European Journal of Forest Research
https://doi.org/10.1007/s10342-024-01676-y

RESEARCH

Effects of plant leaf traits, abundance and phylogeny on differentiation of herbivorous insect assemblages in Mediterranean mixed forest

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Received: 7 August 2023 / Revised: 2 February 2024 / Accepted: 27 February 2024

Abstract

Herbivorous insect assemblages are functionally diverse, with each species exploiting plant tissues in different ways. Availability and palatability of plant tissues influence the diversity and composition of herbivorous insect assemblages. However, few studies have compared herbivorous insect assemblages and their ecological correlates across multiple plant species within the same plant community. Here, we sampled insect assemblages from the canopies of 1060 plants belonging to 36 woody species in two mixed Mediterranean forest stands. 401 insect species were classified as herbivores and grouped into sucker or chewer guilds. We explored differences in the diversity and composition of each insect guild across plant species, and tested their relationships with plant leaf traits, abundance or phylogeny, and explored whether the structures of plant-herbivorous insect networks depended on any of the studied plant traits. Plant identity accounted for the highest proportion of variation in the composition of each insect guild. Plant species abundance showed a positive effect on both insect guilds' diversity. Suckers' diversity was higher in plant species with deciduous leaves and low SLA, while the composition was more similar between phylogenetically closer plant species. Chewers diversity increased with the leaf area, while plants with similar LA, leaf nitrogen, SLA and distinct leaf habit showed more similar assemblages. Similarly, closely related angiosperms showed similar chewer assemblages. Plant–insect interaction networks present a modular structure, in which plants belonging to the same module tend to be related and share more sucker species. We add to the evidence supporting the role of plant species features as filters for structuring their associated herbivore insect assemblages.

Keywords Chewers · Mediterranean mixed forest · Plant-herbivorous insect interactions · Suckers

Introduction

Plants and herbivorous insects share a long history of coadaptation and coevolution with consequences on individual plant fitness, population-level processes, and community assembly (Coley et al. 1985; Crawley 1989; Agrawal 2007). Plants, to avoid or limit insect herbivory, have evolved physical (e.g. leaf indumenta, spines, tough leaves) and chemical (e.g. wax, resins, secondary metabolites or volatile compounds) traits acting as defensive, deterrent mechanisms or defensive mutualisms (Peeters 2002a, b; Peeters et al. 2007; Agrawal 2007; Clissold et al. 2009; Carmona et al. 2011; Pereira et al. 2020). Other plant traits, such as leaf phenology or leaf nutrient content, can control insect development, fecundity, and performance (Southwood et al. 2004; Wetzel et al. 2016; Barton et al. 2019). On their part, herbivorous insects have also developed multiple adaptations to feed on

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Communicated by Gediminas Brazaitis.

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plant tissues of different qualities (War et al. 2018). Herbivorous insects can be grouped into feeding guilds, i.e. groups of species exploiting the same resources in a similar way (Simberloff and Dayan 1991), typically defined by the combination of one or various features as: feeding mode (e.g. sucking–piercing or chewing mouthparts), feeding habit (e.g. endophagous or exophagous), behavior (e.g. sessile or mobile) or developmental (e.g. larvae or adults) (Peeters 2002a, b; Southwood et al. 2004; Peeters et al. 2007; Novotny et al. 2010).

Plant-herbivorous insect interactions do not occur randomly, but are strongly determined by plants' phenotypes (Ibanez et al 2016), i.e. interactions are functionally or phylogenetically conserved. Despite that, the richness and composition of plant-herbivorous insect assemblages vary widely within and between plant species (Basset and Novotny 1999; Southwood et al. 2004; Novotny et al. 2010; Wardhaugh 2014; Harrison et al. 2018; Rego et al. 2019; Tielens and Gruner 2020). Such variation has been frequently linked to the quality and quantity of resources offered by distinct plant species (Robinson et al. 2012; Harrison et al. 2018; Wang et al. 2020; Tielens and Gruner 2020; Lu et al. 2021; Keith et al. 2023), abundance effects (Cornell and Kahn 1989; Basset and Novotny 1999) or host plant phylogeny (Ødegaard et al. 2005; Grandez-Rios et al. 2015). However, most studies lack a community-level approach, focusing on one or few plant species and a particular insect guild or a single taxonomic group, what can limit our understanding of what determines the richness and composition of herbivorous insect assemblages associated with different plant species in a community, and how these associations translate into a network of plant-herbivorous insect interactions.

The quality and quantity of resources provided by plants are determinants of which kind of insect herbivores interact with a particular plant species. In general, herbivorous insects prefer young, tender and soft plant tissues of high nutritive quality (Clissold et al. 2009; Carmona et al. 2011), but this resource is temporary and spatially scarce (Barton et al. 2019). In turn, more available mature or perennial leaves may provide more abundant and stable resources and, consequently, could support richer insect communities. The effects of plant traits on insects probably depend on their feeding behaviors, physiology and ability to solve and manage direct and indirect plant-imposed barriers. As a result, each feeding guild can respond differently to the same plant traits (Basset and Novotny 1999; Peeters 2002a, b; Peeters et al. 2007; Novotny et al. 2010; Harrison et al. 2018; Caldwell et al. 2016; Tielens and Gruner 2020). Even, within the same feeding guild, species might react differently to plant traits, because of spatiotemporal partitioning of resources used by distinct insect species or because of different degrees of specialization (Novotny et al. 2010; Pimentel et al. 2023).

Several plant traits related to leaves quality and quantity have been found to be functional for herbivorous insect communities affecting their abundance, richness and composition. While biochemical traits are known to be poor predictors (Carmona et al. 2011; Harrison et al. 2018), leaf physical and nutritional-related traits seem to widely affect the richness and composition of herbivorous insect assemblages (Peeters 2002a, b; Dial et al. 2006; Robinson et al. 2012; Caldwell et al. 2016; Harrison et al. 2018; Tielens and Gruner 2020; Lu et al. 2021; Keith et al. 2023). According to the *resource availability hypothesis* (Coley et al. 1985), leaf size, palatability and nutritive value can be strong predictors of arthropod richness and composition (Basset and Novotny 1999; Peeters et al. 2007; Harrison et al. 2018; Tielens and Gruner 2020; Wang et al. 2020; Lu et al. 2021; Keith et al. 2023). For example, the richness and composition of chewers tends to correlated positively with leaf area, SLA and nitrogen content (Kagata and Ohgushi 2011; Peeters 2002a, b; Dial et al. 2006; Caldwell et al. 2016; Lu et al. 2021; Schön et al. 2023). This is explained because chewing insects ingest entire plant tissues, and are therefore more exposed to secondary and structural compounds (Clissold et al. 2009). While in the suckers' guild, although would be expected a similar trend, evidences are contradictory, especially for the SLA and nitrogen content (Whitham 1978; Peeters 2002a, b; Dial et al. 2006; Caldwell et al. 2016; Lu et al. 2021). In the case of the suckers' guild is assumed to be less constrained by structural or nutritional of leaf traits since they ingest fluids from different plant tissues, e.g. phloem, xylem or mesophyll cells (Peeters 2002a, b; Peeters et al. 2007; Caldwell et al. 2016). In addition, as expected by Root`s (1973) *resource concentration hypothesis*, abundant or dominant plant species that provide much of the vegetative tissues should support richer insect assemblages than rare plant species (Cornell and Kahn 1989; Basset and Novotny 1999; Southwood et al. 2004; Lewinsohn et al. 2005).

Plant phylogeny synthesizes the shared evolutionary history of a set of species, including multiple traits potentially affecting herbivorous insects (Kraft et al. 2007), many of which are not feasible to measure. To circumvent this limitation, phylogenetic distance has been used as a surrogate for trait dissimilarity and specialization (Ødegaard et al. 2005; Lewinsohn et al. 2005; Grandez-Rios et al. 2015). Because most traits are more or less evolutionarily conserved, trait dissimilarity is expected to increase with phylogenetic distance. If dissimilarity in functional traits between two plants involves extreme or unique combinations of traits, it may be difficult for herbivorous insects to exploit both (Hill and Kotanen 2009). This led to the prediction, that an increase in phylogenetic distance is associated with a high dissimilarity of herbivorous insect assemblages and a decrease in species richness hosted (*taxonomic isolation hypothesis*, Kennedy and Southwood 1984; Vialatte et al. 2010; Grandez-Rios et al. 2015).

Due to this tight ecological and evolutionary history, and in contrast with mutualistic networks that tend towards generalization, antagonistic plant-herbivorous insect interactions are more specialized and structured, with groups of species interacting intensively with each other, while maintaining few interactions with other groups (Lewinsohn et al. 2006; Cirtwill et al. 2020). Therefore, is expected that plant species with similar traits, i.e. traits with a functional role for herbivorous insects, or phylogenetically related tend to share partners and potentially structure the plant-herbivorous insect interaction networks (Ibanez et al. 2016; Cirtwill et al. 2020). Nevertheless, within antagonistic networks, the degree of specialization and modularity depends on the interacting guild, being highly specialized in the case of endophagous insects (galling insects), but less specialized in the case of free living (suckers and chewers) with sucker tending to be more specialized than chewers (Novotny et al. 2010; Oliveira et al. 2020). Also, variation in the proportion of generalist and specialist species within a guild might have effects on the structure and specialization of plant-herbivorous insect interaction networks (Araújo and Oliveira 2021).

The main goal of our study is to understand the differentiation of herbivorous insect assemblages across woody plant species of Mediterranean mixed forests. We hypothesize that, (1) given the interspecific differences among plant species in their trait profiles and abundances, their associated herbivorous insect communities should differ. In such case, (2) some specific plant features should be behind such differentiation, probably affecting differently to each guild. According to the different evolutionary history of plants and feeding mode of each guild (i.e. suckers and chewers), we expect for both guilds that (2.1) closely related plant species should show similar insect assemblages and (2.2) abundant plant species should have richer insect assemblages. Additionally, (2.3) suckers should be mainly affected by leaf quantity related traits; while, (2.4) chewers should be mainly affected by leaf quality and quantity. Finally, (3) such differentiation should influence the structure of plant–insect interaction networks.

Material and methods

Study sites and dominant plant species

This work was carried out in two Mediterranean pine-oak mixed forest communities of the south-eastern Iberian Peninsula: Sierra Sur de Jaén and Sierra de Segura (Jaén and Segura, hereafter). The study area at Jaén is characterized by mixed forests of *Pinus halepensis*, *Quercus ilex*, and *Q. faginea* while Segura is characterized by mixed forests of *P. nigra* subsp. *salzmanii*, *Q. faginea*, and *Q. pyrenaica*. Both areas have calcareous soils and Mediterranean climate. Jaén has a mean annual temperature of 14.1 °C, a mean annual rainfall of 715 mm, and a mean altitude of 1010 m, and Segura has a mean annual temperature of 11.6 °C, a mean annual rainfall of 890.5 mm, and a mean altitude of 1338 m. We chose for this study the dominant woody species (trees and shrubs) in each community: 22 species in Jaén and 14 species in Segura (Table S1).

Arthropod sampling and characterization of herbivorous insect assemblages

Arthropod communities are inherently variable at multiple scales. To address as many as possible sources of variation we sampled 36 plant species, with 26 to 31 individuals sampled per species, across two sites, over two seasons (spring and summer) and three consecutive years (2016–2018), which resulted in a total effort of 1060 samples (Table S1). In this way, we addressed the multiple sources of variation at spatial, inter-annual, intra-annual, between-species, and within-species. Arthropod sampling was carried out by the beating method. This is a standard method for sampling foliage and is frequently used to sample arthropods associated with the canopies of shrubs and trees (e.g. caterpillars, aphids, scale insects, other hemipterans, some beetles, and other plant-feeding or plant-dwelling arthropods (Montgomery et al. 2021).

Individual plants were sampled in the four cardinal directions using beating trays (40 cm × 50 cm or 20 cm × 30 cm depending to plant size) with soapy water to reduce the loss by escape of the collected arthropods (Ballare et al. 2019). Beating trays were placed under the canopy of the sampled individual and branches hitted until no more arthropods fell into the trays. Due to sampling plant species of contrasting canopy sizes, we adjusted the number of the trays to the sampled plant canopy to avoid sampling bias. In the case of trees, we sampled individuals which were able to beat completely from the lower to the upper canopy layer.

Samples were taken to the lab, where specimens were sorted under the stereomicroscope and identified to morphospecies or at the lower taxonomic level possible (specimens are preserved in 75% ethanol at the Department of Animal and Plant Biology and Ecology in the University of Jaén, Spain). Arthropod species were classified into trophic groups: phytophagous, zoophagous (including active predators, parasites, parasitoids, scavengers and sarcophagous), saprophagous, mycophagous and omnivorous. The trophic group was ascribed based on mouthparts and considering the available information at the species level or from close relatives (see Table S2).

Here, we focused on insects that feed on vegetative plant tissues. Pollinivores, nectarivores and florivores were excluded unless their larvae feed on vegetative plant tissues. Gall-forming insects also were excluded since our sampling was not properly designed for them. We classified phytophagous insects into feeding guilds (Table S2), according to whether their mouthparts are adapted to suck-pierce vascular fluids (external, mobile and sessile phloem, mesophyll or xylem suckers), suckers hereafter, or to chew plant tissues (external and internal chewers including boring and mining insects, and rostrum chewers), chewers hereafter.

Diversity of herbivorous insect assemblages

To estimate insect diversity of each guild, we used both rarefaction/extrapolation curves and Hill numbers, as a way to get more robust and meaningful comparisons (Chao et al. 2014; Roswell et al. 2021). Diversity indices were calculated from incidence data (0/1) to avoid abundance biases caused by differences in the gregarious behaviour between insect species (e.g. aphids vs. leafhoppers). Diversity was approximated by using Hill numbers, the computation was performed for three increasing values of the order parameter q, corresponding to increasing weight on the species relative abundances: $q=0$, counts interacting species equally, irrespective of their relative abundances, correspond to richness; $q=1$, counts interactions equally, thus representing species proportional to their frequency of interaction, correspond to the Hill-Shannon index; $q=2$, exclusively pertains to the dominant interactions across the surveys, correspond to the Hill-Simpson index. While richness tends to be sensitive to rare species since it uses an arithmetic rarity scale. The Hill-Shannon index uses a logarithmic scale and the Hill-Simpson index uses a reciprocal scale which emphasizes the abundant species (Chao et al. 2014; Hsieh et al. 2016; Roswell et al. 2021).

To avoid estimation bias, plant species with extremely low number of recorded insects were excluded: *Thymus mastichina* and *Daphne laureola,* in the sucker guild, and *Phillyrea angustifolia, P. latifolia, Phlomis purpurea, Pistacia lentiscus, P. terebinthus* and *Acer granatensis* in the chewer guild.

Plant leaf traits and abundance

We used leaf plant traits frequently found to affect herbivorous insect assemblages. Namely, specific leaf area (SLA, mm^2/mg) and leaf nitrogen content (LN, %) as measures of leaf quality; and leaf area (LA, mm^2) as a proxy for resource quantity (Basset and Novotny 1999; Peeters 2002a, b; Harrison et al. 2018; Wang et al. 2020). In addition, we included the mean cover (m^2) of each plant species at each site (evaluated through vegetation surveys), as a proxy for the resource concentration (Cornell and Kahn 1989; Basset and Novotny 1999). Leaf habit (evergreen vs. deciduous) was included as a life history trait related to plant phenology, with potential effects on insects' development and degree of specialization (Southwood et al. 2004; Barton et al. 2019). In each site we choose 10 adult individuals per plant species for sampling leaf traits. We collected 5 healthy and mature leaves from each individual. These leaves were collected 2–3 h after sunrise and 3–4 h before the sunset, and were placed individually into plastic zip-bags. These bags were placed inside a portable fridge to avoid water loss. We used the average of the five collected leaves to estimate the leaf traits. Leaf area was measured by taking a picture of the leaves of each individual with a reference scale and processing with the image analysis software ImageJ (Abràmoff et al. 2004). To obtain the SLA, the leaf area was divided by the oven-dried mass. Leaf Nitrogen content was obtained from 0.2 g of homogenized oven-dried leaves for each sample, and analyzed on an automated CHNS elemental analyzer (Thermo Fisher). However, some species like *Thymus mastichina* or *Juniperus oxycedrus* show relatively small leaves, so several leaves were taken and weighted until a minimum of 2 gr of leaf fresh weight was reached, and leaf traits averaged by the number of leaves. It also should be noted that other species like *Juniperus phoenicea* or *Ulex parviflorus* present photosynthetic stems with small modified leaves, so we used 5 cm of the stem tip to calculate the traits. All the protocols followed for the measurement of functional traits follow Cornelissen et al. (2003), and are described in detail in Perea et al. (2021). Plant traits are available and described in detail in Perea et al. (2021). Since environmental conditions and soil properties are similar at both sites (Perea et al. 2021), we assumed that traits do not differ within species in these two communities (Zhao et al. 2022).

Plant phylogenetic relatedness metrics

To incorporate in the analyses phylogenetic information from plant species, we used an in situ time-calibrated barcoded phylogeny from the same study sites (Alcántara et al. 2019). Depending on the analysis nature, the phylogenetic information must be provided on a species or on a pairwise basis. Thus, the phylogenetic distance of a given plant species relative to a whole plant community was estimated using the "evolutionary distinctiveness" index (Isaac et al. 2007), which informs about how isolated or distant a species is within a given phylogeny. It was calculated using the evol.distinct function from the picante package in R (version 1.8.2) (Kembel et al. 2010). Pairwise distances were calculated using the cophenetic function from the vegan package in R (version 2.5–7) (Oksanen et al. 2022).

Data analysis

Differentiation of herbivorous insect assemblages across plant species

To explore the variation in herbivorous insect assemblages among plant species, we used the total β diversity based on the Sørensen index (Baselga 2010; Baselga et al. 2022). We used the matrices of insect presence-absence separately for each site (Jaén and Segura) and feeding guild (suckers and chewers).

Differences in β diversity of insect assemblages were tested by means of PERMANOVA (Anderson 2001), including as factors, plant species identity, and also sampling year and month, to account for a possible temporal variation across samplings. To estimate p values, we run 999 permutations randomizing individuals only between samples taken on the same date. β diversity matrices were computed using the betapart package in R (version 1.5.4) (Baselga et al. 2022).

Plant traits and diversity of herbivorous insect assemblages

To test for the effect of plant traits on the diversity of herbivorous insect communities, we fitted a generalized linear model separately for each insect's guild and diversity index. All diversity estimates (i.e. $q0$, $q1$, $q2$) were modelled with Gaussian family distribution, while $q1$ for the chewers guild was modeled with tweedie family distribution. The model included, as a dependent variable, each diversity index per plant species, and, as explanatory variables, leaf area (LA), specific leaf area (SLA), leaf nitrogen content (LN), mean plant cover, plant evolutionary distinctiveness, and site (Jaén and Segura). All models were checked for residuals diagnostics.

Plant traits and composition of herbivorous insect assemblages

To test whether plant species differences in the composition of their associated insect assemblages were related to plant differences in ecological and functional leaf traits, and/or phylogenetic distances, we fitted a generalized linear mixed model separately for each feeding guild.

Betadiversity was modelled with Beta family distribution (suckers) and Gamma family distribution (chewers). All models were checked for residuals diagnostics.

Pairwise β diversity was estimated from a plant–insect matrix of the mean incidence of insect species among samples. β diversity was calculated based on the Bray–Curtis index using the betapart package in R (version 1.5.4) (Baselga et al. 2022). Distances for each plant trait were calculated using Gower distance (Gower 1971) using the FD package in R (version 1.0–12) (Laliberté and Legendre 2010). This metric yields a standardized distance between 0 and 1, which is recommended because it facilitates interpretations of dissimilarity and allows comparisons between traits with different units (de Bello et al. 2021).

The model included, as a dependent variable, the pairwise β diversity. As explanatory variables: Gower distances in leaf area (LA), specific leaf area (SLA), leaf Nitrogen content (LN), and mean plant cover, similarity in leaf habit (same (0) or different (1)), phylogenetic distances (squared-root transformed) and site (Jaén and Segura). Since every plant species appears in multiple pairwise distances with all other species, data from those pairs sharing plant species are not independent. To account for this non-independence, we included two random factors coding the identity of each species in a pair, considering their site provenance. To control for phylogenetic autocorrelation, we included in our models the squared-root of the phylogenetic distances as a covariable. However, the correlation between betadiversity and phylogenetic distances can be mainly driven by the differences between gymnosperms and angiosperms (for example, see Brändle and Brandl 2006). Therefore, we analysed also our data including only distances within angiosperms.

Plant traits and structure of plant–insect interaction networks

We explored whether plant ecological and functional leaf traits, and phylogenetic relatedness can leave an imprint on the structure of plant-herbivorous insect interaction networks. Thus, we built a weighted bipartite network for each site and feeding guild using bipartite package in R (version 2.17) (Dormann et al. 2008). Modularity was assessed with the meta Compute Modules function of the bipartite package in R (version 2.17) (Dormann et al. 2008) with the Beckett algorithm (Beckett 2016). To test for modularity significance, we used 999 permutations of a non-sequential algorithm for quantitative matrices that preserves column sums and cells within each column are shuffled, using the c0_samp option of the nullmaker function of the metacom package in R (version 1.5.3) (Dallas 2014).

Once the plant–insect networks were built and their modularity calculated, we tested the influence of plant ecological and functional leaf traits, and phylogenetic distances on the belonging of each plant species pairs to the same or different module. For that, we used as a dependent variable, a binary variable coding whether two plant species belonged to the same or different module (0 and 1, respectively). Leaf functional traits and mean plant cover dissimilarities (i.e. Gower distances as in the previous section), leaf habit similarity (same (0) or different (1)), phylogenetic distances (squared-root transformed) and site (Jaén and Segura) were included as explanatory variables.

We used generalized linear mixed model with binomial family distribution, and included the identity of both plant species in the pair as a random factor.

All analyses were performed in R (R Core Team 2021). PERMANOVAs were run using the vegan package in R (version 2.5–7) (Oksanen et al. 2022). Models were performed using the glmmTMB package (version 1.1.2.3) (Brooks et al. 2017). Model residuals diagnostics were checked with the DHARMa package (version 0.4.5) (Hartig 2022). Model predictions were evaluated with the ggeffects package (version 1.1.1) (Lüdecke 2018) and the stats package (R Core Team 2021). All graphics were done with ggplot2 package (version 3.3.5) (Wickham 2016).

Results

A total of 6635 individual arthropod specimens were collected, of which 2176 were classified as herbivorous insects and involved 401 species. The taxonomic composition was dominated by Hemiptera (66.33%) followed by Coleoptera (20.45%), Diptera (4.49%), Orthoptera (4.74%), Hymenoptera (2.00%), Lepidoptera (1.50%) and Phasmatodea (0.50%) (Fig. 1, see Table S2). Regarding feeding guilds, suckers represented 66.33% (all Hemipterans), while chewers represented 33.67%, mainly including exophagous species from Coleoptera, Orthoptera and Phasmatodea (76.3%), and some species from Diptera, Hymenoptera and Lepidoptera whose larvae feed on plant tissues (23.7%).

Differentiation of herbivorous insect assemblages across plant species

Plant species differed in their associated herbivorous insect assemblages, accounting significantly for the largest proportion of variation in each insect feeding guild. In the case of sucker insects, plant identity explained 19.30% of the variation in Jaén, and 15.60% in Segura (Table 1). In the case of chewer insects, plant identity explained 17.54% of the variation in Jaén, and 8.13% in Segura (Table 1). The explained variation by plant species identity was much more than that explained by year or month (Table 1).

Plant traits and diversity of herbivorous insect assemblages

Regarding suckers' guild, both the Hill-Shannon and Hill-Simpson diversity indexes indicated that plants with low SLA and deciduous leaves hosted more diverse sucker assemblages, in terms of common and dominant insect species, respectively (Table 2; Fig. 2). In the chewers' guild, the Hill-Simpson index (that takes into account dominant species) indicated that plants with large leaf areas can support more diverse assemblages and mainly composed by dominant chewer species (Table 3; Fig. 3). In addition, independently of the estimator considered, mean plant cover showed a general significant positive relationship with the diversity

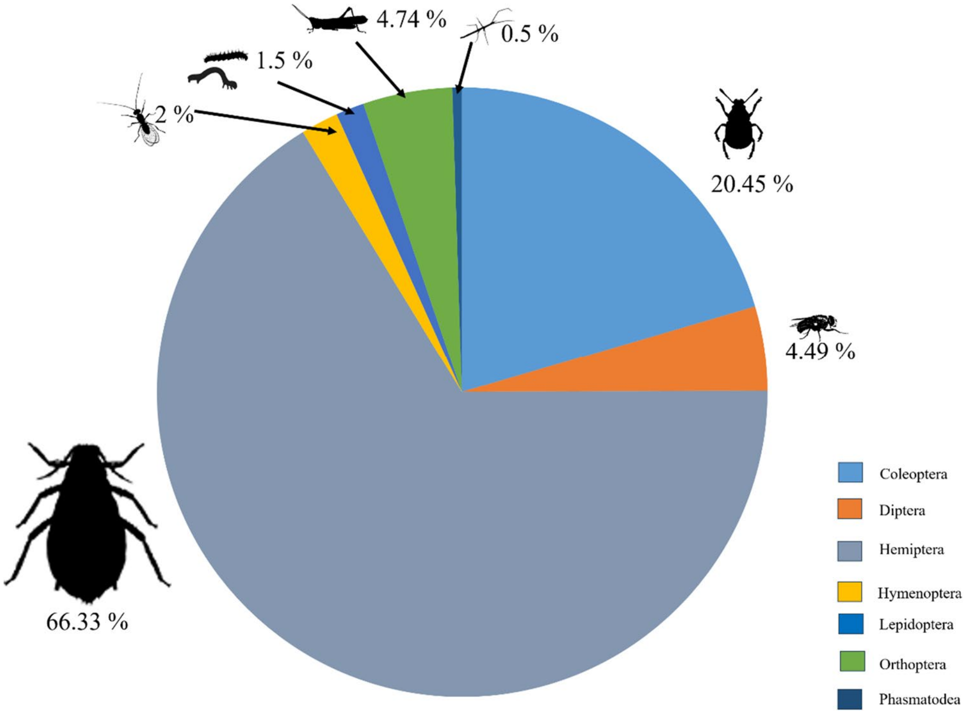

Fig. 1 Percentage of sampled arthropod species by taxonomic Order (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera and Phasmatodea). Silhouettes from http://phylopic.org/: Coleoptera (by Samanta Orellana), Diptera, Calliphoridae (by Robert Baird); Hemiptera, Aphididae (by Christoph Schomburg); Hymenoptera, *Leptopilina clavipes* (by Kamil S. Jaron); Lepidoptera. Geometridae larva (by Colleen Nell) and *Vanesa carduii* larva (by Gareth Monger); Orthoptera, *Phaeoparia lineaalba* (by Fernando Domenico) and Phasmatodea, *Medauroidea extradentata* (by Christoph Schomburg), all license at https://creativecommons.org/licenses/by-nc/3.0/ or https://creativecommons.org/publicdomain/mark/1.0/

Table 1 PERMANOVA analyses to explore patterns of differentiation of herbivorous insect assemblages among plant species, years and months

Model	df	SS	R^2	F	*p*(perm)
$\beta_{total\_Sucker\_SJ}$					
Species	21	38.63	0.193	4.87	**0.001**
Year	2	2.04	0.010	2.70	**0.01**
Month	3	5.43	0.034	4.79	**0.001**
Residual	404	153.73	0.767		
Total	430	200.41	1.000		
$\beta_{total\_Sucker\_SS}$					
Species	13	22.62	0.156	4.42	**0.001**
Year	2	2.23	0.015	2.83	0.45
Month	2	2.77	0.019	3.52	*0.07*
Residual	295	117.57	0.815		
Total	312	145.32	1.000		
$\beta_{total\_Chewer\_SJ}$					
Species	21	15.39	0.175	1.80	**0.001**
Year	2	1.08	0.012	1.32	0.13
Month	3	2.74	0.031	2.24	**0.02**
Residual	168	68.53	0.78		
Total	194	88.19	1.000		
$\beta_{total\_Chewer\_SS}$					
Species	13	8.24	0.081	1.49	**0.001**
Year	2	2.22	0.022	2.59	0.29
Month	2	3.73	0.035	4.36	0.11
Residual	206	87.98	0.863		
Total	223	101.90	1.000		

Analyses were conducted separately for each sampling site (Jaén and Segura) and for each insect guild, i.e. sucker and chewer. The degrees of freedom (df), Sum of Squares (SS), the amount of explained variance (R2), the Pseudo-F (F) and the associated *P* values (*p*(perm)) are given. Statistically significant effects are bold typed

Table 2 Generalized linear models analyses exploring the variation of suckers' diversity with plant leaf traits, abundance, phylogenetic distances and sampling sites

	df	Estimate	Wald χ^2	*p*
Richness (q0)				
LA	1, 25	– 0.10	0.27	0.60
LN	1, 25	0.07	0.01	0.92
SLA	1, 25	– 0.44	0.66	0.41
Leaf habit	1, 25	– 13.18	3.28	*0.07*
Cover	**1, 25**	**0.09**	**27.59**	**< 0.001**
Evolutionary distinctiveness	1, 25	– 0.05	0.93	0.33
Site	1, 25	6.92	1.25	0.26
Hill-Shannon (q1)				
LA	1, 25	– 0.07	0.36	0.55
LN	1, 25	0.24	0.33	0.56
SLA	*1, 25*	*– 0.61*	*3.42*	*0.06*
Leaf habit	**1, 25**	**– 13.93**	**9.93**	**< 0.01**
Cover	**1, 25**	**0.05**	**26.26**	**< 0.001**
Evolutionary distinctiveness	1, 25	– 0.02	0.50	0.48
Site	1, 25	1.89	0.26	0.61
Hill-Simpson (q2)				
LA	1, 25	– 0.003	0.61	0.43
LN	1, 25	0.02	2.09	0.15
SLA	**1, 25**	**– 0.04**	**9.99**	**< 0.01**
Leaf habit	**1, 25**	**– 0.70**	**21.11**	**< 0.001**
Cover	**1, 25**	**0.001**	**21.71**	**< 0.001**
Evolutionary distinctiveness	1, 25	0.0001	0.01	0.91
Site	1, 25	– 0.10	0.73	0.39

Models were fitted separately for each diversity estimators (i.e. *q*0, *q*1 and *q*2). For each plant trait, we provide its estimated effect according to the fitted model and its significance evaluated by means of a Wald χ^2 test. Significant effects ($p < 0.05$) are bold typed and marginally significant effects are in italics. *LA* leaf area; *LN* leaf Nitrogen content; *SLA* Specific Leaf Area, Leaf habit, deciduous/evergreen; Cover, mean plant cover; Evolutionary distinctiveness, a measure of phylogenetic distance between plants of the community and sampling sites, Jaén and Segura.

of sucking and chewing insects (Tables 2, 3; Figs. 2, 3). Evolutionary distinctiveness did not show any effects on herbivorous insect diversity.

Plant traits and composition of herbivorous insect assemblages

Plant traits did not show any effect on the variation in composition of suckers' assemblages. Phylogenetic distance revealed that closely related plants hosted more similar suckers' assemblages (Table 4, Fig. 4a). This relationship was held when we analysed exclusively distances between angiosperms (Table S1, Fig. 4b). Regarding chewers, the dissimilarity of their assemblages between plant species pairs was higher in Jaén than in Segura. We showed that betadiversity of chewing insect assemblages (dissimilarity) increases with differences in plant leaf traits. That is, plants with similar leaf functional traits, i.e. leaf area, SLA and nitrogen content, tend to host similar chewing insect assemblages (Table 4, Fig. 5a–c). However, when we analysed the chewing insect associated exclusively to angiosperm species, we showed that betadiversity increases with differences in leaf area and phylogenetic distances (Table 4, Fig. 5d, f). By contrast, betadiversity was higher in plant species with the same leaf habit (Fig. 5e). That is, angiosperm species with similar leaf area, phylogenetically close and with different leaf habit tend to show similar chewing insect assemblages.

Plant traits and structure of plant-herbivorous insect interaction networks

Interaction networks showed a modular structure for both feeding guilds (Fig. S1-2): plant-sucker insect networks were

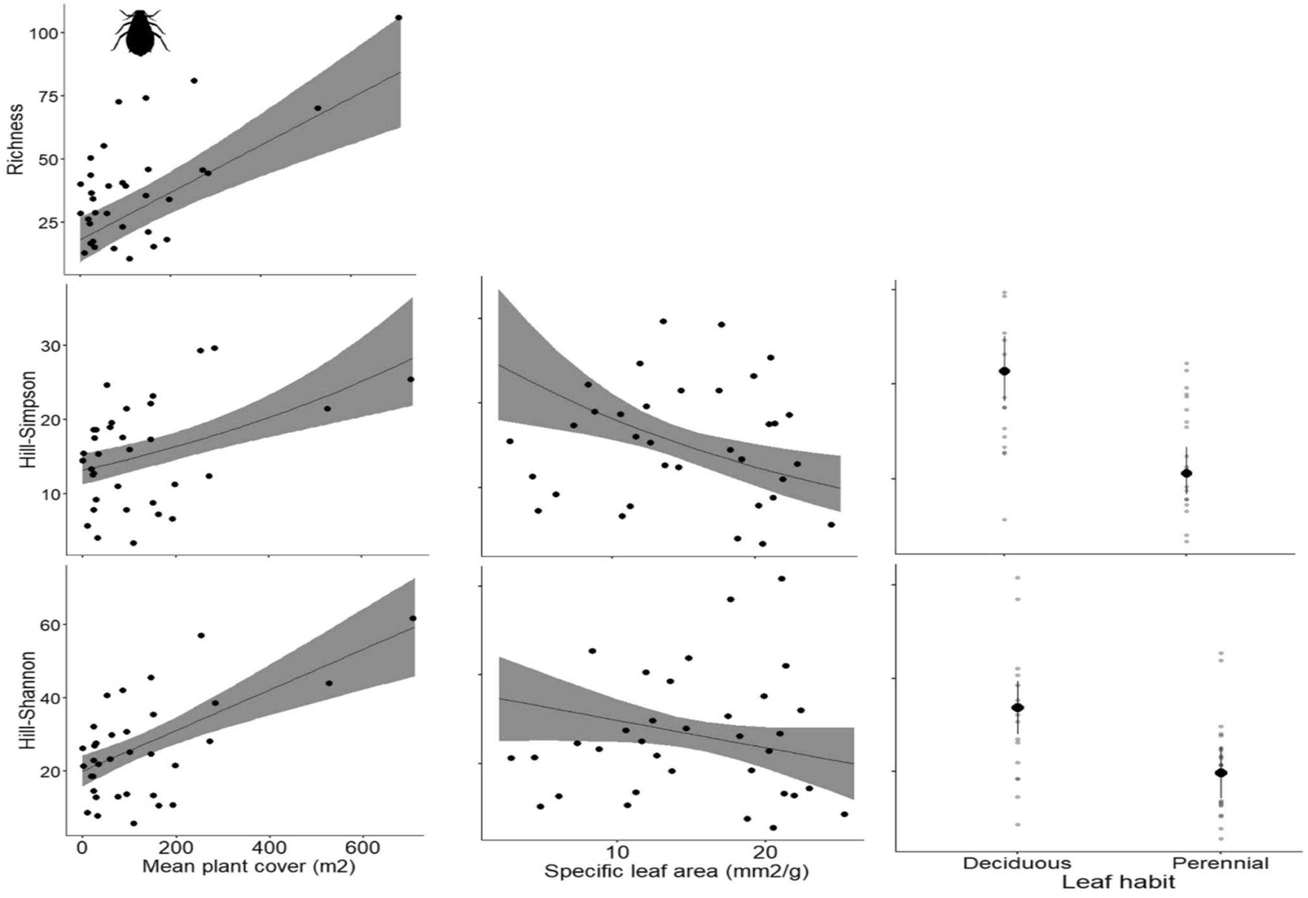

Fig. 2 Predictions of the relationship between plant associated sucking insect assemblages' diversity and plant leaf traits and abundance. Lines and 95% ICs are extracted from GLMs. The y-axis represents the model-predicted diversity estimates for each index. Silhouettes from http://phylopic.org/. Aphididae (by Christoph Schomburg), license at https://creativecommons.org/licenses/by-sa/3.0/

composed by 12 modules in Jaén (modularity score = 0.47, $p < 0.01$) and 9 in Segura (modularity score = 0.47, $p < 0.01$). On the other hand, plant-chewer insect networks consisted of 12 modules in Jaén (modularity score = 0.46, $p < 0.05$) and 8 in Segura (modularity score = 0.35, $p < 0.05$).

GLMMs performed to assess the relationships of plant leaf traits, abundance and phylogenetic distance with the modular structure of plant-herbivorous insect networks found significant influences of plant phylogenetic distances on the probability of two plant species belong to the same module (Table 5, Fig. 6). Plant species from the same modules tended to be phylogenetically closer. In contrast, GLMMs did not detect any traits related to the modular structure of the plant-chewer network (Table 5).

Discussion

Herbivorous insect assemblages are highly diverse and variable across multiple scales (Southwood et al. 2004; Lewinsohn et al. 2005; Wardhaugh 2014). To understand how this variability is structured within local plant communities, we identified plant features acting as potential biotic filters for regional herbivorous insect pools and explored their effects on plant-herbivorous insect interaction networks. In the present study, herbivorous insect assemblages were much more variable at fine than at large spatial and temporal scales, and a relevant part of their variability could be attributed to host plant species.

Variability of insect assemblages between samples mostly reflects small-scale spatial variation among samples taken throughout the study sites, since temporal variation explained a very small fraction of the variance. Despite the wide variability of herbivorous insect assemblages among samples, those taken from the same plant species tended to be more similar than those taken from different species. These results concur with many other studies reporting distinct plant species to harbour different associated herbivorous insect assemblages (Cornell and Kahn 1989; Basset and Novotny 1999; Peeters 2002a, b; Peeters et al. 2007; Southwood et al. 2004, 2005; Lewinsohn et al. 2005; Rego et al. 2019). Such differentiation can reflect the effect of

Table 3 Generalized linear models analyses exploring the variation of chewers' diversity with plant leaf traits, abundance, phylogenetic distances and sampling sites

	df	Estimate	Wald χ^2	*p*
Richness (q0)				
LA	1, 21	0.01	1.46	0.23
LN	1, 21	0.03	0.90	0.34
SLA	1, 21	0.01	0.32	0.57
Leaf habit	1, 21	0.28	0.74	0.39
Cover	**1, 21**	**0.001**	**8.48**	**< 0.01**
Evolutionary distinctiveness	1, 21	0.003	1.13	0.28
Site	1, 21	0.15	0.33	0.56
Hill-Shannon (q1)				
LA	1, 21	0.01	2.63	0.10
LN	1, 21	0.03	1.55	0.21
SLA	1, 21	0.006	0.11	0.74
Leaf habit	1, 21	0.12	0.26	0.61
Cover	**1, 21**	**0.002**	**7.36**	**< 0.01**
Evolutionary distinctiveness	1, 21	0.002	1.72	0.19
Site	1, 21	0.35	2.97	0.09
Hill-Simpson (q2)				
LA	**1, 21**	**0.15**	**3.91**	**0.05**
LN	1, 21	0.33	2.71	0.10
SLA	1, 21	− 0.05	0.12	0.72
Leaf habit	1, 21	− 0.25	0.01	0.90
Cover	**1, 21**	**0.02**	**10.39**	**< 0.01**
Evolutionary distinctiveness	1, 21	0.01	0.73	0.39
Site	**1, 21**	**4.02**	**4.95**	**0.03**

Models were fitted separately for each diversity estimators (i.e. $q0$, $q1$ and $q2$). For each plant trait, we provide its estimated effect according to the fitted model and its significance evaluated by means of a Wald chi−square test. Significant effects ($p < 0.05$) are bold typed and marginally significant effects are in italics. *LA* leaf area; *LN* leaf Nitrogen content; *SLA* Specific Leaf Area, Leaf habit, deciduous/evergreen; Cover, mean plant cover; Evolutionary distinctiveness, a measure of phylogenetic distance between plants of the community and sampling sites, Jaén and Segura

plant traits and evolutionary features. For example, variation in herbivorous insect composition has been found to be mainly related to traits that directly or indirectly reduce herbivory, such as leaf toughness, leaf indumenta, SLA, leaf nitrogen content or leaf area (Lawton and Price 1979; Peeters 2002a, b; Peeters et al. 2007; Hanley et al. 2007; Clissold et al. 2009; Carmona et al. 2011). Moreover, there is increasing evidence that certain insect guilds vary between and within plant species depending on their ecological and functional traits. For example, suckers are negatively related to leaf water content and positively related to leaf nitrogen content (in Australian species Peeters 2002a, b; Lewinsohn et al. 2005; or within *Metrosideros polymorpha* Tielens and Gruner 2020); while chewers are positively related to leaf area or leaf nitrogen content and negatively by the leaf indumenta (in Australian species Peeters 2002a, b; Lewinsohn et al. 2005; or within *Metrosideros polymorpha* Tielens and Gruner 2020).

Plant traits and diversity of herbivore insect assemblages

The diversity of sucker and chewer assemblages was related to different plant features. In the sucker guild, diversity decreased with SLA and was lower in evergreen than in deciduous plants. On the one hand, species with low SLA (e.g. *Juniperus phoenicea*, *J. communis*, *Pinus halepensis*, *P. nigra* or *Quercus ilex*), that is, strong and tough leaves, supported more diverse sucker assemblages than plants with soft and thin leaves, high SLA (e.g. *Sorbus torminalis, Berberis hispanica*, *Daphne gnidium* or *Cistus albidus*). A similar trend was found by Caldwell et al. (2016), who showed that the density of sucker species was negatively correlated with the specific leaf area (i.e. SLA), although others have found the opposite trend (Peeters 2002a, b a, b; Peeters et al. 2007; Lu et al. 2021). On the other hand, deciduous plants (e.g. *Pistacia terebinthus*, *Quercus_faginea*, *Crataegus monogyna* or *Rosa* spp.) supported more diverse sucker assemblages than perennials (e.g. *Cistus albidus, Phillyrea* spp. *or Phlomis purpurea*). This result is supported by studies on different tree species from the British islands (Cornell and Kahn 1989) and for *Quercus* species (Southwood et al. 2004, 2005) where deciduous species supported higher diversity of sucker species. Jointly, these traits can be interpreted as mechanical and temporal constraints to the sucker guild. First, plants with tough and thick leaves with large lifespan can provide more resistance and for longer times to damage by suckers, which only need to pierce the cuticle; but also provide resources for long time, and, in this way, they could support more diverse assemblages along seasons (Peeters 2002a, b; Peeters et al. 2007; Hanley et al. 2007; Caldwell et al. 2016). Indeed, the feeding behaviour of suckers (e.g. the use of enzymatic secretions to facilitate penetration, the reuse of stylet tracks or the use of stomata to penetrate) do not remove leaf tissues, therefore, it would be less harmful and costly in species with low SLA leaves (Peeters et al. 2007; Hanley et al. 2007; Caldwell et al. 2016). Second, deciduous species can have high photosynthetic rates during bud break resulting in a faster translocation of sap, and probably more nutritive, which may make new and young tissues or growing meristems more attractive for suckers (Coley 1983; Peeters 2002a, b; Peeters et al. 2007; Barton et al. 2019). Besides, like plants, sucker life cycles show seasonality and synchrony with the development of new plant structures (Awmack and Leather 2002; Southwood et al. 2004; Barton et al. 2019).

In turn, in the chewer guild, plants providing large leaves (e.g. *S. torminalis* or *Q. pyrenaica*) harboured more diverse

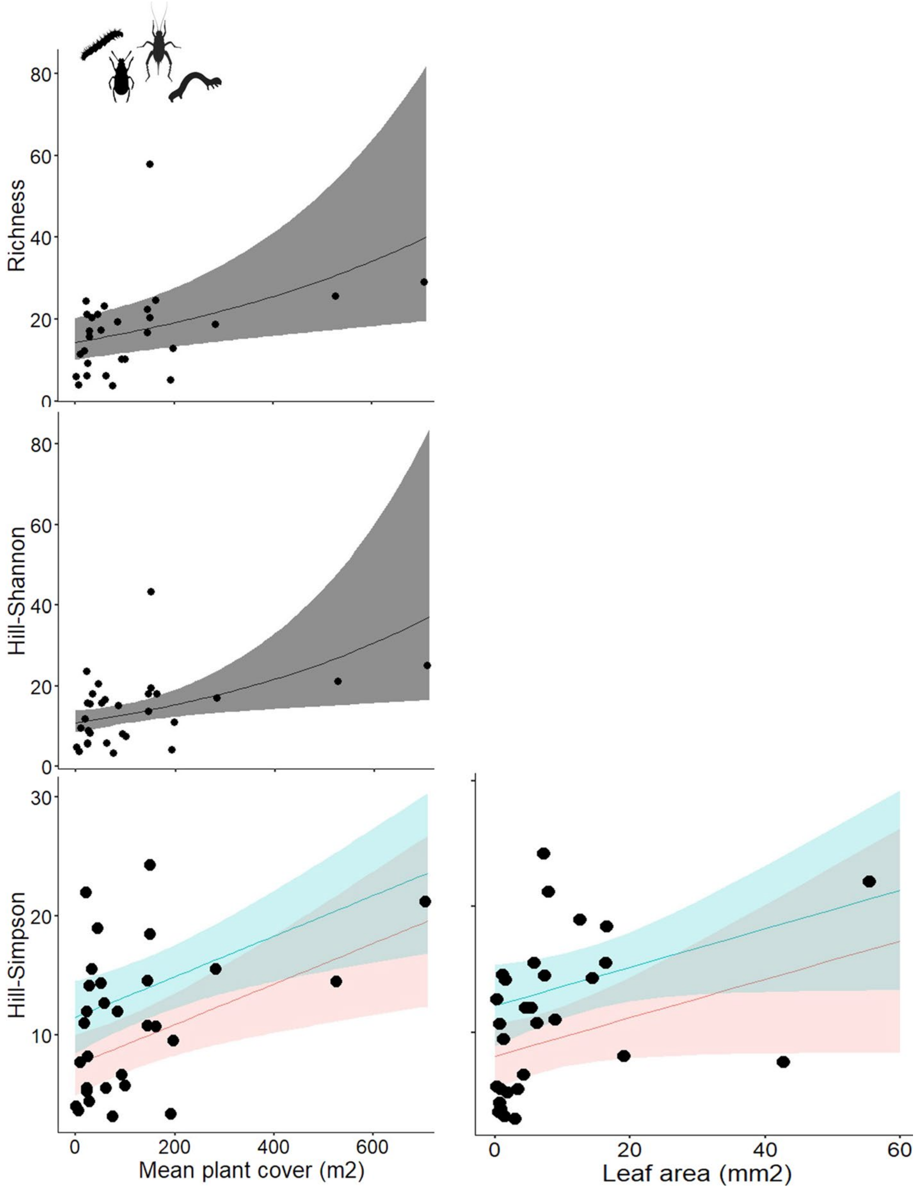

Fig. 3 Predictions of the relationship between plant associated chewing insect assemblages' diversity and plant leaf traits and abundance. Lines and 95% ICs are extracted from GLMs. Blue and red colours represent each sampling site, Segura and Jaén, respectively. The y-axis represents the model-predicted diversity estimates for each index. Silhouettes from http://phylopic.org/. Geometridae larva (by Colleen Nell) license at https://creativecommons.org/licenses/by-sa/3.0/; *Vanesa carduii* larva (by Gareth Monger) and Orthoptera (by Melissa Broussard) licenses at https://creativecommons.org/licenses/by/3.0/; and Coleoptera (by Samanta Orellana) license at https://creativecommons.org/licenses/by-nc/3.0/

chewer assemblages than those with small leaves (e.g. *Genista cinerea*, *D. gnidium*, *Juniperus* spp. or *Thymus mastichina*), as expected by the *resource availability hypothesis* (Coley 1983; Coley et al. 1985). Other authors also reported similar trends; for example, in the Australian flora, Peeters (2002a, b) and Peeters et al. (2007) found densities of total chewer species positively related to leaf area. While, in the British flora, Umbellifera species (Lawton and Price 1979) and trees (Moran and Southwood 1982; Kennedy and Southwood 1984) with large leaf areas and less divided supported more diverse insect communities.

The diversity of both insect guilds was positively affected by mean plant cover, as expected by the *resource concentration hypothesis* (Root 1973). Species providing most of the resources in our community (e.g. *P. halepensis*, *P. nigra*, *Q. ilex*, *Q. faginea* or *Q. pyrenaica*) supported richer and more diverse herbivorous insect assemblages. Similar results have been reported for the British arboreal insects, where sucker and chewer richness increased with host abundance (Cornell and Kahn 1989; Kelly and Southwood 1999) or for sucker assemblages on *Ficus* species (Basset and Novotny 1999). Besides, some of the more abundant species co-occur with phylogenetically close relatives which would facilitate host shifts by insects, especially for specialist insects (Hill and Kotanen 2009; Vialatte et al. 2010). At the same time, the fact that some of the most abundant species are gymnosperms (e.g. *P. halepensis* or *P. nigra*), which are phylogenetically distant with respect to the rest of co-occurring plant species, may explain the lack of a phylogenetic effect on the richness and diversity of each assemblage.

Table 4 Generalized linear mixed models analyses exploring the relationship between plant leaf traits, abundance, phylogenetic distances and sampling sites on the composition of herbivore insect assemblages

	Suckers				Chewers			
	df	Estimates	Wald χ^2	*p*	df	Estimates	Wald χ^2	*p*
LA	1, 310	0.16	2.08	0.15	**1, 310**	**0.13**	**14.05**	**< 0.001**
LN	1, 310	0.19	2.26	0.13	**1, 310**	**0.09**	**5.30**	**< 0.05**
SLA	1, 310	0.16	2.72	0.10	**1, 310**	**0.07**	**4.50**	**< 0.05**
Leaf habit	1, 310	0.02	0.25	0.62	1, 310	− 0.02	3.14	0.08
Cover	1, 310	− 0.05	0.31	0.58	1, 310	− 0.004	0.01	0.91
Phylogenetic distance	**1, 310**	**0.02**	**6.78**	**< 0.01**	1, 310	0.003	1.64	0.20
Site	1, 310	− 0.13	0.99	0.32	**1, 310**	**− 0.20**	**27.12**	**< 0.001**
Dispersion model	df	Estimates	z-value	*p*	df	Estimates	**z-value**	***p***
Phylogenetic distance	**1, 310**	**0.06**	**3.33**	**< 0.001**	1, 310	0.03	1.64	0.10

The composition of herbivore insect assemblages is measured as β diversity based on the Bray–Curtis distance. Models were fitted separately for each feeding guild. For each trait, we provide its estimated effect according to the fitted model and its significance evaluated by means of a Wald chi−square test. Significant effects ($p < 0.05$) are bold typed. LA, leaf area; LN, leaf Nitrogen content; SLA, Specific Leaf Area, Leaf habit, deciduous/evergreen; Cover, mean plant cover; square root of phylogenetic distances, and sampling sites, Jaé^n and Segura

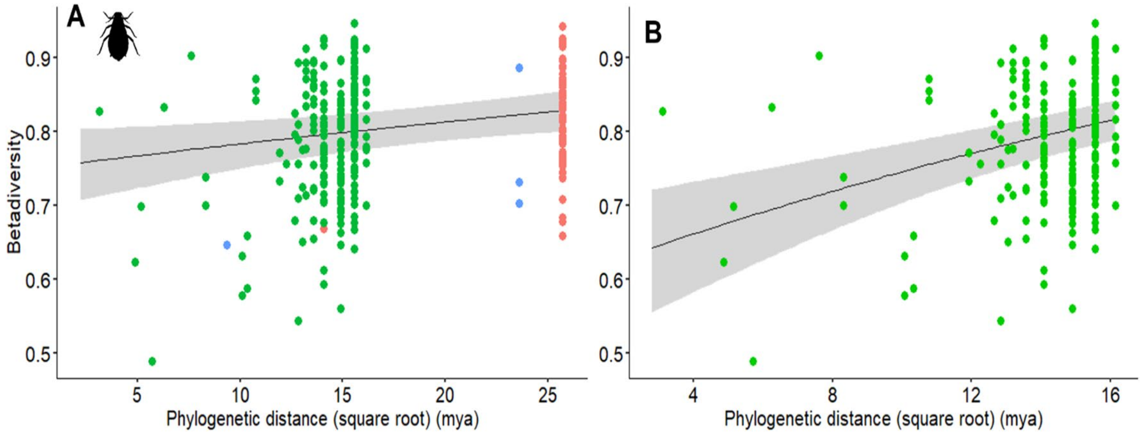

Fig. 4 Predictions of the relationship between plant associated sucking insect assemblages' β diversity and plant phylogenetic distances. Panel A shows the relationship for the full dataset, i.e. angiosperms and gymnosperms. Panel B shows the relationship exclusively for the angiosperms. For each plot, observed data are shown with different colours according to whether they are distances between angiosperms and gymnosperms (red), within angiosperms (green) and within gymnosperms (blue). The dissimilarity was measured as β diversity based on the Bray–Curtis distance. Lines and 95% ICs are extracted from GLMMs. The y-axis represents the model-predicted estimates. Silhouettes from http://phylopic.org/. Aphididae (by Christoph Schomburg), license at https://creativecommons.org/licenses/by-sa/3.0/. (Color figure online)

Plant traits, assemblage composition and interaction network structure

We found that insect assemblages were more different with increasing functional or phylogenetic distances between co-occurring plant species (Lewinsohn et al. 2005; Ødegaard et al. 2005; Grandez-Rios et al. 2015). In the sucker guild, variation in composition was related to phylogenetic distance between pairs of plant species. Moreover, the analysis of the interaction network structure reveals a clustering of plant species into modules with similar sucker assemblage composition, and that this clustering also reflects the signal of the phylogenetic distance between plants. By contrast, the variation in the composition of chewers was related to resource availability-palatability leaf traits (LA, LN and SLA) when consider angiosperms and gymnosperms together. However, when consider only angiosperm pairs, chewer's composition was related to the LA and leaf habit, both traits related to resource availability, and the phylogenetic distance. The phylogenetic distance effect may be indicating two non-mutually exclusive processes contributing to the assembly of both herbivorous insect guilds. On

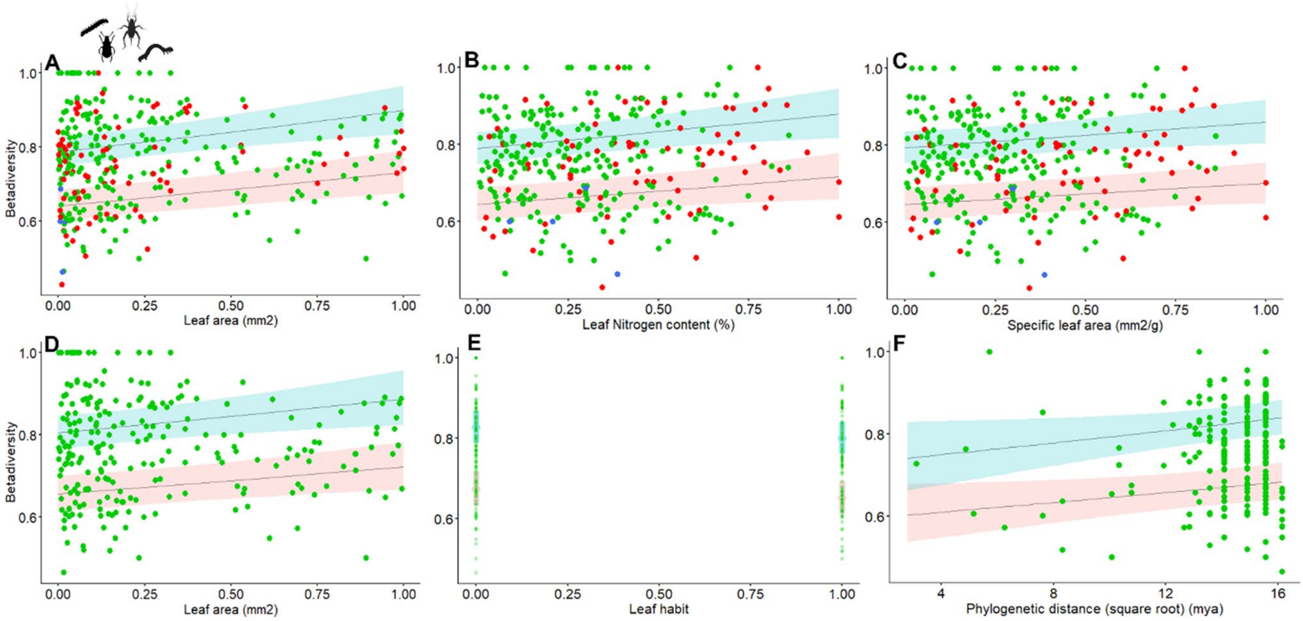

Fig. 5 Predictions of the relationship between plant associated chewing insect assemblages' β diversity and plant leaf traits dissimilarities. Panels **a**–**c** shows the relationship for the full dataset, i. e. angiosperms and gymnosperms. Panels **d**–**f** shows the relationship exclusively for the angiosperms. For each plot, observed data are shown with points of different colours according to whether they are distances between angiosperms and gymnosperms (red), within angiosperms (green) and within gymnosperms (blue). In light blue and pink are represent each sampling site, Jaén and Segura, respectively. The dissimilarity was measured as β diversity based on the Bray–Curtis distance. Lines and 95% ICs are extracted from GLMMs. The y-axis represents the model-predicted estimates. Silhouettes from http://phylopic.org/. Geometridae larva (by Colleen Nell) license at https://creativecommons.org/licenses/by-sa/3.0/; *Vanesa carduii* larva (by Gareth Monger) and Orthoptera (by Melissa Broussard) licenses at https://creativecommons.org/licenses/by/3.0/; and Coleoptera (by Samanta Orellana) license at https://creativecommons.org/licenses/by-nc/3.0/. (Color figure online)

Table 5 Generalized linear mixed models analysis exploring the relationships of plant module structure with plant leaf traits, abundance, phylogenetic distances and sampling sites

		Suckers			Chewers		
	df	Estimate	Wald χ^2	*p*	Estimate	Wald χ^2	*p*
LA	1,312	− 0.39	0.23	0.63	0.52	0.25	0.61
LN	1,312	0.52	0.13	0.72	− 0.23	0.03	0.86
SLA	1,312	1.76	1.90	0.17	0.88	0.63	0.43
Leaf habit	1,312	0.14	0.09	0.76	0.86	2.49	0.11
Cover	1,312	2.32	3.34	*0.07*	1.32	0.18	0.28
Phylogenetic distance	1,312	**0.14**	**4.57**	**0.03**	0.02	0.13	0.72
Site	1,312	− 0.69	1.85	0.17	0.04	0.003	0.95

Models were fitted separately for each feeding guild. For each plant trait, we provide its estimated effect according to the fitted model and its significance evaluated by means of a Wald χ^2 test. Significant effects ($p < 0.05$) are bold typed and marginally significant effects are in italics. *LA* leaf area; *LN* leaf Nitrogen content; *SLA* Specific Leaf Area, Leaf habit, deciduous/evergreen; Cover, mean plant cover; square root of phylogenetic distances between plants and sampling sites, Jaén and Segura

the one hand, it seems likely that phylogenetically conserved traits not included in this study (e.g. leaf indumenta, spines, waxes, resins, secondary metabolites or volatile compounds) are contributing to the assembly of the studied communities (Ødegaard et al. 2005; Kraft et al. 2007; Ibanez et al. 2016). On the other hand, it is also possible that the evolution of sucker and chewer lineages has occurred in concert with the diversification of plant lineages (Agrawal 2007; Lewinsohn et al. 2005). Plant functional traits seems to be important for chewers, species with similar LA, SLA, LN showed more similar assemblages of chewers. For example, Wang et al. (2020) found that the composition of Lepidopteran caterpillars was affected by SLA; while Tielsen and Gruner (2020) and Whitfeld et al. (2012) found positive effects of LN on the abundance of chewers species (including caterpillars and leaf miners); and Pitteloud et al. (2020) found a relationship

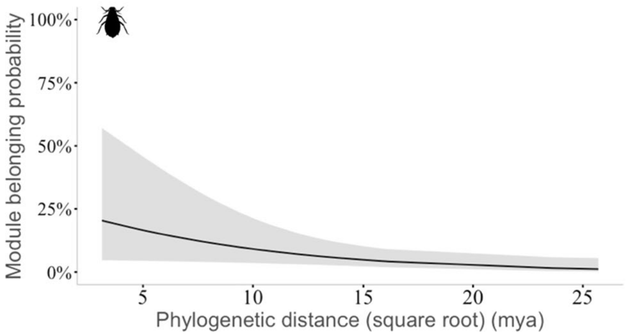

Fig. 6 Prediction of the relationship between the probability of plant species belonged to the same module and plant phylogenetic distances in the plant-sucker interaction network. Lines and 95% ICs are extracted from GLMMs. Silhouettes from http://phylopic.org/. Aphididae (by Christoph Schomburg), license at https://creativecommons.org/licenses/by-nc/3.0/

between Orthopteran species composition and changes in SLA and LDMC. Indeed, chewer insects, unlike suckers, tend to consume whole leaves and are directly exposed to leaf material secondary compounds and toxins. Therefore, variation in some of these traits could represent filters to the composition of chewers. However, despite the clustering of host species into modules with similar chewer composition, such interaction structure was not related to any of the studied plant traits. These results can reflect the heterogeneous composition of our chewer guild, which includes several Orders of insects, and also the more generalist feeding behaviour of chewers in comparison with suckers (Ødegaard et al. 2005; Novotny et al. 2010; Oliveira et al. 2020). Alternatively, other traits correlated with the SLA, LA, LN or deciduousness can be involved in the patterns detected here for the diversity and composition. For example, SLA is positively related to photosynthetic rates (Reich et al. 1991; Wright et al. 2001) and relative growth rates (Poorter and Remkes 1990), and negatively with leaf life span (Reich et al. 1991). Besides, the reduction in SLA is accompanied by an increase in lignin and fibres, and consequently, a dilution of leaf nitrogen content (Clissold et al. 2009). In addition, other plant features such as size and branch density patterns (Lawton 1983) or symbiosis with mycorrhizas (Koricheva et al. 2009) and N-fixing organisms (Lewinsohn et al. 2005) can be involved.

Conclusions

Based on a wide sampling of herbivore insect communities associated with the most important woody species dominating Mediterranean mixed forests, we show that the diversity and compositional variation of sucker and chewer insect assemblages are strongly determined by plant species identity and are structured by plant features that act as biotic filters of the insect species pool. The effects of such plant features vary with respect to the guild considered, so they are guild-specific. The sucker's assemblage was affected by the SLA, leaf habit and plant abundance, while chewers were affected by the SLA, LA, LN and plant abundance. The effect of plant phylogenetic distance only was important for the sucker guild. Both plant-sucker and plant-chewer interaction networks showed a modular structure. Plant-sucker network modularity is related to plant phylogenetic distance, where more closely related plants tend to share more suckers with each other, than with distantly related plants from different modules. Exploring the causes and consequences of plant features over their associated—herbivore insect assemblages within local plant communities may provide insights to understand their role in multiple community processes and ecological functions.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10342-024-01676-y.

Acknowledgements JMB was supported by FEDER SUMHAL-Sustainability for Mediterraean Hospost in Andalusia integrating LifeWatch ERIC [Work Package 5. Task 5.1.2. Development of the data standard. Repository development.] (LifeWatch ERIC—FEDER, POPE 2014-2020; Ministerio de Ciencia e Innovación, Spain).

Author contributions All authors have contributed to this study. JMA and JLG designed this study and carried out the field sampling. LCP and DC-S carried out the taxonomy of insects. AJP provided plant functional traits. JMB carried out statistical analyses and wrote the draft, all co-authors contribute to the final version.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. COEXMED II: Especificidad de las interacciones adulto-juvenil durante el reclutamiento de plantas leñosas: complementariedad de caracteres funcionales e interacciones plant-antagonista (CGL2015-69118-C2-1-P, FEDER y Ministerio de Economia y Competitividad, Spain); REPNETS-Redes de reemplazamiento en bosques: variación ecogeográfica e influencia de las comunidades de hongos de la filosfera y de las interacciones planta-suelo (PGC2018-100966-B-I00, FEDER—Agencia Estatal de Investigación, Ministerio de Ciencia e Innovación, Spain); and FEDER SUMHAL-Sustainability for Mediterraean Hospost in Andalusia integrating LifeWatch ERIC [Work Package 5. Task 5.1.2. Development of the data standard. Repository development.] (LifeWatch ERIC—FEDER, POPE 2014–2020; Ministerio de Ciencia e Innovación, Spain).

Data availability The data are publicly available in Zenodo https://doi.org/https://doi.org/10.5281/zenodo.10611074

Declarations

Conflict of interest The contact author has declared that none of the authors has any competing interests.

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