



A snapshot in time: composition of native primary fauna of gall wasps in Spanish contact zones with chestnut trees infested by *Dryocosmus kuriphilus*

Research Paper

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Abstract

One of the most prominent problems related to biological invasions is the variation of local species composition, which often leads to *ex novo* interspecific interactions. Here, we explored and analysed the native species composition of gall inducers and their associated parasitoids and inquilines in Spanish areas invaded by *Dryocosmus kuriphilus* Yasumatsu 1951 (Hymenoptera: Cynipidae), an invasive pest of chestnut trees. After a quantitative description of these species' assemblages, we analysed through bipartite networks the level of the trophic specialisation of parasitoids and inquilines when considering either the host taxonomic identity, the host plant species or the host gall morphological type. We sampled galls of *D. kuriphilus* and native species of Cynipidae in different Spanish areas, including those where the exotic parasitoid *Torymus sinensis* Kamijo 1982 (Hymenoptera: Torymidae) had been released for *D. kuriphilus* biological control. The results indicate that the native parasitoids recruited by *D. kuriphilus* come almost exclusively from native communities on *Quercus* galls, except for one species from *Rosa*. Galls of *D. kuriphilus* had the second most diverse species composition; despite this species assemblage arose *ex novo* in less than a decade. The bipartite networks resulted more specialised when considering host plant taxa than when gall types and the host taxa were accounted. In such trophic webs, there were few parasitoid/inquiline specialist and many generalist species, which agrees with the rapid recruitment by *D. kuriphilus*. Higher parasitoid species richness in *D. kuriphilus* galls is likely due to their being a largely unexploited available resource for the native natural enemies of cynipid wasps.

Introduction

Exotic and invasive species are one of the most important drivers for biodiversity loss (Vitousek *et al.*, 1997; IPBES, 2019). The introduction of an alien species in a non-native area can produce different types of biological perturbations, such as an increased species competition, overpopulations and greater pest damages, and changes in trophic interactions (Pyšek and Richardson, 2010; Mollot *et al.*, 2017). A new species established in an area is a new component in a biological system and may potentially alter interactions between native fauna and flora. These *ex novo* interactions can result in competition for species by a resource (Brown *et al.*, 2002; MacDougall and Turkington, 2005) or the generation of new top-down and bottom-up dynamics with the native flora and fauna (Keeler *et al.*, 2006; Strange *et al.*, 2019). An example of these new interactions is the recruitment of species, i.e. the emergence of *ex novo* trophic interactions among a community founder species and native taxa that exploit it as a resource (Tecco *et al.*, 2006; Matošević and Melika, 2013). In this case, the community founder – e.g. an invasive species – becomes a new component of food webs whose relationships with other species were not established until the time of recruitment. Hence, although exotic species are often considered more invasive when producing an economic or health damage than when producing ecosystem disturbance (Pimentel *et al.*, 2005), their alterations of within-community species interactions can be detrimental (Pyšek *et al.*, 2020).

On the other hand, species can be categorised according to their trophic niche width, i.e. the number of taxa or functional groups of taxa that they can consume (Bearhop *et al.*, 2004; Olsson *et al.*, 2009). Thus, we can set generalists (euryphagous or with a wide trophic range) or specialists (stenophagous or with a narrow trophic range). For parasitoids and parasites, such trophic range corresponds to the host range (Askew, 1971; Quicke, 1997), and because many of these organisms are trophically specialised (Futuyma and Moreno, 1988; Agosta *et al.*, 2010), it

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is relevant to study their recruitment patterns and specifically by invasive host species. We can hypothesise, for example, that the more generalist species are the first to be recruited and the most represented in the newly formed trophic webs and that the more specialist species will be more rarely recruited by the alien species. Here, we explored and analysed the species composition of gall inducers and their associated parasitoids and inquiline in Spanish areas invaded by *Dryocosmus kuriphilus* Yasumatsu 1951 (Hymenoptera: Cynipidae), an invasive galling pest of chestnut trees.

D. kuriphilus is a pest of *Castanea* and its galls cause important economic losses (Battisti *et al.*, 2014) as well as the deterioration of the quality and vigorosity of the trees (Gehring *et al.*, 2020), leading to a serious concern on the chestnut production sector, which is already facing tree disorders such as blight or ink disease (Vannini and Vettrano, 2001; Rigling and Prospero, 2018). This species belongs to the so-called gall wasps, which are secondarily herbivorous hymenopterans characterised by the induction (or in some cases the usurpation (inquilinity) (Ronquist, 1994)) of particular structures on plants called galls, in which the larvae feed and develop (Nieves-Aldrey, 2001; Stone *et al.*, 2002). Apart from inquiline cynipids, the galls are also attacked by a variety of hymenopteran parasitoid species in the superfamilies (Chalcidoidea and Ichneumonoidea), which use the host larvae to feed their own brood (Askew *et al.*, 2006, 2013).

In the areas where it has been introduced, *D. kuriphilus* has recruited several native parasitoid species from the close native cynipid communities (Aebi *et al.*, 2006; Matošević and Melika, 2013; Quacchia *et al.*, 2013; Bonsignore *et al.*, 2020; Gil-Tapetado *et al.*, 2021a). It is noteworthy that in the Western Palearctic, chestnut trees did not possess any associated or gall-inducing cynipid species. Hence, the arrival of *D. kuriphilus* is producing a new biological community, which has been rapidly formed through the 'emerged islands-on-mainland effect' (Gil-Tapetado *et al.*, 2021a). Together with the recruited native parasitoid species, the galls of *D. kuriphilus* are also attacked by *Torymus sinensis* Kamijo 1982 (Hymenoptera: Torymidae), which has been also introduced in many infested regions to control this pest (Quacchia *et al.*, 2008; Borowiec *et al.*, 2018) or has colonised areas with *D. kuriphilus* close to other areas where *T. sinensis* has been released (Nieves-Aldrey *et al.*, 2019). This parasitoid is not only forming part of the chestnut pest communities but is engaging in new interspecific relationships with native gall wasp species (Ferracini *et al.*, 2017, 2018; Gil-Tapetado *et al.*, 2023). Thus, the native species composition of parasitoids and inquilines associated with *D. kuriphilus* and with native gall wasps provides a 'snapshot in time' of the status of these species during the first years of establishment of an invasive species that is essentially developing an *ex novo* community. Previous contributions (Kos *et al.*, 2015; Jara-Chiquito *et al.*, 2020) reported a list of parasitoids found in both *D. kuriphilus* and native cynipid-gall communities in Slovenia and Catalonia (north-eastern Spain), respectively. Their results showed that the pest galls harbour a rich assemblage of species, often more than those found in the native wasp galls. However, these studies did not analyse the data in order to assess quantitatively how these associated faunas overlap or differ among the alien wasp and the native wasps.

Our study aims specifically to answer to the following questions: (1) which parasitoid/inquiline species have been actually recruited to date by *D. kuriphilus* in confluence zones with native cynipids? (2) How different is the overlap of parasitoid/inquiline diversity between *D. kuriphilus* and native fauna depending on

the cynipid taxa/host plant taxa? (3) Is host specialisation variation across parasitoid/inquiline species of the whole cynipid assemblage mostly driven by host wasp taxa, host plant taxa, or gall morphology? and (4) Are more generalist parasitoid/inquiline species more diverse and abundant in *D. kuriphilus* galls than specialist ones?

Materials and methods

Study area

Field samplings were carried out from May 2016 to May 2019 in different areas of Spain: in the north, northwest (Galicia), central area (Central System), and the south (Andalucía, mainly the province of Málaga). The northern and northwestern areas are characterised by an Atlantic and temperate climate (according to Peel *et al.*, 2007), with relatively high rainfall and mild temperatures, and with dominance of *Quercus robur* L. The area of the Central System is a mountain range in the centre of Spain, characterised by a milder climate than the northern and southern plateaus with their steppe climate, characterised by forests of *Quercus pyrenaica* Willd. The southern areas are related to humid valleys surrounded by mountain ranges with high rainfall, but with a typical Mediterranean climate, with more presence of *Quercus ilex* L. and *Quercus suber* L. than the other areas. All these areas have *Castanea sativa* trees and are known to be infested by *D. kuriphilus* (Gil-Tapetado *et al.*, 2018) and *T. sinensis* is also present there (Nieves-Aldrey *et al.*, 2019) (table S1; fig. S1), or with a high suitability for its establishment (as is the case in the areas of Andalusia other than Málaga) (following Gil-Tapetado *et al.*, 2018). In addition, we selected these areas because we previously studied the parasitoid and inquiline communities associated with *D. kuriphilus* (Gil-Tapetado *et al.*, 2021a). A total of 74 sites were sampled (see table S1) in at least 2 consecutive years.

Field sampling and collection of native cynipid galls

To evaluate the composition of parasitoid and inquiline species associated with native cynipid-gall species close to infested chestnuts with *D. kuriphilus*, we collected all the available galls in the nearest host plants of cynipid (fig. 1). We consider both parasitoids and inquiline species, as the primary fauna associated with gall inducer cynipids because they are found during the period of the gall wasp is present inside the gall, differentiating it from the secondary fauna, which is present after the emergence of the cynipid specimen. We collected all the galls within a buffer of 250 m around a centroid of the coordinates according to Gil-Tapetado *et al.* (2021a) by active sampling with two collectors in approximately 1 h by site, searching known host plants for Cynipidae. The galls were collected mainly from trees of *Q. robur*, *Quercus petraea* (Matt.) Liebl., *Quercus canariensis* Willd., *Q. pyrenaica*, *Quercus faginea* Lam. (grouped on section *Quercus*), *Q. ilex*, *Quercus coccifera* L. (grouped on *Q. ilex + cocc*), *Q. suber*, and *C. sativa* as well as from bushes of *Rosa* sp. and *Rubus* sp., and herbaceous *Asteraceae* of genera *Rhaponticum* Ludw. (= *Leuzea*) and *Centaurea*. These galls were collected, identified at the species level, shipped, transported under cold, and sorted by species of Cynipidae and sampling date in emergency card boxes, equipped with skylight extractors, under indoor room conditions. A total of 4484 galls of native Cynipidae were collected (table S2). Adult emerged primary



Figure 1. Galls of sampled native cynipid species: (A) *B. pallida*, (B) *An. curvator* (sex.), (C) *Andricus coriarius* (asex.), (D) *Andricus grossulariae* (asex.), (E) *An. hispanicus* (asex.), (F) *Andricus pictus* (asex.), (G) *Cynips quercus* (asex.), (H) *Neuroterus quercusbaccarum* (sex.), (I) *Trigonaspis mendesi* (asex.), (J) *Andricus quercusramuli* (sex.), (K) *Pl. quercusilicis* (sex.), (L) *An. crispator* (sex.), (M) *Diastrophus rubi*, (N) *Diplolepis rosae*, and (O) *Isocolus lichtensteini*. (A), (B), (G), (H), (K), (L), (M), and (O) species are examples of simple galls; (C), (D), (E), (F), and (I) of complex lignified galls; (J) and (N) of complex hairy galls. © J.L. Nieves-Aldrey.

fauna was collected, and specimens were stored in ethanol 70% and deposited in the Entomological Collection of the *Museo Nacional de Ciencias Naturales* of Madrid (MNCN-CSIC).

Cynipid-gall wasps, chalcid parasitoids, and cynipid inquilines were identified by the senior author using available taxonomic key references (De Vere Graham and Gisjwist, 1998;

Nieves-Aldrey, 2001; Gómez *et al.*, 2008) and unpublished information of Askew and Thüroczy (unpublished) and Nieves-Aldrey (unpublished).

Composition and diversity analyses

We computed our data as a compilation of information of primary fauna species from May 2016 to May 2019, which show a temporal framework of a snapshot of species composition of Chalcidoidea and Cynipidae, but not as a biological community, because our data are not sufficiently powerful to be able to separate the assemblages among the study areas. Although we cannot consider our data as a biological community, we use strategies of community analyses to obtain information about the species composition. The raw dataset is available in the Supplementary file DataSET.xlsx.

We used the abundance data of parasitoids by host species of Cynipidae as a dataset to investigate the recent species composition of these assemblages in the studied areas. To check that our data can be analysed at the level of diversity, that the number of samplings and galls collected are sufficient, and that the samples are representative, we first estimated the sampling effort. We performed this analysis at the individual level using a species accumulation curve based on the Chao2 estimator calculated with EstimateS 9.1.0 software. Biodiversity Estimation software (Colwell, 2013) and the smoothened Clench curve was calculated with CurveExpert Basic 2.0 (Hyams, 2020). We considered the following criteria as indicators for sufficient sampling effort and good sample quality: slope <0.1, registered species percentage >70%, and realised sampling effort >70%. Species accumulation curve indicates that at this level the data are representative and have a sufficient and high sampling effort, fulfilling all the above criteria (fig. S2).

We performed analyses of species aggrupation/segregation by the host plant of the Cynipidae using different Venn diagrams. These analyses show using coincident and exclusive compartments the aggrupation and segregation of species complex considering each host plant. As we focused on *D. kuriphilus*, we first compared the composition of primary fauna on this species with the galls of native species that are not presented in trees in a regular Venn diagram. Second, we performed another regular Venn diagram with the species on the galls of *D. kuriphilus*, on *Quercus*, and those of the previous Venn analysis. For a better result of the aggrupation/segregation of the primary fauna for each host plant, we performed a proportional Venn diagram showing the comparative size of each compartment and the percentage that each represents of the total. These analyses were performed with the packages *venn* (for regular Venn diagrams; Dusa 2022) and *eulerr* (for the proportional Venn diagram; Larsson *et al.*, 2022) in R version 4.2.2 (R Development Core Team, 2023) in RStudio 2022.12.0+353 'Elsbeth Geranium' (RStudio Team, 2022). We performed an additional non-metric multidimensional scaling analysis to observe the similarity among the composition of species based on host plants. These similarities are based on Bray–Curtis distances among the groups. This analysis was performed with the package *vegan* (Dixon, 2003) in RStudio.

To perform the analyses detailed below, we selected only host species of Cynipidae with a representation of collected galls (>30), emerged species (>6), and individuals (>20) of parasitoids and inquilines; we can consider them as common host species and with an abundant and diverse primary fauna at least in our

study areas and sampling period. To calculate the total diversity of species, we used the true diversity indices (Jost, 2006), obtaining the values of observed (q_0), effective species (q_1), and dominant species richness (q_2). For this purpose, we use the package *SpadeR* (Chao *et al.*, 2016) in RStudio.

Bipartite network analyses

We tested the relationships among the species compositions through bipartite food webs using three different categories: host species (taxonomy), plant host species, and gall morphological type (the latter being functional ecology traits). The type of the morphology and structure of the galls was categorised following Gil-Tapetado *et al.* (2022), but separating complex galls into two categories, those with a large, spherical shape or with rigid extensions, lignified structure (lignified) and those with a cottony shape or a spiky ball (hairy) (see fig. 1). For this categorisation, we also considered and adapted the proposed character states of Stone and Cook (1998). Thus, we created three different networks based on the three above-mentioned traits: host taxa, plant taxa, and gall type. Hereafter, we refer to these three networks, respectively, as HT-web, PT-web, and GS-web.

We obtained different parameters for each network. Among the network-level parameters, we calculated complementary specialisation (H_2'), nestedness (which describes a network topology in which the interactions of the more specialised nodes are subsets of the interactions made by the more generalised nodes) (*NODF*), and linkage density (diversity of interactions *per species*). Among the group-level parameters (i.e. for lower (LL) and higher trophic level (HL)), we calculated the niche overlap and the togetherness (the mean number of co-occurrences across all pairwise species combinations). We then generated random food webs and compared their calculated indices with the empirical ones through null models based on random permutations.

At the species level, we calculated the specialisation (d') for each parasitoid/inquiline species in each of the three created networks, and we compared it across networks both using an analysis of variance (ANOVA) and ranking the species by increasing specialisation.

Specialisation, both at network-level and species-level analysis, may suggest which cues are important to guide the parasitoids/inquilines while searching for/detecting a host. For example, if specialisation is higher in the HT-web, we may suggest that the gall volatiles are more important than the plant volatiles and the gall type while searching for a host. On the contrary, specialisation would be higher in the PT-web likely if plant volatiles are relevant, and specialisation would be higher in the GS-web likely if visual cues are important for host detection. All these analyses and the display of the food webs were performed with the package *bipartite* (Dormann *et al.*, 2014) in RStudio.

Results

Composition and diversity analyses

We collected a total of 25,277 galls of *D. kuriphilus* on *Castanea* and 4484 galls of native cynipid species, from which 4258 on *Quercus* species (42 species of Cynipidae), and 5047 specimens of parasitoids and inquilines (3792 and 1,255, respectively) of 76 different species (64 and 15 respectively) (see DataSET.xlsx). Out of the parasitoid species, we have obtained representatives of the following families of Chalcidoidea: 16 species belonging to

Eulophidae, 5 to Eupelmidae, 11 to Eurytomidae, 2 to Megastigmidae, 2 to Ormyridae, 16 to Pteromalidae, 13 to Torymidae, and 1 species of Ichneumonidae (Ichneumonoidea) (perhaps as part of a secondary community in the galls of Cynipidae that does not parasitise the galling wasp). Of the Cynipidae inquiline species, we have obtained 14 species belonging to Synergini and 1 to Diastrophini. Of the host species of Cynipidae, we obtained 1 species from *C. sativa* (*D. kuriphilus*); 26 from section *Quercus*; 4 from *Q. suber*, *Q. ilex*, and *Q. coccifera*; 4 from *Rosa*, 1 from *Rubus*, and 3 from Asteraceae species.

Segregation analyses showed that *D. kuriphilus* did not share any parasitoid or inquiline species with gall-inducing cynipids on Asteraceae or *Rubus*, except for two species from *Rosa* (fig. 2A), namely *Eurytoma setigera* Mayr 1878 and *Eupelmus urozonus* Dalman 1820. For this reason, we have included the composition of *Rosa*'s primary fauna in the segregation analyses with *Quercus* and *Castanea*. This analysis indicated a single species exclusive from galls on *Castanea* (fig. 2B), namely *Pachyneuron concolor* (Förster 1841), while the rest of the species has been recruited from other biological communities. This result

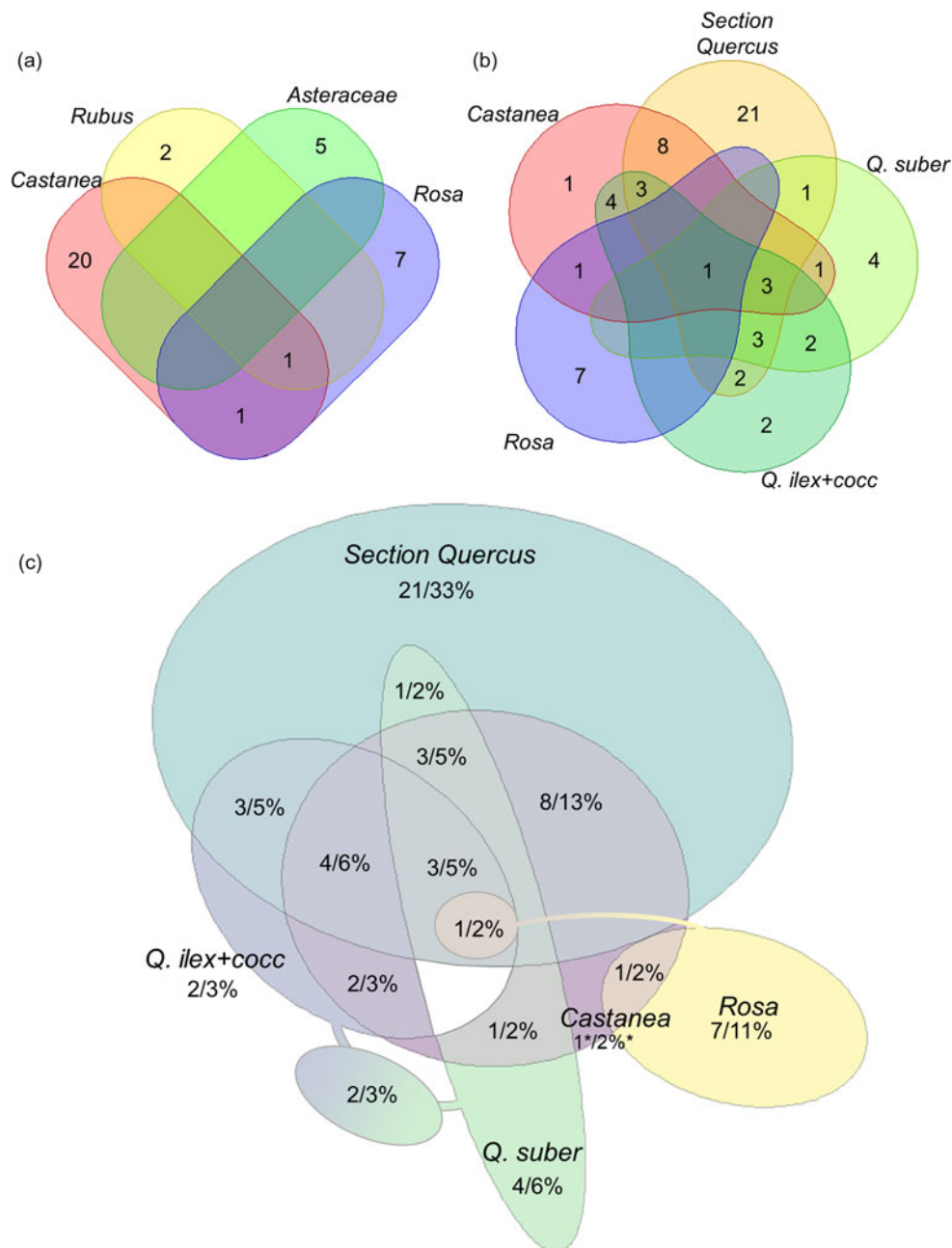


Figure 2. Segregation Venn analysis of parasitoid and inquiline species that we have found in our samplings in different host plants comparing with those founded on *D. kuriphilus* on *Castanea*: (A) herbaceous (Asteraceae) and bushes (*Rosa* and *Rubus*). (B) trees (*Quercus*), categorised in section *Quercus* (*Q. robur*, *Q. petraea*, *Q. canariensis*, *Q. pyrenaica*, and *Q. faginea*), *Q. ilex + cocc* (*Q. ilex* and *Q. coccifera*), and *Q. suber*. We also included parasitoids and inquilines on *Rosa* due to the sharing species it has with *D. kuriphilus*. (C) Proportional Venn analysis showing the numbers and percentages of species that share and are exclusive to each host plant category. For a better interpretation of the figure, the percentage values are rounded. *The exclusive species of *D. kuriphilus*, *Pa. concolor*, is a parasitoid of the secondary fauna inhabiting the galls of *D. kuriphilus* and does not really represent a trophic relationship with this cynipid.

Table 1. Bray–Curtis' similarity (in percentage) among the primary fauna of each five categories of the host plant

Host plants	<i>Rosa</i>	<i>Q. suber</i>	<i>Q. ilex + cocc</i>	Section <i>Quercus</i>	<i>Castanea</i>
<i>Castanea</i>	12.9	27.03	52.38	44.44	–
Section <i>Quercus</i>	4.00	28.57	39.34	–	–
<i>Q. ilex + cocc</i>	6.90	51.43	–	–	–
<i>Q. suber</i>	8.33	–	–	–	–
<i>Rosa</i>	–	–	–	–	–

indicated that there were both specialist and generalist species considering the host plant taxa for each cynipid-gall species, showing that there were both exclusive species from each one and species that attack galls on different host plants, as is the case of *E. urozonus*. Considering the proportionality of sharing species, the fauna of *D. kuriphilus* was almost entirely recruited from *Quercus* communities and marginally from *Rosa* (fig. 2C), indicating that was immersed in the native parasitoid and inquiline assemblages of gall inducer cynipids. The primary fauna belonging to section *Quercus* is the most recruited species by *D. kuriphilus*, being 8 species coming only from this host plant (~13%), 14 species (~23%) were also shared with other *Quercus* hosts. The section *Quercus* also had the richest exclusive primary fauna (21 species, ~33%). However, the compositions of species most similar to *D. kuriphilus* were the *Q. ilex* and *Q. coccifera* groups (52.38%; table 1). The plant categories also showed a similar percentage of exclusive species and shared species (~46 vs. ~54%, respectively), being section *Quercus* and *Rosa* (7 species, 11%) the categories with most exclusive species. The most different group of species was *Rosa*

(table 1), while the *Castanea* and all *Quercus* constituted a unique group (fig. S2).

Among the host species, which we selected and that fulfil the requirements (see above) (fig. 3, table S3), the species with the richest primary fauna was *Biorhiza pallida*, followed by *D. kuriphilus*. This indicates that this alien species is the second most species-diverse among the common hosts of parasitoids and inquiline of cynipid galls. The other top five species with the total richness were *Andricus hispanicus*, *Plagiotrochus quercusilicis*, and *Plagiotrochus australis*, the last two in *Q. ilex* and *Q. coccifera*. *D. kuriphilus* had a 41.87% of effective species and a 27.40% of dominant species, being a host with a large complex of accessory species (58.12%), as also were *B. pallida*, *An. hispanicus*, or *Pl. quercusilicis*. The host species with less dominant richness was *Andricus crispator* in *Q. suber*, which had a species composition dominated by the newly described species *Mesopolobus delafuentei* Nieves-Aldrey and Askew 2020. Curiously, we have only found *M. delafuentei* in the south of the Iberian Peninsula (Málaga) and not in the galls of *An. crispator* in other territories such as Galicia (Nieves-Aldrey et al., 2020).

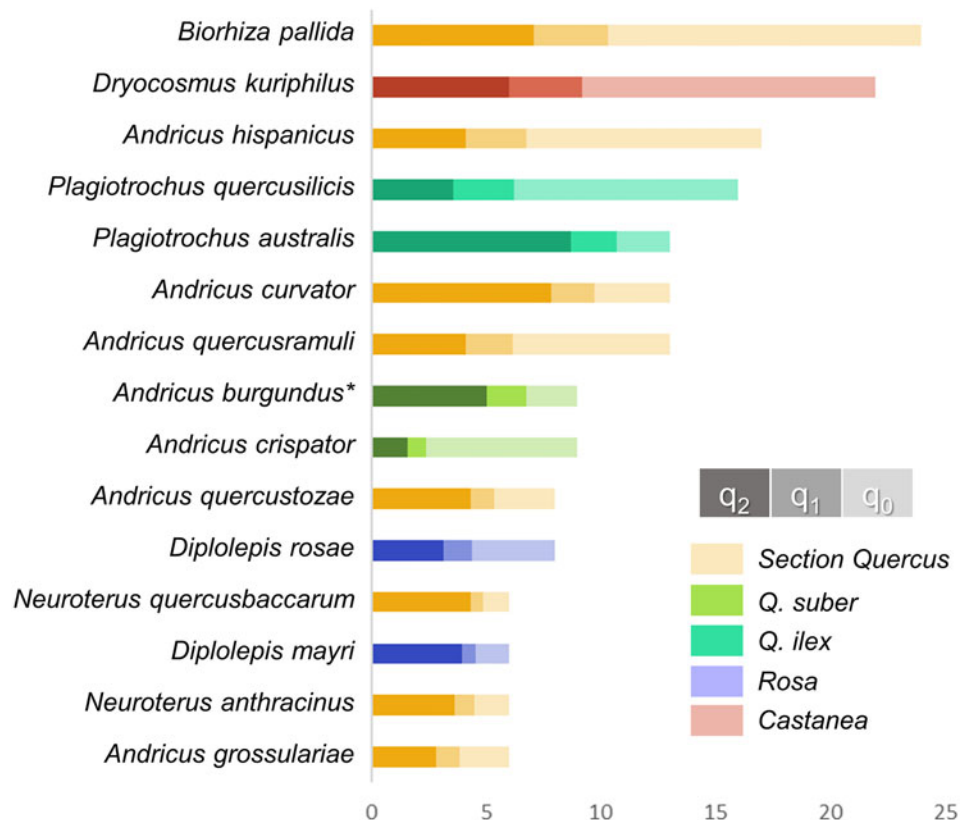


Figure 3. True diversity of primary fauna by host species of Cynipidae with a representation of collected galls (>30), emerged species (>6), and individuals (>20) of parasitoids and inquilines. Colours denote each host plant category. Light tones represent the value of total species richness (q_0); medium tones, the effective species (q_1); and dark tones, the dominant species (q_2). **Andricus burgundus* is a cryptic species complex formed by different bisexual generations of species of *Andricus* in *Q. suber* with a quite similar morphology.

Network analyses

The three types of food webs (HT-web, PT-web, and GS-web) showed different topologies, having the highest number of nodes and links for the HT-web and the lowest values for the GS-web (fig. 4). There were significant differences in all the considered network parameters for the network types, except in the case of the *NODF* in the GS-web, in comparison with the random networks (table 2). By comparing the parameters among network types (table 2), we have found that the GS-web has greater linkage density, niche overlap, and togetherness. On the other hand, the PT-web showed intermediate values except for H_2' and *NODF*, which had the highest values in this web, together with the lowest niche overlap of the lower trophic level.

The species-level specialisation (d') of the parasitoids/inquilines was highest, on average, in the HT-web and lowest in the GS-web (fig. 5A). However, the d' values' distribution indicates that in the HT-web there was a similar number of specialists and generalists, while the GS-web harboured many generalist species and few specialised ones. The PT-web showed intermediate values of d' . The most specialised species is *M. delafuentei* in galls of *An. crispator*, and eight species associated with gall on *Rosa* (*Diplolepis*), following to *Aulogymsus arsames* (Walker 1838) and *T. sinensis*. On the other hand, the most generalist species were *Eurytoma brunniventris* Ratzeburg 1852, *Hyssopus pallidus* (Askew 1964), *Mesopolobus mediterraneus* (Mayr 1903), *Mesopolobus sericeus* (Förster 1770), *Torymus flavipes*, *E. urozonus*, and *Torymus auratus* (fig. 5B).

Discussion

The snapshot of the species composition

Our results reflect the species compositions of Cynipidae and their primary fauna in areas infested by *D. kuriphilus* from mid-2016 to mid-2019 in the Iberian Peninsula and other adjacent areas. This time is not the initial period of the biological invasion of *D. kuriphilus* in the study areas (Gil-Tapetado *et al.*, 2018, 2021b), but it represents the term when such *ex novo* biological community, recruited by this alien species in *Castanea*, appeared. The formation of new biological communities is a complicated process to observe, since in natural environments native species have been coexisting with each other for millions of years (Cody *et al.*, 1975; Thompson, 1999). However, we can observe the formation of new communities after a biological invasion since this appears in a much shorter time. In the case of *D. kuriphilus*, we are not only observing how new interactions are created between species that had never interacted *a priori*, but we are observing how multiple species are recruited by a founder species, giving birth to an assemblage of species which European chestnut trees did not account before (Askew *et al.*, 2013). From this point of view, it is striking that *D. kuriphilus* is the second most parasitised species and the second having most species-rich primary fauna, after the native species on *Q. ilex* and *Q. coccifera* and the section *Quercus*. The primary fauna associated with *D. kuriphilus* resulted in fully nested within the communities of native cynipids, and additionally *T. sinensis* – the alien biological control agent of this pest – has not been found as a parasitoid of native Cynipidae.

The paradigmatic result that *D. kuriphilus*, the last species to be established in the study area (and in Europe as a whole), has one of the richest primary faunal assemblages among Cynipidae, outcompeting all native species except for *B. pallida*,

has been addressed in previous studies (Kos *et al.*, 2015; Jara-Chiquito *et al.*, 2020). Here, we also analysed in a quantitative and detailed way, such pattern of host use.

The very rich assemblages found in *D. kuriphilus* galls is likely since they represent new resources to be exploited, and the species (parasitoids and inquilines) that can potentially use them as resources were already part of biological communities located very close. On the one hand, chestnut trees and *Quercus* are both part of the hardwood forests of the Mediterranean regions (Pividori *et al.*, 2016), while chestnut trees are also cultivated near of oak stands. In this primary fauna recruitment, the landscape and the composition of tree species have been very relevant, since the close disposition between the galls that were already resources for parasitoids and inquilines, have found a new unexplored resource in the nearby chestnut trees when have been infested by *D. kuriphilus*. In an alternative theoretical scenario in which there were not oak trees nearby, recruitment of native primary fauna would not have been possible and only *T. sinensis* would have been present due to releases. On the other hand, according to our species composition results, there are more parasitoids with a wide host range (i.e. generalists), than specialists. Parasitoids and inquilines of galls on *Rosa* are less recruited by *D. kuriphilus*, showing the most different composition and almost all are the most specialised species. Also, the galls of *D. kuriphilus* and *B. pallida*, together with others, such as *Pl. quercusilicis*, *Pl. australis* (in *Q. ilex* and *Q. coccifera*), and *Andricus curvator* (also *B. pallida*, both in section *Quercus*), have similar traits, being simple, without defence structures, multilocular, and usually aggregated, unlike other Cynipidae galls (Stone and Schönrogge, 2003). These galls do not seem to have a specific defence to avoid parasitism, but rather they seem to have an aggregation strategy, based on both the multilocularity of their galls, the joint arrangement of many of them, and the production of numerous offspring. This, together with the strategy of empty larval chambers (Cooper and Rieske, 2010), means that despite not having a physical strategy against parasitism, the mortality is distributed among the population (i.e. they are easier to parasitise, but they are numerous). These statements coincide with the 'emerged islands-on-mainland effect' (Gil-Tapetado *et al.*, 2021a), which explains the rapid recruitment of species by *D. kuriphilus*.

The exclusive species in the composition of *D. kuriphilus*, *Pa. concolor*, is a hyperparasitoid of other parasitoids of Encyrtidae related to Coccidae or Aphididae (Hemiptera) (Noyes, 2019), species that can cohabit between or inside the cynipid galls, therefore, although we have found it inside the galls of *D. kuriphilus*, it does not have a direct relationship with this cynipid and is not part of the primary fauna but belongs to the secondary fauna. Also, *H. pallidus* is an occasional, rare, and marginal species in the oak gall-wasp communities, and which is associated with Cecidomyiidae (Diptera) and Tortricidae (Lepidoptera) (Noyes, 2019). The presence of *H. pallidus* in our samplings seems to be due to chance, and the results related to this species should not be taken into consideration in the context of species specialisation.

In previous contributions, higher parasitoid activity and richness has been reported mostly in warmer and Mediterranean areas than colder or temperate ones (Bonsignore *et al.*, 2019; Gil-Tapetado *et al.*, 2021a, 2021c). In this article we have not compared the possible differences between the biological communities of cynipids in *Castanea* and *Quercus* in the three areas sampled, although we had previously focused on the variability of the communities of *D. kuriphilus* in the north-western (Galicia) and southern (Andalusia) regions of the Iberian Peninsula (Gil-Tapetado

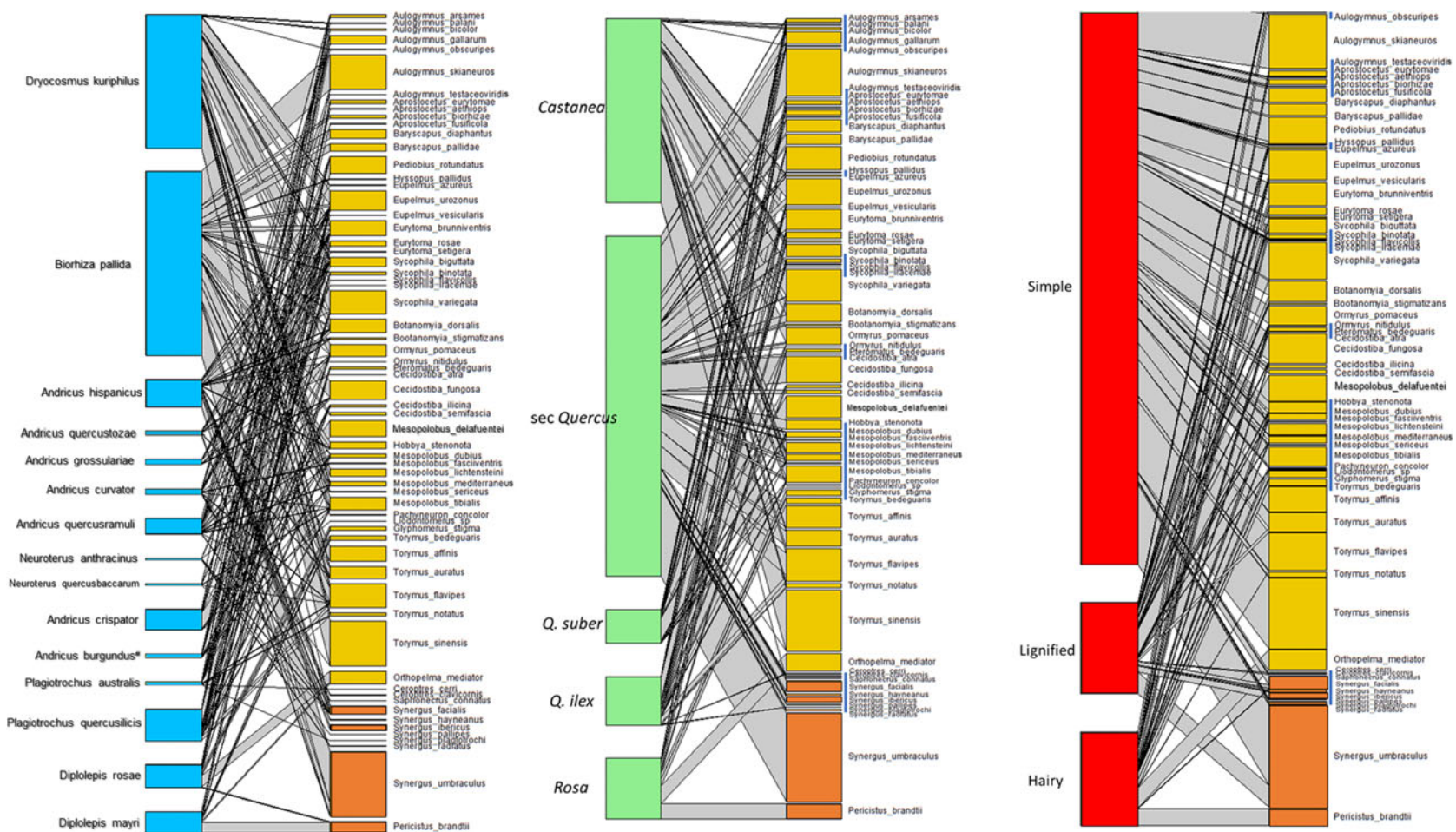


Figure 4. Food webs performed with three different categorisations of the lower level: host species (left, in blue), host plant of the Cynipidae (centre, in green), and the type of the gall induced by the host species (right, in red).

Table 2. Values of the network parameters, considering three different traits: the host species of Cynipidae, the host plant of the host species, and the gall type of the hosts

Parameter	Host species			Host plant			Gall type		
	Empirical web	Random web		Empirical web	Random web		Empirical web	Random web	
Linkage density	5.149	5.107	***	6.324	6.654	***	10.111	10.361	***
H_2	0.709	0.733	***	0.805	0.813	***	0.658	0.647	***
<i>NODF</i>	27.167	20.234	***	36.269	26.727	***	46.296	35.628	
Niche overlap HL/LL	0.149/ 0.095	0.144/0.08	***/**	0.323/ 0.033	0.310/ 0.037	***/**	0.542/ 0.149	0.529/ 0.167	***/**
Togetherness HL/LL	0.084/ 0.139	0.065/ 0.068	***/**	0.251/ 0.164	0.221/ 0.088	***/**	0.310/ 0.162	0.403/ 0.505	***/**

We calculated complementary specialisation (H_2'), nestedness (which describes a network topology in which the interactions of the more specialised nodes are subsets of the interactions made by the more generalised nodes) (*NODF*) and linkage density (diversity of interactions *per* species). Among the group-level parameters (i.e. for lower (LL) and higher trophic level (HL)), we calculated the niche overlap and the togetherness (the mean number of co-occurrences across all pairwise species combinations). We generated food webs at random, comparing their calculated values with the empirical ones through null models based on random permutations.

>0.01, *>0.001.

et al., 2021a). Future research on how cynipid-gall communities in *Quercus* and *Castanea* might vary along a temperature gradient would further explore these questions.

Specialisation of parasitoids

Most of the native recruited species by *D. kuriphilus* are considered generalist taxa (Askew *et al.*, 2013; Noyes, 2019; Gil-Tapetado *et al.*, 2021a). It has even been reported that in the first year of introduction of *D. kuriphilus* in a new area there is usually recruitment of generalist parasitoids (Pérez-Otero *et al.*, 2017; Gil-Tapetado *et al.*, 2020). This coincides with the idea that the first parasitoids to be recruited to *D. kuriphilus* are those that have a wider host range and are more opportunistic, and in successive years, other species with a narrower host range are incorporated into the species composition. Following this idea, the more specialist native species would be the last to be recruited because their host range is the narrowest, and only if the galls of *D. kuriphilus* fulfil the characteristics of its host selection, they can incorporate them as a new resource. Thus, there would be a succession of parasitoid recruitment not due to the distance between resources (galls are very close to each other, since chestnut and oak form common forests), but due to the host range of the recruited species. Inquiline species of the cynipid galls tend to have a narrower and more specific range of gall and host plant than parasitoids. This is due to the physiological specificity of inquilines towards the cynipid species they attack, occupying their galls, producing new larval chambers within them or even producing secondary induction in the gall (Nieves-Aldrey, 2001; Gobbo *et al.*, 2020). It is to be expected that more specialist inquilines will not become part of the primary faunal composition of *D. kuriphilus*, at least in the short-to-medium term, as *a priori* the indigenous inquilines do not possess the modifying mechanisms for the galls of this invasive species. Furthermore, only the more generalist inquilines and those, which do not exhibit gall induction or modification responses, will be recruited by *D. kuriphilus*. Analyses by network type suggest that the primary fauna studied are likely to use gall morphological type and host plant volatiles rather than traits (e.g. odour) associated with the host cynipid taxa. However, we also found that specialisation was greatest in the network with host taxa at the lower trophic level. This may

suggest that parasitoids/inquilines first use plant volatiles to detect host plants (Turlings and Benrey, 1998), then approach preferred galls depending on their type (Tumlinson *et al.*, 1993; Lucchetta *et al.*, 2008), and then continue and finally select the cynipid host species at a closer distance. Following this observation, the identity of the host species seems to be the least relevant trait during host searching, except for a few species with high specialisation towards a host(s) (e.g. *M. delafuentei* with *An. crispator*) (Nieves-Aldrey *et al.*, 2020). This suggests that in the most cases there is no taxonomic specialisation but ecological or functional specialisation of the primary fauna. There are examples of parasitoid–host networks, which suggest similar results to those found by us. For example, mutillid wasps (Mutillidae) seem to be rather generalist at the host taxon level, but each species seems to be specialised to attack bee and wasp hosts sharing certain ecological traits (nest type, social behaviour) (Ronchetti and Polidori, 2020).

Here, *T. sinensis* appear as a high specialised species because we only detected this species in galls of *D. kuriphilus* in the wild. However, in other studies *T. sinensis* has been detected parasitising native galls, both in laboratory trials and in the field (Ferracini *et al.*, 2017; Gil-Tapetado *et al.*, 2023). The galls of native Cynipidae in which *T. sinensis* has been detected are those that have a similar morphology with the galls of *D. kuriphilus* (simple gall developing in spring, soft in appearance, and either a swelling on the leaf or an irregular ellipsoid related to the number of larval chambers it contains, e.g. *An. curvator* or *B. pallida*). Hence, also based on the attacked host gall morphological types and on previous results on the potential host range of *T. sinensis* (Gibbs *et al.*, 2011; Ferracini *et al.*, 2017; Gil-Tapetado *et al.*, 2023), it is quite possible that this alien parasitoid is an ecology-specialist species. A similar situation appeared for *Au. arsames*, one of the species cited as an ecology-specialist. This also suggests that, along the ecological succession of parasitoid recruitment exerted by the native species, *T. sinensis* would lose specialisation (d') over the years and would have a similar value to its sister species, *Torymus notatus* (Walker 1833). The high abundance of *D. kuriphilus* relative to native cynipids in the sampling areas probably results in a high availability of alien galls relative to native galls. Because of this high abundance, we believe that *T. sinensis* is more closely associated with *D. kuriphilus* than with native cynipids. However, we are not certain about what

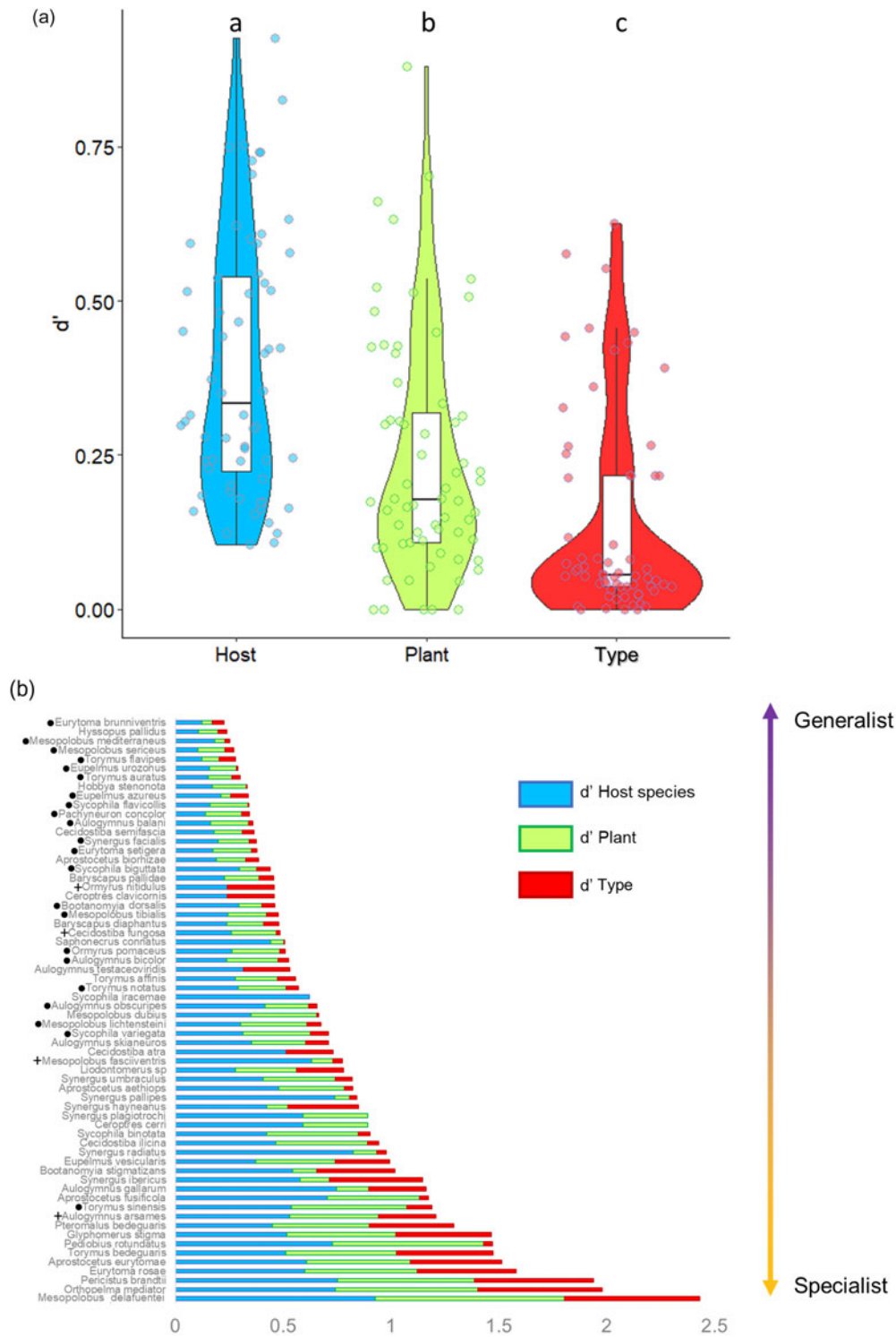


Figure 5. (A) Violin diagrams with the comparison between the d' (individual specialisation) of the primary fauna of Cynipidae by each category. ANOVA test, $F = 28.73$, $P < 0.00001$. (B) Ranking of primary fauna species with the sum of d' of each category, indicating a gradient of generalist and specialist species. Dots mark the primary fauna associated with *D. kuriphilus* studied in this article (data of samplings of Gil-Tapetado *et al.*, 2021a) and cross mark the primary fauna associated with this host detected in the Iberian Peninsula (data compilation of Gil-Tapetado *et al.*, 2021a).

could happen in the future if the population of *D. kuriphilus* is eventually regulated and the availability of its galls becomes equitable to that of native galls susceptible to parasitism, such as those already reported, e.g. *B. pallida* or *An. curvator* (Ferracini *et al.*, 2015; Gil-Tapetado *et al.*, 2023).

The analyses of our study can be considered as a first attempt or an initial snapshot of the composition and network topology of the primary fauna associated with native cynipid galls in areas with the presence of *D. kuriphilus* and can be compared in the future by performing the same sampling campaigns and carry

out the sample methodology in the Iberian Peninsula. This can be seen both as an approach to observing how biological communities are formed and reshaped from their inception over the years, and how alien species can affect and change native fauna.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0007485324000774>.

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