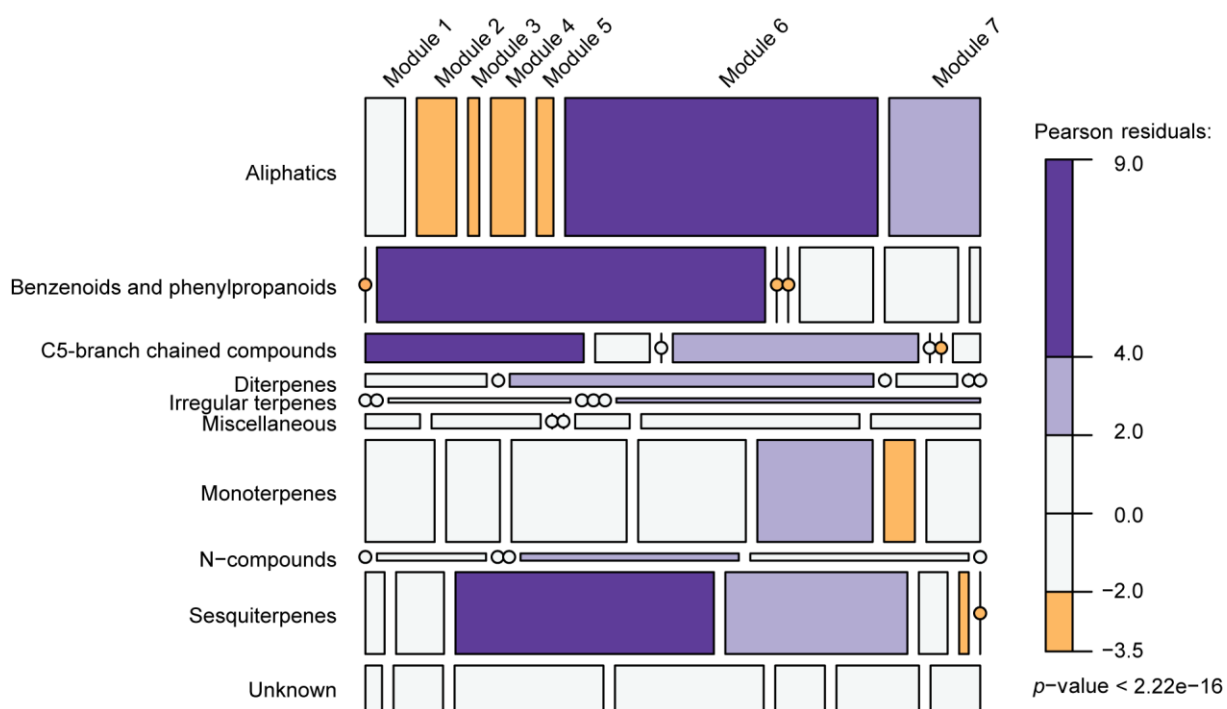
Fig. 3.S7. Chemical characterization of the seven modules of the plant–VOC network in the study community. The frequency distribution of VOCs of each class within the modules is presented in a mosaic plot. Shading shows the module–class combinations that are more (violet) or less (orange) probable corresponding to the magnitude of the standardized residuals of the Pearson χ^2 test. Shaded cells with residual values >|2| and >|4| correspond to residuals that are individually significant at 0.05 and 0.0001, respectively.
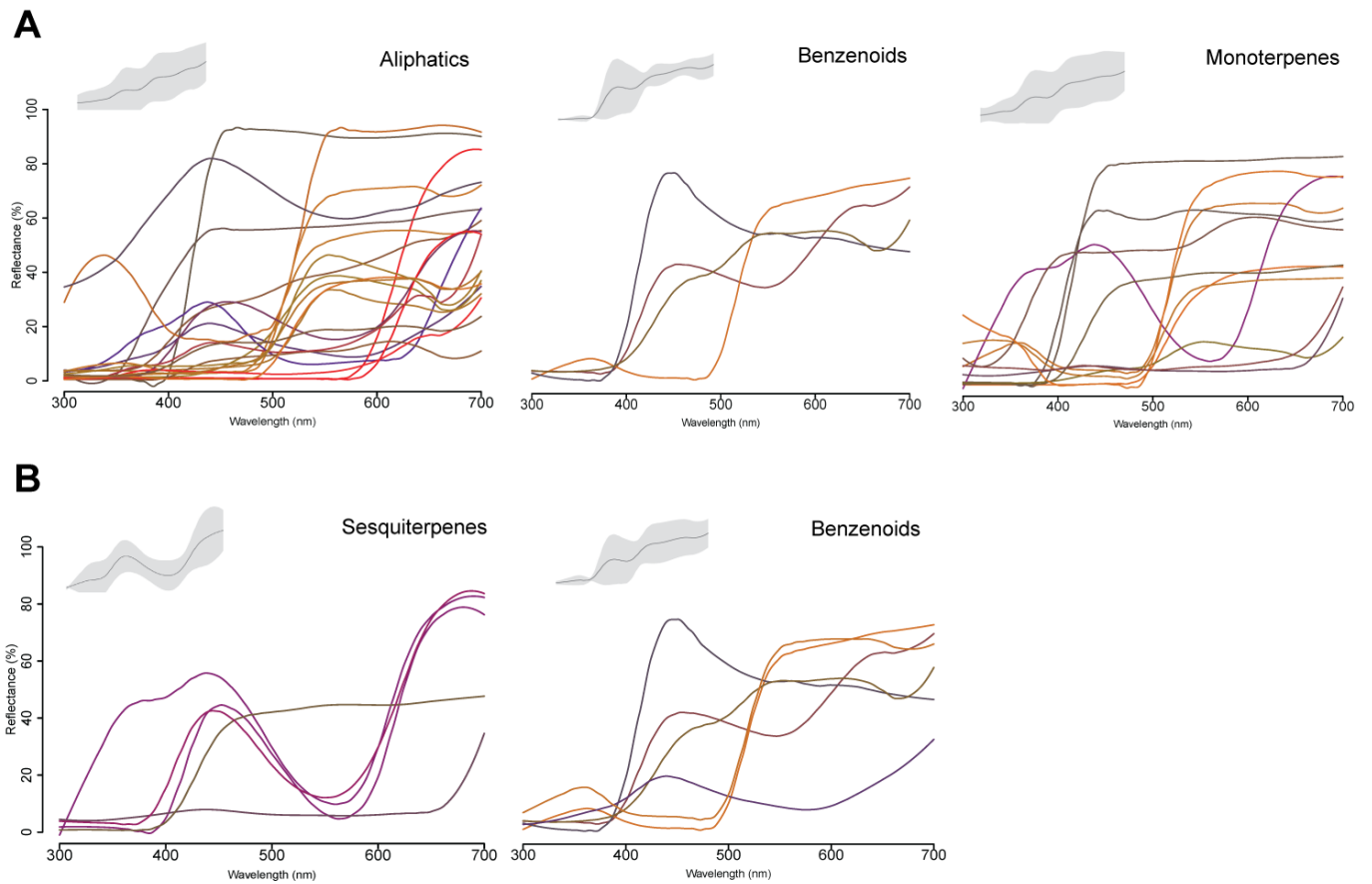
Fig. 3.S8. Spectral patterns associated with VOC classes in the floral phenotypes. (**A**) Spectra in the groups where aliphatics, benzenoids, and monoterpenes prevail in the total emissions. (**B**) Spectra of the plants included in Modules 3-4 and Module 2 of the plant−volatilome network, which have been characterized for sesquiterpenes and benzenoids, respectively (Pearson $\chi2$ conditional independence test, fig. S7). Insets in spectra plots correspond to the average spectrum of the group/module ± SD. Line colors encoded according to the RGB model.

Table 3.S1. Color and scent samples of the entomophilous plants in the study community at Aghios Stefanos. For one plant we provide the number of records in FReD. Plane families follow APG III (*59*).

Family	Plant	Corolla part sampled for color	#color samples	#scent samples
Primulaceae	*Anagallis arvensis*	petals	10	3
Ranunculaceae	*Anemone pavonina*	tepals	15	4
Asteraceae	*Anthemis auriculata*	ligulate florets	13	4
Fabaceae	*Anthyllis hermanniae*	petals	10	4
Xanthorrhoeaceae	*Asphodelus ramosus*	petals	12	4
Gentianaceae	*Blackstonia perfoliata*	petals	1	1
Asteraceae	*Centaurea solstitialis*	ligules	5	2
Gentianaceae	*Centaurium pulchellum*	petals	4	3
Cistaceae	*Cistus creticus*	petals	16	9
Cistaceae	*Cistus salviifolius*	petals	17	2
Asteraceae	*Crepis neglecta*	ligules	10	2
Convolvulaceae	*Cuscuta epithymum*	petals	12	4
Boraginaceae	*Echium plantagineum*	petals	17	1
Cistaceae	*Fumana arabica*	petals	20	4
Fabaceae	*Genista acanthoclada*	petals (banner)	15	4
Geraniaceae	*Geranium robertianum*	petals	16	3
Asteraceae	*Hedypnois cretica*	ligules	7	3
Boraginaceae	*Heliotropium lasiocarpum*	petals	8	7
Apiaceae	*Lagoecia cuminoides*	umbel	5	1
Lamiaceae	*Lavandula stoechas* subsp. *stoechas*	corolla	18	3
Linaceae	*Moenchia mantica*	petals	7	6
Fabaceae	*Linum trigynum*	petals	4	1
Caryophyllaceae	*Medicago minima*	petals (banner)	1	1
Asteraceae	*Onopordum tauricum*	ligules	5	6
Orchidaceae	*Orchis sancta*	lip	14	3
Asparagaceae	*Ornithogalum* sp.	tepals	5	1
Papaveraceae	*Papaver argemone*	petals	9	3
Lamiaceae	*Prasium majus*	FReD n. 4051, 4052	-	3
Ranunculaceae	*Ranunculus paludosus*	petals	16	4
Apiaceae	*Scandix* sp.	center of the umbel	7	2
Crassulaceae	*Sedum confertiflorum*	petals	8	1
Orchidaceae	*Serapias cordigera*	lip	16	2
Orchidaceae	*Serapias vomeracea*	lip	6	2
Asteraceae	*Taraxacum* sp.	ligules	10	3
Lamiaceae	*Teucrium divaricatum*	lip	14	8
Asteraceae	*Tolpis barbata*	ligules	11	4
Fabaceae	*Trifolium angustifolium*	petals	9	2
Fabaceae	*Trifolium arvense*	petals	8	4
Fabaceae	*Trifolium campestre*	petals	12	5
Fabaceae	*Trifolium glanduliferum*	petals	16	5
Cistaceae	*Tuberaria guttata*	petals	12	2

Table 3.S2. Colorimetric, spectral, and chemical floral properties of the plants in the study community. For details on the variables, see Materials and Methods. #Class: percentage of class in the total number of VOCs. %Class ER: percentage of class in the total emissions. Alip: Aliphatics; Benz: Benzenoids and phenylpropanoids; Mono: Monoterpenes; Sesq: Sesquiterpenes.

Plant	r_{hex}	θ_{hex}	NMDS1	NMDS2	θ_{tet}	φ_{tet}	r_{tet}	Brightness	Chroma	Hue	#Alip	#Benz	#Mono	#Sesq	Total VOCs	%Alip ER	%Benz ER	%Mono ER	%Sesq ER	c	z	d'
Anagallis arvensis	0.205	-1.064	0.195	-0.147	-2.177	-0.705	0.130	13.955	0.080	0.676	3	4	1	0	10	0.656	0.198	0.016	0.000	0.580	0.587	0.371
Anemone pavonina	0.084	-0.548	-0.440	-0.399	-0.500	-0.354	0.656	17.081	0.925	1.547	15	1	6	0	27	0.654	0.025	0.245	0.000	0.604	2.688	0.541
Anthemis auriculata	0.471	0.598	0.121	0.180	0.413	-1.516	0.235	63.208	0.353	0.198	10	2	14	4	41	0.204	0.012	0.394	0.277	0.711	4.595	0.598
Anthyllis hermanniae	0.213	-1.363	-0.171	0.000	0.412	-0.549	0.318	36.954	0.532	0.952	2	9	9	6	34	0.023	0.154	0.775	0.022	0.574	3.550	0.689
Asphodelus ramosus	0.174	0.924	0.178	0.079	-0.061	-1.501	0.172	44.868	0.268	0.176	6	0	1	0	7	0.977	0.000	0.023	0.000	0.449	0.322	0.316
Blackstonia perfoliata	0.412	0.030	-0.115	0.180	0.584	-0.778	0.332	18.235	0.567	0.645	6	0	3	1	11	0.897	0.000	0.033	0.054	0.628	0.607	0.361
Centaurea solstitialis	0.517	-0.382	-0.314	0.237	0.295	-0.638	0.410	20.461	0.688	0.945	8	0	4	0	12	0.421	0.000	0.579	0.000	0.653	0.322	0.332
Centaurium pulchellum	0.228	1.499	0.168	-0.061	-1.237	-0.787	0.240	30.808	0.205	1.020	2	3	5	7	19	0.087	0.186	0.224	0.456	0.643	1.503	0.459
Cistus creticus	0.473	0.976	0.324	0.081	-1.537	-0.772	0.324	27.477	0.291	1.238	7	2	16	29	71	0.023	0.098	0.233	0.423	0.551	7.000	0.599
Cistus salviifolius	0.658	0.570	0.100	0.255	0.667	-1.533	0.244	62.864	0.370	0.227	3	5	7	7	28	0.312	0.079	0.079	0.299	0.615	2.961	0.476
Crepis neglecta	0.397	-0.323	-0.194	0.168	0.413	-0.672	0.371	26.885	0.630	0.849	4	0	5	0	12	0.521	0.000	0.141	0.000	0.542	0.891	0.449
Cuscuta epithymum	0.227	0.700	0.054	0.028	0.081	-1.125	0.218	30.676	0.348	0.632	17	10	2	1	33	0.460	0.225	0.012	0.008	0.562	3.705	0.544
Echium plantagineum	0.313	-0.673	0.245	-0.292	-2.256	0.044	0.173	17.148	0.114	2.121	3	0	1	0	4	0.962	0.000	0.038	0.000	0.375	-0.248	0.452
Fumana arabica	0.127	1.148	-0.114	-0.128	0.377	-0.406	0.239	54.742	0.387	1.141	10	5	4	0	21	0.655	0.091	0.132	0.000	0.667	2.031	0.545
Genista acanthoclada	0.345	-1.088	-0.252	0.087	0.373	-0.576	0.369	34.643	0.628	0.971	6	17	16	4	48	0.171	0.458	0.255	0.065	0.628	4.735	0.481
Geranium robertianum	0.234	-0.511	0.212	-0.244	-1.568	0.081	0.163	41.163	0.156	2.212	7	3	17	17	51	0.033	0.012	0.644	0.274	0.651	4.855	0.697
Hedypnois cretica	0.323	-0.793	-0.218	0.100	0.417	-0.620	0.367	34.363	0.618	0.896	10	2	7	0	24	0.500	0.048	0.227	0.000	0.660	2.031	0.465
Heliotropium lasiocarpum	0.432	0.632	0.156	0.155	1.352	-1.542	0.221	49.753	0.332	0.071	8	4	13	2	32	0.108	0.160	0.566	0.007	0.592	3.691	0.434
Lagoecia cuminoides	0.259	0.303	-0.018	0.074	0.713	-0.917	0.267	8.842	0.452	0.529	0	1	9	1	11	0.000	0.114	0.855	0.031	0.545	0.773	0.811
Lavandula stoechas	0.168	-0.712	0.149	-0.226	-1.874	-0.934	0.056	7.385	0.154	1.324	2	0	23	12	39	0.013	0.000	0.893	0.078	0.601	3.322	0.817
Moenchia mantica	0.126	-1.022	0.240	-0.189	-2.520	-0.787	0.061	63.578	0.069	-0.600	0	0	3	0	3	0.000	0.000	1.000	0.000	0.000	-0.199	0.245
Linum trigynum	0.239	1.367	-0.168	-0.084	0.414	-0.425	0.273	24.061	0.447	1.084	1	0	0	0	3	0.640	0.000	0.000	0.000	0.000	-0.248	0.394
Medicago minima	0.201	-0.449	-0.105	0.033	0.565	-0.679	0.311	15.648	0.509	0.780	10	0	1	1	15	0.915	0.000	0.003	0.004	0.436	2.031	0.511
Onopordum tauricum	0.332	0.983	0.172	0.022	-1.470	-1.104	0.227	21.590	0.267	0.843	18	2	7	3	33	0.641	0.038	0.158	0.036	0.669	2.891	0.283
Orchis sancta	0.292	0.781	0.089	0.037	-0.730	-1.178	0.227	36.852	0.305	0.656	2	15	0	3	24	0.001	0.948	0.000	0.027	0.479	2.760	0.953

Plant	r_{hex}	θ_{hex}	NMDS1	NMDS2	θ_{tet}	φ_{tet}	r_{tet}	*Brightness*	*Chroma*	*Hue*	#Alip	#Benz	#Mono	#Sesq	Total VOCs	%Alip ER	%Benz ER	%Mono ER	%Sesq ER	c	z	d'
Ornithogalum sp.	0.069	-1.527	0.129	-0.090	-0.065	-1.245	0.118	49.570	0.194	0.302	3	0	5	0	10	0.131	0.000	0.666	0.000	0.480	0.530	0.284
Papaver argemone	0.039	-0.213	-0.375	-0.434	-0.501	-0.351	0.635	10.596	0.919	1.559	23	3	3	0	34	0.751	0.008	0.050	0.000	0.396	4.722	0.854
Prasium majus	0.536	0.563	0.068	0.188	0.450	-1.365	0.243	29.927	0.388	0.377	5	0	11	6	29	0.164	0.000	0.497	0.263	0.497	3.332	0.425
Ranunculus paludosus	0.459	-1.417	-0.355	0.043	0.383	-0.519	0.361	41.328	0.586	1.032	3	2	7	0	13	0.154	0.016	0.809	0.000	0.592	0.773	0.444
Scandix sp.	0.385	0.720	0.195	0.145	-2.729	-1.289	0.228	44.316	0.313	-0.223	4	7	4	2	18	0.012	0.972	0.010	0.005	0.586	1.575	0.880
Sedum confertiflorum	0.328	0.611	0.046	0.146	0.096	-1.176	0.249	7.432	0.389	0.390	4	2	8	3	19	0.385	0.037	0.309	0.239	0.709	1.260	0.422
Serapias cordigera	0.074	-0.524	-0.004	-0.192	-0.461	-0.398	0.295	6.380	0.530	1.461	27	0	0	0	27	1.000	0.000	0.000	0.000	0.140	4.519	0.750
Serapias vomeracea	0.169	1.269	0.071	-0.053	-0.553	-0.833	0.227	14.667	0.362	1.115	12	0	0	0	14	0.990	0.000	0.000	0.000	0.245	1.874	0.908
Taraxacum sp.	0.461	-0.537	-0.288	0.180	0.358	-0.623	0.400	16.756	0.670	0.902	3	0	0	0	5	0.656	0.000	0.000	0.000	0.320	0.037	0.353
Teucrium divaricatum	0.283	1.231	0.198	-0.033	-1.272	-0.796	0.271	30.701	0.291	1.209	9	0	8	20	46	0.083	0.000	0.253	0.581	0.612	4.665	0.428
Tolpis barbata	0.312	-0.167	-0.120	0.119	0.429	-0.716	0.336	18.790	0.570	0.807	2	0	1	1	6	0.667	0.000	0.022	0.088	0.500	0.037	0.373
Trifolium angustifolium	0.251	0.744	0.065	0.037	0.334	-1.232	0.209	13.092	0.331	0.447	6	1	1	0	11	0.831	0.032	0.012	0.000	0.545	0.891	0.460
Trifolium arvense	0.342	0.654	0.075	0.095	0.680	-1.303	0.223	19.011	0.360	0.329	0	1	5	0	9	0.000	0.080	0.426	0.000	0.346	0.773	0.318
Trifolium campestre	0.215	-0.453	-0.117	0.066	0.618	-0.671	0.317	20.909	0.526	0.687	8	2	9	1	22	0.767	0.097	0.115	0.006	0.645	2.315	0.401
Trifolium glanduliferum	0.281	0.563	0.039	0.079	0.491	-1.168	0.231	35.924	0.383	0.457	12	15	9	4	44	0.082	0.802	0.072	0.025	0.637	4.143	0.564
Tuberaria guttata	0.177	-0.266	0.081	-0.246	-0.369	-0.460	0.076	9.586	0.252	1.528	7	0	1	1	29	0.062	0.000	0.808	0.003	0.709	2.973	0.313

Table 3.S3. Results of the univariate tests of the multivariate generalized linear models, showing which response variables (i.e. VOCs) in the community plant–volatilome network show significant effects ($p<0.050$) against nectar or the colorimetric and spectral properties of floral reflectance. Explanatory variables are those that showed statistically significant effects in Table 3.1. Statistics were acquired with ANOVA (likelihood ratio tests) using 999 bootstrap iterations via PIT-trap residual resampling. For details on the models applied see Materials and Methods.

Class	VOC[1]	r_{hex}		$r_{hex}{:}\theta_{hex}$		NMDS1		NMDS2		φ_{tet}		*Brightness*		Nectar	
		Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p.
Aliphatics	1-Hexadecanol, 2-methyl-			9.39	0.018	9.393	0.016								
	2-Heptadecanone											4.784	0.047	5.974	0.017
	2-Pentadecanone											4.784	0.047	5.974	0.017
	2-Tridecanone											4.784	0.047	5.974	0.017
	(Z)-3-Hexenal	9.399	0.014					9.287	0.021	4.822	0.045	5.224	0.04		
	(Z)-5-Nonadecene	9.363	0.018												
	(Z)-7-Hexadecene									9.163	0.007				
	9-Nonadecene					4.165	0.041	9.336	0.007						
	Acetic acid, decyl ester	9.363	0.018												
	AL 55, 43, 41, 69, 83, 57	12.134	0.004					6.558	0.018			7.277	0.017	5.974	0.017
	AL 43, 72, 57, 58, 42, 39					9.38	0.019	5.354	0.035						
	AL 57, 71, 85, 56, 41, 197					9.38	0.019	5.354	0.035						
	AL 57, 71, 43, 85, 41, 56									8.254	0.024				
	AL 131, 43, 84, 113, 56, 69													5.974	0.015
	AL 55, 83, 69, 97, 57, 41											9.13	0.009		
	AL 83, 97, 55, 69, 57, 43	9.363	0.018			4.165	0.041	9.336	0.007						
	AL 43, 71, 55, 41, 82, 69											9.13	0.009		
	AL 88, 55, 101, 41, 185, 69											9.13	0.009		
	AL 57, 43, 71, 41, 85, 55	9.363	0.018			4.165	0.041	9.336	0.007						
	AL 57, 43, 75, 85, 41, 99	9.363	0.018			4.165	0.041	9.336	0.007						
	AL 57, 71, 43, 85, 41, 55	9.605	0.003					4.969	0.031					12.754	0.004
	AL 57, 71, 43, 85, 55, 99	9.363	0.018			4.165	0.041	9.336	0.007						
	Decanal													7.363	0.015
	Dodecanal	4.611	0.034												

Class	VOC[1]	r_{hex}		$r_{hex}{:}\theta_{hex}$		NMDS1		NMDS2		φ_{tet}		*Brightness*		Nectar	
		Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p.*
	Dodecanoic acid, 1-methylethyl ester											9.13	0.009		
	Dodecanoic acid, ethyl ester	9.363	0.018												
	Eicosane					4.165	0.041	9.336	0.007						
	Ethyl 9-hexadecenoate											9.13	0.009		
	Heptadecane													7.309	0.012
	Heptanol											9.13	0.009		
	Hexadecane, 2,6,10,14-tetramethyl-	9.363	0.018			4.165	0.041	9.336	0.007						
	Hexadecane, 2-methyl-									7.274	0.016				
	Hexadecane, 4-methyl-	10.742	0.003			15.822	0.001	15.976	0.001					5.974	0.006
	Hexadecanoic acid, ethyl ester											9.13	0.009		
	Hexanoic acid, methyl ester									10.063	0.004				
	Nonadecane	9.964	0.004					5.169	0.031			7.336	0.014	9.247	0.002
	Nonanal									4.173	0.043				
	Nonanoic acid, 9-oxo-, ethyl ester											9.13	0.009		
	Octadecanal							4.387	0.048						
	Octane, 1,1'-oxybis-											9.13	0.009		
	Palmitic acid, isopropyl ester											5.534	0.037		
	Tetradecanal	12.134	0.004					6.558	0.018			7.277	0.017	5.974	0.017
	Tetradecanoic acid, ethyl ester											9.13	0.009		
	Tricosane	9.363	0.018			4.165	0.041	9.336	0.007						
Benzenoids and phenylpropanoids	Anisole, *o*-methyl-													2.901	0.02
	BE 124, 137, 55, 180, 125, 51	9.399	0.014					9.287	0.021	4.822	0.045	5.224	0.04		
	Benzoic acid, methyl ester			5.012	0.041					8.942	0.004				
	Benzyl Alcohol			6.275	0.017										
	Benzyl isovalerate									8.254	0.024				
	p-Cresol									8.254	0.024				
	Phenylethyl alcohol											4.241	0.04		
C5 Branch-chained compounds	2-Methylbutyric acid, butyl ester											5.534	0.037		
	2-Methylbutyric acid, 3-methylbutyl ester											5.534	0.037		

Class	VOC[1]	r_{hex}		$r_{hex}{:}\theta_{hex}$		NMDS1		NMDS2		φ_{tet}		*Brightness*		Nectar	
		Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	$p.$
	C5 85, 57, 70, 43, 41, 71											5.534	0.037		
	C5 85, 70, 57, 43, 71, 41											5.534	0.037		
	C5 84, 43, 69, 71, 89, 55											5.534	0.037		
	C5 54, 57, 85, 69, 43, 41											5.534	0.037		
Diterpenes	DI 68, 93, 67, 81, 121, 107									8.254	0.024				
	DI 43, 108, 95, 275, 257, 81			9.39	0.018	9.393	0.016								
	DI 257, 285, 81, 192, 95, 177			9.39	0.018	9.393	0.016								
	DI 189, 93, 119, 107, 190, 133			9.39	0.018	9.393	0.016								
	Manoyl oxide			4.364	0.05										
	Sclarene			9.39	0.018	9.393	0.016								
	Sclareoloxide			9.39	0.018	9.393	0.016								
Irregular terpenes	Dihydro-β-ionone			9.39	0.018	9.393	0.016								
	Hexahydrofarnesyl acetone													4.664	0.04
Miscellaneous	1,3-Cyclopentanedione					9.38	0.019	5.354	0.035						
	2-Cyclopentene-1,4-dione					9.38	0.019	5.354	0.035						
	Cyclopentadecanone											9.13	0.009		
	UN 69, 79, 41, 107 150 135	9.363	0.018			4.165	0.041	9.336	0.007						
Monoterpenes	3-Carene					6.217	0.031								
	Bornyl acetate									8.254	0.024				
	Camphor											9.489	0.002		
	(Z)-Citral									9.163	0.007				
	Citronellol					9.38	0.019	5.354	0.035						
	(Z)-Cyclohexanemethanol, 4-(1-methylethyl)-					7.426	0.024								
	(E)-Cyclohexanemethanol, 4-(1-methylethyl)-					9.38	0.019	5.354	0.035						
	Cymene													5.069	0.05
	Limonene					4.508	0.04								
	Eucalyptol	4.263	0.043									4.595	0.034		
	Fenchone					6.217	0.031								
	Isopinocamphone											5.534	0.037		

Class	VOC[1]	r_{hex}		$r_{hex}{:}\theta_{hex}$		NMDS1		NMDS2		φ_{tet}		*Brightness*		Nectar	
		Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p.*
	Isopinocarveol											5.534	0.037		
	MO 121, 105, 136, 79, 28, 91									9.163	0.007				
	MO 93, 91, 77, 79, 136, 41	9.793	0.002												
	MO 93, 91, 77, 79, 92, 121									9.163	0.007				
	MO 121, 93, 136, 91, 77, 79									9.163	0.007				
	MO 91, 134, 119, 105, 92, 117									9.163	0.007				
	MO 95, 93, 110, 121, 41, 136			9.39	0.018	9.393	0.016								
	β-Myrcene													5.402	0.028
	Myrtenol											9.489	0.002		
	Perillene									8.254	0.024				
	α-Pinene	5.707	0.038												
	p-Menth-1-en-8-ol			9.39	0.018	9.393	0.016								
	Terpinen-4-ol											5.534	0.037		
	(*Z*)-*β*-Terpineol											4.707	0.039		
	Terpinolene									9.163	0.007				
	(*Z*)-Verbenone	4.167	0.04												
N-compounds	2-Pentanone, 4-methyl-, oxime	9.399	0.014					9.287	0.021	4.822	0.045	5.224	0.04		
	Butyl aldoxime, 2-methyl-, anti-	9.363	0.018			4.165	0.041	9.336	0.007						
	Butyl aldoxime, 2-methyl-, syn-	3.898	0.05												
	NI 73, 87, 56, 41, 100, 69	9.399	0.014					9.287	0.021	4.822	0.045	5.224	0.04		
Sesquiterpenes	Aristolene									8.254	0.024				
	Aromadendrene			10.642	0.003	8.661	0.021								
	β-Bergamotene			10.223	0.001	7.091	0.021								
	β-Bourbonene	9.895	0.004	17.629	0.001	5.116	0.038								
	1,4-Cadinadiene			9.39	0.018	9.393	0.016								
	δ-Cadinene					11.713	0.002								
	Carotol									9.163	0.007				
	α-Caryophyllene					6.06	0.021								
	L-Calamenene			9.39	0.018	9.393	0.016								

Class	VOC[1]	r_{hex}		r_{hex}:θ_{hex}		NMDS1		NMDS2		φ_{tet}		*Brightness*		Nectar	
		Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p.
	α-Cubebene			9.39	0.018	9.393	0.016								
	β-Cubebene			13.508	0.001	8.797	0.014								
	β-Elemene			9.39	0.018	9.393	0.016								
	α-Gurjunene			10.642	0.003	8.661	0.021								
	Nerolidol													2.901	0.031
	SE 119, 105, 133, 93, 91, 107											5.534	0.037		
	SE 95, 147, 96, 94, 91, 79			9.39	0.018	9.393	0.016								
	SE 57, 43, 41, 161, 119, 105	15.831	0.001	4.686	0.043			8.723	0.017	6.423	0.018				
	SE 161, 120, 105, 91, 93, 133			5.172	0.032	7.226	0.012								
	SE 93, 81, 67, 107, 147, 168									9.163	0.007				
	SE 161, 91, 93, 105, 119, 107			9.39	0.018	9.393	0.016								
	SE 161, 105, 91, 79, 81, 93					10.904	0.001								
	SE 119, 121, 189, 93, 79, 204											5.534	0.037		
	SE 204, 81, 119, 134, 39, 162			9.39	0.018	9.393	0.016								
	SE 189, 133, 204, 109, 95, 147			9.39	0.018	9.393	0.016								
	SE 105, 91, 93, 107, 121, 94			9.39	0.018	9.393	0.016								
	SE 161, 105, 91, 119, 81, 79							9.287	0.021	4.822	0.045	5.224	0.04		
	SE 91, 107, 133, 204, 95, 55	9.399	0.014	4.346	0.049	5.396	0.028								
	SE 161, 105, 91, 119, 204, 162					13.133	0.001								
	SE 93, 123, 119, 81, 107, 121			9.39	0.018	9.393	0.016								
	SE 119, 105, 91, 55, 81, 41			9.39	0.018	9.393	0.016								
	SE 81, 135, 204, 43, 71, 109			9.39	0.018	9.393	0.016								
	SE 81, 80, 123, 161, 79, 41									9.163	0.007				
	SE 81, 93, 68, 41, 107, 67			9.39	0.018	9.393	0.016								
	SE 161, 105, 93, 91, 41, 119									9.163	0.007				
	β-Selinene			9.39	0.018	9.393	0.016								
	Spathulenol					10.904	0.001								
Unknown	UN 67, 107, 95, 109, 138, 81					9.38	0.019	5.354	0.035						
	UN 105, 109, 81, 123 , 207, 69			9.39	0.018	9.393	0.016								

Class	VOC[1]	r_{hex}		$r_{hex}{:}\theta_{hex}$		NMDS1		NMDS2		φ_{tet}		*Brightness*		Nectar	
		Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p.*
	UN 204, 109, 133, 81, 43, 93			9.39	0.018	9.393	0.016								
	UN 91, 92, 65, 39, 63, 51									8.254	0.024				
	UN 67, 107, 123, 138, 95, 109					9.38	0.019	5.354	0.035						
	UN 79, 110, 95, 77, 93, 94									9.163	0.007				
	UN 59, 43, 132, 131, 71, 117									8.254	0.024				
	UN 57, 71, 43, 85, 41, 56													2.901	0.02
	UN 119, 43, 59, 134, 91, 79									9.163	0.007				
	UN 41, 111, 83, 159, 243, 55													2.901	0.02
	UN 207, 161, 105, 119, 43, 121					6.217	0.031								
	UN 68, 95, 82, 43, 57, 123													2.901	0.031
	UN 161, 207, 105, 43, 121, 204			9.39	0.018	9.393	0.016								
	UN 79, 45, 67, 91, 81, 41	9.363	0.018			4.165	0.041	9.336	0.007						
	UN 80, 43, 79, 94, 91, 69									9.163	0.007				
	UN 119, 161, 105, 204, 179, 82			9.39	0.018	9.393	0.016								
	UN 109, 121, 107, 81, 91, 59			9.39	0.018	9.393	0.016								
	UN 43, 91, 93, 121, 79, 107	6.298	0.02												
	UN 189, 93, 119, 107, 190, 133			9.39	0.018	9.393	0.016								
	UN 112, 57, 70, 71, 43, 211											5.534	0.037		
	UN 275, 173, 159, 185, 270, 69	9.399	0.014					9.287	0.021	4.822	0.045	5.224	0.04		
	UN 191, 81, 69, 95, 109, 192			9.39	0.018	9.393	0.016								
	UN 43, 333, 255, 190, 135, 81			9.39	0.018	9.393	0.016								
	UN 41, 69, 55, 39, 70, 53					9.38	0.019	5.354	0.035						

[1]Unless otherwise verified with an authentic standard, positions of double bonds and methyl groups are only suggestive based on the NIST 05 Mass Spectral Library hits and are not intended to imply precise chemical determination. See Table S8 for the verification status of each compound.

Table 3.S4. Results of the univariate tests of the multivariate generalized linear models, showing which response variables (i.e. VOCs) in each one of the plant–volatilome network subsets (containing only aliphatics or benzenoids or monoterpenes or sesquiterpenes) show significant effects ($p<0.050$) against nectar or the colorimetric and spectral properties of floral reflectance. Explanatory variables are those that showed statistically significant effects in Table 3.1. Statistics were acquired with ANOVA (likelihood ratio tests) using 999 bootstrap iterations via PIT-trap residual resampling. For details on the models applied see Materials and Methods.

Sub-network	VOC[1]	r_{hex} Dev.	p	NMDS2 Dev.	p	*Brightness* Dev.	p	Nectar Dev.	p	*Chroma* Dev.	p	r_{tet} Dev.	p	φ_{tet} Dev.	p	$r_{hex}:\theta_{hex}$ Dev.	p	NMDS1 Dev.	p
Aliphatics	1-Heptadecanol					5.534	0.03												
	1-Octen-3-yl-n-propionate					5.534	0.03												
	1-Undecene					5.534	0.03	2.901	0.035										
	2-Heptadecanone					4.784	0.047	5.974	0.015										
	2-Pentadecanone					4.784	0.047	5.974	0.015										
	2-Tridecanone					4.784	0.047	5.974	0.015										
	(Z)-3-Hexenal	9.399	0.009	9.287	0.023														
	AL 55, 43, 41, 69, 83, 57	12.134	0.003	6.558	0.027	7.277	0.025	5.974	0.011										
	9-Nonadecene	9.363	0.013	9.336	0.015														
	Acetic acid, pentyl ester							2.901	0.044										
	AL 43, 72, 57, 58, 42, 39			5.354	0.042														
	AL 57, 71, 85, 56, 41, 197			5.354	0.042														
	AL 131, 43, 84, 113, 56, 69							5.974	0.01										
	AL 55, 83, 69, 97, 57, 41					9.13	0.01												
	AL 83, 97, 55, 69, 57, 43	9.363	0.013	9.336	0.015														
	AL 43, 71, 55, 41, 82, 69					9.13	0.01												
	AL 88, 55, 101, 41, 185, 69					9.13	0.01												
	AL 57, 71, 43, 85, 55, 99	9.363	0.013	9.336	0.015														
	Decanal							7.363	0.008										
	Dodecanal	4.611	0.043																
	AL 57, 43, 71, 41, 85, 55	9.363	0.013	9.336	0.015														
	Dodecanoic acid, ethyl ester					9.13	0.01												
	Eicosane	9.363	0.013	9.336	0.015														

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Sub-network	VOC[1]	r_{hex}		NMDS2		*Brightness*		Nectar		*Chroma*		r_{tet}		φ_{tet}		$r_{hex}:\theta_{hex}$		NMDS1	
		Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*
	Ethyl 9-hexadecenoate					9.13	0.01												
	Heptadecane							7.309	0.016										
	AL 57, 43, 75, 85, 41, 99	9.363	0.013	9.336	0.015														
	Heptanol					9.13	0.01												
	Hexadecane, 2,6,10,14-tetramethyl-	9.363	0.013	9.336	0.015														
	Hexadecane, 4-methyl-	10.742	0.001	15.976	0.001					5.974	0.006								
	Hexadecanoic acid, ethyl ester					9.13	0.01												
	Palmitic acid, isopropyl ester					5.534	0.03												
	Nonadecane	9.964	0.004	5.169	0.044	7.336	0.023	9.247	0.001										
	Nonanoic acid, 9-oxo-, ethyl ester					9.13	0.01												
	Octane, 1,1'-oxybis-					9.13	0.01												
	AL 57, 71, 43, 85, 41, 55	9.605	0.003	4.969	0.036			12.754	0.001										
	Tetradecanal	12.134	0.003	6.558	0.027	7.277	0.025												
	Tetradecanoic acid, ethyl ester					9.13	0.01			5.974	0.011								
	Tricosane	9.363	0.013	9.336	0.015														
	(*Z*)-5-Nonadecene	9.363	0.013	9.336	0.015														
Benzenoids	Benzoic acid, 3-methyl-2-buten-1-ol ester									8.724	0.012								
	3-Methoxy-4-propoxybenzaldehyde									8.724	0.012								
	BE 105, 77, 68, 67, 41, 123									8.724	0.012								
	BE 103, 77, 51, 132, 104, 102									8.724	0.012								
	Benzyl Alcohol									4.641	0.039								
	Benzoic acid, benzyl ester									10.618	0.003								
	Benzyl isovalerate									8.724	0.012								
	Benzyl nitrile									5.741	0.044								
	Benzyl pentanoate									8.724	0.012								
	Estragole									6.182	0.028								
	p-Allylphenol									8.724	0.012								
	p-Cresol									5.741	0.044								
Monoterpenes	Myrtenyl acetate											8.683	0.019						

Sub-network	VOC[1]	r_{hex}		NMDS2		Brightness		Nectar		Chroma		r_{tet}		φ_{tet}		$r_{hex}{:}\theta_{hex}$		NMDS1	
		Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p	Dev.	p
	(Z)-Citral													9.163	0.016				
	Fenchol											8.683	0.019						
	Fenchyl acetate											8.683	0.019						
	L-Bornyl acetate											8.683	0.019						
	MO 93, 91, 77, 79, 92, 121													9.163	0.016				
	MO 121, 93, 136, 91, 77, 79													9.163	0.016				
	MO 91, 134, 119, 105, 92, 117													9.163	0.016				
	MO 121, 105, 136, 79, 28, 91													9.163	0.016				
	MO 95, 93, 121, 136, 109, 110													8.254	0.024				
	p-Cymen-8-ol											5.607	0.037						
	Perillene													8.254	0.024				
	Terpinolene													9.163	0.016				
	Verbenol											8.683	0.019						
Sesquiterpenes	Aromadendrene															10.642	0.001	8.661	0.023
	1,4-Cadinadiene															9.39	0.026	9.393	0.014
	L-Calamenene															9.39	0.026	9.393	0.014
	SE 95, 147, 96, 94, 91, 79															9.39	0.026	9.393	0.014
	SE 57, 43, 41, 161, 119, 105															4.686	0.043		
	SE 161, 120, 105, 91, 93, 133															5.172	0.037	7.226	0.008
	SE 161, 91, 93, 105, 119, 107															9.39	0.026	9.393	0.014
	SE 161, 105, 91, 79, 81, 93																	10.904	0.005
	SE 204, 81, 119, 134, 39, 162															9.39	0.026	9.393	0.014
	SE 189, 133, 204, 109, 95, 147															9.39	0.026	9.393	0.014
	SE 105, 91, 93, 107, 121, 94															9.39	0.026	9.393	0.014
	SE 91, 107, 133, 204, 95, 55															4.346	0.044	5.396	0.024
	SE 161, 105, 91, 119, 204, 162															4.13	0.05	13.133	0.002
	SE 93, 123, 119, 81, 107, 121															9.39	0.026	9.393	0.014
	SE 119, 105, 91, 55, 81, 41															9.39	0.026	9.393	0.014
	SE 81, 135, 204, 43, 71, 109															9.39	0.026	9.393	0.014

Sub-network	VOC[1]	r_{hex}		NMDS2		*Brightness*		Nectar		*Chroma*		r_{tet}		φ_{tet}		$r_{hex}{:}\theta_{hex}$		NMDS1	
		Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*	Dev.	*p*
	SE 81, 93, 68, 41, 107, 67															9.39	0.026	9.393	0.014
	α-Caryophyllene																	6.06	0.03
	α-Cubebene															9.39	0.026	9.393	0.014
	α-Gurjunene															10.642	0.001	8.661	0.023
	β-Bergamotene															10.223	0.002	7.091	0.019
	β-Bourbonene															17.629	0.001	5.116	0.031
	β-Cubebene															13.508	0.002	8.797	0.012
	β-Elemene															9.39	0.026	9.393	0.014
	β-Selinene															9.39	0.026		
	δ-Cadinene																	11.713	0.004

[1] Unless otherwise verified with an authentic standard, positions of double bonds and methyl groups are only suggestive based on the NIST 05 Mass Spectral Library hits and are not intended to imply precise chemical determination. See Table S8 for the verification status of each compound.

Table 3.S5. The effect of nectar on the floral colorimetric and spectral properties of the plants in the community. The results of ten phylogenetic GLS models are presented. Response variables are shown in rows. AIC values are presented both for the fitted and for the null models (~1). Bold digits denote statistical significance (≤ 0.050).

		Nectar	~1
r_{hex}	$F_{1,39}$	13.10	
	p-value	**<0.001**	
	AIC	-50.3	-41.2
θ_{hex}	$F_{1,39}$	0.76	
	p-value	0.388	
	AIC	116.6	104.1
NMDS1	$F_{1,39}$	2.77	
	p-value	0.104	
	AIC	-19.0	-18.0
NMDS2	$F_{1,39}$	16.63	
	p-value	**<0.001**	
	AIC	-30.7	-25.2
θ_{tet}	$F_{1,39}$	0.01	
	p-value	0.910	
	AIC	135.0	133.8
φ_{tet}	$F_{1,39}$	8.75	
	p-value	**0.005**	
	AIC	73.0	79.3
r_{tet}	$F_{1,39}$	0.03	
	p-value	0.861	
	AIC	-51.3	-53.3
Chroma	$F_{1,39}$	1.05	
	p-value	0.311	
	AIC	-16.9	-17.8
Hue	$F_{1,39}$	2.31	
	p-value	0.137	
	AIC	63.1	65.3
Brightness	$F_{1,39}$	2.00	
	p-value	0.124	
	AIC	337.5	345.6

Table 3.S6. Results of phylogenetic GLS models showing the relationship of colorimetric and chemical properties of the floral phenotype in the community. Response variables are shown in rows. AIC values for each model, including the null model (~1) are given. For details on the models, see Materials and Methods. Alip: Aliphatics; Benz: Benzenoids and phenylpropanoids; Mono: Monoterpenes; Sesq: Sesquiterpenes. %Class ER: proportion of the class in the sum of emission rates. %Class count: proportion of the class in the sum of VOCs. For the interpretation of NMDS1 and NMDS2, refer to Fig. 3.S4. Numbers in bold denote statistical significance ($p \leq 0.050$).

		Trichromatic vision					Tetrachromatic vision				Spectral properties				~1
		r_{hex}	θ_{hex}	$r_{hex}{:}\theta_{hex}$	NMDS1	NMDS2	θ_{tet}	φ_{tet}	r_{tet}	$\theta_{tet}{:}\varphi_{tet}{:}r_{tet}$	*Chroma*	*Hue*	*Brightness*	*Chr:Bri:Hue*	
%Alip ER	$F_{1,39}$	1.85	0.01	0.47	3.26	0.55	0.88	2.52	3.42	0.62	3.97	2.69	5.84	0.31	
	p-value	0.182	0.911	0.499	0.079	0.462	0.353	0.120	0.072	0.437	0.053	0.109	**0.020**	0.580	
	AIC	53.8	55.6	55.2	52.4	55.1	54.7	53.1	52.2	55.0	51.7	52.9	49.9	55.3	53.7
%Benz ER	$F_{1,39}$	0.41	0.04	1.59	0.88	1.65	0.73	3.57	0.11	5.27	0.43	3.71	3.30	0.21	
	p-value	0.524	0.210	0.215	0.354	0.207	0.399	0.066	0.746	**0.027**	0.516	0.061	0.077	0.646	
	AIC	32.7	31.4	31.5	32.2	31.4	32.3	29.5	33.0	27.9	32.6	29.4	30.2	32.9	31.1
%Mono ER	$F_{1,39}$	0.00	8.26	4.12	0.24	0.61	0.07	0.00	3.18	1.28	1.75	0.39	2.23	0.00	
	p-value	0.939	**0.007**	**0.049**	0.626	0.440	0.789	0.933	0.082	0.265	0.194	0.537	0.144	0.937	
	AIC	45.3	39.0	41.1	45.0	44.6	45.2	45.3	42.1	44.0	43.5	44.9	43	45.3	43.3
%Sesq ER	$F_{1,39}$	5.61	5.69	11.22	7.82	3.29	0.50	1.94	0.14	1.25	1.50	0.05	4.61	0.06	
	p-value	**0.023**	**0.022**	**0.002**	**0.008**	0.077	0.482	0.172	0.706	0.271	0.228	0.818	**0.038**	0.810	
	AIC	-4.7	-4.6	-9.5	-6.7	-3.0	-0.2	-1.5	0.2	-0.9	-1.1	0.3	-3.7	0.3	-1.7
%Alip count	$F_{1,39}$	1.87	0.03	0.32	4.53	0.93	0.32	4.53	6.03	0.03	6.34	5.53	5.03	0.63	
	p-value	0.180	0.871	0.575	**0.040**	0.342	0.574	**0.040**	**0.019**	0.827	**0.016**	**0.024**	**0.031**	0.432	
	AIC	25.8	27.3	31.4	23.0	26.3	26.9	23.0	21.7	27.3	21.3	21.9	22.3	31.0	25.3
%Benz count	$F_{1,39}$	0.17	0.36	0.14	0.02	0.77	0.00	2.62	0.00	1.02	0.11	1.73	6.75	0.61	
	p-value	0.686	0.550	0.708	0.877	0.384	0.931	0.113	0.949	0.319	0.739	0.196	**0.013**	0.441	
	AIC	6.4	6.2	6.4	6.5	5.7	6.54	4.1	6.54	5.5	6.4	4.8	2.0	5.9	4.6
%Mono count	$F_{1,39}$	0.02	6.45	2.82	0.95	0.01	0.06	0.55	4.43	1.87	1.97	4.09	2.79	1.40	
	p-value	0.896	**0.015**	0.101	0.336	0.934	0.805	0.463	**0.042**	0.180	0.168	**0.050**	0.103	0.244	

		Trichromatic vision					Tetrachromatic vision				Spectral properties				
		r_{hex}	θ_{hex}	$r_{hex}{:}\theta_{hex}$	NMDS1	NMDS2	θ_{tet}	φ_{tet}	r_{tet}	$\theta_{tet}{:}\varphi_{tet}{:}r_{tet}$	Chroma	Hue	Brightness	Chr:Bri:Hue	~1
	AIC	21.3	15.3	18.6	20.3	21.3	21.3	20.8	17.4	19.5	19.4	17.3	18.9	19.9	19.3
%Sesq count	$F_{1,39}$	3.18	2.39	6.20	7.76	2.17	1.18	1.57	0.45	2.07	2.47	0.00	0.87	0.51	
	p-value	0.082	0.131	**0.017**	**0.008**	0.148	0.285	0.217	0.505	0.159	0.124	0.957	0.356	0.481	
	AIC	-5.8	-4.9	-8.4	-10.2	-5.0	-3.9	-4.4	-3.2	-4.8	-5.2	-2.7	-3.6	-3.3	-4.7
c	$F_{1,39}$	3.79	0.00	0.75	0.00	2.79	0.91	1.93	0.07	0.00	0.03	0.13	0.32	1.57	
	p-value	0.059	0.958	0.392	0.955	0.103	0.347	0.173	0.788	0.970	0.869	0.722	0.575	0.218	
	AIC	-27.7	-24.1	-24.4	-24.5	-26.8	-25.4	-26.4	-24.5	-24.5	-24.5	-24.5	-24.8	-26.0	-26.5
z	$F_{1,39}$	0.02	0.76	3.00	0.00	0.60	0.11	0.00	0.78	0.69	0.09	3.22	0.46	1.55	
	p-value	0.894	0.390	0.091	0.955	0.444	0.737	0.936	0.383	0.412	0.770	0.080	0.502	0.221	
	AIC	167.1	166.4	164.1	167.0	166.5	167	167.2	166.4	166.5	167.1	163.9	166.7	165.6	165.2
d'	$F_{1,39}$	0.67	0.20	0.12	0.00	0.80	1.20	0.02	0.64	2.00	0.20	1.38	0.10	0.95	
	p-value	0.416	0.656	0.731	1.000	0.375	0.281	0.890	0.429	0.165	0.659	0.247	0.753	0.336	
	AIC	-26.9	-26.4	-26.3	-26.2	-27.0	-27.4	-26.2	-26.8	-28.2	-26.4	-27.6	-26.3	-27.1	-28.2

Table 3.S7. Chromatic characterization of the seven modules of the plant–volatilome network of the community. Results of phylogenetic ANOVA are shown (*p*-phylo: *p*-value given phylogenetic relationships within the plant assemblage). Numbers in bold denote statistical significance ($p \leq 0.050$).

	$F_{6,34}$	*p*	*p*-**phylo**
r_{hex}	1.19	0.333	0.414
θ_{hex}	0.26	0.951	0.967
NMDS1	2.11	0.078	0.112
NMDS2	1.60	0.177	0.220
r_{tet}	1.87	0.114	0.155
φ_{tet}	1.16	0.353	0.453
θ_{tet}	1.15	0.353	0.405
Chroma	2.00	0.093	0.127
Hue	**2.67**	**0.031**	**0.047**
Brightness	1.55	0.192	0.252

Table 3.S8. Volatile organic compounds (VOCs) trapped in the floral headspace of the 41 entomophilous plants in the community. Compounds have been arbitrarily assigned to major classes based on the convention in the literature on floral volatiles (see *85*). For each compound, the Kovats retention index (KI) has been calculated using the retention times for n-alkane standards in the same chromatographic conditions. Compounds are presented in four categories of putative identification: (i) compounds written in bold match the KI and mass spectra (MS) of authentic standard compounds on the polar GC column, (ii) named compounds match published KI (footnotes) and MS library values but could not be verified with an authentic standard, (iii) compounds marked with § show strong MS library match (> 90%) but KI were not available or did not match, and (iv) compounds not vetted in any of these ways were left as unidentified, listing distinctive MS ion fragments in descending order of abundance and assigning to a putative class when fragments allowed. Note that the methods used (headspace–GC/MS) are not sufficient to establish the absolute configuration of these compounds; thus, positions of double bonds, methyl groups and specific enantiomers are only suggestive based on the NIST 05 Mass Spectral Library hits and are not intended to imply precise chemical determination.

Class	VOC	KI this study	KI literature	CAS number
Aliphatics	AL 57, 43, 41, 71, 85, 29	1071	-	-
	(Z)-3-Hexenal §	1118	-	6789-80-6
	1-Undecene §	1121	-	000821-95-4
	Acetic acid, pentyl ester §	1155	-	000628-63-7
	2-Heptanone	1164	-	000110-43-0
	Heptanal	1167	1163-1222[1]	000111-71-7
	Hexanoic acid, methyl ester §	1169	-	000106-70-7
	(E)-2-Hexenal	1204	1201 [2]	006728-26-3
	1-Tetradecene §	1231	-	1120-36-1
	(Z)-3-Hexen-1-ol, formate	1259	1258 [2]	033467-73-1
	Acetic acid, hexyl ester	1266	1268 [3]	000142-92-7
	Octanal §	1282	-	000124-13-0
	AL 55, 43, 41, 69, 83, 57 §	1282	-	-
	(E)-2-Hexenoic acid, methyl ester §	1283	-	013894-63-8
	1-Octen-3-one §	1295	-	000109-25-1
	9-Nonadecene §	1301	-	031035-07-1
	(Z)-3-Hexen-1-ol, acetate	1313	1308 [2]	003681-71-8
	(Z) or (E)-2-Heptenal §	1319	1318 [4]	018829-55-5
	(E)-2-Hexen-1-ol, acetate	1328	1323 [2]	002497-18-9
	1-Hexanol	1349	1351 [2]	000111-27-3
	Octen-1-ol acetate §	1377	-	-
	(Z)-3-Hexen-1-ol	1382	1378 [2]	000928-96-1
	2-Nonanone	1385	1386 [4]	000821-55-6
	Nonanal	1390	1396 [5]	000124-19-6
	(E)-2-Hexen-1-ol	1402	1400 [2]	000928-95-0
	(E)-2-Octenal	1427	1434 [5]	002548-87-0
	(Z)-4-Octenoic acid, methyl ester	1427	1418-1434[1]	021063-71-8
	1-Octen-3-ol-n-propionate §	1433	-	063156-02-5
	1-Octen-3-ol	1446	1456 [5]	003391-86-4

Class	VOC	KI this study	KI literature	CAS number
	AL 57, 43, 72, 29, 41, 55	1450	-	589-98-0
	Heptanol	1453	1457 [4]	053535-33-4
	AL 57, 71, 43, 85, 41, 55	1455	-	-
	AL 43, 72, 57, 58, 42, 39	1467	-	-
	AL 82, 67, 57, 85, 55, 41	1473	-	-
	(Z)-3-Hexenyl isovalerate §	1483	-	035154-45-1
	Decanal	1499	1498 [6]	000112-31-2
	(E)-2-Nonenal	1537	1542 [5]	018829-56-6
	(Z)-7-Decen-1-al §	1548	-	21661-97-2
	1-Octanol	1556	1546 [3]	000111-87-5
	AL 57, 71, 85, 56, 41, 197 §	1564	-	-
	(E,E)-2,6-Nonadienal §	1586	-	017587-33-6
	Hexadecane	1596	1600	000544-76-3
	2-Undecanone	1598	1592 [7]	000112-12-9
	Undecanal	1603	1609 [5]	000112-44-7
	Hexanoic acid, hexyl ester	1613	1599 [3]	006378-65-0
	AL 57, 43, 71, 41, 85, 55	1615	-	-
	(Z)-7-Hexadecene §	1622	-	035507-09-6
	Hexadecane, 4-methyl- §	1648	-	025117-26-4
	AL 57, 43, 75, 85, 41, 99	1652	-	-
	Hexadecane, 2-methyl-	1652	1661 [8]	001560-92-5
	1-Nonanol	1658	1666 [5]	000143-08-8
	AL 57, 71, 43, 85, 41, 56	1664	-	-
	AL 131, 43, 84, 113, 56, 69	1664	-	-
	Hexadecane, 2,6,10,14-tetramethyl- §	1664	-	000638-36-8
	Acetic acid, decyl ester	1683	1679 [4]	000112-17-4
	Heptadecane	1697	1700	000629-78-7
	Dodecanal	1711	1709 [5]	000112-54-9
	AL 55, 83, 69, 97, 57, 41	1729	-	-
	Octane, 1,1'-oxybis- §	1749	-	000629-82-3
	1-Decanol §	1759	-	000112-30-1
	AL 55, 43, 56, 70, 41, 69	1763	-	-
	Octadecane	1794	1800	000593-45-3
	2-Tridecanone	1809	1805 [7]	000593-08-8
	(Z)-5-Decen-1-ol	1809	1803 [1]	51652-47-2
	Octanoic acid, hexyl ester §	1812	-	001117-55-1
	Dodecanoic acid, 1-methylethyl ester §	1831	-	010233-13-3
	Dodecanoic acid, ethyl ester	1842	1844 [3]	000106-33-2
	Nonadecane	1896	1900	000629-92-5
	AL 57, 82, 41, 43, 55, 68	1922	-	-
	Tetradecanal	1923	1906-1947 [1]	000124-25-4
	Eicosane	1994	2000	000112-95-8
	2-Pentadecanone	2020	2011 [7]	002345-28-0
	Tetradecanoic acid, ethyl ester	2047	2027 [3]	000124-06-1

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	Nonanoic acid, 9-oxo-, ethyl ester §	2094	-	003433-16-7
	Heneicosane	2095	2100	000629-94-7
	AL 83, 97, 55, 69, 57, 43	2112	-	-
	AL 57, 41, 55, 96, 83, 68	2134	-	-
	Hexadecanal	2134	2098-2164 [1]	000629-80-1
	Pentadecanal	2134	1999-2060 [1]	002765-11-9
	2-Heptadecanone	2232	2196-2255 [1]	002922-51-2
	Palmitic acid, isopropyl ester	2237	2210-2251 [1]	000142-91-6
	Hexadecanoic acid, ethyl ester	2248	2243 [9]	000628-97-7
	AL 43, 71, 55, 41, 82, 69	2261	-	-
	Ethyl 9-hexadecenoate §	2295	-	054546-22-4
	(Z)-5-Nonadecene §	2295	-	1000131-11-8
	Tricosane	2295	2300	638-67-5
	AL 88, 55, 101, 41, 185, 69	2310	-	-
	Octadecanal	2347	2343 [10]	000638-66-4
	Octadecanoic acid, methyl ester	2423	2445 [11]	000112-61-8
	2-Nonadecanone §	2443	-	000629-66-3
	AL 57, 71, 43, 85, 55, 99	2495	-	-
	1-Heptadecanol §	2581	-	036653-82-4
	1-Hexadecanol, 2-methyl- §	2585	-	2490-48-4
	Hexacosane	2594	2600	000630-01-3
	AL 57, 71, 85, 69, 83, 97	2885	-	-
Benzenoids and phenylpropanoids	Styrene	1246	1254 [16]	000100-42-5
	Anisole, o-methyl- §	1405	-	000578-58-5
	BE 151, 166, 138, 54, 152, 119	1453	-	-
	Benzaldehyde	1526	1525 [12]	000100-52-7
	Benzoic acid, methyl ester	1624	1624 [13]	000093-58-3
	Phenylacetaldehyde	1643	1640 [13]	000122-78-1
	Acetophenone	1653	1611-1675 [1]	000098-86-2
	Benzoic acid, ethyl ester	1670	-	000093-89-0
	Estragole	1678	1685 [14]	000140-67-0
	Acetic acid, phenylmethyl ester	1731	1682-1759 [1]	000140-11-4
	1,4-Dimethoxybenzene §	1739	-	000150-78-7
	Benzenepropanal	1781	1723-1809 [1]	000104-53-0
	p-Anethole	1829	1798-1847 [1]	000104-46-1
	3,5-Dimethoxytoluene §	1855	-	004179-19-5
	2-Butanone, 3-phenyl- §	1863	-	000769-59-5
	Benzyl isovalerate §	1871	-	000103-38-8
	Benzyl alcohol	1876	1879 [15]	000100-51-6
	Benzyl pentanoate	1895	-	010361-39-4
	BE 131, 132, 103, 77, 78, 51	1902	-	-
	Phenylethyl alcohol	1913	1912 [16]	000060-12-8
	Benzyl nitrile	1928	1938 [5]	000140-29-4

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	Acetic acid, phenylpropyl ester	1946	1930 [17]	000122-72-5
	BE 131, 103, 162, 77, 16, 51	1958	-	-
	BE 117, 91, 132, 92, 45, 78	1992	-	-
	Phenol	1999	1962-2039[1]	000108-95-2
	Eugenol methyl ether	2009	2003 [9]	000093-15-2
	(*Z*)-Cinnamyl acetate §	2018	-	-
	***p*-Anisaldehyde**	2030	2011 [16]	000123-11-5
	(*E*)-Cinnamaldehyde	2044	2043 [18]	014371-10-9
	Benzoic acid, 3-methyl-2-buten-1-ol ester §	2058	-	005205-11-8
	BE 105, 77, 68, 67, 41, 123	2061	-	-
	2-methoxy benzoic acid, methyl ester	2067	2032-2088[1]	000606-45-1
	p-Cresol	2077	2050-2126[1]	000106-44-5
	Cinnamic acid methyl ester	2083	2047-2105[1]	000103-26-4
	BE 103, 77, 51, 132, 104, 102	2091	-	-
	Benzyl tiglate	2119	2109 [13]	037526-88-8
	Benzoic acid, (*Z*)-3-Hexen-1-ol ester	2133	2051-2148[1]	025152-85-6
	Acetophenone, 4'-methoxy-	2146	2115-2164[1]	000100-06-1
	(*E*)-Cinnamyl acetate	2153	2176 [19]	000103-54-8
	BE 124, 137, 55, 180, 125, 51	2160	-	-
	Eugenol	2168	-	000097-53-0
	(*Z*)-Cinnamyl alcohol	2172	-	-
	(*E*)-Cinnamyl alcohol	2286	2234-2289[1]	000104-54-1
	p-Allylphenol	2334	2234-2289[1]	000501-92-8
	3,4-Dimethoxybenzaldehyde	2392	2234-2289[1]	000120-14-9
	3-Methoxy-4-propoxybenzaldehyde §	2509	-	-
	(*E*)-4-Methoxycinnamaldehyde	2565	2544 [1]	024680-50-0
	3-Methoxycinnamaldehyde	2565	2565 [1]	056578-36-0
	BE 105, 123, 77, 122. 51, 106	2616	-	-
	BE 105, 123, 77, 56, 57, 69	2625	-	-
	Benzoic acid, benzyl ester	2645	-	000120-51-4
C5-branch chained compounds	3-Methylbutanoic acid, ethyl ester	1034	1041-1114 [1]	000108-64-5
	Butanoic acid, isobutyl ester	1143	1160 [9]	000539-90-2
	3-Methylbutyric acid, isobutyl ester	1182	1165 [20]	000589-59-3
	Butanoic acid, butyl ester	1209	-	000109-21-7
	2-Methylbutyric acid, butyl ester	1222	1239 [21]	015706-73-7
	3-Methylbutyric acid, butyl ester §	1244	-	000109-19-3
	Butanoic acid, 2-methylbutyl ester	1262	1272 [21]	051115-64-1
	2-Methylbutyric acid, 3-methylbutyl ester §	1272	-	027625-35-0
	C5 85, 57, 70, 43, 41, 71	1274	-	-
	2-Methylbutyric acid, 2-methylbutyl ester	1278	1284 [21]	002445-78-5
	C5 85, 70, 57, 43, 71, 41	1291	-	-
	Isovaleric acid, 2-methylbutyl ester §	1294	-	002445-77-4
	C5 84, 43, 69, 71, 89, 55	1299	-	-

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	Hexanoic acid, isobutyl ester	1352	1328-1373 [1]	-
	C5 54, 57, 85, 69, 43, 41	1384	-	-
	Butanoic acid, hexyl ester	1414	1419 [5]	002639-63-6
	2-Methylbutanoic acid, hexyl ester	1429	1431 [5]	010032-15-2
	Butanoic acid, (Z)-3-hexenyl ester	1460	1448 [2]	016491-36-4
	C5 82, 67, 71, 43, 41, 27	1464	-	-
	3-Methyl-2-butenoic acid, 3-methylbut-2-enyl ester §	1600	-	72779-06-7
Diterpenes	Sclarene	2232	2233 [22]	511-02-4
	DI 187, 119, 189, 105, 161, 91	2257	-	-
	DI 68, 93, 67, 81, 121, 107	2265	-	-
	Sclareoloxide §	2276	2223 [23]	-
	DI 109, 148, 257, 105, 133, 106	2301	-	-
	DI 43, 108, 95, 275, 257, 81	2375	-	-
	DI 257, 285, 81, 192, 95, 177	2375	-	-
	Manoyl oxide §	2376	-	001227-93-6
	DI 189, 93, 119, 107, 190, 133	2462	-	-
Irregular terpenes	(E)-4,8-dimethyl-1,3,7-nonatriene	1301	-	-
	6-Methyl-5-hepten-2-one	1332	1339 [5]	000110-93-0
	Dihydro-β-ionone	1828	-	031499-72-6
	Geranyl acetone	1854	1859 [5]	003796-70-1
	Neryl acetone	1858	1862 [5]	003796-70-1
	Hexahydrofarnesyl acetone	2125	-	000502-69-2
Miscellaneous	3-Cyclohexen-1-ol, acetate §	1428	-	10437-78-2
	1,3-Cyclopentanedione §	1559	-	003859-41-4
	2-Cyclopentene-1,4-dione §	1584	-	000930-60-9
	Naphthalene	1753	1762 [24]	000091-20-3
	Propanoic acid, 2-methyl-, 1-(1,1-dimethylethyl)-2-methyl-1,3-propanediyl ester	1879	-	-
	4-Methyl-5H-furan-2-one §	1895	1909-1912 [1]	006124-79-4
	(Z)-Jasmone	1953	1955 [15]	000488-10-8
	Cyclopentadecanone §	2061	-	000502-72-7
Monoterpenes	**α-Pinene**	939	1008-1052 [1]	80-56-8
	β-Pinene	942	1074-1133 [1]	000127-91-3
	α-Thujene §	957	1003-1038 [1]	002867-05-2
	Camphene §	1031	1040-1114 [1]	000079-92-5
	MO 93, 91, 77, 79, 136, 41	1095	-	-
	MO 93, 91, 77, 79, 92, 121	1126	-	-
	MO 93, 91, 77, 92, 136, 94	1144	-	-
	α-Phellandrene	1145	1140-1186 [1]	000099-83-2
	β-Myrcene	1145	1128-1180 [1]	000123-35-3
	MO 121, 93, 136, 91, 77, 79	1161	-	-
	Limonene	1186	1187 [13]	005989-27-5
	MO 93, 91, 77, 136, 79, 94	1193	-	-

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	β-Phellandrene	1195	1196 [13]	000555-10-2
	Eucalyptol	1197	1181-1231 [1]	000470-82-6
	(*Z*)-*β*-Ocimene	1225	1232 [25]	003779-61-1
	γ-Terpinene	1235	1238 [26]	000099-85-4
	3-Carene	1241	1242 [26]	013466-78-9
	(*E*)-*β*-Ocimene	1242	1238 [5]	003338-55-4
	Cymene	1263	1246-1296 [1]	-
	Terpinolene	1279	1274 [26]	000586-62-9
	MO 93, 121, 136, 91, 79, 77	1281	-	-
	MO 121, 105, 136, 79, 28, 91	1368	-	-
	(*Z*)-Neo-allo-ocimene	1368	1373 [27]	007216-56-0
	α-Pinene oxide §	1379	-	001686-14-2
	Fenchone	1403	1388-1432 [1]	004695-62-9
	Perillene	1414	1409-1431 [1]	000539-52-6
	MO 91, 134, 119, 105, 92, 117	1426	-	-
	MO 119, 91, 134, 77, 79, 93	1443	-	-
	(*Z*)-β-terpineol §	1466	1437-1444 [1]	007299-41-4
	MO 71, 93, 43, 81, 111, 121	1469	-	-
	(*Z*)-Linalool oxide (furanoid)	1473	1478 [5]	005989-33-3
	Fenchyl acetate	1476	-	013851-11-1
	Camphor	1528	-	000464-49-3
	Linalool	1543	1549 [15]	000078-70-6
	MO 93, 91, 79, 80, 77, 41	1544	-	-
	Pinocarvone	1550	1539-1600 [1]	030460-92-5
	Isopinocamphone	1554	1482-1578 [1]	000547-60-4
	Verbenol acetate §	1573	-	-
	MO 95, 93, 121, 136, 109, 110	1585	-	-
	Fenchol	1588	1574-1580 [27]	001632-73-1
	L-Bornyl acetate	1589	1584 [27]	092618-89-8
	Terpinen-4-ol	1605	1594 [26]	000562-74-3
	3,7-dimethyl-1,6-Nonadien-3-ol (ethyl linalool) §	1614	-	-
	4-Thujen-2α-yl acetate §	1628	-	53833-85-5
	Isopinocarveol	1661	1651 [28]	005947-36-4
	(*E*)-Pinocarveol	1667	1658 [29]	000547-61-5
	MO 95, 93, 110, 121, 41, 136	1678	-	-
	Verbenol	1688	1680 [30]	000473-67-6
	(*Z*)-Citral §	1690	-	005392-40-5
	Myrtenyl acetate §	1697	1720 [27]	-
	α-Terpinyl acetate	1700	1679-1709 [1]	80-26-2
	p-menth-1-en-8-ol	1705	1698 [5]	98-55-5
	Borneol	1710	1700 [31]	000507-70-0
	(*Z*)-Verbenone	1719	1676-1735 [1]	001196-01-6
	Verbenone	1724	1730 [32]	80-57-9

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	MO 67, 71, 69, 41, 43, 84	1746	-	-
	Geranyl acetate	1757	1756 [33]	000105-87-3
	Citronellol	1763	-	001117-61-9
	Nerol	1797	1806 [5]	000106-25-2
	Myrtenol	1799	1767 [16]	000515-00-4
	(*E,E*)-2,6-Dimethyl-3,5,7-octatrien-2-ol §	1815	-	-
	(*E*)-Cyclohexanemethanol, 4-(1-methylethyl)- §	1829	-	013674-19-6
	p-Menthan-7-ol §	1850	1800-1836 [1]	013828-37-0
	p-Cymen-8-ol §	1851	1843 [34]	001197-01-9
	(Z)-Cyclohexanemethanol, 4-(1-methylethyl)- §	1851	1823-1836 [1]	013828-37-0
	(Z)-Myrtanol	1879	1861 [35]	15358-92-6
	MO 150, 91, 107, 135, 79, 77	2062	-	-
	Carvacrol	2208	2173-2246 [1]	000499-75-2
N-compounds	NI 73, 87, 56, 41, 100, 69	794	-	-
	2-Pentanone, 4-methyl-, oxime (*m/z* 73, 43, 100, 115, 56, 69) §	828	-	000105-44-2
	Butyl aldoxime, 2-methyl-, *syn-*	1491	-	49805-56-3
	Butyl aldoxime, 2-methyl-, *anti-*	1510	-	49805-55-2
	Indole	2450	2398-2478 [1]	000120-72-9
Sesquiterpenes	*α*-Cubebene	1465	1472 [28]	017699-14-8
	SE 119, 105, 133, 93, 91, 107	1475	-	-
	SE 95, 147, 96, 94, 91, 79	1483	-	-
	SE 121, 93, 107, 91, 79, 94	1483	-	-
	Copaene	1488	1488 [33]	003856-25-5
	SE 161, 105, 119, 204, 91, 94	1489	-	-
	SE 57, 43, 41, 161, 119, 105	1493	-	-
	SE 161, 120, 105, 91, 93, 133	1499	-	-
	β-Bourbonene	1526	1531 [36]	005208-59-3
	SE 81, 80, 123, 161, 79, 41	1526	-	-
	SE 81, 93, 68, 41, 107, 67	1542	-	-
	α-Gurjunene	1542	1549 [37]	000489-40-7
	β-Cubebene	1547	1541 [32]	013744-15-5
	Aristolene	1578	1552-1589 [1]	006831-16-9
	SE 119, 69, 91, 107, 55, 105	1582	-	-
	SE 93, 81, 67, 107, 147, 168	1586	-	-
	β-Bergamotene	1588	1590 [27]	017699-05-7
	SE 161, 105, 91, 119, 120, 162	1593	-	-
	β-Elemene	1597	1536-1611 [1]	033880-83-0
	β-Caryophyllene	1609	1617 [27]	000087-44-5
	SE 161, 91, 93, 105, 119, 107	1621	-	-
	SE 161, 105, 91, 79, 81, 93	1650	-	-
	SE 161, 105, 91, 81, 79, 119	1655	-	-
	SE 91, 105, 161, 107, 133, 119	1661	-	-
	Aromadendrene	1661	1660-1683 [27]	000489-39-4

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	β-Farnesene	1667	1668-1671 [27]	007212-44-4
	SE 119, 121, 189, 93, 79, 204	1667	-	-
	SE 204, 81, 119, 134, 39, 162	1673	-	-
	SE 161, 105, 93, 91, 41, 119	1674	-	-
	SE 119, 81, 162, 93, 77, 133	1679	-	-
	α-Caryophyllene (= α-Humulene)	1680	1672 [27]	006753-98-6
	SE 189, 133, 204, 109, 95, 147	1689	-	-
	SE 161, 105, 91, 119, 79, 81	1691	-	-
	SE 105, 91, 93, 107, 121, 94	1696	-	-
	SE 93, 119, 107, 91, 41, 105	1709	-	-
	SE 161, 105, 91, 119, 81, 79	1720	-	-
	SE 91, 107, 133, 204, 95, 55	1721	-	-
	SE 161, 105, 91, 119, 204, 162	1731	-	-
	β-Selinene	1736	1727-1767 [27]	017066-67-0
	α-Selinene	1739	1729-1759 [27]	000473-13-2
	SE 121, 93, 161, 91, 107, 105	1744	-	-
	(E,E)-α-Farnesene	1747	1752 [5]	000502-61-4
	SE 134, 105, 81, 41, 55, 162	1763	-	-
	δ-Cadinene	1768	1761-1785 [27]	000483-76-1
	SE 69, 93, 161, 120, 79, 105	1773	-	-
	1,4-Cadinadiene	1795	1786 [27]	016728-99-7
	L-Calamenene	1846	1837-1842 [27]	000483-77-2
	SE 161, 105, 204, 43, 81	1951	-	-
	SE 93, 123, 119, 81, 107, 121	1999	-	-
	Caryophyllene oxide	2002	2000 [27]	001139-30-6
	Carotol	2027	-	000465-28-1
	Nerolidol	2034	2000-2044 [27]	007212-44-4
	SE 119, 105, 91, 55, 81, 41	2075	-	-
	SE 109, 161, 43, 107, 69, 93	2100	-	-
	Spathulenol	2138	2153 [27]	006750-60-3
	SE 81, 135, 204, 43, 71, 109	2271	-	-
Unknowns	UN 91, 92, 65, 39, 63, 51	984	-	-
	UN 41, 69, 55, 39, 70, 53	1118	-	-
	UN 69, 79, 41, 107 150 135	1298	-	-
	UN 67, 83, 69, 41, 82, 55	1353	-	-
	UN 69, 41, 82, 55, 39, 95	1391	-	-
	UN 67, 107, 123, 138, 95, 109	1437	-	-
	UN 79, 110, 95, 77, 93, 94	1469	-	-
	UN 67, 107, 95, 109, 138, 81	1487	-	-
	UN 79, 81, 77, 41, 93, 53	1487	-	-
	UN 81, 67, 55, 41, 82, 96	1570	-	-
	UN 59, 43, 132, 131, 71, 117	1601	-	-
	UN 57, 71, 43, 85, 41, 56	1664	-	-
	UN 81, 67, 96, 55, 82, 41	1768	-	-

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	UN 119, 43, 59, 134, 91, 79	1805	-	-
	UN 67, 81, 79, 95, 41, 55	1810	-	-
	UN 41, 111, 83, 159, 243, 55	1879	-	-
	UN 71, 43, 159, 111, 41, 56	1881	-	-
	UN 207, 161, 105, 119, 43, 121	1899	-	-
	UN 68, 95, 82, 43, 57, 123	1920	-	-
	UN 161, 207, 105, 43, 121, 204	1952	-	-
	UN 79, 45, 67, 91, 81, 41	2042	-	-
	UN 80, 43, 79, 94, 91, 69	2044	-	-
	UN 68, 67, 81, 54, 41, 95	2047	-	-
	UN 105, 109, 81, 123 , 207, 69	2082	-	-
	UN 119, 161, 105, 204, 179, 82	2083	-	-
	UN 43, 108, 93, 126, 111, 95	2374	-	-
	UN 109, 121, 107, 81, 91, 59	2415	-	-
	UN 43, 91, 93, 121, 79, 107	2437	-	-
	UN 189, 93, 119, 107, 190, 133	2462	-	-
	UN 112, 57, 70, 71, 43, 211	2512	-	-
	UN 275, 173, 159, 185, 270, 69	2518	-	-
	UN 191, 81, 69, 95, 109, 192	2766	-	-
	UN 204, 109, 133, 81, 43, 93	3037	-	-

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Table 3.S9. The phylogenetic signal in all variables used in the present Chapter. Different methods have been used according to variable type. Details are provided in Materials and Methods. K^*: Blomberg's K^*. Mantel r: Mantel statistic. D: statistic for binary traits. Only p-values implying significance shown ($p \leq 0.050$).

Trait	K^*	p	Mantel r	p	D	p[1]	Transitions observed[2]	Transitions randomized	p
r_{hex}	**0.32**	**0.041**							
θ_{hex}	0.22	ns							
Chroma	**0.46**	**0.004**							
Hue	**0.39**	**0.014**							
Brightness	0.24	ns							
NMDS1	**0.37**	**0.020**							
NMDS2	**0.43**	**0.006**							
r_{tet}	**0.49**	**0.008**							
φ_{tet}	0.21	ns							
θ_{tet}	0.36	ns							
Spectral DM[3]			0.04	ns					
Hexagon loci DM[3]			0.08	ns					
NMDS loci DM[3]			**0.17**	**0.014**					
%Aliphatics (ER)[4]	0.13	ns							
%Benzenoids (ER)[4]	0.24	ns							
%Monoterpenes (ER)[4]	0.30	ns							
%Sesquiterpenes (ER)[4]	**0.42**	**0.044**							
%Aliphatics (count)	0.17	ns							
%Benzenoids (count)	0.24	ns							
%Monoterpenes (count)	0.24	ns							
%Sesquiterpenes (count)	0.29	ns							
Total network – DM[3]			**0.18**	**0.008**					
Aliphatics sub-network – DM[3]			0.07	ns					
Benzenoids sub-network – DM[3]			0.04	ns					
Monoterpenes sub-network – DM[3]			**0.18**	**0.020**					
Sesquiterpenes sub-network – DM[3]			0.08	ns					
d'	**0.39**	**0.028**							
c	0.18	ns							
z	0.18	ns							

Trait	$K*$	p	Mantel r	p	D	p[1]	Transitions observed[2]	Transitions randomized	p
Module ID							24	25	ns
Nectar					0.09	**0.006**			

[1]Probability of D resulting from no (random) phylogenetic structure.
[2]Phylogenetic signal exists if only the observed transitions are significantly le
[3]DM: distance matrix.
[4]ER: emission rate.

SM CHAPTER 4
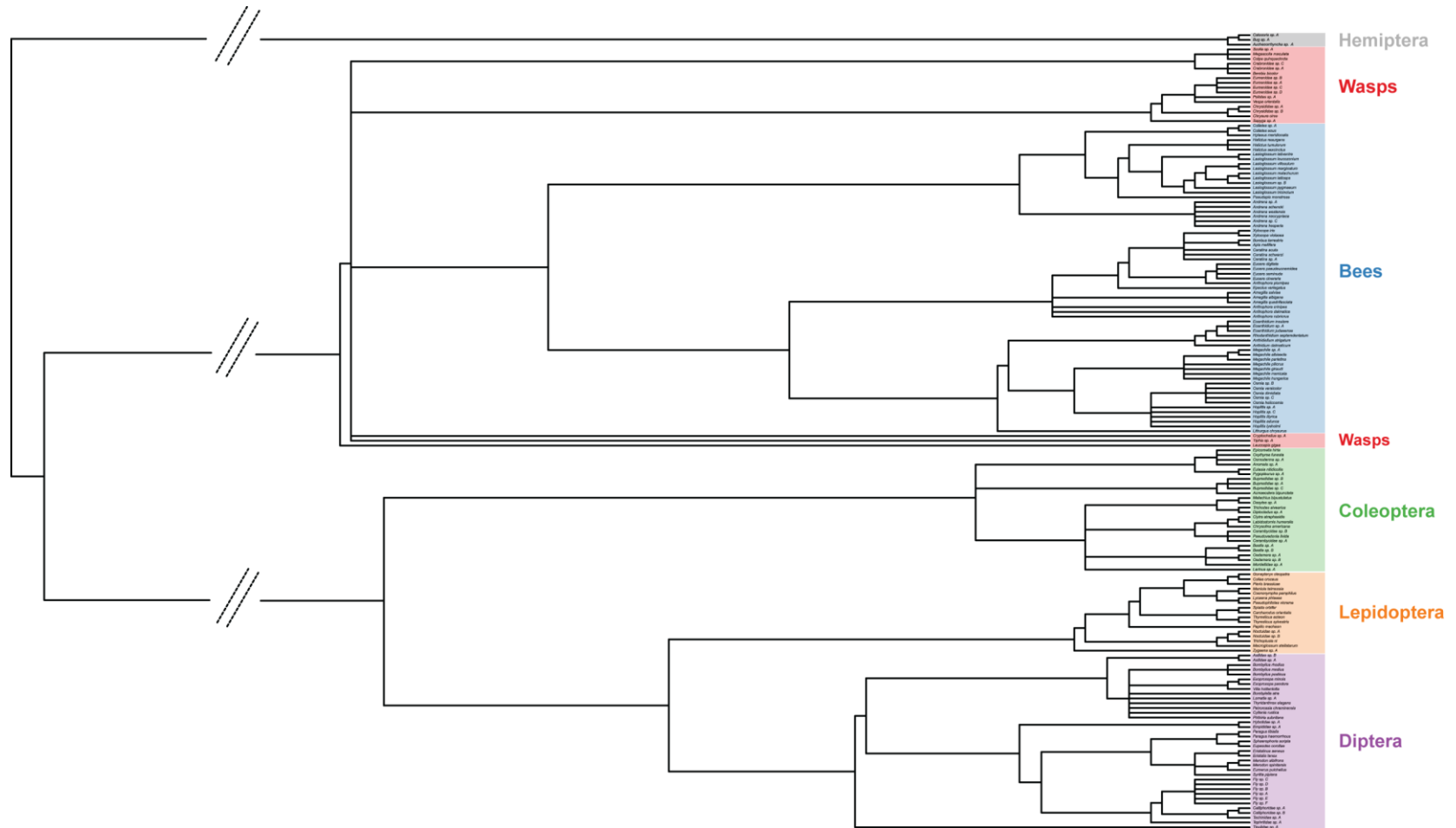
Fig. 4.S1. Phylogenetic relationships among the insects of the community. The rectangular cladogram (no branch lengths) was created using the online tool Open Tree of Life (*95*).
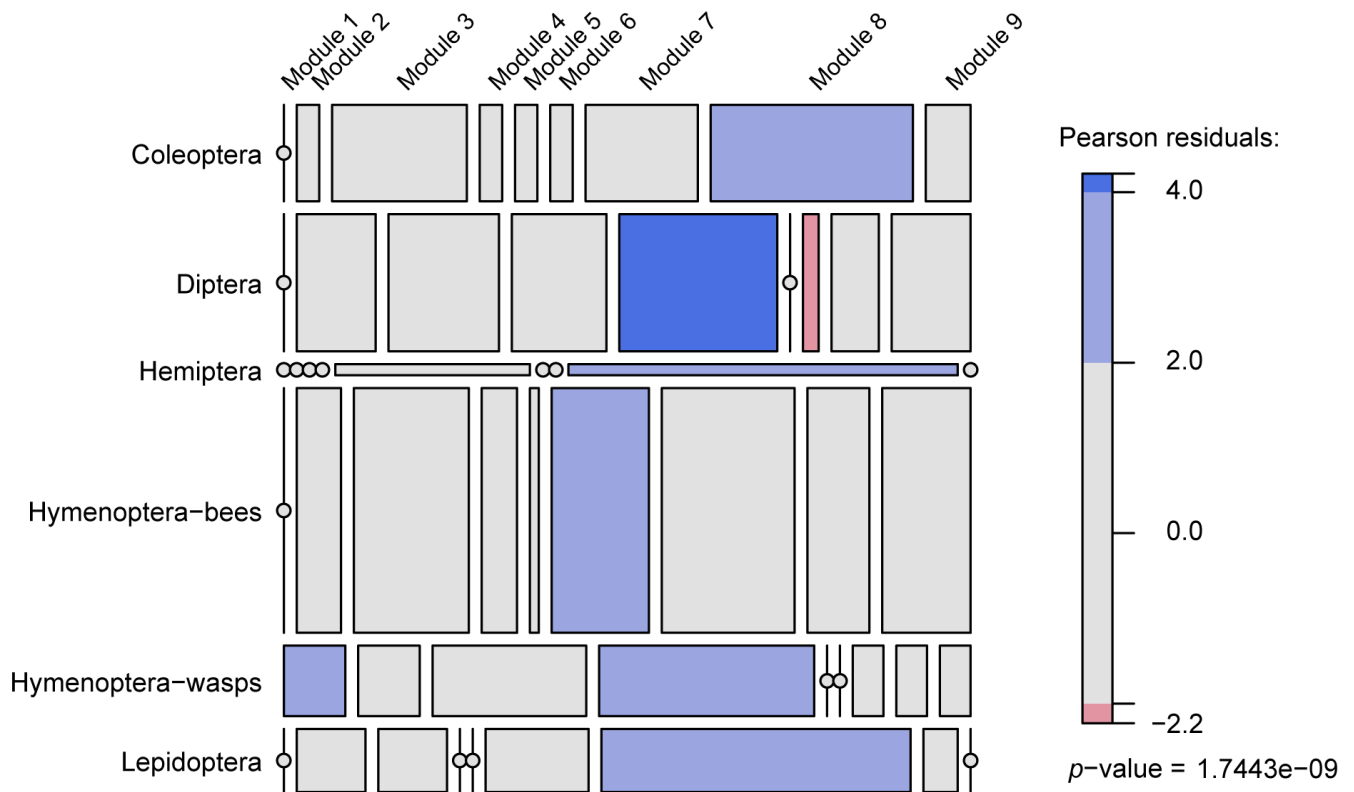
Fig. 4.S2. Significant associations between pollinator groups and the nine modules of the p–p network in the study community. The frequency distribution of insects of each group within the modules is presented in a mosaic plot. Shading shows the module–class combinations that are more (blue) or less (red) probable corresponding to the magnitude of the standardized residuals of the Pearson χ^2 test. Shaded cells with residual values >|2| and >|4| correspond to residuals that are individually significant at 0.05 and <0.0001, respectively.
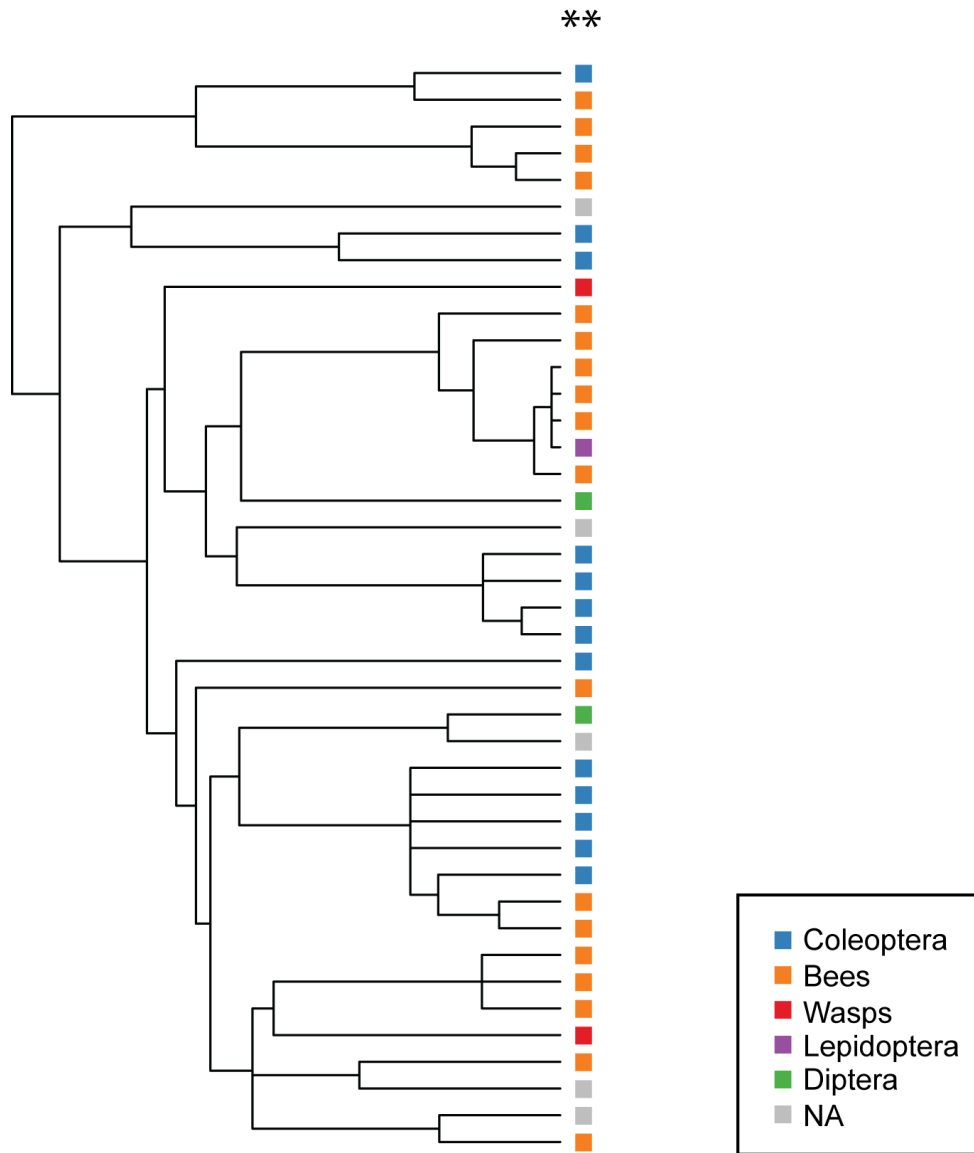
Fig. 4.S3. Phylogenetically relative plants are mainly visited by the same group of pollinator. Significance (**: $p=0.008$) was acquired by applying the algorithm 'phylo.signal.disc' for discrete traits implemented in R, developed by Enrico Rezende (pers. comm.; see *94* for detailed description of the method and example).
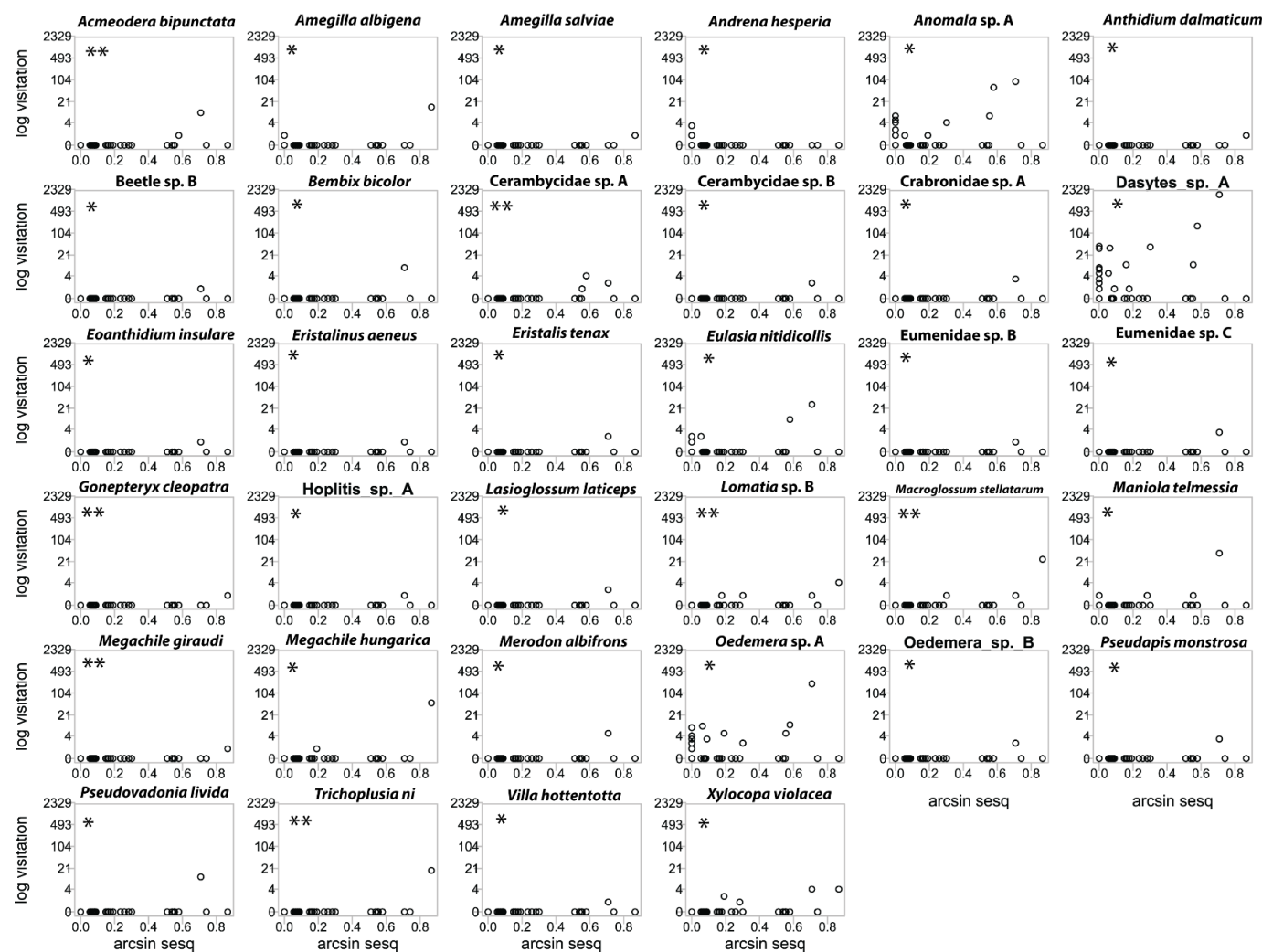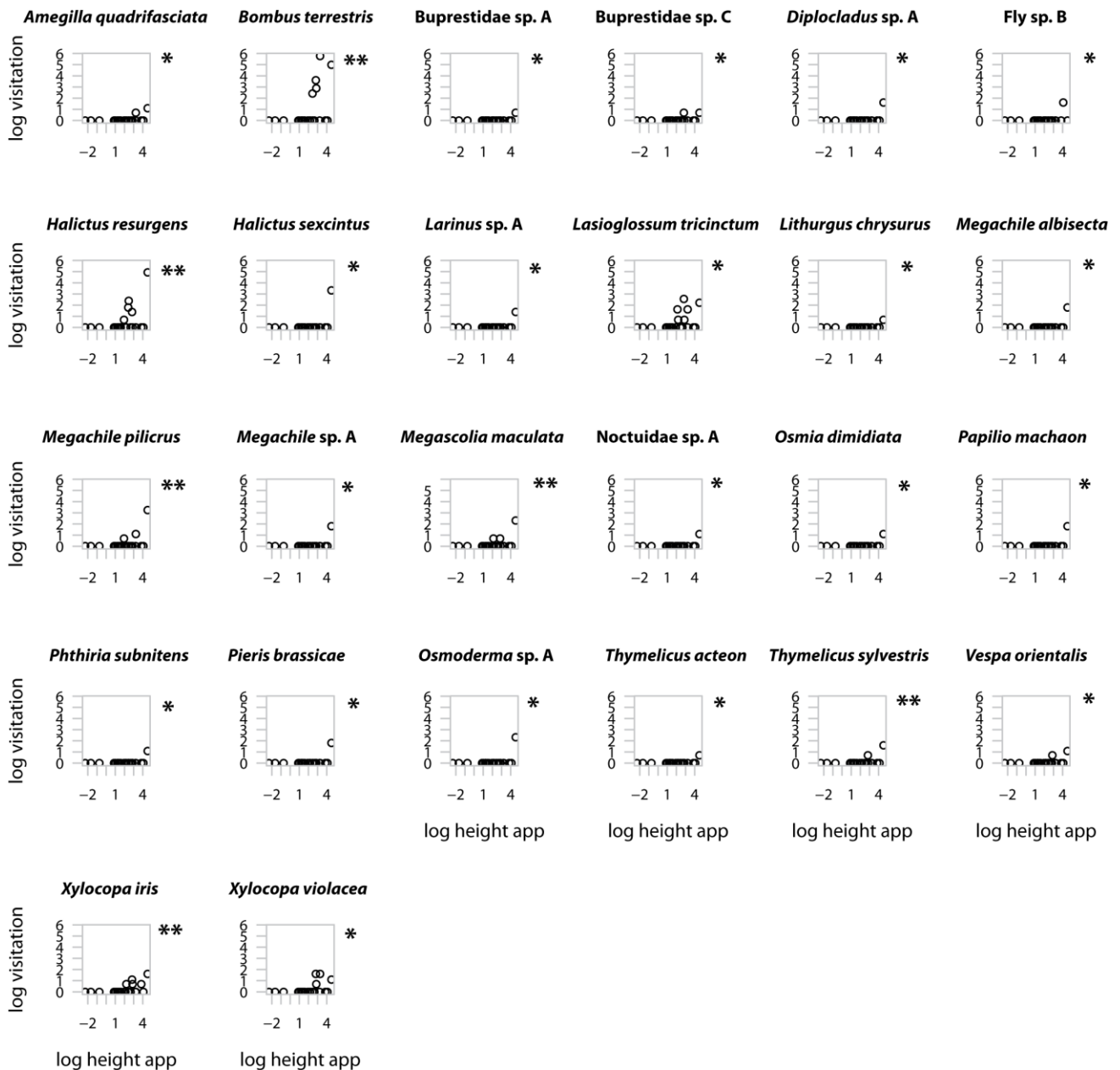
Fig. 4.S4. The insects in the **total** network showing significant associations of number of visits (visitation) and the **proportion of sesquiterpenes** in plant emissions (sesq). The independent variable was arcsine transformed. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
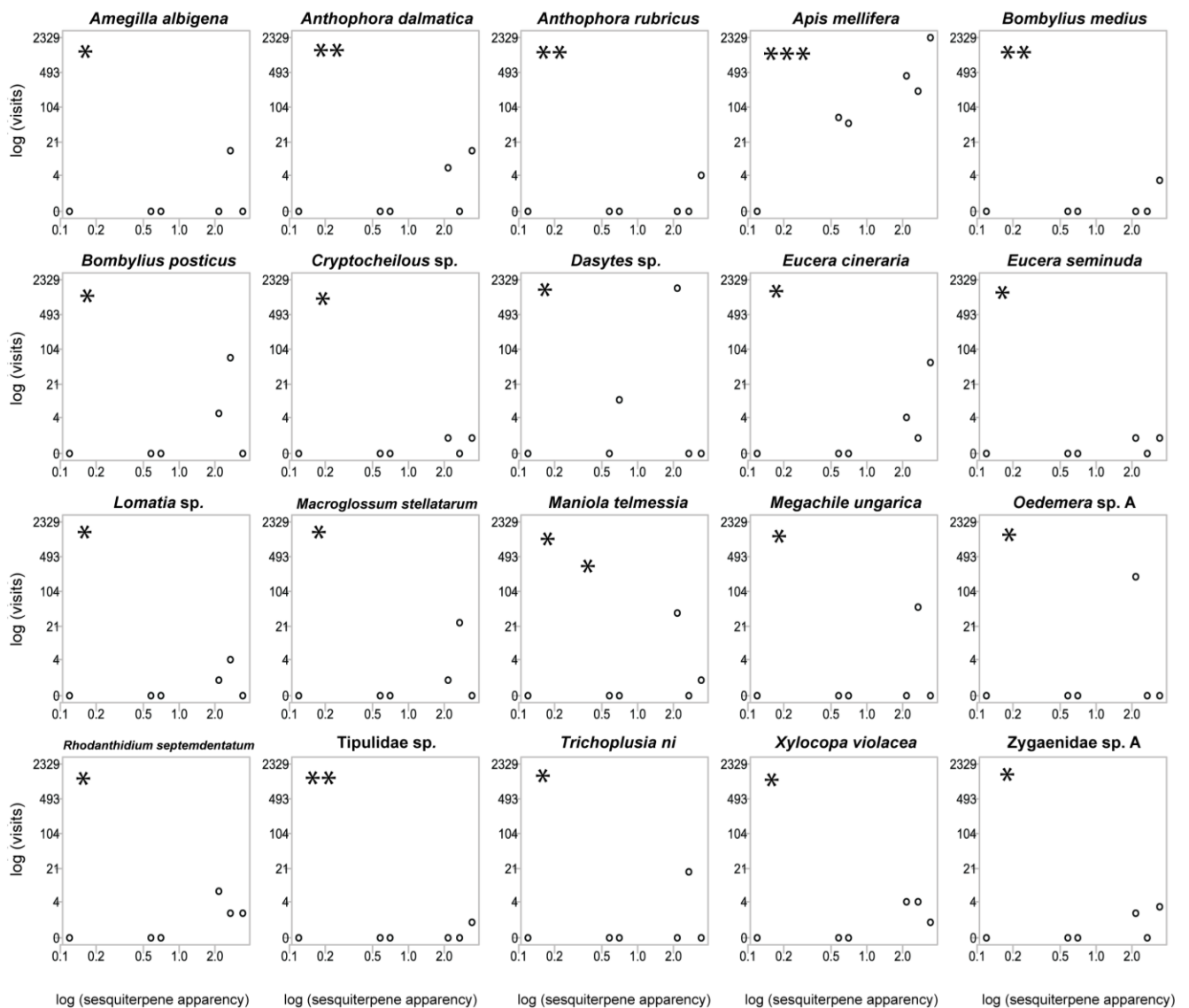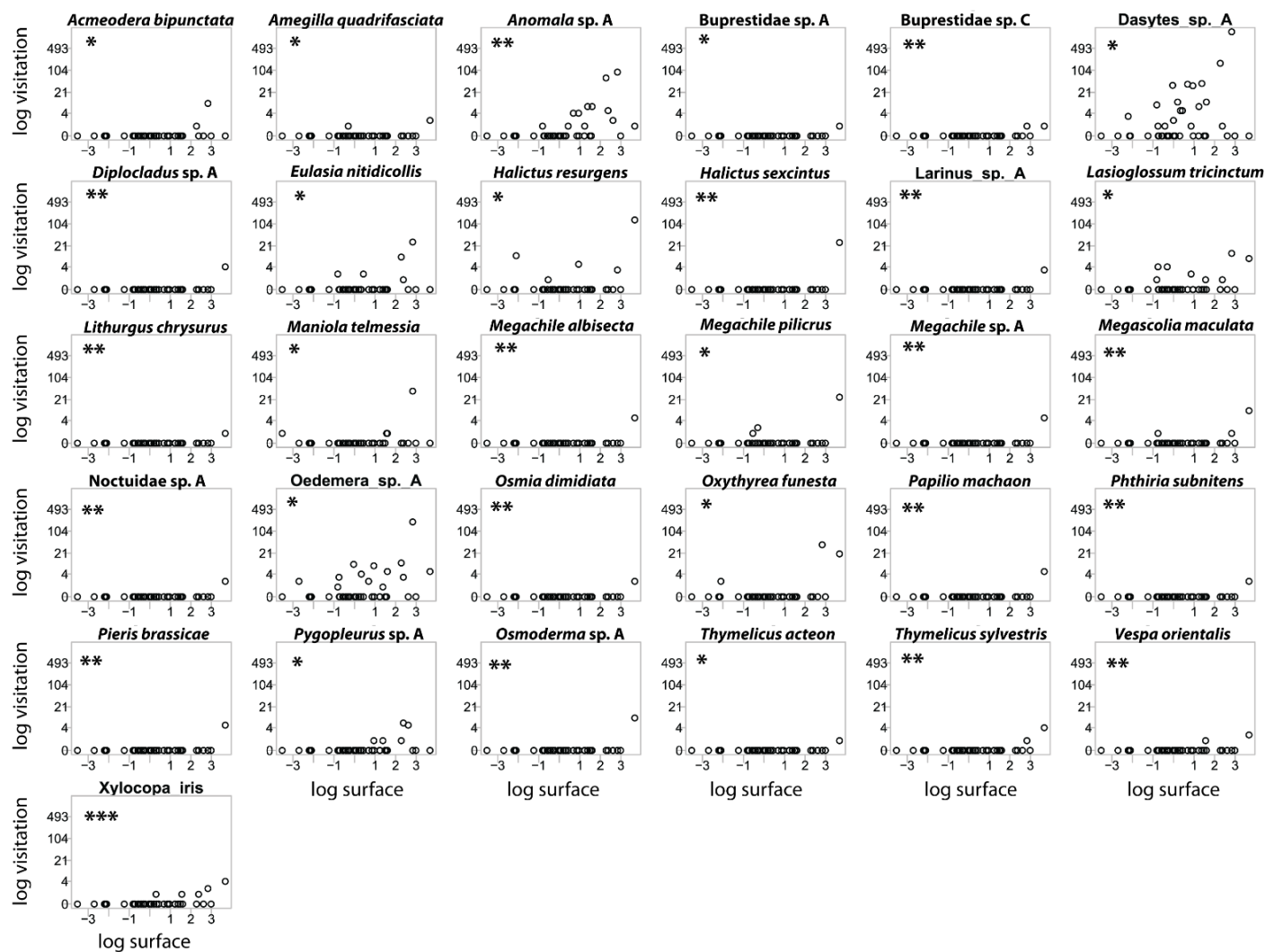
Fig 4.S5. The insects in the **total** network showing significant associations of number of visits (visitation) and the **apparency of sesquiterpene emissions**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
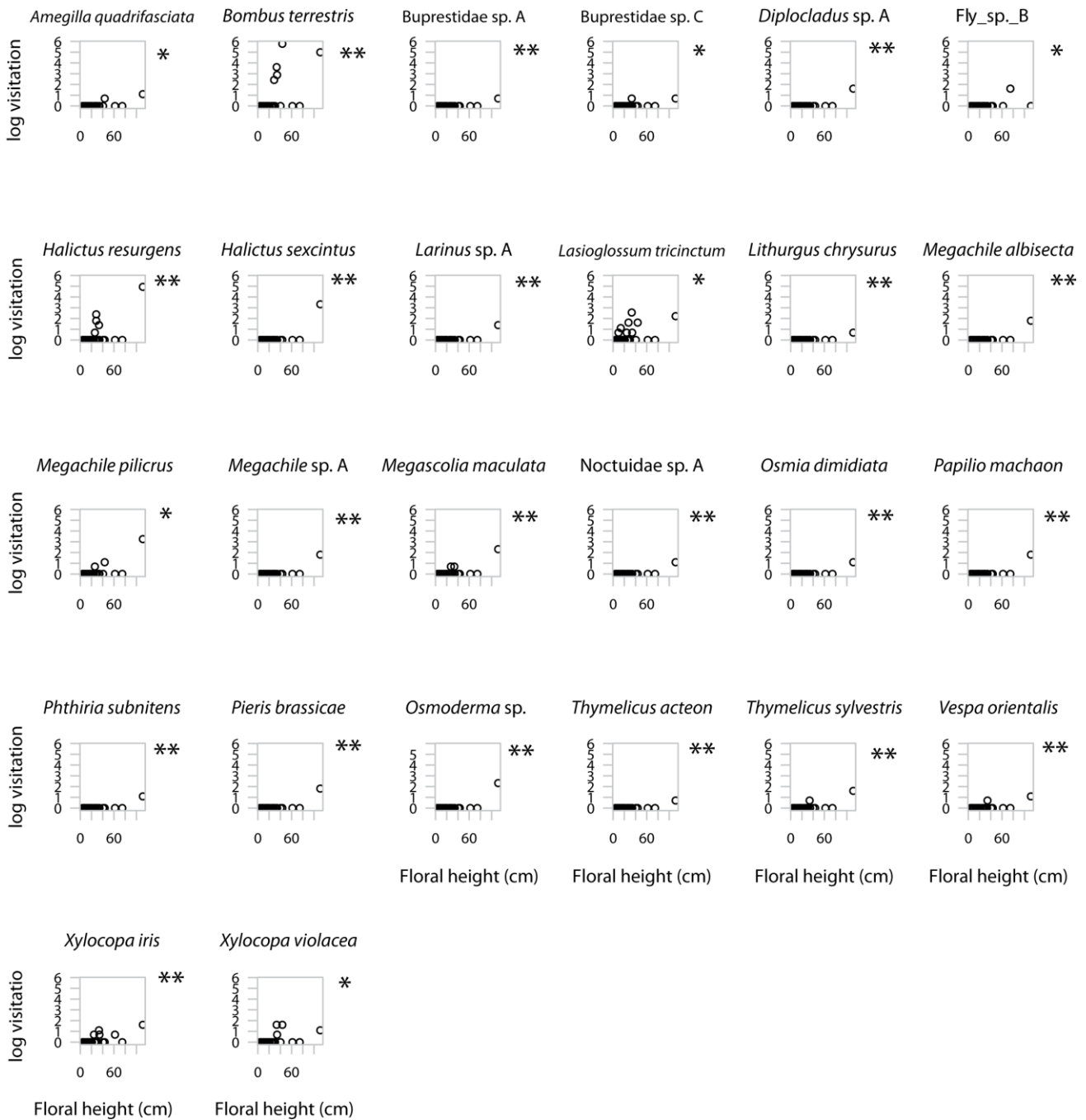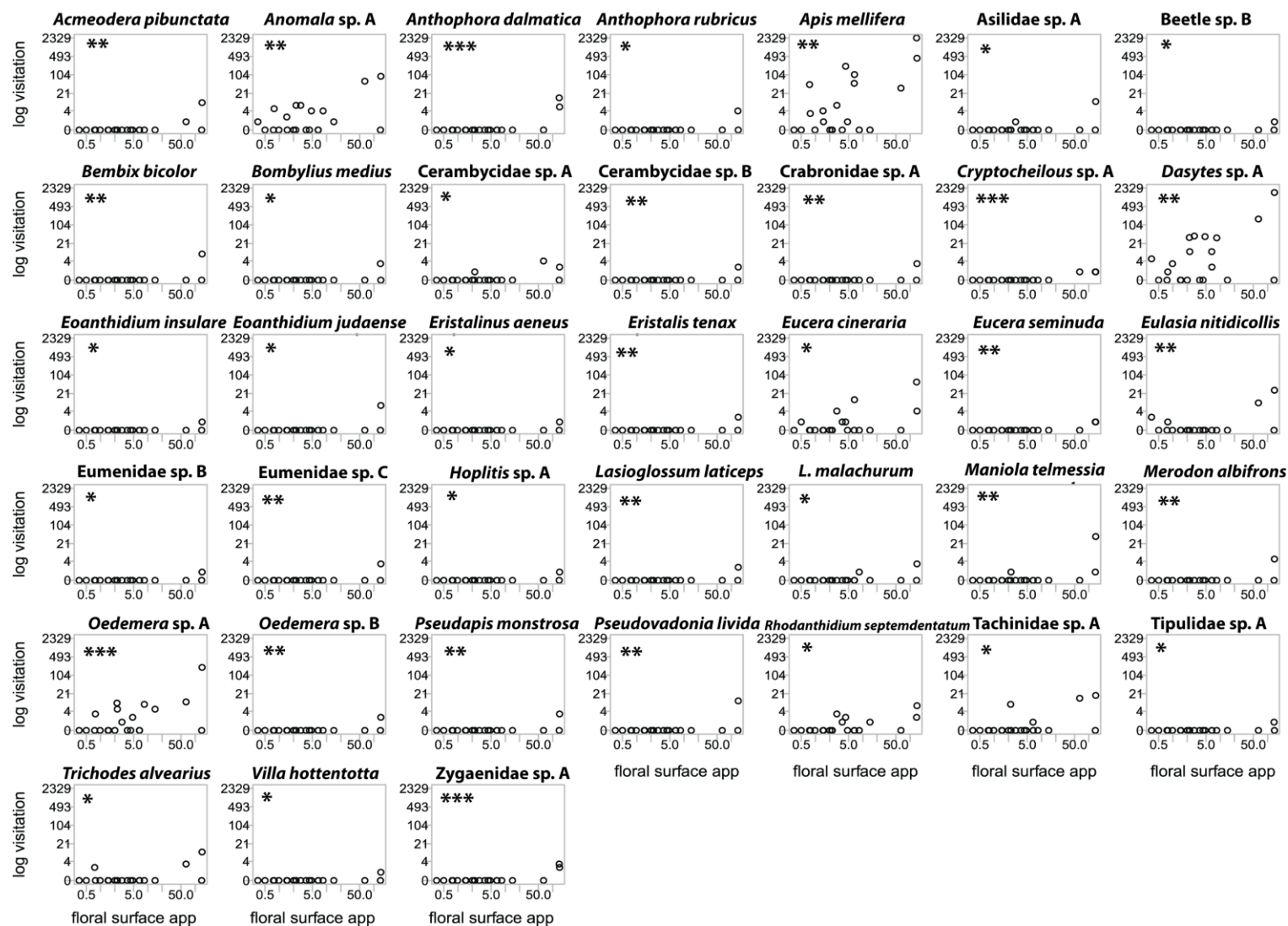
Fig 4.S6. The insects in the **total** network showing significant associations of number of visits (visitation) and **floral height**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).

Fig 4.S7. The insects in the **total** network showing significant associations of number of visits (visitation) and **floral height apparency**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
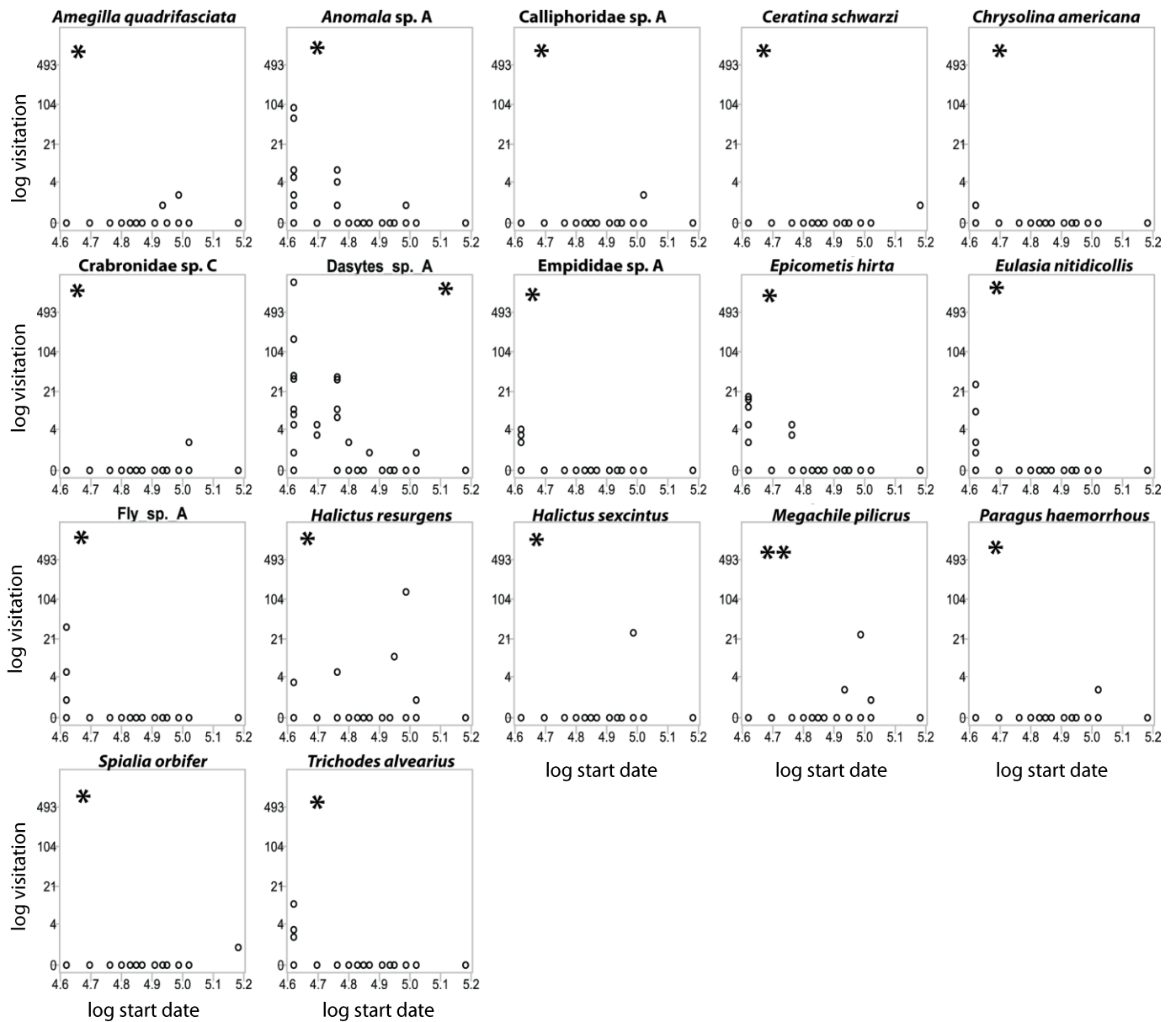
Fig 4.S8. The insects in the **total network** showing significant associations of number of visits (visitation) and **floral surface**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).

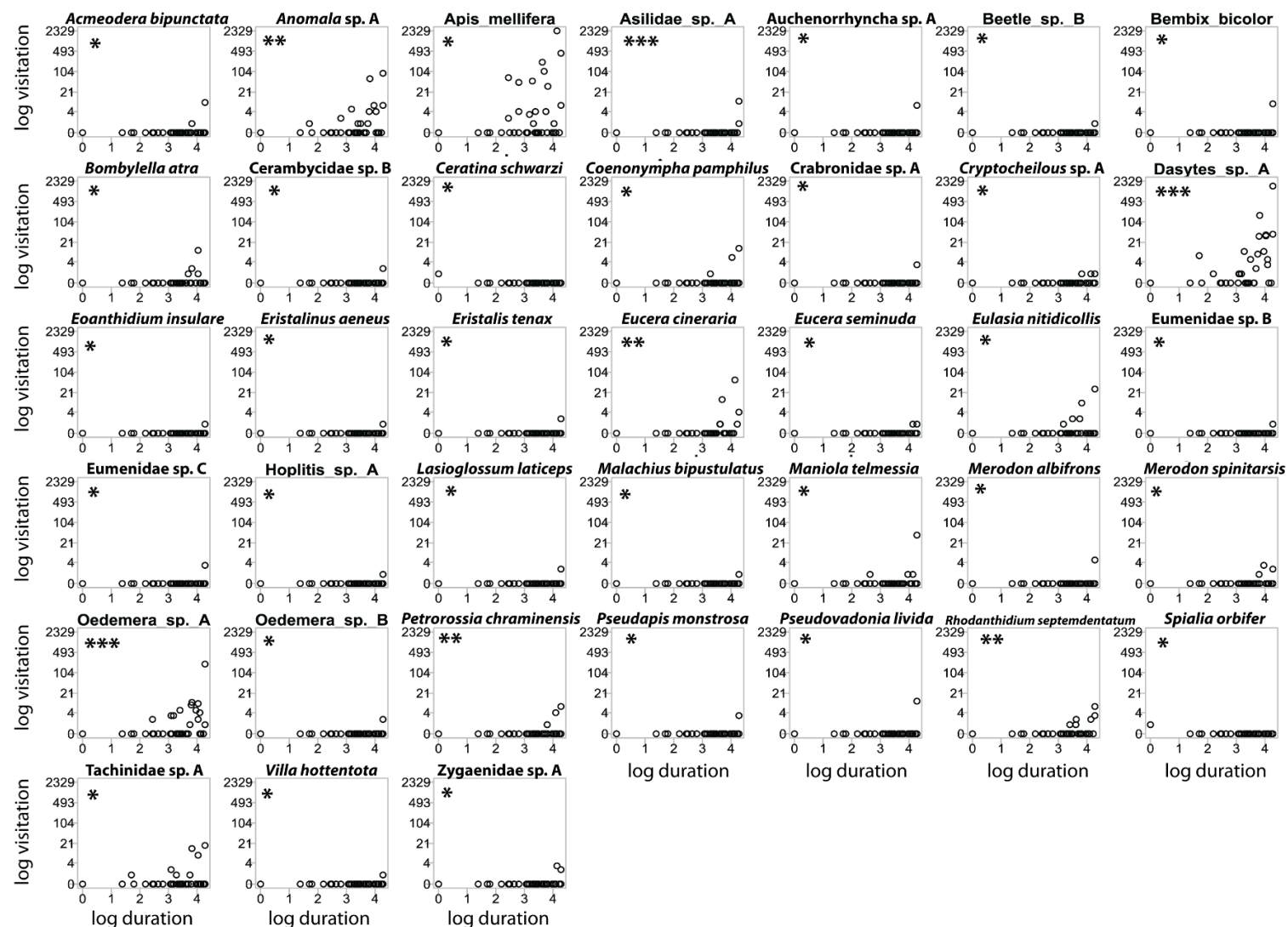**Fig 4.S9.** The insects in the **total network** showing significant associations of number of visits (visitation) and **floral surface apparency** (surface app). The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).

Fig 4.S10. The insects in the **total network** showing significant associations of number of visits (visitation) and the **start of flowering** (start date). The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
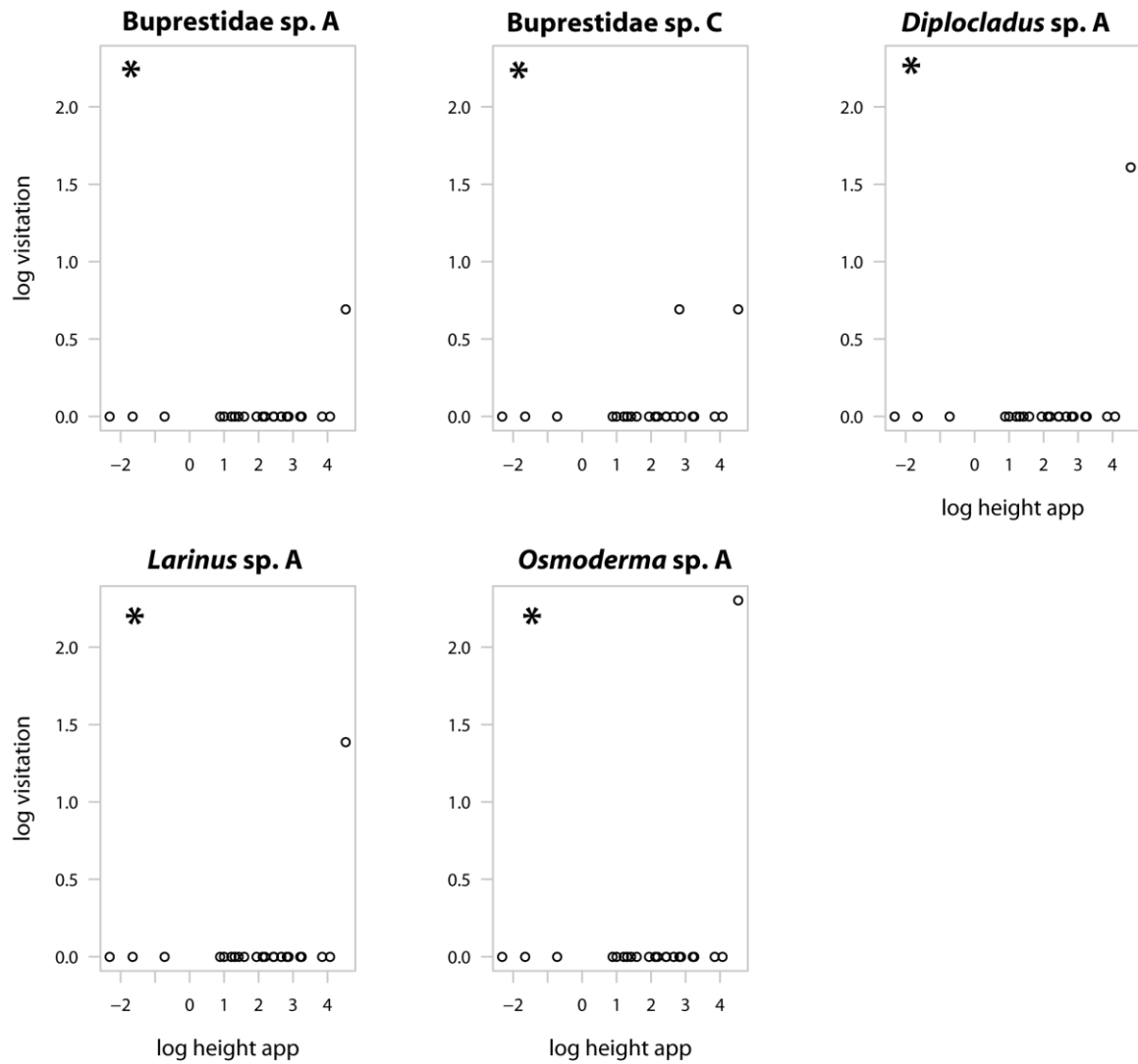
Fig 4.S11. The insects in the **total network** showing significant associations of number of visits (visitation) and the **duration of flowering** (duration). The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
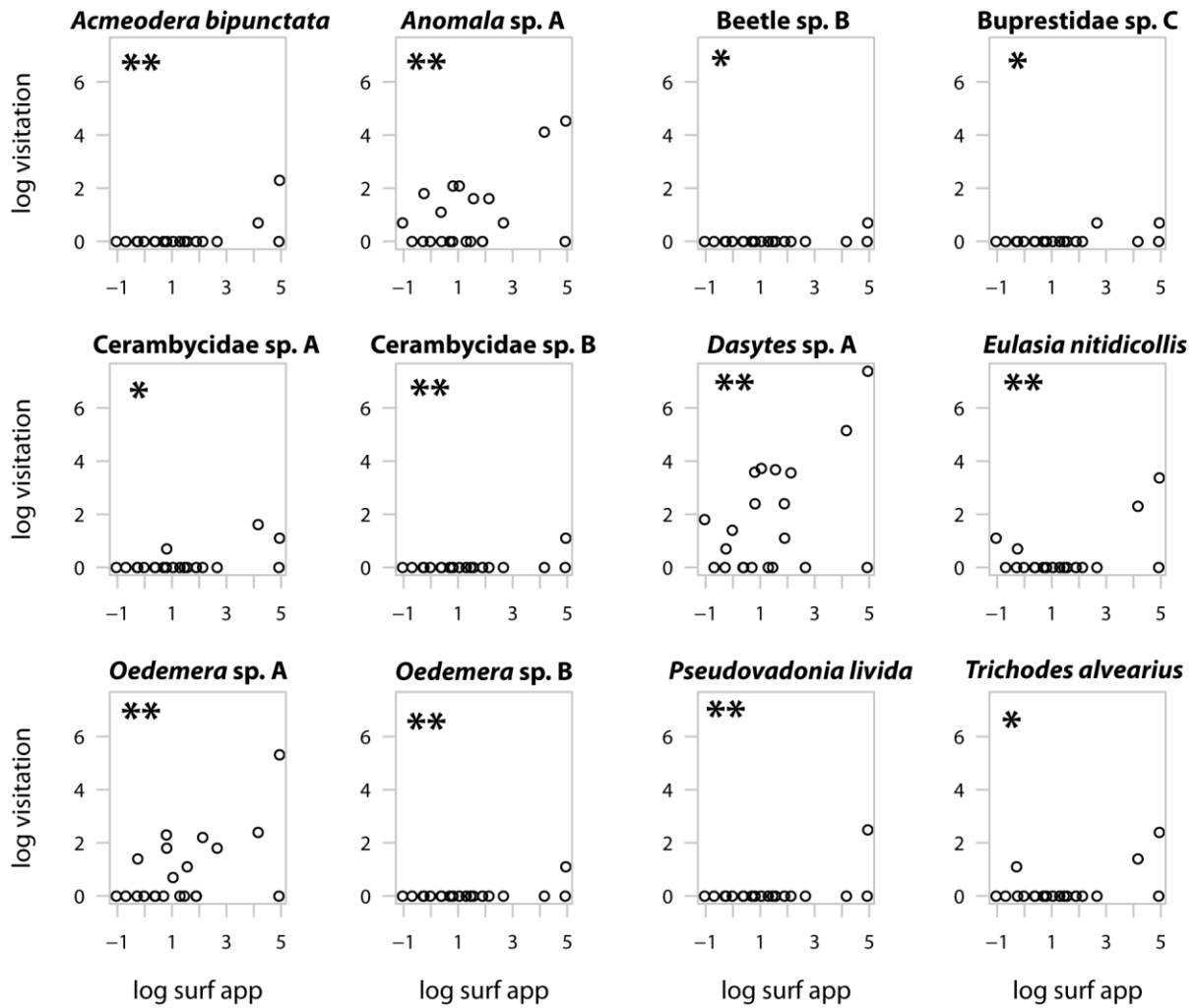
Fig 4.S12. The insects in the **Coleoptera** sub-network that show significant associations of number of visits (visitation) and **floral height apparency** (height app). The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).

Fig 4.S13. The insects in the **Coleoptera** sub-network that show significant associations of number of visits (visitation) and **floral surface apparency** (surf app). The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
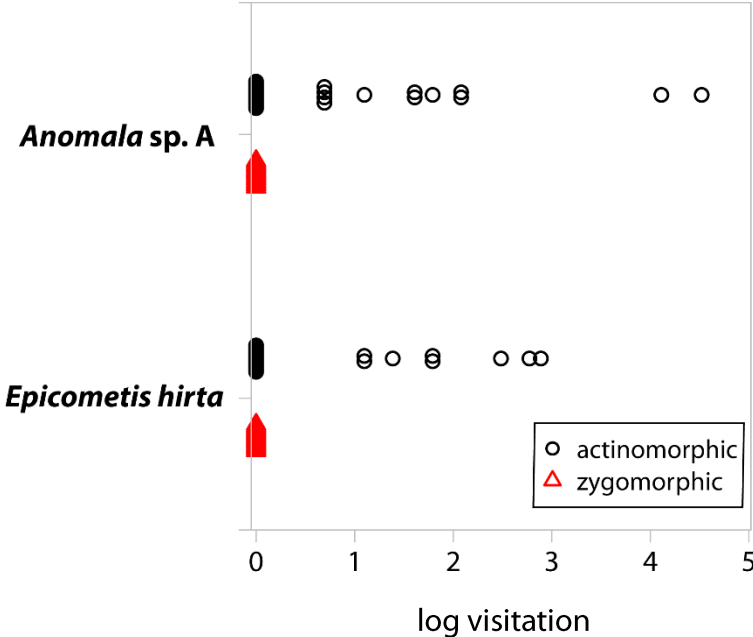
Fig 4.S14. The insects in the **Coleoptera** sub-network that show significant associations of number of visits (visitation) and **floral symmetry**.
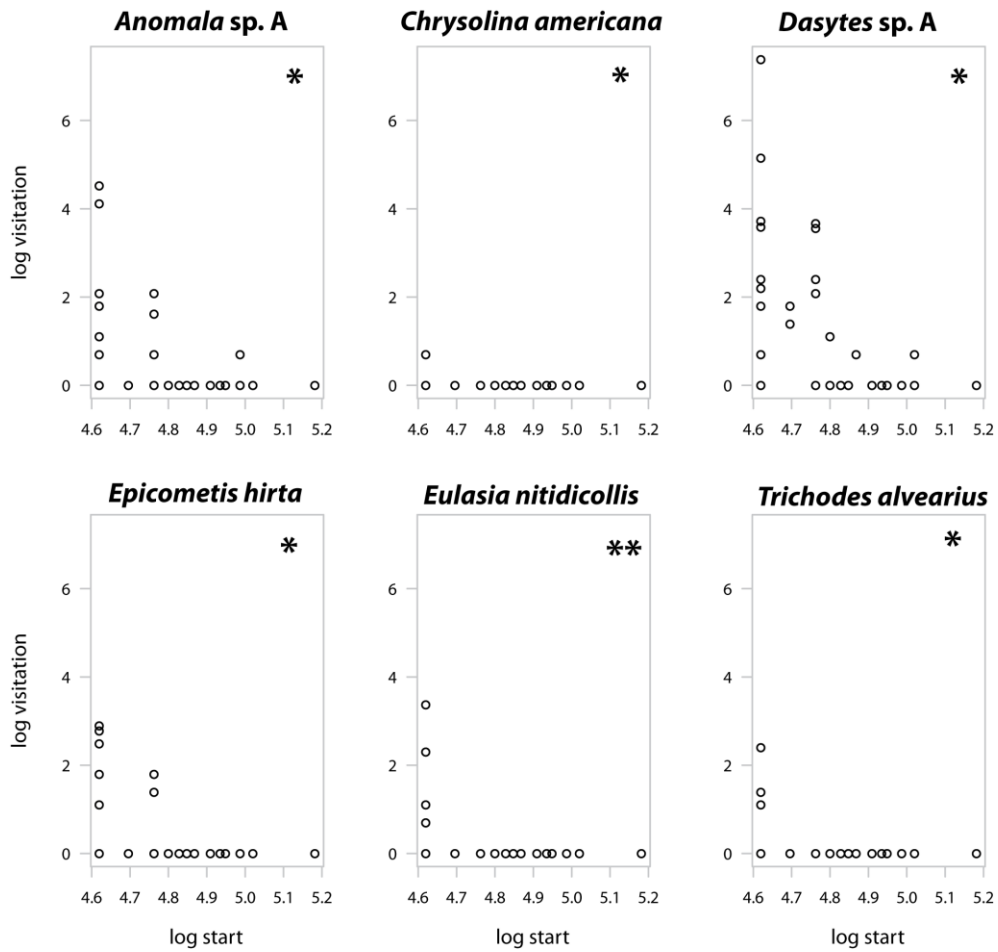
Fig. 4.S15. The insects in the **Coleoptera** sub-network that show significant associations of number of visits (visitation) and the **start of flowering** (start). The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
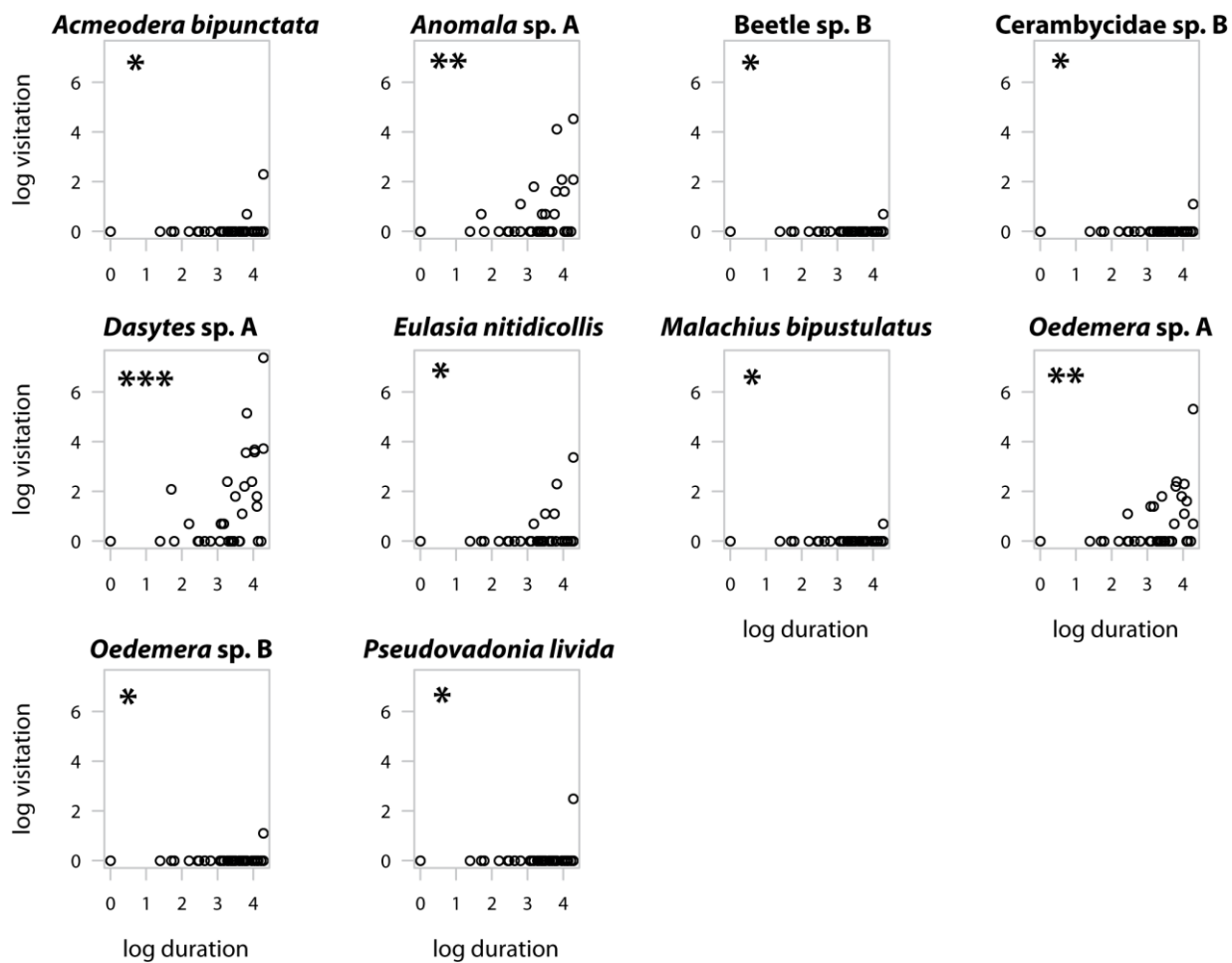
Fig 4.S16. The insects in the **Coleoptera** sub-network that show significant associations of number of visits (visitation) and the **duration of flowering**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
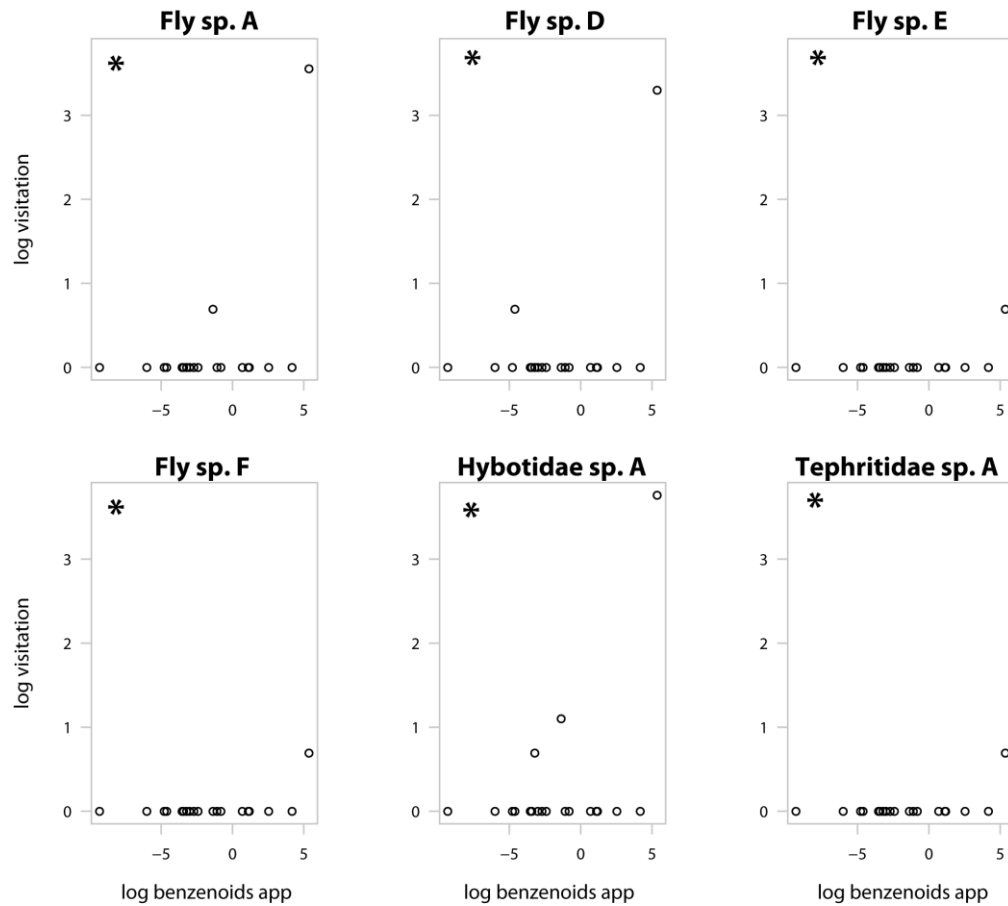
Fig 4.S17. The insects in the **Diptera** sub-network that show significant associations of number of visits (visitation) and **benzenoid emissions apparency** (benzenoids app). The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
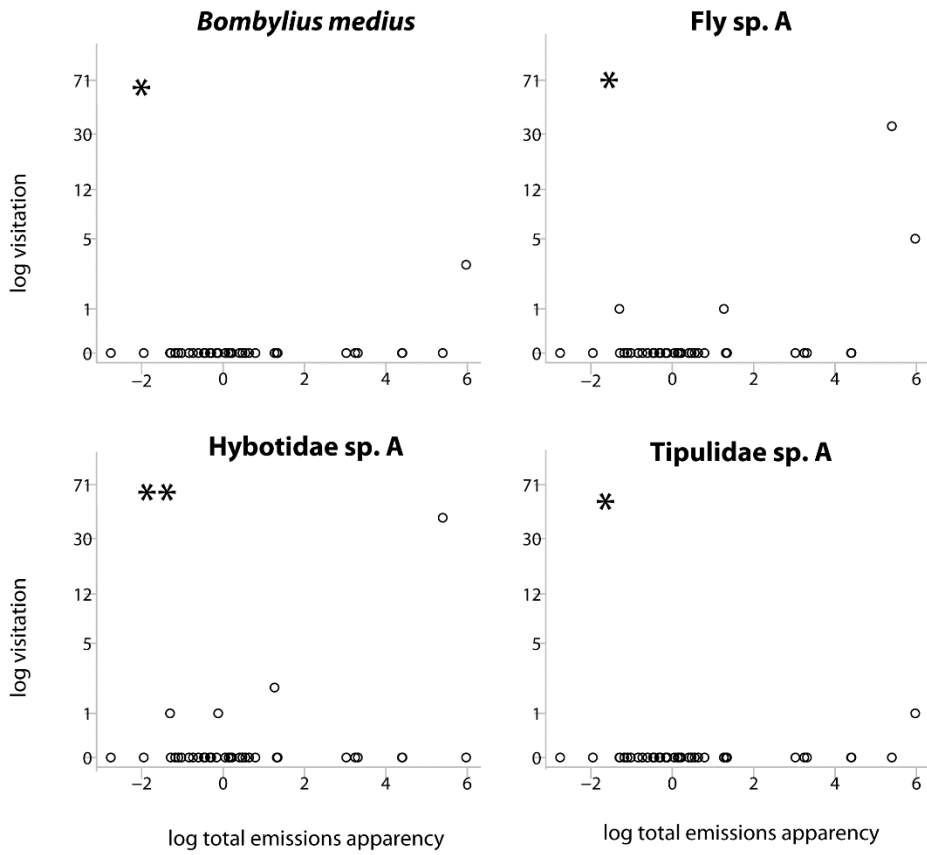
Fig 4.S18. The insects in the **Diptera** sub-network that show significant associations of number of visits (visitation) and **total emissions apparency**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
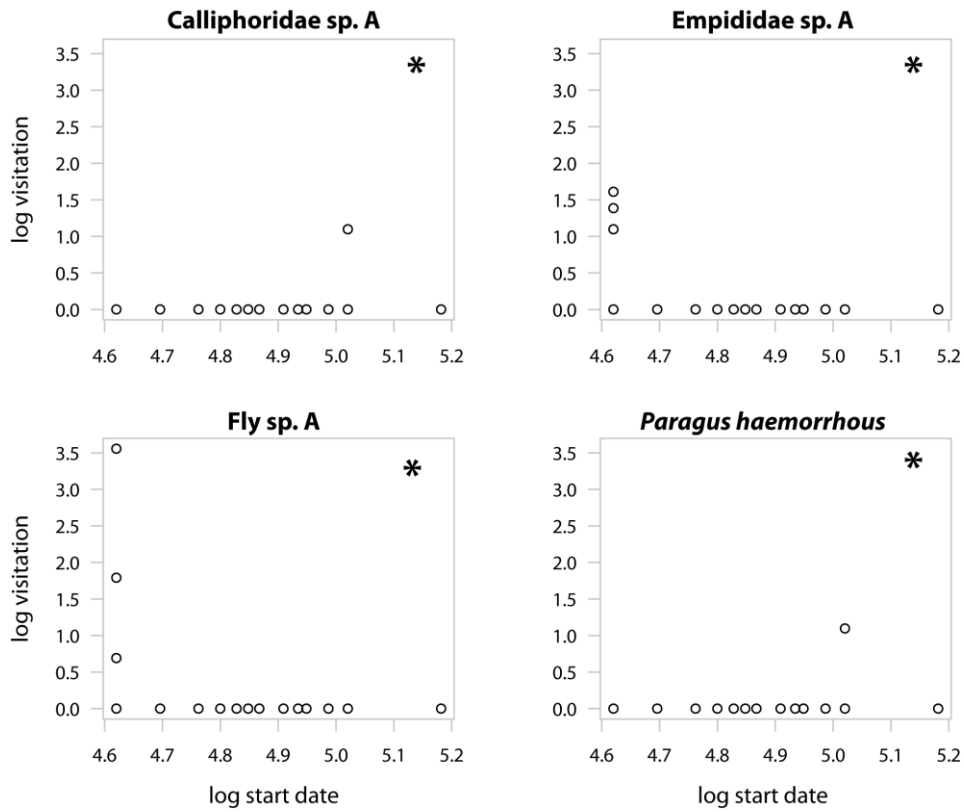
Fig 4.S19. The insects in the **Diptera** sub-network that show significant associations of number of visits (visitation) and the **start date of flowering**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).

Fig 4.S20. The insects in the **Diptera** sub-network that show significant associations of number of visits (visitation) and the **duration of flowering**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).

Fig 4.S21. The insects in the **bees** sub-network that show significant associations of number of visits (visitation) and the **apparency of sesquiterpene emissions** (sesq app). The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).

Fig 4.S22. The insects in the **bees** sub-network that show significant associations of number of visits (visitation) and **floral height apparency** (height app). The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
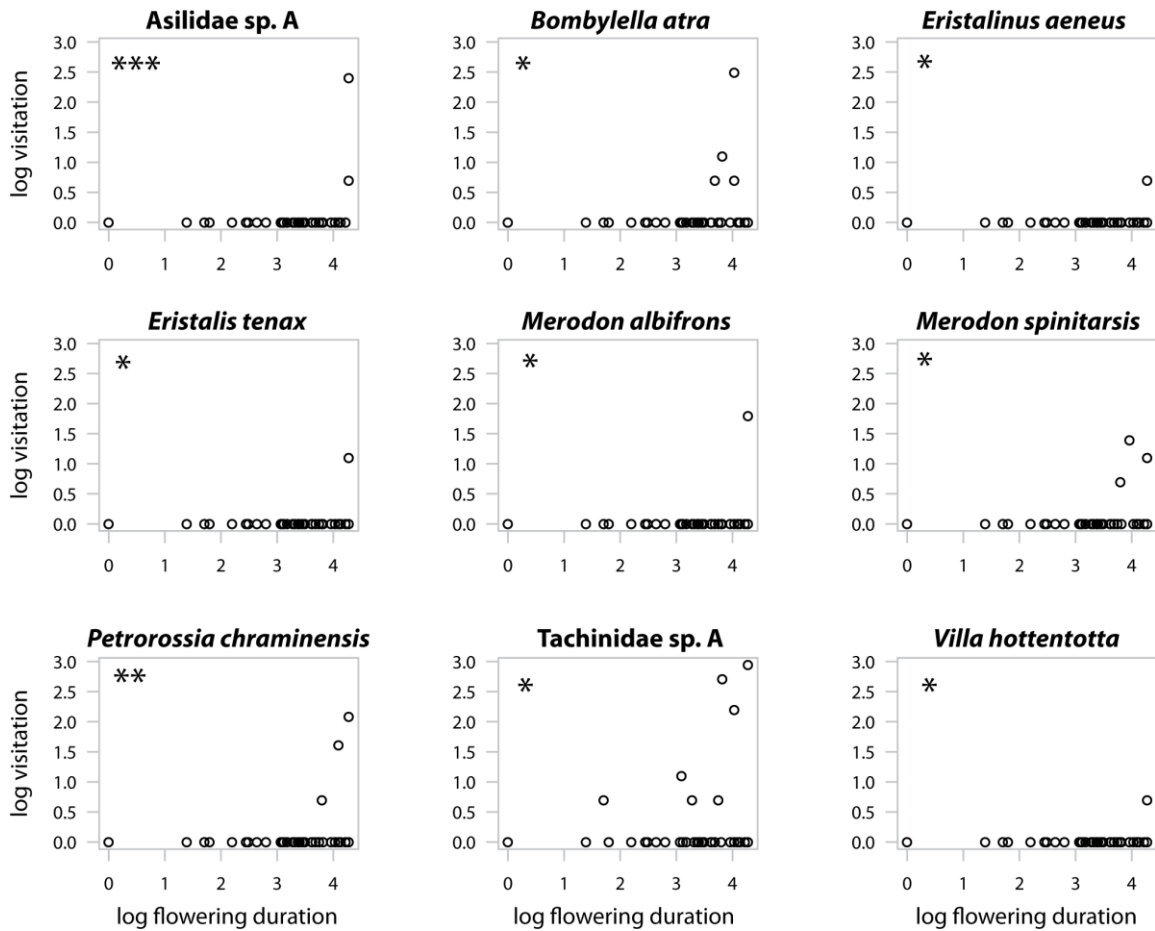
Fig 4.S23. The insects in the **bees** sub-network that show significant associations of number of visits (visitation) and **floral surface apparency** (surface app). The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).

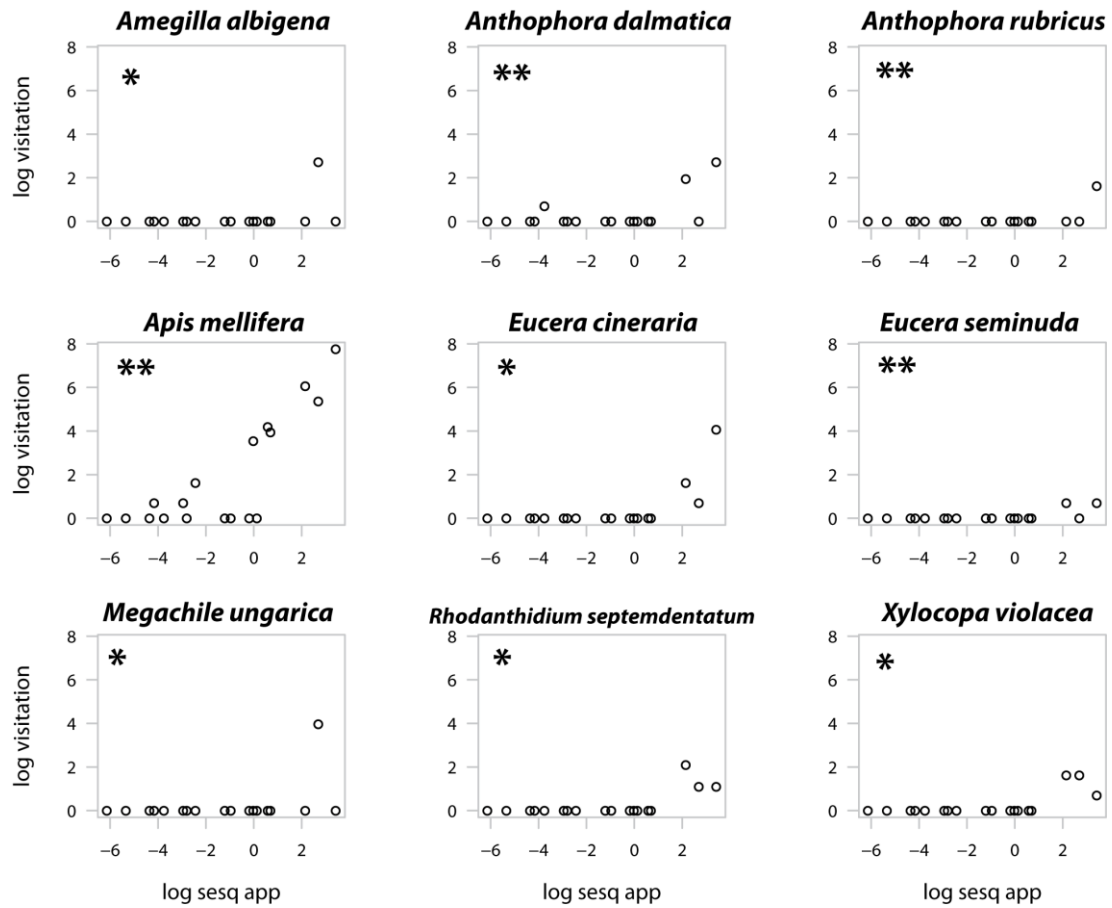**Fig 4.S24.** The insects in the **bees** sub-network that show significant associations of number of visits (visitation) and **corolla depth**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).

Fig 5.S25. The insects in the **bees** sub-network that show significant associations of number of visits (visitation) and the **duration of flowering**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **: $p \leq 0.010$; ***: $p \leq 0.001$).
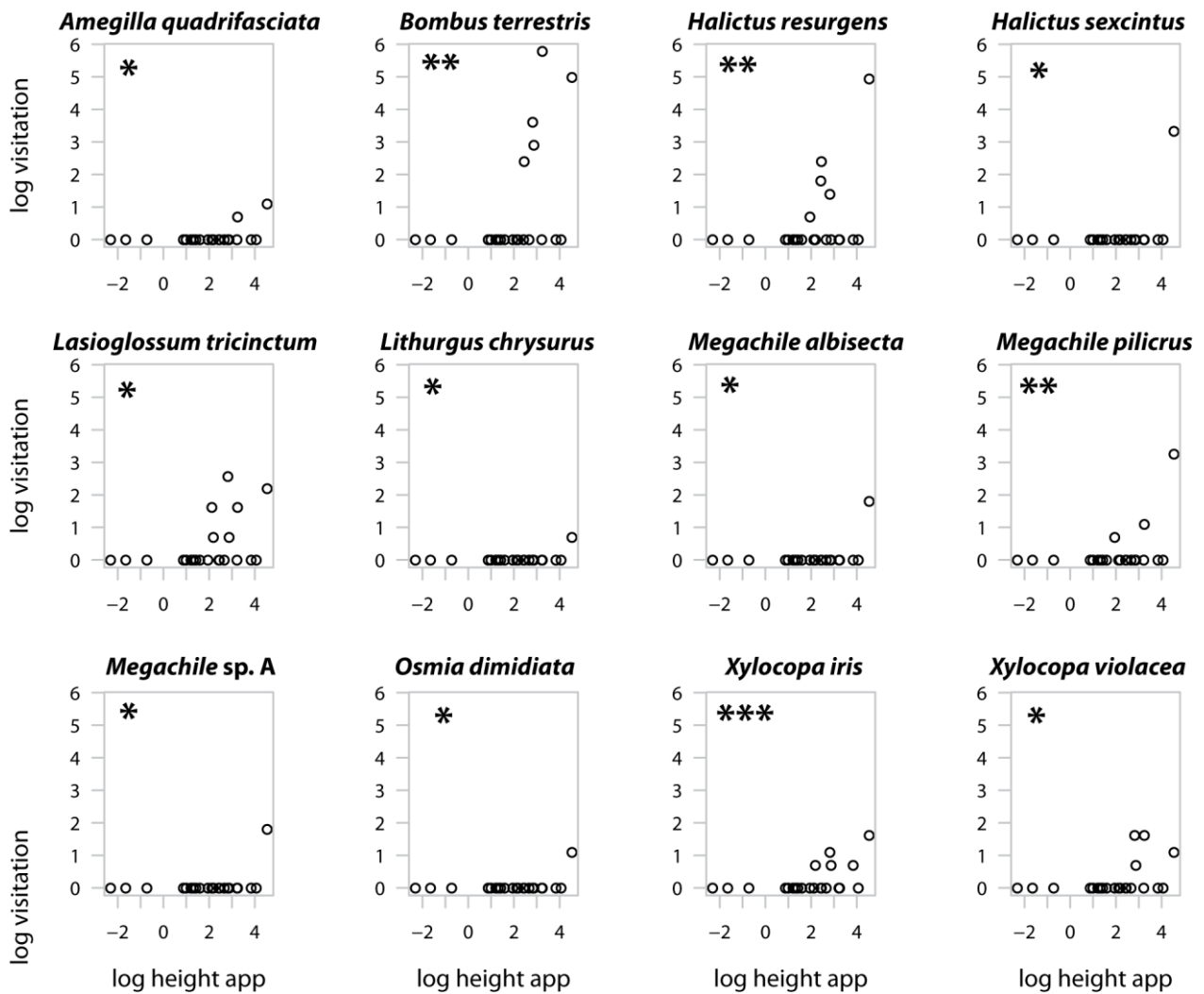
Fig 4.S26. The insects in the **wasps** sub-network that show significant associations of number of visits (visitation) and **floral surface**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
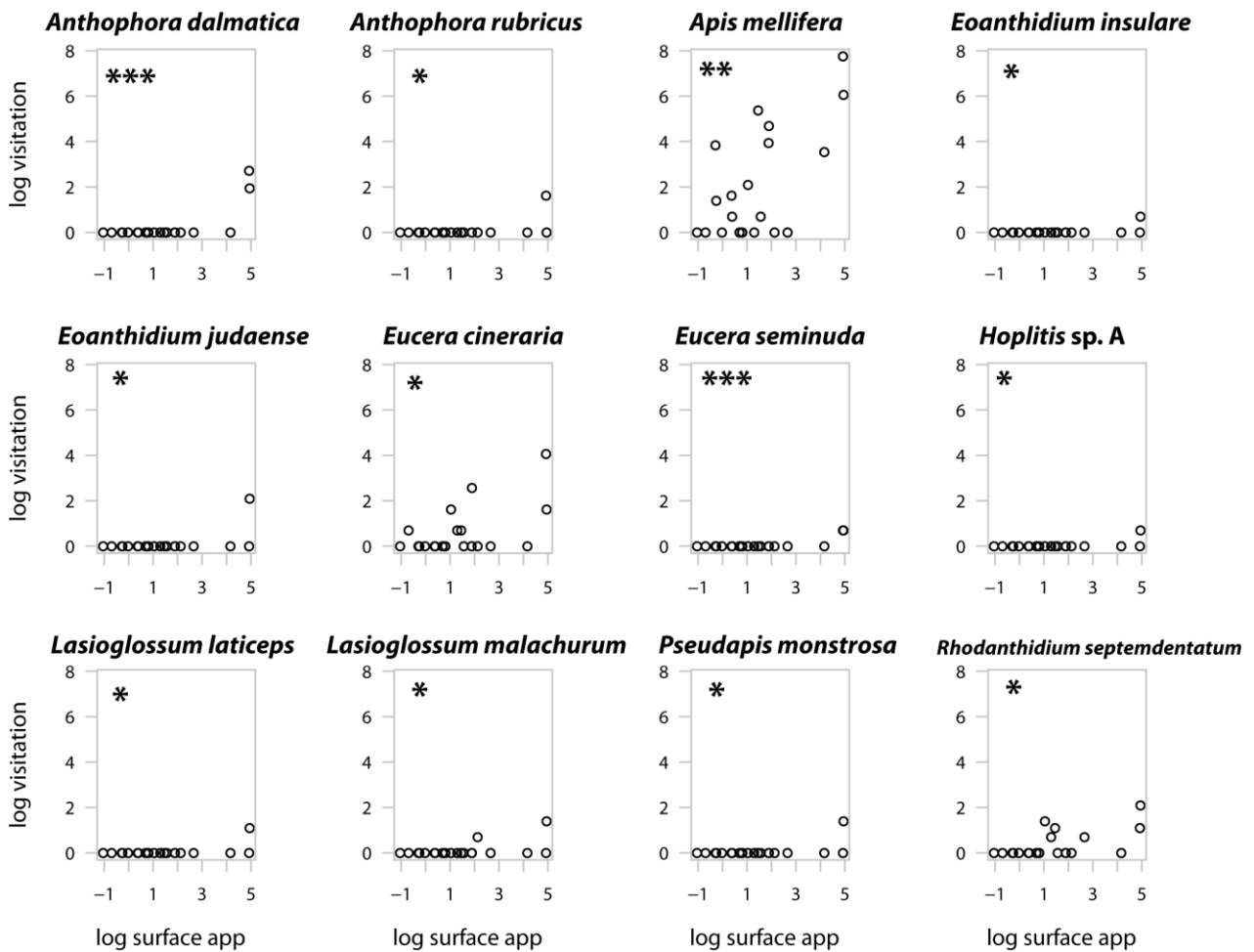
Fig 4.S27. The insects in the **wasps** sub-network that show significant associations of number of visits (visitation) and **floral surface apparency**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
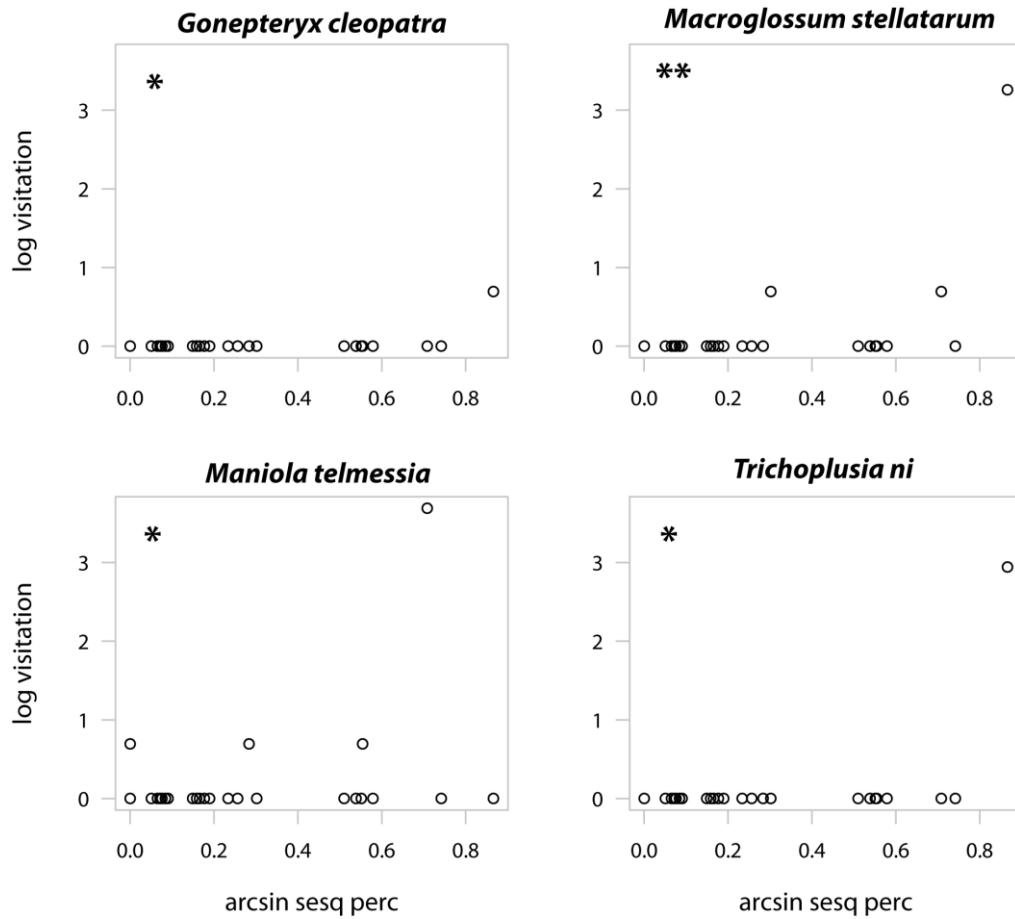
Fig 4.S28. The insects in the **Lepidoptera** sub-network that show significant associations of number of visits (visitation) and the **proportion of sesquiterpenes** in the floral emissions. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
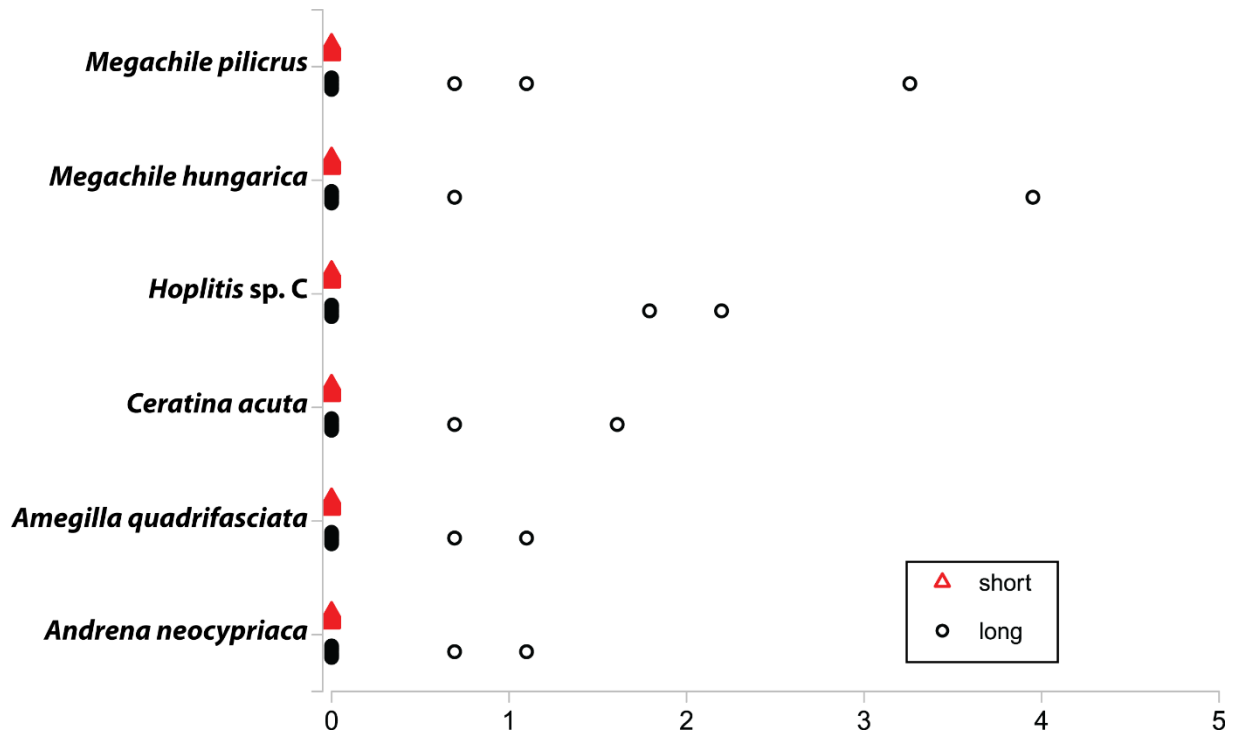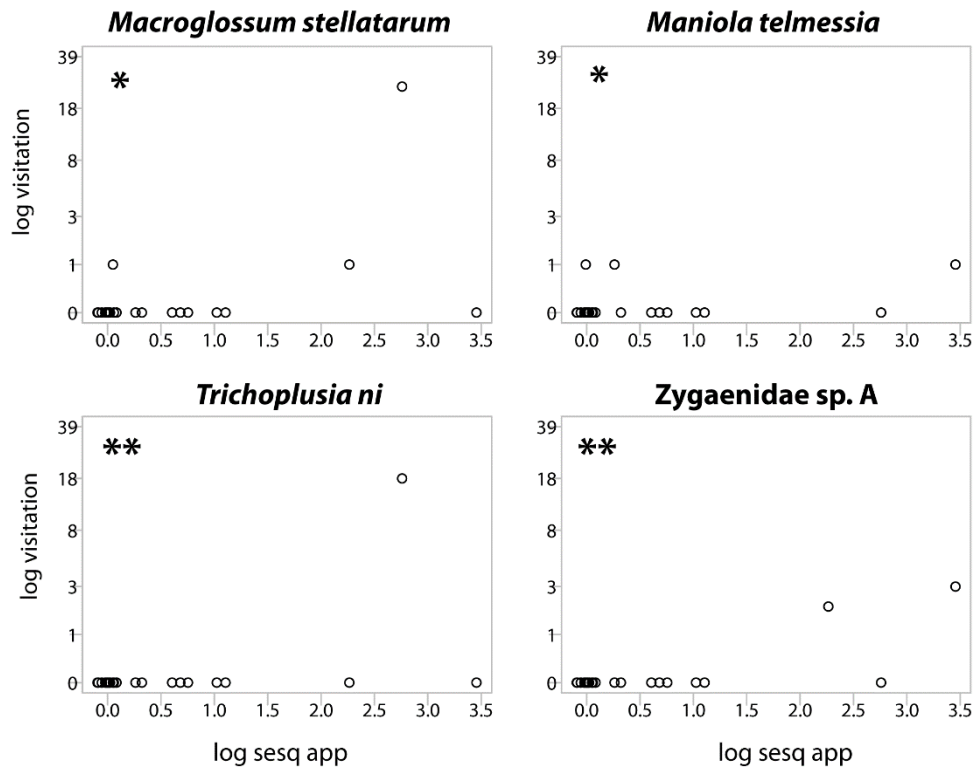
Fig 4.S29. The insects in the **Lepidoptera** sub-network that show significant associations of number of visits (visitation) and **sesquiterpenes apparency** (sesq app). The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
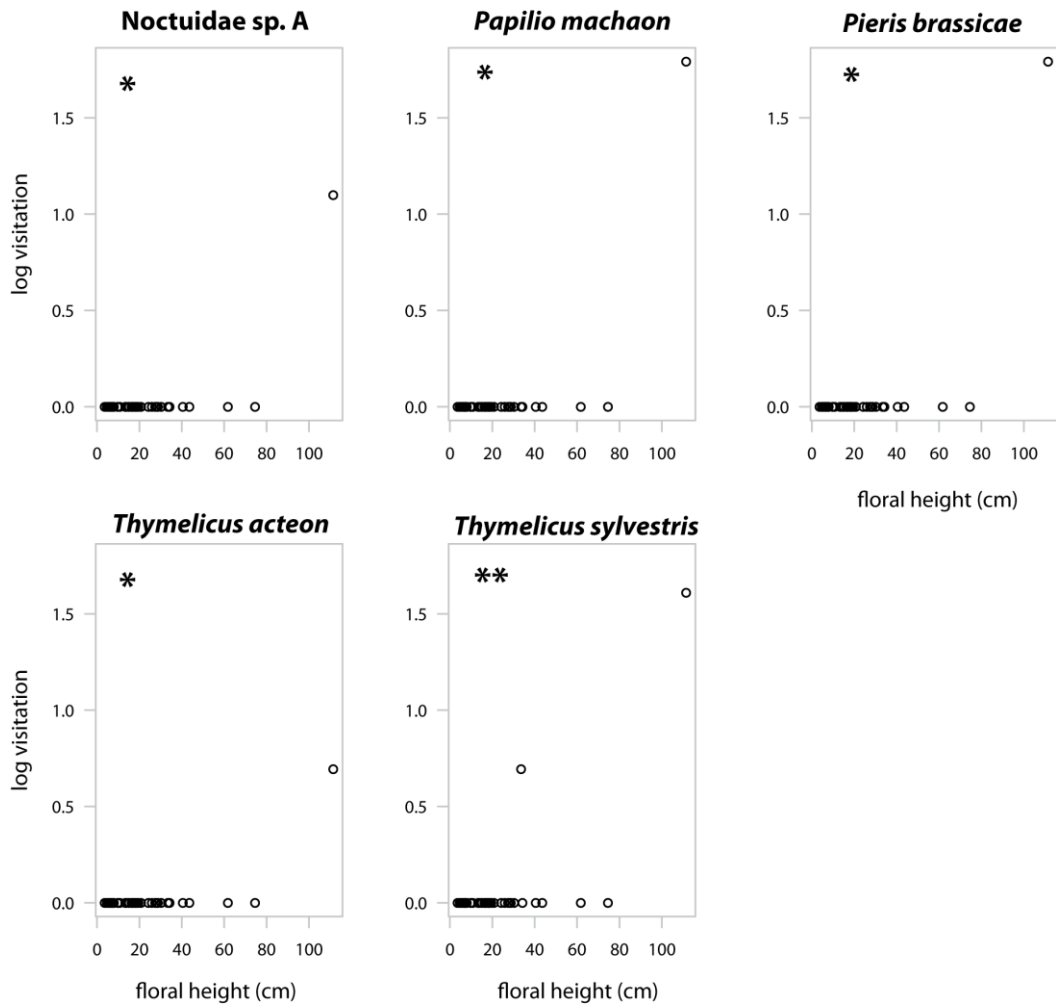
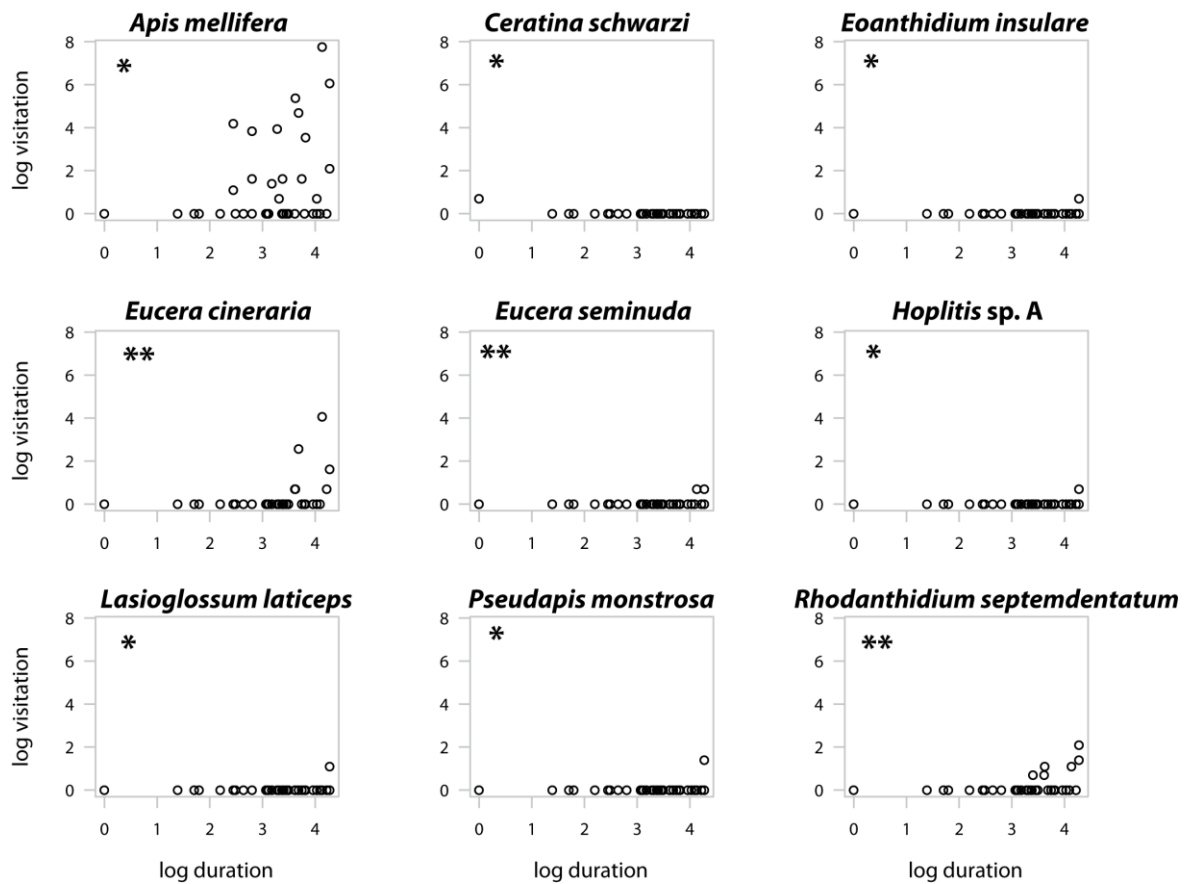**Fig 4.S30.** The insects in the **Lepidoptera** sub-network that show significant associations of number of visits (visitation) and **floral height**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
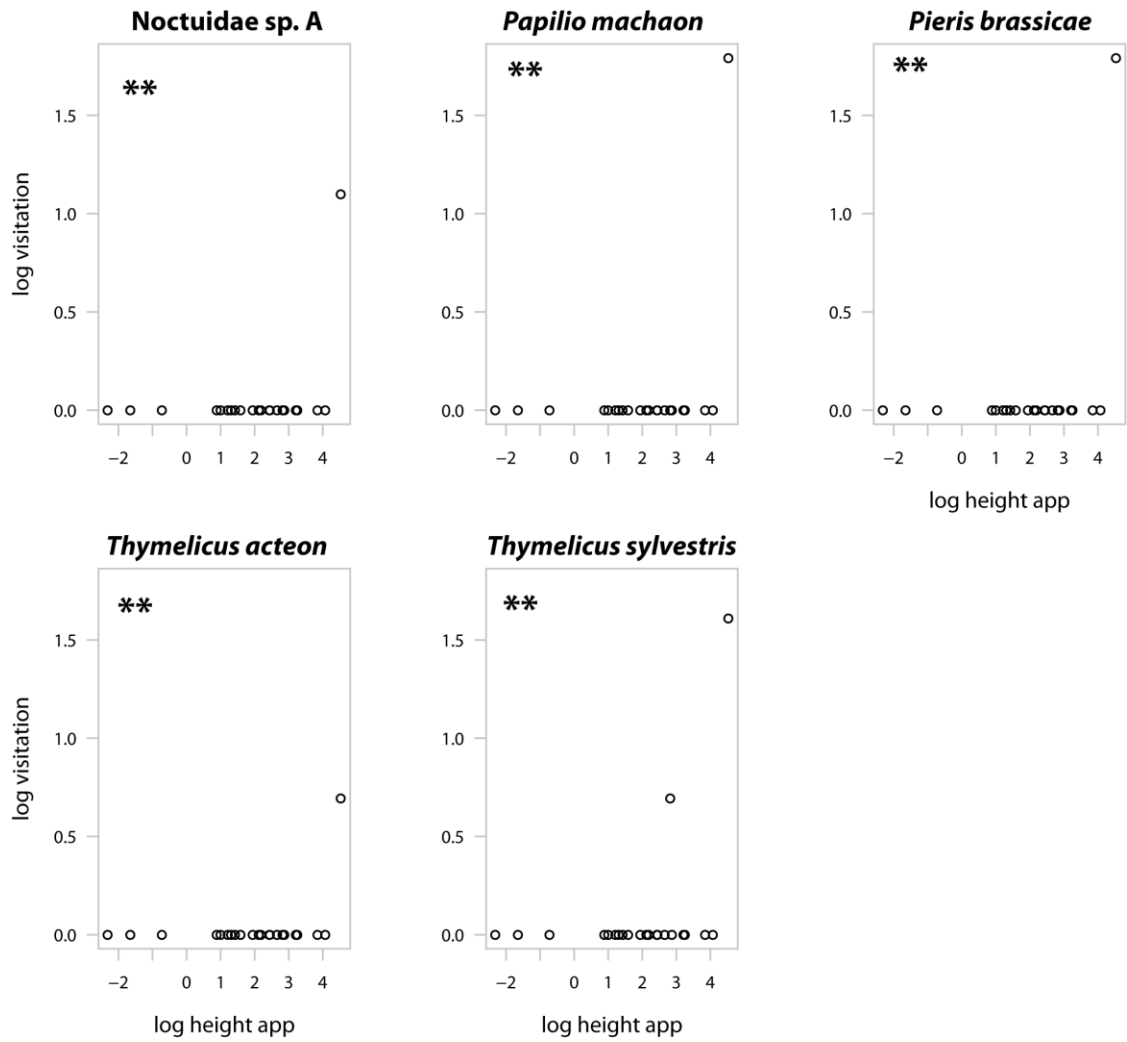
Fig 4.S31. The insects in the **Lepidoptera** sub-network that show significant associations of number of visits (visitation) and **floral height apparency**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
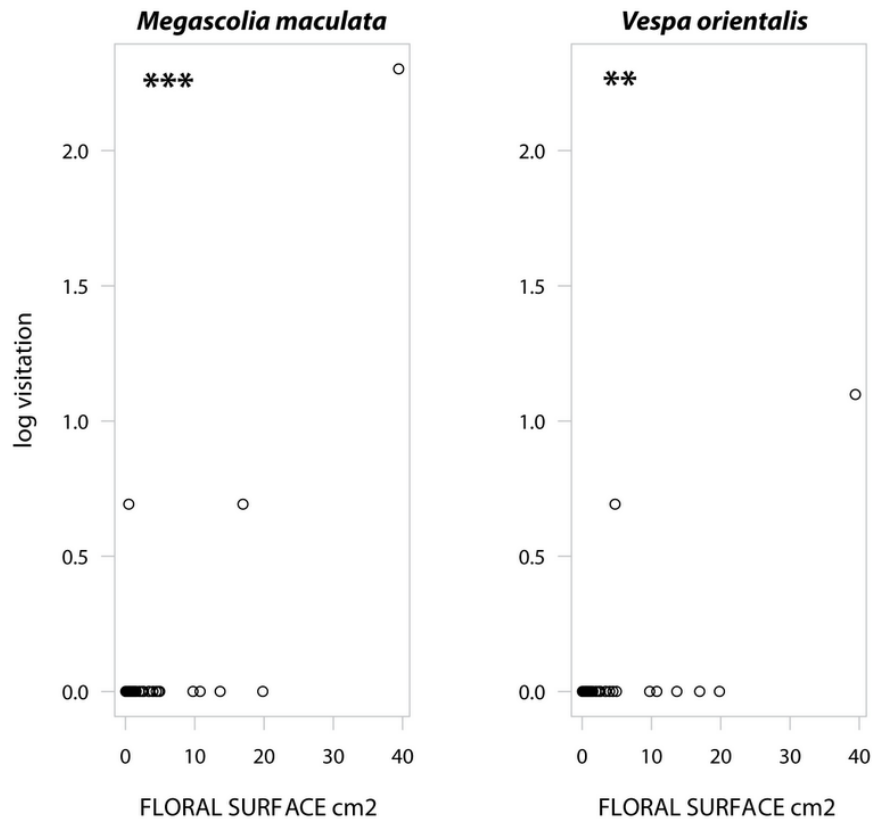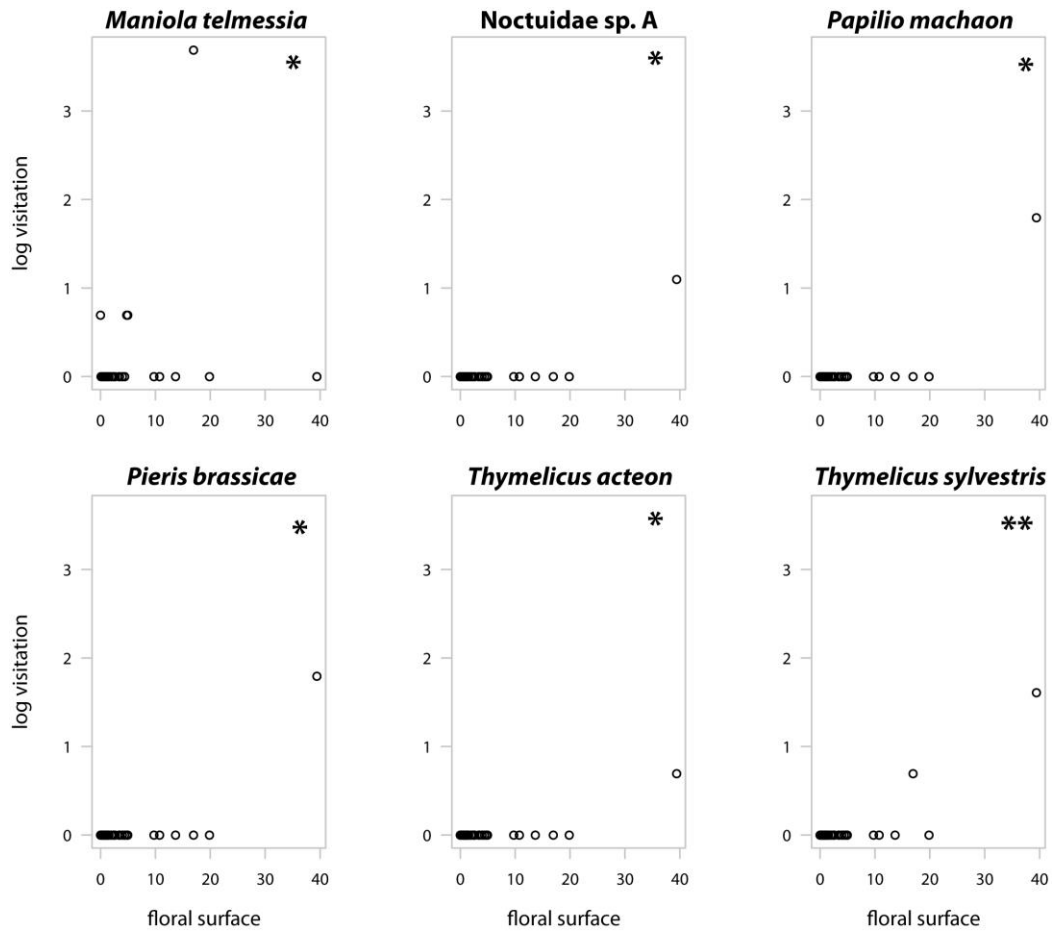
Fig 4.S32. The insects in the **Lepidoptera** sub-network that show significant associations of number of visits (visitation) and **floral surface**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
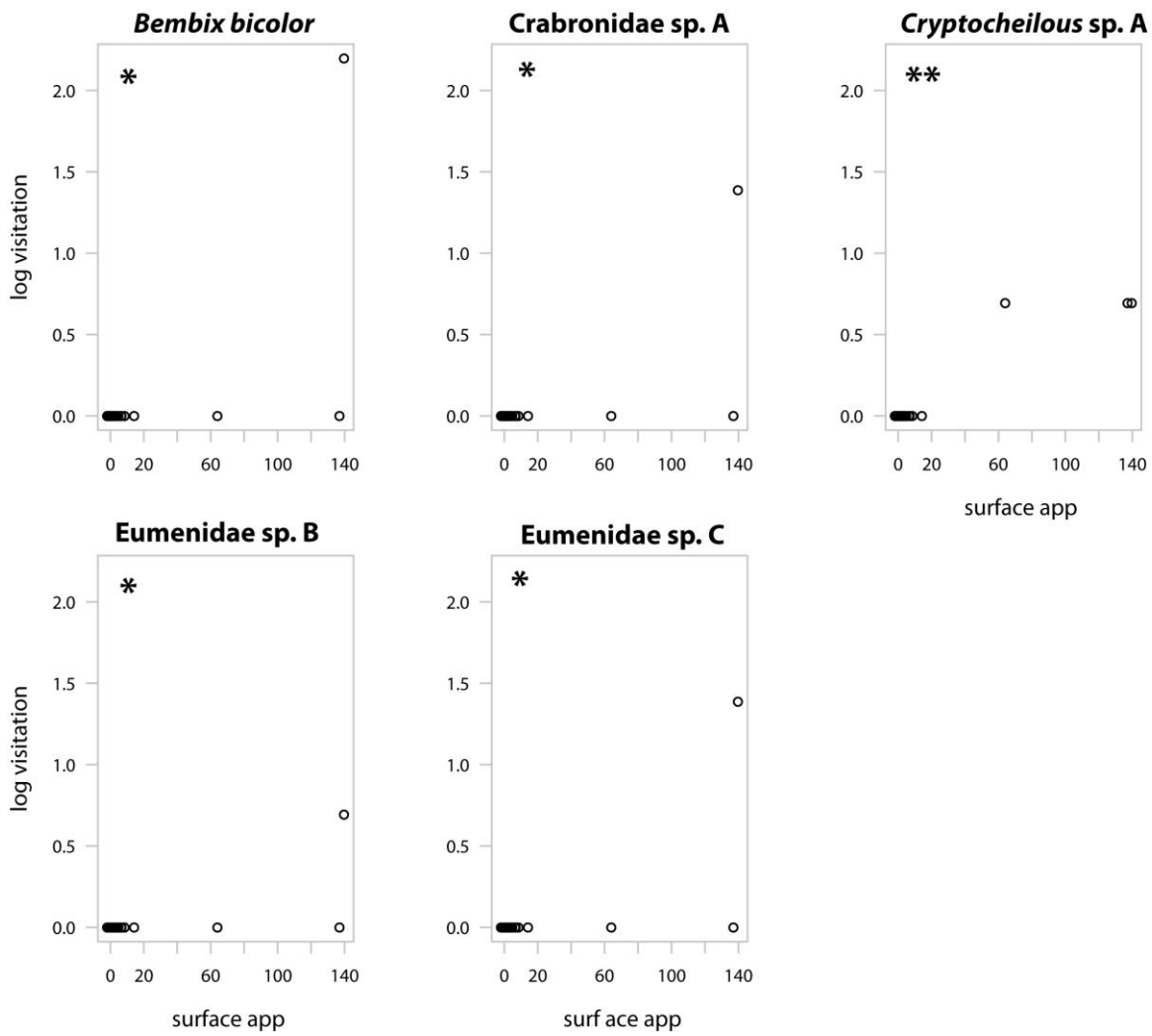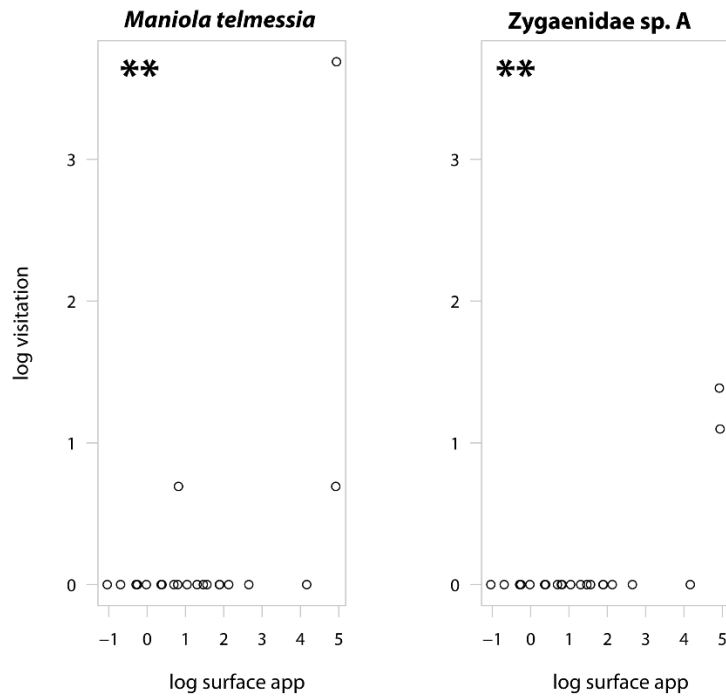
Fig 4.S33. The insects in the **Lepidoptera** sub-network that show significant associations of number of visits (visitation) and **floral surface apparency** (surface app). The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).
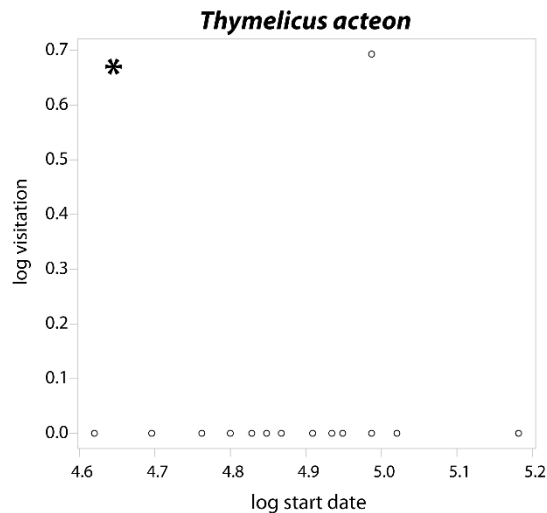
Fig 4.S34. The only insect in the **Lepidoptera** sub-network that shows a significant association of number of visits (visitation) and the **start date of flowering**. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling (*: $p \leq 0.050$; **$p \leq 0.010$; ***$p \leq 0.001$).

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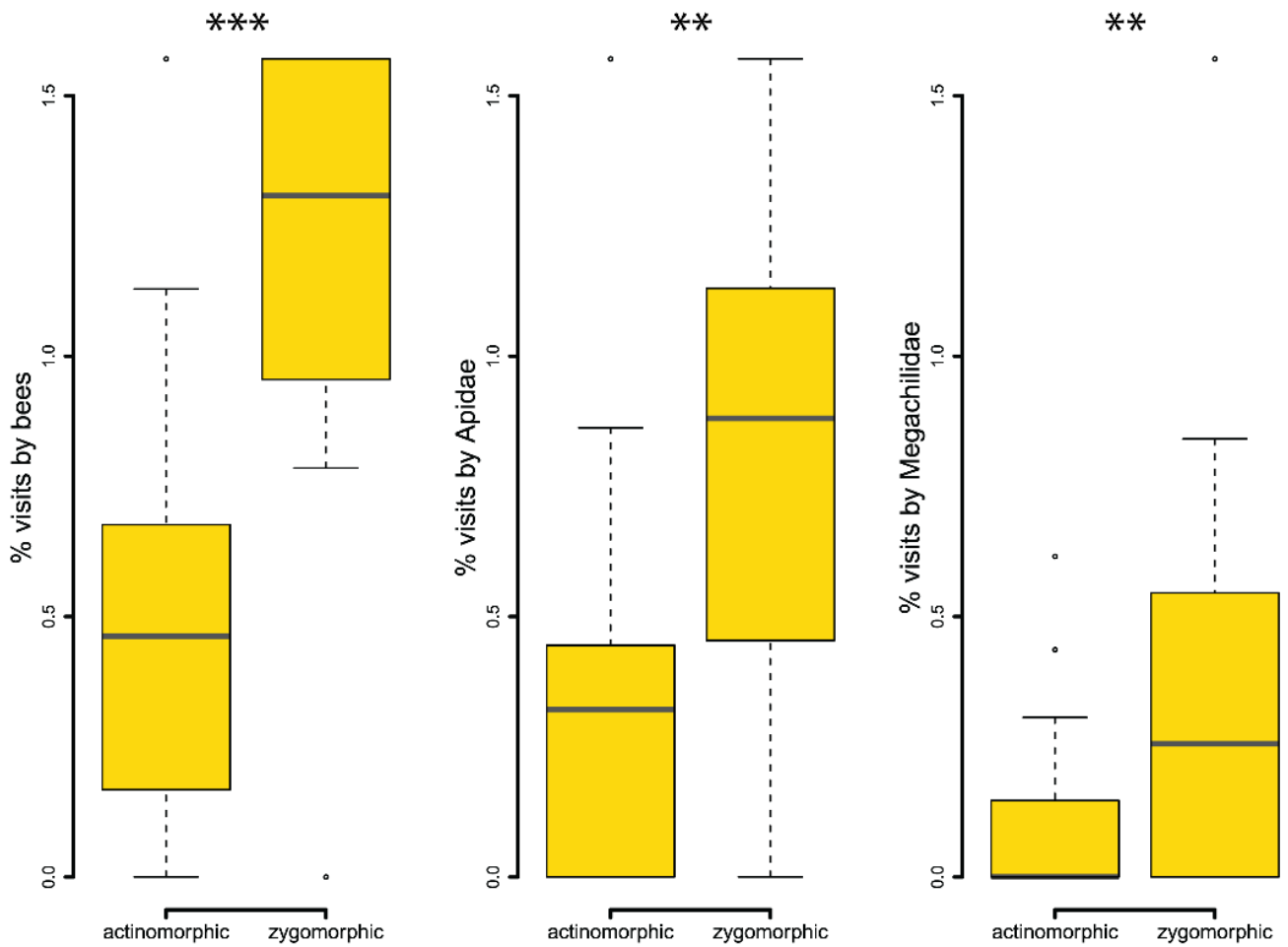
**Fig 4.S35.** The relationship of floral symmetry and visitation by bees (left), and separately by Apidae (middle), and Megachilidae (right). Results were acquired with phylogenetically informed GLS models. Response variables were arcsine-transformed.
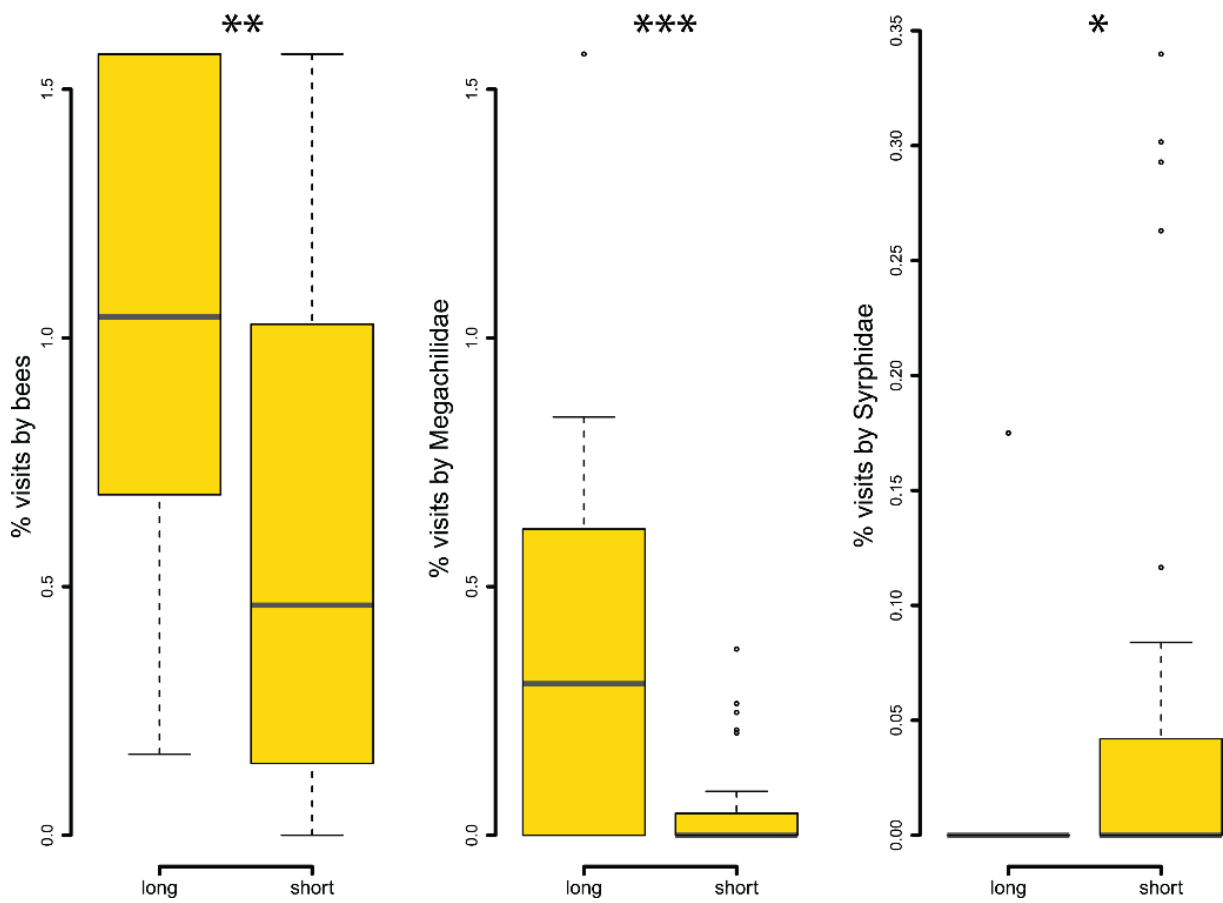
Fig 4.S36. The relationship of corolla depth and visitation by bees (left), separately by Megachilidae (middle), and by Syrphidae (right). Results were acquired with phylogenetically informed GLS models. Response variables were arcsine-transformed.
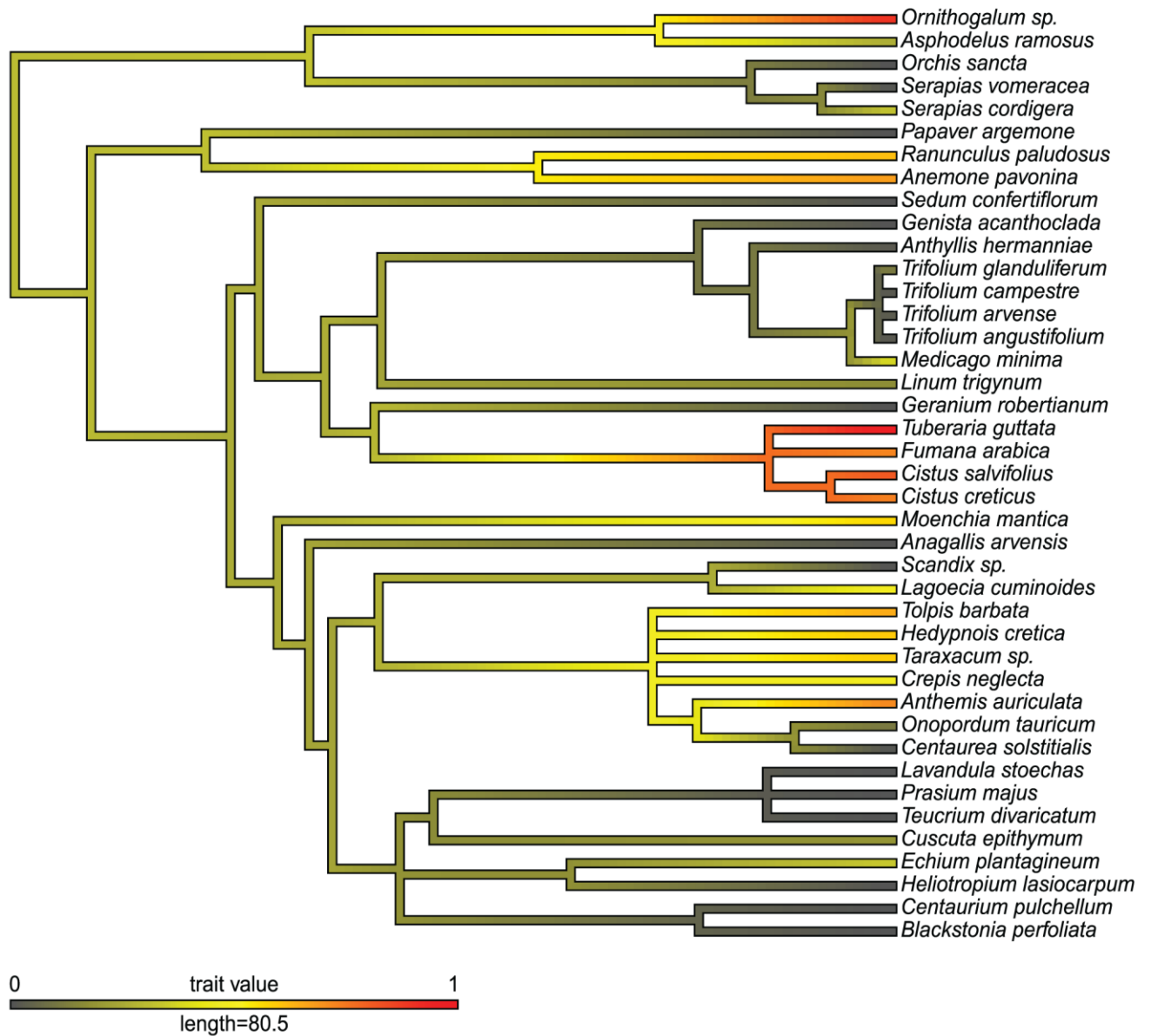
Fig. 4.S37. The percentage of visits by Coleoptera for each plant, distributed within the phylogram of the plants in the community (branch length: Ma). A significant phylogenetic signal is found (Blomberg's K^*=0.47, p=0.009 in Table 4.S6).

Table 4.S1. Flowering phenology, floral morphology and the volatility of the scent blends of the plants in the community. Days of flowering and floral density represent mean values of the two years of sampling, except for *Geranium robertianum* and *Heliotropium europaeum* that were observed in the community only in the second year. Note that *Cuscuta epithymum* is a parasitic vine found on *Cistus creticus* towards the end of its flowering period.

Plant	First day of flowering[1]	Last day of flowering[1]	Floral density (fl. units/m^2)	Corolla depth[2]	Symmetry	Floral surface (cm^2)	Floral height (cm)	Mean nBP (ºC)
Anagallis arvensis	102	169	3.23	short	actinomorphic	0.47	3.71	218.1
Anemone pavonina	102	117	0.23	short	actinomorphic	13.67	20.67	222.9
Anthemis auriculata	117	169	0.67	short	actinomorphic	4.95	13.97	207.7
Anthyllis hermanniae	141	152	8.58	short	zygomorphic	0.12	28.79	227.5
Asphodelus ramosus	102	117	0.71	short	actinomorphic	3.39	74.65	206.7
Blackstonia perfoliata	117	138	1.09	short	actinomorphic	0.29	6.74	188.8
Centaurea solstitialis	152	155	0.01	long	actinomorphic	0.58	25.95	213.1
Centaurium pulchellum	147	152	0.01	short	actinomorphic	0.49	10.11	228.5
Cistus creticus	102	173	8.29	short	actinomorphic	16.97	33.48	235.2
Cistus salvifolius	102	146	6.70	short	actinomorphic	9.74	30.28	209.6
Crepis neglecta	117	161	3.69	long	actinomorphic	2.56	28.20	205.6
Cuscuta epithymum	152	173	1.50	short	actinomorphic	0.47	27.35	221.4
Echium plantagineum	110	169	0.32	long	zygomorphic	1.39	7.25	169.9
Fumana arabica	102	173	0.96	short	actinomorphic	3.97	20.75	206.3
Genista acanthoclada	102	117	0.73	long	zygomorphic	0.73	40.53	208.2
Geranium robertianum	125	153	0.08	short	actinomorphic	0.56	4.63	226.8
Hedypnois cretica	102	143	1.99	long	actinomorphic	0.44	9.82	202.2
Heliotropium lasiocarpum	178	178	0.10	short	actinomorphic	4.42	16.71	200.9
Lagoecia cuminoides	130	152	1.30	short	actinomorphic	0.66	17.21	180.5
Lavandula stoechas	102	163	28.99	long	zygomorphic	4.76	34.23	209.1
Linum trigynum	110	169	18.05	short	actinomorphic	0.11	10.87	166.0
Medicago minima	136	146	0.56	short	zygomorphic	0.07	5.10	201.2
Moenchia mantica	102	157	3.34	long	actinomorphic	0.96	13.33	222.1

Plant	First day of flowering[1]	Last day of flowering[1]	Floral density (fl. units/m^2)	Corolla depth[2]	Symmetry	Floral surface (cm^2)	Floral height (cm)	Mean nBP (ºC)
Onopordum tauricum	147	176	0.40	long	actinomorphic	39.43	111.47	202.5
Orchis sancta	102	130	0.07	long	zygomorphic	1.01	18.33	261.8
Ornithogalum sp.	117	122	0.12	short	actinomorphic	3.44	7.00	194.8
Papaver argemone	128	141	0.02	short	actinomorphic	19.81	16.31	244.6
Prasium majus	122	133	0.04	long	zygomorphic	1.35	61.75	205.6
Ranunculus paludosus	102	110	0.16	short	actinomorphic	2.35	13.70	198.2
Scandix sp.	102	132	3.01	short	actinomorphic	1.08	18.00	237.8
Sedum confertiflorum	102	117	0.54	short	actinomorphic	0.12	4.66	211.1
Serapias cordigera	102	138	1.86	long	zygomorphic	2.60	18.68	268.3
Serapias vomeracea	102	130	1.43	long	zygomorphic	0.72	19.56	274.5
Taraxacum sp.	102	125	0.20	long	actinomorphic	10.77	24.25	247.0
Teucrium divaricatum	139	176	7.80	long	zygomorphic	0.74	43.50	215.1
Tolpis barbata	117	173	2.93	short	actinomorphic	1.98	14.96	212.1
Trifolium angustifolium	117	130	1.94	short	zygomorphic	0.03	6.55	202.9
Trifolium arvense	122	161	7.66	short	zygomorphic	1.00	7.75	200.1
Trifolium campestre	102	128	3.48	short	zygomorphic	0.80	7.95	206.8
Trifolium glanduliferum	102	127	6.54	short	zygomorphic	1.22	5.99	217.7
Tuberaria guttata	102	134	1.02	short	actinomorphic	1.54	15.12	202.3

[1]Julian day numbers.
[2]Limit set at 3 mm.

Table 4.S2. The 168 flower-visiting insects recorded in the study community, their phenology and the module they have been classified to by the Simulated Annealing algorithm (see Materials and Methods). For each Order, number of taxa is given in parentheses. Insects found only in the first year are marked with (1), and insects found only in the second year, with (2). For the rest insects, days of activity (Julian day numbers) represent the mean values of the two years. Specimens are deposited at the Melissotheque of the Aegean, University of the Aegean.

Order	Family	Insect	First day of activity	Last day of activity	Module ID
Coleoptera (26; 15.5%)	Buprestidae	*Acmaeodera bipunctata*	157	173	Module 3
		Buprestidae sp. A	152	155	Module 7
		Buprestidae sp. B (1)	150	150	Module 9
		Buprestidae sp. C (1)	157	173	Module 7
	Cerambycidae	Cerambycidae sp. A	124	130	Module 2
		Cerambycidae sp. B (2)	153	153	Module 3
		Pseudovadonia livida	143	143	Module 3
	Chrysomelidae	*Chrysolina americana* (1)	103	129	Module 3
		Clytra atraphaxidis (1)	103	129	Module 9
		Labidostomis humeralis (1)	105	105	Module 8
	Cleridae	*Diplocladus* sp. A	147	152	Module 7
		Trichodes alvearius	101	139	Module 5
	Curculionidae	*Larinus* sp. A (1)	157	173	Module 7
	Glaphyridae	*Eulasia nitidicollis*	117	124	Module 8
		Pygopleurus sp. A	101	102	Module 8
	Melyridae	*Dasytes* sp. A	103	103	Module 8
		Malachius bipustulatus (1)	102	160	Module 8
	Mordellidae	Mordellidae sp. A (1)	167	167	Module 4
	Oedemeridae	*Oedemera* sp. A	109	166	Module 8
		Oedemera sp. B	168	168	Module 3
	Scarabaeidae	*Anomala* sp. A	101	143	Module 8
		Epicometis hirta	101	117	Module 8

Order	Family	Insect	First day of activity	Last day of activity	Module ID
		Osmoderma sp. A	130	169	Module 6
		Oxythyrea funesta	133	133	Module 7
	Unknown	Beetle sp. A (1)	103	120	Module 8
		Beetle sp. B (2)	153	153	Module 3
Diptera (37; 22.0%)	Asilidae	Asilidae sp. A (1)	105	120	Module 3
		Asilidae sp. B (2)	153	153	Module 4
	Bombyliidae	*Bombylella atra* (1)	103	157	Module 8
		Bombylius medius (1)	103	120	Module 3
		Bombylius posticus	147	166	Module 2
		Bombylius rhodius	101	102	Module 5
		Cyllenia rustica	157	157	Module 2
		Exoprosopa minois	147	161	Module 2
		Exoprosopa pandora	147	176	Module 2
		Lomatia sp. A (1)	150	157	Module 8
		Petrorossia chraminensis (2)	153	178	Module 9
		Phthiria subnitens (1)	173	173	Module 7
		Thyridanthrax elegans (1)	167	167	Module 4
		Villa hottentotta (2)	164	164	Module 3
	Calliphoridae	Calliphoridae sp. A (1)	167	167	Module 4
		Calliphoridae sp. B (1)	103	142	Module 9
	Empididae	Empididae sp. A (2)	98	98	Module 5
	Hybotidae	Hybotidae sp. A (1)	103	105	Module 5
	Syrphidae	*Eristalinus aeneus* (2)	164	164	Module 3
		Eristalis tenax	136	150	Module 3
		Eumerus pulchellus	102	150	Module 5
		Eupeodes corollae (2)	113	113	Module 2
		Merodon albifrons (1)	150	150	Module 3

Order	Family	Insect	First day of activity	Last day of activity	Module ID
		Merodon spinitarsis	121	121	Module 9
		Paragus haemorrhous (1)	167	167	Module 4
		Paragus sp. A (1)	173	173	Module 4
		Sphaerophoria scripta (1)	142	142	Module 9
		Syritta pipiens (1)	167	167	Module 4
	Tachinidae	Tachinidae sp. A	142	166	Module 8
	Tephritidae	Tephritidae sp. A (1)	103	105	Module 5
	Tipulidae	Tipulidae sp. A (1)	105	105	Module 3
	Unknown	Fly sp. A	103	105	Module 5
		Fly sp. B	105	105	Module 5
		Fly sp. C	103	120	Module 5
		Fly sp. D (1)	108	117	Module 5
		Fly sp. E (1)	129	129	Module 9
		Fly sp. F	105	105	Module 5
Hemiptera (3; 1.8%)	Auchenorrhyncha	*Auchenorrhyncha* sp. A	142	150	Module 8
	Miridae	*Calocoris* sp. A	103	105	Module 5
		Bug sp. A	105	120	Module 8
Hymenoptera – Bees (66; 39.3%)	Andrenidae	*Andrena* aff. *hesperia*	102	102	Module 8
		Andrena aff. *neocypriaca*	128	128	Module 9
		Andrena panurgimorpha (1)	135	142	Module 9
		Andrena schencki (2)	113	113	Module 8
		Andrena sp. A (1)	103	129	Module 5
		Andrena sp. C (1)	120	129	Module 9
		Andrena westensis (2)	98	178	Module 8
	Apidae	*Amegilla albigena*	152	169	Module 7
		Amegilla quadrifasciata	163	176	Module 7

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Order	Family	Insect	First day of activity	Last day of activity	Module ID
		Amegilla salviae (1)	173	173	Module 7
		Anthophora crinipes (2)	113	125	Module 3
		Anthophora dalmatica	109	127	Module 3
		Anthophora plumipes (1)	103	103	Module 3
		Anthophora rubricrus (1)	105	105	Module 3
		Apis mellifera	101	176	Module 8
		Bombus terrestris	114	155	Module 7
		Ceratina acuta (2)	125	153	Module 6
		Ceratina schwarzi (2)	113	178	Module 2
		Ceratina sp. A (1)	167	167	Module 6
		Epeolus variegatus (1)	157	157	Module 6
		Eucera cineraria group	124	143	Module 3
		Eucera digitata	130	138	Module 2
		Eucera aff. *pseudeucnemidea* (2)	125	125	Module 9
		Eucera seminuda	139	139	Module 3
		Xylocopa iris	114	169	Module 3
		Xylocopa violacea	141	166	Module 7
	Colletidae	*Colletes eous* (2)	136	136	Module 6
		Colletes sp. A	147	147	Module 4
		Hylaeus meridionalis (1)	167	167	Module 4
	Halictidae	*Halictus resurgens*	147	176	Module 7
		Halictus sexcinctus (1)	167	173	Module 7
		Halictus aff. *tumulorum.confusus* (2)	153	153	Module 9
		Lasioglossum laticeps/mediterraneum (2)	136	153	Module 3
		Lasioglossum aff. *lativentre/haesitans* (2)	136	136	Module 2
		Lasioglossum leucozonium	109	155	Module 6
		Lasioglossum malachurum group	152	157	Module 9
		Lasioglossum marginatum (1)	129	129	Module 9

Order	Family	Insect	First day of activity	Last day of activity	Module ID
		Lasioglossum pygmaeum/pauperatum	101	133	Module 3
		Lasioglossum sp. B (2)	113	113	Module 6
		Lasioglossum tricinctum group	101	160	Module 8
		Lasioglossum villosulum group (2)	136	136	Module 9
		Pseudapis monstrosa (2)	136	153	Module 3
	Megachilidae	*Anthidiellum strigatum*	155	155	Module 6
		Anthidium aff. *dalmaticum* (2)	153	153	Module 7
		Eoanthidium insulare (2)	178	178	Module 3
		Eoanthidium aff. *judaense* (2)	160	160	Module 4
		Eoanthidium sp. A	164	164	Module 4
		Hoplitis adunca group (2)	125	125	Module 6
		Hoplitis aff. *illyrica*	141	141	Module 2
		Hoplitis aff. *lysholmi*	152	155	Module 2
		Hoplitis sp. A (2)	125	125	Module 3
		Hoplitis sp. C (1)	142	142	Module 9
		Lithurgus chrysurus (1)	173	173	Module 7
		Megachile albisecta	163	163	Module 7
		Megachile giraudi (2)	136	136	Module 7
		Megachile hungarica	147	173	Module 7
		Megachile manicata (2)	98	153	Module 6
		Megachile parietina (2)	98	136	Module 6
		Megachile pilicrus	155	176	Module 7
		Megachile sp. A (1)	167	167	Module 7
		Osmia dimidiata	163	163	Module 7
		Osmia aff. *helicosmia* (2)	125	125	Module 6
		Osmia sp. B (2)	125	125	Module 8
		Osmia sp. C (2)	125	125	Module 9
		Osmia versicolor (2)	125	125	Module 8

Order	Family	Insect	First day of activity	Last day of activity	Module ID
		Rhodanthidium septemdentatum (2)	125	178	Module 3
Hymenoptera – Wasps (19; 11.3%)	Chrysididae	*Chrysididae* sp. A (1)	157	157	Module 2
		Chrysididae sp. B (2)	113	113	Module 1
		Chrysura circe (1)	103	103	Module 1
	Crabronidae	*Bembix bicolor* (2)	136	153	Module 3
		Crabronidae sp. A (1)	150	150	Module 3
		Crabronidae sp. C (2)	164	178	Module 4
	Eumenidae	Eumenidae sp. A (1)	167	167	Module 4
		Eumenidae sp. B (2)	136	136	Module 3
		Eumenidae sp. C (2)	136	136	Module 3
		Eumenidae sp. D (2)	136	136	Module 8
	Leucospidae	*Leucospis gigas* (1)	167	167	Module 4
	Pompilidae	*Cryptocheilus* sp. A	117	124	Module 3
	Sapygidae	*Sapyga* sp. A (1)	135	135	Module 2
	Scoliidae	*Colpa quinquecincta* (2)	178	178	Module 4
		Megascolia maculata	147	155	Module 4
		Scolia sp. A (2)	164	178	Module 4
	Tiphiidae	*Tiphia* sp. A (2)	113	113	Module 9
	Vespidae	*Polistes* sp. A	164	173	Module 4
		Vespa orientalis (1)	142	167	Module 7
Lepidoptera (17; 10.1%)	Hesperiidae	*Charcharodus orientalis* (2)	153	178	Module 2
		Spialia orbifer (2)	178	178	Module 2
		Thymelicus acteon (1)	157	157	Module 7
		Thymelicus sylvestris	160	160	Module 7
	Lycaenidae	*Lycaena phlaeas*	143	161	Module 6
		Pseudophilotes vicrama	128	155	Module 6

Order	Family	Insect	First day of activity	Last day of activity	Module ID
	Noctuidae	Noctuidae sp. A (1)	167	167	Module 7
		Noctuidae sp. B (2)	136	136	Module 6
		Trichoplusia ni (1)	157	157	Module 7
	Nymphalidae	*Coenonympha pamphilus*	141	157	Module 8
		Maniola telmessia	130	143	Module 3
	Papilionidae	*Papilio machaon* (1)	157	167	Module 7
	Pieridae	*Colias crocea*	128	155	Module 7
		Gonepteryx cleoptatra (2)	136	136	Module 7
		Pieris brassicae (1)	157	167	Module 7
	Sphingidae	*Macroglossum stellatarum* (2)	136	153	Module 7
	Zygaenidae	Zygaenidae sp. A (2)	125	125	Module 3

Table 4.S3. Sizes of the phenonets in the study community. Connectance represents the realized proportion of the possible links within each phenonet. Metrics are also shown for the phenonets of the plants that received no visits.

phenonet	Connectance	# Insects	# Plants
Anagallis arvensis	0.067	158	37
Anemone pavonina	0.139	47	24
Anthemis auriculata	0.066	165	36
Anthyllis hermanniae	0.165	51	20
Asphodelus ramosus	0.144	47	23
Blackstonia perfoliata	0.092	68	36
Centaurea solstitialis	0.190	42	16
Centaurium pulchellum	0.198	42	15
Cistus creticus	0.067	158	37
Cistus salviifolius	0.083	99	34
Crepis neglecta	0.078	115	35
Cuscuta epithymum	0.143	77	16
Echium plantagineum	0.068	143	37
Fumana arabica	0.067	158	37
Genista acanthoclada	0.137	47	24
Geranium robertianum	0.089	91	32
Hedypnois cretica	0.085	96	33
Heliotropium lasiocarpum	NA	NA	NA
Lagoecia cuminoides	0.114	68	27
Lavandula stoechas	0.071	139	37
Linum trigynum	0.068	143	37
Medicago minima	0.152	46	18
Moenchia mantica	0.072	135	37
Onopordum tauricum	0.135	88	16
Orchis sancta	0.099	72	31
Ornithogalum sp.	0.171	30	24
Papaver argemone	0.114	49	28
Prasium majus	0.140	41	25
Ranunculus paludosus	0.155	39	19
Scandix sp.	0.099	72	31
Sedum confertiflorum	0.138	48	24
Serapias cordigera	0.090	83	31
Serapias vomeracea	0.098	72	30
Taraxacum sp.	0.124	54	27
Teucrium divaricatum	0.118	99	20
Tolpis barbata	0.071	136	35
Trifolium angustifolium	0.118	50	29
Trifolium arvense	0.082	109	33
Trifolium campestre	0.108	67	28
Trifolium glanduliferum	0.113	64	27
Tuberaria guttata	0.099	72	31

Table 4.S4. Comparison of the node properties computed for the 'static' network of the entire flowering season and for the plant phenonets (pn) in the community. Properties were calculated using the function 'specieslevel' in the R package *bipartite* v.2.05, except for the functional role which was computed with *NetCarto* software (*69*). Plants with no insect visitors are not included. For details on each property see Materials and Methods.

Plant	Normalized degree		Betweenness centrality		Closeness centrality		Functional role	
	static	phenonet	static	phenonet	static	phenonet	static	phenonet
Anagallis arvensis	0.006	0.006	0.000	0.000	0.020	0.021	Peripheral	Peripheral
Anemone cf. *pavonina*	0.024	0.085	0.007	0.020	0.028	0.043	Peripheral	Connector
Anthemis auriculata	0.071	0.073	0.062	0.052	0.031	0.032	Connector	Connector
Anthyllis hermanniae	0.071	0.137	0.025	0.040	0.029	0.050	Module hub	Peripheral
Asphodelus ramosus	0.065	0.213	0.008	0.034	0.027	0.045	Peripheral	Peripheral
Blackstonia perfoliata	0.006	0.015	0.000	0.000	0.021	0.023	Peripheral	Peripheral
Centaurea solstitialis	0.018	0.048	0.004	0.015	0.023	0.052	Peripheral	Peripheral
Cistus creticus	0.411	0.430	0.207	0.194	0.035	0.035	Network hub	Network hub
Cistus salviifolius	0.113	0.182	0.020	0.025	0.031	0.035	Peripheral	Connector
Crepis neglecta	0.155	0.200	0.124	0.138	0.030	0.032	Module hub	Module hub
Cuscuta epithymum	0.143	0.260	0.021	0.114	0.030	0.068	Module hub	Connector
Echium plantagineum	0.054	0.063	0.025	0.027	0.030	0.030	Peripheral	Peripheral
Fumana arabica	0.077	0.082	0.059	0.066	0.032	0.033	Connector	Connector
Genista acanthoclada	0.012	0.043	0.000	0.000	0.020	0.029	Peripheral	Peripheral
Hedypnois cretica	0.054	0.094	0.013	0.017	0.031	0.035	Peripheral	Peripheral
Lagoecia cuminoides	0.012	0.029	0.001	0.002	0.027	0.036	Peripheral	Peripheral
Lavandula stoechas	0.125	0.137	0.102	0.107	0.032	0.032	Connector	Peripheral
Linum trigynum	0.048	0.056	0.032	0.025	0.030	0.030	Peripheral	Module hub
Medicago minima	0.018	0.065	0.014	0.047	0.029	0.058	Peripheral	Peripheral
Moenchia mantica	0.065	0.074	0.009	0.010	0.029	0.029	Connector	Connector
Onopordum tauricum	0.208	0.375	0.033	0.049	0.029	0.059	Module hub	Module hub
Orchis sancta	0.012	0.028	0.008	0.021	0.026	0.032	Peripheral	Peripheral
Ornithogalum sp.	0.030	0.100	0.004	0.009	0.028	0.043	Peripheral	Peripheral

Plant	Normalized degree		Betweenness centrality		Closeness centrality		Functional role	
	static	phenonet	static	phenonet	static	phenonet	static	phenonet
Prasium majus	0.024	0.073	0.000	0.000	0.020	0.029	Peripheral	Peripheral
Ranunculus paludosus	0.024	0.103	0.004	0.011	0.028	0.055	Peripheral	Peripheral
Scandix sp.	0.065	0.153	0.001	0.002	0.023	0.029	Module hub	Module hub
Sedum confertiflorum	0.012	0.042	0.000	0.000	0.000	0.000	Peripheral	Peripheral
Serapias cordigera	0.018	0.036	0.001	0.001	0.021	0.025	Peripheral	Peripheral
Serapias vomeracea	0.006	0.014	0.000	0.000	0.016	0.021	Peripheral	Peripheral
Taraxacum sp.	0.089	0.278	0.046	0.117	0.031	0.044	Peripheral	Connector
Teucrium divaricatum	0.119	0.172	0.050	0.106	0.030	0.050	Peripheral	Module hub
Tolpis barbata	0.077	0.081	0.047	0.029	0.032	0.033	Peripheral	Peripheral
Trifolium angustifolium	0.006	0.020	0.000	0.000	0.019	0.025	Peripheral	Peripheral
Trifolium arvense	0.060	0.092	0.050	0.055	0.032	0.036	Connector	Peripheral
Trifolium campestre	0.006	0.015	0.000	0.000	0.025	0.034	Peripheral	Peripheral
Trifolium glanduliferum	0.054	0.094	0.021	0.025	0.031	0.042	Peripheral	Peripheral
Tuberaria guttata	0.018	0.042	0.002	0.002	0.027	0.034	Peripheral	Peripheral

Table 4.S5. Vertical, horizontal, and chemical floral apparency in the study community. Values correspond to the flowering time of each plant species, not to the entire sampling season. Apparency values of zero indicate that the focal trait of the plant does not differ from the median of the co-flowering plants. For chemical apparency, we have taken into account the per m^2 emission rate of each plant (see Materials and Methods for details).

Plant	Vertical apparency	Horizontal apparency	Total emissions apparency	Aliphatics apparency	Benzenoids apparency	Monoterpenes apparency	Sesquiterpenes apparency
Anagallis arvensis	-12.89	0.50	-0.15	0.18	0.09	-0.09	0.00
Anemone pavonina	4.91	1.44	-0.45	-0.10	0.00	-0.04	0.00
Anthemis auriculata	-2.80	2.26	0.50	0.13	0.01	0.36	0.30
Anthyllis hermanniae	11.56	-0.37	80.94	1.69	12.61	63.25	1.78
Asphodelus ramosus	58.94	0.75	-0.73	-0.29	-0.01	-0.10	0.00
Blackstonia perfoliata	-8.59	-0.96	-0.52	-0.07	-0.01	-0.09	0.00
Centaurea solstitialis	6.98	-1.62	-1.12	-0.24	-0.01	-0.24	-0.05
Centaurium pulchellum	-9.77	-1.82	-1.43	-0.29	-0.02	-0.34	-0.09
Cistus creticus	16.86	139.73	19.56	0.31	1.97	4.63	8.63
Cistus salvifolius	14.28	64.10	2.55	0.81	0.26	0.15	0.98
Crepis neglecta	11.40	8.41	0.90	0.77	0.00	0.14	0.00
Cuscuta epithymum	8.35	-0.96	-0.86	-0.12	0.05	-0.23	-0.05
Echium plantagineum	-9.38	-0.54	-0.57	-0.14	0.00	-0.08	0.00
Fumana arabica	4.15	2.83	-0.11	0.16	0.04	-0.02	0.00
Genista acanthoclada	24.86	-1.12	0.24	-0.13	0.45	0.15	0.06
Geranium robertianum	-12.21	-1.25	0.61	-0.23	0.01	0.80	0.38
Hedypnois cretica	-5.79	-0.14	0.73	0.53	0.07	0.21	-0.01
Heliotropium lasiocarpum	0.10	-0.56	-0.38	-0.13	0.03	0.05	0.00
Lagoecia cuminoides	0.19	-0.26	26.36	-0.23	3.08	23.07	0.83
Lavandula stoechas	17.68	137.13	391.45	4.96	0.00	350.03	30.70
Linum trigynum	-5.69	0.98	-0.26	-0.16	0.00	0.26	0.00
Medicago minima	-10.32	-1.54	-1.33	-0.39	-0.01	-0.31	-0.08
Moenchia mantica	-3.38	2.22	1.21	1.50	0.00	-0.05	0.00

Plant	Vertical apparency	Horizontal apparency	Total emissions apparency	Aliphatics apparency	Benzenoids apparency	Monoterpenes apparency	Sesquiterpenes apparency
Onopordum tauricum	92.94	14.19	-1.15	-0.24	-0.01	-0.27	-0.05
Orchis sancta	2.72	-1.18	2.74	-0.20	3.25	-0.12	0.09
Ornithogalum sp.	-9.06	-1.16	-0.64	-0.28	-0.01	-0.07	-0.01
Papaver argemone	0.48	-0.72	-0.94	-0.27	-0.01	-0.18	-0.02
Petrorhagia velutina	0.69	-1.70	-0.93	-0.42	-0.02	-0.13	-0.01
Prasium majus	46.57	-1.26	-0.72	-0.26	-0.01	-0.07	0.02
Ranunculus paludosus	-4.00	-1.51	-0.25	-0.28	-0.02	0.43	-0.01
Scandix sp.	2.41	2.01	219.88	2.47	214.56	2.09	1.13
Sedum confertiflorum	-10.98	-1.62	-0.67	-0.28	0.00	-0.07	0.01
Serapias cordigera	3.36	3.68	0.14	0.64	-0.01	-0.11	0.00
Serapias vomeracea	3.69	-0.15	0.19	0.65	-0.01	-0.10	0.00
Taraxacum sp.	8.90	0.78	-0.69	-0.24	-0.01	-0.11	-0.01
Teucrium divaricatum	25.87	4.34	24.66	4.00	-0.01	6.28	14.79
Tolpis barbata	-1.87	4.76	0.06	0.26	0.00	-0.05	0.05
Trifolium angustifolium	-9.29	-1.27	-0.36	0.06	0.00	-0.09	-0.01
Trifolium arvense	-8.73	6.66	-0.27	-0.21	0.03	0.10	-0.01
Trifolium campestre	-7.53	1.47	2.83	2.46	0.34	0.30	0.02
Trifolium glanduliferum	-9.23	6.60	80.12	6.60	64.84	5.80	2.02
Tuberaria guttata	-0.54	0.35	-0.28	-0.14	-0.01	0.22	-0.01

Table 4.S6. The phylogenetic signal in all variables used in the present Chapter. Different methods have been used according to variable type (alternately shaded groups of columns). Details are provided in Materials and Methods. K^*: Blomberg's K^*. Mantel r: Mantel statistic. D: statistic for binary traits. Only p-values implying significance shown ($p \leq 0.050$).

	K^*	p-value	r	p-value	D^1	p random	p Brownian	Transitions observed[2]	Transitions randomized[2]	p-value
% Bees visits	0.15	0.605								
% Andrenidae visits	0.19	0.784								
% Apidae visits	0.14	0.641								
% Colletidae visits	0.42	0.394								
% Halictidae visits	**0.55**	**0.011**								
% Megachilidae visits	0.26	0.409								
% Coleoptera visits	**0.47**	**0.009**								
% Oedemeridae visits	0.18	0.544								
% Scarabaeidae visits	**0.85**	**0.001**								
% Diptera visits	**0.62**	**0.003**								
% Bombyliidae visits	0.46	0.056								
% Syrphidae visits	**0.54**	**0.046**								
% Lepidoptera visits	0.04	0.938								
% Wasps visits	**0.90**	**0.010**								
pn Normalized degree	0.23	0.382								
pn Betweenness centrality	0.39	0.065								
pn Closeness centrality	0.07	0.979								
pn Functional role								13	13	0.999
Module ID								24	23	0.999
Predominating insect order in visits								16	20	**0.008**
Total p–p network			0.09	0.066						
Bees sub-network			0.02	0.375						
Coleoptera sub-network			0.11	0.065						

	K*	p-value	r	p-value	D[1]	p random	p Brownian	Transitions observed[2]	Transitions randomized[2]	p-value
Diptera sub-network			0.01	0.398						
Lepidoptera sub-network			0.05	0.176						
Wasp sub-network			0.02	0.371						
Corolla depth					-0.15	0	**0.641**			
Floral symmetry					-0.75	0	**0.955**			
Floral height	0.35	0.162								
Floral surface	0.29	0.404								
Vertical apparency	0.35	0.192								
Horizontal apparency	0.27	0.572								
Total Emissions apparency	0.23	0.624								
Aliphatics apparency	0.06	0.931								
Benzenoids apparency	0.19	0.752								
Monoterpenes apparency	0.27	0.619								
Sesquiterpenes apparency	0.34	0.467								

[1]Probability of D resulting from no (random) phylogenetic structure or from Brownian model of evolution.
[2]Phylogenetic signal exists if only the observed transitions are significantly less than the randomized median.

Table 4.S7. Number of visits by each one of the main pollinator groups recorded in the two years of sampling for each plant of the community, and the distribution of plants into the p–p network modules computed with the SA algorithm (*69*).

Plant	Coleoptera	Diptera	Lepidoptera	Bees	Wasps	Total visits	Module ID
Anagallis arvensis	0	0	0	1	0	1	Module 3
Anemone pavonina	9	0	0	4	0	13	Module 8
Anthemis auriculata	25	6	1	1	1	34	Module 2
Anthyllis hermanniae	2	0	10	122	0	134	Module 6
Asphodelus ramosus	20	10	0	48	0	78	Module 5
Blackstonia perfoliata	0	0	0	2	0	2	Module 2
Centaurea solstitialis	0	1	0	2	0	3	Module 7
Centaurium pulchellum	0	0	0	0	0	0	NA
Cistus creticus	2017	71	62	539	19	2708	Module 3
Cistus salviifolius	271	21	0	34	1	327	Module 8
Crepis neglecta	49	8	3	38	1	99	Module 9
Cuscuta epithymum	9	11	7	8	13	48	Module 4
Echium plantagineum	9	0	4	13	0	26	Module 6
Fumana arabica	50	2	0	16	0	68	Module 8
Genista acanthoclada	0	0	0	8	0	8	Module 6
Geranium robertianum	0	0	0	0	0	0	NA
Hedypnois cretica	17	1	0	10	0	28	Module 8
Heliotropium lasiocarpum	0	2	2	1	0	5	Module 2
Lagoecia cuminoides	1	1	0	0	0	2	Module 8
Lavandula stoechas	0	13	6	2430	2	2451	Module 3
Moenchia mantica	3	12	0	3	0	18	Module 2
Linum trigynum	2	0	0	3	0	5	Module 8
Medicago minima	44	30	0	2	0	76	Module 5
Onopordum tauricum	48	2	20	367	12	449	Module 7
Orchis sancta	0	0	0	9	0	9	Module 6
Ornithogalum sp.	12	1	0	0	0	13	Module 8
Papaver argemone	0	0	0	0	0	0	NA
Prasium majus	0	0	0	37	0	37	Module 3
Ranunculus paludosus	5	0	0	3	0	8	Module 8
Scandix sp.	0	130	0	18	0	148	Module 5
Sedum confertiflorum	0	0	0	0	3	3	Module 1
Serapias cordigera	1	0	0	2	0	3	Module 3
Serapias vomeracea	0	0	0	1	0	1	Module 9
Taraxacum sp.	24	0	0	16	0	40	Module 8
Teucrium divaricatum	0	75	45	625	0	745	Module 7
Tolpis barbata	49	15	8	1	1	74	Module 8
Trifolium angustifolium	0	0	1	0	0	1	Module 3
Trifolium arvense	2	4	2	178	1	187	Module 2
Trifolium campestre	0	0	0	1	0	1	Module 8
Trifolium glanduliferum	10	1	1	61	0	73	Module 8
Tuberaria guttata	8	0	0	0	0	8	Module 8

Table 4.S8. Insects in the **total network** showing significant effects to at least one of the **interaction terms** of floral traits examined in this Chapter. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling.

Order	Insect	Trichromatic color		Tetrachromatic color		Height:Surface		Height:Surface apparency		Phenology	
		Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value
Coleoptera	*Acmaeodera bipunctata*	18.10	0.001					9.522	0.005		
	Anomala sp. A	6.96	0.026					10.165	0.011	8.792	0.011
	Beetle sp. B	7.42	0.017					5.751	0.023		
	Buprestidae sp. A					7.427	0.011				
	Buprestidae sp. C	7.48	0.004	4.203	0.034	5.564	0.009	6.864	0.005		
	Cerambycidae sp. A	11.45	0.002					4.586	0.033		
	Cerambycidae sp. B	9.95	0.016					6.718	0.032	7.156	0.026
	Dasytes sp. A	9.97	0.03			6.09	0.043	15.899	0.003	18.942	0.003
	Diplocladus sp. A			3.539	0.049	11.406	0.011				
	Eulasia nitidicollis							7.208	0.011	5.033	0.048
	Larinus sp. A			3.44	0.05	10.849	0.011				
	Malachius bipustulatus									6.017	0.032
	Mordellidae sp. A	4.75	0.029								
	Oedemera sp. A	7.47	0.037			6.02	0.03	14.755	0.008	18.526	0.001
	Oedemera sp. B	9.95	0.016					6.718	0.032	7.156	0.026
	Osmoderma sp. A			3.704	0.024	12.787	0.011				
	Oxythyrea funesta			4.814	0.017			7.072	0.005		
	Pseudovadonia livida	13.09	0.016					6.827	0.022	7.02	0.026
	Trichodes alvearius	6.91	0.015					5.425	0.028		
Diptera	Asilidae sp. A	5.03	0.037					5.856	0.028	14.935	0.001
	Bombylella atra									7.141	0.019
	Bombylius medius							10.594	0.01		

Order	Insect	Trichromatic color		Tetrachromatic color		Height:Surface		Height:Surface apparency		Phenology	
		Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value
	Bombylius posticus			6.988	0.011						
	Eristalinus aeneus	7.42	0.017					5.751	0.023	6.017	0.027
	Eristalis tenax	9.95	0.016					6.718	0.032	7.156	0.026
	Eumerus pulchellus			10.128	0.008						
	Fly sp. A			5.667	0.042						
	Fly sp. F			7.427	0.008						
	Hybotidae sp. A	6.12	0.04	5.436	0.048						
	Merodon albifrons	11.80	0.016					6.792	0.022	7.044	0.034
	Merodon spinitarsis									6.687	0.027
	Petrorossia chraminensis									9.023	0.006
	Phthiria subnitens					9.957	0.011				
	Tachinidae sp. A							4.336	0.049		
	Tephritidae sp. A			4.325	0.035						
	Tipulidae sp. A							7.241	0.01		
	Villa hottentotta	7.42	0.017					5.751	0.023	6.017	0.027
Hemiptera	*Auchenorrhyncha* sp. A									7.031	0.025
Hymenoptera – Bees	*Amegilla quadrifasciata*	5.13	0.028	5.182	0.033	7.932	0.01				
	Andrena hesperia aff.	5.64	0.035								
	Andrena schencki	3.14	0.05								
	Andrena sp. A			18.79	0.001						
	Anthophora crinipes							5.598	0.04		
	Anthophora dalmatica							17.618	0.001		
	Anthophora plumipes							4.995	0.041		
	Anthophora rubricrus							11.132	0.01		
	Apis mellifera							10.181	0.003	7.787	0.028
	Bombus terrestris			5.542	0.01						
	Ceratina schwarzi			7.426	0.024					7.404	0.014

Order	Insect	Trichromatic color		Tetrachromatic color		Height:Surface		Height:Surface apparency		Phenology	
		Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value
	Eoanthidium insulare	7.42	0.017					5.751	0.023	6.017	0.027
	Eoanthidium judaense aff.	5.22	0.036					5.571	0.05		
	Eucera cineraria group							5.457	0.021	12.831	0.004
	Eucera seminuda							12.014	0.001	6.184	0.017
	Halictus resurgens							4.628	0.045		
	Halictus sexcinctus			3.826	0.047	14.422	0.011				
	Hoplitis sp. A	7.42	0.017					5.751	0.023	6.017	0.027
	Lasioglossum laticeps.mediterraneum	9.95	0.016					6.718	0.032	7.156	0.026
	Lasioglossum malachurum group							5.307	0.039	5.21	0.049
	Lasioglossum pygmaeum.pauperatum							3.44	0.044		
	Lasioglossum tricinctum group			6.716	0.012			6.555	0.009		
	Lithurgus chrysurus					7.427	0.011				
	Megachile albisecta			3.597	0.048	11.808	0.011				
	Megachile hungarica	6.85	0.026								
	Megachile parietina			3.496	0.048						
	Megachile pilicrus					10.091	0.009				
	Megachile sp. A			3.597	0.048	11.808	0.011				
	Osmia dimidiata					9.957	0.011				
	Osmia sp. B							6.63	0.027		
	Osmia versicolor							5.638	0.03		
	Pseudapis monstrosa	10.84	0.016					6.758	0.022	7.08	0.026
	Rhodanthidium septemdentatum			5.709	0.015			7.565	0.006	12.762	0.001
	Xylocopa iris			4.383	0.038	9.37	0.004	9.894	0.001		
	Xylocopa violacea			10.027	0.001			4.763	0.027	5.612	0.019
Hymenoptera – Wasps	*Bembix bicolor*	12.59	0.016					6.815	0.022	7.027	0.034
	Crabronidae sp. A	10.84	0.016					6.758	0.022	7.08	0.026
	Cryptocheilus sp. A							10.965	0.001		

Order	Insect	Trichromatic color		Tetrachromatic color		Height:Surface		Height:Surface apparency		Phenology	
		Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value
	Eumenidae sp. B	7.42	0.017					5.751	0.023	6.017	0.027
	Eumenidae sp. C	10.84	0.016					6.758	0.022	7.08	0.026
	Megascolia maculata	5.63	0.034	5.968	0.019	14.186	0.004	6.415	0.026		
	Vespa orientalis					8.199	0.007	6.756	0.016		
Lepidoptera	*Charcharodus orientalis*	5.84	0.018								
	Coenonympha pamphilus									5.191	0.048
	Colias crocea	10.06	0.004							4.625	0.03
	Maniola telmessia	6.35	0.03	5.224	0.047			12.721	0.005	6.393	0.038
	Noctuidae sp. A					9.957	0.011				
	Papilio machaon			3.597	0.048	11.808	0.011				
	Pieris brassicae			3.597	0.048	11.808	0.011				
	Spialia orbifer									7.404	0.014
	Thymelicus acteon					7.427	0.011				
	Thymelicus sylvestris	5.65	0.023			11.392	0.003	7.043	0.005		

Table 4.S9. Insects in the **Coleoptera** sub-network showing significant effects to at least one of the **interaction terms** of floral traits examined in this Chapter. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling.

Family	Insect	Height:Surface apparency Dev.	p-value	Phenology Dev.	p-value
Buprestidae	*Acmaeodera bipunctata*	9.522	0.008		
	Buprestidae sp. C	6.864	0.011		
Cerambycidae	Cerambycidae sp. B	6.718	0.031	7.156	0.023
	Pseudovadonia livida	6.827	0.024	7.02	0.023
Cleridae	*Trichodes alvearius*	5.425	0.029		
Glaphyridae	*Eulasia nitidicollis*	7.208	0.014		
Melyridae	*Malachius bipustulatus*			6.017	0.036
	Dasytes sp. A	15.899	0.01		
Oedemeridae	*Oedemera* sp. A	14.755	0.008	18.526	0.001
	Oedemera sp. B	6.718	0.031	7.156	0.023
Scarabaeidae	*Anomala* sp. A	10.165	0.014	8.792	0.018
	Oxythyrea funesta	7.072	0.01		
Unknown	Beetle sp. B	5.751	0.025	6.017	0.023

Table 4.S10. Insects in the **Diptera** sub-network showing significant effects to at least one of the **interaction terms** of floral traits examined in this Chapter. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling.

Family	Insect	Height:Surface apparency Dev.	p-value	Phenology Dev.	p-value
Asilidae	Asilidae sp. A	5.856	0.033	14.935	0.002
Bombyliidae	*Bombylella atra*			7.141	0.019
	Bombylius medius	10.594	0.016		
	Exoprosopa minois	5.538	0.048		
	Petrorossia chraminensis			9.023	0.007
	Villa hottentotta	5.751	0.017	6.017	0.018
Syrphidae	*Eristalinus aeneus*	5.751	0.017	6.017	0.018
	Eristalis tenax	6.718	0.026	7.156	0.018
	Merodon albifrons	6.792	0.016	7.044	0.026
	Merodon spinitarsis			6.687	0.034
Tachinidae	Tachinidae sp. A	4.336	0.035	4.533	0.047
Tipulidae	Tipulidae sp. A	7.241	0.017		

Table 4.S11. Insects in the **bees** sub-network showing significant effects to at least one of the **interaction terms** of floral traits examined in this Chapter. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling.

Family	Insect	Trichromatic color Dev.	*p*-value	Tetrachromatic color Dev.	*p*-value	Height:Surface apparency Dev.	*p*-value	Phenology Dev.	*p*-value
Andrenidae	*Andrena hesperia* aff.	5.635	0.023						
	Andrena schencki	3.136	0.05						
	Andrena sp. A			18.79	0.003				
Apidae	*Amegilla quadrifasciata*	5.128	0.037	5.182	0.028				
	Anthophora dalmatica					5.598	0.042		
	Anthophora plumipes					4.995	0.042		
	Anthophora rubricrus					11.132	0.009		
	Apis mellifera					10.181	0.004	7.787	0.019
	Bombus terrestris			5.542	0.009				
	Ceratina schwarzi			7.426	0.02			7.404	0.016
	Eucera cineraria group					5.457	0.036	12.831	0.003
	Eucera seminuda					12.014	0.003	6.184	0.013
	Xylocopa iris			4.383	0.04	9.894	0.003		
	Xylocopa violacea	5.645	0.025	10.027	0.003	4.763	0.032	5.612	0.036
Halictidae	*Halictus resurgens*					4.628	0.047		
	Lasioglossum laticeps.mediterraneum	9.948	0.029			6.718	0.032	7.156	0.021
	Lasioglossum malachurum group					5.307	0.034	5.21	0.045
	Lasioglossum pygmaeum.pauperatum					3.44	0.048		
	Lasioglossum tricinctum group			6.716	0.006	6.555	0.009		
	Pseudapis monstrosa	10.839	0.029			6.758	0.021	7.08	0.036
Megachilidae	*Eoanthidium insulare*	7.419	0.033			5.751	0.021	6.017	0.021
	Eoanthidium judaense aff.	5.221	0.048			5.571	0.048		

Family	Insect	Trichromatic color		Tetrachromatic color		Height:Surface apparency		Phenology	
		Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value
	Hoplitis illyrica aff.					5.56	0.049		
	Hoplitis lysholmi aff.					5.563	0.049	6.017	0.021
	Hoplitis sp. A	7.419	0.033			5.751	0.021		
	Megachile hungarica	6.853	0.027	5.503	0.038				
	Megachile pilicrus			5.589	0.037				
	Osmia sp. B					6.63	0.027		
	Osmia versicolor					5.638	0.029		
	Rhodanthidium septemdentatum			5.709	0.013	7.565	0.005	12.762	0.001

Table 4.S12. Insects in the **wasps** sub-network showing significant effects to at least one of the **interaction terms** of floral traits examined in this Chapter. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling.

Family	Insect	Trichromatic color		Height:Surface		Height:Surface apparency	
		Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value
Chrysididae	*Chrysididae* sp. B			2.913	0.048		
Crabronidae	*Bembix bicolor*	12.587	0.023			6.815	0.021
	Crabronidae sp. A	10.839	0.023			6.758	0.021
Eumenidae	Eumenidae sp. B	7.419	0.024			5.751	0.023
	Eumenidae sp. C	10.839	0.023				
Pompiliidae	*Cryptocheilus* sp. A					10.965	0.001
Sapygidae	*Sapyga* sp. A					4.912	0.044
Scoliidae	*Megascolia maculata*	5.628	0.04	14.186	0.002	6.415	0.028
Vespidae	*Vespa orientalis*			8.199	0.003	6.756	0.023

Table 4.S13. Insects in the **Lepidoptera** sub-network showing significant effects to at least one of the **interaction terms** of floral traits examined in this Chapter. The significance of the univariate tests was assessed with ANOVA (likelihood ratio tests), and it was acquired after 999 bootstrap iterations via PIT-trap residual resampling.

Family	Insect	Trichromatic color		Tetrachromatic color		Height:Surface		Height:Surface apparency	
		Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value	Dev.	*p*-value
Hesperiidae	*Charcharodus orientalis*	5.837	0.021						
	Spialia orbifer			7.426	0.021				
	Thymelicus acteon					7.427	0.014		
	Thymelicus sylvestris	5.645	0.032	6.894	0.02	11.392	0.005	7.043	0.009
Noctuidae	Noctuidae sp. A			3.227	0.05	9.957	0.013		
Nymphalidae	*Maniola telmessia*	6.346	0.035					12.721	0.003
Papilionidae	*Papilio machaon*			3.597	0.047	11.808	0.013	3.596	0.05
Pieridae	*Colias crocea*	10.06	0.003					3.594	0.046
	Pieris brassicae			3.597	0.047	11.808	0.013	3.596	0.05
Zygaenidae	Zygaenidae sp. A							18.033	0.002

SM CHAPTER 5

Table 5.S1. Normalized degree (ND) of the 111 insects participating in the insect–VOC network, and their distribution among the modules identified by the SA algorithm. Insects are ordered according to descending ND values.

Order	Family	Insect	ND	Module ID
Hymenoptera-bees	Apidae	*Apis mellifera*	0.683	Module 5
Coleoptera	Merylidae	*Dasytes* sp. A	0.546	Module 5
Coleoptera	Oedemeridae	Oedemera sp. A	0.516	Module 5
Hymenoptera-bees	Apidae	*Bombus terrestris*	0.500	Module 2
Coleoptera	Scarabaeidae	*Anomala* sp. A	0.480	Module 5
Coleoptera	Mordellidae	Mordellidae sp. A	0.438	Module 3
Hymenoptera-bees	Halictidae	*Lasioglossum tricinctum*	0.435	Module 3
Coleoptera	Scarabaeidae	*Epicometis hirta*	0.408	Module 5
Hymenoptera-bees	Apidae	*Eucera digitata*	0.402	Module 2
Hymenoptera-bees	Halictidae	*Halictus resurgens*	0.399	Module 2
Hymenoptera-bees	Megachilidae	*Rhodanthidium septemdentatum*	0.399	Module 4
Diptera	Tachinidae	Tachinidae sp. A	0.395	Module 3
Coleoptera	Scarabaeidae	*Oxythyrea funesta*	0.386	Module 1
Hymenoptera-bees	Apidae	*Xylocopa violacea*	0.379	Module 4
Coleoptera	Glaphyridae	*Eulasia nitidicollis*	0.369	Module 5
Hymenoptera-bees	Megachilidae	*Megachile parietina*	0.366	Module 4
Diptera	Calliphoridae	Calliphoridae sp. B	0.350	Module 1
Lepidoptera	Lycaenidae	*Pseudophilotes vicrama*	0.346	Module 3
Hymenoptera-bees	Apidae	*Eucera cineraria*	0.340	Module 1
Diptera	Syrphidae	*Merodon spinitarsis*	0.333	Module 1
Hymenoptera-bees	Halictidae	*Lasioglossum leucozonium*	0.320	Module 1
Hymenoptera-bees	Apidae	*Xylocopa iris*	0.314	Module 1
Diptera	Bombyliidae	*Exoprosopa pandora*	0.310	Module 1
Lepidoptera	Lycaenidae	*Lycaena phlaeas*	0.310	Module 1
Diptera	Bombyliidae	*Bombylius posticus*	0.307	Module 1
Coleoptera	Cleridae	*Trichodes alvearius*	0.304	Module 1
Hymenoptera-bees	Apidae	*Anthophora dalmatica*	0.291	Module 1
Lepidoptera	Zygaenidae	Zygaenidae sp. A	0.291	Module 1
Coleoptera	Cerambycidae	Cerambycidae sp. A	0.288	Module 1
Diptera	Syrphidae	*Eumerus pulchellus*	0.278	Module 1
Diptera	Syrphidae	*Sphaerophoria scripta*	0.252	Module 1
Hymenoptera-bees	Halictidae	*Lasioglossum pygmaeum*	0.248	Module 1
Lepidoptera	Pieridae	*Colias crocea*	0.245	Module 1
Lepidoptera	Nymphalidae	*Coenonympha pamphilus*	0.239	Module 1
Diptera	Bombyliidae	*Petrorossia chraminensis*	0.235	Module 1
Hymenoptera-bees	Megachilidae	*Eoanthidium judaense*	0.232	Module 1
Hymenoptera-bees	Halictidae	*Lasioglossum malachurum*	0.232	Module 1
Lepidoptera	Nymphalidae	*Maniola telmessia*	0.232	Module 1

Order	Family	Insect	ND	Module ID
Diptera	Asilidae	Asilidae sp. A	0.232	Module 1
Coleoptera	Buprestidae	*Acmaeodera bipunctata*	0.232	NA
Hymenoptera-wasps	Crabronidae	*Bembix bicolor*	0.232	Module 1
Coleoptera	Cerambycidae	Cerambycidae sp. B	0.232	Module 1
Hymenoptera-wasps	Crabronidae	Crabronidae sp. A	0.232	Module 1
Diptera	Syrphidae	*Eristalis tenax*	0.232	Module 1
Hymenoptera-wasps	Eumenidae	Eumenidae sp. C	0.232	Module 1
Hymenoptera-bees	Halictidae	*Lasioglossum laticeps*	0.232	Module 1
Diptera	Syrphidae	*Merodon albifrons*	0.232	Module 1
Coleoptera	Oedemeridae	*Oedemera* sp. B	0.232	Module 1
Hymenoptera-bees	Halictidae	*Pseudapis monstrosa*	0.232	Module 1
Coleoptera	Cerambycidae	*Pseudovadonia livida*	0.232	Module 1
Hymenoptera-bees	Megachilidae	*Megachile pilicrus*	0.229	Module 4
Diptera		Fly sp. A	0.173	Module 2
Diptera	Empididae	Empididae sp. A	0.173	Module 2
Hymenoptera-bees	Megachilidae	*Megachile manicata*	0.157	Module 5
Diptera	Bombyliidae	*Lomatia* sp. A	0.150	Module 4
Lepidoptera	Sphingidae	*Macroglossum stellatarum*	0.150	Module 4
Hymenoptera-bees	Megachilidae	*Megachile hungarica*	0.150	Module 4
Hymenoptera-bees	Apidae	*Amegilla albigena*	0.150	Module 4
Lepidoptera	Noctuidae	*Trichoplusia ni*	0.150	Module 4
Hymenoptera-bees	Megachilidae	*Osmia* sp. B	0.144	Module 5
Diptera	Hybotidae cf.	Hybotidae sp. A	0.137	Module 5
Hymenoptera-bees	Apidae	*Anthophora rubricrus*	0.127	Module 2
Diptera	Bombyliidae	*Bombylius medius*	0.127	Module 2
Hymenoptera-bees	Megachilidae	*Anthidiellum strigatum*	0.111	Module 2
Hymenoptera-bees	Colletidae	*Colletes eous*	0.111	Module 2
Hymenoptera-bees	Apidae	*Epeolus variegatus*	0.111	Module 2
Hymenoptera-wasps	Scoliidae	*Megascolia maculata*	0.108	Module 3
Hymenoptera-wasps	Vespidae	*Polistes* sp. A	0.108	Module 3
Hymenoptera-wasps	Scoliidae	*Scolia* sp. A	0.108	Module 3
Lepidoptera	Hesperiidae	*Thymelicus sylvestris*	0.108	Module 3
Hymenoptera-wasps	Vespidae	*Vespa orientalis*	0.108	Module 3
Hymenoptera-bees	Apidae	*Amegilla quadrifasciata*	0.108	Module 3
Diptera	Calliphoridae	Calliphoridae sp. A	0.108	Module 3
Hymenoptera-wasps	Crabronidae	Crabronidae sp. C	0.108	Module 3
Coleoptera	Cleridae	*Diplocladus* sp. A	0.108	Module 3
Hymenoptera-bees	Halictidae	*Halictus sexcinctus*	0.108	Module 3
Coleoptera	Curculionidae	*Larinus* sp. A	0.108	Module 3
Hymenoptera-bees	Megachilidae	*Megachile albisecta*	0.108	Module 3
Hymenoptera-bees	Megachilidae	*Megachile* sp. A	0.108	Module 3
Lepidoptera	Noctuidae	Noctuidae sp. A	0.108	Module 3
Hymenoptera-bees	Megachilidae	*Osmia dimidiata*	0.108	Module 3
Lepidoptera	Papilionidae	*Papilio machaon*	0.108	Module 3
Diptera	Syrphidae	*Paragus haemorrhous*	0.108	Module 3

Order	Family	Insect	ND	Module ID
Diptera	Bombyliidae	*Phthiria subnitens*	0.108	Module 3
Lepidoptera	Pieridae	*Pieris brassicae*	0.108	Module 3
Coleoptera	Scarabaeidae	Scarabaeidae sp. A	0.108	Module 3
Diptera	Bombyliidae	*Bombylella atra*	0.098	Module 5
Coleoptera	Glaphyridae	*Pygopleurus* sp. A	0.095	Module 4
Diptera		Fly sp. D	0.095	Module 2
Diptera	Bombyliidae	*Bombylius rhodius*	0.095	Module 2
Hymenoptera-bees	Apidae	*Anthophora crinipes*	0.095	Module 5
Hymenoptera-bees	Megachilidae	*Hoplitis* sp. C	0.082	Module 5
Hemiptera	Auchenorrhyncha	Auchenorrhyncha sp. A	0.069	Module 5
Hymenoptera-wasps	Chrysididae	Chrysididae sp. B	0.062	Module 4
Hymenoptera-bees	Andrenidae	*Andrena* sp. A	0.059	Module 2
Diptera		Fly sp. C	0.049	Module 2
Coleoptera		Beetle sp. A	0.042	Module 4
Hymenoptera-bees	Andrenidae	*Andrena neocypriaca*	0.039	Module 4
Hymenoptera-bees	Andrenidae	*Andrena panurgimorpha*	0.039	Module 4
Hymenoptera-bees	Apidae	*Eucera pseudeucnemidea*	0.039	Module 4
Hymenoptera-bees	Halictidae	*Lasioglossum villosulum*	0.039	Module 4
Diptera	Bombyliidae	*Exoprosopa minois*	0.029	Module 4
Hymenoptera-bees	Megachilidae	*Hoplitis illyrica*	0.029	Module 4
Hymenoptera-bees	Megachilidae	*Hoplitis lysholmi*	0.029	Module 4
Hemiptera	Miridae	*Calocoris* sp. A	0.023	Module 3
Diptera		Fly sp. B	0.023	Module 3
Hymenoptera-bees	Andrenidae	*Andrena hesperia*	0.016	Module 3
Coleoptera	Chrysomelidae	*Clytra atraphaxidis*	0.016	Module 3
Hymenoptera-bees	Andrenidae	*Andrena westensis*	0.016	Module 3
Hymenoptera-bees	Apidae	*Ceratina acuta*	0.013	Module 4
Hymenoptera-bees	Megachilidae	*Hoplitis adunca*	0.013	Module 4

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ΠΕΡΙΛΗΨΗ

Εννέα στα δέκα ανθοφόρα φυτά χρειάζονται επικονιαστές για την αναπαραγωγή τους. Το μέγεθος αυτό καταδεικνύει από μόνο του ότι η βιοτική επικονίαση είναι μία οικοσυστημική λειτουργία-κλειδί για τη διατήρηση της φύσης και της παγκόσμιας πρωτογενούς παραγωγής. Κατά τα τελευταία ~65 εκατομμύρια χρόνια, μετά την έναρξη της μεγάλης ακτινωτής εξέλιξης των αγγειόσπερμων κατά την Κρητιδική περίοδο, οι συνεξελικτικές σχέσεις μεταξύ των ανθοφόρων φυτών και των επικονιαστών τους συγκροτούν έναν κύριο παράγοντα διαφοροποίησης των ειδών φυτών και των ζώων στον πλανήτη. Πράγματι, τα ανθοφόρα φυτά και τα έντομα αποτελούν τις πλέον ποικιλόμορφες ομάδες ζωντανών οργανισμών. Οι παράλληλες μειώσεις επικονιαστών και αγγειόσπερμων φυτών κατά τη διάρκεια του 20ου αι. που τεκμηριώθηκαν πρόσφατα για χώρες της Βόρειας Ευρώπης, καταδεικνύουν την αλληλεξάρτηση των ομάδων αυτών και επισημαίνουν το γεγονός ότι οι συνέπειες από τη διατάραξη των διαειδικών σχέσεων αμοιβαιότητας αφορούν και τους δύο εταίρους (φυτά και ζώα). Είναι προφανές ότι η διατήρηση καθώς και η εξέλιξη της χερσαίας βιοποικιλότητας της Γης εξαρτώνται από την ποιότητα και την αποτελεσματικότητα των αλληλεπιδράσεων αμοιβαιότητας μεταξύ ανθοφόρων φυτών και επικονιαστών.

Η επιβίωση των ανθρώπων βασίζεται, επίσης σε μεγάλο βαθμό, στους επικονιαστές, δεδομένου ότι περισσότερα από 1500 καλλιεργούμενα είδη φυτών παγκοσμίως επικονιάζονται από ζώα, κυρίως έντομα. Στις εύκρατες περιοχές του πλανήτη, δε, είναι οι άγριοι επικονιαστές, και όχι οι ήμερες μέλισσες, που υποστηρίζουν το μεγαλύτερο μέρος των επικονιαστικών υπηρεσιών. Μόνο κατά το έτος 2005, η οικονομική αξία των υπηρεσιών επικονίασης αποτιμήθηκε στα 153 δισεκατομμύρια ευρώ, αντιστοιχώντας στο 9,5% της αγροτικής παραγωγής εκείνου του έτους. Ωστόσο, εκτός από το να στηρίζει την παγκόσμια οικονομία μέσω της διατροφής του ανθρώπινου πληθυσμού, η επικονίαση βρίσκεται πίσω από την εκπληκτική ανθική ποικιλότητα των αγγειόσπερμων, η οποία έχει εμπνεύσει και επηρεάσει από τους προϊστορικούς χρόνους ακόμη, πολιτισμούς σε ολόκληρο τον κόσμο. Η ίδια λειτουργία συνεχίζει και σήμερα να έχει αγοραστική αξία ή να είναι ουσιαστικά ανεκτίμητη: για την αισθητική απόλαυση που προσφέρει, την τέχνη, τον αρχιτεκτονικό σχεδιασμό, τις χρωστικές ουσίες, και τα αρώματα. Συνεπώς, με μία ανθρωποκεντρική προσέγγιση, η επικονίαση θα μπορούσε να ιδωθεί ως μια οικοσυστημική/βιοτική λειτουργία που συνδέει το ζην με το ευ ζην των ανθρώπων στη Γη.

Στις μέρες μας, η υπερεκμετάλλευση των ειδών, οι επιθετικές γεωργικές πρακτικές, οι αλλαγές χρήσης γης, οι βιολογικές εισβολές, η ρύπανση του περιβάλλοντος και η κλιματική αλλαγή αποτελούν τις κύριες απειλές κατά της βιοποικιλότητας σε παγκόσμια κλίμακα. Δεδομένου ότι όλα τα παραπάνω φαινόμενα αποδεδειγμένα απειλούν και τις επικονιαστικές σχέσεις, έρευνες σε όλον τον κόσμο επικεντρώνονται ολοένα και συχνότερα στην κατανόηση της δομής και της δυναμικής των αλληλεπιδράσεων φυτών–επικονιαστών, προκειμένου οι πρακτικές οικολογικής διατήρησης και αποκατάστασης να σχεδιάζονται και να εφαρμόζονται αποτελεσματικά.

Η παρούσα διδακτορική διατριβή επικεντρώνεται στην *αισθητηριακή οικολογία* (sensory ecology) της επικονίασης, ειδικότερα στον τρόπο με τον οποίο τα σήματα που εκπέμπονται από τα άνθη και στοχεύουν στα αισθητηριακά συστήματα των επικονιαστών (όραση και όσφρηση) σχετίζονται με την πραγματοποιούμενη ανθική επισκεψιμότητα. Τα φυτά, ως οργανισμοί με πολύ περιορισμένες

δυνατότητες μετακίνησης, βασίζονται στην εκπομπή σημάτων ως τις μόνες διόδους επικοινωνίας με τους υπόλοιπους οργανισμούς. Έτσι, τα ανθικά σήματα, οπτικά και οσφρητικά, με την τεράστια ποικιλία χρωμάτων, σχημάτων και αρωμάτων, έχουν ως πρωταρχική λειτουργία τη διαμεσολάβηση στην επικοινωνία μεταξύ φυτών και επικονιαστών. Είναι γνωστό ότι τα διαφορετικά ανθικά σήματα δρουν συνεργητικά ή προσθετικά, έτσι, ώστε να επηρεάζουν τις επιλογές, τη συμπεριφορά και εν τέλει την πιστότητα των επικονιαστών, οι οποίοι αποδεδειγμένα αποτελούν φορείς επιλογής της ανθικής ποικιλότητας. Εδώ εφαρμόζεται μία ολιστική προσέγγιση στο *αισθητηριακό τοπίο* που διαμορφώνεται από τα άνθη των εντομόφιλων φυτών σε κλίμακα ολόκληρης βιοκοινότητας, και παρότι ο τίτλος της διατριβής αναφέρεται αποκλειστικά στο *οσμοτοπίο*, η έρευνα επεκτάθηκε στην πορεία, ώστε να συμπεριλάβει και τη χρωματική διάσταση του ανθικού φαινότυπου.

Το ανθικό χρώμα συνίσταται από μίγματα χρωστικών ουσιών, δηλ. δευτερογενών μεταβολιτών, που ανήκουν σε τρεις κατηγορίες: (α) *ανθοκυανίνες*, μία κλάση φλαβονοειδών που δίνουν ποικίλες αποχρώσεις από πορτοκαλί έως γαλάζιο, (β) *καροτενοειδή*, ισοπρενοειδείς ενώσεις που δίνουν αποχρώσεις από κίτρινο έως κόκκινο, και (γ) *βεταλαΐνες*, οι οποίες αντικαθιστούν τις ανθοκυανίνες στα περισσότερα γένη της τάξης των Caryophyllales και δίνουν αποχρώσεις πορτοκαλί ή πορφυρές. Η πρωταρχική λειτουργία του ανθικού χρώματος είναι η προσέλκυση επικονιαστών, αν και έχει επιπλέον συνδεθεί με τη θερμορύθμιση των ανθέων και με την προστασία από καταναλωτές. Η μεγάλη πρόοδος που έχει συντελεστεί τα τελευταία χρόνια αφενός στην τεχνολογία της φασματομέτρησης του φωτός και αφετέρου στην κατανόηση των οπτικών συστημάτων των εντόμων-επικονιαστών έχει επιτρέψει την παραμετροποίηση του ανθικού χρώματος με βάση τη φυσιολογία της όρασης των μελισσών και μερικών ακόμα ειδών εντόμων. Έτσι, είναι δυνατή η περιγραφή των χρωματομετρικών ιδιοτήτων των ανθέων σύμφωνα με τα οπτικά συστήματα των επικονιαστών, διευρύνοντας σημαντικά τις δυνατότητες διερεύνησης των διαειδικών αλληλεπιδράσεων και αποκαλύπτοντας ενδιαφέροντα πρότυπα φαινοτυπικών προσαρμογών σε σύνολα ανθοφόρων φυτών από διάφορες περιοχές του κόσμου.

Τα φυτικά αρώματα αποτελούν μίγματα Πτητικών Οργανικών Ενώσεων (ΠΟΕ) με σχετικά χαμηλά μοριακά βάρη (συνήθως <300 Da) και σχετικά υψηλή πτητικότητα (δες παρακάτω), τα οποία εκπέμπονται, ως προϊόντα του δευτερογενούς μεταβολισμού, από όλα σχεδόν τα φυτικά μέρη (βλαστοί, φύλλα, άνθη, ρίζες, καρποί, σπέρματα). Πρόσφατες έρευνες έχουν δείξει ότι η εκπομπή πτητικών μιγμάτων είναι μία λειτουργία συνδεδεμένη με τον χερσαίο τρόπο ζωής των φυτών από πολύ νωρίς στην εξελικτική τους ιστορία: γένη βρύων και λυκοφύτων, που αποτελούν τα πρώτα φυτά που εποίκησαν την ξηρά, είναι γνωστό ότι μπορούν να εκπέμπουν μίγματα ΠΟΕ ακόμα και προς διαμεσολάβηση διαειδικής επικοινωνίας. Οι ανθικές εκπομπές ΠΟΕ από τα αγγειόσπερμα φυτά εξυπηρετούν (α) την προσέλκυση επικονιαστών, (β) την απώθηση ανεπιθύμητων ανθικών επισκεπτών, όπως π.χ. τους καταναλωτές ανθικών ιστών, (γ) την προσέλκυση εχθρών των καταναλωτών, π.χ. παρασιτοειδή, κατά τις λεγόμενες *τριτροφικές αλληλεπιδράσεις*, (δ) την αλληλεπίδραση με μικροοργανισμούς, (ε) την προστασία από φυτοπαθογόνους παράγοντες και (στ) αλληλοπαθητικά φαινόμενα. Μέχρι στιγμής, έχουν αναγνωρισθεί περισσότερες από 1700 ανθικές ΠΟΕ σε 90 οικογένειες αγγειόσπερμων, οι οποίες ομαδοποιούνται σε τέσσερις κύριες κατηγορίες ανάλογα με το μεταβολικό μονοπάτι που οδηγεί στη σύνθεσή τους: *αλειφατικές ενώσεις* (μονοπάτι λιποξυγενάσης), *βενζενοειδή/φαινυλοπροπανοειδή* (μονοπάτι σικιμικού οξέος), *μονοτερπένια* (μονοπάτι φωσφορικής

μεθυλερυθριτόλης), και *σεσκιτερπένια* (μονοπάτι μεβαλονικού οξέος). Σημειώνεται ότι η έρευνα της αισθητηριακής αντίληψης των οσμών από τους επικονιαστές και των προτιμήσεων ή τάσεων που αυτοί παρουσιάζουν, έχει προχωρήσει αρκετά, αλλά όχι τόσο, ώστε να γνωρίζουμε τις προτιμήσεις έστω των κυριότερων εντόμων-επικονιαστών σε κάθε μία από πολυάριθμες ΠΟΕ ανθικής προέλευσης.

Στο πλαίσιο της παρούσας διατριβής, το ερευνητικό ενδιαφέρον εστιάζεται αρχικά στην αξία των ΠΟΕ ως φυσικών προϊόντων. Η τεράστια χημική ποικιλότητα των φυτών αποτελεί πρώτη ύλη για πληθώρα εφαρμογών στη γεωργία, στην τεχνολογία τροφίμων, στη φαρμακευτική, στην κοσμετολογία και στην τέχνη. Ωστόσο, βάσεις δεδομένων που να συνοψίζουν τη χημική ποικιλότητα των αρωμάτων φυτικών ειδών και να εμπεριέχουν γεωγραφική πληροφορία είναι εξαιρετικά σπάνιες. Έτσι, στο Κεφάλαιο 2, αναπτύχθηκε μία γεω-βάση δεδομένων της χημικής ποικιλότητας των φυτικών αρωμάτων στην Ελλάδα, συγκεντρώνοντας ερευνητικά αποτελέσματα από 116 επιστημονικά άρθρα δημοσιευμένα κατά την τελευταία 25ετία. Η γνώση της κατανομής της χημικής ποικιλότητας των ΠΟΕ των φυτών είναι απαραίτητη για τη μελέτη βιολογικών διεργασιών, την αποτίμηση της αξίας των φυτών, και την εφαρμογή μεθόδων αειφορικής διαχείρισης των καλλιεργειών. Ωστόσο, προσπάθειες για τη συλλογή και μελέτη δεδομένων χημικής ποικιλότητας των φυτικών αρωμάτων και των ιδιοτήτων τους, σε καθορισμένες γεωγραφικές περιοχές είναι σπάνιες. Τα δεδομένα που συγκεντρώθηκαν περιλαμβάνουν 999 ΠΟΕ που κατανέμονται σε 178 φυτικά είδη και υποείδη, 59 γένη και 19 οικογένειες. Ως μέθοδος ανάκτησης των αρωμάτων χρησιμοποιείται σχεδόν αποκλειστικά η υδροαπόσταξη, ενώ απουσιάζουν οι μέθοδοι συλλογής υπερκείμενης αέριας φάσης (headspace sampling), οι οποίες θα επέτρεπαν τη μελέτη οικολογικών διεργασιών. Τα σεσκιτερπένια παρουσιάζουν τη μεγαλύτερη ποικιλότητα ΠΟΕ, ακολουθούμενα από τα μονοτερπένια και τις αλειφατικές ενώσεις. Στην παρούσα έρευνα, εκτιμάται για πρώτη φορά η *πτητικότητα* των ΠΟΕ στα μίγματα αρωμάτων σε επίπεδο φυτικού γένους χρησιμοποιώντας το κανονικό σημείο ζέσεως (ΚΣΖ) ως αντίστροφο δείκτη, και παρουσιάζονται τα φάσματα πτητικότητας των αρωμάτων 58 γενών. Τα μέσα ΚΣΖ ποικίλουν ανάμεσα στα μελετώμενα γένη, με μέγιστη παρατηρούμενη διαφορά τους 118,4ºC. Η *πτητικότητα* αποτελεί μία φυσικοχημική ιδιότητα του φυτικού αρώματος που συνδέεται άμεσα με τις περιβαλλοντικές συνθήκες (θερμοκρασία, ατμοσφαιρική πίεση). Η μελέτη της *πτητικότητας* των εκπομπών για τα είδη μπορεί να εξηγήσει μερικώς τις αλλαγές στις εκπεμπόμενες ΠΟΕ από τα φυτά λόγω κλιματικής υπερθέρμανσης, και να βρει εφαρμογές τόσο στη βασική έρευνα, όσο και στη βελτιστοποίηση της ανάκτησης των φυτικών αρωμάτων υπό διαφορετικές συνθήκες. Τέλος, παρουσιάζονται οι βασικοί χάρτες χημικής ποικιλότητας για τρία αρωματικά φυτά της ελληνικής χλωρίδας και συζητείται η σημασία και οι προοπτικές τους ως μία ειδική περίπτωση χαρτογράφησης φυσικών πόρων.

Στις αρχές του 20ου αι., η βιολογία υιοθέτησε τη *θεωρία δικτύων* από τα μαθηματικά (γνωστή αρχικά ως *«θεωρία γράφων»*) προκειμένου να περιγράψει τη δομή περίπλοκων συστημάτων διαειδικών αλληλεπιδράσεων, όπως είναι τα τροφικά δίκτυα. Σήμερα, στην οικολογία υπάρχουν τρεις κατηγορίες δικτύων αλληλεπιδράσεων: τα τροφικά δίκτυα, τα δίκτυα ξενιστών–παρασιτοειδών, και τα δίκτυα αμοιβαιότητας (π.χ. επικονίασης). Η ανάλυση δικτύων έχει πλέον καταστεί ένα πολυεργαλείο μελέτης, το οποίο «αναβάθμισε» την επικονίαση από μια βιοτική λειτουργία παραδοσιακά μελετώμενη κατά ζεύγη ειδών (υλοποιώντας το δαρβινικό παράδειγμα της συνεξέλιξης φυτών και επικονιαστών) σε μία οικοσυστημική διεργασία θεμελιώδους σημασίας για τη διατήρηση των βιοκοινοτήτων. Κατά τα τελευταία 30 χρόνια, η δικτυακή προσέγγιση των σχέσεων αμοιβαιότητας φυτών–επικονιαστών έχει

εξελιχθεί σε μια ολοκληρωμένη μέθοδο για τη μελέτη των αλληλεπιδράσεων αμοιβαιότητας επικονιαστών–ανθοφόρων φυτών, για την πρόβλεψη της σταθερότητας των βιοκοινοτήτων απέναντι σε διαταραχές, και για την κατάρτιση σχεδίων λειτουργικής αποκατάστασης οικοτόπων. Εν τούτοις, παρά τις πολυάριθμες έρευνες δικτύων επικονίασης που έχουν διεξαχθεί, από τους Τροπικούς μέχρι τον Αρκτικό Κύκλο, και την τεράστια πρόοδο που έχει σημειωθεί προκειμένου να κατανοηθούν η δομή και οι ιδιότητες των δικτύων επικονίασης, ο ρόλος των ανθικών σημάτων σε επίπεδο βιοκοινότητας σε αυτά δεν έχει ποτέ ληφθεί υπόψιν και ενσωματωθεί στην ανάλυση των δικτύων αυτών. Παρόλα αυτά, η αλληλεπίδραση των οπτικών και οσφρητικών σημάτων των φυτών και των αισθητηριακών συστημάτων των εντόμων-επικονιαστών είναι δεδομένη. Ο ρόλος του *ανθικού αισθητηριακού τοπίου* (floral sensory landscape), δηλαδή των ποσοτικοποιημένων παραμέτρων του ανθικού φαινότυπου των ειδών σε επίπεδο βιοκοινότητας, στη δομή των διμερών δικτύων αμοιβαιότητας έχει μελετηθεί σε ελάχιστες περιπτώσεις και ποτέ ολιστικά, συμπεριλαμβάνοντας κυρίως μη-αντικειμενικές ή ανθρωποκεντρικές παραμετροποιήσεις των κύριων ανθικών χαρακτήρων που διαμεσολαβούν στις αλληλεπιδράσεις ανθέων και επικονιαστών.

Στο Κεφάλαιο 3 διερευνάται *το ανθικό αισθητηριακό τοπίο*, δηλαδή το σύνολο των ανθικών σημάτων που εκπέμπονται με στόχο τα αισθητηριακά συστήματα των επικονιαστών (άρωμα και χρώμα), σε μία φυσική βιοκοινότητα. Η αναπαραγωγή των ανθοφόρων φυτών συνεπάγεται την παραγωγή σύνθετων μιγμάτων πτητικών και χρωστικών ουσιών, τα οποία, συγκροτώντας το άρωμα και το χρώμα των ανθέων, εξυπηρετούν κατά κύριο λόγο την προσέλκυση επικονιαστών. Παρά την τεράστια πρόοδο που έχει σημειώσει η οικολογία της επικονίασης σε επίπεδο βιοκοινότητας, μέχρι στιγμής δεν έχει αποπειραθεί την μελέτη φυσικών *ανθικών αισθητηριακών τοπίων*. Εφόσον τα τελευταία διαμεσολαβούν στις σχέσεις αμοιβαιότητας φυτών–επικονιαστών, αναμένεται ότι θα επηρεάζουν τη δυναμική της βιοκοινότητας. Ορισμένα κοινά βιοσυνθετικά μονοπάτια των πτητικών και των χρωστικών ουσιών καθώς και η εξελικτική τους ιστορία θα μπορούσαν να δικαιολογήσουν έναν βαθμό *φαινοτυπικής συνδιακύμανσης* (phenotypic covariation or integration) μεταξύ του αρώματος και του χρώματος των ανθέων, σε συνάφεια με συγκεκριμένα οικολογικά πλεονεκτήματα. Μέχρι στιγμής, σποραδικές έρευνες μεμονωμένων φυτικών ειδών έχουν δείξει ότι τέτοια *φαινοτυπική συνδιακύμανση* μπορεί να συμβεί, ωστόσο, στη συντριπτική τους πλειονότητα τα ευρήματα προέρχονται από ανθρωποκεντρική ποιοτική παραμετροποίηση του ανθικού χρώματος, δηλ. κατηγοριοποίηση σε χρώματα όπως τα αντιλαμβάνεται το ανθρώπινο μάτι (π.χ. λευκό, κίτρινο κ.λπ.). Στην παρούσα έρευνα, που διεξήχθη σε μία φρυγανική βιοκοινότητα στη Λέσβο (Άγιος Στέφανος Μανταμάδου), συλλέχθηκαν *in vivo* και *in situ* (α) τα μίγματα πτητικών οργανικών ουσιών με συλλογή υπερκείμενης αέριας φάσης (headspace sampling) και (β) τα φάσματα ανάκλασης των ανθέων με φορητό φασματοφωτόμετρο, από 41 είδη και υποείδη εντομοεπικονιαζόμενων φυτών. Τα ευρήματα δείχνουν ότι, πράγματι, σε συγκεκριμένες φυτικές ομάδες, το ανθικό άρωμα συμμεταβάλλεται με το ανθικό χρώμα όπως το αντιλαμβάνονται οι μέλισσες και οι πεταλούδες του γένους *Papilio* (Papilionidae). Επιπλέον, οι δύο αυτοί φαινοτυπικοί χαρακτήρες μεταβάλλονται ανάλογα με την παρουσία του νέκταρος. Παρόμοια σύνθεση ανθικού αρώματος μπορεί ακόμα να προβλέψει το φάσμα ανάκλασης της στεφάνης. Συγκεκριμένα, παρουσιάζονται δύο ενδιαφέρουσες σχέσεις (α) μεταξύ των πορφυρών ανθέων και των υψηλών εκπομπών σεσκιτερπενίων, και (β) μεταξύ των κόκκινων ανθέων και των αλειφατικών ενώσεων. Τα αποτελέσματα οδηγούν στο συμπέρασμα ότι στη φρυγανική βιοκοινότητα υφίσταται συντονισμένη εκμετάλλευση των αισθητηριακών ικανοτήτων των εντόμων-επικονιαστών

από τα φυτά, με ιδιαίτερη έμφαση στην προσέλκυση των μελισσών, που είναι και οι κυριότεροι επικονιαστές στο μελετώμενο σύστημα και τα μεσογειακά οικοσυστήματα εν γένει. Το φαινόμενο αυτό πιθανότατα αντανακλά αρχέγονες σχέσεις μεταξύ του φυτικού μεταβολισμού και της φυσιολογίας όρασης και όσφρησης των εντόμων. Η μελέτη του *ανθικού αισθητηριακού τοπίου* σε άλλα οικοσυστήματα με διαφορετική σύνθεση ειδών και διαφορετικές αβιοτικές συνθήκες θα μπορούσε να αποκαλύψει περισσότερα ενδιαφέροντα πρότυπα ανθικής *φαινοτυπικής συνδιακύμανσης*. Μια ολοκληρωμένη συνθεώρηση του ανθικού χρώματος και του αρώματος καθίσταται πλέον σημαντική για τη μελέτη της οικολογίας της επικονίασης σε επίπεδο βιοκοινότητας.

Δεδομένων των παραπάνω ευρημάτων, στο Κεφάλαιο 4 διερευνάται ο ρόλος του ανθικού αισθητηριακού τοπίου στη δομή και λειτουργία του δικτύου επικονίασης της εν λόγω φρυγανικής βιοκοινότητας. Συγκεκριμένα, αναλύεται το δίκτυο επικονίασης με χρήση μεθοδολογικών καινοτομιών, και ελέγχεται η υπόθεση ότι τα αισθητηριακά ανθικά σήματα συσχετίζονται με τη βασική δομή του δικτύου επικονίασης, την *κεντρικότητα* (centrality), και την επικάλυψη θώκου των φυτών που αφορά στην ποικιλότητα των ανθικών επισκεπτών. Στη βιοκοινότητα μελέτης, που είναι η ίδια με το Κεφάλαιο 3, πραγματοποιήθηκαν δειγματοληψίες ανθικών επισκέψεων σε δύο διαδοχικές κύριες περιόδους ανθοφορίας (Απρίλιος-Ιούλιος). Η πρώτη μεθοδολογική καινοτομία που εισάγεται στην παρούσα έρευνα είναι τα *φαινο-δίκτυα* (phenonets), τα οποία αντιπροσωπεύουν ένα νέο τρόπο ομαδοποίησης δεδομένων των διμερών δικτύων αμοιβαιότητας, ο οποίος βασίζεται στην απλή αρχή ότι δύο είδη δεν μπορούν να αλληλεπιδράσουν αν δεν είναι ταυτόχρονα ανθισμένα (φυτά) ή δραστήρια (έντομα) στη βιοκοινότητα. Σε όλες τις δημοσιευμένες μελέτες δικτύων επικονίασης, ακόμη και σε εκείνες όπου τα δεδομένα έχουν συλλεγεί ανά ημέρα, η εξειδίκευση των ειδών (κόμβων) είναι υπερεκτιμημένη διότι υπολογίζεται με βάση το συνολικό δίκτυο ολόκληρης της περιόδου ανθοφορίας της περιοχής. Στην παρούσα εργασία, για κάθε τροφικό επίπεδο, δημιουργήθηκαν τόσα *φαινο-δίκτυα* όσα και τα είδη του κάθε τροφικού επιπέδου και περιλαμβάνουν τις αλληλεπιδράσεις που πραγματοποιήθηκαν μόνο κατά τη χρονική διάρκεια της ανθοφορίας ή δραστηριότητάς τους. Έτσι, οι ιδιότητες κόμβων των ειδών υπολογίστηκαν στα *φαινο-δίκτυά* τους. Με τον τρόπο αυτό, τα *φαινο-δίκτυα* εξυπηρετούν στον περιορισμό της επίδρασης της φαινολογίας των ειδών στη μελέτη της συμπεριφοράς τους εντός του δικτύου και της υπερεκτίμησης της οικολογικής εξειδίκευσής τους. Η δεύτερη μεθοδολογική καινοτομία αφορά στην εισαγωγή της έννοιας της *φαινοτυπικής διακριτότητας* ενός είδους σε μία βιοκοινότητα. Έχει παρατηρηθεί ότι η ανθική αφθονία επηρεάζει τις ιδιότητες των ειδών στα δίκτυα επικονίασης. Υιοθετώντας μία λειτουργική προσέγγιση και προκειμένου να εστιάσουμε καθαρά στον ρόλο των φαινοτυπικών χαρακτήρων των ανθέων στην επισκεψιμότητα από επικονιαστές, θεωρούμε ότι η ανθική αφθονία είναι, στην ουσία, η αφθονία των φαινοτυπικών χαρακτήρων. Με το σκεπτικό αυτό, δημιουργήθηκαν δείκτες *ανθικής διακριτότητας* (floral apparency) ως προς τις χημικές εκπομπές, το ανθικό ύψος, και την ανθική επιφάνεια. Τα αποτελέσματα αποκαλύπτουν ότι, πράγματι, οι ανθικοί χαρακτήρες συσχετίζονται σημαντικά με τη συμπεριφορά (λειτουργικό ρόλο) των φυτών στο δίκτυο επικονίασης. Συγκεκριμένα, με την εφαρμογή πολυμεταβλητών γενικευμένων γραμμικών μοντέλων και φυλογενετικών μοντέλων ελαχίστων τετραγώνων, παρατηρείται ότι η *κεντρικότητα εγγύτητας* (closeness centrality) των φυτών στο δίκτυο, δηλ. η επικάλυψη θώκου όσον αφορά στους ανθικούς επισκέπτες, σχετίζεται σημαντικά με το ανθικό άρωμα. Επιπλέον, η *κεντρικότητα διαμεσότητας* (betweenness centrality) των φυτών, δηλ. η σημασία του είδους για την συγκράτηση της συνεκτικότητας του δικτύου, σχετίζεται σημαντικά με τις εκπομπές

σεσκιτερπενίων και με την οπτική διακριτότητα των φυτών, δηλ. με το πόσο ξεχωρίζουν οπτικά από το σύνολο. Τέλος, η ποικιλότητα ειδών επικονιαστών που δέχονται τα φυτά συνδέεται με τα οπτικά ανθικά σήματα, καθώς και με την παρουσία νέκταρος. Δεδομένων όλων αυτών, διατυπώνεται μία λειτουργική υπόθεση για την εξ αποστάσεως προσέλκυση των επικονιαστών στους μεσογειακούς θαμνώνες, και αναδεικνύεται η λειτουργική διάσταση της θεμελιώδους σχέσης των μελισσών και των ανθέων στα οικοσυστήματα αυτού του τύπου. Επιβεβαιώνοντας τα ευρήματα του Κεφαλαίου 3 καταδεικνύεται ότι οι εκπομπές σεσκιτερπενίων, οι οποίες είναι αυξημένες σε άνθη με υψηλότερο *χρωματικό κορεσμό* (color saturation) για το οπτικό σύστημα της μέλισσας, πράγματι συσχετίζονται θετικά με την επισκεψιμότητα των μελισσών. Επιπλέον, περιγράφονται και συζητούνται οι ειδικές σχέσεις που αναδείχθηκαν μεταξύ των διαφορετικών ομάδων εντόμων της βιοκοινότητας και των διαφόρων στοιχείων του ανθικού φαινότυπου. Η *αισθητηριακή ποικιλότητα* (sensory diversity) των εντομόφιλων φυτών αναδεικνύεται ως σημαίνον συστατικό της *λειτουργικής ποικιλότητας* (functional diversity), και η μελέτη της οδηγεί στην επισήμανση των ειδών με τη μεγαλύτερη επιρροή στο δίκτυο επικονίασης και κατ' επέκταση στη δομή ολόκληρης της βιοκοινότητας. Συνεπώς, η διερεύνηση της *αισθητηριακής ανθικής ποικιλότητας* μπορεί να χρησιμοποιηθεί ως εργαλείο για τον σχεδιασμό στοχευμένων πρακτικών αποκατάστασης βιοκοινοτήτων, με διατήρηση της δυναμικής των δικτύων διαειδικών αλληλεπιδράσεων.

Στο Κεφάλαιο 5, παρουσιάζεται μία νέα μεθοδολογία για την ανάλυση δεδομένων χημικά διαμεσολαβούμενων αλληλεπιδράσεων, βασιζόμενη στην ανάλυση διμερών δικτύων. Η αισθητηριακή επικοινωνία φυτών και εντόμων που διαμεσολαβείται από χημικά σήματα αποτελεί ένα πεδίο οικολογικής έρευνας με πολυάριθμες εφαρμογές, εξαιτίας της πολλαπλής λειτουργικότητας των πτητικών οργανικών ενώσεων που εκπέμπουν τα φυτά. Στην παρούσα έρευνα, παρουσιάζεται το πρώτο δίκτυο εντόμων–ΠΟΕ συντεθειμένο από (α) τα δεδομένα του δικτύου ανθικής επισκεψιμότητας από έντομα-επικονιαστές, και (β) από τα χημικά δεδομένα του ανθικού αρώματος των φυτών που έχουν συλλεγεί στη βιοκοινότητα μελέτης στη Λέσβο. Εφαρμόζοντας απλά μέτρα *κεντρικότητας* κόμβων και υπολογίζοντας τον βαθμό *διαμερισματοποίησης* (modularity) του δικτύου επικονιαστών– ΠΟΕ, ανιχνεύονται ενδιαφέροντα μοτίβα συνδέσεων μεταξύ ειδών που ανήκουν στις *δικτυακές μονάδες* (modules) που συσχετίζονται θετικά με ομάδες εντόμων (συρφίδες και σφήκες) και χημικών κλάσεων ΠΟΕ. Τέλος, επιβεβαιώνεται η αυξημένη επιρροή των σεσκιτερπενίων στο δίκτυο επικονιαστών–ΠΟΕ της φρυγανικής βιοκοινότητας, γεγονός το οποίο χρήζει διερεύνησης και σε άλλα οικοσυστήματα μεσογειακού τύπου στον πλανήτη, που φιλοξενούν παρόμοια χημική ποικιλότητα πτητικών εκπομπών των φυτών (π.χ. Chaparral στην Καλιφόρνια). Τα διμερή δίκτυα ειδών– μεταβολιτών αναδεικνύονται σε ένα εργαλείο μελέτης (α) της *αισθητηριακής ποικιλότητας* σε επίπεδο βιοκοινότητας και (β) της χημικής επικοινωνίας φυτών και αρθροπόδων.

ΚΑΤΑΛΟΓΟΣ ΣΧΗΜΑΤΩΝ[2]

ΚΕΦΑΛΑΙΟ 1

Σχήμα 1.1. Οι πολλαπλοί οικολογικοί ρόλοι των πτητικών οργανικών ενώσεων των φυτών. Από Dudareva *et al.* (*59*).

ΚΕΦΑΛΑΙΟ 2

Σχήμα 2.1. Η κατανομή του αριθμού Πτητικών Οργανικών Ενώσεων (VOCs) στα φυτικά taxa που έχουν μελετηθεί στην Ελλάδα. Στα σύνολα συμπεριλαμβάνονται τα ίχνη ενώσεων, όπως αναφέρονται στις πηγές.

Σχήμα 2.2. Χάρτης θερμότητας (heat map) της κατανομής των χημικών κλάσεων των ΠΟΕ στις φυτικές οικογένειες που μελετήθηκαν (*: η οικογένεια αντιπροσωπεύεται από ένα taxon). Η αφθονία των κλάσεων παρουσιάζεται σε κλίμακα για διευκόλυνση της σύγκρισης.

Σχήμα 2.3. Δεξιά: Διαγράμματα μη-μετρικής πολυδιάστατης κλιμάκωσης (non-metric multidimensional scaling, NMDS) των πινάκων κατανομής των ΠΟΕ στα φυτικά δείγματα με εφαρμογή καμπυλών (a) υψομέτρου και (b) γεωγραφικού πλάτους (δείκτης καταπόνησης: 0,115). Αριστερά: Οι περισσότερο αποκλίνοντες πληθυσμοί καταδεικνύονται στο χάρτη με αριθμούς. (c) Χάρτης χημειοποικιλότητας σε επίπεδο κλάσεων του είδους *Origanum vulgare* subsp. *hirtum* στην Ελλάδα. Για κάθε περιοχή συλλογής δίνονται οι αναλογίες των χημικών κλάσεων στα αναλυθέντα δείγματα.

Σχήμα 2.4. Χημειοποικιλότητα σε επίπεδο κλάσεων για τα γένη *Hypericum* και *Mentha* στην Ελλάδα. Για κάθε περιοχή συλλογής δίνονται οι αναλογίες των χημικών κλάσεων στα αναλυθέντα δείγματα. Οι αριθμοί αντιστοιχούν στα μελετημένα είδη ως εξής: (1) *H. perfoliatum*; (2) *H. perforatum*; (3) *H. tetrapterum*; (4) *H. olympicum*; (5) *M. pulegium*; (6) *M. spicata*; (7) *M. piperita*; (8) *M. longifolia*; (9) *M. × villoso-nervata*.

Σχήμα 2.S1. (A) Χημική σύνθεση σε επίπεδο κλάσεων και φάσματα πτητικότητας των αρωμάτων των 59 φυτικών γενών που έχουν μελετηθεί στην Ελλάδα. Οι κατανομές των κανονικών σημείων ζέσεως (nBP) διακρίνονται ανάλογα με το μεταβολικό μονοπάτι κάθε κύριας χημικής κλάσης. LOX: μονοπάτι λιποξυγενάσης. MVA: μονοπάτι μεβαλονικού οξέος. MEP: μονοπάτι φωσφορικής μεθυλερυθριτόλης. (B) Η μέση πτητικότητα των αρωμάτων των φυτών στην Ελλάδα, εκφρασμένη με το nBP (± SE). Σε όλες τις περιπτώσεις, πλην του γένους *Paeonia*, τα αρώματα παρελήφθησαν με απόσταξη.

Σχήμα 2.S2. Τα hotspot της έρευνας φυτικών πτητικών οργανικών ουσιών στην Ελλάδα (A) Κατανομή των περιοχών συλλογής. (B) Κατανομή των μελετημένων φυτικών taxa στις διοικητικές περιοχές της χώρας. Τα επίπεδα σκίασης αντιστοιχούν στο αριθμό φυτικών taxa που μελετήθηκαν σε κάθε περιοχή.

Σχήμα 2.S3. Μεθοδολογία ανάπτυξης της γεω-βάσης δεδομένων. Ο σχεδιασμός βασίστηκε στο διάγραμμα κλάσεων της ενοποιημένης γλώσσας σχεδιασμού (UML) και περιλαμβάνει 17 κλάσεις διασυνδεόμενες με 15 δυαδικές σχέσεις. Για την κατασκευή της βάσης χρησιμοποιήθηκαν το περιβάλλον της MS Access relational DBMS και το λογισμικό διαχείρισης χωρικών δεδομένων ESRI ArcCatalog. Η τελική βάση αποτελείται από 20 πίνακες. Τα αλφαριθμητικά δεδομένα διαχειρίστηκαν

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[2] Οι αναφορές αντιστοιχούν στη βιβλιογραφία του εκάστοτε Κεφαλαίου. Τα Σχήματα των Παραρτημάτων συμπεριλαμβάνονται εδώ, ακολουθώντας τα Σχήματα του κυρίως κειμένου κατά αύξουσα αριθμητική σειρά.

με φόρμες MS Access, ενώ η εφαρμογή των χαρτών έγινε με το λογισμικό ESRI ArcMap GIS (ArcGIS™ 10.0).

ΚΕΦΑΛΑΙΟ 3

Σχήμα 3.1. Ο χημικός και οπτικός φαινότυπος των εντομοεπικονιαζόμενων φυτών στην μελετώμενη βιοκοινότητα. (Α) Οι φυλογενετικές σχέσεις μεταξύ των φυτών. (Β) Το δίκτυο φυτών–ΠΟΕ. Οι ενώσεις ομαδοποιούνται ανά χημική κλάση. Τα μαύρα αστέρια καταδεικνύουν την παρουσία νέκταρος. Ενώσεις που δεν ταυτοποιήθηκαν, δεν συμπεριλαμβάνονται εδώ. (C) Τα φάσματα ανθικής ανάκλασης των φυτών παρουσιάζονται σε διαγράμματα ορίζοντα (horizon plots), όπου οι επικαλύπτουσες σκουρόχρωμες περιοχές αντιπροσωπεύουν υψηλότερη ανάκλαση στο συγκεκριμένο νανομετρικό εύρος.

Σχήμα 3.2. Οι σημαντικές συσχετίσεις μεταξύ των χημικών και των χρωματομετρικών ή φασματικών ιδιοτήτων στους ανθικούς φαινότυπους της βιοκοινότητας. Τα αποτελέσματα προέκυψαν από φυλογενετικά μοντέλα γενικευμένων ελαχίστων τετραγώνων (PGLS). Στα διαγράμματα παρουσιάζονται οι φυλογενετικά ανεξάρτητες διαφορές (phylogenetically independent constrasts) για τους μελετούμενους ανθικούς χαρακτήρες. Τα διαφορετικά χρώματα καταδεικνύουν διαφορετικές χημικές κλάσεις. Alip: Αλειφατικές ενώσεις· Benz: Βενζενοειδή· Mono: Μονοτερπένια· Sesq: Σεσκιτερπένια. %Class ER: αναλογία της χημικής κλάσης στο σύνολο των ανθικών εκπομπών. %Class count: αναλογία της χημικής κλάσης στο σύνολο των ΠΟΕ (*≤0,050 και **≤0,010).

Σχήμα 3.3. Ανθικά φάσματα που συσχετίζονται με χημικές κλάσεις. (Α) Φάσματα των φυτών που περιλαμβάνονται στη δικτυακή Μονάδα #6 του δικτύου φυτών–ΠΟΕ που έχει χαρακτηριστεί ως η μονάδα των αλειφατικών ενώσεων (Σχήματα 3.S6-3.S7). (Β) Μέση απόσταση Manhattan των ζευγών φασμάτων ανάκλασης σε κάθε μία δικτυακή μονάδα που έχει χαρακτηριστεί χημικά (αλειφατικές ενώσεις: Μονάδα #6· βενζενοειδή: Μονάδα #2· σεσκιτερπένια: Μονάδες #3-4, Σχήματα S6-3.S7). (C) Φάσματα ανάκλασης των φυτών στων οποίων τις ανθικές εκπομπές κυριαρχούν τα σεσκιτερπένια. (D) Μέση απόσταση Manhattan των ζευγών φασμάτων ανάκλασης στις ομάδες των φυτών που διακρίθηκαν ανάλογα με το ποια χημική κλάση κυριαρχεί στις ανθικές τους εκπομπές. Τα ένθετα αντιπροσωπεύουν το μέσο φάσμα των δικτυακών μονάδων ή ομάδων ± SD. Οι φασματικές καμπύλες είναι χρωματισμένες ανάλογα με το ανθικό χρώμα του είδους κωδικοποιημένο στο σύστημα RGB. Al: Αλειφατικές ενώσεις, Be: Βενζενοειδή, Mo: Μονοτερπένια, Se: Σεσκιτερπένια (*p≤0,05 και ***p≤0,001, Kruskal–Wallis rank sum test).

Σχήμα 3.S1. Βορειοανατολική άποψη της μελετώμενης βιοκοινότητας στον Άγιο Στέφανο Λέσβου (φωτο: Αφροδίτη Καντσά).

Σχήμα 3.S2. Η τοπογραφία των ανθέων της βιοκοινότητας στον εξαγωνικό χρωματικό χώρο του τριχρωματικού οπτικού συστήματος της μέλισσας (ένθετο). Στο διάγραμμα παρουσιάζεται η απόλυτη συχνότητα των τόπων (loci) σε κάθε έναν από τους 36 τομείς του εξαγώνου (οριζόμενοι ανά 10°). Ο αναγνώστης παραπέμπεται στις αναφορές 19 και 20 για σύγκριση με σύνολα φυτών από διαφορετικές περιοχές του κόσμου. Πορτοκαλί κουκίδες: φυτά που παράγουν νέκταρ· μαύρα κουκίδες: φυτά που δεν παράγουν νέκταρ.

Σχήμα 3.S3. Η τοπογραφία των ανθέων της βιοκοινότητας στον τετραεδρικό χρωματικό χώρο του τετραχρωματικού οπτικού συστήματος της πεταλούδας *Papilio xuthus* (Lepidoptera, Papilionidae). Πορτοκαλί κουκίδες: φυτά που παράγουν νέκταρ· μαύρα κουκίδες: φυτά που δεν παράγουν νέκταρ. Η γκρίζα κουκίδα αντιστοιχεί στη θέση ενός αχρωματικού αντικειμένου.

Σχήμα 3.S4. Οι στατιστικά σημαντικές συσχετίσεις Pearson μεταξύ των φασματικών ή των χρωματομετρικών ιδιοτήτων των φυτών της βιοκοινότητας και των δύο NMDS αξόνων που υπολογίστηκαν από τα ακατέργαστα δεδομένα. Για λεπτομέρειες σχετικά με τις φασματικές και χρωματικές ιδιότητες, ο αναγνώστης παραπέμπεται στο Κεφ. 3, Υλικά και Μέθοδοι.

Σχήμα 3.S5. Η συνδεσιμότητα μεταξύ μονάδων (among-module connectivity, *c*) των φυτών στο δίκτυο φυτών–ΠΟΕ ανάλογα με την παρουσία/απουσία νέκταρος. Η σχέση μετρήθηκε με εφαρμογή φυλογενετικών μοντέλων γενικευμένων τετραγώνων ($F_{1,39}$=7,85, p=0,008). Παρουσιάζονται οι μέσες τιμές ± SE.

Σχήμα 3.S6. Οι επτά μονάδες του δικτύου φυτών–ΠΟΕ, όπως προέκυψαν από τον αλγόριθμο Προσομοιωμένης Ανόπτησης (*77-78*). Το δίκτυο απεικονίζεται ως μονομερές (one-mode), περιλαμβάνοντας μόνο τα φυτά. Οι αριθμοί αντιστοιχούν στο Σχήμα 3.S7. Οι κόμβοι είναι χρωματισμένοι ανάλογα με το ανθικό χρώμα του είδους κωδικοποιημένο στο σύστημα RGB.

Σχήμα 3.S7. Χημικός χαρακτηρισμός των επτά μονάδων του δικτύου φυτών–ΠΟΕ στη μελετώμενη βιοκοινότητα. Η κατανομή των ΠΟΕ κάθε χημικής κλάσης στις δικτυακές μονάδες απεικονίζεται σε διάγραμμα μωσαϊκό (mosaic plot). Η σκίαση καταδεικνύει εκείνους τους συνδυασμούς κλάσης–μονάδας που είναι περισσότερο (βιολετί) ή λιγότερο (πορτοκαλί) πιθανοί, ανάλογα με την τάξη μεγέθους των τυποποιημένων υπολοίπων (standardized residuals) του Pearson χ^2 test. Τα χρωματισμένα κελιά με τιμές υπολοίπων >|2| και >|4| αντιστοιχούν σε υπόλοιπα που είναι στατιστικά σημαντικά στα επίπεδα 0,05 και 0,0001, αντίστοιχα.

ΚΕΦΑΛΑΙΟ 4

Σχήμα 4.1. Ο λειτουργικός ρόλος κάθε φυτού στα φαινο-δίκτυα των άλλων φυτών της βιοκοινότητας (αναφορά 8, Υλικά και Μέθοδοι). Τα φαινο-δίκτυα βρίσκονται στην πρώτη σειρά (μαύρη σκίαση) και παρατάσσονται με χρονική σειρά ανάλογα με (α) την πρώτη μέρα που παρατηρήθηκε ανθοφορία και (β) τη διάρκεια της ανθοφορίας του συγκεκριμένου είδους, έτσι, ώστε τα φυτά που ανθίζουν νωρίτερα και έχουν μικρότερη διάρκεια ανθοφορίας βρίσκονται στα αριστερά. Οι μήνες αντιστοιχούν αποκλειστικά στην ανθοφορία.

Σχήμα 4.2. Η συνολική ανθική διακριτότητα (apparency) των φυτών της βιοκοινότητας. Η διάμετρος των κύκλων είναι ανάλογη της διακριτότητας των ανθικών εκπομπών ΠΟΕ (χημική διακριτότητα). Το χρώμα τον κύκλων αντιστοιχεί στο ανθικό χρώμα κάθε είδους κωδικοποιημένο στο σύστημα RGB.

Σχήμα 4.3. Οι σημαντικές συσχετίσεις μεταξύ των διαφόρων χαρακτήρων του ανθικού φαινότυπου, του ομαλοποιημένου βαθμού (normalized degree) και της κεντρικότητας ενδιαμεσότητας (betweenness centrality) στη μελετώμενη βιοκοινότητα. Τα διαγράμματα διασποράς παρουσιάζουν τις φυλογενετικά ανεξάρτητες διαφορές (Πίνακας 4.1).

Σχήμα 4.4. Σκαθάρια σε άνθη της μελετώμενης βιοκοινότητας. Η επικονίαση τύπου "mess and soil" σύμφωνα με τους Fægri και van der Pijl (*5*) είναι εμφανής. (A) *Dasytes* sp. (Melyridae) σε *Cistus creticus*. (B) *Clytra atraphaxidis* (Chrysomelidae) σε *Crepis neglecta*. (C) *Eulasia nitidicollis* σε *Cistus salvifolius*. (D) *Pygopleurus* sp. (Glaphyridae) σε *Anemone coronaria*. (E) *Epicometis hirta* (Scarabaeidae) σε *Asphodelus ramosus*. (F) *Oxythyrea funesta* (Scarabaeidae) σε *Onopordum tauricum*. (G) *Oedemera* sp. (Oedemeridae) σε *Tolpis barbata*. (H) *Trichodes alvearius* (Cleridae) σε *C. creticus*. (I) *Chrysolina americana* (Chrysomelidae) σε *Lavandula stoechas*. Φώτο: Αφροδίτη Καντσά.

Σχήμα 4.S1. Φυλογενετικές σχέσεις των εντόμων της μελετώμενης βιοκοινότητας. Το ορθογώνιο κλαδόγραμμα (χωρίς μήκη κλάδων) δημιουργήθηκε με το λογισμικό Open Tree of Life (*95*).

Σχήμα 4.S2. Οι σημαντικές συσχετίσεις μεταξύ των ομάδων των εντόμων-επικονιαστών και των εννέα μονάδων του δικτύου φυτών–επικονιαστών στη μελετώμενη βιοκοινότητα. Η κατανομή κάθε ομάδας στις δικτυακές μονάδες απεικονίζεται σε μωσαϊκό διάγραμμα (mosaic plot). Η σκίαση καταδεικνύει εκείνους τους συνδυασμούς κλάσης–μονάδας που είναι περισσότερο (γαλάζιο) ή λιγότερο (κόκκινο) πιθανοί, ανάλογα με την τάξη μεγέθους των τυποποιημένων υπολοίπων (standardized residuals) του Pearson χ^2 test. Τα χρωματισμένα κελιά με τιμές υπολοίπων >|2| και >|4| αντιστοιχούν σε υπόλοιπα που είναι στατιστικά σημαντικά στα επίπεδα 0,05 και 0,0001, αντίστοιχα.

Σχήμα 4.S3. Τα φυλογενετικά συγγενή φυτά δέχονται επισκέψεις κυρίως από την ίδια ομάδα επικονιαστών. Το επίπεδο σημαντικότητας (**: p=0,008) προέκυψε από την εφαρμογή του αλγόριθμου

'phylo.signal.disc' του Enrico Rezende που χρησιμοποιείται για την ανίχνευση φυλογενετικού σήματος σε διακριτές μεταβλητές (προσωπική επικοινωνία· ο αναγνώστης παραπέμπεται στην αναφορά 94 για αναλυτική περιγραφή και παράδειγμα εφαρμογής).

Σχήμα 4.S4. Έντομα του συνολικού δικτύου φυτών–επικονιαστών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με την αναλογία των σεσκιτερπενίων στις ανθικές εκπομπές (sesq). Η ανεξάρτητη μεταβλητή υπέστη γωνιακό μετασχηματισμό (arcsine). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: $p \leq 0,050$· **$p \leq 0,010$· ***$p \leq 0,001$).

Σχήμα 4.S5. Έντομα του συνολικού δικτύου φυτών–επικονιαστών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα των σεσκιτερπενίων στις ανθικές εκπομπές. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: $p \leq 0,050$· **$p \leq 0,010$· ***$p \leq 0,001$).

Σχήμα 4.S6. Έντομα του συνολικού δικτύου φυτών–επικονιαστών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με το ανθικό ύψος. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: $p \leq 0,050$· **$p \leq 0,010$· ***$p \leq 0,001$).

Σχήμα 4.S7. Έντομα του συνολικού δικτύου φυτών–επικονιαστών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα του ανθικού ύψους. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: $p \leq 0,050$· **$p \leq 0,010$· ***$p \leq 0,001$).

Σχήμα 4.S8. Έντομα του συνολικού δικτύου φυτών–επικονιαστών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με την ανθική επιφάνεια. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: $p \leq 0,050$· **$p \leq 0,010$· ***$p \leq 0,001$).

Σχήμα 4.S9. Έντομα του συνολικού δικτύου φυτών–επικονιαστών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα της ανθικής επιφάνειας (surface app). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: $p \leq 0,050$· **$p \leq 0,010$· ***$p \leq 0,001$).

Σχήμα 4.S10. Έντομα του συνολικού δικτύου φυτών–επικονιαστών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με την έναρξη της ανθοφορίας (start date). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: $p \leq 0,050$· **$p \leq 0,010$· ***$p \leq 0,001$).

Σχήμα 4.S11. Έντομα του συνολικού δικτύου φυτών–επικονιαστών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διάρκεια της ανθοφορίας (duration). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: $p \leq 0,050$· **$p \leq 0,010$· ***$p \leq 0,001$).

Σχήμα 4.S12. Έντομα του υπο-δικτύου φυτών–Κολεόπτερων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα του ανθικού ύψους (height app). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: $p \leq 0,050$· **$p \leq 0,010$· ***$p \leq 0,001$).

Σχήμα 4.S13. Έντομα του υπο-δικτύου φυτών–Κολεόπτερων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα της ανθικής επιφάνειας (surface app). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: $p \leq 0,050$· **$p \leq 0,010$· ***$p \leq 0,001$).

Σχήμα 4.S14. Έντομα του υπο-δικτύου φυτών–Κολεόπτερων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με την ανθική συμμετρία. Η σημαντικότητα υπολογίστηκε με

ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling).

Σχήμα 4.S15. Έντομα του υπο-δικτύου φυτών–Κολεόπτερων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με την έναρξη της ανθοφορίας (start). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S16. Έντομα του υπο-δικτύου φυτών–Κολεόπτερων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διάρκεια της ανθοφορίας (duration). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S17. Έντομα του υπο-δικτύου φυτών–Διπτέρων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα των βενζενοειδών στις ανθικές εκπομπές (benz app). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S18. Έντομα του υπο-δικτύου φυτών–Διπτέρων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα των συνολικών ανθικών εκπομπών (total emissions apparency). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S19. Έντομα του υπο-δικτύου φυτών–Διπτέρων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με την έναρξη της ανθοφορίας (start date). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S20. Έντομα του υπο-δικτύου φυτών–Διπτέρων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διάρκεια της ανθοφορίας (duration). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S21. Έντομα του υπο-δικτύου φυτών–μελισσών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα των σεσκιτερπενίων στις ανθικές εκπομπές (sesq app). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S22. Έντομα του υπο-δικτύου φυτών–μελισσών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα ανθικού ύψους (height app). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S23. Έντομα του υπο-δικτύου φυτών–μελισσών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα της ανθικής επιφάνειας (surface app). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S24. Έντομα του υπο-δικτύου φυτών–μελισσών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με το βάθος στεφάνης. Η σημαντικότητα υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling).

Σχήμα 5.S25. Έντομα του υπο-δικτύου φυτών–μελισσών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διάρκεια ανθοφορίας (duration). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S26. Έντομα του υπο-δικτύου φυτών–σφηκών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με την ανθική επιφάνεια (floral surface). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S27. Έντομα του υπο-δικτύου φυτών–σφηκών, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα της ανθικής επιφάνειας (surface app). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S28. Έντομα του υπο-δικτύου φυτών–Λεπιδόπτερων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με την αναλογία των σεσκιτερπενίων στις ανθικές εκπομπές (sesq). Η ανεξάρτητη μεταβλητή υπέστη γωνιακό μετασχηματισμό (arcsine). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S29. Έντομα του υπο-δικτύου φυτών–Λεπιδόπτερων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα των σεσκιτερπενίων στις ανθικές εκπομπές (sesq app). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S30. Έντομα του υπο-δικτύου φυτών–Λεπιδόπτερων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με το ανθικό ύψος (floral height). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S31. Έντομα του υπο-δικτύου φυτών–Λεπιδόπτερων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα του ανθικού ύψους (height app). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S32. Έντομα του υπο-δικτύου φυτών–Λεπιδόπτερων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με την ανθική επιφάνεια (floral surface). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S33. Έντομα του υπο-δικτύου φυτών–Λεπιδόπτερων, τα οποία παρουσιάζουν αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με τη διακριτότητα της ανθικής επιφάνειας (surface app). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S34. Το μοναδικό έντομο του υπο-δικτύου φυτών–Λεπιδόπτερων, το οποίο παρουσιάζει αριθμό επισκέψεων (visitation) σημαντικά συσχετιζόμενο με την έναρξη της ανθοφορίας (start date). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling) (*: p≤0,050· **p≤0,010· ***p≤0,001).

Σχήμα 4.S35. Η σχέση μεταξύ ανθικής συμμετρίας και ποσοστού επισκεψιμότητας των μελισσών (αριστερά) και ξεχωριστά των ειδών της οικογένειας Apidae (μέσο) και της οικογένειας Megachilidae (δεξιά). Εφαρμόστηκαν φυλογενετικά μοντέλα γενικευμένων ελαχίστων τετραγώνων (PGLS). Η εξαρτημένη μεταβλητή υπέστη γωνιακό μετασχηματισμό (arcsine).

Σχήμα 4.S36. Η σχέση μεταξύ βάθους στεφάνης και ποσοστού επισκεψιμότητας των μελισσών (αριστερά), ξεχωριστά των ειδών της οικογένειας Megachilidae (μέσο), και των Διπτέρων της οικογένειας Syrphidae (δεξιά). Εφαρμόστηκαν φυλογενετικά μοντέλα γενικευμένων ελαχίστων τετραγώνων (PGLS). Η εξαρτημένη μεταβλητή υπέστη γωνιακό μετασχηματισμό (arcsine).

Σχήμα 4.S37. Τα ποσοστά επισκεψιμότητας από Κολεόπτερα για κάθε φυτό κατανεμημένα στο φυλόγραμμα των φυτών της βιοκοινότητας (μήκος κλάδων: εκατ. χρόνια). Ανιχνεύθηκε στατιστικά σημαντικό φυλογενετικό σήμα (Blomberg's K^*=0,47, p=0,009 στον Πίνακα 4.S6).

ΚΕΦΑΛΑΙΟ 5

Σχήμα 5.1. Το θεωρητικό πλαίσιο της κατασκευής του δικτύου εντόμων–ΠΟΕ στη μελετώμενη βιοκοινότητα. Τα δύο δίκτυα, φυτών–επικονιαστών (αριστερά) και φυτών–ΠΟΕ (δεξιά), απεικονίζονται σε διάγραμμα κυψέλης (*35*), όπου κάθε άξονας απεικονίζει τους γραμμικά τοποθετημένους κόμβους κάθε τροφικού επιπέδου. Οι επικονιαστές συνδέονται με τις ΠΟΕ διά των επισκέψεών τους στα ανθοφόρα φυτά. Έτσι, το δίκτυο εντόμων–ΠΟΕ συντίθεται από το δίκτυο φυτών–επικονιαστών, αντικαθιστώντας κάθε φυτό με τις ΠΟΕ που αυτό εκπέμπει.

Σχήμα 5.2. Το δίκτυο εντόμων–ΠΟΕ της βιοκοινότητας. Μόνο τα 111 είδη εντόμων που συμμετείχαν σε >2 αλληλεπιδράσεις με κάθε ΠΟΕ συμπεριλαμβάνονται. Οι ΠΟΕ (στήλες) ομαδοποιούνται σε χημικές κλάσεις. Τα βάρη των αλληλεπιδράσεων έχουν τυποποιηθεί (κλίμακα 0-1).

Σχήμα 5.3. Χαρακτηρισμός των πέντε μονάδων του δικτύου εντόμων–ΠΟΕ που προέκυψαν από τον αλγόριθμο Προσομοιωμένης Ανόπτησης για (Α) τις χημικές κλάσεις και (Β) για τις ομάδες επικονιαστών. Η σκίαση καταδεικνύει εκείνους τους συνδυασμούς χημικής κλάσης–μονάδας ή ομάδας επικονιαστών–μονάδας που είναι περισσότερο (γαλάζιο) ή λιγότερο (κόκκινο) πιθανοί, ανάλογα με την τάξη μεγέθους των τυποποιημένων υπολοίπων (standardized residuals) του Pearson χ^2 test. Τα χρωματισμένα κελιά με τιμές υπολοίπων >|2| και >|4| αντιστοιχούν σε υπόλοιπα που είναι στατιστικά σημαντικά στα επίπεδα 0,05 και (Α) <0,0001 ή (Β) 0,004, αντίστοιχα.

Σχήμα 5.4. Σφήκες του είδους *Megascolia maculata* (Scoliidae) συλλέγουν τροφή από *Onopordum tauricum* (αριστερά) και *Anthyllis hermanniae* (δεξιά) στη μελετώμενη βιοκοινότητα. Φωτο: Αφροδίτη Καντσά.

Σχήμα 5.5. Μέσος ομαλοποιημένος βαθμός (normalized degree) των κύριων χημικών κλάσεων στο δίκτυο εντόμων–ΠΟΕ. Οι διαφορές μεταξύ των κλάσεων προέκυψαν με Kruskal-Wallis rank sum test και Nemenyi post-hoc test (Tukey-Dist. Approximation).

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ΚΑΤΑΛΟΓΟΣ ΠΙΝΑΚΩΝ[3]

ΚΕΦΑΛΑΙΟ 1

Πίνακας 1.1. Οι ανθικοί χαρακτήρες που σχετίζονται με την επισκεψιμότητα των ανθέων από τις τέσσερις κύριες τάξεις εντόμων-επικονιαστών, σε πέντε μελετημένες βιοκοινότητες. Σε κάθε περίπτωση δίνονται ο τύπος βλάστησης και η γεωγραφική περιοχή. Διακρίνεται η ανθική ανάκλαση από το χρώμα διότι στην πρώτη περίπτωση έγινε ποσοτική μέτρηση με φασματοφωτόμετρο ενώ η δεύτερη αποτελεί ανθρωποκεντρική ποιοτική παραμετροποίηση (π.χ. κίτρινο, κόκκινο κλπ). Για τις στατιστικές μεθόδους ανάλυσης που χρησιμοποιήθηκαν, ο αναγνώστης παραπέμπεται στις εκάστοτε αναφορές.

ΚΕΦΑΛΑΙΟ 2

Πίνακας 2.1 Πτητικές οργανικές ενώσεις (ΠΟΕ) που έχουν ανιχνευθεί σε περισσότερα από τα μισά μελετημένα φυτικά taxa. Για κάθε ΠΟΕ, δίνεται ο αριθμός οικογενειών στις οποίες έχει ταυτοποιηθεί.

Πίνακας 2.2 Τα περισσότερο μελετημένα αρωματικά φυτά στην Ελλάδα. Περιλαμβάνονται τα φυτικά taxa που μελετήθηκαν σε τουλάχιστον τέσσερις περιοχές.

Πίνακας 2.S1. Η χημική σύσταση των μιγμάτων ΠΟΕ των φυτικών taxa που μελετήθηκαν στην Ελλάδα κατά τα χρόνια 1988-2013.

ΚΕΦΑΛΑΙΟ 3

Πίνακας 3.1 Η επίδραση του ανθικού χρώματος ή της παρουσίας νέκταρος στην κατανομή των ΠΟΕ στα φυτά της βιοκοινότητας. Ο έλεγχος πραγματοποιείται στο συνολικό δίκτυο φυτών–ΠΟΕ, καθώς και στα τέσσερα υπο-δίκτυα που περιλαμβάνουν τις ΠΟΕ από κάθε μία κύρια χημική κλάση. Παρουσιάζονται τα αποτελέσματα 70 πολυμεταβλητών γενικευμένων γραμμικών μοντέλων. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling).

Πίνακας 3.S1. Δείγματα ανθικού χρώματος και αρώματος των εντομόφιλων φυτών της υπό μελέτη βιοκοινότητας στον Άγιο Στέφανο Λέσβου. Για ένα φυτό παρατίθενται οι αριθμοί καταγραφών στη βάση δεδομένων FReD. Η ταξινόμηση σε οικογένειες ακολουθεί το σύστημα APGIII (*59*).

Πίνακας 3.S3. Αποτελέσματα από τα μονομεταβλητά τεστ των πολυμεταβλητών γενικευμένων γραμμικών μοντέλων, που καταδεικνύουν ποιες εξαρτημένες μεταβλητές (ΠΟΕ) στο δίκτυο φυτών–ΠΟΕ της βιοκοινότητας σχετίζονται σημαντικά με την παρουσία νέκταρος ($p < 0,050$) ή με τις χρωματικές και φασματικές ιδιότητες της ανθικής ανάκλασης. Οι ανεξάρτητες μεταβλητές είναι αυτές που έδωσαν στατιστικά σημαντικές συσχετίσεις στον Πίνακα 3.1. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling).

Πίνακας 3.S4. Αποτελέσματα από τα μονομεταβλητά τεστ των πολυμεταβλητών γενικευμένων γραμμικών μοντέλων, που καταδεικνύουν ποιες εξαρτημένες μεταβλητές (ΠΟΕ) σε κάθε ένα υπο-δίκτυο φυτών–ΠΟΕ της βιοκοινότητας (που περιέχει μόνο αλειφατικές ενώσεις, βενζενοειδή, μονοτερπένια ή σεσκιτερπένια) σχετίζονται σημαντικά με την παρουσία νέκταρος ($p < 0,050$) ή με τις χρωματικές και φασματικές ιδιότητες της ανθικής ανάκλασης. Οι ανεξάρτητες μεταβλητές είναι αυτές που έδωσαν

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[3]Οι αναφορές αντιστοιχούν στη βιβλιογραφία του εκάστοτε Κεφαλαίου. Οι Πίνακες των Παραρτημάτων συμπεριλαμβάνονται εδώ, ακολουθώντας τους Πίνακες του κυρίως κειμένου κατά αύξουσα αριθμητική σειρά.

στατιστικά σημαντικές συσχετίσεις στον Πίνακα 3.1. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling).

Πίνακας 3.S5. Η συσχέτιση της παρουσίας νέκταρος και των ανθικών χρωματικών ή φασματικών ιδιοτήτων των φυτών της μελετώμενης βιοκοινότητας. Παρουσιάζονται τα αποτελέσματα 10 φυλογενετικών μοντέλων γενικευμένων ελαχίστων τετραγώνων. Οι εξαρτημένες μεταβλητές παρουσιάζονται στις γραμμές του πίνακα. Οι τιμές του AIC παρουσιάζονται για όλα τα μοντέλα, συμπεριλαμβανομένων των μηδενικών (~1). Τιμές με έντονη γραφή καταδεικνύουν στατιστική σημαντικότητα (≤0,050).

Πίνακας 3.S6. Αποτελέσματα των φυλογενετικών μοντέλων γενικευμένων ελαχίστων τετραγώνων που καταδεικνύουν τη σχέση μεταξύ των χρωματικών και των χημικών ιδιοτήτων του ανθικού φαινότυπου των φυτών της μελετώμενης βιοκοινότητας. Οι τιμές του AIC παρουσιάζονται για όλα τα μοντέλα, συμπεριλαμβανομένων των μηδενικών (~1). Alip: Αλειφατικές ενώσεις· Benz: Βενζενοειδή· Mono: Μονοτερπένια· Sesq: Σεσκιτερπένια. %Class ER: αναλογία της χημικής κλάσης στο σύνολο των ανθικών εκπομπών. %Class count: αναλογία της χημικής κλάσης στο σύνολο των ΠΟΕ. Για την ερμηνεία των αξόνων NMDS1 and NMDS2 ο αναγνώστης παραπέμπεται στο Σχήμα 3.S4. Τιμές με έντονη γραφή καταδεικνύουν στατιστική σημαντικότητα (≤0,050).

Πίνακας 3.S7. Χρωματικός χαρακτηρισμός των επτά μονάδων (modules) του δικτύου φυτών–ΠΟΕ της βιοκοινότητας. Παρουσιάζονται τα αποτελέσματα φυλογενετικής ANOVA (p-phylo: p-value δεδομένων των φυλογενετικών σχέσεων μεταξύ των μελετώμενων φυτών). Τιμές με έντονη γραφή καταδεικνύουν στατιστική σημαντικότητα (≤0,050).

Πίνακας 3.S8. Οι ΠΟΕ που ανιχνεύθηκαν στη ανθική υπερκείμενη φάση των 41 εντομόφιλων φυτών της βιοκοινότητας. Οι ενώσεις κατηγοριοποιούνται σε χημικές κλάσεις με βάση τη βιβλιογραφία (*85*). Για κάθε ΠΟΕ, ο δείκτης συγκράτησης Kovats (KI) υπολογίσθηκε χρησιμοποιώντας τους χρόνους συγκράτησης προτύπων ενώσεων (ν-αλκάνια) στις ίδιες χρωματογραφικές συνθήκες. Οι ΠΟΕ παρουσιάζονται σε τέσσερα επίπεδα αναγνώρισης: (α) ΠΟΕ με έντονη γραφή έχουν προκύψει από ταύτιση του KI και των φασμάτων μάζας με αυθεντικές πρότυπες ενώσεις που εισήχθησαν στο σύστημα GC/MS, (ii) ενώσεις με κανονική γραφή έχουν προκύψει από επαλήθευση του KI (υποσημειώσεις πίνακα) με δημοσιευμένες τιμές του ίδιου δείκτη για πολική στήλη, (γ) ΠΟΕ σημειωμένες με § έχουν προκύψει από συμφωνία (>90%) του φάσματος μάζας με τη διαθέσιμη βιβλιοθήκη φασμάτων, ενώ ο KI είτε δεν ταίριαζε απόλυτα είτε δεν ήταν διαθέσιμος, και (δ) ΠΟΕ που δεν μπόρεσαν να ταυτοποιηθούν με κανέναν από τους παραπάνω τρόπους, παραμένουν άγνωστες, αντιπροσωπεύονται από τα κυριότερα ιόντα στα φάσματα μάζας παρατιθέμενα κατά φθίνουσα σειρά αφθονίας και σε περίπτωση που αυτό ήταν δυνατό, κατηγοριοποιήθηκαν σε χημικές κλάσεις. Σημειώνεται ότι η μεθοδολογία χημικής ανάλυσης που χρησιμοποιήθηκε (GC/MS) δεν επιτρέπει την απόλυτη αναγνώριση της διάταξης των ενώσεων· συνεπώς, οι θέσεις των διπλών δεσμών και των μεθυλιωμένων ομάδων καθώς και η διάκριση σε εναντιομερή βασίζονται μόνο στα αποτελέσματα ταυτοποίησης με βάση τη βιβλιοθήκη φασμάτων NIST 05 Mass Spectral Library και δεν καταδεικνύουν πλήρη χημική αναγνώριση.

Πίνακας 3.S9. Το φυλογενετικό σήμα για τις μεταβλητές που χρησιμοποιούνται στο παρόν Κεφάλαιο. Ανάλογα με τον τύπο της μεταβλητής, χρησιμοποιήθηκε διαφορετική μεθοδολογία. Λεπτομέρειες παρατίθενται στις Μεθόδους. *K**: Blomberg's *K**. Mantel r: Mantel statistic. *D*: statistic for binary traits. Μόνο οι p-values που καταδεικνύουν στατιστική σημαντικότητα παρουσιάζονται (p≤ 0,050).

ΚΕΦΑΛΑΙΟ 4

Πίνακας 4.1. Ανθικοί χαρακτήρες που συσχετίζονται με τουλάχιστον μία από τις ιδιότητες κόμβων των φυτών που αντιστοιχούν στα φαινοδίκτυα. Παρουσιάζονται τα αποτελέσματα 14 φυλογενετικών μοντέλων γενικευμένων ελαχίστων τετραγώνων. Μόνο οι στατιστικά σημαντικές σχέσεις παρουσιάζονται (p≤ 0.050), με την εξαίρεση του τριχρωματικού συστήματος. Οι ανεξάρτητες μεταβλητές

ομαδοποιούνται στον πίνακα με εναλλασσόμενα σκιασμένες ζώνες (χρώμα, άρωμα, διαστάσεις, νέκταρ). Γαλάζια γραφή σημαίνει συντελεστή παλινδρόμησης >0.

Πίνακας 4.2. Οι σημαντικές συσχετίσεις των ανθικών χαρακτήρων και της ποιοτικής κατανομής των συνδέσεων στο δίκτυο επικονίασης της μελετώμενης βιοκοινότητας. Οι δοκιμές αφορούν το συνολικό δίκτυο καθώς και τα πέντε υπο-δίκτυα που περιλαμβάνουν τις αλληλεπιδράσεις των φυτών με κάθε μία από τις κύριες τάξεις εντόμων-επικονιαστών. Παρουσιάζονται τα αποτελέσματα 55 πολυμεταβλητών γενικευμένων γραμμικών μοντέλων (αρνητική διωνυμική κατανομή). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling). Οι ανεξάρτητες μεταβλητές ομαδοποιούνται στον πίνακα με εναλλασσόμενα σκιασμένες ζώνες (χρώμα, άρωμα, διαστάσεις, μορφολογία, φαινολογία).

Πίνακας 4.3. Οι σημαντικές συσχετίσεις των ανθικών χαρακτήρων και της ποσοτικής κατανομής των συνδέσεων στα υπο-δίκτυα που περιλαμβάνουν τις αλληλεπιδράσεις των φυτών με κάθε μία από τις πλουσιότερες σε είδη οικογένειες ανθόφιλων εντόμων στη μελετώμενη βιοκοινότητα. Παρουσιάζονται τα αποτελέσματα 38 πολυμεταβλητών γενικευμένων γραμμικών μοντέλων (αρνητική διωνυμική κατανομή). Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling). Οι ανεξάρτητες μεταβλητές ομαδοποιούνται στον πίνακα με εναλλασσόμενα σκιασμένες ζώνες (χρώμα, άρωμα, διαστάσεις, μορφολογία, φαινολογία).

Πίνακας 4.4. Ανθικοί χαρακτήρες που συσχετίζονται με την επισκεψιμότητα από τις κύριες ομάδες επικονιαστών στη μελετώμενη βιοκοινότητα. Παρουσιάζονται μόνο οι στατιστικά σημαντικές σχέσεις (p≤0,050) που προέκυψαν από 32 φυλογενετικά μοντέλα γενικευμένων ελαχίστων τετραγώνων. Οι ανεξάρτητες μεταβλητές ομαδοποιούνται στον πίνακα με εναλλασσόμενα σκιασμένες ζώνες (χρώμα, άρωμα, διαστάσεις, μορφολογία, φαινολογία). Γαλάζια γραφή σημαίνει συντελεστή παλινδρόμησης >0. Η επισκεψιμότητα από σφήκες δεν συσχετίζεται με κανέναν ανθικό χαρακτήρα και δεν συμπεριλαμβάνεται εδώ.

Πίνακας 4.S1. Ανθική φαινολογία, μορφολογία και πτητικότητα των αρωμάτων των φυτών της μελετώμενης βιοκοινότητας. Για τις ημέρες άνθισης και την ανθική πυκνότητα, οι τιμές αντιπροσωπεύουν το μέσο όρο των δύο περιόδων δειγματοληψίας, με εξαίρεση τα *Geranium robertianum* και *Heliotropium lasiocarpum*, τα οποία παρατηρήθηκαν στη βιοκοινότητα μόνο κατά τη δεύτερη χρονιά. Σημειώνεται ότι η *Cuscuta epithymum* είναι αναρριχητικό παράσιτο που βρέθηκε επάνω στο *Cistus creticus* στο τέλος της περιόδου ανθοφορίας του τελευταίου.

Πίνακας 4.S2. Τα 168 έντομα που καταγράφηκαν ως ανθικοί επισκέπτες στη μελετώμενη βιοκοινότητα, η φαινολογία τους και η δικτυακή μονάδα (module) στην οποία έχουν ταξινομηθεί σύμφωνα με τον αλγόριθμο Προσομοιωμένης Ανόπτησης (Υλικά και Μέθοδοι). Για κάθε τάξη εντόμων, ο αριθμός των taxa δίνεται σε παρένθεση. Έντομα που παρατηρήθηκαν μόνο στην πρώτη χρονιά δειγματοληψίας σημειώνονται με (1), ενώ αυτά που παρατηρήθηκαν μόνο στη δεύτερη χρονιά σημειώνονται με (2). Για τα υπόλοιπα έντομα, οι ημέρες δραστηριοποίησης (Ιουλιανές ημέρες) αντιπροσωπεύουν το μέσο όρο των δύο ετών. Τα δείγματα των εντόμων έχουν κατατεθεί στη Μελισσοθήκη του Αιγαίου, στο Πανεπιστήμιο Αιγαίου.

Πίνακας 4.S3. Τα μεγέθη των φαινοδικτύων στη μελετώμενη βιοκοινότητα. Η συνδεσιμότητα (connectance) αντιπροσωπεύει την αναλογία των πραγματοποιημένων συνδέσεων προς τις δυνατές συνδέσεις σε κάθε φαινοδίκτυο. Οι τιμές έχουν υπολογιστεί και για τα φαινοδίκτυα των φυτών στα οποία δεν παρατηρήθηκαν επισκέψεις από έντομα.

Πίνακας 4.S4. Σύγκριση των τιμών των ιδιοτήτων των κόμβων για τα φυτά του «στατικού» δικτύου της μελετώμενης βιοκοινότητας που αναφέρεται σε ολόκληρη την περίοδο ανθοφορίας και αυτών των φαινοδικτύων των φυτών (pn). Οι ιδιότητες υπολογίστηκαν με τη λειτουργία 'specieslevel' στο πακέτο bipartite v.2.05 της R, εκτός από το λειτουργικό ρόλο (functional role) που υπολογίστηκε στο

λογισμικό NetCarto (*69*). Φυτά στα οποία δεν παρατηρήθηκαν επισκέπτες δεν συμπεριλαμβάνονται εδώ.

Πίνακας 4.S5. Κάθετη, οριζόντια, και χημική ανθική διακριτότητα (apparency) στη μελετώμενη βιοκοινότητα. Οι τιμές αντιστοιχούν στην περίοδο ανθοφορίας κάθε είδους και όχι στη συνολική περίοδο ανθοφορίας της βιοκοινότητας. Μηδενική διακριτότητα ως προς έναν ανθικό χαρακτήρα σημαίνει ότι η τιμή του εν λόγω χαρακτήρα δεν διαφέρει από το διάμεσο των συν-ανθοφορούντων φυτών. Η χημική διακριτότητα υπολογίστηκε λαμβάνοντας υπόψιν τον ανά m^2 ρυθμό εκπομπής αρώματος για κάθε φυτό (λεπτομέρειες στα Υλικά και Μέθοδοι).

Πίνακας 4.S6. Το φυλογενετικό σήμα για τις μεταβλητές που χρησιμοποιούνται στο παρόν Κεφάλαιο. Ανάλογα με τον τύπο της μεταβλητής, χρησιμοποιήθηκε διαφορετική μεθοδολογία. Λεπτομέρειες παρατίθενται στις Μεθόδους. *K**: Blomberg's *K**. Mantel r: Mantel statistic. *D*: statistic for binary traits. Μόνο οι p-values που καταδεικνύουν στατιστική σημαντικότητα παρουσιάζονται (p≤ 0,050).

Πίνακας 4.S7. Αριθμός επισκέψεων κάθε μίας από τις κυριότερες ομάδες εντόμων-επικονιαστών που παρατηρήθηκαν κατά τις δύο διαδοχικές περιόδους δειγματολειψίας στη μελετώμενη βιοκοινότητα και η κατανομή των φυτών στις δικτυακές μονάδες (modules) όπως υπολογίστηκε με τον αλγόριθμο Προσομειωμένης Ανόπτησης (*69*).

Πίνακας 4.S8. Έντομα τα οποία στο συνολικό δίκτυο σχετίζονται σημαντικά με τουλάχιστον έναν όρο αλληλεπίδρασης ανθικών χαρακτήρων στο παρόν Κεφάλαιο. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling).

Πίνακας 4.S9. Έντομα τα οποία, στο δίκτυο των Κολεόπτερων, σχετίζονται σημαντικά με τουλάχιστον έναν όρο αλληλεπίδρασης ανθικών χαρακτήρων στο παρόν Κεφάλαιο. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling).

Πίνακας 4.S10. Έντομα τα οποία, στο δίκτυο των Διπτέρων, σχετίζονται σημαντικά με τουλάχιστον έναν όρο αλληλεπίδρασης ανθικών χαρακτήρων στο παρόν Κεφάλαιο. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling).

Πίνακας 4.S11. Έντομα τα οποία, στο δίκτυο των μελισσών, σχετίζονται σημαντικά με τουλάχιστον έναν όρο αλληλεπίδρασης ανθικών χαρακτήρων στο παρόν Κεφάλαιο. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling).

Πίνακας 4.S12. Έντομα τα οποία, στο δίκτυο των σφηκών, σχετίζονται σημαντικά με τουλάχιστον έναν όρο αλληλεπίδρασης ανθικών χαρακτήρων στο παρόν Κεφάλαιο. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling).

Πίνακας 4.S13. Έντομα τα οποία, στο δίκτυο των Λεπιδόπτερων, σχετίζονται σημαντικά με τουλάχιστον έναν όρο αλληλεπίδρασης ανθικών χαρακτήρων στο παρόν Κεφάλαιο. Το επίπεδο σημαντικότητας υπολογίστηκε με ANOVA (likelihood ratio tests) μετά από 999 bootstrap επαναδειγματοληψίες (PIT-trap residual resampling).

ΚΕΦΑΛΑΙΟ 5

Πίνακας 5.S1. Ομαλοποιημένος βαθμός (ND) για τα 111 έντομα που περιλαμβάνονται στο δίκτυο εντόμων–ΠΟΕ, και η κατανομή τους στις δικτυακές μονάδες (modules) που προέκυψαν από τον αλγόριθμο Προσομοιωμένης Ανόπτησης. Τα είδη αναφέρονται κατά φθίνουσα σειρά τιμών ND.

SHORT BIO

Aphrodite Kantsa was born and raised in Thessaloniki, Greece. She studied Biology at the Aristotle University of Thessaloniki, including one semester at Tor Vergata University of Rome, Italy, in the context of the Erasmus exchange program. Her first research interest focused on urban ecology and biodiversity, a topic that she had the opportunity to study both in Thessaloniki and in Rome at the Department of Environmental Biology of Sapienza University. In 2007, she acquired her Master's degree on Environmental Biology from the Aristotle University of Thessaloniki. Her thesis focused on the analysis of the urban plant diversity of the city of Ioannina (Western Greece), under the supervision of Prof. Stella Kokkini. In 2013, the published results of this work were highlighted by the European Commision's *Science for Environment Policy*. In 2007, she worked as a research assistant for the Department of Geography, University of the Aegean, conducting fieldwork for an international research project studying the pollination ecology of the noxious weed *Solanum elaeagnifolium* in its native and invasive range, coordinated by Prof. Theodora Petanidou. Since 2009, she has been living on the island of Lesvos, where she fulfilled her PhD at the Laboratory of Biogeography and Ecology, supervised by T. Petanidou and co-financed by Greece and the European Union (Heraclitus II program). Her research focuses on floral sensory diversity, inlcuding color as perceived by the different pollinators and scent, at a community level and studies its functional role in structuring plant–pollinator interaction networks. Furthermore, she is particularly interested in plant volatile organic compounds both as olfactory signals and as natural products. During her PhD studies, she participated in two side projects regarding (a) the relationship of floral diversity and plant vulnerability, and (b) the functionality of vegetative and floral scents of aromatic plants in Mediterranean scrublands. She deliberately thinks that Euripides, Shakespeare, Darwin and Camus explained pretty much most of everything, she hates cumin, and she loves crime novels. She cannot stay for long without theatre.

Google Scholar