What feeds on *Quercus ilex* L.? A biogeographical approach to studying trophic interactions in a Mediterranean keystone species

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Abstract

**Aim:** Holm oak (*Quercus ilex* L.) is regarded as a keystone plant species. Trophic interactions may affect the distribution and abundance of phytophagous species, but the number of arthropod species that use holm oak as a food resource and their levels of host specificity are not yet known. Here, we aimed to quantify these species, their feeding strategies and conservation status, the taxonomic relatedness in each trophic guild and their degree of host specificity on holm oak.

**Location:** Our study covered the whole distribution area of *Q. ilex* in the central-western Mediterranean Basin.

**Methods:** We reviewed the existing literature and compiled information about all arthropod species that feed on *Q. ilex*, as well as their feeding strategies and conservation status. We also investigated the relationships between trophic guilds and the taxonomic relatedness of species, and assessed the degree of climatic niche overlap with holm oak.

**Results:** We found that 605 species feed on seven different parts of the holm oak plant (*i.e.* feeding strategies). More than 90% of these species lack a conservation status assessment, and eight are threatened by human activities, either as vulnerable, endangered or critically endangered. A significant phylogenetic relationship was found between taxonomic relatedness and groups of arthropods that feed on the same part of the plant (*i.e.* trophic guilds). Twenty per cent of the species had similar niches, thereby indicating the potentially high host dependence of these species.

**Main conclusions:** This study highlights the significance of a keystone tree species for arthropod conservation and the need for further research into the distribution and conservation status of arthropod species in Mediterranean holm oak woodlands.

**Keywords**

arthropod biodiversity, climatic niche, feeding strategy, IUCN red list, phytophagous species, trophic guild
The concept of keystone species was first proposed by Paine (1966) who suggested that certain species have impacts on many others, and often far more than those expected considering their biomass or abundance (Simberloff, 1998). Keystone species are distributed among various trophic guilds, including carnivores (Paine, 1969) [e.g. grey wolf (Canis lupus) or sea otter (Enhydra lutris) (Hale & Kropowski, 2018)], herbivores (Poelmann & Kessler, 2016) [e.g. white-tailed deer (Odocoileus virginianus) (Waller & Alverson, 1997) and long-spined sea urchin (Diadema antillarum) (Lessios et al., 2001)], detritivores [e.g. Marion flightless moth (Pringleophaga marioni) (Haupt et al., 2014)] and primary producers (Terborgh, 1986) [e.g. Azorella selago (Nyakatya & McGeoch, 2008) and saguaro (Carnegiea gigantea) (Drezner & Balling, 2008)].

Among primary producers, species such as Acacia peuce, Vachellia erioloba and Vachellia haematoxylon can be considered keystone species in arid or semi-arid ecosystems (Nano et al., 2012; Shadwell & February, 2017; Tews et al., 2004). Large isolated trees belonging to these species can ameliorate harsh climatic conditions (Joffre et al., 1999) and increase soil nutrient levels (Joffre & Rambal, 1993; Munzbergova & Ward, 2002), plant species richness (Guevara et al., 1992) and structural complexity, as well as provide habitats for animals (Manning et al., 2004). Other trees that are considered keystone species include Quercus douglasii, Sclerocarya birrea, Quercus griffithii, Schinziopython rautanenii, Corymbia calophylla and Populus tremula (Chidumayo, 2016; Helm & Witkowski, 2012; Kivinen et al., 2020; Paap et al., 2017; Rice et al., 1993; Singh et al., 2015). They provide resources (Messeder et al., 2020) and shelter to a large number of bird, mammal and insect species, some of which have a high degree of host specificity, that is specialization on host species used by phytophagous species (Ødegaard, 2004; Wardhaugh, Stork, & Edwards, 2013, 2014). Given the importance of these species for biological communities and considering the ongoing biodiversity crisis, conservation biology needs to devote more attention to identifying and conserving keystone species (Jordán, 2009).

The holm oak, Quercus ilex (Linneo, 1753), is considered a keystone tree species in the central-western Mediterranean Basin (Carnicer et al., 2014; Pérez-Ramos et al., 2013; Sirami et al., 2008). Holm oak not only represents a dominant species in Mediterranean woodlands and maquis vegetation, but can also form mixed stands throughout its distributional range (de Rigo & Caudullo, 2016). Holm oak forests have been reported to harbour high biodiversity in several taxa, including ectomycorrhizal fungi (Richard et al., 2005),lichens (Loppi & Frati, 2004) and plants (Diaz et al., 1997; Ihaddaden et al., 2013). Similar to other Quercus species in Mediterranean ecosystems, holm oak is suffering from the effects of a disease produced by the invasive oomycete Phytophthora cinnamomi (Brasier, 1996), which may have been increasing mortality since the 1980s (de Sampaio e Paiva Camilo-Alves et al., 2013). Holm oak-dominated dehesas (“human-made” ecosystems characterized by a savanna-likephysiognomy used to maintain livestock and hunting activity, and to obtain other forest products) are also home to a large number of protected species (Diaz et al., 1997). In addition, holm oak may be an important trophic resource for various groups of organisms. In particular, Ruiz-Carbayo et al. (2017) identified 24 Lepidoptera species that feed on Q. ilex in Spain, and 86 saproxylic beetle species were reported to feed on holm oak trunks in France (Sirami et al., 2008). However, at present, it is not known how many arthropod species feed on Q. ilex, as well as the trophic guilds in which they are organized, or their host specificity.

It has been proposed that trophic guilds (i.e. a group of organisms with a similar feeding strategy) are phylogenetically conserved (Potapov et al., 2019). In arthropods, a relationship is expected between feeding strategies and taxonomy because feeding is known to be a significant driving force associated with evolutionary morphological changes (Maas et al., 2007). This relationship has been demonstrated in different families or orders of insects that preferentially feed on flowers, leaves, wood, fruits or sap, but mostly in tropical environments (Novotny et al., 2010; Wardhaugh, Stork, & Edwards, 2013, 2014). In addition, host specificity (i.e. the degree of host dependence) may affect the distribution of phytophagous insects, with highly specialized species exhibiting distributional ranges that are enclosed within the range of their host (Arnal et al., 2019; Du et al., 2020). In these cases, the climatic niche of the phytophagous species is expected to be constrained by that of the tree host. Host specificity has been shown to vary among arthropods with different feeding strategies ranging from the most specialized group comprising granivores to the least specialized group comprising root feeders (Novotny & Basset, 2005).

In this study, we aimed to review the importance of Q. ilex as a trophic resource for arthropods. In particular, our specific goals were as follows: (a) to quantify how many arthropod species feed on holm oak (Q. ilex L.), as well as assessing their feeding strategies and conservation status throughout its distributional range; (b) to investigate the relationships between trophic guilds and the taxonomic relatedness of species; and (c) to assess the degree of host specificity for phytophagous arthropod species that feed on holm oak by comparing their feeding strategies across climatic niches. We hypothesized that: (a) Q. ilex will provide food resources for a high number of arthropod species, thereby confirming its role as a keystone species; (b) closely related species will have similar feeding strategies compared with distantly related species in accordance with the “taxonomic signal” hypothesis (Potapov et al., 2019); and (c) host specificity will be widespread among arthropods that feed on holm oak, but higher for the most specialized feeding groups, such as acorn feeders. To the best of our knowledge, no previous studies have reviewed how many arthropod species feed on a keystone tree species in this much detail, and those that focused on investigations of trophic guilds were mostly conducted in tropical environments (Novotny et al., 2010; Wardhaugh et al., 2013, 2014). Trophic interactions are likely to fundamentally affect the distribution and abundance of organisms, so our results may provide a baseline and important insights regarding arthropod conservation in Mediterranean holm oak woodlands.
2 | MATERIALS AND METHODS

2.1 | Study species

Holm oak is a widespread tree or shrub, which has been historically managed as coppice forests or in pastures with large isolated trees (i.e., dehesas) where livestock feed on grass and acorns (Díaz et al., 1997). It can be found in the central-western part of the Mediterranean Basin from coastal zones to up to 1,800 m.a.s.l. in southern Spain or 2,900 m.a.s.l. in the High Atlas (Rigo & Caudullo, 2016). It is a shade-tolerant species and can grow in semi-arid to very humid climates.

Holm oak refers to two currently accepted species names comprising *Quercus ilex* L. and *Q. rotundifolia* Lam (Ferrer-Galego & Sáez, 2019). The latter is mostly distributed in the western Mediterranean, including the Iberian Peninsula and Morocco. There is a consensus that the morphological variation in these trees is very high and the taxonomic characters typically used to separate these two species (related to the shape, toughness and spinescence of the leaves) are extremely plastic, and thus of very limited value in taxonomy. Therefore, this complex was resolved at the subspecies level in the Iberian Flora (Castroviejo et al., 1990), where *Q. ilex* subsp. *ilex* L. is found in areas with a greater oceanic influence and *Q. ilex* subsp. *ballota* (Desf.) Samp. (*Q. rotundifolia*) is found in inland zones. Therefore, we use *Q. ilex* sensu lato to refer to either of these taxonomical interpretations at the species level (*Q. rotundifolia*) and/or the subspecies level (*Q. ilex* subsp. *ballota*).

2.2 | Study area

Our study covered the whole distribution area of *Q. ilex* in the central-western Mediterranean Basin (Figure 1), which is considered a major biodiversity hotspot (Myers et al., 2000). This area is characterized by a Mediterranean climate, with mild wet winters and warm-to-hot, dry summers (Lionello et al., 2004), and high human usage during the last 300 human generations (~7,500 years). This human usage is mainly characterized by forest management, agriculture and livestock production, or landscape modification, which led to the disappearance of 85% of the potential forest area (Blondel, 2006).

2.3 | Literature search

To quantify how many arthropod species feed on *Q. ilex* and assess their feeding strategies and conservation status (goal 1), we conducted a literature search using Google Scholar, Dialnet, ResearchGate and Web of Science with pairwise combinations of the following two groups of keywords: “insect,” “invertebrate” and “arthropod,” and “Quercus ilex,” “Quercus rotundifolia,” “holm oak” and “evergreen oak,” in English and the equivalent French, Italian or Spanish terms. These languages are spoken in at least eight out of the 17 countries where the holm oak is found, and they cover more than 90% of its distribution area. We reviewed all papers retrieved from the literature search and excluded studies that did not specifically report trophic interactions between arthropod species and *Q. ilex* regardless of the region where the study was conducted. We did not include pollinators in this study because *Q. ilex* is an anemophilous species. In addition to the literature search, we: (a) examined all references in the selected publications; (b) browsed all articles published in “Boletín de Sanidad Vegetal y Plagas,” which is a Spanish journal published between 1975 and 2012 that focused on plant pest species, as well as all volumes of “Fauna Iberica” and “Faune de France” referring to terrestrial arthropods; and (c) reviewed all books available in the Rey Juan Carlos University (URJC), Madrid Autonomous University (UAM) and Madrid Polytechnic University (UPM) libraries covering aspects related to the feeding ecology of arthropod species in the Mediterranean region, including field guides. We annotated the parts of the plant consumed and geographical coordinates of the locations where arthropod species were recorded feeding on holm oak when available. We assumed that the identifications provided in the cited papers were correct without independent corroboration, although we checked for synonyms to avoid duplicating data. Finally, we conducted a search in the International Union for Nature Conservation (IUCN) Red List database (www.iucnredlist).

![FIGURE 1 Study area and distribution of Quercus ilex (in green) based on Beck et al. (2020). Red dots represent the locations of studies that reported trophic interactions between holm oak and arthropod species based on our literature search. Dots outside the distributional range of Quercus ilex represent interactions in ornamental holm oaks.](image)
org) to retrieve information about the conservation status of each species found in our literature search.

2.4 Investigating the relationships between trophic guilds and taxonomic relatedness

To investigate the relationships between trophic guilds and the taxonomic relatedness of species (goal 2), we conducted both phylogenetic and cluster analyses. We identified seven different feeding strategies: gall feeders (i.e. species that produce and feed via galls in leaves or stems), leaf feeders (including species that feed on both dead or living leaves and sprouts), wood feeders (including both xylophagous and saproxylic species that feed on trunks and stems), acorn feeders, sap feeders, root feeders and flower feeders.

We used the $\delta$ statistic (Borges et al., 2019) to test whether the feeding strategy was phylogenetically conserved. This metric measures the entropy contained in ancestral inferences in order to translate the principle of a phylogenetic signal into categorical data. Ancestral reconstructions using categorical data return the probability of each trait category occurring in each node (Borges et al., 2019).

The $\delta$ statistic can be any positive real number, where a higher value indicates that the degree of a phylogenetic signal is higher between a given trait and the phylogeny. We used the phylogenetic tree published by Chesters (2017) and pruned it to include the phytophagous species associated with Q. ilex for which we had trophic information. To test for the statistical significance of $\delta$, we randomized the feeding strategies of arthropods across the phylogenetic tree tips 200 times and compared the measured $\delta$ statistic ($\delta_{\text{obs}}$) with the simulated statistic ($\delta_{\text{sim}}$) to calculate a $p$-value.

We then conducted hierarchical cluster analysis to analyse the similarities of the feeding strategies among genera and to establish trophic guilds. The proportions of taxa with each feeding strategy were estimated at the genus level. We only used those genera and feeding strategies with more than three species for the analysis. If a species had more than one feeding strategy, we counted that species several times rather than using fractional assignment. Clustering was performed using the Manhattan dissimilarity measure and Ward’s algorithm (Strauss & von Maltitz, 2017), and the optimal number of clusters was determined with the R package “factoextra” (Kassambara & Mundt, 2017) based on the k-means method with 999 bootstrap replicates (Monte Carlo resampling simulation).

2.5 Environmental niche analysis

To assess the degree of host specificity for phytophagous arthropod species that feed on holm oak (goal 3), we estimated the climatic niche of both the holm oak and each arthropod species found in the literature search and calculated their climatic niche overlap. To achieve this, we downloaded the geographical coordinates of all records available for Q. ilex and Q. rotundifolia and their phytophagous arthropod species from the Global Biodiversity Information Facility (GBIF) using the R package “rgbif” (Chamberlain et al., 2020). The downloaded data were curated using the R package “CoordinateCleaner” (Zizka et al., 2019), which removed (0, 0) coordinates, sea coordinates and incorrect geolocations, such as records allocated to the centroids of countries or institutions where specimens were stored (e.g. herbaria at botanical gardens or universities), country capitals and identical coordinates (Figure 2). In addition, coordinates were aggregated to the resolution of the climatic variables (2.5 arc min) to avoid overrepresentation of locally clustered species records.

The climatic niche of each arthropod species and the holm oak was calculated for the same area, which encompassed most of Europe (excluding the northernmost part), northern Africa and western Asia, (24°N–60°N/18°W–42°E; Figure 1), and it included the entire distribution of holm oak. We downloaded 19 climatic raster layers from the WorldClim database (Hijmans et al., 2005) with a resolution of 2.5 min. We conducted principal component analysis (PCA) with all climatic variables across the entire study area (bounded area shown in Figure 1) using the R package “ade4” (Dray & Dufour, 2007) based on the method proposed by Broennimann et al. (2012). The first two PCA axes were used to quantify the observed climatic niches of species by creating a bidimensional representation of the environmental variables based on the 2.5-arc-min grid cells with records of species occurrences (Figure 2). To accurately estimate the climatic niches of species, we only used those species present in at least 30 cells (Franklin, 2010; Supplementary Material 1), with a total of 294 species. We evaluated the climatic niche overlap between holm oak and its phytophagous species using the R package “ecospat” (Figure 2; Broennimann et al., 2020). We ran similarity analyses to test the overlap of two niches using the D metric proposed by Schoener (1968), which ranges between 0 (no overlap) and 1 (complete overlap). Based on this metric, a similarity test was conducted with function “ecospat.niche.similarity.test” in R (Broennimann et al., 2020) to determine which of the arthropod species distributions was explained by the holm oak distribution (a host dependence relationship) (Warren et al., 2008). This analysis was conducted based on the assumption that climate is the main driver of species distribution, although it is important to consider that other factors can also affect species distribution, including abiotic factors such as soils, or biotic factors such as predators or competitors (Gaston, 2003). This similarity test comprised a background test to assess whether two niches were more or less similar than expected by chance. A permutation approach (using 100 permutations) was employed to assess the significance of tests, where a $p$-value > .05 indicated that niches were no more similar than expected by chance (i.e. different). We considered that the host specificity of an arthropod species was holm oak when the similarity test between the host and phytophagous species obtained a value that differed significantly from that expected by chance ($p$-value < .05) (Figure 2). This approach has been used widely in previous studies of patterns of future species stability (Molina-Henao & Hopkins, 2019), predictions of suitability for...
invasive species (Beukema et al., 2018; Zemanova et al., 2018), spatial differentiation of subspecies (Ashrafzadeh et al., 2018), comparisons of climatic niches for species under present and future scenarios (Hamid et al., 2019), and assessing phytophagous species–host niche overlap (Arnal et al., 2019).

Finally, we fitted a generalized linear model with a beta error distribution to test for differences in Schoener’s D metric among feeding strategies in order to assess differences in host specificity between feeding guilds. This analysis was conducted with the R package “betareg” (Cribari-Neto & Zeileis, 2010).

3 | RESULTS

3.1 | Literature search

We identified 605 species from 342 genera, 90 families and eight arthropod orders (Table 1; Hernández-Agüero et al., 2021) based on 198 sources found during the two years of consult (Figure S2a), including research papers (69%, \( n = 136 \)) and books (31%, \( n = 62 \)) (Supplementary Material 2: Figure S2c), with 271 (44.8%) species cited in research papers, 269 (44.4%) in books, and 75 (12.3%) in both sources. (A list of the data sources is found in Appendix 1.) We found bibliographic information from 17 different countries, where the highest number of sources came from Spain, followed by France and Italy (Figure S2b), which corresponds to the countries with the largest holm oak distributions (Figure 1).

![FIGURE 2 Workflow diagram illustrating the niche overlap analysis conducted in this study, data preparation and the possible outcomes in terms of similarity](image)

![TABLE 1 List of arthropod orders that feed on holm oak and families with the highest number of species. Numbers of species and their percentage relative to the total (605) are also presented for both orders (left) and families (right)](table)

| Order         | Most common families | Number of species | % of species |
|---------------|----------------------|-------------------|--------------|
| Coleoptera    | Cerambycidae         | 72                | 11.86        |
|               | Curculionidae         | 50                | 8.24         |
|               | Chrysomelidae         | 42                | 7.24         |
|               | Buprestidae           | 35                | 5.77         |
| Lepidoptera   | Geometridae           | 27                | 4.45         |
|               | Erebidae              | 20                | 3.29         |
|               | Noctuidae             | 16                | 2.64         |
| Hemiptera     | Miridae               | 32                | 5.27         |
|               | Aphididae             | 22                | 3.62         |
| Hymenoptera   | Cynipidae             | 75                | 12.39        |
| Trombidiiformes| Cynipidae             | 35                | 5.77         |
| Diptera       | 12                    | 1.98              |
| Psocoptera    | 2                     | 0.33              |
| Blattodea     | 2                     | 0.33              |
| TOTAL         | 605                   |                   |              |
Among the 605 species found to feed on Q. ilex, 71 (11.73%) were included in the IUCN Red List with assessments conducted at the global (n = 11), European (n = 66) or Mediterranean geographical scope (n = 33) (Hernández-Agüero et al., 2021). At the global geographical scope, three species were identified as data deficient (DD), four as least concern (LC), two as near threatened (NT) and two as vulnerable (VU) (Table 2). At the European geographical scope, four species were identified as DD, 49 as LC, seven as NT, three as VU, two as endangered (EN) and one as critically endangered (CR). Finally, at the Mediterranean geographical scope, two species were identified as DD, 26 as LC, three as NT, one as EN and one as CR (Table 2).

3.2 | Feeding strategies

Among the 605 species included in this study, we obtained information about the feeding strategies of 527 species, where 42% fed on leaves (n = 222), 31% on wood (n = 164) and 13% on galls (n = 70), and 9% were sap feeders (n = 45). The remaining 5% of the species fed on flowers (n = 16), acorns (n = 10) and roots (n = 2). We found that 98% of the species fed only on one part of the Q. ilex plant, 1.3% on two parts and 0.5% on three or more parts. The pruned phylogenetic tree contained 205 out of the 527 species for which we obtained information about their feeding strategies (Figure 3). A strong phylogenetic signal was associated with feeding strategies (δ̄ = 1.582, δlim 95% confidence interval = 0.881–1.179, p-value = 0.005).

Based on the feeding strategies of the different genera, we identified six major clusters (trophic guilds) with Ward’s clustering algorithm. One of the two main partitions split into two clusters dominated by leaf feeders (Figure 4, purple and blue) in genera from Coleoptera (Cryptocephalus, Polydrusus, Rhynchites, Coeloides, Smaragdina, Pachyrachis, Lachnaia and Labidostomis), Lepidoptera (Catocala, Phyionoryctery, Eupithecia, Stigmella, Ectoedemia and Dryobotodes) and Hymenoptera (Pericolista). The second partition split into four clusters encompassing wood feeders in genera (Figure 4, green) in genera from Hemiptera (Myzocallis and Kerme); acorn feeders (Figure 4, brown) in genera from Trombidiformes (Aceteria), Lepidoptera (Cydia) and Coleoptera (Curculio); and gall feeders (Figure 4, pink) in genera from Hymenoptera (Plagiotochus, Andricus, Mesopolobus and Synergus) and Diptera (Contarinia). Flower feeders did not constitute a cluster but they were present in others.

3.3 | Environmental niche analysis

Records were available in the GBIF for 491 (80%) of the 605 arthropod species that feed on Q. ilex, but only 294 species had a sufficiently high number of records (n > 30, ~48%) to reliably estimate their environmental niche, with a range between 31 and 13,149 records, and a mean of 1,136 coordinates per species. The first and second principal components obtained by PCA explained 64.63% and 17.65% of the climatic variation, respectively. Only 53 (18.02%) of the species studied had similar climatic niches (p-value < .05) to Q. ilex (see Figure 5 for an example). All of the climatic niche analysis results are available in Supplementary Material 3.

Finally, we found no statistically significant differences in the degree of overlapping with the climate niche of holm oak among arthropod feeding strategies (p-value = 0.275).

| Species               | Global | European | Mediterranean |
|-----------------------|--------|----------|--------------|
| Alocerus moesiacus    |        | NT       |              |
| Alocerus siculus      |        | CR       | CR           |
| Bothrideres interstitialis |    |          | EN           |
| Brachygonus megerlei  |        |          |              |
| Calchaenesthes sexmaculata |  NT | EN       | NT           |
| Cerambyx cerdo       | VU     | NT       | LC           |
| Cerambyx dux          |        | NT       | LC           |
| Cerambyx miles        |        | NT       | LC           |
| Cerambyx welensi      |        | NT       | NT           |
| Chlorophorus javieri  |        | NT       | NT           |
| Lichenophanes varius  |        | NT       |              |
| Nectalis ulmi         |        | VU       |              |
| Pachyta iamed         |        | VU       |              |
| Pedostrangalia revestita |  VU | VU       |              |
| Stictoleptura oblongomaculata |  |          | EN           |

Abbreviations: CR, critically endangered; EN, endangered; NT, near threatened; VU, vulnerable.

TABLE 2  List of species evaluated under the IUCN Red List criteria at different geographical scopes (global, European and Mediterranean), excluding the data deficient (DD) and least concern (LC) categories.
Based on our literature analysis, we found more than 600 species that feed on holm oak (Q. ilex). More than 90% of the species lack a conservation status assessment, where only 71 of the species were found in the IUCN Red List, with 56 in the DD category. Among the other 15 species, eight species are threatened by extinction at either global, European or Mediterranean geographical scopes. Most of the species feed on leaves, wood, sap or galls, and about 20% of the arthropod species were found to have niche similarity to holm oak, but we detected no differences in niche overlap between feeding strategies.

4.1 | Arthropod species that feed on holm oak

Tropical tree species can sustain a high number of arthropod species. For example, the number of phytophagous Coleoptera species...
found on *Brosimum utile* in tropical forests across the Neotropics was estimated as ca. 900 (Ødegaard, 2004), which contrasts with the 250 Coleoptera species found in our study. However, the amounts of species are much lower in temperate ecosystems. For example, based on a literature review, it was proposed that two oak species in the UK can support ca. 300 insect herbivore species (Southwood, 1961). However, in the present study, we found that over twice that amount of species feed at least partially on *Q. ilex*, thereby indicating a high level of biodiversity, at least compared with other oak species in temperate ecosystems. This number should not be treated as the actual amount because many species have yet to be formally described and catalogued (Whittaker et al., 2005), while others may have not been observed feeding on holm oak and/or reported in the scientific literature, and finally, our knowledge of the global, regional and even local distributions of many taxa, particularly arthropods, is far from being complete (Lomolino, 2004). In addition,
it should be noted that each arthropod species that feeds on holm oak can easily attract an average of 5–15 parasitoids and predators (Price, 2002), and thus, the number of arthropod species indirectly supported by holm oak woodlands might potentially range between 3,650 and 9,750 based on current figures for known taxa. This estimate only considers direct and indirect trophic interactions, and it could be higher if we consider species that use holm oak for shelter. *Q. ilex* is also known to be suitable for the establishment of other non-arthropod species, including lichens (Loppi & Frati, 2004), fungi (Richard et al., 2005) and vertebrates (Díaz et al., 1997). Overall, our results support the role of holm oak as a keystone tree species in Mediterranean ecosystems, as shown in previous studies (Carnicer et al., 2014; Pérez-Ramos et al., 2013; Sirami et al., 2008).

### 4.2 Is there a relationship between the degree of feeding strategies and taxonomic relatedness of species?

Our results indicated a relationship between the feeding strategies and taxonomic relatedness of species, and this is in agreement with the "taxonomic signal" hypothesis, which suggests that closely related species have more similar species’ traits compared with distantly related species (Potapov et al., 2019). However, our results indicated some variability in the phylogenetic composition of some trophic guilds, especially between acorn feeders, possibly as a response to strong trophic competition within taxonomically related species only allowing the coexistence of some phytophagous species, that is only 10 species in our study. This can be explained by the "limiting similarity" hypothesis (Potapov et al., 2019). Thus, many taxonomic groups seem to have developed specialized feeding strategies, such as Buprestidae, Cerambycidae and Cynipidae, whereas others have not, including Curculionidae.

The two trophic guilds of leaf feeders mostly comprised genera from Coleoptera and Lepidoptera, as well as one genus from Hymenoptera (Figure 4). These results are similar to those obtained by Novotny et al. (2010) in tropical forests, although they also found a substantial number of Orthoptera and Phasmatodea species with the leaf-feeding strategy, whereas these orders were not found to feed on holm oak. The trophic guild dominated by wood feeders in our study mostly comprised genera from Coleoptera in a similar manner to previous studies conducted in tropical forests (Novotny et al., 2010; Wardhaugh et al., 2013). The use of wood as a food resource appeared to be dominated by this order of insects. Indeed, dehesas (the most representative holm oak ecosystem) are considered a key ecosystem for saproxylic feeders (Ramírez-Hernández et al., 2014), and this might explain why we detected a disproportionate number of species that feed on this resource (wood) compared with other holm oak plant parts. In addition, the wood obtained from holm oak is economically important and much research has been conducted to minimize the economic losses caused by insect pests during its production. The trophic guild dominated by sap feeders entirely comprised Hemiptera species. A previous study also found that Hemiptera species are the most important sap feeders in tropical forests (Novotny et al., 2010), probably due to the highly specialized structures that they have evolved to obtain this resource (Goodchild, 1966). In contrast to our findings for other trophic guilds, the guild dominated by acorn feeders did not exhibit a taxonomic clustering pattern. The number of species that feed on this resource was relatively low and most belonged to three genera. The gall feeder trophic guild is extensive on holm oak (see references by Nieves-Aldrey in Hernández-Agüero et al., 2021), and we found that it mainly comprised genera from Cynipidae, a highly specialized family in the production of galls. Flower feeders did not constitute a trophic guild. Root feeders were not considered in our analysis due to the low number of species found, and the lack of literature regarding this trophic guild might have led to underestimation of the proportion of species that use this resource. However, it has been shown that this trophic guild has the lowest level of host specificity (Novotny & Basset, 2005).

### 4.3 Does environmental niche overlap occur between holm oak and phytophagous arthropods?

Among the 294 species considered for niche analysis, we found that 53 (18.02%) exhibited niche similarity to holm oak. Niche similarity indicates climatically driven species co-occurrence patterns that might be caused by different underlying ecological processes. For example, some of the arthropod species that exhibited niche similarity to holm oak might depend entirely on this resource because they have developed specificity for this host as a resource, for example *Satyrium esculi* or *Plagiotochus quercusilicis*. In contrast to our expectations, no differences in niche overlap were detected between feeding strategies, although this pattern might have been obscured by: (a) the lack of relevant data for specific trophic guilds such as root feeders, which typically exhibit less host specificity (Novotny & Basset, 2005); and (b) the possible influence of microhabitats on arthropods niches, which could not be accurately depicted with the spatial resolution of the WorldClim climatic layers used in this study.

### 4.4 Prospects for arthropod conservation

*Quercus ilex* is currently threatened by the invasive fungal species *Phytophthora cinnamomi* (Brasier, 1996; de Sampaio e Paiva Camilo-Alves et al., 2013), drought-induced tree mortality (Gea-Izquierdo et al., 2011), lack of regeneration (Plieninger et al., 2010; Pulido & Díaz, 2005) and land use changes (de Rigo & Caudullo, 2016). These threats have reduced the distribution of holm oak to ca. 22% of its potential distribution, at least in the Iberian Peninsula (Felícísimo et al., 2012). Thus, our results highlight the vulnerability of arthropod species that feed on this keystone species, particularly for species with small geographical ranges or population sizes. However,
details are lacking regarding basic aspects of the ecology of most arthropod species, such as where a species is found, which contrasts sharply with other groups such as mammals, birds, reptiles and plants (Cardoso et al., 2011). Thus, insufficient data were available to reliably describe the distributional ranges of more than 50% of the arthropod species. The lack of information was even more obvious when we considered the conservation status of the arthropod species because conservation status assessments were not available for over 90% of the species. Among the 71 species with full conservation assessments, 15 were threatened by extinction at global, European or Mediterranean geographical scopes, and thus, it is reasonable to assume that the number of threatened arthropod species was vastly underestimated in our study (Cardoso et al., 2020).

5 | CONCLUSIONS

Holm oak supports a huge number of arthropod species, thereby supporting its role as a keystone species in Mediterranean woodlands. In general, closely related species have similar feeding strategies compared with distantly related species, which supports the “taxonomic signal” hypothesis (Potapov et al., 2019). Finally, we found a moderate degree of host specificity among arthropods that feed on holm oak (ca. 20% of the species), and contrary to our expectations, we did not identify higher host specificity in the most specialized feeding groups. Overall, this study provides novel insights and offers a quantitative approach to identify keystone species important for conservation purposes, particularly in the current context of ongoing biodiversity crisis. However, further research is needed in many aspects of arthropod ecology, including the distributional ranges of species, degree of habitat specialization, population sizes and network analysis. Many arthropod species that thrive in holm oak woodlands might be at risk of extinction, and they could become extinct in the near future if the current threats to holm oak persist.

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CONFLICTS OF INTEREST

The authors confirm to not have any interest conflicts.

PEER REVIEW

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All of the data and R scripts used in this study are available at Dryad (Hernández-Agüero et al., 2021): https://doi.org/10.5061/dryad.r2280gbdg.

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Supporting Information
Additional supporting information may be found online in the Supporting Information section.

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Appendix 1

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