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2 # Time-since fire and cynipid gall wasp assemblages on oaks

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6 **Abstract**
7 Fires are ubiquitous features of many terrestrial ecosystems and can greatly impact the
8 structure and evolution of plant communities. However, much less is known about how fire
9 history impacts higher trophic levels. Using detailed records on the history and intensity of
10 fires at the Archbold Biological Station (ABS) in central Florida, USA, we examined how
11 time-since-fire affects the cynipid gall wasp assemblage (Hymenoptera: Cynipidae) associ-
12 ated with four oak species (*Quercus*) that are dominant components of the plant commu-
13 nity in this region. Cynipid abundance, richness and diversity were quantified from 1249
14 oak trees/shrubs in 20 sites that varied in time-since-fire from 1.5 to 91 years. Among all
15 sites and oaks, we found 24 species of cynipids and there was very little species overlap
16 among oak species, even within the same site. Gall abundance increased with time-since-
17 fire and was correlated with tree height, suggesting that available host material or plant
18 architecture may be a primary driver of cynipid recovery. Within 3 years of a fire, 14 of
19 the 23 cynipid species were detected among the sites, and by seven years since fire, all but
20 two species could be detected. Overall, species richness and diversity reached an asymptote
21 within ≈ 7 years. Given how quickly the cynipid assemblage recovers after a fire, frequent
22 fires at ABS are unlikely to negatively impact these insects. However, in smaller or more
23 isolated scrub-oak fragments, recovery could be much slower.

24 **Keywords** Fire management · *Quercus* spp. · Species richness · Time-since fire

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Introduction

Understanding how communities assemble and the factors that affect community structure have been central issues in the field of ecology. Natural and anthropogenic disturbances such as fires, droughts and hurricanes are ubiquitous features of terrestrial communities that can profoundly influence community structure (Dayton 1971; Connell 1978; Sousa 1984; Petraitis et al. 1989; Collins 1992). Fire is a particularly important disturbance to plant communities because it removes biomass, affects the quality and quantity of soil nutrients and water, and can be a key selective agent in the evolution of natural communities (Bond and Keeley 2005; Certini 2005; Keeley et al. 2011; Pausas and Keeley 2019). To date, much less attention has been paid to the impacts of fire on higher trophic levels, such as insect herbivores (Kim and Holt 2012). Depending on the scale and intensity of fires, the impacts on herbivore populations and higher trophic levels can range from minimal to complete local extirpation; at least in the short term (Swengel 2001; Knight and Holt 2005). Less mobile species such as flightless insects or species in a sedentary life stage (e.g., egg and pupal stages, leaf miners and galls) are particularly vulnerable to fires.

Insect populations may recover from fires by in situ survival of individuals or through recolonization from nearby unburned areas or refugia (Harper et al. 2000; Panzer 2003). Following an intense fire, herbivore abundances and species richness are expected to be low in early successional stands and then increase over time (Kim and Holt 2012). If recruitment is primarily by recolonization, early successional stands may be dominated by highly mobile taxa or those with strong refuge-seeking strategies (Kim and Holt 2012). Later successional stages should have a greater proportion of herbivore species that are less mobile or more fire sensitive (Swengel 2001; Joern 2005; Knight and Holt 2005; Kim and Holt 2012). For example, Mutz et al. (2017) found that the abundance of a tortoise beetle of saw palmetto (*Hemisphaerota cyanea*) generally increased with time-since fire. Similarly, Garcia et al. (2016) found that specialist herbivores (seed-feeding weevil and myrid bug), but not generalist herbivores, were less abundant on their host plants in recently burned compared to unburned sites. Interestingly, Kaynaş and Gürkan (2008) found the opposite relationship between time-since-fire and abundance for herbivores of pine forest of the Mediterranean (see also Uehara-Prado et al. 2010). Clearly, more studies are needed that examine the relationship between fire histories and how herbivore communities are assembled following fires.

Prescribed fires are increasingly being used to manage fire-dependent systems. In addition to reducing fuel loads to mitigate threats to urban areas (North et al. 2015), the priority of fire management plans is usually to improve plant biodiversity or provide habitat for game animals, endangered species or other charismatic species (Parr and Andersen 2006; Clarke 2008). Promoting insect herbivore or higher trophic level diversity may be an implicit goal of fire-management programs but it is rarely explicitly considered (Parr and Andersen 2006; but see Martinez-Torres et al. 2015). Given the immeasurable importance of arthropod herbivores and their natural enemies to ecosystem function (Price et al. 2011), it is essential that they be more carefully considered in the development and evaluation of fire management plans.

The Lake Wales Ridge in Peninsular Florida is composed of relict sand dunes within which the plant communities are highly fire dependent (Abrahamson 1984a; Myers 1990; Platt et al. 1991) and at the Archbold Biological Station (ABS) at the southern end of the Lake Wales Ridge, prescribed fires have been implemented since 1977. Although much research has been conducted on the impact of fires on components of the plant community

(e.g., Abrahamson 1984b; Menges and Hawkes 1998; Weekley and Menges 2003; Kettenring et al. 2009; Evans et al. 2010; Dee and Menges 2014) and with regard to some vertebrate species (e.g., Ashton et al. 2008; Ashton and Knipps 2011; Schrey et al. 2011; Fitzpatrick and Bowman 2016), very little is known about its impact on the arthropods (but see Menges and Deyrup 2001; Carrel 2008; Kim and Holt 2012).

Here, we take advantage of ABS's detailed records on the history and intensity of fires to examine how time-since-fire affects the cynipid gall wasp assemblage associated with oaks (*Quercus*) that are dominant components of the plant community in this region. Although cynipids have been the subject of numerous community-ecology studies (e.g., Cornell 1985a, b, 1986; Abrahamson et al. 1998b; Price et al. 2004; Williams and Cronin 2004; Maldonado-López et al. 2015), no studies to date have examined how their communities assemble following a disturbance. Using replicated forest/scrub sites that were subjected to high-intensity burns ranging from 1.5 to 91 years ago, we determined cynipid gall abundance, species richness and diversity on four oak species. We tested the prediction that abundance, richness and Shannon–Wiener diversity increased with time-since-fire. We also examined whether members of the cynipid assemblage were fire sensitive (i.e., limited to sites with a long time-since-fire) or were specialists of particular post-fire successional stages.

Materials and methods

Study area

The research was conducted at the ABS, 12 km south of Lake Placid, Florida (27.183° N, 81.350° W). Soils are typically comprised of xeric white or yellow sands that are excessively well drained, acidic and nutrient poor. Three common habitats in this region are scrubby flatwoods (also known as oak scrub), sand pine scrub and ridge sandhills (Abrahamson et al. 1984). Scrubby flatwoods are dominated by the evergreen, xeromorphic oaks *Quercus inopina* (scrub oak), *Quercus chapmanii* (Chapman's oak), and *Quercus geminata* (sand live oak), as well as *Serenoa repens* (saw palmetto) and *Sabal etonia* (scrub palmetto). The oak *Quercus myrtifolia* (myrtle oak) is relatively rare and the pines, *Pinus clausa* (sand pine) and *Pinus elliottii* (slash pine), are also present but widely scattered. In contrast, sand pine scrub has an overstory of *P. clausa* and an intermediate canopy of shrubby oaks including *Q. geminata*, *Q. chapmanii*, *Q. myrtifolia* and less commonly *Quercus laevis* (turkey oak). Finally, southern ridge sandhills are open woodlands with a slash pine overstory and mid-canopy of *Q. geminata*, *Q. chapmanii*, *Q. myrtifolia*, *Q. laevis*, and *Carya floridana* (scrub hickory). Details of the vegetation in these habitats are available in Abrahamson et al. (1984), Abrahamson and Hartnett (1990) and Myers (1990). Today, only remnants of these habitats exist (approximately 85% has been lost due to human activities) and this region is of significant conservation concern (Abrahamson 1984a; Myers 1990; Deyrup and Eisner 1993; Stap 1994; Weekley et al. 2008).

Historically, lightning-ignited fire has been a natural and common phenomenon in Florida and has played an integral role in shaping the landscape (Myers 1990; Platt et al. 1991; Glitzenstein et al. 1995). Periodically burned scrubby flatwoods are resilient to fire and within a few years can return compositionally and structurally to their pre-burn states (Abrahamson 1984a; Schmalzer and Hinkle 1992; Abrahamson and Abrahamson 1996a, b). Sand pine scrub becomes ignited only rarely and under natural conditions fire frequency

is likely on the order of every 20–100 years (Webber 1935; Abrahamson 1984a; Menges et al. 2017). Scrubby flatwoods and southern ridge sandhill burn more frequently, with fire-return intervals of 6–19 years for the former and 2–5 years for the latter habitat (Harper 1927; Abrahamson 1984a; Menges et al. 2017).

At ABS, active fire suppression began in the late 1920s and continued until 1977 (Main and Menges 1997). Beginning in 1977, prescribed fires have been used at ABS and in 1997, ABS implemented a formal fire-management plan with the goals of mimicking natural processes (fire-return intervals, fire intensity), enhancing biodiversity and reducing fire hazards through the reduction of fuel levels (Main and Menges 1997; Menges et al. 2017). ABS maintains an extensive GIS database for the station property that includes detailed maps of vegetation composition, and the location and intensity of fires dating back to early 1990s. Records of fires predating this period are available but not part of the current database. Overall, these detailed records of fire history, intensity and vegetation composition provide an ideal opportunity to assess how fire influences community assembly in oak-gall wasps.

Oak–cynipid system

The oak-gall wasps in the Cynipini Tribe (Hymenoptera: Cynipidae) are comprised of 750–800 species worldwide (Melika and Abrahamson 2000a). The host range of these cynipines is generally restricted to one or a few closely related oak species in the genus *Quercus* (Abrahamson and Weis 1997; Abrahamson et al. 1998a, b, 2003) and the wasp attacks a specific plant part; e.g., a leaf vein, stem node, dormant bud, flower part, or fruit. Upon hatching, the wasp larva initiates the production of a morphologically complex gall structure (Askew 1980) which provides the developing wasp with nutrition and a degree of protection from the elements and natural enemies (Askew 1975, 1980; Washburn and Cornell 1981, 1983; Abrahamson and Weis 1987; Stone et al. 2002). Gall structure is highly distinctive and, in most cases, can be used for accurate species identification (Cornell 1983, 1985a; Abrahamson et al. 2003; Maldonado-López et al. 2015).

Experimental plan

Using archived ABS fire-history data, we selected 20 sites that varied in time-since-fire from 1.5 to 91 years (Fig. 1, Appendix 1). Sites were also limited to three habitat types: scrubby flatwoods, southern ridge sandhill and sand pine scrub. With the exception of our oldest time-since-fire sites (> 19 years), we selected sites that were standardized with regard to fire severity—choosing sites classified in the highest severity burn category, category four. Fire severity was determined from ground and aerial surveys conducted shortly after a burn with a precision of ca. 3 m (Menges et al. 2017). According to Menges et al. (2017), high-severity burn sites exhibited consumption of litter, leaves, twigs, and palmetto leaf blades and it is unlikely that the oak–cynipid community could have survived. This conclusion is supported by our own observations that there are no live cynipids in galls shortly after a high-intensity burn (Cronin and Abrahamson personal observation). Consequently, we conclude that our sites with a time-since-fire of < 19 years must have been recolonized by cynipids following the burn. This was important because we wanted our younger sites to begin cynipid community assembly from a clean slate. For sites burned prior to 1989, we do not have information on burn severity. Oaks in these latter sites were substantially more mature (19–91 years since fire) than those in which burn severity was
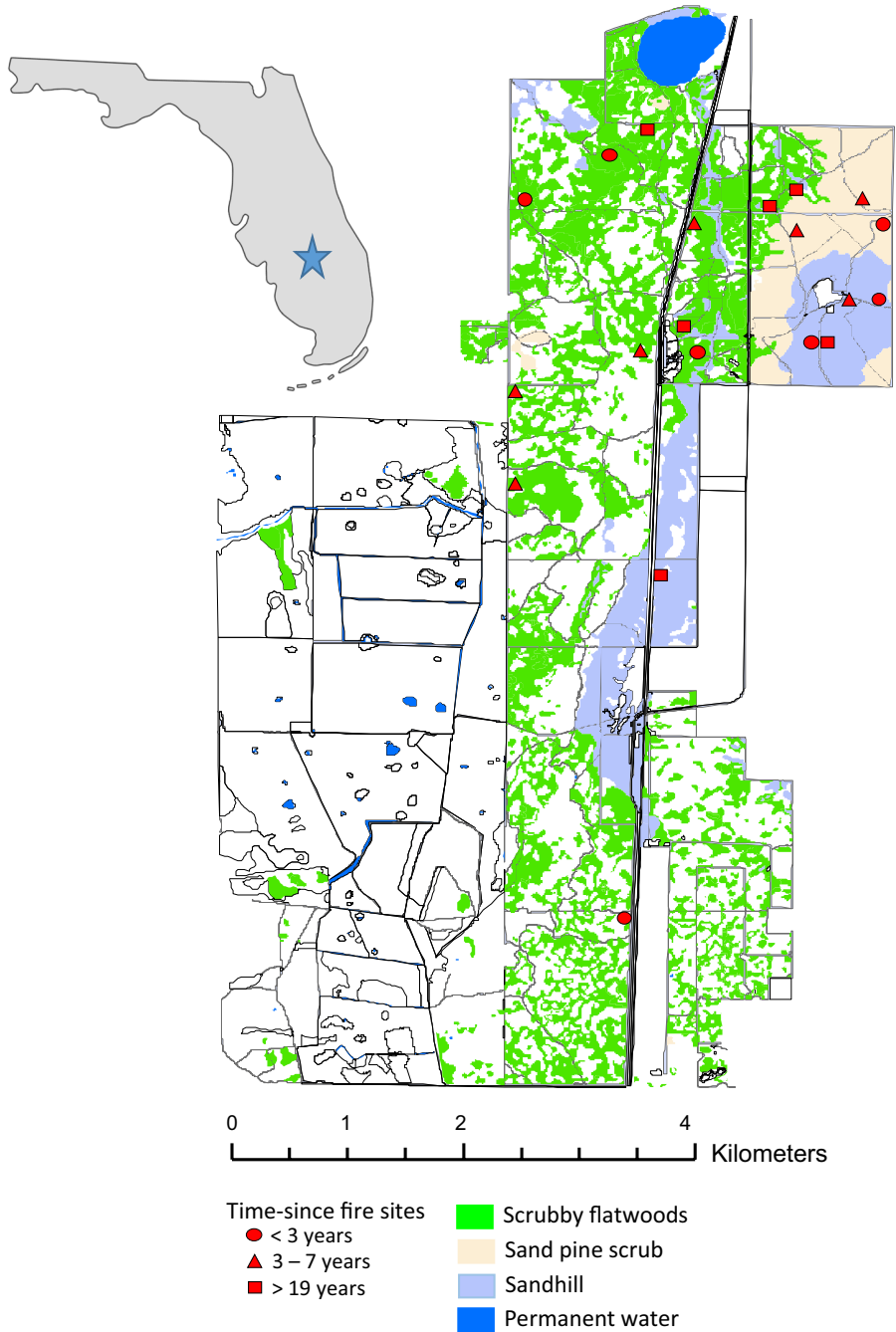
Fig. 1 Map of field sites at Archbold Biological Station, Highlands County, Florida, USA

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known. We assumed with these older sites that the signal remaining from the fire's severity would be weak and have little impact on cynipid community metrics. Based on the above criteria, maps of candidate sites were produced from the ABS GIS database and the suitability of these sites was confirmed via brief on-site inspection. Except in the case of sites #1 and #5 (ABS section 2B, Appendix 1), each burned site represented a different burn. Section 2B represented a large burn and the two sites were 800 m apart.

We conducted our surveys in two different years, late January to early February, 2018 and late January, 2019. Because of time constraints, surveys in two different years were necessary to achieve sufficient replication of sites for the study. We acknowledge here that, although the oaks we sampled are evergreen, galls are more ephemeral and seasonal plant parts (e.g., catkins or acorns) with galls would be missed in our samples. For example, a multiple-year, year-round sampling at ABS found 12 cynipid gallers on *Q. geminata* (Price et al. 2004) whereas our winter sampling found only 7 species. Therefore, our surveys reflect the abundance and richness of persistent galls, not the entire cynipid gall-wasp community.

At each site, we walked transects perpendicular to the adjacent fire road or jeep trail. Every five paces, the nearest oak (in front or to the side of the investigator), for each species present at the site, was selected for inspection. *Quercus chapmanii* and *Q. geminata* occurred in abundance at all 20 sites but *Q. inopina* was often scarce in ridge sandhill and sand pine scrub and *Q. myrtifolia* was rarely found in scrubby flatwoods. As a result, only three sites were represented by all four oak species. The remainder of sites had three oak species each. We measured stem height with a tape measure or measuring pole (to the nearest cm) and stem diameter at the base of the plant with Vernier calipers (to the nearest mm). Oaks in the Florida scrub are dwarf trees and heights in our study sites rarely exceeded 6 m. For oaks less than ca. 3 m tall, we carefully inspected every bud, leaf, twig and stem for the presence of a gall and counted the number of individual galls for each species. For taller trees, we inspected plant parts within reach and did the same for branches cut from the middle and crown of the tree using a pole trimmer. In these cases, we also estimated the proportion of the tree/shrub that was inspected. Only for the older sites (> 19 years since burned) did we need to subsample oaks. However, 86% of all oaks in those sites were fully sampled and of those that were subsampled, an average of 55% of the tree was inspected. To account for this incomplete sampling of larger trees at some sites, we obtained a corrected gall abundance per tree by dividing gall counts per tree by the proportion of the tree sampled. At each site, we continued walking a transect (or parallel ones at least 5 m away) until we inspected 20 trees per oak species.

The oak cynipids present at ABS have been studied extensively by Abrahamson and colleagues (Melika and Abrahamson 1997a, b, 2000a, b, 2007; Abrahamson et al. 1998a, b, 2003; Price et al. 2004). Seventy-four species have been identified from five species of oaks at ABS and a pinned reference collection of wasps and their galls is available in the Arthropod Collection. We consulted this collection in developing a pictorial guide to cynipid species found on each oak species during the period when we conducted our census (see Appendix 2).

Statistical analyses

Our primary interests focus on how time-since fire influences oak cynipid abundance, richness, diversity and composition at the scale of the burned plot. As there were many individual oaks with zero galls, particularly in the recently burned sites, we opted to combine

the 20 trees/shrubs per oak species at each site to compute gall abundance, richness and Shannon–Wiener diversity. We note here that analyses conducted at the tree scale or the site scale yielded nearly identical results.

We used the Vegan package in R (version 3.4.3; R Core Team 2013) to compute the Shannon–Wiener diversity index. Also, to assess whether our richness estimates were asymptotic, we computed Chao 1 for each oak species and site (Gotelli and Colwell 2010). In only one of 63 cases did we obtain an estimate of asymptotic richness that was greater than our actual count (Site 16, 4.5 years since burned, *Q. chapmanii*, 7.5 versus 7 species). We conclude that our surveys were sufficiently extensive to reflect the asymptotic richness of these sites and we therefore use our raw data on species richness. Moreover, this finding suggests that incomplete sampling of larger trees in sites with long time-since-fires had no effect on our estimates of richness.

We used separate generalized linear mixed models (GLMMs) to test whether gall abundance, cynipid species richness or cynipid diversity per site was related to oak species, time-since-fire, oak species×time-since-fire interaction and mean tree/shrub height. To test for the possibility that the above response variables were asymptotic with regard to time-since-fire, we also included time-since-fire^2 as a predictor in the model. Site and year of data collection were treated as random effects in the model to account for the potential nonindependence among oak species within a site and interannual variation in cynipid community metrics, respectively. Because stem diameter was strongly correlated with tree height ($R=0.87$, $P<0.001$, $n=1249$), we excluded diameter from the analysis. Although our site surveys were conducted in three distinct vegetation types (scrubby flatwoods, sand-pine scrub or ridge sandhill), we did not have sufficient statistical power to include this as a fixed effect in our model. Tree height and time-since-fire were *ln*-transformed to satisfy model assumptions about normality and homogeneity of variances. Also, for the mixed-effects model for gall abundance, the error term was defined as Poisson. For all other response variables, the error terms were defined as normally distributed. Finally, the data were analyzed using Proc GLIMMIX in SAS® version 9.4 (SAS Institute, Inc., Cary, NC, USA).

Pairwise differences among oak species in response variables were assessed using Tukey–Kramer tests. Differences among oak species in the slopes of the relationship between time-since-fire and our response variables were assessed with *t*-statistics using the Estimate command in SAS Proc PLM. To control for type I errors associated with multiple comparisons, *P*-values for differences among slopes were Bonferroni corrected.

Results

During the course of this study, we inspected 1249 oak tree/shrubs divided among 20 sites and four oak species common at ABS: *Q. geminata* ($n=406$), *Q. chapmanii* ($n=411$), *Q. inopina* ($n=224$) and *Q. myrtifolia* ($n=208$). As expected, mean oak height was the shortest in sites that had burned recently and increased linearly with time-since-fire (Fig. 2a; Table 1). Independent of time-since-fire, *Q. chapmanii* and *Q. myrtifolia* were similar in height, with least-squares means of 122 ± 7 cm and 115 ± 7 cm, respectively (Tukey–Kramer test, $t_{37}=1.18$, $P=0.24$). Both of these oaks were significantly taller than *Q. geminata* (93 ± 5 cm) and *Q. inopina* (87 ± 6 cm) (Tukey–Kramer test for all comparisons, $P<0.006$). The increase in height with time-since-fire also differed among oak species (Table 1): *Q. chapmanii* and *Q. geminata* had similarly steep slopes (0.49 ± 0.15 and
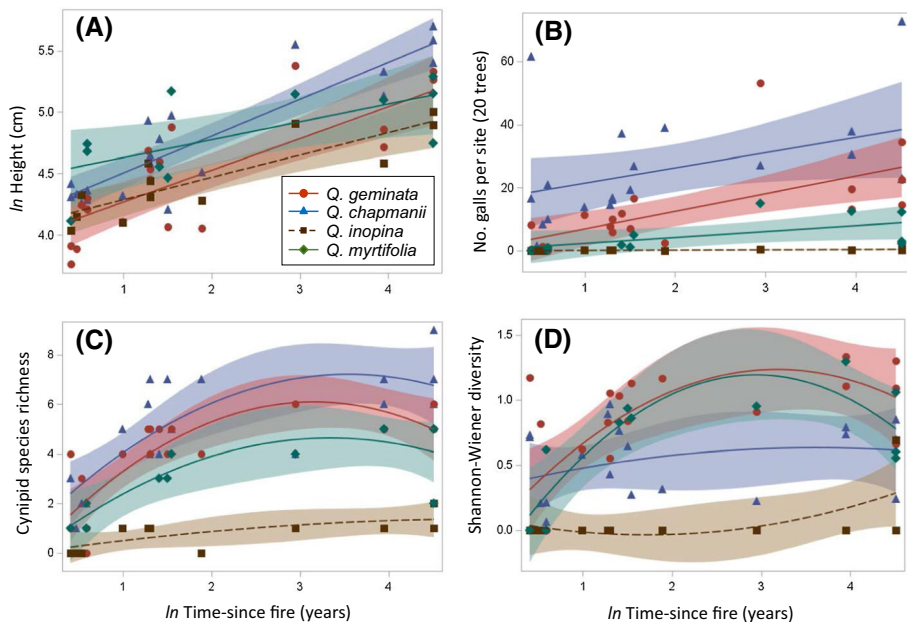
Fig. 2 The relationship between time-since-fire and oak species on **a** mean tree height (*ln*-transformed), **b** mean gall abundance (20 trees combined), **c** species richness and **d** Shannon–Wiener diversity per site. Lines for each oak species are fit by least-squares regression and a quadratic term was included in the models for species richness and diversity. Significance of the relationship between each response variable and time-since-fire can be found in Table 2

251   0.45 ± 0.15, respectively; $t_{37} = 1.41$, $P = 0.99$), averaging 26% higher than the slopes for
252   the other two oaks (*Q. myrtifolia*: 0.34 ± 0.16, *Q. inopina*: 0.36 ± 0.15; all comparisons,
253   $P < 0.05$).
254   Gall abundance per site (summed over 20 trees) was strongly dependent on oak spe-
255   cies (Table 1; Fig. 2b). There was also a strong oak species × time-since-fire interaction
256   in the GLMM indicating that the oak species have significantly different slopes in the
257   relationship between gall abundance and time-since-fire (Table 1; Fig. 2b). *Quercus chap-*
258   *manii* had the greatest overall abundance, averaging 386 ± 36 galls per site ($\pm$ SE) in sites
259   burned < 2 years ago and increasing by an average of 73% from the most recent to the old-
260   est time-since-fire sites (based on a least-squares regression model; Fig. 2b). Interestingly,
261   one of the youngest and oldest time-since-fire sites had the highest gall abundance on *Q.*
262   *chapmanii*, 1220 ± 308 and 1266 ± 416 galls, respectively. *Quercus geminata* had the sec-
263   ond highest gall abundance, with 64 ± 34 galls per 20 trees for sites burned < 2 years ago
264   and a predicted 5.8-fold increase across the entire range of time-since-fire ($1.5 = 91$ years;
265   Fig. 2b). *Quercus myrtifolia* had fewer galls on average with gall abundances rising from
266   a predicted 22 galls per 20 trees in sites burned just < 2 years ago to 170 galls per 20 trees
267   in the oldest burn sites, a 7.8-fold increase. In contrast, *Q. inopina* had very few galls
268   regardless of time-since-fire (2.8 ± 1.2; Fig. 2b). All pairwise comparisons of gall abun-
269   dance between oak species were statistically significant based on a Tukey–Kramer test
270   ($P \leq 0.02$ in all cases). There was no evidence that the relationship between time-since-fire
271   and gall abundance was nonlinear (i.e., the quadratic term in the model was not significant;

Table 1 Results from separate GLMMs for the effects of time-since-fire, time-since-fire^2, oak species and the interaction of time-since-fire and oak species (Fire × Oak) on mean tree height, mean gall abundance per tree, species richness and Shannon–Wiener diversity per site

Response variable	Effect	Num DF	Den DF	F	P
Tree height	*ln* Time-since-fire	1	37	6.69	0.0138
	ln Time-since-fire^2	1	37	1.54	0.2223
	Oak species	3	37	7.43	0.0005
	Fire × Oak	3	37	9.64	< 0.0001
	ln Time-since-fire	1	36	1.77	0.1912
	ln Time-since-fire^2	1	36	0.62	0.4345
Gall abundance	Oak species	3	36	41.4	< 0.0001
	Fire × Oak	3	36	12.55	< 0.0001
	ln Height	1	36	5.99	0.0194
	ln Time-since-fire	1	36	17.62	0.0002
	ln Time-since-fire^2	1	36	13.03	0.0009
Richness	Oak species	3	36	8.19	0.0003
	Fire × Oak	3	36	1.87	0.1524
	ln Height	1	36	0.66	0.4226
	ln Time-since-fire	1	36	5.59	0.0236
Shannon diversity	*ln* Time-since-fire^2	1	36	4.51	0.0406
	Oak species	3	36	4.62	0.0078
	Fire × Oak	3	36	1.59	0.2091
	ln Height	1	36	0.59	0.4476

For the latter three response variables, height was included as a covariate in the model. Time-since-fire and height were *ln*-transformed prior to the analyses. Random factors in each model included the survey site and year of survey. Reported are the numerator and denominator degrees of freedom (Num DF and Den DF, respectively), F statistic and P-value

Table 1). The slope of the linear relationship between time-since-fire and gall abundance was 1.9 and 2.5 times lower for *Q. chapmanii* than *Q. geminata* (t_{36} = 5.89, P < 0.001) and *Q. myrtifolia* (t_{36} = 3.32, P = 0.012), respectively. All other comparisons among slopes were not significant. Finally, there was also a significant positive effect of mean tree/shrub height on gall abundance ($F_{1,36}$ = 5.99, P = 0.019; Table 1; Fig. 3). Time-since-fire and mean tree/shrub height are necessarily confounded variables. With mean tree height included as a predictor variable in the GLMM, time-since-fire category on its own was not a significant factor (Table 1). However, if tree height is removed from the analysis, time-since-fire ($F_{1,37}$ = 7.49, P = 0.010) and its interaction with oak species ($F_{3,37}$ = 10.88, P < 0.001) are significant factors affecting gall abundance. Specifically, the slope of the relationship between time-since-fire and gall abundance was significantly positive for all four oak species (all cases, t_{37} ≥ 2.18, P ≤ 0.035).

Cynipid species richness was also strongly affected by oak species and fire history (Table 1; Fig. 2c). For all four oak species, richness increased with time-since-fire ($F_{1,36}$ = 17.62, P < 0.001) but tended to level off after ≈ 7 years (time-since-fire^2: $F_{1,36}$ = 13.02, P < 0.001). Least-squares mean number of cynipid species among 20 oak trees/shrubs was 4.88 ± 0.26 for *Q. chapmanii*, 4.00 ± 0.25 for *Q. geminata*, 3.01 ± 0.34 for *Q. myrtifolia* and 0.84 ± 0.32 for *Q. inopina*. All possible pairwise comparisons were significantly different (Tukey–Kramer test, P ≤ 0.002). Maximum species richness for a site

Fig. 3 The relationship between mean gall abundance per site (20 trees combined) and mean tree height for each oak species. Each point represents a different site and lines are fit by least-squares regression
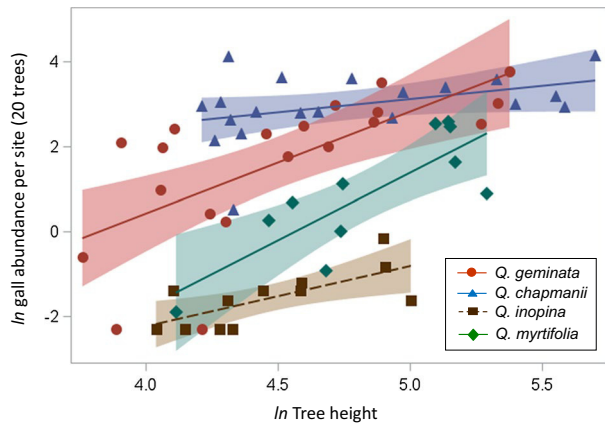
was 9 (time-since-fire = 91 years), 6 (19 and 91 years since fire), 5 (≥ 52 years since fire) and 2 (91 years since fire) for *Q. chapmanii*, *Q. geminata*, *Q. myrtifolia* and *Q. inopina*, respectively. Unlike for gall abundance, there was no significant interaction between oak species and fire history or effect of mean tree/shrub height on species richness (Table 1).

Finally, Shannon–Wiener diversity mostly followed the same pattern as that for species richness. Independent of oak species, diversity was generally lowest in the most recently burned sites and increased asymptotically with time-since-fire (Table 1; Fig. 2d). This relationship was driven primarily by the cynipids on *Q. geminata* and *Q. myrtifolia*. Separate tests for each species revealed significant time-since-fire and time-since-fire^2 effects for *Q. geminata* and *Q. myrtifolia* [*Q. geminata*: time-since-fire ($F_{1,15} = 6.69$, $P = 0.021$), time-since-fire^2 ($F_{1,15} = 5.20$, $P = 0.037$)]; *Q. myrtifolia*: time-since-fire ($F_{1,6} = 18.68$, $P = 0.005$), time-since-fire^2 ($F_{1,6} = 16.12$, $P = 0.007$) but not for the other two species (all tests, $P > 0.15$). Pairwise-comparison's tests based on least-squares means yielded the following rankings of diversity (highest to lowest): *Q. geminata* (0.81 ± 0.07) > *Q. myrtifolia* (0.66 ± 0.09) > *Q. chapmanii* (0.50 ± 0.07) > *Q. inopina* (0.08 ± 0.09). However, the only statistically significant differences were between *Q. geminata* and *Q. chapmanii* ($t_{36} = 3.21$, $P = 0.003$) and between *Q. inopina* and all other oak species (all comparisons, $P < 0.001$).

To better visualize the compositional change in cynipid communities as time-since-fire increases, we divided our sites into burn categories. Sites were divided according to natural breaks in the distribution of times-since-fire: < 3 years ($n = 7$), 3–7 years ($n = 7$) and ≥ 19 years ($n = 6$) (Appendix 3). Compositionally, the change in the cynipid assemblage as time-since-fire increased was only the result of new species being added to the assemblage. No species dropped out of the assemblage as the shrub/forest community matured. For *Q. chapmanii*, 3 of the 10 cynipid species found on this oak species were not detected until the time-since-fire was greater than three years: *Sphaeroterus melleum*, *Disholcaspis quercusomnivora* and *Bassettia pallida* (Appendix 3). These cynipid species were present in at least one site in each of the older two fire categories. All but one of the seven cynipid species found on *Q. geminata* were present in sites from each fire category. The exception was *Belonocnema quercusvirens* which only appeared in sites burned ≥ 19 years ago. *Quercus myrtifolia* had a total of six cynipid species, four of which were not detected in the most recently burned sites: *Callirhytis quercusclavigera*, *C. difficilis*, *C.* sp. 1 (rough stem gall) and *C.* sp. 2 (leaf cigar). *Quercus inopina* had very low gall abundance and only

323 a total of two cynipid species. Finally, because there was almost no overlap in gall species
324 among the four oaks (only one case: *Amphibolips murata* on the red oaks *Q. myrtifolia* and
325 *Q. inopina*), an analysis of compositional differences among oaks was unnecessary.

Discussion

327 Fires are a common occurrence in oak-dominated communities (Abrams 1992; Callaway
328 and Davis 1993; Peterson and Reich 2001) and in the face of predicted climate change,
329 fire frequency is likely to increase in many of these areas (Flannigan et al. 2000, 2009;
330 Abatzoglou and Williams 2016). This study is the first to demonstrate how fire history can
331 affect one of the most important and diverse herbivore assemblages of oaks, the cynipid
332 gall wasps. For oaks in xeric scrub/forest habitats in central Florida, we find that although
333 gall number steadily increases with time-since-fire, richness and diversity tend to asymp-
334 tote within 7 years. The fire-return intervals employed in the ABS fire-management plan
335 are within this time frame (Main and Menges 1997; Menges et al. 2017) and, thus, are
336 likely near optimal for the conservation of cynipid biodiversity (see below).
337 Twenty-four species of cynipid gall wasps were found in our winter surveys of the four
338 most common *Quercus* species at ABS. The near complete absence of shared cynipid spe-
339 cies among oaks (the only exception was *A. murata* on the two oaks, *Q. myrtifolia* and
340 *Q. inopina*), even for oaks growing in physical contact with each other, is in accordance
341 with the findings of Abrahamson et al. (1998b, 2003). In particular, red and white oaks are
342 known to have sufficiently different chemistry that they have unique cynipid assemblages
343 (Abrahamson et al. 1998a, 2003). This high degree of host specificity is common among
344 gall-forming insects (Csoka et al. 1998; Redfern 2011; Knuff et al. 2019). After a fire,
345 when oaks are resprouting, there should be an abundance of actively growing, undifferenti-
346 ated plant tissues that are ideal for gall induction (Price 1991). However, even under these
347 circumstances, host-specificity of the cynipid assemblages remained intact (Appendix 3).
348 Given the extreme oak species and plant organ specialization by the cynipids, we would
349 expect that suitable host tissues would be a serious limiting factor immediately following
350 a fire. Indeed, gall-forming herbivores are commonly limited by the abundance of their
351 hosts (Cuevas-Reyes et al. 2014; Altamirano et al. 2016). Our more recently burned sites
352 (time-since-fire < 19 years) were chosen because they experienced high-intensity fires.
353 Under these circumstances, recovery of the cynipid wasp assemblage must have been initi-
354 ated from recruitment outside of the burned stand. As such, the immediate and short-term
355 effects of fire on the cynipid assemblage are direct. Direct effects of fire on herbivores,
356 which could include killing or injuring the herbivores or causing their starvation following
357 the temporary elimination of suitable hosts, are particularly likely to be detrimental to sed-
358 entary species or life stages. Such direct effects have been generally overlooked (Vermeire
359 et al. 2004; Knight and Holt 2005; Vogel et al. 2010; Kim and Holt 2012). Fires are widely
360 reported to have significant long-term effects on plant abundance, distribution, chem-
361 istry and vegetation structure (e.g., branching, seed production) which can subsequently
362 impact herbivore assemblages (Evans 1984; Bock and Bock 1991; Kerstyn and Stiling
363 1999; Swengel 2001). Following the recolonization of a burned site by herbivores, these
364 fire effects on plants are likely to have strong indirect effects on structuring the herbivore
365 assemblage (Knight and Holt 2005; Kim and Holt 2012).
366 Accumulation of cynipid species and an increase in their abundances are expected
367 to be concomitant with the regrowth of the oaks, both in terms of increased biomass

368 and architectural complexity. For all four oak species, we found that cynipid abundance
369 increased with plant height (Fig. 3). It was also the case that the small-statured *Q. inopina*
370 had the fewest galls and the tallest of our four species, *Q. chapmanii*, had the most galls
371 per tree (Fig. 2b). Although a positive host-size–herbivore abundance relationship has been
372 commonly reported for other herbivore taxa (e.g., Garcia et al. 2016; Mutz et al. 2017), our
373 results are in the opposite direction of that reported by Price et al. (2004) for their survey of
374 cynipids at ABS. This latter study was limited to sites with no recent fire history but even
375 if we constrain our analysis to mature sites (i.e., time-since-fire > 19 years), we still find a
376 positive linear relationship between tree height and gall abundance (least-squares regres-
377 sion: $R^2 = 0.33$, $P = 0.006$, $n = 21$; all oak species combined). One possible explanation for
378 the difference between our two studies is that Price et al. (2004) conducted their surveys in
379 October when less persistent galls (e.g., on acorns) were present.

380   Naturally, time-since-fire and plant biomass or height should be positively correlated.
381 In our analyses, time-since-fire was only related to cynipid abundance when oak height
382 was excluded from the analysis. This result suggests that cynipid abundance in our system
383 may be driven primarily by availability of host material or complexity of tree architecture
384 (Denno 1983; Lawton 1983; Campos et al. 2006; Neves et al. 2014). In fact, for many
385 gall-forming species, plant architecture (e.g., height, number of shoots, leaves, branching
386 structure) is strongly related to gall abundance (Quiring et al. 2006; Lara et al. 2008; Spaw-
387 ton and Wetzel 2015). In future studies with the oak cynipids at ABS, it would be inform-
388 ative to investigate what architectural aspects associated with plant height are primarily
389 responsible for the strong plant height–gall abundance correlation. In contrast with gall
390 abundance, time-since-fire but not oak height was an important predictor of richness and
391 diversity. We suggest that recruitment of cynipid species proceeds at relatively fast rate,
392 saturating within seven years. With shrub/tree heights steadily increasing with time-since-
393 fire, height and cynipid richness become decoupled. The presence of a plant architecture
394 effect on gall species richness has been reported in some (Espírito-Santo et al. 2007; Spaw-
395 ton and Wetzel 2015) but not all cases (de Araújo et al. 2013).

396   Our study of oak cynipids provides support for the prediction that herbivore abundance
397 and species richness generally increase with time-since-fire (Swengel 2001; Kim and Holt
398 2012), regardless of whether or not it is mediated through changes in resource availability
399 or architectural complexity. This result appears consistent regardless of the oak species at
400 ABS. The very low gall abundance and cynipid species richness on *Q. inopina* is likely
401 related to its small stature and architectural simplicity (see above) as well as the fact that it
402 is a Florida endemic (Christman and Judd 1990) and has the smallest distributional range
403 of our four oak species (Price 1980; Strong et al. 1984; Price et al. 2004). In fact, Cornell
404 (1985a) concluded that at the regional scale, a primary determinant of cynipid species rich-
405 ness was the range of its host.

406   Interestingly, tree/shrub height and gall abundance per tree generally increased with
407 time-since-fire but species richness and diversity appeared to asymptote within seven
408 years after a fire. Although a number of studies have reported a similar increase in her-
409 bivore abundance and richness with time-since-fire, the opposite finding is also common
410 (for review, see Swengel 2001). For example, insect species spanning a number of families
411 are known to be attracted to recently burned sites; thus favoring a negative relationship
412 between time-since-fire and community metrics (Swengel 2001; Kaynaş and Gürkan 2008;
413 Uehara-Prado et al. 2010). Even studies in the same habitat have shown different relation-
414 ships for different tree species (Swengel 2001). For example, Kim and Holt (2012) work-
415 ing in the scrubby flatwoods at ABS found a positive non-asymptotic relationship between
416 time-since-fire and the abundance and species richness of free-living herbivores (caught in

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insect nets) associated with *Q. inopina*. No time-since-fire effects were observed for free-living herbivores associated with *Q. geminata* or *Q. chapmanii*.

Our surveys suggest that within 3 years of a fire, 14 of the 23 cynipid species have recolonized the site (Appendix 3). By seven years since fire, all but two species were present, *B. quercusvirens* on *Q. geminata* and *Zapatella quercusmedullae* on *Q. inopina*. All of our sites were embedded in a scrub/forest mosaic with different burn histories and, as such, sources of cynipid colonists were always nearby. So, it is not too surprising that these sites were colonized relatively quickly. Had the sites been discrete and isolated scrub habitats, as are common along the Lake Wales Ridge (Abrahamson 1984a; Myers 1990), we would expect a much slower accumulation of cynipid species.

To our knowledge, there has never been an explicit study of cynipid dispersal. In a comparative study involving both gall-forming cecidomyid flies and cynipids on Florida oaks, Price et al. (2004) determined that the cynipids had more localized distributions than the cecidomyids and inferred from this that the former were more dispersal limited. In another large-scale study, Gilioli et al. (2013) used a reaction–diffusion model to show that the discontinuous spread of the chestnut gall wasp (*Dryocosmus kuriphilus*; Cynipidae) in Italy could be the result of both short and long-distance dispersal mechanisms. From a conservation perspective, smaller-scale dispersal experiments would be quite valuable in determining whether movement from nearby sources is gradual; e.g., diffusive spread from neighboring unburned trees or through longer-distance dispersal. If it is only by the former, recolonization of intensively burned and isolated scrub fragments may occur at a pace far slower than the normal burn periodicity in this region (for scrubby flatwoods and ridge sandhill, this can be as frequent as once every several years; Harper 1927; Abrahamson 1984a).

Life-history traits such as the presence/absence of wings, wing size, body size, number of generations per year, mode of reproduction, and fecundity have been linked to dispersal ability or rate of population spread of a species (Denno 1994; Turchin 1998; Stevens et al. 2012). All of our oak cynipids are winged and body sizes are comparably small. Fecundity is largely unknown for our species but mode of reproduction is available for most of the described species in Appendix 3. At present, we know that 11 species are parthenogenic, two reproduce only sexually and 5 species have both modes of reproduction and likely alternate generations of sexual and asexual reproduction (see Appendix 3). Asexual reproduction can mitigate Allee effects (i.e., the positive effects of increasing density on fitness) and increase the likelihood of successful colonization because mate finding at low density is no longer a problem (Allee et al. 1949; Gascoigne et al. 2009; Castel et al. 2014). However, despite our limited data, we have no evidence to suggest that obligate asexual species more quickly colonize post-burn sites than species with sexual reproduction. 55% (6 of 11) of the asexual-only species recolonized sites within 3 years whereas 71% of the species (5 of 7) that reproduce sexually, at least in some generations, recolonized sites within 3 years ($\chi^2 = 0.51$, $P = 0.47$). Clearly, more information is needed on the dispersal ability and life histories of cynipids for us to provide a mechanistic understanding of the reassembly of the cynipid communities following a burn. In general, this is a common limitation of the study of community assembly (Zalewski and Ulrich 2006).

Oak–cynipid conservation

ABS encompasses one of the largest and southernmost fragments of natural habitat on the Lake Wales Ridge and therefore is vital to the conservation of this unique region. The

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fire-management plan at ABS (Main and Menges 1997) emphasizes frequent but variable fires, reflective of historical patterns (Myers 1990; Platt et al. 1991; Glitzenstein et al. 1995). As in most cases, the fire-management plan was designed with the plant community and several charismatic vertebrate species in mind (e.g., Abrahamson 1984b; Menges and Hawkes 1998; Weekley and Menges 2003; Ashton et al. 2008; Evans et al. 2010; Ashton and Knipps 2011; Schrey et al. 2011; Dee and Menges 2014). We add to the small but growing database on the impact of fires on arthropod members of the scrub community (Menges and Deyrup 2001; Carrel 2008; Kim and Holt 2012). The cynipid assemblage we studied reaches asymptotic richness and diversity within ≈ 7 years, which for most habitats on the Lake Wales Ridge is a time period that is at or below historical fire-return levels (Harper 1927; Abrahamson 1984a; Menges et al. 2017). Consequently, the fire-management plan for ABS is well suited for the conservation of cynipid biodiversity. In the other remaining forest/scrub habitat reserves along the Lake Wales Ridge, the implementation of a similar fire-management strategy likely would not only secure the dominance of oaks in these areas but also promote high cynipid biodiversity (likely indirectly through an increase in availability of host material or complexity of tree architecture).

An important next step in our understanding of the ecology and conservation of this system would be an investigation of the role of fragment isolation and size and burn history and intensity on cynipid species richness, abundance and population-genetic structure. Landscape features, such as proximity to unburned habitat, the types of unburned habitat within the surrounding landscape, and the amount of edge, may all be important factors to consider as well (Swengel 2001; Panzer 2003; Saint-Germain et al. 2004; Knight and Holt 2005; Maldonado-López et al. 2016). The maintenance of a viable metacommunity (Leibold and Chase 2017) is also strongly dependent on an understanding of species dispersal among habitat fragments. Finally, we echo the recommendations of other ecologists that the study of disturbances such as fires should include multitrophic and broader food–web interactions (e.g., Swengel 2001; Vickery 2002; Alves-Silva and Del-Claro 2013; Cherry et al. 2016; Geary et al. 2018). For the oak–cynipids, this includes a diverse group of parasitoids, predators, parasites, inquilines and mutualists (e.g., Ronquist 1994; Schonrogge et al. 1996; Rokas et al. 2002; Stone et al. 2002; Inouye and Agrawal 2004).

Appendix 1

See Table 2.   AQ2

Time-since-fire is measured in years. Vegetation type is sand pine scrub (SS, $n = 4$), southern ridge sandhill (RS, $n = 5$) and scrubby flatwoods (SF, $n = 11$).

Table 2 Oak-gall wasp survey sites at Archbold Biological Station

Site	Date sampled	Burn unit	Burn date	Time since fire	Latitude	Longitude	Vegetation type
1	1/29/2018	2B North	4/20/2016	1.8	27.19344	− 81.33302	SS
2	1/30/2018	18 South	2/17/1999	19	27.19372	− 81.34268	SF
3	1/31/2018	15 Southwest	1927	91	27.19555	− 81.34202	SS
4	2/1/2018	41A Southwest	7/4/2016	1.6	27.19385	− 81.36411	SF
5	2/5/2018	2B Southeast	4/20/2016	1.8	27.18627	− 81.33424	RS
6	2/5/2018	36	5/12/2016	1.7	27.18166	− 81.34963	SF
7	2/5/2018	29A	1927	91	27.18495	− 81.34963	SF
8	2/6/2018	11	5/17/2013	4.7	27.19261	− 81.34028	SS
9	2/7/2018	48B West	7/11/2012	5.6	27.16996	− 81.36603	SF
10	2/8/2018	46	5/28/2014	3.7	27.18233	− 81.35349	SF
11	1/21/2019	61A	7/5/2017	1.5	27.13497	− 81.35513	SF
12	1/22/2019	51	1967	52	27.16465	− 81.35266	RS
13	1/23/2019	40B	1967	52	27.20117	− 81.35324	SF
14	1/23/2019	41A	5/11/2016	2.7	27.19852	− 81.35766	SF
15	1/25/2019	26	5/12/2015	3.7	27.19293	− 81.35025	SF
16	1/28/2019	4A	7/22/2014	4.5	27.18655	− 81.33633	RS
17	1/28/2019	4B	1927	91	27.18311	− 81.33900	RS
18	1/29/2019	5	8/9/2017	1.5	27.18279	− 81.33914	RS
19	1/30/2019	47A	7/10/2012	6.6	27.17857	− 81.36555	SF
20	1/30/2019	13	1/7/2015	4.1	27.19422	− 81.33536	SS

504 **Appendix 2**

505 See Fig. 4.

Scrub oak (*Quercus inopina* [red oak])

Callirhytis quercusclavigera
(Ashmead 1881)

Callirhytis difficilis
(Ashmead 1887)

Callirhytis quercusventricosa
(Bassett 1864)

Zapatella quercusmedullae
(Ashmead 1885)

Zapatella quercusphellos (=Callirhytis q.similis)
(Osten Sacken 1861)

Amphibolips murata Weld 1957

Fig. 4 Pictorial guide to the cynipid galls present on four common oaks during the winter at Archbold Biological Station. Photographs were taken by J. T. Cronin, W. G. Abrahamson, J. Nicholls and G. Melika

Myrtle oak (*Quercus myrtifolia* [red oak])

Callirhytis quercusclavigera
(Ashmead 1881)

Callirhytis difficilis
(Ashmead 1887)

Zapatella quercusphellos (=quercussimmilis)
(Osten Sacken 1861)
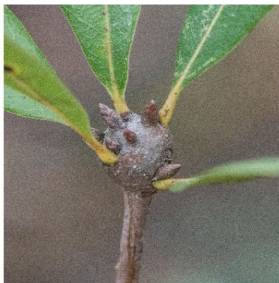
Callirhytis sp. nova 1

Amphibolips murata Weld 1957

Callirhytis sp. nova 2

Fig. 4   (continued)

Sand-live oak (*Quercus geminata* [white oak])

Disholcaspis quercusvirens (=*quercussuccinipes*) (Ashmead 1881)

Callirhytis quercusbatatoides
(Ashmead 1881)

Belonocnema quercusvirens
(Osten Sacken 1861)

Andricus quercusfoliatus
(Ashmead 1881)

Andricus quercuslanigera
(Ashmead 1881)

Neuroterus quercusminutissimus
(Ashmead 1885)

Bassettia pallida
Ashmead 1896

Fig. 4 (continued)

Chapman's oak (*Quercus chapmanii* [white oak])

Disholcaspis quercusomnivora (Ashmead 1885)

Andricus stropus Ashmead 1887
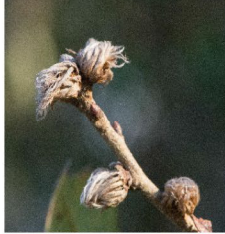
Andricus quercuspetiolicola (Bassett 1863)

Sphaeroterus melleum (Ashmead 1887)

Sphaeroterus carolina (Ashmead 1887)

Xystoterus sp. nova 1

Neuroterus quercusverrucarum Osten Sacken 1861

Neuroterus sp. nova 1

Neuroterus weldi Melika and Abrahamson 1997

Bassettia pallida Ashmead 1896

Andricus cinnamomeus Ashmead 1887

Fig. 4 (continued)

Appendix 3

See Table 3.

Table 3 Frequency of occurrence of each cynipid wasp species among sites for each oak species and time-since-fire (divided into three categories: <3 years, 3–7 years and ≥19 years)

Cynipid species	Generations	Oak species												
		Q. chapmanii			Q. geminata			Q. myrtifolia			Q. inopina		
		<3 years	3–7 years	>19 years	<3 years	3–7 years	>19 years	<3 years	3–7 years	>19 years	<3 years	3–7 years	>19 years
Disholcaspis quercusvirens (=*quercussuccinipes*)	Asexual and sexual	0	0	0	0.428571	1	1	0	0	0	0	0	0
Callirhytis quercusbatatoides	Asexual only	0	0	0	0.142857	0.714286	1	0	0	0	0	0	0
Belonocnema quercusvirens	Asexual only	0	0	0	0	0	0.333333	0	0	0	0	0	0
Andricus quercusfoliatus	Asexual only	0	0	0	0.142857	0.857143	1	0	0	0	0	0	0
Andricus quercuslanigera	Asexual and sexual	0	0	0	0.571429	1	1	0	0	0	0	0	0
Neuroterus quercusminutissimus	Unknown	0	0	0	0.571429	1	1	0	0	0	0	0	0
Neuroterus quercusverrucarum	Asexual and sexual	1	1	1	0	0	0	0	0	0	0	0	0
Disholcaspis quercusomnivora	Asexual and sexual	0	0.714286	0.8333333	0	0	0	0	0	0	0	0	0
Andricus stropus (mop)	Asexual only	0.857143	1	1	0	0	0	0	0	0	0	0	0

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Table 3 (continued)

Cynipid species	Generations	Oak species											
		Q. chapmanii			Q. geminata			Q. myrtifolia			Q. inopina		
		<3 years	3–7 years	>19 years	<3 years	3–7 years	>19 years	<3 years	3–7 years	>19 years	<3 years	3–7 years	>19 years
Andricus quercuspetiolicola	Sexual only	0.142857	0.714286	0.6666667	0	0	0	0	0	0	0	0	0
Sphaeroterus melleum	Asexual only	0	0.857143	1	0	0	0	0	0	0	0	0	0
Sphaeroterus carolina	Asexual and sexual	0.142857	0.285714	0.8333333	0	0	0	0	0	0	0	0	0
Xystoterus sp.	Unknown	0.142857	0	0.1666667	0	0	0	0	0	0	0	0	0
Neuroterus sp. R67	Unknown	0.142857	0.571429	0.6666667	0	0	0	0	0	0	0	0	0
Bassettia palida	Sexual only	0	0.285714	0.1666667	0	0	0	0	0	0	0	0	0
Andricus cinnamomeus	Asexual only	0.142857	0.285714	0.1666667	0	0	0	0	0	0	0	0	0
Callirhytis quercusclavigera	Asexual only	0	0	0	0	0	0	0	0.333333	0.8	0	0	0
Callirhytis difficilis	Asexual only	0	0	0	0	0	0	0	0.333333	0.6	0	0	0
Zapatella quercusphellos	Asexual only	0	0	0	0	0	0	0.333333	0.666667	0.8	0	0	0
Amphibolips murata	Asexual only	0	0	0	0	0	0	1	1	1	0.25	0.75	0.75
Callirhytis sp. 1 (rough stem)	Unknown	0	0	0	0	0	0	0	0.333333	0.2	0	0	0

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Table 3 (continued)

Cynipid species	Generations	Oak species											
		Q. chapmanii			Q. geminata			Q. myrtifolia			Q. inopina		
		<3 years	3–7 years	>19 years	<3 years	3–7 years	>19 years	<3 years	3–7 years	>19 years	<3 years	3–7 years	>19 years
Callirhytis sp. 2 (leaf cigar)	Unknown	0	0	0	0	0	0	0	0.666667	0.8	0	0	0
Zapatella quercusmedullae	Asexual only	0	0	0	0	0	0	0	0	0	0	0	0.5
Sites (n)		7	7	6	7	7	6	3	3	5	4	4	4
Richness		7	9	10	5	5	6	2	6	6	1	1	2

508 Generations reflects the current knowledge about whether the species reproduces sexu-
509 ally, asexually or status unknown.

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