ORIGINAL PAPER

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Life inside a gall: diversity, phenology and structure of Portuguese gall communities, their hosts, parasitoids and inquilines

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Abstract

Plant galls sustain diverse and complex communities of gallers, parasitoids and inquilines that provide exceptional systems to explore evolutionary, ecological and conservation questions. However, the structure and phenology of such communities are still largely unknown. In order to fill these gaps, we sampled plant galls along the Portuguese coast aiming to (1) characterize the diversity of gall-associated communities (plants, gallers, their parasitoids, and inquilines); (2) evaluate how richness and abundance of gallers are shaped by plant life-form; and (3) explore the phenology (i.e. emergence time) of the different guilds. For 1 year, we collected 31,737 galls from 33 plant species, revealing remarkably diverse communities centred on 49 gallers, 65 parasitoids and 88 inquiline species. The plant families with more galls were Fabaceae, Fagaceae and Cistaceae, while most gallers were Cynipidae and Cecidomyiidae. Regarding parasitoids, *Torymidae* and *Eulophidae* were the richest families, and most inquilines belonged to the families Cecidomyiidae, Thripidae, Aphidiidae and Psocoptera. Shrubs hosted a significantly greater abundance and richness of gallers. Overall community composition was highly variable in time, frequently with turnover rates greater than 50% between consecutive months. An asynchrony between life cycles of each guild could be explained by the sequential availability of resources for gallers and parasitoids and by the relaxed physiological constraints between galls and inquilines. This baseline information is vital for revealing a hidden component of biodiversity and shedding light on its community structure and resilience.

Keywords Gall-inducing insects · Iberia · Multitrophic relationships · Parasitoids · Inquilines · Hidden biodiversity

Introduction

Insects have been increasingly recognized as "the small things that run the world" (Wilson 1987); however, a few guilds, particularly pollinators, pests and decomposers, gathered most of the attention to date (Brian 2012; Copping 2009; Losey and Vaughan 2006). One often neglected group is that of gall-inducing insects (hereafter gallers for simplicity) and their associated communities. Plant galls are formed by the growth of plant tissues as a reaction to the oviposition by a galler. During this process, the plant cells suffer an abnormal growth characterized by hypertrophy and hyperplasia, resulting from biochemical compounds secreted by galler larvae (Dorchin et al. 2009; Giron et al. 2016; Redfern and Shirley 2011). In turn, both the galler and the gall tissue can be resources for other trophic and non-trophic interactions, namely with parasitoids and inquilines, respectively, forming complex communities. These communities are exceptional systems to explore evolutionary, ecological and conservation questions (Hayward and Stone 2005). Most gallers are midges (Diptera:Cecidomyiidae) and wasps (Hymenoptera:Cynipidae), although several other insect families can induce gall formation (e.g. Coleoptera:Apionidae, Homoptera:Aphidiidae) as well as Acari (Eriophyidae), bacteria and fungi (Price et al. 1998; Redfern 2011). Most studies on galls have been centred on a single species, genus or family (Stone et al. 2002),

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sometimes exploring the trophic relationships with their parasitoids, as the case of Palearctic region (particularly in Iberia), where the diversity of gallers, parasitoids and inquilines is relatively well studied (Bellido and Pujade-Villar 1999; Garbin et al. 2008; László and Tóthmérész 2006; Nieves-Aldrey 2001a, b; Nieves-Aldrey and Askew 2002; Pujade-Villar and Ros-Farré 1998; Ros-Farré and Pujade-Villar 1998; Skuhravá et al. 1996; Stone and Cook 1998). However, community level assessments of the interactions structuring gall communities (Kaartinen et al. 2010; Bunnefeld et al. 2018) and the importance of temporal dynamics of these communities (which influence the composition and abundance of species and consequently ecosystem functioning) have been largely ignored (but see Cuevas-Reyes et al. 2004; Hawkins and Goeden 1984; Joseph et al. 2011; Veldtman and McGeoch 2003). Although less explored, some studies highlight the impact of inquilines in the fitness of gallers and in nutrient cycles (Begon et al. 1999; Brooks and Shorthouse 1998; László and Tóthmérész 2006; Shorthouse 1998).

In Portugal, there is only a handful of studies of gall communities, including the seminal work of Joaquim Tavares in the beginning of twentieth century (Tavares 1900, 1902, 1905, 1907) and some more recent work with *Quercus* and *Eucalyptus* galls (Askew et al. 2006, 2013; Branco et al. 2006, 2009; Inácio et al. 2002).

Different gallers induce the formation of highly characteristic galls and the association between plants and gallers is highly specific, to the point that it is possible to identify the galler based on the plant species and on the morphology of the gall (Redfern 2011; Redfern and Shirley 2011; Russo 2006). Given their specificity, galls have been used as biocontrol agents of invasive plants (Impson et al. 2008; Moran and Goolsby 2009); e.g. the Australian gall-wasp *Trichilogaster acaciaelongifoliae* Froggatt (Hymenoptera:Pteromalidae) has been used in South Africa since the early 1980s to control *Acacia longifolia* (Andrews) Willd (Hoffmann et al. 2002) and was recently introduced in coastal habitats in Portugal (Marchante et al. 2017). On the other hand, some gallers have become invasive (Csóka et al. 2017), as is the case of chestnut gall wasp *Dryocosmus kuriphilus* Yasumatsu, 1951 (Hymenoptera:Cynipidae) in Europe (Brussino et al. 2002), including in Portugal where it has significant economic costs (EPPO Reporting Service no. 06-2014). Nevertheless, and despite their high host specificity, some gallers or galls may share parasitoids and inquilines, respectively (Aebi et al. 2007; Quacchia et al. 2013; Askew et al. 2006, 2013; Csóka et al. 2005; Holt and Lawton 1993; Ronquist and Liljeblad 2001), which is likely to be determinant for their potential impacts either as invasive species or as biocontrol agents (López-Núñez et al. 2017; Veldtman et al. 2011).

The Iberian Peninsula, and Portugal in particular, is included in one of the world's biodiversity hotspots (Hewitt 2011). Within this region, coastal habitats are particularly vulnerable to many rapidly growing threats, such as direct pressure from anthropogenic activities, urban development, coastal erosion, sea level rise and invasive species (Heslenfeld et al. 2004). However, although a network approach has been previously used to analyse network interactions of Portuguese coastal gall communities in the context of biological invasions and biological control (López-Núñez et al. 2017), no studies have explored the diversity, taxonomy and phenology of gall communities. In this context, we wanted to explore the communities of galls along the Portuguese coast in order to (1) characterize the diversity of gall-associated communities (plants, gallers, their parasitoids and inquilines); (2) evaluate how richness and abundance of gallers are shaped by plant life-form; and (3) explore the differences in annual phenology and turnover among the different guilds, namely testing if they have different emergence times. Additionally, this knowledge may change the perception about the importance of these hidden communities throughout the coastal habitats of Portugal; and at the same time can form an important baseline information for understanding future changes on native gall communities.

Materials and methods

Sample sites

Ten sites were selected along the Portuguese coast (Online Resource 1: Figure 1), including sand dunes, pine forests and oak woodlands with dominance of different species of shrubs and trees (Table 1). Sites were predominantly located up to 1 km from the ocean and all have mild winters and dry summers typical of Mediterranean climate. Four of the sites were visited monthly for 1 year and the other six were visited every 3 months (Table 1 and Online Resource 1: Figure 1). Sampling was uneven because the large number of galls and intensive lab work made it impossible to sample all sites monthly. The seasonal sampling of six of the sites, although less frequent, allowed a better representation of the whole diversity of the study region.

Collection of galls and rearing of insects

Sampling took place between August 2013 and July 2014, during which period a random transect of $20 \times 2 \times 2$ m (length × width × height) was run in each visit and site. Transects were separated by at least 50 m. In each transect, all plants were recorded and identified to the species level following Bingre et al. (2007) for trees and shrubs, and other

sources for herbaceous plants (Franco 1971, 1984; Franco and Rocha Afonso 1994, 1998, 2003).

Galls detected in each transect were collected and individually stored in closed plastic containers at room temperature. When the abundance of similar galls on the same host plant made collection impossible, all galls were counted and a sub-sample was collected. Collected galls were monitored once a week during 15 months or until they rot or were damaged by fungi. Emerging insects were stored in Eppendorfs in 70% ethanol and identified to the lowest taxonomical level possible, usually species, by professional taxonomists.

Emerging insects were sorted into three different guilds: gallers, parasitoids or inquilines (Online Resource 2: Table 1) based on available literature (Chinery 2013; Nieves-Aldrey 2001a; Noyes 2016; Redfern and Shirley 2002). Although many of the inquilines do not feed or develop strictly within galls, the term "inquiline emergence" was used for simplicity. For species with no available information, the guild was attributed based on information relative to the closest genus with a known feeding strategy. When there were no emergences from collected galls, the species of galler was inferred from gall morphology (shape, size, aspect, colour, etc.) and the identity of the host plant following Chinery (2013), Jürgen Buhr (2012), Nafría and Durante (2002), Nieves-Aldrey (2001a) and Redfern and Shirley (2002). Furthermore, since the formation of galls in organs is indicative of the contact with a galler insect, and because the effective fecundity of each species of gall is difficult to determine, we assumed that galls of each morphotypes produce the same number of gallers, in order to use the frequency of gall types as a proxy of galler abundance and diversity.

Data analysis

We characterized the diversity of each guild, as well as their phenology and emergence period, as follows.

Diversity analysis

We assessed the overall richness and abundance of plants, gallers, their parasitoids and inquilines. Plant species were classified according to their life-form as herbs, vines, sub-shrubs, shrubs or trees. Abundance and richness of galls were corrected by each plant species cover.

Using a Generalized Linear Mixed Models (GLMMs), we evaluated the relationship between plant family, life-form, and cover (as fixed factors) and the abundance and richness of gall species. In order to incorporate spatial autocorrelation in these models, we considered the sampling site as random factor. Dependent variables and plant cover were transformed as $x' = \frac{-1}{(x+1)^2}$ and $\log(x)$, respectively, in order

to reach normality and homoscedasticity of the model residuals. When the model detected significative differences, it was followed by a post hoc Tukey test. GLMMs and post hoc analyses were carried with the R packages lme4 and multcomp (Hothorn et al. 2008; Bates et al. 2015).

Rank-abundance curves

Rank-Abundance curves were constructed and plotted in R (R Development Core Team 2011) using package Vegan (Oksanen et al. 2013). These curves characterize the taxocenosis diversity (richness and relative species abundances) and the slope informs about species dominance (Whittaker 1965).

Species turnover rate

We calculated the monthly turnover of each guild using the equation: $TR = \frac{(G + L)}{T}$, where G is the number of species gained, L is the number of species lost and T is the total number of species observed in both months (Collins et al. 2008). Turnover rates thus vary between 0 (no change) and 1 (all species change). Turnover rates were calculated with the codyn package (Hallett et al. 2016).

Insect emergence

In order to analyse the differences in the emergence phenology of insects of the different guilds, two measures were considered: (1) insect emergence distribution throughout the year, and (2) the number of days between gall collection and the emergence of insects. For this, medians and their 95% confidence interval of the median bootstrap were calculated based on the four sites with monthly samplings. Differences were analysed with non-parametric Kruskal–Wallis tests, followed by a Dunn's multiple comparisons test with a Bonferroni correction. Post hoc analyses were carried using the FSA package (Ogle 2016).

Results

Diversity analysis

A total of 203 plant species, distributed through 54 families, were recorded (Online Resource 2: Table 1). Galls were observed in 33 of these plant species from 13 families (Fig. 1a). Among these, Fabaceae, Fagaceae and Cistaceae the most common, encompass 33%, 15% and 12% of the plant host species, respectively. Although galls were observed in all sampled species of Fagaceae, Salicaceae, Anacardiaceae, Lauraceae and Rhamnaceae, these families were represented by only a few plant species. On the other

(a) Plant Families

(b) Gall Families

(c) Parasitoid Families

(d) Inquiline Families
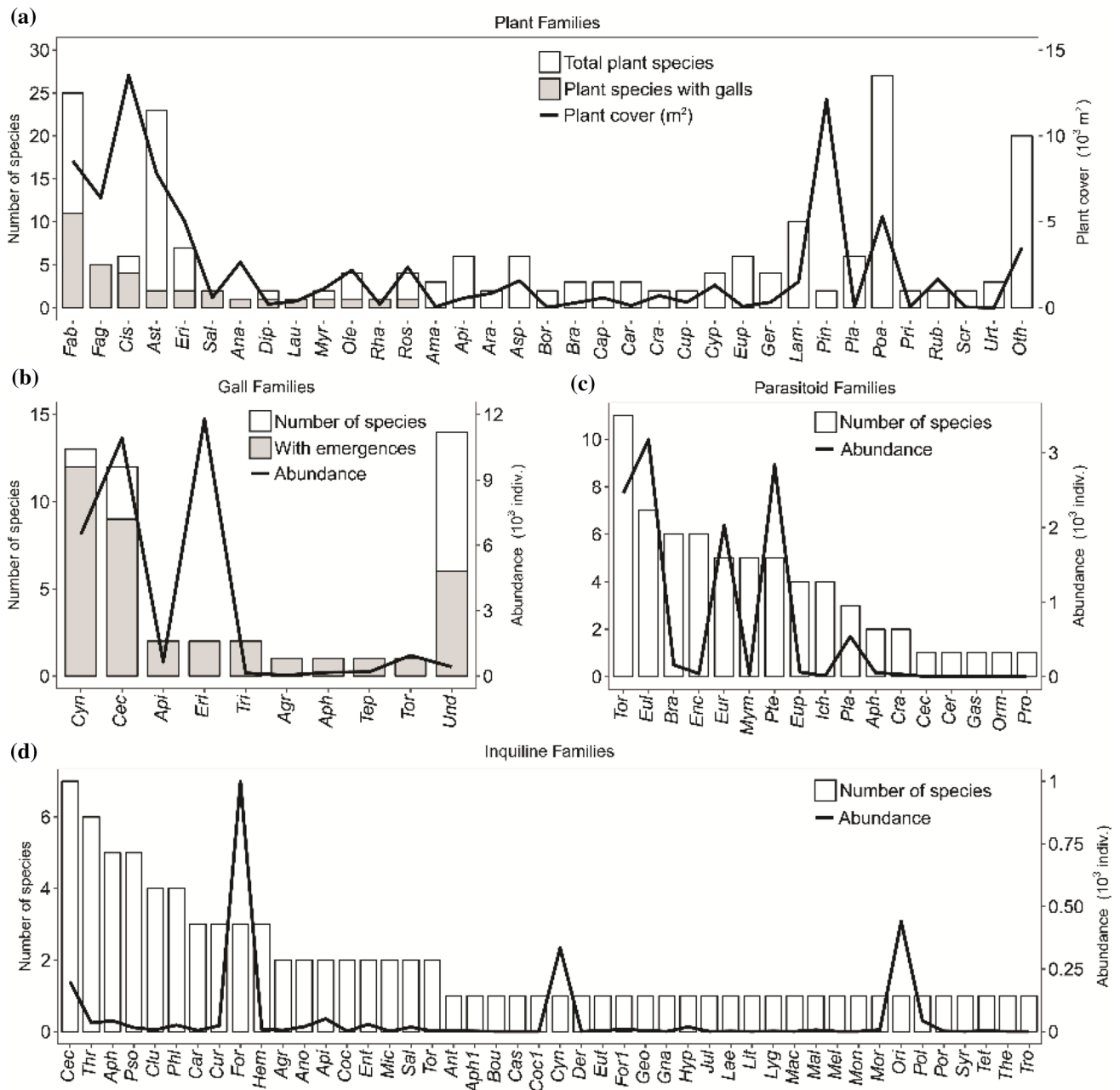
hand, in some of the richer plant families, such as Poaceae and Lamiaceae, no galls were detected, or only a small percentage of species had galls, e.g. Asteraceae (Fig. 1a).

Overall, 31,737 galls were collected, belonging to 49 species or morphospecies (hereafter referred collectively as "species") (Fig. 1b); of these only 13 gallers could not be identified to species level. The most represented and diverse families of gallers were Cynipidae and Cecidomyiidae (with 13 and 12 gall species, respectively), which were also the families with higher percentage of gall species with emergencies (92% and 69%, respectively). When considering the abundance of gallers besides these two

dominant families, a third family stands out: Eriophyidae, with only two species of very abundant gallers (Fig. 1b).

As for parasitoids, 11,435 insects from 65 species distributed by 17 families emerged from the galls, with families Torymidae, Eulophidae, Braconidae, Encyrtidae, Eurytomidae, Mymaridae and Pteromalidae being the ones with greater species richness (Fig. 1c). The families with higher abundance of individuals were Eulophidae, Pteromalidae, Torymidae and Eurytomidae. Although Torymidae almost is twofold the number of species of Pteromalidae, both families had similar abundance. Braconidae,

◀**Fig. 1** Number of species and abundance of specimens per family of **a** plants, considering both species where galls were observed and species with no galls; **b** gallers; **c** parasitoids; and **d** inquilines. All field sites and samplings were considered for this analysis. *Plant families*: Fab (Fabaceae), Fag (Fagaceae), Cis (Cistaceae), Ast (Asteraceae), Eri (Ericaceae), Sal (Salicaceae), Ana (Anacardiaceae), Dip (Dipsacaceae), Lau (Lauraceae), Myr (Myricaceae), Ole (Oleaceae), Rha (Rhamnaceae), Ros (Rosaceae), Ama (Amaryllidaceae), Api (Apiaceae), Apo (Apocynaceae), Ara (Araceae), Asp (Asparagaceae), Bor (Boraginaceae), Bra (Brassicaceae), Cap (Caprifoliaceae), Car (Caryophyllaceae), Cra (Crassulaceae), Cup (Cupressaceae), Cyp (Cyperaceae), Eup (Euphorbiaceae), Ger (Geraniaceae), Lam (Lamiaceae), Pin (Pinaceae), Pla (Plantaginaceae), Poa (Poaceae), Pri (Primulaceae), Rub (Rubiaceae), Scr (Scrophulariaceae), Urt (Urticaceae), Oth (Others): including all families with only one plant species and without the presence of galls; *Gall families*: Cyn (Cynipidae), Cec (Cecidomyiidae), Api (Apionidae), Eri (Eriophyidae), Tri (Triozidae), Agr (Agromyzidae), Aph (Aphidiidae), Tep (Tephritidae), Tor (Tortricidae) and Und (Undetermined); *Parasitoid families*: Tor (Torymidae), Eul (Eulophidae), Bra (Braconidae), Enc (Encyrtidae), Eur (Eurytomidae), Mym (Mymaridae), Pte (Pteromalidae), Eup (Eupelmidae), Ich (Ichneumonidae), Pla (Platygastridae), Aph (Aphelinidae), Cra (Crabronidae), Cec (Cecidomyiidae), Cer (Ceraphronidae), Gas (Gasteruptiidae), Orm (Ormyridae), Pro (Proctotrupidae) and *Inquiline families*: Cec (Cecidomyiidae), Thr (Thripidae), Aph (Aphididae), Pso (Psocoptera), Clu (Clubionidae), Phl (Phlaeothripidae), Car (Carabidae), Cur (Curculionidae), For (Formicidae), Hem (Hemiptera: Heteroptera), Agr (Agromyzidae), Ano (Anobiidae), Api (Apionidae), Coc (Coccinellidae), Ent (Entomobryidae), Mic (Microcoryphia), Sal (Salticidae), Tor (Tortricidae), Ant (Anthocoridae), Aph1 (Aphrophoridae), Bou (Bourletidae), Cas (Cassidae), Coc1 (Coccidae), Cyn (Cynipidae), Der (Dermestidae), Eut (Eutichuridae), For1 (Forficulidae), Geo (Geophilomorpha), Gna (Gnaphosidae), Hyp (Hypogastruridae), Jul (Julidae), Lae (Laemophloeidae), Lit (Lithobiomorpha), Lyg (Lygaeidae), Mac (Machilidae), Mal (Malachiidae), Mel (Melyridae), Mon (Monophlebidae), Mor (Mordellidae), Ori (Oribatida), Pol (Polyxenidae), Por (Porcellionidae), Syr (Syrphidae), Tet (Tettigoniidae), The (Theridiidae), Tro (Trombidiidae)

Encyrtidae and Mymaridae were represented by several species, but with a very low abundance (Fig. 1c).

Finally, 2391 inquilines, distributed by 88 species and 46 families, emerged from the collected galls (Fig. 1d). The richest families were Cecidomyiidae and Thripidae, followed by a diverse array of poorly represented arthropod groups, namely: aphids (Aphidiidae), booklice (Psocoptera), spiders (Clubionidae) and thrips (Phlaeothripidae). Ants (Formicidae) and Cynipidae wasps and mites (Oribatida) were the most abundant inquilines (Fig. 1d).

Life-form and plant cover were identified as important variables that influenced the abundance ($F = 4.309$, $df = 4$, $p = 0.040$ and $F = 4.361$, $df = 4$, $p = 0.002$, respectively) of galls (Online Resource 2: Table 2). However, plant family was strong associated ($F = 2.27$, $df = 166$, $p < 0.001$) with the richness of galls. More species of galls were found in shrubs (0.052 ± 0.303 (mean $\pm$ SD)) and trees (0.007 ± 0.03) while only a few species were found in subshrubs and herbs (Fig. 2). However in average, abundance of galls was substantially higher on shrubs (3.475 ± 13.328 galls/m^2 of plant cover) than in subshrubs, tress and herbs (1.26 ± 5.227; 0.007 ± 0.03 and 0.0004 ± 0.005 galls/ m^2 of plant cover, respectively) (Fig. 2).

Rank-abundance curves

Rank-abundance curves revealed the dominance of only a few species per guild (Fig. 3; see Online Resource 2: Table 3 for details). The most abundant plant species with galls was *Cistus salviifolius*, followed by *Artemisia campestris, Quercus coccifera, Pistacia lentiscus, Ulex europaeus, Halimium calycinum, Halimium halimifolium* and *Quercus robur* (Fig. 3, grey line). In the case of gallers, the midge *Aceria quercina* (Eriophyidae) was by far the most abundant species, followed by the midges *Rhopalomyia baccarum* and *R. santolinae* (Cecidomyiidae), and by the wasp *Plagiotrochus quercusilicis* (Cynipidae) (Fig. 3, pink line).

Regarding the parasitoids that emerged from the collected galls (Online Resource 2: Table 1) (Fig. 3, green line), there were four most frequent wasps: *Torymus flavipes* (Torymidae) [attacking *Plagiotrochus quercusilicis* (Cynipidae) and *Andricus kollari* (Cynipidae)], *Mesopolobus tibialis* (Pteromalidae) (attacking the cynipid *P. quercusilicis, Cynips* sp., undeterminated Q. robur gall and the cecidomyiid *Rhopalomyia baccarum*), *Pediobius rotundantus* (Eulophidae) (attacking *P. quercusilicis*) and *Sycophila variegata* (Eurytomidae) (attacking *P. quercusilicis* and the cecidomyiid *Contarinia* sp.). Finally, concerning inquilines (Fig. 3, blue line), the ants (*Temnothorax* sp.), the mites (mainly Acari: Oribatidae), the cynipid *Synergus* sp. and the Cecidomyiidae *Clinodiplosis* sp. were the most abundant and dominated over all other groups.

Monthly phenology and turnover

The number of species per guild was highly variable throughout the year (Fig. 4, Online Resource 1: Figure 2), but there was a trend for a higher diversity in winter and spring (Fig. 4). Although the number of plant species per month was high (usually above 40 species, Fig. 4a), only about 20–30% of those had galls (min. = 10; max. = 14 species, Fig. 4a). Approximately, the same numbers of galler and parasitoid species were observed per month (6–16 galler species and 6–19 parasitoid species; Fig. 4b, c), while inquiline diversity was lower (ranging from 1 to 13, Fig. 4d).

Species turnover rates were generally above 50% and somewhat variable for all guilds (Fig. 4). Plants showed the lower turnover rates (mean = 31.9%; min. = 8.3%; max. = 46.7%), followed by gallers with values around 50% (mean = 49.6%; min. = 27.3%; max. = 71.4%), while parasitoids (mean = 60.1%; min. = 37.5%; max. = 76.2%) and inquilines (mean = 87.8%; min. = 70%; max. = 100%)

Table 1 Habitat classification and conservation status of each sampling sites

	Site (coordinates)	Dominant plant species	Habitat type	Conservation status
Sites sampled every month	Quaios1 (Lat: 40.22476 Lon: −8.88622)	*Artemisia campestris* L. *Carpobrotus edulis* (L.) N.E.Br *Corema album* (L.) D.Don *Crucianella maritima* L.	Sand Dune	National Forest Natura 2000 Network
	Quiaios2 (Lat: 40.251896 Lon: −8.798968)	*Pinus pinaster* Aiton *Corynephorus* sp. *P.Beauv* *Halimium halimifolium* (L.) Willk *Scirpoides holoschoenus* (L.) Soják	Pine forest	Natura 2000 Network
	Boa Viagem (Lat: 40.20037 Lon: −8.88969)	*Pistacia lentiscus* L. *Cistus salviifolius* L. *Smilax aspera* L. *Rosmarinus officinalis* L.	Oak woodland	National Forest
	Coimbra (Lat: 40.18588 Lon: −8.41358)	*Quercus robur* L. *Arbutus unedo* L. *Quercus suber* L. *Ulex minor* Roth	Oak woodland	–
	São Pedro de Moel (Lat: 39.75711 Lon: −9.02338)	*Pinus pinaster* Aiton *Cistus salviifolius* L. *Quercus coccifera* L. *Phillyrea angustifolia* L.	Pine Forest	National Forest
Sites sampled every 3 months	Santo André (Lat: 37.993975 Lon: −8.850893)	*Santolina impressa* Hoffmanns. and Link *Stauracanthus spectabilis* Webb *Artemisia campestris* L. *Halimium calycinum* (L.) K.Koch	Sand Dune	Natural Reserve, Natura 2000 Network
	Esposende (Lat: 41.508999 Lon: −8.784351)	*Artemisia campestris* L. *Ammophila arenaria* H.Lindb *Cistus salviifolius* L. *Aetheorhiza bulbosa* Cass	Sand Dune	Natural Park, Natura 2000 Network
	São Jacinto1 (Lat: 40.698608 Lon: −8.735636)	*Artemisia campestris* L. *Carpobrotus edulis* (L.) N.E.Br *Corema album* (L.) D.Don *Helichrysum italicum* subsp. *picardii* (Boiss. and Reut.) Franco	Sand Dune	Natural Reserve, Natura 2000 Network
	São Jacinto2 (Lat: 40.697669 Lon: −8.729265)	*Cistus salviifolius* L. *Pinus pinaster* Aiton *Avena sterilis* L. *Ulex europaeus* L.	Pine Forest	Natural Reserve, Natura 2000 Network
	Tocha (Lat: 40.34837 Lon: −8.81704)	*Stauracanthus genistoides* (Brot.) Samp *Pinus pinaster* Aiton *Halimium halimifolium* (L.) Willk *Cistus salviifolius* L.	Pine Forest	National Forest Natura 2000 Network

showed high turnover rates changing almost all species in some consecutive months (Fig. 4).

As for general specimens' abundance, more galls were collected and more insects emerged from these galls during late spring, mostly in April to June (Online Resource 2: Table 5).

Insect emergence

At least some individuals of all insect guilds emerged throughout the year, however, each guild showed a characteristic phenology (Fig. 5). Gallers emerged mainly from late April to late June, with only smaller peaks outside this

period. For parasitoids, there were two nearly overlapping peaks in mid-May and mid-June. Finally, the emergence of inquilines (Fig. 5a) was more evenly distributed throughout the year, with only two broad peaks in early-April and June. Differences in the mean emergence date of the different guilds were statistically significant ($H^2 = 1776.8$, $p < 0.05$), with inquilines "emerging" earlier than gallers and parasitoids (Fig. 5b).

When considering the number of days that insects took to emerge after collection of the galls in the field, most insects emerged within a month, but there was a large variation and some insects emerged only after ca. 6 months (Fig. 6a). When median values were analysed, gallers emerged in
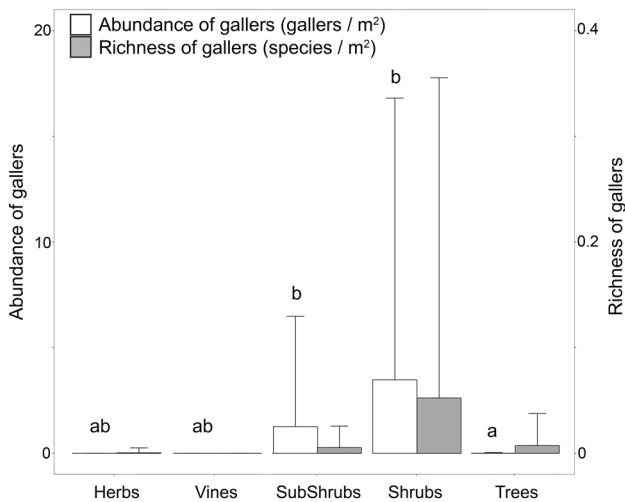
Fig. 2 Average richness and abundance of galler species according to the life-form of the host plants. Error bars show the standard deviation. Letters above bars show the results of the multiple comparison of means by Tukey test

14 days (min. = 0; max. = 284), followed by parasitoids that emerged in 17 days (min. = 0; max. = 389), and inquilines in 49 days (min. = 0; max. = 335, Fig. 6b); differences on the time until emergence were statistically significant ($H^2 = 5236$, $p < 0.05$) for all guilds (Fig. 6b).

Discussion

Our results show a remarkable diversity associated with gall communities in Portuguese coastal habitats, as well as a strong temporal structure of such communities. In comparison with previous taxonomic studies of Iberia, our study revealed a relatively richer community of galls, parasitoids and inquilines (Nieves-Aldrey 2001a; Skuhravá et al. 1996,

2006). As could be anticipated, more gall species were observed in large plant families, particularly in Fabaceae and in families frequently associated with galls in the northern hemisphere such as Fagaceae and Cistaceae (Nieves-Aldrey 2001a; Ronquist et al. 2015). Considering the 140 species of Cynipidae described for the Iberian Peninsula and Balearic Islands (Nieves-Aldrey 2001a) and the 122 species of Cecidomyiidae given for Portugal (Skuhravá and Skuhravý 2009), it was found a considerable percentage of such species (9.3% and 10.3% of Cynipidae and Cecidomyiidae, respectively) only in coastal habitats. This is even more surprising considering the range of plant species observed in such habitats, many of which were not associated with galls (Fig. 1a). Moreover, plants species that are typically known to harbour many gall species, particularly *Quercus* spp. (Skuhravý et al. 1998; Stone and Cook 1998), were absent from most study sites, although they had galls whenever present. Eriophyidae, which is also an important gall-inducing family (Amrine and Stasny 1994), was represented only by two species, although very abundant due to *Aceria quercina*, the most frequent gall species in our study, forming small copious galls in the leaves of *Quercus coccifera* .

As for parasitoids and inquilines, several families co-occurred in the same gall species some of which co-occured simultaneously. But while parasitoids belonged to a few families with several representatives, inquilines were generally scattered among many families, within different orders, each of them represented by only a few species. This reflects, on one hand the complex morphologies of some galls (*e.g. Plagiotrochus quercusilicis* with different morphotypes) that provided more niches for several inquilines, and on the other hand the lower physiological constraints for inquilines as many of them only use the gall as a protective structure. In fact, although all inquilines were included in the same category, it must be acknowledged that their ecology and life-history traits may be quite diverse (Sanver and Hawkins

Fig. 3 Rank-abundance curves of plants with galls, gallers, parasitoids and inquilines in Portuguese coastal habitats. Species abundance ranks were based on plant cover (m²) and abundance of individuals of each animal guild (gallers, parasitoids and inquilines), see Online Resource 2 and Table 3 for details
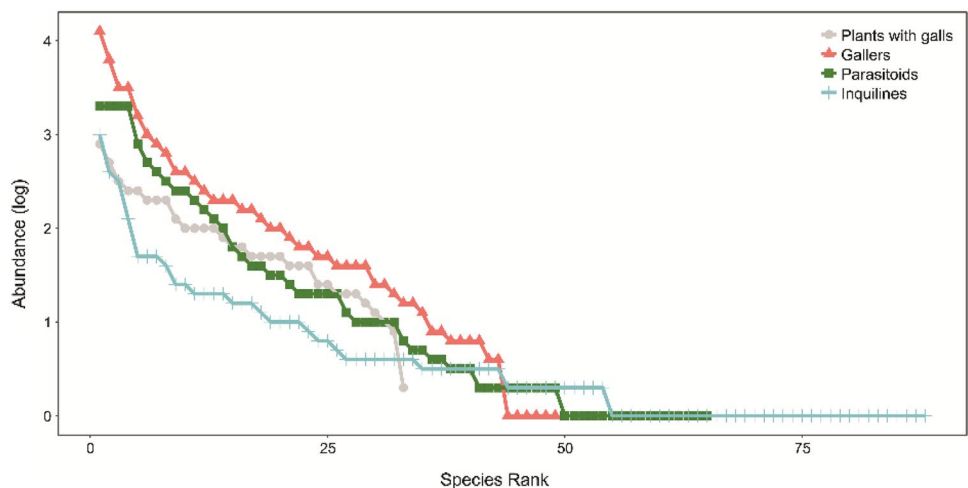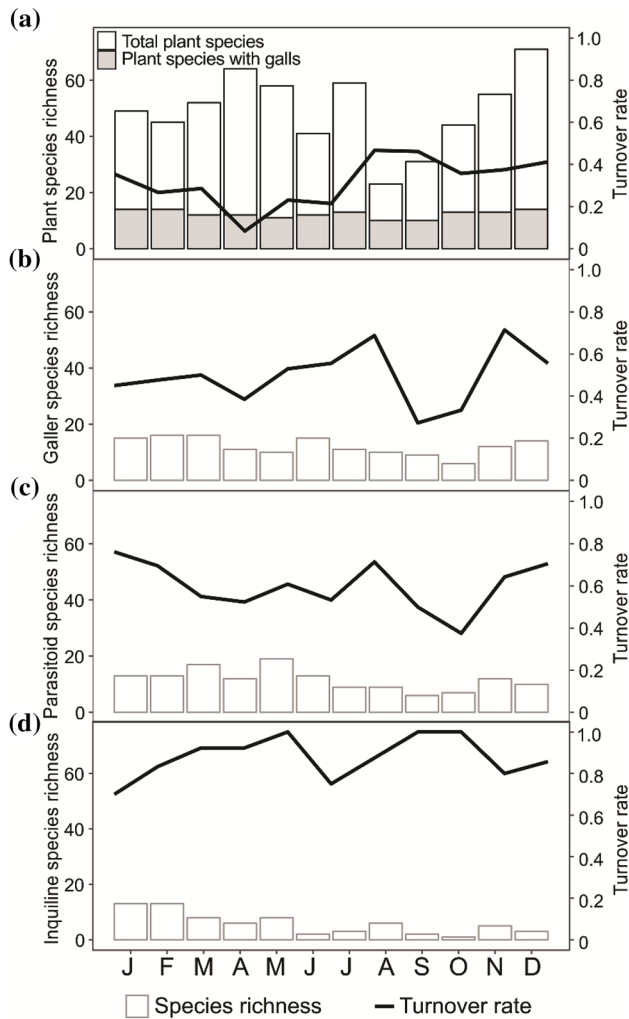
Fig. 4 Number of species (bars) and monthly turnover rate (lines) for **a** plants, **b** gallers, **c** parasitoids and **d** inquilines. Only data from the sites sampled every month were considered for these analyses

2000). For example, the cynipoid inquiline *Synergus* feeds within the gall tissues (Nieves-Aldrey 2001a), while many spiders, ants and beetles only use the gall as shelter or nest site (Blanche 2012). Additionally, parasitoids are likely more specialized, due to the physiological requirements of this intimate interaction, while the relationship between galls and inquilines is less constrained and therefore more generalized (Paniagua et al. 2009). The diverse gall morphology observed may have also contributed for the diversity of species parasitizing them, e.g. parasitoids with long ovipositors can easily reach the galler chamber in large galls, while species with short ovipositors prefer smaller galls or galls with peripheric chambers (Joseph et al. 2011).

Accordingly, we found that parasitoids of *Plagiotrochus quercusilicis* (Cynipidae; < 1 cm plurilocular gall formed on *Quercus coccifera*) were mainly Torymids (*Torymus* spp.) with long ovipositors, while parasitoids of
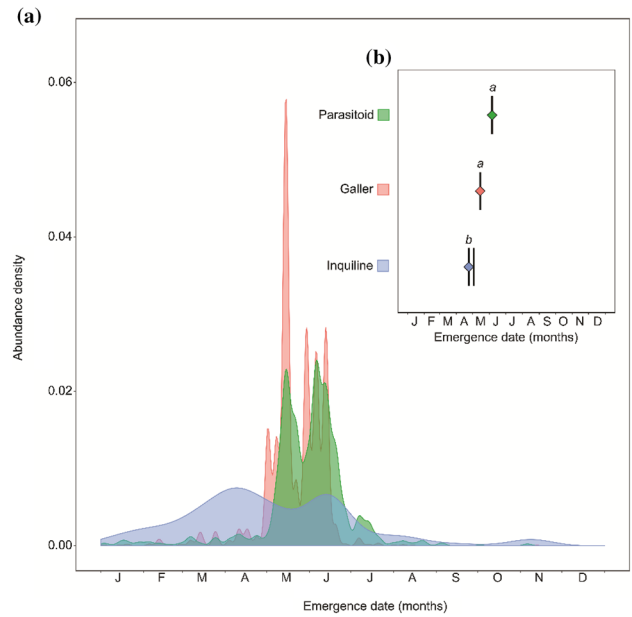

Fig. 5 Annual phenology of insect guilds emerging from collected galls. **a** Emergence phenology, **b** median emergence time and 95% confidence intervals of the bootstrapped median. Only the data from the four sites sampled in each month were included in this analysis
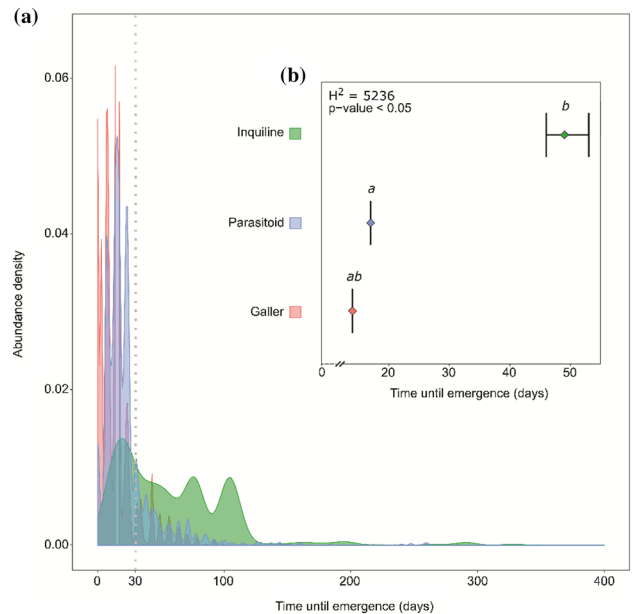

Fig. 6 Time until insect emergence per guild. **a** Distribution of emergence frequency, **b** median time until emergence per guild and 95% confidence intervals of the bootstrapped median. All field sites and samplings were considered for this analysis

Rhopalomyia baccarum (Cecidomyiidae; < 0.5 cm unilocular gall from *Artemisia campestris*) were mostly Pteromalids (*Mesopolobus* spp.) and Eulophids (*Aprostocetus* spp.)

with short ovipositors. Species of Torymidae, Eulophidae and Pteromalidae known to parasitize Cynipidae and Cecidomyiidae (Goulet and Huber 1993; Grissell 1995) were very common in our sites, suggesting that these two gall families represent important trophic resources for parasitoids.

As often documented for biological communities, insect guilds, particularly parasitoids and inquilines, were dominated by a few very abundant species and by a long tail of rare species (Fisher et al. 1943; Preston 1948). Most study sites were spatially heterogeneous with high plant diversity, including a mixture of plant species and life-forms that frequently promote gall formation, e.g. oak woodlands included *Quercus coccifera*, *Q. robur* and *Ulex* spp., sand dunes had *Artemisia campestris* and *Cistus salviifolius*, pine forests included several species of *Halimium* and there were several schlerophiyllous plant species (such as *Stauracanthus* spp. and *Ulex* spp.) which are reported to frequently form galls (Fernandes and Price 1992). This means that the high spatial heterogeneity in environmental conditions associated with the distribution of host plants, and possibly asynchronous plant phenology may have conferred high diversity of niches all year long for different gallers and consequently parasitoids and inquilines. As expectable, galls predominate on shrubs and trees (Cuevas-Reyes et al. 2004; Lawton 1983), a vast majority of galls species on littoral habitats of Portugal were observed in shrubs and trees, while the abundance was higher in shrubs and subshrubs, suggesting that such plant life-forms are important for maintaining diverse gall communities in these habitats. Consequently, disturbances that keep habitats into early successional stages or prevent diversity and abundance of shrubs and trees, such as frequent fires, overgrazing or invasive plants, can negatively affect gall communities (see López-Núñez et al. 2017).

Even though turnover rates revealed a high variation in gall communities along the whole year, richness and abundance of galls and insects tended to be higher during winter and spring. This may be partially explained because gall communities are coupled with the life cycles of the host plants, since the development of meristematic tissues and the growth of young buds are essential for gall development (Redfern and Shirley 2011), which occurs in spring in Mediterranean ecosystems. It must be noticed that because our sampling was destructive, we had to sample different transects each month and as such the plant species were not always exactly the same, although transects were in the same habitat type; since gallers are highly specific, this type of sampling necessarily influenced the turnover rate beyond the normal seasonal variation. Nevertheless, the turnover of gallers, parasitoids and inquilines was greater than that of plants, suggesting that high turnover rates are mostly a consequence of intrinsic insect phenology and not a simple consequence of different plant communities.

Regarding insect phenology, parasitoids and inquilines can only enter the galls after the gallers and consequently they usually emerge later. In general, gallers were the first to emerge followed by parasitoids and later by inquilines, suggesting an inter-guild regulation with a lag-time, which, together with variable environmental conditions, is likely to cause fluctuations in the seasonal dominance of the different guilds (Ananthakrishnan 1998). The presence of several peaks of galler emergence could be explained either by the presence of galler species with multiple generations through the year, as is the case of *Plagiotrochus quercusilicis*, by the emergence of multiple generations from the same gall, or can be an artefact related to the context-specific sampling of each month (i.e. different transects and different environmental conditions in each visit). As for parasitoids, the infection of the galler larvae is generally performed during the first stages of gall development (Askew 1961), and parasitoids usually take longer until they are ready to emerge and complete their life cycle, explaining why they emerge slightly after the gallers. Inquilines have a broad ecological amplitude in terms of the galls used as many of them are only looking for shelter and tend to use the galls only after the gallers or parasitoids have already emerged (Sanver and Hawkins 2000). In this context, although galls are frequently ignored as an important biological resource, gall communities can provide resources across the whole year, which might be important for many insectivorous species. Additionally, the galls themselves may be a precious resource through the year, making them an interesting niche exploited by several groups of terrestrial mesofauna. For example, several large herbivores, such as goats, are known to specifically search for galls while foraging (Otília, pers. commun).

As in any ecological study, the observed species richness and abundances should be interpreted as minimum reference values. First, because despite the high investment in fieldwork, considering different sites and habitats and the yearlong sampling, we might still have missed some of the species present. Secondly, because we have only detected insect emergencies in 21% of all collected galls. This low emergence rate may be explained by several reasons, namely (1) some gallers or parasitoids may have emerged in the field before the galls were collected, (2) some gallers may have been killed by parasitoids failing to complete their cycle, and (3) the optimal conditions for the development of insects may have not been reached for all species in the lab. These limitations are common to all studies involving insect rearing in laboratorial conditions (Fisher et al. 1999).

In conclusion, and despite a relatively low emergence rate, our results revealed highly diverse gall communities in coastal habitats, both in terms of richness and abundance of these underexplored guilds. Turnover rates and phenology of the different guilds provide a much deeper

understanding of the dynamics of gall communities and revealed how different guilds dominate these poorly known communities along the year, potentially affecting other species that depend on these resources. Naturally, the composition, structure and resilience of these communities are contingent upon several biotic and environmental factors. Therefore, the baseline information reported here is likely to prove highly valuable in the future to monitor community changes as a response of the many external threats such as biological invasions and climate change.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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