Environmental Variables Influencing Cynipid Gall Distribution in Southwest Florida

by

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A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science in Conservation Biology
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Date of Approval:
March 27, 2020

Keywords: Time Since Fire, Latitude, *Quercus* spp., Insect Diversity, Hymenoptera

Dedication

I dedicate this thesis to my family and friends, who have continuously supported and encouraged me through even my darkest times, and who graciously share in my appreciation for the insects that have captured my heart. I could not have found the courage to continue pushing forward without them.

I would like to give special thanks to my mother, Carolyn, and her parents and grandparents, for their undying commitment to my education. I would also like to thank the dedicated researchers that have guided me through the academic world and provided invaluable mentorship: Melanie Riedinger-Whitmore, Ph.D. and Thomas Whitmore, Ph.D. Finally, I want to thank my hardworking and supportive circle of classmates, all of whom are dedicated to protecting our natural world for future generations. Their commitment gives me hope for us all.

Acknowledgements

I would like to acknowledge the critical support offered to me by the dedicated professionals within the Southwest Florida Water Management District, Florida Forest Service, Florida Department of Environmental Protection, Florida Fish and Wildlife Conservation Commission, Bok Tower Gardens, Boyd Hill Nature Preserve, and Brooker Creek Preserve. Their assistance and knowledge were crucial for the efficient collection of data used in this study. I would also like to acknowledge the invaluable input from Alison Gainsbury, Ph.D., Deby Cassill, Ph.D., and Colin Shea of FWC towards sample design and statistical analysis. Also critical to this thesis was the generous advice and expertise of Warren Abrahamson, Ph.D., of Bucknell University.

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Abstract

Insect galls are a common feature in many xeric environments, where hiding away inside a plant host offers developing larvae consistent food and shelter from harsh conditions. This study aimed to identify the most significant environmental factors that affect local populations of oak-galling wasps (Hymenoptera: Cynipidae) associated with three *Quercus* species found in xeric habitats located in southwest Florida, USA. Cynipid gall diversity, richness, and abundance were quantified for 35 sample sites across 11 counties, counting only winter-season galls. All sample sites were located within xeric, fire-managed, vegetative communities. It was hypothesized that time since last fire, habitat size, latitude, and tree size would have significant and positive correlations with cynipid Shannon-Weiner diversity (H'), species richness, and gall abundance per site. It was also hypothesized that individual host *Quercus* species and *Quercus* species richness would influence cynipid populations. A total of 4,305 individual galls from 21 cynipid species were counted. Time since fire was the strongest predictor tested in this study, significantly correlating with both cynipid diversity and richness. It was also a predictor of mean tree height, which was the only predictor found for gall abundance. Leaving unburned refugia within fire-managed areas should therefore be considered an important management tool for the protection of galling insect diversity. Individual *Quercus* species and *Quercus* richness also affected local cynipid assemblages, but played more minor roles in community-level metrics than time since fire.

Introduction

Cynipid wasps (Hymenoptera: Cynipidae) are small, solitary parasites with highly specialized reproductive strategies and often complex, cyclically parthenogenic life cycles (Stone et al., 2002). The phytophagous members of this family chemically induce the growth of protective and nutritive structures on their host plants (“galls”) in which the larvae feed and develop. Once hatched, the adults do not feed and are only concerned with reproduction, be it sexually or asexually. The galls they induce are highly diverse across species, and can be either very simple or astonishingly complex in structure (Askew, 1984).

Taxonomy and Life Strategies

Though a widespread and diverse family, there is still much to learn about Cynipidae natural histories and taxonomy. Hymenoptera is, in general, understudied and underdescribed in relation to other orders (LaSalle & Gauld, 1991), and may in fact rival, or even surpass, Coleoptera as the most speciose on the planet. Recent estimates suggest that Hymenoptera may contain 2.5-3.2x more species than Coleoptera (Forbes et al., 2018). Parasitica, the Apocritan infraorder that includes wasp species whose larvae are assumed to be obligate parasites of arthropod hosts (the other infraorder, Aculeata, includes ants, bees, and stinging wasps), is thought to make up most of the order’s diversity, but exact percentages have not yet been calculated. However, their typically small size and complex life cycles likely contribute to a lag in new species being described. The galling wasps of Cynipidae, which parasitize plant tissues, are similarly elusive but have garnered attention as examples of complex insect-plant and parasite-hyperparsitoid relationships (Ronquist & Liljeblad, 2001; Hayward & Stone, 2005; Inouye & Agrawal, 2004).

Cynipidae currently includes four major and four minor tribes whose approximate 1,400 species parasitize a wide range of plant genera (Ronquist & Liljeblad, 2001). Species within the tribe Cynipini (Hymenoptera: Cynipidae: Cynipini), the most abundant group of gall wasps, parasitize *Quercus* and a few other genera of Fagaceae. Two other major galling tribes—Aylacini and Diplolepidini—find refuge in woody genera like *Castanea* or in herbaceous species of Asteraceae, Lamiaceae, Rosaceae, and Papaveraceae (Ronquist et al., 2015). Members of the final major tribe, Synergini, do not induce galls and instead feed and develop within the galls of other Cynipids as inquilines or parasitoids, though only on those induced on woody plants. Additionally, two minor tribes have been traditionally included in Cynipidae: Pediaspidini (*Acer* gallers) and Eschatocerini (*Acacia* gallers). Two new, small tribes have also recently been described based on morphology: one species of Qwaqwaiini (*Scolopia* [Salicaceae] galler) (Liljeblad et al., 2011), and two inquiline genera of Paraulacini (Nieves-Aldrey et al., 2009).

For the galling tribes of Cynipidae, reproduction begins by locating specific, usually meristematic organs on their host plant species (Shorthouse & Rohfritsch, 1992; LeBlanc & Lacroix, 2001). Mating may or may not precede this; Cynipini and Pediaspidini are rare examples of cyclical parthenogenesis, or heterogony. Generally, one sexual generation and one asexual generation occur each year, with some species involving two different types of asexual females at a time (Folliot, 1964; Askew, 1984). In those species, sexual haploid male offspring are produced by asexual androphores, while sexual diploid female offspring are produced by asexual gynephores. Likewise, the sexual females of those species, such as *Neuroterus quercusbaccarrum*, can be divided into two groups based on whether they produce androphore or gynephore daughters. Other species' asexual females, such as *Bassettia pallida*, can produce both male and female offspring from unfertilized eggs (Suomalainen & Lokki, 1987).

After emerging from their own galls, adults (rarely longer than 5 mm) are not known to feed; instead immediately begin searching for mates or ideal spots for planting the next generation. Little is known about their dispersal preferences or capabilities, but the search is aided by the wasps' keen ability to detect the chemical signatures of their host plants (Abrahamson et al., 2003; Romani et al., 2010), allowing them to not only distinguish between species, but also between different organs. Once an ideal spot has been located by the gravid female, they attach either one egg, or several at a time, to the target organ, and the surrounding plant cells lyse to form a chamber around the subsequent larvae. The method of gall induction is not entirely clear, although chemical redirection of plant organ development by growth hormones and enzymes synthesized and injected by the mother at time of oviposition, but also by the eggs and larvae, is suspected as the main driver (Egan et al., 2018; Harper et al., 2004; Shorthouse et al., 2005). Meristematic tissue is generally popular for ovipositioning sites among galling cynipids, as the tissue is already actively differentiating. For the Cynipini tribe, the apical buds, young leaves, flower buds, catkins, and acorns of *Quercus* are common target organs, though some species prefer woody twigs or subterranean roots.

Once a larva has hatched and is surrounded by the early gall tissue, it can begin to feed on the nutritive tissue produced only in the innermost layer of the gall, or larval chamber. Vacuolate parenchyma tissue develops around the larval chamber, as well as a layer of sclerenchyma that will lignify once the larva begins to pupate (LeBlanc & Lacroix, 2001). Incredible variations of the outer parenchyma tissue and epidermis have evolved to achieve different morphological characteristics, most commonly for avoiding Synergini parasitoids and other predators (Shorthouse & Rohfristch, 1992). These morphological variations are even evident between sexual and asexual generations of the same species (Melika et al., 2013). Especially in oak gallers, the tissue outside of the larval chamber produces relatively large amounts of tannins and phenolics, likely for deterring fungal parasites or other threats (Taper & Case, 1987). This is where the structure gets its name; Merriam-Webster defines “gall” as: “bile,” “something bitter to endure,” or “a bitterness of spirit.” The bitter and astringent properties that the tannins and phenolics lend to the gall have also led to its past and present use in the production of pigments and medicines (Larew, 1987). Iron gall ink, made by combining ground oak galls with ferrous sulfate, was one of the most important inks used throughout the history of western civilization (Kolar et al., 2006). Thomas Jefferson wrote the Declaration of Independence in iron gall ink, which has caused document preservation issues due to its acidity.

As the gall matures, the growth of parenchyma tissue slows and the larva consumes the last of the nutritive layer within the sclerenchymatous chamber wall (Stone et al., 2002). Lignification of the surrounding tissue begins, controlled by and for the protection of the larva, which then initiates pupation. The gall may drop to the ground or remain on the tree until the adult wasp emerges. Typically, in Cynipini, galls containing the sexual generation develop in the Spring, with adults emerging by late Summer. The asexual generation then develops through Fall and either emerges and lays eggs in late Fall or remains dormant and overwinters in the gall.

Although the cynipid galls provide nutrition and protection to their hosts, the developing larvae and pupae still face threats from the outside. Inquilines and parasitoids, be they Lepidopterans (Eliason & Potter, 2000b) or fellow Hymenopterans, can have remarkable impacts on their hosts' populations (Washburn & Cornell, 1981; Cornell & Hawkins, 1995; Roy et al., 2011). Invertebrate and vertebrate predators can also feed on the protein-rich larvae hidden away in galls, provided they have the machinery necessary to reach them. Large and heavily-lignified galls can be cracked open by woodpeckers and rodents, while smaller birds can break into softer galls with thinner shells (Schönrogge et al., 1999). However, the effect of vertebrate and fungal predation on galling communities has not been well studied among most species and could apply significant pressure on cynipid populations (Abrahamson & Weis, 1997; Taper & Case, 1987; Zargaran et al., 2012).

Distribution

Generally, galling species richness is usually highest in the northern hemisphere, particularly in areas around 35° latitude, and are more abundant in dry habitats (Fernandes & Price, 1988). However, particularly high richness has been found in the dry cerrado biome in Brazil (Lara & Fernandes, 1996). Infertile soils also appear to encourage higher galling insect richness (Blanche & Westoby, 1995).While free-feeding insect herbivores have been found to prefer riparian sites over dry sites, the opposite is true of galling insects. Inducing and taking refuge in galls can be an effective way to escape harsh environmental conditions, and is thus more likely to evolve where those conditions are present. Gall induction has evolved independently several times in arthropods, including Diptera, Coleoptera, Lepidoptera, and Homoptera (Raman et al., 2005).

Within Cynipidae, oak galling cynipids—Cynipini, sometimes referred to as “cynipines” but more often simply as “cynipids”—are found in both the Eastern and Western hemispheres, but are most abundant in the Nearctic, particularly in Mexico (Weld, 1960). Cynipines are represented by approximately 1,000 described species across 41 genera (Ronquist, 1999), though a revision to 26 genera has recently been recommended (Melika & Abrahamson, 2002). There have been no comprehensive surveys of cynipine richness since the late 1970s, which placed the total number of cynipines native to continental America, north of Mexico, at 485 species (Krombein et al., 1979). Florida’s collection of approximately 26 native oak species are host to least 66 described cynipine species (Price et al., 2004). However, the sexual and asexual generations are both known for relatively few species, so some sister generations may be wrongly classified as separate species. At the same time, it has been suggested that there is still available niche space in cynipid communities, such that there is good reason to believe that there are still undescribed species (Cornell, 1985).

Previous Research in Florida

The Cynipidae family has received scientific attention as parts of model systems for studying complex plant-insect and host-parasite interactions (Stone et al., 2009; Gaylord, 1996). Though most of the cynipid research performed in the U.S. has been conducted in California, several notable discoveries have stemmed from Florida's cynipids, including key insights into the taxonomy, phylogeny, and host specificity of cynipid wasps, as well as the applicability of ecological theory to interspecies population dynamics (Melika & Abrahamson, 2002; Abrahamson et al., 2003; Price et al., 2004). These include finding strong host species and organ fidelity among cynipids (Abrahamson et al., 1998), so much so that arranging host *Quercus* species by their cynipid parasite assemblages produces a dendogram similar to botanical arrangements that depict phylogenetic relationships. Although Florida has higher oak-galling cynipid richness than other areas of the U.S. (Price et al., 2004), investigation into the state's populations and assemblages is lacking in comparison. Only very recent publications have focused on cynipid responses to environmental variables, especially time since fire (Cronin et al., 2020). Considering its high richness and the lag in cynipine research, Florida could prove to be a diversity hotspot for cynipids and yield new insights into their natural histories, evolutionary histories, and species- and community-level interactions.

Florida is home to 25 species of *Quercus,* which equates to a relatively high diversity of oak species when compared to better-studied regions like California, which has only ~20 species of *Quercus* despite being 2.65x larger in land area. Additionally, the Atlantic region has a higher cynipine-to-oak species ratio (378 cynipine to 28 oak species censused) compared to California (159/14 species censused) (Weld, 1957;1959). This may suggest that Florida, with its 25 *Quercus* species, could have relatively high total cynipine diversity when compared to other states; most recent estimates hover around 130 species in Florida alone (Price et al., 2004).

Project Scope

This project included a regional survey of oak-galling cynipid species on three oak species commonly found in upland communities of Florida, with subsequent investigations into species assemblage, richness, and diversity patterns. The main objectives for this survey were to map the geographic ranges of cynipid species within the target region to identify significant variables that influence cynipid population metrics, and to determine whether the individual population metrics respond to those variables equally. It is hoped that this information could then be used by local land managers to protect, or give special consideration, to any areas with rare or isolated populations. This is extremely important with respect to fire regimes, as frequent, wide-ranging burns could harm vulnerable populations. Species-level responses to fire are largely unknown for most North American cynipids, aside from one-time mortality rates of herbaceous gallers in prairie fires (Fay & Samenus, 1993). However, new attention now being given to individual cynipid species responses to fire (Bakhshandeh-Savadroodbari et al., 2017; Abrahamson & Cronin, 2019) lends new insights into prospective fire management tactics for protecting populations.

Mapping the geographic ranges of the cynipid species found on the three target oak species is simple compared to the statistical components of this project, but could prove to be more telling in the end. Climate change will likely have some degree of effect on oak-galling cynipids, especially with respect to their short, seasonally-cued, emergence and reproduction periods. As climate patterns in Florida are expected to become drier and hotter, with longer fire seasons (Fill et al., 2019), cynipid reproductive timelines may be altered or impacted by changes in growing season timing or intensity.

Insect herbivores, in general, will have to adapt to a warming climate (Bale et al., 2002); tracking any shifts in distribution patterns will be an important part of assessing a population's response to climate change.

Identifying the important environmental variables that influence oak-galling cynipid populations will also be a key component for managing populations, both generally and in a warming climate. This project aimed to collect data on several variables that could influence cynipid populations on the three target oak species, and to then find the best combinations of these variables, as determined by lowest Akaike information criterion (AIC) in multiple linear regressions predicting important cynipid population metrics like diversity, richness, and abundance. Findings could be then be used to help identify critical areas for cynipid populations, and suggest ways in which land managers can better protect them. Such insights could prove to be important not only for the cynipids, but also for any other arthropods that utilize their galls (Eliason & Potter, 2000a: Washburn, 1984).

Research hypotheses.

Previous studies point to several important environmental factors that can affect cynipid populations, though many details are still unknown. Cynipids have been observed aligning with the species-area relationship derived from island biogeography theory (Simberloff & Abele, 1976) but the degree to which host geographic range affects cynipid richness is greater in the Pacific region of the U.S. than in the Atlantic (Cornell & Washburn, 1979). This could be due to several other compounding variables, such as taxonomic isolation of both hosts and parasites (Lawton & Shroder, 1977), size of individual host plants (Cornell, 1986), and habitat diversity (Opler, 1974). However, galling insects are known to be more abundant in regions with low soil fertility (Blanche & Westoby, 1995; Cuevas-Reyes et al., 2004), and are most abundant in subtropical latitudes (25-38° N or S), decreasing only if altitude rises (Price et al., 1998). Galling insect communities are also known to be highly influenced by temperature and moisture, supporting the harsh environment hypothesis of distribution (Fernandes & Price, 1988). Hot, dry environments seem to encourage galling insect richness, as stowing away inside of a plant is a clever, albeit evolutionarily complicated, way to escape harsh conditions.

Florida's pine upland communities provide ideal combinations of these constraining factors to encourage high cynipid richness (Carr et al., 2010). Sandy soils encourage quick drainage, low nutrient retention, and often low pH levels among upland soil types; overall soil fertility varies little between these upland communities, except for scrubby flatwoods (Kalisz & Stone, 1984). Florida also lies within the ideal latitudinal range (25-31° N) and has only marginal altitudinal variation (0-105 m). Further, many of Florida's oak species vary markedly in distribution and phenolics due to water availability, soil fertility, and fire regimes (Ewel & Myers, 1990; Long & Jones, 1996; Menges & Kohfeldt, 1995), providing ample opportunity for specialization among the cynipids that parasitize them. Many of these characteristics likely play a role in Mexico's high cynipid richness (Weld, 1960).

Fire is a dominant feature in Florida's upland communities. The destructiveness of fire to galling insects depends to some degree upon its intensity (Fay & Samenus, 1993), and cynipid richness and diversity have been observed increasing with time since fire (Bakhshandeh-Savadroodbari et al., 2017; Cronin et al., 2020). Most scrub oak species have evolved to be able to completely burn above ground during a fire and then resprout (Abrahamson, 1984) but their galling insects usually do not survive moderate to high intensity burns. Re-establishment of a burned cynipid community relies on immigration, and for some species it can take six years or more (W. G. Abrahamson, personal communication, February 27, 2018). Fire can thus reduce cynipid richness in an area for several years but may also open new habitat space for colonization. The periods of intense post-fire sprouting may be beneficial to some species, as many choose meristematic tissues for oviposition sites (Stone et al., 2002). However, the abundance of parasitoid and inquiline species which prey on cynipids can also increase with time since fire (Washburn & Cornell, 1981) but at the same time can suffer in fragmented habitats (Kruess & Tscharntke, 2000). Parasitoids apply significant pressure on cynipid populations (Stone et al., 2002) so the variables controlling their population dynamics can indirectly affect cynipid populations. Fragmentation can also have direct effects on cynipids (Kaartinen & Roslin, 2000), though it is not always guaranteed (Chust et al., 2007). In this way, habitat size and fire history can have varied influences on cynipids; a goal of this project was to determine how these possible influences manifest in Florida. With the aforementioned environmental factors and their possible influences on cynipid populations in mind, the hypotheses for this study are as follows:

Hypothesis 1: Oak-galling cynipid Shannon-Weiner species diversity (H’) will increase as habitat size, time since fire, tree size, latitude, and oak species richness increases.

Hypothesis 2: Oak-galling cynipid species richness will increase as habitat size, time since fire, tree size, latitude, and oak species richness increases.

Hypothesis 3: Oak-galling cynipid abundance will increase as habitat size, time since fire, tree size, latitude, and oak species richness increases.

Methods

Target *Quercus* Species Selection

Florida is home to 25 species in the oak genus, *Quercus*, making it a rich and diverse region for cynipid gallers (Price et al., 2004). Winter is an opportune period for sampling and collecting cynipid galls as the pupating young are typically fully encased in an airtight, sclerenchymatous kernel by the onset of Winter and then ready to emerge in the Spring (Askew, 1984). Collected galls can therefore yield live adult specimens to aid in identification, demonstrate emergence rates, and to provide insights into the parasitoid and inquiline assemblages for the cynipid species collected.

Quercus geminata Small, *Quercus myrtifolia* Wildenow, and *Quercus chapmanii* Sargent were selected to be surveyed for cynipid wasp galls from November, 2018 to the end of March, 2019. These three species were selected due to their physiological characteristics, geographic distributions, and documented abundance of cynipid gallers. *Q. geminata* and *Q. chapmanii* are white oaks (section *Quercus*), while *Q. myrtifolia* is a red oak (section *Lobatae*). All three species are xerophytic and produce hardy, waxy leaves that typically do not drop in the Fall and persist at least for one year. As a result, galling insects can utilize leaf tissue and galls can stay attached to the host tree year-round. They are also short-statured trees, typically 1-3 meters tall, but capable of exceeding 12 meters if not subjected to periodic fires, making sampling the entire tree for galls more feasible. Lastly, these species of *Quercus* are typically found in the same vegetative community types (Carr et al., 2010), thereby nullifying most potential differences in cynipid gall assemblages between species due to habitat characteristics. Most of their geographic ranges are in Florida, though *Q. geminata* and *Q. myrtifolia* extend north along the coasts of Georgia and South Carolina (Nixon, 1997). Because the distributions of cynipid gallers are restricted to that of their host plants, tree species that are almost solely found in Florida are more likely to host cynipids that are similarly limited, and possibly endemic, to Florida. The three selected *Quercus* species also host an extremely high proportion of Florida's estimated number of cynipids. Of the 25 species of oaks found in the state, *Q. geminata*, *Q. myrtifolia*, and *Q. chapmanii* host a combined 59% of its known oak-galling cynipids (Price et al., 2004).

The goal of this study was to survey the three selected species of oak for all winter-season, non-subterranean cynipid galls that were active at the time of sampling. The galls from a large number of cynipid species can persist long after the adult emerges (Askew, 1984), such as *Disholcaspis quercusomnivora* Ashmead (Figs. 2.1 & 2.2). In order to avoid any potential skew in the count data (from overcounting long-persisting galls) it was important that these were excluded from the survey. Therefore, only the currently- or very recently active-galls were counted during sampling so as to build more accurate snapshots of cynipid assemblages and abundances. The status and age of a gall can be determined not only by the presence or absence of escape holes chewed out by the emerging wasps, but also by color, texture, and/or volume changes of the gall. The exclusion of expired galls from the count data means that only the winter season generations were counted, though the presence of expired galls was recorded for anecdotal purposes.

Cynipid wasps can produce drastically different galls between their sexual and asexual generations (Askew, 1984), and galls for both generations are still not identified for some species. Some species also switch between inducing galls above and below ground between their two generations (Lund et al., 1998). Only galls occurring above ground were counted in this survey, and any unknown galls were counted and collected in order to rear adults for identification.

Site Selection

For this study, sampling was conducted in the Southwest region of Florida, bordered on the north by Marion county, on the east by Polk county, on the west by Pinellas county, and on the south by Charlotte county. Few previous surveys of Florida cynipids on oaks exist, and the most recent and extensive survey (Abrahamson et al., 1998) did not sample large portions of the state, particularly in the Southwestern region. Therefore, this study focused more intensively on a smaller geographic area with an attempt to reveal more subtle patterns in species distributions. This study also surveyed a smaller number of *Quercus* species than the Abrahamson survey, in an effort to identify significant factors affecting species assemblages and abundances other than oak species assemblages.

The three target species of *Quercus* are typically found in xeric, upland community types, such as sandhill, scrub, xeric hammock, and scrubby (pine) flatwoods (Carr et al., 2010). Of the four, scrubby flatwoods is the most common, but all four communities are found within the geographic range of this survey (Ewell & Myers, 1990). To identify possible sampling sites, 10-year management plans were obtained for protected areas managed by the Florida Forest Service, Southwest Florida Water

Management District, Florida Fish and Wildlife Conservation Commission, Florida Department of Environmental Protection, Bok Tower Gardens, Pinellas County Parks and Conservation Resources, and St. Petersburg Park and Recreation. These management plans included maps of the Florida Natural Areas Inventory (FNAI) natural communities found within the boundaries of the sites. These maps are generally created using remote sensing to differentiate vegetative or geological designations and to produce fairly accurate representations of the communities present at particular sites. Only sites with at least one of the four target community types known to regularly host the three target *Quercus* species were selected for sampling.

A total of 44 sites within 22 protected areas were selected throughout the survey area, but only 36 sites within 19 protected areas contained at least one of the target *Quercus* species (Table 1). One of the 36 sites had no cynipid wasp galls present and was removed from statistical analyses. More northerly sites tended to contain the sandhill community type, while more southerly sites tended to contain scrubby flatwoods, likely due to a latitudinal topographic gradient throughout the region (Carr et al., 2010). Sandhills are found in higher, better draining-soils than scrubby flatwoods (Myers, 1990), and are therefore more likely to be present at the higher elevations found at the northern end of the survey region, and vice versa. Scrub communities are typically found on high, sandy ridges, but are more or less evenly distributed throughout the survey area (Table 1). Xeric hammocks are relatively rare throughout the survey area, occurring in only three sites. They are typically considered advanced stages of scrub communities (Florida Natural Areas Inventory, 1990).

Once a specific sampling site was identified, five individuals of each *Quercus* species were selected, their heights and trunk circumferences measured, and their active cynipid gall assemblages and abundances recorded. Individual trees were selected randomly by walking from a central location at random angles from due North until a tree of one of the target species was found. A random number generator (0-360) was used to produce the angles. This was repeated five times for each species present at each sampling location.

Typically, two sites were sampled within each protected area, with exceptions only made when there were adequate populations of target oak species for two sites. These sister sites were labeled as “Site nameA” and “Site nameB.” Choosing sampling sites within each protected area that were far from each other was preferred, but not always possible. At the time of sampling, each site was first surveyed to confirm the presence of any of the three target *Quercus* species. The FNAI natural communities maps for each property were used as guides for identifying these preliminary sampling sites by identifying areas of appropriate vegetative communities. If a preliminary site did not have, or did not contain enough of, at least one of the target oak species, the surrounding areas were scouted on foot for alternative sites. On only two occasions were alternative sites not found: once at Half Moon Wildlife Management Area and Potts Preserve. A second site was originally sampled from the Wingate parcel of Beker State Park, but no galls were found at that site despite the presence of all three target *Quercus* species, and the site was excluded from analyses. The Serenova tract and Starkey Wilderness Preserve sites were technically sister sites as the two parcels are contiguous, but their individual names were kept.

Site Descriptions

Originally, 22 natural areas protected by state, county, city, and private entities were identified for sampling within the southwest region of Florida. However, only 19 of the protected areas contained one or more of the target oak species, and were therefore eligible for sampling in this survey. Each protected area was generally able to produce two distinct sampling sites; there were a few exceptions where the target oak species were only present in a small area and therefore could only yield one sampling site. Below are brief descriptions of each sampling site, with information drawn from management plans, historical documents, and vegetative surveys.

Allen D. Broussard Catfish Creek Preserve State Park.

Allen D. Broussard Catfish Creek Preserve State Park is an 8,157 acre preserve located on Polk County, FL. Acquisition of the property began in 1991 and management authority was conveyed to the Department of Environmental Protection (DEP), Division of Recreation and Parks (DRP). The preserve partially covers a portion of the Lake Wales Ridge and subsequently hosts endemic scrub ridge habitat, but also contains 14 other xeric to mesic natural communities. Cultural sites located within the preserve include Seminole burial mounds and middens dating back as far as 3,000 years.

Sample site “ADB Catfish CreekA” was located at the southern end of management zone CF-12b, in an area designated as scrub community. The site would generally be considered “overgrown” for scrub, with many large (>3 m) sand live oaks (*Q. geminata*) providing variable degrees of canopy cover. Few sand pines (*Pinus clausa*) or other pines, if any, occurred at this site and relatively low densities of groundcover plant species revealed wide patches of white sugar sand (Astatula fine sand). These patches likely helped to distinguish this site as scrub community rather than xeric hammock. The site was last burned in January, 2017, but the abundance of bare ground made it difficult for fire to spread.

Sample site “ADB Catfish CreekB” was located at the western end of the management zone CF-7b, which was also designated as scrub community on Astatula fine sand. However, this site contained a much denser population of scrub oaks (including all three target species), though none as tall as those found in the previous site. Even further, this site contained no substantial patches of open ground and slash pine (*P. elliottii*) was sparsely scattered throughout the site. The last prescribed burn in this zone was in March of 2015, and the park biologist noted that this site generally had more intense and complete burns than zone CF-12b (E. Egensteiner, personal communication, August 13, 2019).

Beker State Park—Wingate Creek Unit.

The Wingate Creek unit of Beker State Park was acquired in 1988, along with the South Fork unit, as mitigation for phosphate mining in the land to the north by the Beker Phosphate Company. The approximately 615 acre preserve is located in Manatee County and is managed primarily by DEP, Division of Recreation and Parks (DRP). It contains ten distinct natural communities, ranging from xeric to seasonally hydric, plus ruderal and developed areas. The preserve also contains two culturally significant sites, including a prehistoric burial mound within the Weeden Island archeological complex.

Sampling site “Beker WingateA” was located in management zone WC-1b, in an area designated as scrub community. Habitat structure in the area was generally open, with some mature sand pines and the occasional large oak (typically *Q. geminata* or *Q. virginiana*). Small bare patches occurred between stands of shrubby and herbaceous plants, including saw palmetto (*Serenoa repens*) and Lyonia species. All three target oak species were present at this site. The most recent prescribed burn occurred in March of 2015. No notes regarding intensity or completeness of the burn were available.

Another site was also sampled within the Wingate Creek unit—“Beker WingateB”—which was designated as ruderal habitat but contained all three species of target oak. However, no galls were observed throughout this sampling site and it was therefore excluded from this survey.

Bok Tower Gardens—Pine Ridge Preserve.

The Pine Ridge Preserve is located at Bok Tower Gardens in Polk County, which has been in operation since 1929 and includes extensive botanical gardens and a rare plant conservation program focused on Florida endemics. Pine Ridge Preserve is an approximately 25-acre sandhill community situated on a high ridge between the botanical gardens and neighboring citrus groves. While grasses dominated the understory, the open canopy consisted of sparse slash pines and turkey oaks (*Quercus laevis*). The property is managed by Bok Tower and has been subject to regular prescribed burns since 1989 (K. Noland, personal communication, May 9, 2019).

Sampling site “BokA” was located in the main portion of the Pine Ridge Preserve, at the northeastern end of the property and within view of the bell tower. Two of the three target oak species were present: *Q. geminata* and *Q. myrtifolia*. The most recent burn of the area was conducted in March of 2016. Despite the small size of this preserve, wildlife was encountered throughout, including northern bobwhites (*Colinus virginianus*), gopher tortoises (*Gopherus polyphemus*), and a southern coachwhip (*Masticophis flagellum flagellum*).

Sampling site “BokB” was located in a separate portion of the Pine Ridge Preserve, approximately 1 km to the south of the main portion of the preserve. This area was acquired by Bok Tower Gardens in 2007 from a nearby citrus operation and had not previously been managed for ecological purposes. However, the site had generally maintained a similar community structure to the main portion of the preserve and contained both *Q. geminata* and *Q. myrtifolia*. The most recent burn at the site was in May of 2015, and had likely only been burned once prior (January, 2012). This contrast in long-term burn histories between the sister sites could become important for explaining any differences in cynipid species assemblages between them.

Boyd Hill Nature Preserve.

Boyd Hill Nature Preserve is a 245-acre preserve located in Pinellas County, bordered by residential areas and Lake Maggiore. Though managed to varying degrees for several purposes throughout its history, the property has been managed as a preserve by the city of St. Petersburg since 1980. It contains a mosaic of mesic and xeric communities, and is currently undergoing restoration efforts to encourage the expansion of scrub-type vegetation.

Sampling site “BoydA” was located in management zone 21a, within one of the preserve’s minor patches of scrub community. The diagnosis of this area as scrub community was not determined via FNAI natural communities maps, as they have not yet been constructed for Boyd Hill Nature Preserve. Instead, a 2015 independent vegetative analysis by botanist Craig Huegel, Ph.D., and my own personal experience were instead used to aid in selecting sample sites within the preserve. Management zone 21a contained all three target species of oak and was last burned in February of 2012. Slash (*P. elliottii*), longleaf (*P. palustris*), and sand pines (*P. clausa*) were the dominant overstory species while wiregrass (*Aristida stricta*) and saw palmetto (*S. repens*) were the dominant understory and groundcover species.

Sampling site “BoydB” was located in management zone 10, which encompasses the largest scrub community in the preserve. This area had generally denser patches of wiregrass and saw palmetto, overall fewer pines, and more frequent patches of bare ground. All three species of target oaks were present at this site, and it was last burned in March of 2015. Another burn was conducted in early 2018, but it did not actually reach the specific sampling site due to bare patches causing low connectivity between patches of vegetation.

Brooker Creek Preserve.

Brooker Creek Preserve is located in northern Pinellas County, and is the county’s largest preserve at almost 9,000 acres. It was established in the early 1990s and is managed by the Pinellas County Department of Environmental Management. About 1,600 acres of the preserve is owned by the Southwest Florida Water Management

District. Communities within the preserve include both upland and wetland communities, such as sandhills, hardwood hammocks, and seasonal blackwater swamps.

The specific management zones in which “BrookerA” and “BrookerB” sampling sites were located could not be determined through the preserve’s management plan. Both were located in separate patches of xeric hammock community, a late successional stage of scrub. “BrookerA” was in an area of both closed and open canopy, mostly by large *Q. viginiana* or *Q. geminata*. The understory was dominated by shrubby oaks, including all three target oak species. Some palmetto and Lyonia species were also present. Pines and grasses were mostly absent. The last prescribed burn occurred in May of 2004.

“BrookerB” was in a similar area as “BrookerA,” though it had denser canopy cover. Plant assemblage and composition were nearly identical at both sites. However, this area was mechanically roller-chopped in mid-2003. Because this treatment would cause similar mortality rates to aboveground cynipid gallers, it was treated as the most recent “burn.” No burns or similar treatments have occurred since.

Charlotte Harbor Preserve State Park—Cape Haze Management Area.

Charlotte Harbor Preserve State Park is located in Charlotte and Lee Counties, and covers a total of 42,600 acres across many discontinuous parcels. Communities within the park range from uplands to estuarine marshes and open shoreline. The Division of Recreation and Parks, under the DEP, has managed the park since 2004. The Cape Haze Management Area is the largest of the five physiographic management units within the park, at just over 20,300 acres. The area is located on the southern and eastern shoreline of the Cape Haze peninsula and includes pine flatwoods, oak scrub, marsh, salt flats, and mangrove islands.

The two sampling sites for this park were both located in management zone CH-21 in the Cape Haze Management Area and both contained all three target oak species. However, the two sites consisted of different communities: “Charlotte HarborA” was located in a scrub community dotted with rosemary balds and “Charlotte HarborB” was located in scrubby flatwoods. A rosemary bald refers to open patches of ground created by the Florida rosemary (*Ceratolia ericoides*), which limits nearby plant growth through allelopathic effects. This species is often characteristic of very dry and stable scrubs as they are exceptionally xerophytic and very easily perish in fires. A slow growing species, a well-developed population suggests longer intervals between fires, as is characteristic of high scrub communities (Myers, 1990). Other species in “Charlotte HarborA” included wiregrass, some saw palmetto, and distantly-spaced slash pines. Also notable was the presence of parasitic love vine (*Cassytha filiformis*), which can grow to cover and choke out its hosts and has even been observed parasitizing cynipid galls (Egan et al., 2018). The presence of *C. filiformis* at any sample site within the survey region was recorded.

Sampling site “Charlotte HarborB” is in a less open, more shaded, area identified as scrubby flatwoods in the FNAI Natural Communities map for the park. The overstory was dominated by slash pine while the understory included relatively dense stands of scrub oaks and saw palmetto. No *C. filiformis* or *C. ericoides* were present at this site, and there was little to no bare ground.

Chinsegut Wildlife and Environmental Area—Nature Center Tract.

Chinsegut WEA is located in Hernando County and is managed by the Florida Fish and Wildlife Conservation Commission (FWC). Portions of the preserve have been protected to some degree since 1932, with management by FWC beginning in 1967 and the final parcels added in 2009. The property consists of two tracts: Nature Center tract and Big Pine tract. Both sampling sites for this preserve were located in the Nature Center tract. The Big Pine tract may contain the largest contiguous stand of old-growth virgin longleaf pines in Florida, with many trees estimated at over 200 years old. Both properties contained a total of eleven natural community types, the most predominant of which were upland pine forest, sandhills, and mesic hammocks.

Sampling site “ChinsegutA” was located in management zone 02 in the Nature Center tract. The zone consisted of mostly sandhill and upland pine communities, which were dominated by longleaf pines but dotted with the occasional large (~2 m) *Q. geminata*. *Q. chapmanii* was also present in this sample site, but was never observed to grow as tall. Groundcover was generally either grassy or herbaceous, with patches of bare ground covered by pine needles and dense clumps of palmetto. The last burn in this zone was in June of 2018, giving this site the shortest time since fire of all sites in the survey.

“ChinsegutB” was located in management zone 05 and had generally fewer pines and a more open canopy. There were subsequently less pine needles covering any patches of bare ground, which at least gave the impression of drier conditions at this site compared to “ChinsegutA.” Only *Q. geminata* occurred at this site, and it was last burned during the Winter of 2017. The particular month of the burn was not available.

Withlacoochee State Forest—Citrus Tract.

The Withlacoochee State Forest is a conservation area made up of seven major tracts totaling 164,000 acres and spanning Citrus, Hernando, Lake, Pasco, and Sumter Counties. While the major management responsibilities fall to the Florida Forest Service, the Florida Fish and Wildlife Conservation Commission (FWC) and the Southwest Florida Water Management District (SWFWMD) also play management roles, with hunting a main public use. The original 115,000 acres of the forest first fell under state management in 1939. The Citrus tract, located in Citrus County, remains one of the largest contiguous stands of longleaf pine in the state, containing approximately 50,000 acres of sandhill.

Sample site “CitrusA” is located just north of Forest Road 2 (FR2), between FR15 and FR13, at the northern end of the forest. The site was near a purported scrub community, but sampling was conducted in a sandhill community. This site contained all three target oak species and was dominated by longleaf and sand pines, with an open understory made up of wiregrass, shrubs, and sparse patches of saw palmetto. The last burn at this site occurred in December of 2017.

“CitrusB” is located at the eastern end of the forest, along FR16, east of FR5. The last burn at this site occurred in September of 2014. Longleaf pine was again the dominant overstory tree, with a grass-dominated understory and the occasional small turkey oak. Saw palmetto was not present and *Q. geminata* was the only target oak species that occurred at this site.

Withlacoochee State Forest—Croom Tract.

The Croom tract of the Withlacoochee State Forest also contains large areas of longleaf pine, with a total of approximately 18,000 acres of sandhill community. It is located in Hernando County and contains a total of six miles of the Withlacoochee River. Public use includes hunting, hiking, trail biking and off-roading.

Sampling site "CroomA" is located southwest of the intersection of FR7 and County Road 480 W, and consists of longleaf pine sandhill. Only Q. *geminata* was found at the site. Understory vegetation was typical for sandhill and mirrored those found in the Citrus tract, though it was generally slightly less xeric than Citrus. Grasses were less abundant as the canopy was denser and subsequent light penetration lower. Pawpaw (*Asimina spp*.) and *Yucca filamentosa* were common. The last burn occurred in April of 2015.

"CroomB" is located along a mountain biking trail to the southeast of the intersection of FR4 and FR9. It was nearly identical to its sister site in plant assemblages but varied in composition due to a more open canopy and greater light availability. *Q. geminata* occurred in relatively dense stands but were not significantly taller than those at the sister site. Neither of the other target oaks were present. The last burn occurred in January of 2016.

Conner Preserve.

Conner Preserve is located in Pasco County and was acquired for habitat and groundwater recharge area preservation in 2003. The property is managed by the SWFWMD and encompasses almost 3,000 acres, including 113 acres of xeric pine flatwoods and sandhill. The majority of the preserve is covered by mesic or hydric communities, including swamps, hammocks, and marches.

“ConnerA” is located near the center of the property, south of State Road 52 and between the two main lakes contained within the preserve. Longleaf pines and turkey oaks were common while saw palmetto densely covered much of the understory. Only *Q. geminata* occurred at this site, and it was last burned in 2017. The exact month of the last burn was not available, but was likely to be during the Spring months.

“ConnerB” was located to the southwest of “ConnerA,” due south of the westernmost lake within the preserve. Both sites were within scrubby flatwoods communities. The exact management zones for each of these sites were not available. Plant assemblage and composition was very similar to its sister site. Both *Q. geminata* and *Q. myrtifolia* were present, and the last burn also occurred in 2017.

Fort Cooper State Park.

Fort Cooper State Park is a relatively small property located in Citrus County, near Inverness. The initial acquisition of the park’s 735 acres began in 1970 and it is managed by the Division of Recreation and Parks within the Department of Environmental Protection. The park’s main community types include sandhill, mesic hammock, and basin marsh.

Sampling site “Fort CooperA” is located on the southeastern boundary of management zone FC-04, in a sandhill community. The area had a very open canopy structure made up of large turkey oaks, post oaks (*Q. stellata*), and pines. Understory and groundcover varied from grasses and shrubs to relatively bare ground covered with pine needles. All three target species of oak were present at this site and the last burn occurred in July of 2017.

“Fort CooperB” is in a more shaded area with denser stands of small oaks, including all three target species. Pines, turkey oaks, and post oaks again made up the overstory but were significantly denser in some areas. Fewer grasses were present and more ground was covered with pine needles. Breaks in the canopy did provide for patches of grasses and shrubs nearby. The last fire occurred in March of 2018, but it did not appear to be a significant burn given the amount of vegetation present.

Half Moon Wildlife Management Area.

Half Moon WMA is a 9,500 acre parcel that is located in Sumter County and managed by the Florida Fish and Wildlife Conservation Commission. The original 4,500 acres first came under state management in 1989, and have been and are currently used for hunting, silviculture, and cattle grazing. The parcel consisted mostly of hydric and mesic communities, but did maintain patches of upland habitat.

Most of those patches of upland habitat did not contain any of the three target oak species, but did occasionally contain dwarf live oak (*Q. minima*). The lone sample site (“Half Moon”) occurred in management zone 27 and, ironically, all three target oak species were present in a relatively small area. The surrounding area consisted of few large trees, mostly water oaks (*Q. nigra*). Also present were small patches of saw palmetto, some sabal palm (*Sabal sp*.), prickly-pear cactus (*Opuntia humifusa*), and several grass species. The last burn occurred in May of 2014.

Halpata Tastanaki Preserve.

The Halpata Tastanaki Preserve is an 8,000 acre property in Marion County, managed by the SWFWMD. The property was acquired between 1994 and 1995, with previous uses including cattle grazing and logging. However, past disturbance across much of the preserve was limited and large stretches are therefore relatively pristine. Vegetative communities range from freshwater marsh and floodplain swamp to scrub and sandhill.

Sampling site “HalpataA” is located in the eastern portion of the preserve, off the SW SR 200 entrance. The FNAI Communities map was not available for Halpata Tastanaki, but this site was most similar to an oak scrub community. The site had an open structure and bare patches of white sand were common, with main overstory trees including large sand live oak, turkey oak, slash and sand pines, and the occasional persimmon (*Diospyros virginiana*). Saw palmetto was not common and groundcover was predominantly comprised of grasses and shrubs. Of the three target oak species, only sand live oak (*Q. geminata*) was present. The last burn occurred in 2016, but the exact month was not available.

“HalpataB” is located near the center of the preserve, in an area of dense longleaf pine sandhill adjacent to an area used for timber production. Understory vegetation was denser and less xeric than at previous sites, with shrubby species like beautyberry (*Callicarpa americana*) and *Smilax spp*. common. Large live oaks (*Q. virginiana*) and smaller laurel oaks (*Q. laurifolia*) were common at the fringes of the dense pine stand. *Q. geminata* were found throughout the site, but neither of the other two target species. The last burn occurred in 2011, with the exact month not being available.

Lake Manatee State Park.

Lake Manatee State Park is located in Manatee County and totals approximately 500 acres. The park is managed by the DEP's Division of Recreation and Parks, and the initial acquisition of the property was in 1970. The northern border of the park occupies much of the southern edge of Lake Manatee, which is popular for recreation and is accessible through the park. The most common vegetative community is mesic flatwoods, but also contains sandhill, scrub, scrubby flatwoods, and xeric hammock.

Sampling site "Lake ManateeA" is located in the management zone LAM-1D, which is nearer to the westernmost entrance to the park and in an area designated as scrubby flatwoods. Habitat structure in this area was very open and low, with no significant overstory trees in the immediate area. Understory vegetation was mostly herbaceous shrubs, wiregrass (*Aristida spp*.), some saw palmetto patches, and stands of ~1 m tall *Q. geminata*. All three species of target oaks were present, and the last burn occurred in June of 2015.

"Lake ManateeB" is located in management zone LAM-3A, nearer to the easternmost entrance to the park and in an area designated as scrubby flatwoods but more resembling scrub. This was partly due to the presence of Florida rosemary (*Ceratolia ericoides*) and sand pine stands. However, the community classification was still recorded as scrubby flatwoods. All three target oak species were again present, and other common species included the prickly-pear cactus, saw palmetto, and several grasses. The last burn occurred in May of 2016.

Little Manatee River State Park.

Little Manatee River State Park is a 2,416- acre property located in the southwestern corner of Hillsborough County. Initial acquisition of the property was in 1974 and it is managed by the Division of Recreation and Parks within the DEP. The park is diverse in composition and includes 20 distinct natural communities, the largest of which are bottomland forest, scrub, mesic flatwoods, and scrubby flatwoods. According to the park's management plan, it also boasts the most pristine blackwater stream system in the county.

Sampling site "Little Manatee RiverA" is located in management zone LMR-19. The area is designated as scrub community and features denser stands of scrub oaks and some sand pines, with only the occasional bare patch of white sand. Few grasses were present and saw palmetto was moderately abundant. Several *Lyonia* species were common, as well as water oaks in the topographically lower areas of the zone. All three species of target oaks were present at this site. The last burn recorded for this area was in 2003, but staff at the park involved with the prescribed burns advised that this burn did not penetrate far in from the edges of the zone.

"Little Manatee RiverB" is located in management zone LMR-17, in an area also designated as scrub. This site had more sand pines and therefore a slightly more closed canopy than the previous site, and the understory was subsequently less dense. Understory species were predominantly large scrub oaks and saw palmetto patches. Most of the open patches of ground were covered with pine needles. The last burn recorded for this area was in 2004, but staff again advised that the last burn did not penetrate deep enough into the zone to affect this particular sampling area.

Oscar Scherer State Park.

Oscar Scherer State Park is located in eastern Sarasota County and includes almost 1,400 acres of mostly mesic and scrubby flatwoods. Mesic hammock, depression marsh, and blackwater stream communities are also present. The initial portion of the park was acquired in 1956, with the last portion preserved in 1991. It is managed by the Division of Recreation and Parks within DEP.

Sampling site "Oscar SchererA" is located in management zone OS-12, in an area designated at scrubby flatwoods. The site had very few overstory trees, and the understory was mostly dense stands of scrub oaks. All three species of target oaks were present. In the few areas with available open space, lupines (*Lupinus*) were common. The last burn occurred in the spring of 2018.

"Oscar SchererB" is located in management zone OS-14B, also designated as scrubby flatwoods. While this site also largely lacked overstory species, the stands of scrub oaks were significantly less dense and more shrub and grass species were able to coexist. All three target oaks were present at this site also. The last burn at this site occurred in the summer of 2015. It could be worth noting that scrub jays (*Aphelocoma coerulescens*) were seen at both sites.

Paynes Creek Historic State Park.

Paynes Creek Historic State Park is located in Hardee County and totals just over 400 acres. The park maintains the site of a mid-19th century trading post that was attacked by rogue Seminole tribe members in 1849; it also protects areas of bottomland forest, mesic hammock and flatwoods, scrubby flatwoods and others. The property has been managed by the Division of Recreation and Parks since it was acquired in 1974.

Sampling site “Paynes CreekA” is located in management zone PC-01A, designated as scrubby flatwoods. The site had an open structure and was bordered by areas with large stands of slash pine, though only sand pines were immediately next to or within the site. Dense grass patches were broken by patches of open sand and scrub oaks. Saw palmetto was not particularly common. All three species of target oak were present at the site and the last burn occurred in the early months of 2018.

“Paynes CreekB” is located at the northern edge of management zone PC-05, near the border between PC-02A and PC-02B. The area was, again, bordered by slash pine forest, but the site itself was almost solely comprised of dense stands of the three species of target oak. The oaks were all of similar age and left almost no room for other species to occupy. The last burn occurred in the summer of 2016, but was recorded as a light burn. This is consistent with the extent to which the oaks dominate the site.

Potts Preserve.

Potts Preserve is a 9,300-acre preserve in northwest Citrus County, within the Withlacoochee River watershed. The Southwest Florida Water Management District began acquiring parts of the property in 1988 and it stands as part of a 122,000-acre contiguous area of protected conservation lands for purposes related to water quality management and aquifer recharge. A total of 16 FNAI communities occur within the preserve, with similar proportions of hydric and xeric types.

Only one sampling site was able to be identified within the preserve (“Potts”), an area designated as scrubby flatwoods near the center of the property. The area immediately adjacent to the sampling site had been burned very recently, and so there was little sampling area available. The other side of the sampling site was bordered by a small lake. While the site itself was xeric with white sands and mature scrub oaks, the hydromorphic red maple (*Acer rubrum*) surrounding the lake were near enough to provide a partial canopy. All three target oak species were present at the site, and it was last burned sometime in 2013.

Starkey Wilderness Preserve—Starkey & Serenova Tracts.

Starkey Wilderness Preserve is a 19,000-acre preserve located in Pasco County and was made up of three contiguous tracts: the Starkey Wilderness Park, the Serenova tract, and the Anclote River Ranch preservation area. The property is owned and managed by the Southwest Florida Water Management District for water management and conservation purposes. The original properties were first acquired in the 1970s.

Sampling site “Serenova” is located in the Serenova tract, which lies to the north of the Starkey tract. The site was in an area designated as xeric hammock, which is characterized by larger and older oaks than those found in scrub. This site had large live oaks making up most of the canopy, and understory vegetation was largely limited by the density of the canopy. In areas where the canopy was more open, sand live oak and myrtle oak were present. The last burn at this site occurred sometime in 2013.

Sampling site “Starkey” is located within the Starkey tract, in an area near the visitor parking lot that was designated as sand pine scrub. The site had some sand pines, but was dominated by large scrub oak stands that inhibited the growth of other understory plants throughout much of the area. All three target oak species were present, including some large live oaks. The exact time of the last burn was not recorded, but it is suspected to have been sometime around 2005.

Data Collection

The location of each tree sampled was marked with a Garmin Dakota™ 10 handheld GPS device and each was given a unique numeric identifier that related to the sampling location in which they were found. Before gall data was collected, the height and trunk circumference for each individual tree was recorded in centimeters. The height was recorded as the length of the trunk, from the ground to the tip of the tallest twig, to the nearest centimeter. If the tree was growing at an angle, the measuring tape was kept at the same angle as the trunk when measuring. The trunk circumference was recorded two centimeters from the ground, to the nearest quarter centimeter. If there were several shoots for the same individual, the circumferences of each were recorded and summed together as a means of accurately representing the available mass of that particular individual (Karlik & McKay 2002). At times, there were large clumps of many shoots (10+), but those were excluded from this study to account for the possibility that the larger clumps could actually contain more than one individual.

Once tree measurements were recorded, each tree was examined from top to bottom for any cynipid galls present. This included searching on the trunk, branches, twigs, leaves, apical buds, and any remnant or emerging acorns or reproductive structures, but not within the root system. Each gall found was examined for activity status and, if active, tentatively identified and counted. Expired galls—those from which adults had already emerged—were not counted, but their presence was recorded for anecdotal evidence, along with any observations of other arthropods using the remnant structures. The holes left by emerging adults were clear indicators of a gall being expired, with supporting evidence provided by marked changes in gall color, volume, and/or texture. Samples of each active species of gall found were collected for off-site identification confirmation, rearing of adult cynipids, and the possible rearing of any parasitoids or inquilines present. Samples were collected in plastic bags, labeled with the same numeric identifier as the tree they were collected from, and their tentative species identification. The bags were subsequently punctured with a small needle for ventilation and hung in a dry room at approximately 21° C. Any adult cynipids, parasitoids, or inquilines that emerged were stored in 90% denatured alcohol in 2-dram clear glass vials, which were then placed back into the bag containing the gall from which the specimens emerged.

Statistical Analyses

Predictor variables for this study were sample site size in acres, latitude, FNAI vegetative community type, oak species richness, species of oak, time since last fire, mean tree height and mean trunk circumference. The response variables were cynipid Shannon-Weiner diversity (H’) per site, cynipid richness per site, and total gall abundance per site. Oak species richness per site was also used as a response variable in several tests, while the other predictor variables were all used as response variables only when compared to community type, shedding light on the connection of the main response variables with community type, a categorical variable. Similarly, some variables within each of the two groups are related to each other by ecological processes, such as time since fire and tree height. These relationships were considered during data analysis not only as ways for two variables to act in conjunction with or at odds with each other, but also to help explain the effects of individual variables. All statistical analyses relating to the hypothesis testing were conducted in R 3.5.3 with an alpha level of 0.05 (R Core Team, 2019).

Parametric assumptions testing.

The first phase of statistical analysis was designed to describe the differences in predictor and response variables across the sample sites and to test for normal distributions. Histograms of each variable were created as visualizations of variable distributions. Both residuals versus fitted plots and Q-Q plots were used to test for normality of residuals for all regression models. Shapiro-Wilk tests were used to more precisely measure both variable and residual distribution normality ($p < 0.05$), for all regression models and ANOVA analyses. Shapiro-Wilk p-values greater than 0.05 indicate normal distribution, while smaller p-values indicate significant skew (Shapiro & Wilk, 1965). Skew was found in the predictor variable target oak species richness and in several ANOVA analyses. The ANOVAs with skewed residuals were subsequently changed to Kruskal-Wallis analyses of variance, a non-parametric test which does not require normality of residuals. All histograms, residuals plots, and Q-Q plots are available in Appendix A.

Univariate difference, dependence, and correlation testing.

The first round of testing used both parametric and non-parametric tests to identify relationships between individual pairs of variables. Pearson's chi-squared analyses were used when both variables were categorical, such as community type and oak species richness per site. Kruskal-Wallis and one-way analyses of variance (ANOVAs) were used when the predictor variable was categorical and response variables were continuous. Post-hoc tests for analysis of variance tests included Tukey and Dunn tests. Linear regression models were used for all pairs of numerical variables.

Multinomial logistic regression models were used when the predictor variable was continuous and the response variable was categorical, specifically oak species richness per site. This method was used as opposed to a linear regression because oak species richness, though technically numeric, behaves more similarly to a categorical variable because there were three levels (1-3 species). When used as a predictor for continuous response variables, oak species richness per site was tested using Kruskal-Wallis one-way analyses of variance, which allows for skewed variable distributions. All statistical tests used an alpha level of 0.05.

Stepwise regressions.

Stepwise regression is a variable selection method that adds ("forward") or subtracts ("backwards") variables, one at a time, from a multiple regression model until the combination of predictor variables that best explains the response variable is found. A forward stepwise regression for each of the three main response variables (cynipid H', cynipid richness per site, and gall abundance per site) was built using the major predictor variables (habitat size, latitude, mean tree height, mean trunk circumference, oak species, and time since fire). Each stepwise regression generated a multiple regression model of best fit for their respective response variables.

The models of best fit were chosen by AIC (Akaike's Information Criteria), with the lowest AIC scores indicating the best models. Lowest scores are preferred because they are the most parsimonious, limiting the addition of variables into the model to only those that account for the most variation. These scores are, however, relative only to other models based on the same response variable. After selecting the final model for each response variable based on the AIC scores, the models were each run individually to produce a p-value and R^2 score. Additionally, residual error, degrees of freedom, regression sum of squares (RSS), and the coefficients of each variable in the final models were reported. These metrics helped to elucidate the efficacy of the model and show how each predictor variable related to the response variable. As each stepwise model was run on individual response variables, a unique combination of predictor variables was created that best explained the variation in that response variable. Each final model is therefore unique from the others.

Ordinations.

Unconstrained principle component analyses, an Eigan analysis-based linear ordination method, were performed for environmental variables by site, species distribution by site, and, subsequently, both environmental variables and species distributions together. This was done as an exploratory method of visualizing how species group together with other species and environmental variables (Gauch, 1982). A linear ordination method was chosen for species data because the data displayed a gradient 3.0 standard deviation units long. Similarly, for the environmental variable data, a linear method was chosen because the data was compositional. Analysis was done on Canoco v5.0 (ter Braak & Smilauer, 2002).

The ordination of only environmental variables included community type as a variable, showing how the different community types occurred amongst the others other variables. The ordination of environmental variables and species distribution together, however, did not include community type as it was not considered a statistically reliable variable. This is because FNAI community types allow for variation within each type, and similar community types are not always clearly delineated. Therefore, community type is considered less statistically reliable as a variable, and is considered more of a rough estimation of variables like plant composition, canopy openness, and hydrologic regime (Florida Natural Areas Inventory, 2010).

Included within the principle component analyses is a species diversity diagram. This diagram displays the species richness of the individual sample sites in the same configuration as that of the sites in the unconstrained PCA of species distributions across sites.

Results

Site Characteristics & Map

Across the 19 protected areas encompassing the 35 sites sampled for this survey, the total acreages of target communities ranged from just six to approximately 50,000 acres (Table 1). These protected areas include state parks and forests, SWFWMD preserves, wildlife or environmental management areas, county and city preserves, and one privately-managed property. Sample sites were concentrated in the southwest region of Florida, bounded on the north by Citrus county, on the east by Polk county, on the south by Charlotte county, and on the west by Pinellas county. This region has, for the most part, not been surveyed for cynipid galls, with a few exceptions from Abrahamson et al.'s 1994-1996 survey (Abrahamson et al., 1998; Price et al., 2004). No record of any previous official cynipid species observations could be found for Pinellas county. Species counts from Abrahamson et al.'s survey were not publicly available and therefore cannot be compared to those from the sites shared by this survey.

Table 1: Sample Site Descriptions

Site	Management Agency	Habitat size (acres)	Latitude	Longitude	FNAI Community Type	Oak Species Present
ADB Catfish CreekA	FDEP	2488	27° 59.065'	81° 29.662'	Scrub	gem, myrt
ADB Catfish CreekB	FDEP	2488	27° 58.839'	81° 29.689'	Scrub	chap, gem, myrt
Beker WingateA	FDEP	214	27° 27.048'	82° 08.740'	Scrub	chap, gem, myrt
BokA	Bok Tower Gardens	25	27° 56.293'	81° 34.435'	Sandhill	gem, myrt
BokB	Bok Tower Gardens	25	27° 55.704'	81° 34.084'	Sandhill	gem, myrt
BoydA	St. Petersburg P&R	6	27° 43.926'	82° 39.472'	Scrub	chap, gem, myrt
BoydB	St. Petersburg P&R	6	27° 43.581'	82° 39.227'	Scrub	chap, gem, myrt
BrookerA	Pinellas P&CR	220	28° 07.778'	82° 39.379'	Xeric hammock	chap, gem, myrt
BrookerB	Pinellas P&CR	220	28° 07.840'	82° 39.314'	Xeric hammock	chap, gem, myrt
Charlotte HarborA	FDEP	763	26° 49.949'	82° 12.785'	Scrub	chap, gem, myrt
Charlotte HarborB	FDEP	763	26° 50.061'	82° 12.843'	Scrubby flatwoods	chap, gem, myrt
ChinsegutA	FWC	545	28° 37.784'	82° 21.437'	Sandhill	chap, gem
ChinsegutB	FWC	545	28° 37.481'	82° 21.090'	Sandhill	gem
CitrusA	FFS	50000	28° 50.618'	82° 24.953'	Sandhill	chap, gem, myrt
CitrusB	FFS	50000	28° 47.541'	82° 23.051'	Sandhill	gem
ConnerA	SWFWMD	113	28° 18.951'	82° 26.927'	Sandhill	gem
ConnerB	SWFWMD	113	28° 18.870'	82° 27.234'	Sandhill	gem, myrt
CroomA	FFS	18000	28° 35.483'	82° 16.286'	Sandhill	gem
CroomB	FFS	18000	28° 36.281'	82° 14.762'	Sandhill	gem
Ft CooperA	FDEP	239	28° 48.675'	82° 18.310'	Sandhill	chap, gem, myrt
Ft CooperB	FDEP	239	28° 48.760'	82° 18.668'	Sandhill	chap, gem, myrt
Half Moon	FWC	167	28° 55.036'	82° 14.287'	Scrubby flatwoods	chap, gem, myrt
Halpata TastanakiA	SWFWMD	1720	29° 01.924'	82° 18.817'	Scrub	gem
Halpata TastanakiB	SWFWMD	1720	29° 01.600'	82° 23.126'	Sandhill	gem
Lake ManateeA	FDEP	155	27° 28.727'	82° 20.800'	Scrubby flatwoods	chap, gem, myrt
Lake ManateeB	FDEP	155	27° 28.623'	82° 19.867'	Scrubby flatwoods	chap, gem, myrt
Little Manatee RiverA	FDEP	155	27° 40.624'	82° 22.679'	Scrub	chap, gem, myrt
Little Manatee RiverB	FDEP	155	27° 40.386'	82° 22.939'	Scrub	chap, gem, myrt
Oscar SchererA	FDEP	421	27° 10.704'	82° 27.641'	Scrubby flatwoods	chap, gem, myrt
Oscar SchererB	FDEP	421	27° 10.899'	82° 27.418'	Scrubby flatwoods	chap, gem, myrt
Paynes CreekA	FDEP	20	27° 37.264'	81° 48.776'	Scrubby flatwoods	chap, gem, myrt
Paynes CreekB	FDEP	20	27° 37.364'	81° 48.601'	Scrubby flatwoods	chap, gem, myrt
Potts	SWFWMD	965	28° 54.717'	82° 18.084'	Scrubby flatwoods	chap, gem, myrt
Serenova	SWFWMD	2745	28° 19.400'	82° 34.474'	Xeric hammock	gem, myrt
Starkey	SWFWMD	2745	28° 15.654'	82° 38.063'	Scrub	chap, gem, myrt

*For management agencies, FDEP = Florida Department of Environmental Protection, FFS = Florida Forest Service, FWC = Florida Fish and Wildlife Conservation Commission, Pinellas P&Cr = Pinellas Co. Parks and Cultural Resources, St. Petersburg P&R = St. Petersburg Parks and Recreation, and SWFWMD = Southwest Florida Water Management District. For oak species present, “chap” = *Quercus chapmanii*, “gem” = *Q. geminata*, and “myrt” = *Q. myrtifolia*.

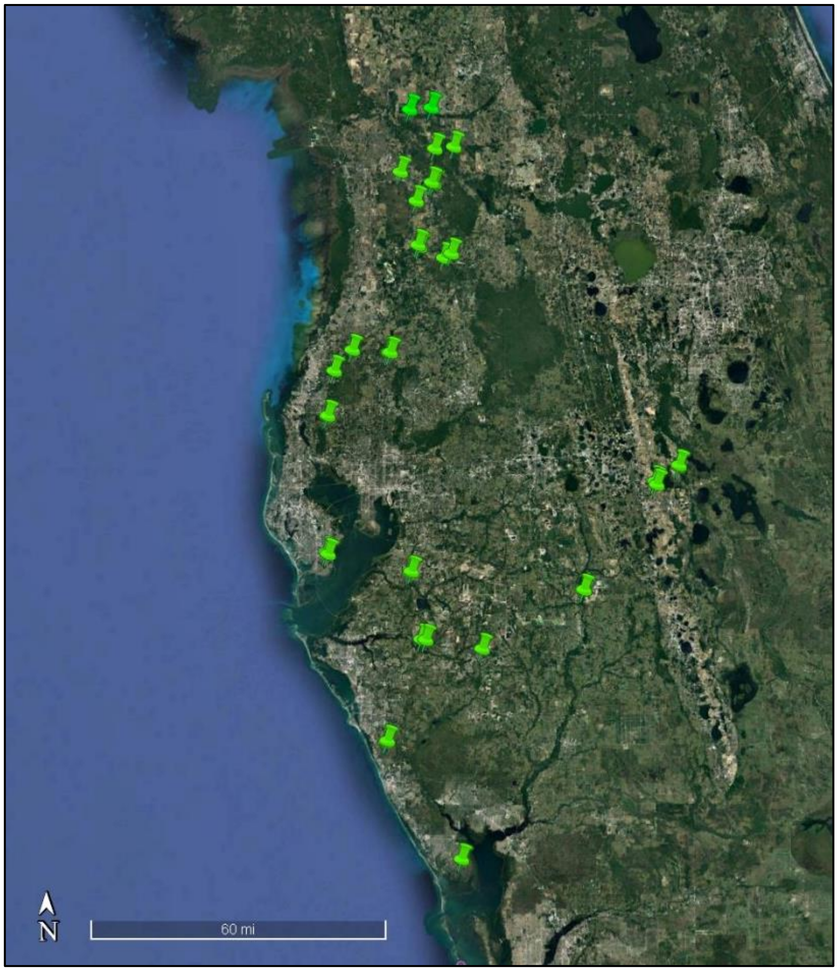


Figure 1: Map of Sampling Sites. The 19 sampling locations containing the 35 individual sampling sites visited between Nov. 2018 to Mar. 2019 are denoted by green pins. Map generated using Google Earth.

Gall and Oak Demographics

Across the 35 sites sampled, active galls of 21 species of cynipid wasps were observed and counted (Table 2). Only one species was unidentifiable and was given the moniker “U12” meaning “unknown species #12” which was found on *Q. myrtifolia*. This number was a remnant of the number of species originally unable to be identified in the field at the time of sampling, and hence given a numerical identifier. All 11 originally-unidentifiable species were later identified as cynipid galls and renamed in the dataset or identified as a non-cynipid gall and removed from the dataset. A total of 4,305 galls were counted. The least common species was *Bassettia pallida* Ashmead, found on *Q. geminata*, followed closely by *Dryocosmus nova* Ashmead, found on *Q. myrtifolia*. The most common species was *Neuroterus quercusminutissimus* Ashmead, also found on *Q. geminata*. *Andricus* and *Callirhytis* were the most common genera with four species each. *Disholcaspsis* was represented by three species, and *Neuroterus* by two species. *Bassettia*, *Belonocnema*, *Dryocosmus*, *Eumayria*, *Sphaeroterus*, *Xanthoterus*, and *Zapatella* were all represented by only one species each.

Interestingly, despite *Q. geminata* hosting the highest total number of galls, *Q. chapmanii* hosted the highest total number of cynipid species (Table 3). *Q. myrtifolia* hosted slightly fewer species but significantly fewer galls in total. *Q. geminata* was found at all 35 sites, while *Q. myrtifolia* was found at 27 and *Q. chapmanii* at 23. These variations in oak assemblages per site can be consequences of natural environmental variation or anthropogenic interference, though it would likely be difficult to identify the specific factors in play.

Table 2: Cynipid Gall Demographics by *Quercus* Species and Total Abundances

Cynipid species	**Quercus species**	**Total abundance**
Andricus pattoni	*chapmanii*	2
Andricus quercusfoliatus	*geminata*	382
Andricus quercuslanigera	*geminata*	120
Andricus stropus	*chapmanii*	33
Bassettia pallida	*geminata*	1
Belonocnema quercusvirens	*geminata*	124
Callirhytis floridana	*chapmanii*	14
Callirhytis quercusbatatoides	*geminata*	46
Callirhytis quercusgemmaria	*myrtifolia*	6
Callirhytis quercussimilis	*myrtifolia*	12
Disholcaspis quercusomnivora	*chapmanii*	209
Disholcaspis quercusvirens	*geminata*	944
Disholcaspis spongiosa	*chapmanii*	19
Dryocosmus nova	*myrtifolia*	3
Eumayria floridana	*myrtifolia*	17
Neuroterus quercusminutissimus	*geminata*	1419
Neuroterus quercusverrucarum	*chapmanii*	824
Sphaeroterus melleum	*chapmanii*	94
Xanthoterus politum	*chapmanii*	17
Zapatella quercusmedullae	*myrtifolia*	11
U12	*myrtifolia*	8
Total		**4305**

Table 3: Number of Sites, Cynipid Species, and Total Galls per Quercus Species

***Quercus* species**	**Number of sites**	**Total cynipid species**	**Total galls observed**
geminata	35	7	3036
chapmanii	23	8	1212
myrtifolia	27	6	57

Figures 2.1-2.12: Cynipid Gall Photographs. (2.1) *Disholcaspis quercusomnivora*, expired. (2.2) *D. quercusomnivora*, active. (2.3*) Andricus quercusfoliatus*. (2.4) *Andricus quercuslanigera*. (2.5) *Andricus pattoni*. (2.6) *Andricus stropus*. (2.7) *Bassettia pallida*, expired. (2.8) *Belonocnema quercusvirens*. (2.9) *Callirhytis floridana*, expired. (2.10) *Callirhytis quercusbatatoides*. (2.11) *Callirhytis quercusgemmaria*, some kernels already dropped. (2.12) *Callirhytis quercussimilis*

Statistical Analyses

Parametric assumptions testing.

Normal distribution of the residuals is required for any parametric analysis, and was tested in this study using Shapiro-Wilk analyses with a significance level of $p < 0.05$. Several ANOVA tests showed significant non-normality of residuals, and were therefore run again as non-parametric Kruskal-Wallis analyses of variance (Table 4). No linear regression analyses showed significant non-normality of residuals. Heteroscedasticity, or significant changes in residual values throughout a regression model, was tested for in each model with a Breusch-Pagan test (Breusch & Pagan, 1979). Models with a Breusch-Pagan p-value less than 0.05 would have been considered heteroscedastic and therefore not reliable, but no models scored below this level.

Patterns among predictor variables.

Community type, though not a quantitatively robust variable, was a significant predictor variable for other variables used elsewhere as predictors. There was variation in latitudinal range across community types (Kruskal-Wallis: KW $\chi2 = 11.399$, $p = 0.01$) (Fig. 3.1). The communities with significantly different latitudinal ranges were scrub-sandhill and scrubby flatwoods-sandhill ($p < 0.05$). Sandhills were the most northerly community type, while scrubby flatwoods were the most southerly, falling in line with the natural latitudinal gradient for the distribution of these communities. Sandhill also had the lowest average oak species richness (2) when compared to the other community types, and scrubby flatwoods sites had no instances of oak species richness less than three (Pearson's chi-square: $\chi^2 = 16.78$; $p = 0.01$) (Fig. 3.3).

Xeric hammock had the longest average time since fire, followed closely by scrub (ANOVA: $F = 8.156$; $p < 0.01$) (Fig. 3.2). Three pairs of communities differed in time since fire: scrub-sandhill, xeric hammock-sandhill, and xeric hammock-scrubby flatwoods ($p < 0.05$). These patterns are generally concurrent with conventional understanding of natural fire frequency for these community types.

Q. geminata had the greatest latitudinal range of the three species, with *Q. chapmanii* and *Q. myrtifolia* more common at lower latitudes (Kruskal-Wallis: KW $\chi2 = 9.3118$; $p < 0.01$) (Fig. 3.5). The species pairings that significantly differed in latitudinal range were *Q. geminata-Q. chapmanii* and *Q. myrtifolia-Q. geminata* ($p < 0.05$). The three species had different distributions within the four community types (Pearson's chi-squared: $\chi2 = 13.34$, $p = 0.38$), though only significantly in sandhills (Fig. 3.4). Oak species richness per site differed more starkly across community types (Pearson's chi-squared: $\chi^2 = 16.78$, $p = 0.0101$), with sandhills mostly commonly containing only one species and scrubby flatwoods most commonly containing all three species (Fig. 3.3)

Time since fire and tree height were also significantly correlated (Linear regression: $R^2 = 0.1313$, $p = 0.012$) (Fig. 3.6). As is typical for species that are periodically burned back in a fire, tree height increased with time since fire.

Table 4: Results from Statistical Analyses Involving Categorical Variables

Predictor	Response	Analysis	DF	p-value	Test Statistic	
Community Type	Latitude	Kruskal-Wallis	3	0.00975	KW χ^2 =	11.399
	Time Since Fire	ANOVA	3	0.00098	F =	8.156
	Oak Species	Pearson's Chi-Squared	3	0.038	χ^2 =	13.34
	Oak Species Richness	Pearson's Chi-Squared	3	0.0101	χ^2 =	16.78
Oak Species	Latitude	Kruskal-Wallis	2	0.00951	KW χ^2 =	9.3118
Oak Species Richness	Cynipid Richness	Kruskal-Wallis	2	0.01448	KW χ^2 =	8.4694

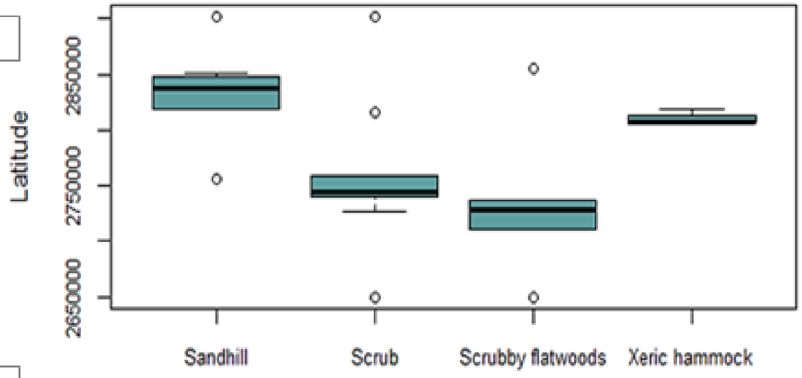
*Only significant results (p > 0.05) are reported above.

Table 5: Results from Statistical Analyses Involving Continuous Variables

		Linear Regression		
Predictor	**Response**	**p-value**	**R^2**	
Habitat Size (acres)	Cynipid H'	0.7487	-0.0271	
	Cynipid Richness	0.5763	-0.0205	
	Gall Abundance	0.3138	0.00136	
Latitude	Cynipid H'	0.08727	0.05833	
	Cynipid Richness	0.6773	0.03483	
	Gall Abundance	0.2105	0.01821	
Mean Tree Height (cm)	Cynipid H'	0.7001	-0.0256	
	Cynipid Richness	0.2183	0.0166	
	Gall Abundance	0.0174	0.1343	+
Mean Trunk Circum. (cm)	Cynipid H'	0.9353	-0.0301	
	Cynipid Richness	0.7007	-0.0256	
	Gall Abundance	0.2518	0.0105	
Time Since Fire (years)	Cynipid H'	0.00448	0.1964	+
	Cynipid Richness	0.00036	0.3037	+
	Gall Abundance	0.114	0.04592	
	Mean Tree Height (cm)	0.01891	0.1303	+

*A (+) symbol indicates significant correlations (p<0.05).

3.1



3.2

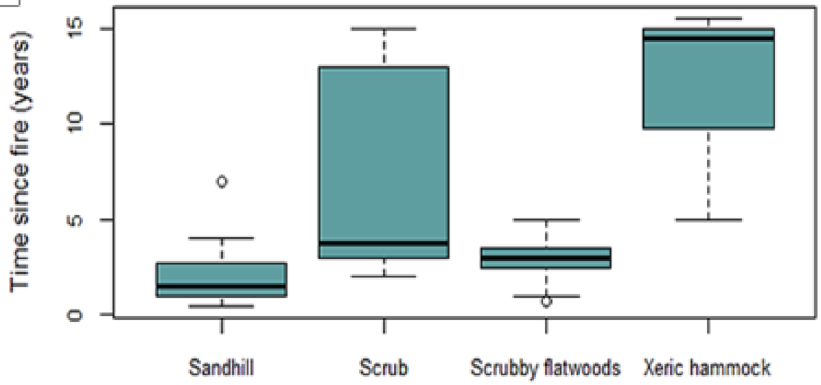
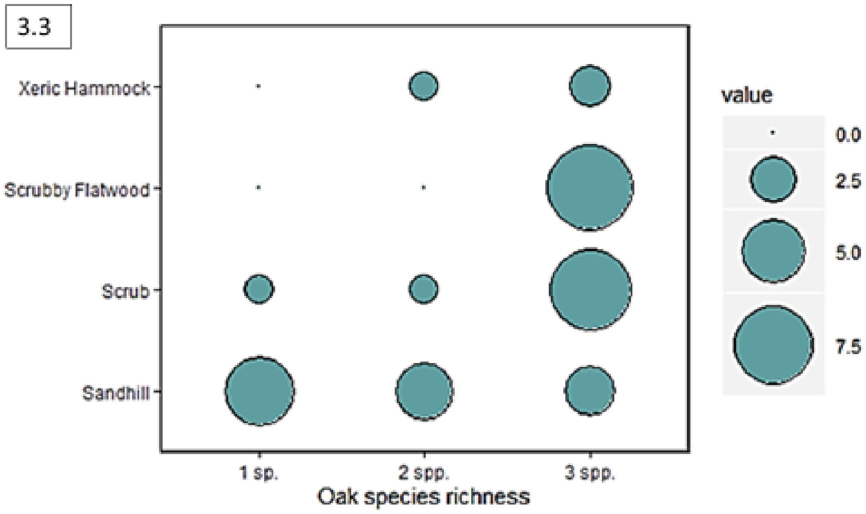


Figure 3.1: Boxplot of Latitudinal Range by Community Type.

Figure 3.2: Boxplot of Time Since Last Fire by Community Type

3.3



3.4

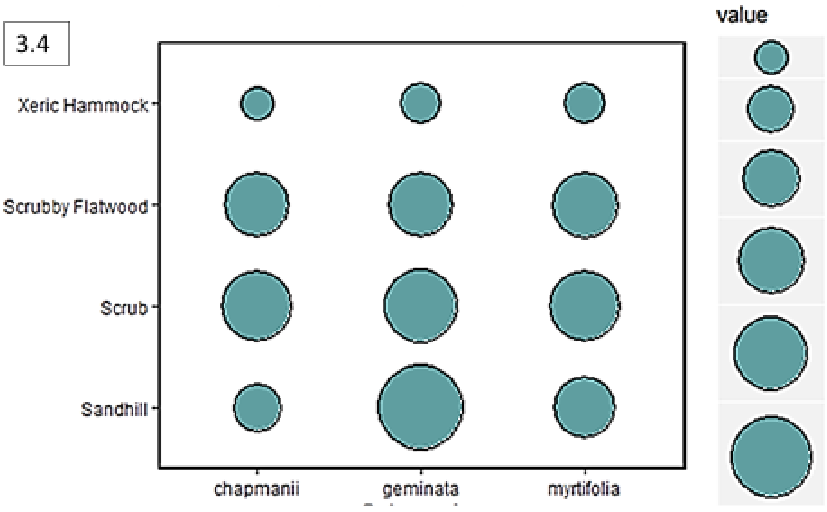
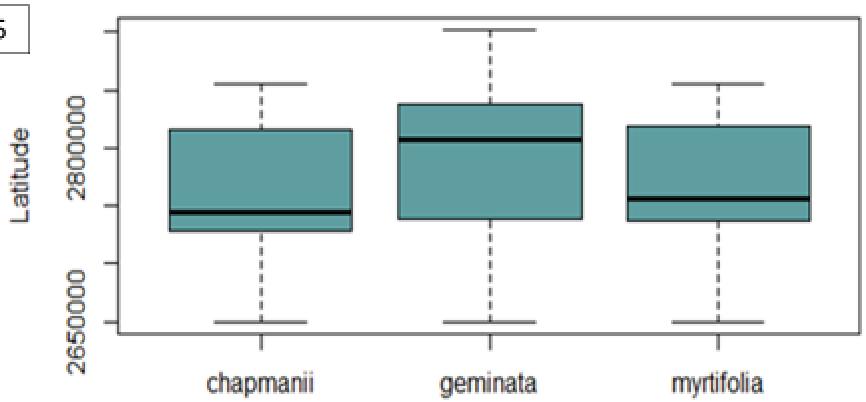


Figure 3.3: Balloon Plot of Target Oak Richness per Site by Community Type.

Figure 3.4: Balloon Plot of Target Oak Species Distributions by Community Type.

3.5



3.6

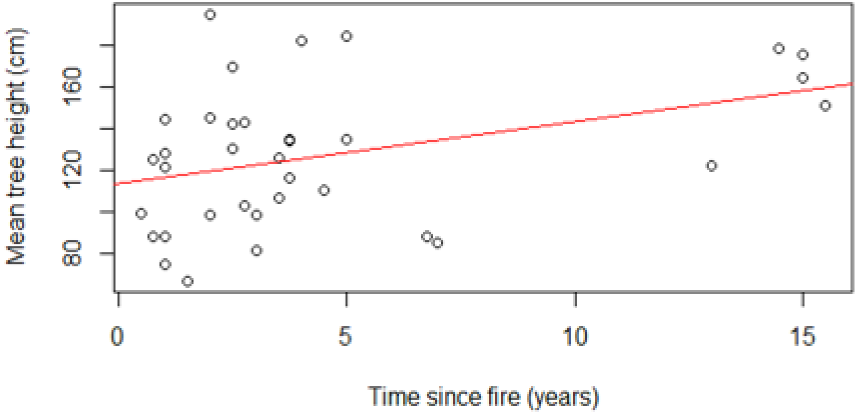


Figure 3.5: Boxplot of Latitudinal Range by Target Oak Species.

Figure 3.6: Scatterplot of Mean Tree Height by Time Since Last Fire. Linear regression line shown in red.

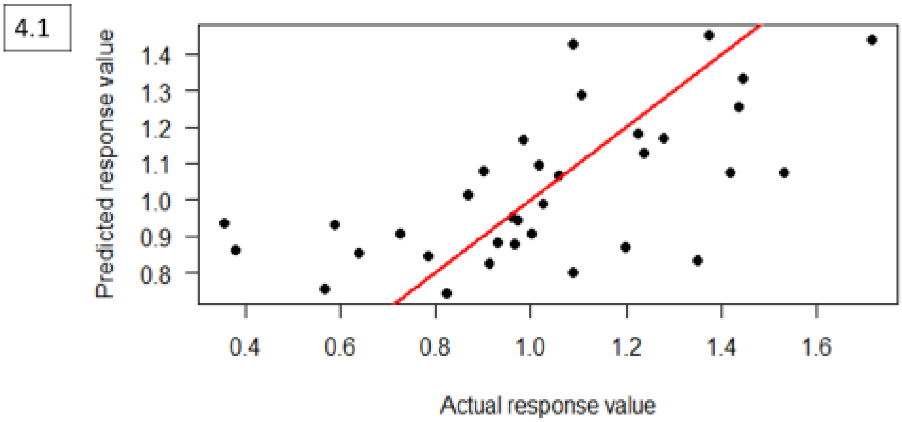
Stepwise regressions.

Cynipid species diversity (H') per site.

Time since fire, latitude, and mean tree height were significant predictors in the final model of the stepwise regression of cynipid species diversity (Fig. 4.1; Multiple linear regression: $R^2 = 0.3382$, $p < 0.01$). However, univariate testing only found significant correlation between cynipid species diversity and time since fire (Fig. 4.3; Linear regression: $R^2 = 0.1962$, $p < 0.01$).

Time since fire and latitude both had positive coefficients in the stepwise regression, meaning that as these two variables increase, cynipid species diversity tends to increase as well. Mean tree height had a negetave coefficient. When these three variables were tested individually, only time since fire was significantly correlated with cynipid species diversity. While latitude was close to a significant correlation (Fig. 4.2; $p = 0.08$), mean tree height was far from it (Fig. 4.4; $p = 0.7$). In addition, mean tree height had a slightly inverse relationship with cynipid diversity, shown in the regression line on Figure 4.4 and its negative coefficient in final multiple linear regression model.

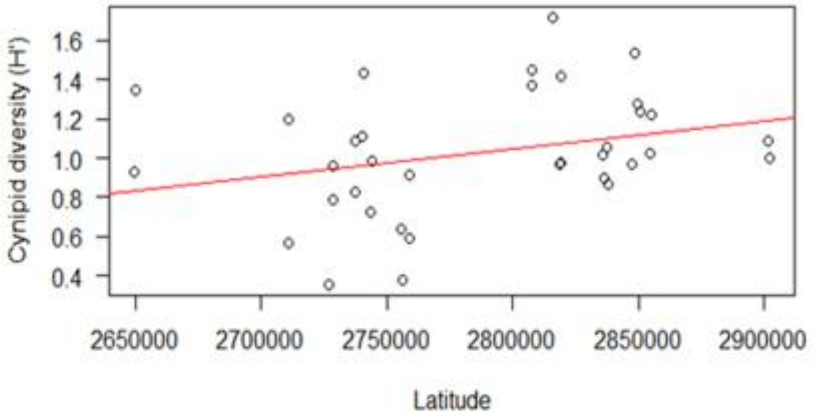
The relationship between cynipid diversity and latitude is likely connected to the different latitudinal ranges of the three oak species surveyed (Fig. 3.5) and the disparities in the cynipid populations observed on them. Sand live oak, *Q. geminata*, ranged the farthest north in the study region and bore the most galls (Table 3). However, the latitudinal ranges of each cynipid species observed were not analyzed for this study; they may show latitudinal gradients in certain species' densities, possibly affecting local diversity metrics. Time since fire and cynipid diversity had a more transparent relationship, showing correlation in both the final multiple regression model and their individual linear regression model. This pattern follows with a recently-documented trend that as a site has more time to recover after a fire, more cynipid species will be able to return and accumulate (Cronin et al., 2020).



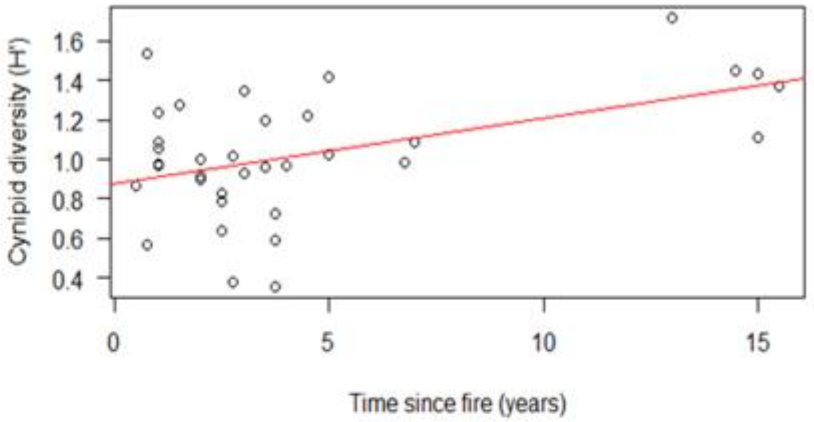
Coefficients:
(Intercept): -3.101e+00
Time since last fire: 4.202e-02
Latitude: 1.544e-06
Avg tree height: -2.866e-03

Figure 4.1: Scatterplot of Final Stepwise Regression For Cynipid Diversity (H’). All major predictor variables included are listed with their coefficients. Multiple linear regression line shown in red.

4.2



4.3



4.4

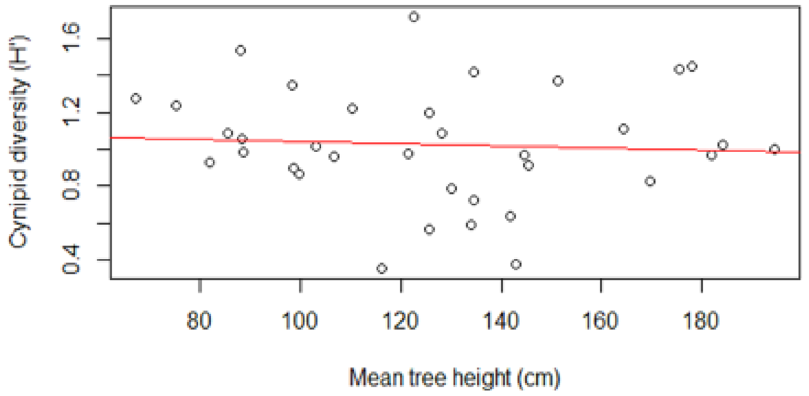


Figure 4.2: Scatterplot of Cynipid Diversity (H') by Latitude. Linear regression line shown in red.

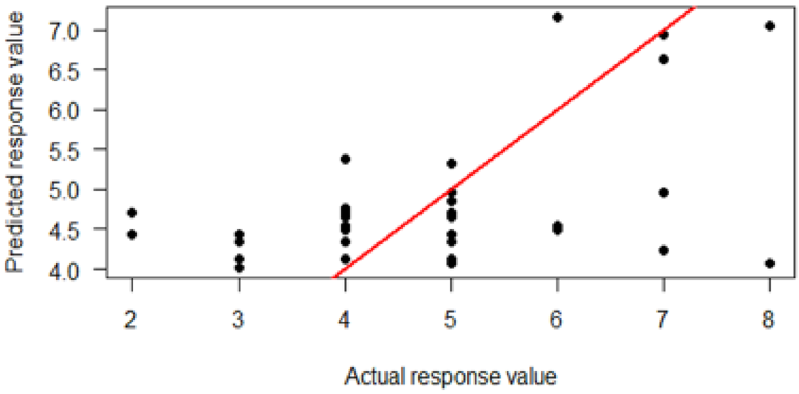
Figure 4.3: Scatterplot of Cynipid Diversity (H') by Time Since Last Fire. Linear regression line shown in red.

Figure 4.4: Scatterplot of Cynipid Diversity (H') by Mean Tree Height. Linear regression line shown in red, though these variables did not show correlation.

Cynipid species richness per site.

Time since fire was the only variable found to be a significant predicator for cynipid species richness in the final model of the stepwise regression (Fig. 5.1; Linear regression: $R^2 = 0.304$, $p < 0.01$) (Fig. 5.2). However, oak species richness also proved to be a significant predictor for cynipid species richness in univariate testing (Kruskal-Wallis: KW $\chi^2 = 8.4694$, $p = 0.015$) (Fig. 5.3). Post-hoc tests showed that each level of species richness (1-3) differed significantly from the others. This pattern follows the assumption that as sites contain more oak species, they should contain more oak-galling cynipid species. Therefore, cynipid species richness per site is likely dependent on both time since fire and oak species richness.

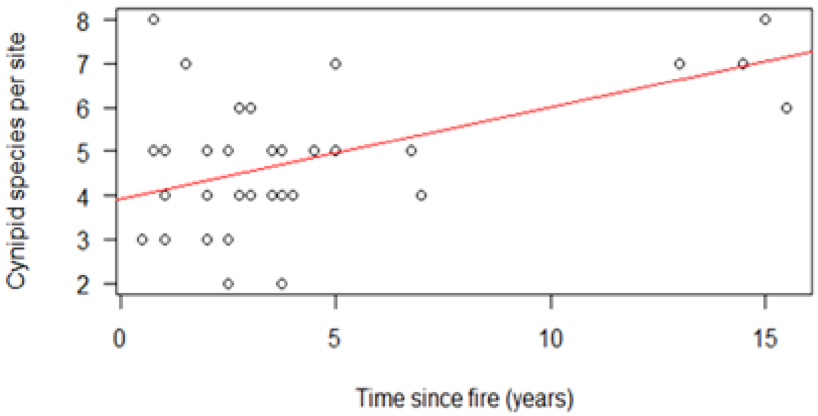
5.1



Coefficients:
(Intercept): -2.469e+01
Time since last fire: 0.2089

Figure 5.1: Scatterplot of Final Stepwise Regression For Cynipid Species Richness. All major predictor variables included are listed with their coefficients. Linear regression line shown in red.

5.2



5.3

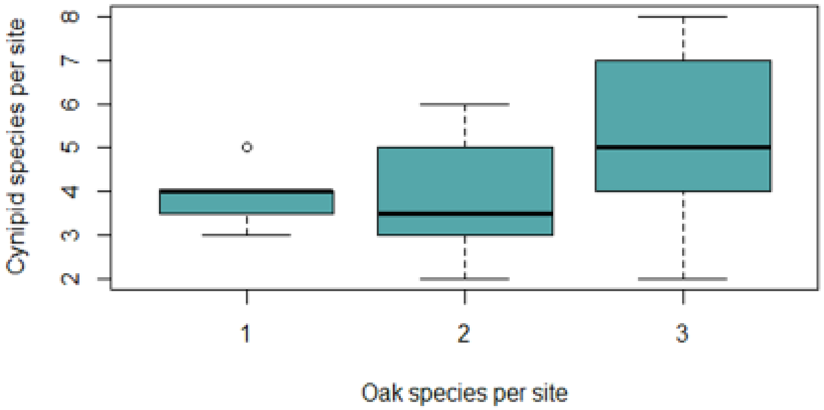


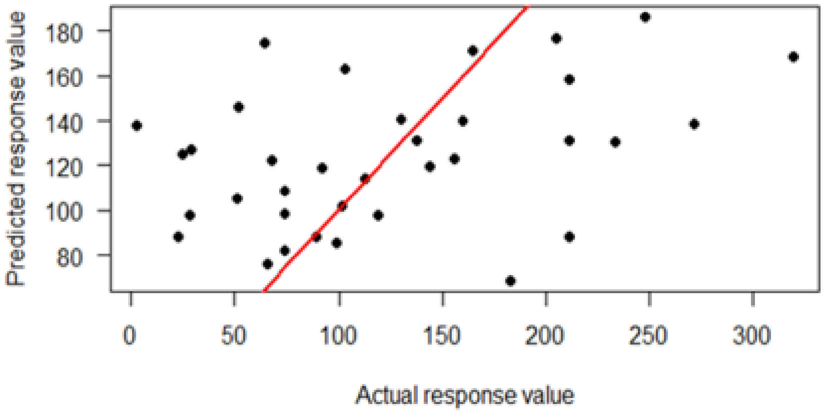
Figure 5.2: Scatterplot of Cynipid Species Richness by Time Since Last Fire. Linear regression line shown in red.

Figure 5.3: Boxplot of Cynipid Species Richness by *Quercus* Species Richness.

Total gall abundance per site.

The stepwise regression for total gall abundance per site included all of the major variables, but the final model included only one variable: mean tree height (Fig. 6.1). As mean tree height (cm) per site increased, total gall abundance per site also increased (Linear regression: $R^2 = 0.1343$, $p = 0.017$) (Fig. 6.2). This suggests that as more tree tissue becomes available, cynipids find increasing amounts of appropriate oviposition sites (stems, buds, leaves, roots, etc.) and therefore produce more galls. There were no other significant relationships identified with total gall abundance.

6.1



Coefficients:
(Intercept): 6.6758
Avg tree height: 0.9234

Figure 6.1: Scatterplot of Final Stepwise Regression For Total Gall Abundance. All major predictor variables included are listed with their coefficients. Linear regression line shown in red.

6.2

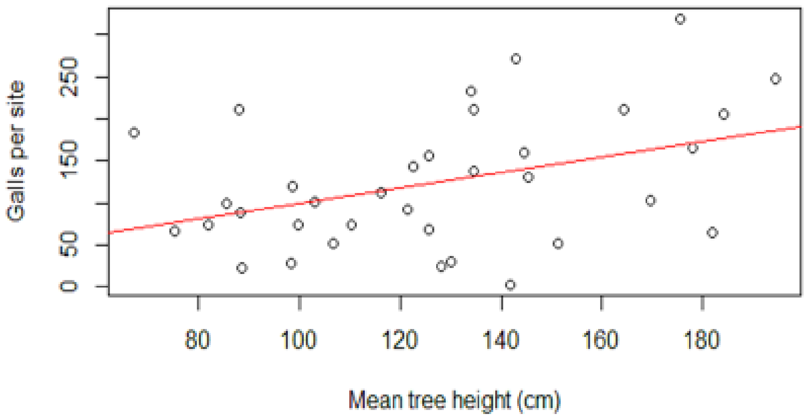


Figure 6.2: Scatterplot of Total Gall Abundance by Mean Tree Height. Linear regression line shown in red.

Ordinations.

A set of exploratory principle component analysis (PCA) ordinations were constructed to visualize any groupings of environmental variables, sites, and species. In the PCA containing only environmental variables (Fig. 7.1, left), arrow length is a measure of fit for the environmental variable, namely the multiple correlation of the variable with the ordination axes. Arrow direction corresponds to the direction of the steepest increase in values for that variable and the angle between arrows (alpha) indicates the sign and degree of correlation between the variables. In Figure 7.1 (left), community type was split into its four categories (sandhill, scrub, scrubby flatwoods, xeric hammock) as several predictor and response variables have been shown to differ significantly between categories. Interestingly, mean tree height fell on the same line as time since last fire, even the latter was not found to predict much of the variance in the former ($R^2 = 0.07$). Xeric hammock and scrub community types grouped together in similar directions, as well. A second grouping included habitat size, latitude, and sandhill. The final grouping was target oak species richness and scrubby flatwoods, which mirrored how the highest average oak species richness was found in scrubby flatwoods (Fig. 3.3).

In the sample site diagram (Fig. 7.1, right), the distance between the symbols approximates the dissimilarity of their environmental variable values as measured by their Euclidean distance. Generally, sister sites were grouped together, denoting high similarity in environmental variables. Approximately four different groups emerged into distinct clusters, primarily dependent on the latitude of the sites. As several environmental (predictor) variables were shown to also vary by latitude (Figs. 3.1. – 4.3), this pattern is likely a reflection of the relationships between those variables and the geographic distributions of the sample sites.

The second round of PCA ordinations plotted oak-galling cynipid species distributions and sample sites according to their species assemblages (Fig. 7.2). With a few exceptions, most species grouped together with those that show host tree species. Species in the lower right quadrant mostly parasitize *Q. chapmanii*, while species in the lower left quadrant mostly parasitize *Q. geminata*, and those in the upper quadrants are mostly parasites of *Q. myrtifolia*. In the sample site by species assemblage diagram (Fig. 7.2, right), the distance between the symbols approximates the dissimilarity of species' compositions as measured by their Euclidean distance. Individual groups of sites are not as easily discerned as when they are plotted using environmental variables, though at least two can be delineated. Generally, sites with higher cynipid species richness and diversity grouped together in the lower right quadrant, while sites with lower scores grouped together in the upper left quadrant. Figure 7.3, a species diversity diagram, shows the same configuration of sample sites, but with the cynipid species richness at each site shown instead of the site name. Additionally, sister sites are also much less likely to be near each other as when compared via environmental variables, suggesting that species assemblages are variable to some degree within similar environmental constraints.

The final PCA ordination included both cynipid species and environmental variables (Fig. 7.4). Arrow length is a measure of fit for the species or variable along the multiple correlation of the species and variables with the ordination axes. Arrow direction corresponds to the direction of the steepest increase in counts for that species or value of environmental variable, and the angle between arrows (alpha) indicates the sign and degree of correlation between the species or variables. Solid arrow points indicate cynipid species and hollow arrow points indicate environmental variables. Community type was withheld from this ordination because it was not considered a significant variable influencing species distribution, but rather only directly influencing other environmental variables already included.

Latitude and target oak species richness appear to be the most influential variables for species assemblage, based on arrow length. Latitude, habitat size, mean tree height, and time since last fire were closely associated and therefore fell out within the same cluster; most were associated with species that parasitize *Q. geminata*. A cluster of species which predominantly parasitize *Q. chapmanii* appear to have weak influences from time since last fire and tree richness, while the *Q. myrtifolia* group of species does not seem to be as closely associated with any environmental variables. This lack of association for *Q. myrtifolia* species is likely a symptom of the scarcity of galls found on that species in this study.

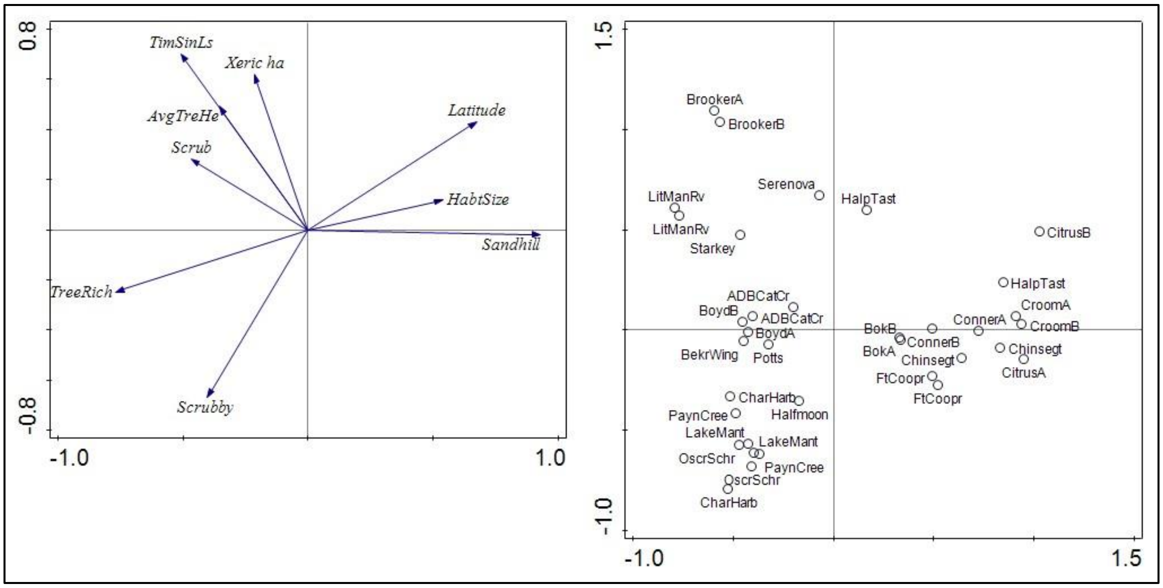


Figure 7.1: Unconstrained PCA of Environmental Variables and Sample Sites. Left: groupings of environmental variable. Right: groupings of sample sites based on environmental variables. Variable name abbreviations: “TimSinLs” = time since last fire, “AvgTreHe” = mean tree height, “HabtSize” = habitat size, “Treerich” = oak species richness, “Xeric ha” = xeric hammock, “Scrubby” = scrubby flatwoods.

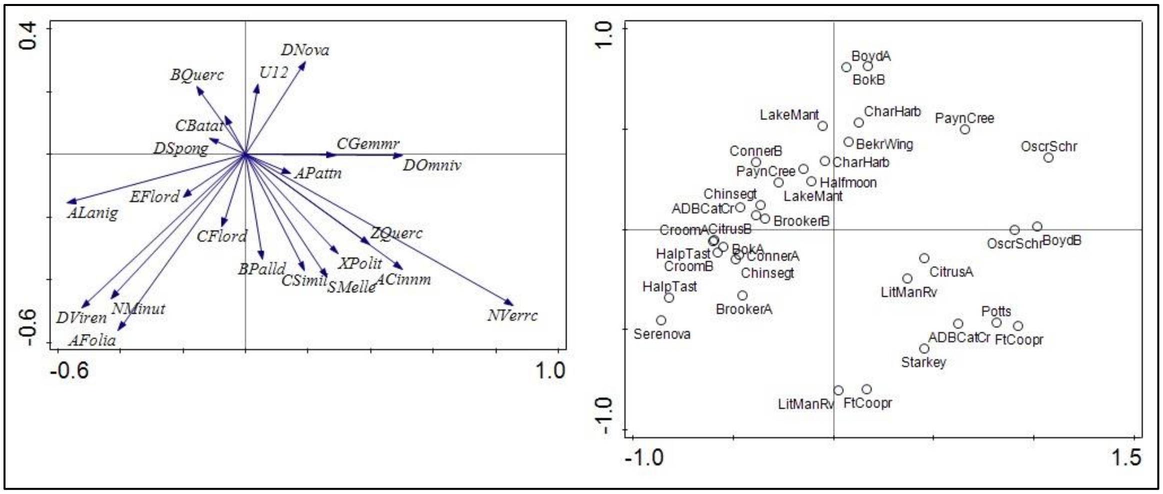


Figure 7.2: Unconstrained PCA of Cynipid Species Distributions and Sample Sites. Left: groupings of cynipid species. Right: groupings of sample sites based on species assemblages (right). Species name abbreviations: “AFolia” = *Andricus quercusfoliatus*, “ALanig” = *A. lanigera*, “ACinnm” = *A. cinnamoneus*, “APattn” = *A. pattoni*, “BPalld” = *Bassettia pallida*, “BQuerc” = *Belonocnema quercusvirens*, “CFlord” = *Callirhytis floridana*, “CGemmr” = *C. gemmaria*, “CBatat” = *C. quercusbatatoides*, “CSimil” = *C. similis*, “DSpong” = *Disholcaspis spongiosa*, “DOmniv” = *D. quercusomnivora*, “DViren” = *D. quercusvirens*, “DNova” = *Dryocosmus nova*, “EFlord” = *Euaymria floridana*, “NMinut” = *Neuroterus quercusminutissimus*, “NVerrc” = *N. quercusverrucarum*, “SMelle” = *Sphaeroterus melleum*, “XPolit” = *Xanthoteras politum*, “ZQuerc” = *Zapatella quercusmedullae*.

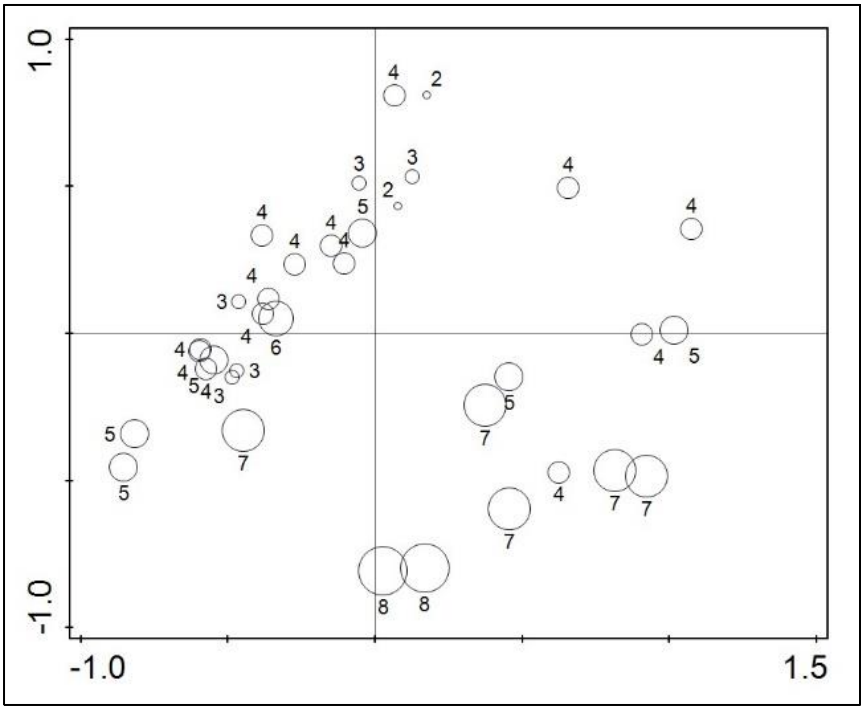


Figure 7.3: Diversity Diagram of Cynipid Species Across Sample Sites. Each circle represents a sample site and are configured as in Figure 7.2. The size of each circle and then number beneath it denotes the number of cynipid species found at that site.

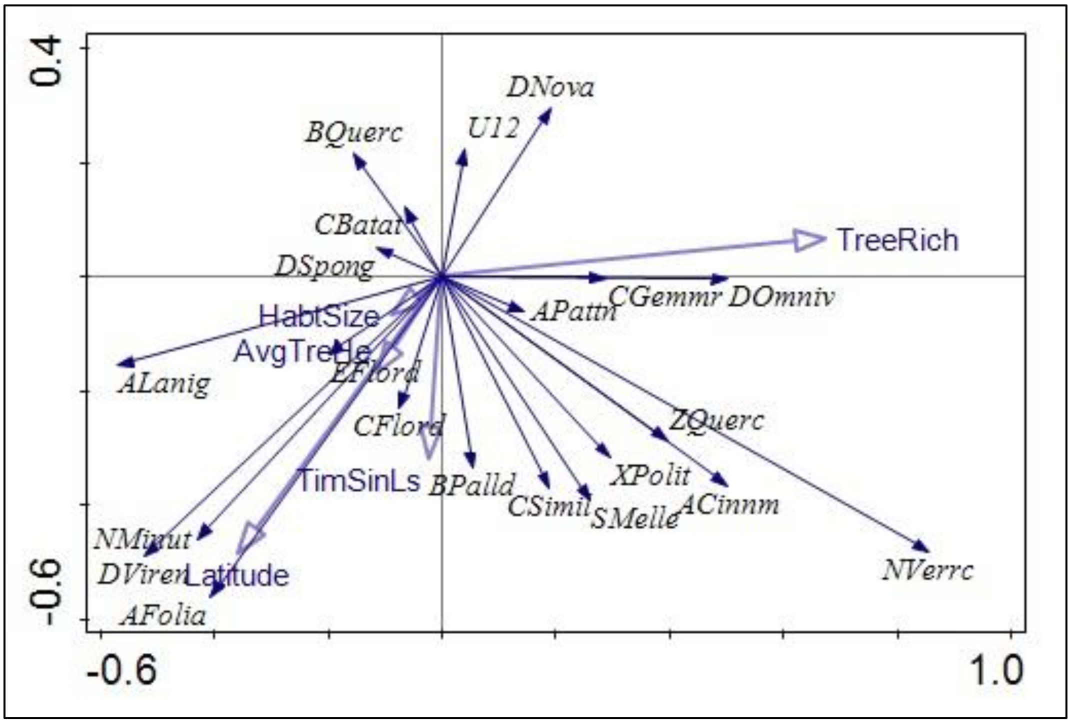


Figure 7.4: Unconstrained PCA of Cynipid Species and Environmental Variables. Environmental variables and species abbreviations are the same as in the previous ordination graphs.

Discussion

The purpose of this survey was to improve our understanding of oak-galling cynipid distributions in southwest Florida and how environmental variables affect their populations. It was hypothesized that cynipid Shannon-Weiner (H') diversity, richness, and gall abundance would increase as habitat size, time since last fire, latitude, tree size, and oak species richness increased. Each hypothesis is discussed individually below, through both univariate analyses and stepwise regressions aimed to create the most parsimonious and effective combinations of predictor variables to explain each response variable. Additionally, unconstrained principle component analysis (PCA) ordinations were used to visualize the relationships between environmental variables, cynipid species, and sample sites. These analyses were more exploratory in nature and therefore used only to help inform and interpret the results of hypothesis testing. This combination of analytical testing revealed a story of how environmental conditions offer different opportunities and challenges for cynipid gallers, and provided a glimpse at the variety of ecological strategies employed by different cynipid species.

Hypothesis 1: Cynipid Diversity

It was hypothesized that cynipid species diversity (H') would increase as habitat size, time since last fire, latitude, tree size, and oak species richness increased. With respect to habitat size, while it has been observed that some cynipids populations increase in smaller, isolated habitat fragments (Chust et al., 2007; Maldonado-López, 2015), this trend was not assumed to be universal for this survey. Cynipid wasps are small (< 5 mm) and generally are not considered to be strong fliers. While considerable dispersal abilities have been observed in some species (Hough, 1951), most notably those that have successfully invaded new geographical areas (Schönrogge, 2012), no observations on the dispersal abilities of Florida cynipid species have been made. It was therefore not assumed that the species found in this survey possessed strong dispersal abilities, and consequently would be more species rich and abundant in larger, contiguous habitat patches.

However, habitat size was not identified as a significant predictor of cynipid diversity in either the individual regressions or the stepwise regressions. Therefore, habitat size does not seem to have a large impact on the total cynipid population for a given site, and small sites should not be discounted for their importance in maintaining local species assemblages.

Cynipid diversity was expected to increase with latitude as the ideal latitudinal region for galling insects extends north of Florida (Fernandes & Price, 1988). However, latitude was not found to be a significant predictor of cynipid diversity during univariate linear regression analyses (Fig. 4.2; $p = 0.087$), although the p-value was nearly significant. At the same time, it was found to be significant enough to be retained in the final multiple linear model produced by the stepwise regression procedure (Fig. 4.1).

As time since fire increased at any particular site, more cynipid species were expected to accumulate in the site and thereby increase species diversity. This pattern has recently been documented in a diverse cynipid community in southern Florida (Cronin et al., 2020) using more highly detailed fire history data than was available for this study. Yet, this study also found time since last fire to be a significant predictor in both univariate regression analysis and in the final model produced by the stepwise regression for cynipid diversity (Figs. 4.1, 4.3).

The final three variables expected to influence cynipid diversity were mean tree height (cm), mean trunk circumference (cm), and target oak species richness. Of these, only mean tree height was found to predict cynipid diversity, though only significantly during the stepwise procedure. Interestingly, tree height was the only variable retained in the multiple linear regression that had a negative coefficient, indicating an inverse relationship between tree height and cynipid diversity. However, when this relationship was tested individually, there was no significant correlation found and any semblance of a pattern that did exist was weakly negative (Fig. 4.4).

The portions of the null of Hypothesis 1 relating to the relationship between cynipid species diversity and habitat size, tree size, and oak species richness, were therefore accepted. The portions relating to latitude and time since fire were rejected. Time since last fire and latitude were both found to significantly influence cynipid species diversity per site.

Some aspects of this relationship may be explainable by other patterns found in this study, both observational and statistical. First, *Q. geminata* was the target oak species on which the most galls were found (3,036), thereby contributing heavily to a site's cynipid diversity. *Q. geminata* was also found the farthest to the North within the study region (Fig. 3.5), and thus the relationship between cynipid diversity and latitude could be, in part, due to the distribution of *Q. geminata* throughout the study region. This pattern was also reflected in several of the ordination figures, most notably Figure 7.4, where the majority of the species that parasitize *Q. geminata* were grouped around the arrow for latitude in the lower left quadrant. However, abundance of galls does not directly equate to higher cynipid diversities on *Q. geminata* and is not likely to account for the entirety of the relationship between latitude and cynipid diversity. Part of this relationship could be due to cynipid diversity simply being greater at the more northerly stretches of the study region, in concurrence with the latitudinal range identified by Fernandes & Price (1988) as having the greatest galling insect diversity.

With regards to time since fire, Cronin et al. (2020) also found that cynipid diversity increased with time since fire, reaching an asymptote at ~7 years. It is not yet known if cynipid diversity may decrease as time since fire increases from that point, but Cronin and colleagues also found that some species can take over 10 years to return to a burned site, even when in close proximity with source populations.

It should be noted that while oak species richness could not be proven to increase cynipid species diversity, the inclusion of more oak species in studies similar to this one may yield different results. In this study, the *Q. myrtifolia* individuals surveyed were found to host a surprisingly small number of galls (57 across the entire study region), but not a comparatively small number of species (6) and *Q. myrtifolia* was the second most common of the three target species. The cause for this stark disparity in gall abundance for this species is unknown, but could be influencing how the relationship between oak richness and cynipid diversity was depicted in this study. *Q. myrtifolia* has previously been known to host the greatest number of cynipid species of any oak species in Florida

(37) (Price et al., 2004), but this could be due to Price et al.'s larger study region (Appendix B) and longer survey period (three winter seasons from 1994 to 1996 at varied time intervals, with shorter surveys conducted up to 2001). Price et al. (2004) may also have included expired galls in their counts, while this study excluded them in order to record only the currently-active breeding populations of cynipid species at each site.

A final possibly for the disparities in species assemblages per *Quercus* species may unfortunately be due to cynipid population declines in the two decades since Price et al.'s survey. Although no studies have been conducted to assess oak-galling cynipid population changes, there is growing evidence for global insect biomass declines during the same time period (Hallman et al., 2017; Leather, 2017; Wagner, 2019). At the same time, some apparent declines in insect populations have been attributed to dramatically-fluctuating populations instead (Saunders, 2019), though interpretations based on either biomass or individual group abundances do not always lead to the same conclusions. To reiterate, there is no clear evidence so far for any decline in cynipid populations in Florida, but continued monitoring should be a priority for ensuring the continuation of the species present in the state.

Hypothesis 2: Cynipid Species Richness

It was hypothesized that cynipid species richness would increase as habitat size, time since last fire, latitude, tree size, and oak species richness increased. Habitat size, latitude, and tree size were not found to have any significant relationships with cynipid species richness, and the null of Hypothesis 2 relating to those variables was accepted.

Time since last fire was a significant predictor of cynipid richness in both individual linear regression and the stepwise procedure, where it was the only variable retained in the final model (Figs. 5.1, 5.2). The null of Hypothesis 2 relating to time since fire was therefore rejected. This relationship mirrored that found by Cronin et al. (2020), where cynipid richness increased with time since fire and reached an asymptote at ~7 years. All but two species had returned by 14 years after fire. Increasing time after fire, therefore, allows more time for cynipids to recolonize an area, although the amount of time required for each species to return has not been studied in detail. It is likely that some species return more quickly than others, taking advantage of different niches than would be available during later stages of habitat regrowth.

Oak species richness, while not included in the stepwise procedure because of its categorical nature, was a significant predictor of cynipid species richness (Fig. 5.3). Cynipid species richness increased as oak species richness increased, showing that the addition of oak species to a site brings with it additional of associated cynipid species. The null of Hypothesis 2 relating to oak species richness was therefore rejected. This trend was also seen by Cronin et al. (2020). There have been no recorded instances of any cynipid species utilizing more than one of the oak species included in this study, making the relationship between oak species richness and cynipid species richness that much stronger.

When examining the ordinations, cynipid richness showed the most definable pattern in Figures 7.2 & 7.3, where oak species richness continued to show its influence over cynipid richness. In Figure 7.2 (right), sample sites are plotted in accordance to their cynipid populations, with sites with higher cynipid richness and diversity grouping together in the lower right quadrant. Actual species counts for those sites are displayed in Figure 7.3. The placement of each site corresponds to similarities in which cynipid species were present, and their abundance in relation to other sites, with more similar sites grouping closer together. The group with the highest number of cynipid species almost exclusively contains sites with all three target oak species, reiterating the relationship between these two variables.

Hypothesis 3: Total Gall Abundance

It was hypothesized that total gall abundance per site would increase as habitat size, time since last fire, latitude, tree size, and oak species richness increased. However, there were no significant relationships found between gall abundance and habitat size, latitude, or oak species richness, and the null of Hypothesis 3 relating to these variables was accepted.

The only direct relationship that occurred with total gall abundance was mean tree height (cm), which was significantly correlated with gall abundance in both individual regression analysis (Fig. 6.2) and the stepwise procedure. It was the only variable retained in the final linear model (Fig. 6.1). These findings agree with the observed trend that more available host tissue supports larger galling insect populations (Cornell, 1986; Cronin et al., 2020). Tree height did not differ by oak species. Therefore, the portion of the null of Hypothesis 3 relating to mean tree height was rejected.

While mean tree height was the only predictor to show a direct relationship with total gall abundance, time since fire had a clear, but indirect, influence on the number of galls per site. Mean tree height was significantly correlated with time since fire (Fig. 3.6), with tree height increasing as time since fire increased. This relationship shows the logical progression of tree regrowth after burning, providing new plant tissue for cynipid gallers to parasitize. The strength of this relationship was such that in Figure 7.1 (right), where the main environmental variables for this study were plotted in relation to how often they occurred together, mean tree height and time since fire fell directly on top of one another. Time since fire is therefore an important factor in predicting total gall abundance per site, and the portion of the null of Hypothesis 3 relating to time since fire was rejected.

A final note on why there is not a direct correlation between gall abundance and time since fire is the possible role of different life strategies across cynipid species. Some species surveyed in this study induce large numbers of small, simple galls (*Neuroterus* spp.), while others induce smaller numbers of larger and more complex galls (*Andricus*, *Disholcaspis* spp.). While statistical analyses to test this relationship were not included in this study and therefore cannot yet be considered reliable, it was anecdotally observed that sites with less time since fire were more likely to host the cynipid species which produce larger numbers of small galls. Sites with longer times since fire more often hosted the species that produced smaller numbers of larger, more complex galls. If this trend could be proven true, it would show a progression of resource competition as cynipids with different life history strategies recolonize an area; the first colonizers' populations are able to boom in the absence of competition and then wane as more species arrive. This is a fascinating concept that regrettably could not be added to this study, as it deserves much more attention and detailed sampling. Further investigation is greatly encouraged.

Interestingly, trunk circumference did not show the same relationship as tree height, and did not differ by, or correlate with, any other variables in this study. The cause for this disparity is not known, but may be connected with how fire affects the growth of these tree species. The oak species included in this study are generally small and shrubby, and therefore the majority of their aboveground biomass is vulnerable to burning during fires. Less intense fires will burn higher, more delicate branches, while doing less damage to thicker, sturdier trunks. In this way, trunk circumference could continue growing even when the height of the tree has been reduced, and therefore not show the same linear relationships as tree height.

Summary of Hypotheses

The aim of this study was to identify and describe the most influential environmental variables for oak-galling cynipid populations. Three hypotheses relating to cynipid Shannon-Weiner (H') species diversity, species richness, and gall abundance were tested, with habitat size, latitude, time since fire, tree size, and oak species richness all assumed to have positive relationships with the three response variables. Time since fire proved to be the most influential predictor throughout the study, significantly correlating with cynipid species diversity and richness directly, and total gall abundance indirectly, via mean tree height. Mean tree height was the only variable to directly influence gall abundance, and was considered influential enough to cynipid diversity to be retained in the final multiple linear regression model from the stepwise procedure. Latitude was also included in that final model, showing a positive correlation with cynipid diversity, but was above the significance level ($p < 0.05$) in an individual regression model. Oak species richness was not included in the stepwise procedures because it was a categorical variable, but it did prove to be an important predictor for cynipid species richness via Kruskal-Wallis analysis of variance, with more oak species equating to more cynipid species. Individual oak species also showed differences in cynipid richness and gall abundances, although the reasons for those differences were not immediately clear.

Clearly, there are many factors that influence the size and diversity of oak-galling cynipid populations. While this study and others have begun identifying and describing the most important variables, there are still unanswered questions and unexplained trends in the data. Cynipid gallers will hopefully continue to gain attention as fascinating parts of their ecosystems and yield new insights into their population dynamics and life history strategies.

Additional Factors Influencing Cynipid Populations

One important feature of cynipid wasp communities that was not included in this survey was predation pressure. While relatively large organisms, like mammals and birds, have been known to crack into galls and eat the protein-rich larvae, the most dangerous predators for a gall wasp are similarly tiny and inconspicuous. Hymenopteran parasitoids, typically from the superfamily Chalcidoidea, are able to oviposit their own eggs inside cynipid galls, usually directly onto the host larvae themselves. Once there, the eggs hatch and the host larvae are consumed by the parasitoid larvae. Some strategies employed by these parasitoids are incredibly complex, such as that employed by *Euderus set*, which allows the infected host to develop enough to cut out an emergence hole in the gall wall, only to be eaten before the parasitoid escapes through its hollowed-out head (Egan et al., 2017). Other parasites, particularly inquilines from the tribe Synergini in the Cynipidae family, infiltrate cynipid galls without killing the host, feeding on the gall tissue instead. Less common are Lepidopteran inquilines, which also feed on gall tissue but are also known to consume the host larvae (Eliason & Potter, 2000b).

Multiple species of inquiline and chalcid parasitoids have been observed attacking the same oak-galling cynipid species, and can often compete for hosts (Washburn & Cornell, 1981). These parasitoids are usually not as picky as their hosts, and can switch between cynipid species depending on availability. The extent of the predation pressure applied by chalcid parasitoids to oak-galling cynipid communities is not yet fully known, but their significant effects on individual populations have been observed (Washburn & Cornell, 1979; Bird et al., 2013). Chalcid parasitoids have even been used as biological control agents for invasive cynipid gallers (Aebi et al., 2006).

The last major source of mortality for cynipid gallers are endophytic fungi, which can cause near total mortality in infected galls (Wilson & Carroll, 1997). As discussed earlier in this manuscript, cynipid galls typically produce high concentrations of tannins and phenolics to prevent fungal infections (Taper & Case, 1987), as well as possibly preferring “low-endophyte space” on their host plants (Wilson & Carroll, 1997). However, endophytic fungi are still significant sources of pressure on cynipid populations.

While this survey did not measure the effects of predation pressure on the observed cynipid populations, samples were taken of each gall type found on each tree counted in the survey. These samples were stored in stable temperature and humidity conditions inside plastic bags, with small holes to allow for ventilation. After several months—and sometimes longer—over half of these samples yielded adult cynipids, inquilines, parasitoids, or combinations of the three. Further study of these gall samples can lend insight into parasitism rates across sample sites and oak-galling cynipid species.

It should also be noted that during the course of this survey, several types of organisms were found to be using the cynipid galls, both while active and expired. Several species of ants, most notably the Florida carpenter ant *Camponotus floridanus*, were observed feeding on the sugary excretions produced by the galls of *Disholcaspis quercusvirens*. This mutualistic interaction provides food for the ants, which in turn protects the galls from potential predators (Bird et al., 2013). Another, unidentified species of ant was found to have based a small colony out of a large, hollowed-out *Callirhytis quercusbatatoides* stem gall. Small spiders were occasionally found within the rosettes of *Andricus quercusfoliatus* galls, and unidentified silk webbing was often found hidden underneath, around, or within several other types of gall. Clearly, cynipid galls provide microhabitats for an assortment of other insects, and their importance as habitat engineers should be investigated further.

Implications for Land Management and Conservation

Fire is an important natural disturbance in the vegetative communities included in this survey (Carr et al., 2010; Menges & Kohfeldt, 1995; Myers, 1985). Natural fire frequencies vary across the four community types, but all sites sampled were subject to controlled burn schedules by their respective management agencies. Generally, natural burn frequencies for sandhills is considered somewhere between 1 and 5 years, with shorter frequencies in Florida’s more northern sandhills (Abrahamson, 1984a). The sandhills included in this survey would be considered closer to the northern sandhills, though the group extends much farther to the north. Second in line, in terms of fire frequency, are scrubby flatwoods, which are thought to burn every 2-3 years. Scrub has more variable fire frequency: 10-100 years, though generally shorter (5-20 years) in some oak-dominated scrub types (Menges, 1999). Xeric hammock is generally considered a late successional stage of scrub in which the resident oaks have either not been subjected to, or have survived fires, long enough to grow relatively tall (>3-4 m) (Menges et al., 1993). Average times since fire for each community type in this survey are significantly different (Fig. 3.2) and generally follow the suspected natural regimes discussed above. However, not included in most of the fire histories for each site were details on fire intensity, which can change the outcomes of post-fire recovery (Myers, 1985; Menges & Hawkes, 1998). Details concerning fire intensity are rarely recorded during prescribed burns, and therefore could not be included in this survey. Cronin et al. (2020) were able to incorporate burn intensity data due to the exceptional record-keeping of Archbold Biological Station in Venus, FL, where they sampled.

Because galls typically perish in fires, local cynipid populations are assumed to effectively reset to zero after any burn of adequate intensity to catch the surrounding woody undergrowth. Data from this study and Cronin et al. (2020) now prove that as the area is recolonized from neighboring populations, the longer the growth period allowed before the next burn translates to more species accumulating in the area. However, the prescribed fire frequency for a particular site should not be elongated solely for the benefit of cynipid populations, as near countless other species in these communities rely upon somewhat frequent fires (Abrahamson, 1984; Carr et al., 2010; Menges & Kohfeldt, 1995; Myers, 1985).

As fire has become more widespread as a management tool, especially in the southeast, the interactions between cynipid gallers and fire has become of greater interest. However, altering an area's burn plan to encourage cynipid population growth is not conducive to effective and comprehensive conservation. Instead, describing cynipid species' dispersal capabilities will be crucial for understanding how likely they are to repopulate an area after a burn, and subsequently altering burn plans to reserve areas that could serve as source populations for burned areas nearby. But dispersal studies have only focused on a few invasive cynipid species that likely do not represent the survival strategies of most of Cynipidae (Gil-Tapetado et al., 2018; Hailes & Crawley, 1991; Walker et al., 2002). Further study of cynipid dispersal is therefore highly encouraged in order to effectively implement fire frequency-based conservation initiatives for cynipid oak-gallers.

Until then, land managers should work to ensure that some portions of quality habitat are left unburned in order to ensure that local cynipid populations are not extirpated due to extensive or frequent prescribed fires. Ideally, these refugia would be directly adjacent to the burned habitat, minimizing any barriers of dispersal for the next generation of cynipids or other arthropods. Indeed, this kind of consideration for maintaining refugia offers many organisms with fragile life cycles means to maintain source populations to recolonize surrounding areas after disturbance. Many land managers in charge of actively burned conservation areas already acknowledge the importance of refugia, but challenges hinder their implementation. If resources for conducting burns are too sparse, or the areas to be burned are small in size, it is more efficient to burn large portions, or all, of the target areas. The idea of maintaining source populations via disturbance refugia is therefore not novel or surprising, but does require collaboration between researchers, land managers, and stakeholders to develop more intricate and thoughtful fire regimes.

Conclusion

In conclusion, several key environmental variables for healthy oak-galling cynipid populations were identified in this study. Time since last fire was the most important variable tested in this survey, which points to its importance as a management tool for cynipid populations. If protecting cynipid populations is a management goal, then allowing for reasonable time between fires and reserving portions of habitat from prescribed burns to act as refugia for source populations should be considered. These reserved areas should have relatively large, mature oaks with high oak species richness, in order to provide oviposition sites for the greatest number of cynipid species.

Oak-galling cynipids have rarely been a priority for wildlife conservation, and that is not expected to change in the near future. Arthropods, in general, are routinely ignored during conservation initiatives, even more so for unpopular groups like wasps and arachnids. However, if the goal is to protect ecosystems as a whole, excluding protections for large, but unpopular, portions of those systems must be avoided. Oak-galling cynipid wasps are a small part of the diverse insect communities in Florida, but they represent the countless, highly specialized species that depend on effective and purposeful land management for survival. It would be impossible to consider the needs of every species present when designing a management plan for a particular area, but indicator species could be used to fill the gaps. Because cynipid gallers have highly-specialized natural histories, and could potentially be important microhabitat engineers, a strong argument could be made that they deserve to be considered as a group of indicator species. Continued research is required to fully elucidate the roles these wasps play in their ecosystems, but this study serves to provide important insight into how best to protect and provide for robust oak-galling cynipid communities and the species they support.

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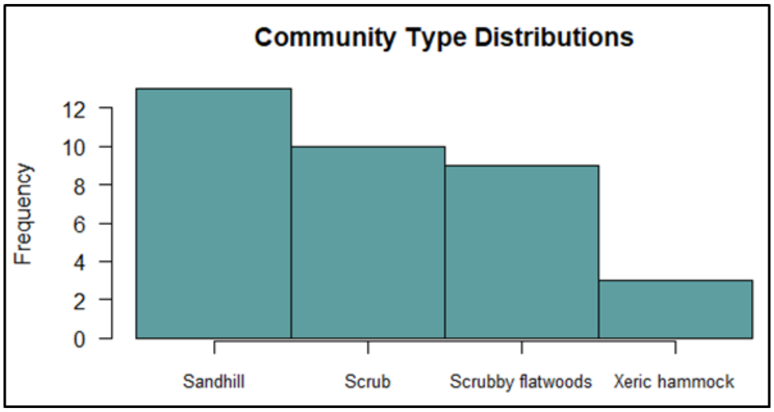
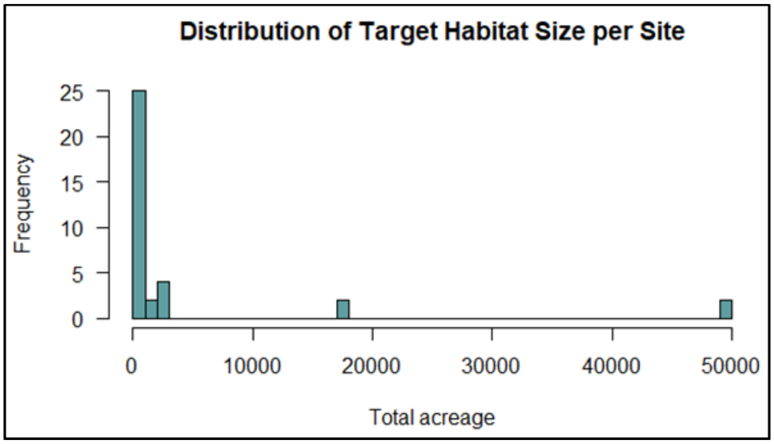
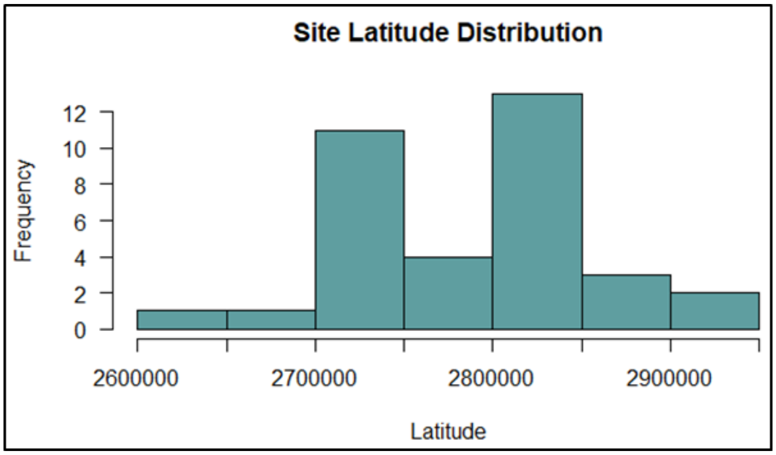
Appendices

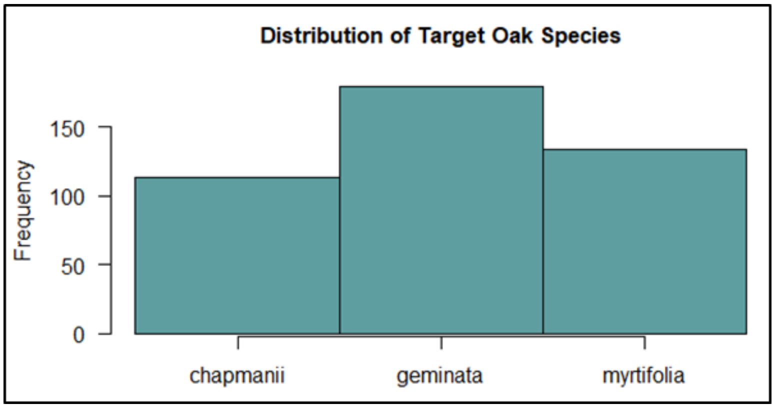
Appendix A: Distribution and Normality Figures

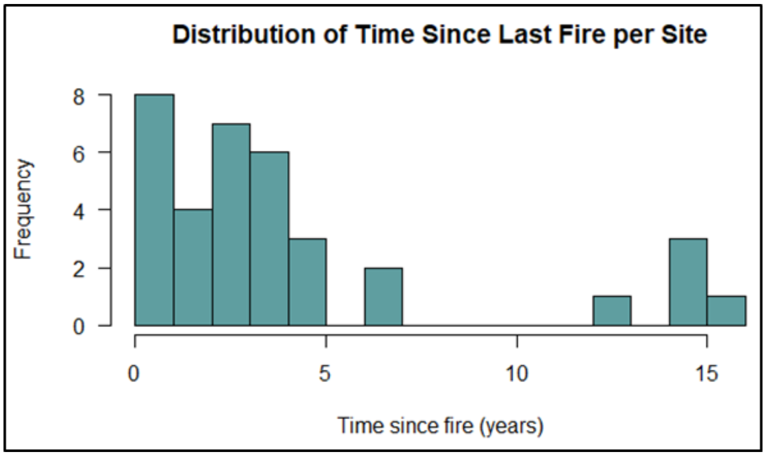
Predictor histograms.

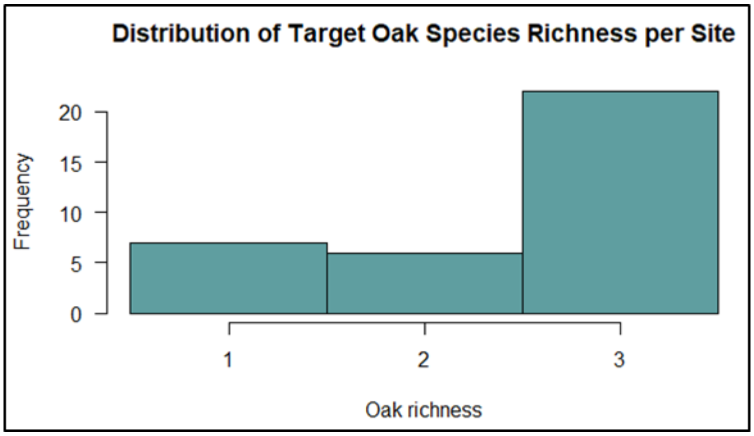


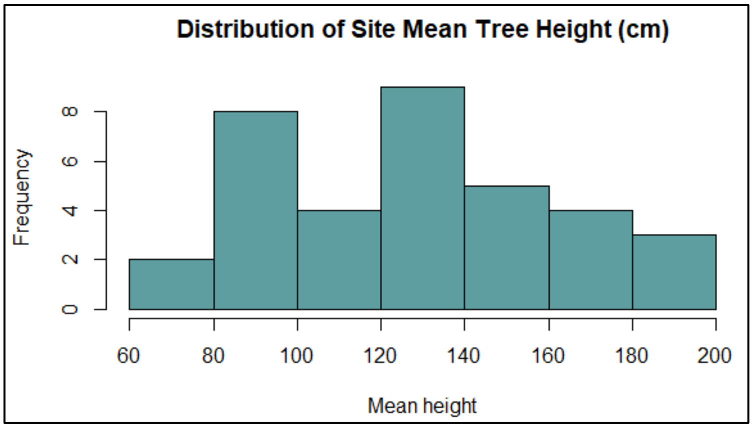


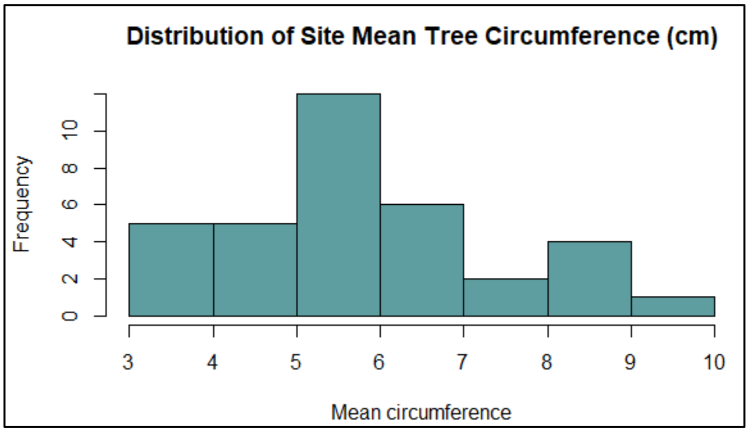



Distribution of Target Oak Species
Frequency
0
50
100
150
chapmanii
geminata
myrtifolia

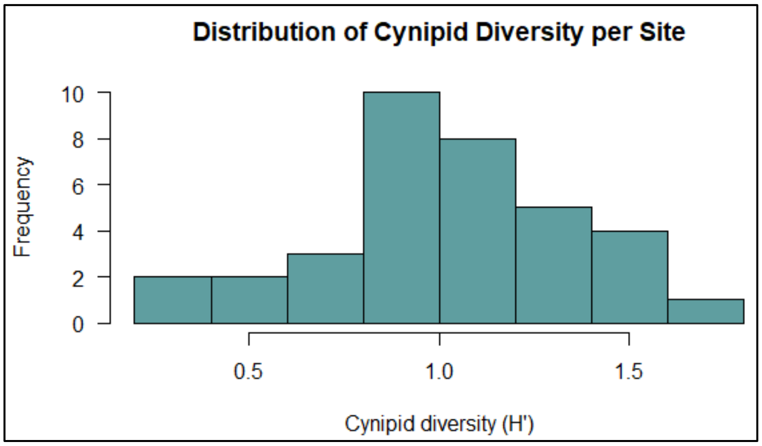

Distribution of Time Since Last Fire per Site
Frequency
0
2
4
6
8
0
5
10
15
Time since fire (years)

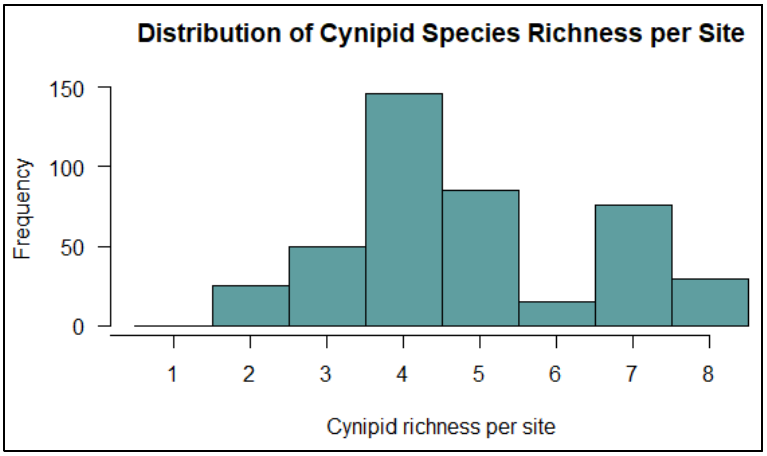

Distribution of Target Oak Species Richness per Site
Frequency
0
5
10
15
20
1
2
3
Oak richness

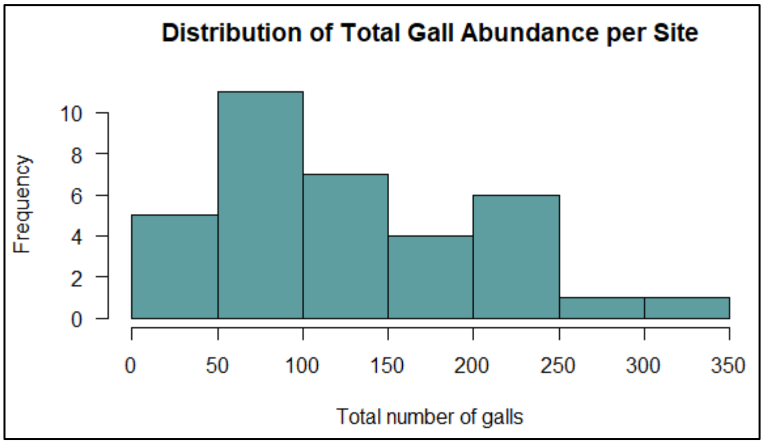

Distribution of Site Mean Tree Height (cm)
Frequency
0
2
4
6
8
60
80
100
120
140
160
180
200
Mean height

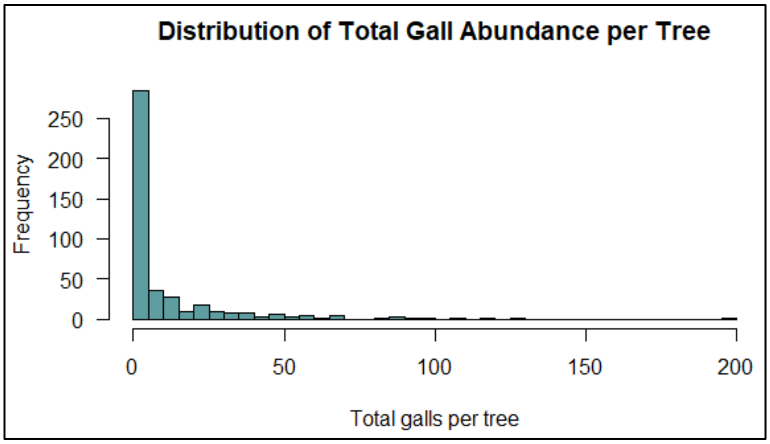

Distribution of Site Mean Tree Circumference (cm)
Frequency
0
2
4
6
8
10
3
4
5
6
7
8
9
10
Mean circumference

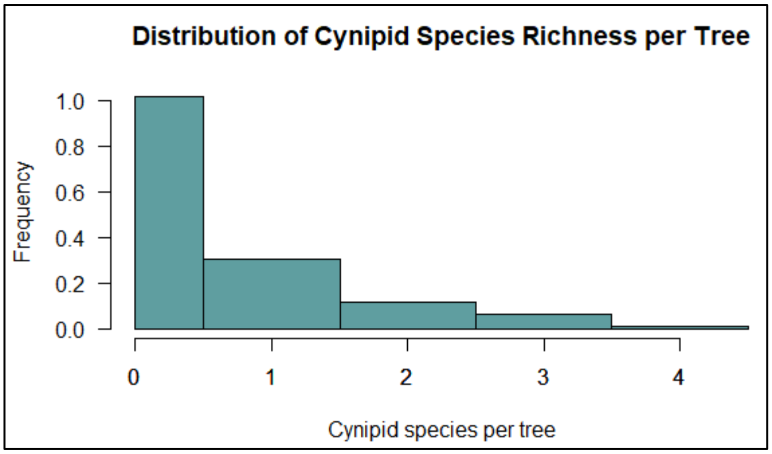
Response histograms.



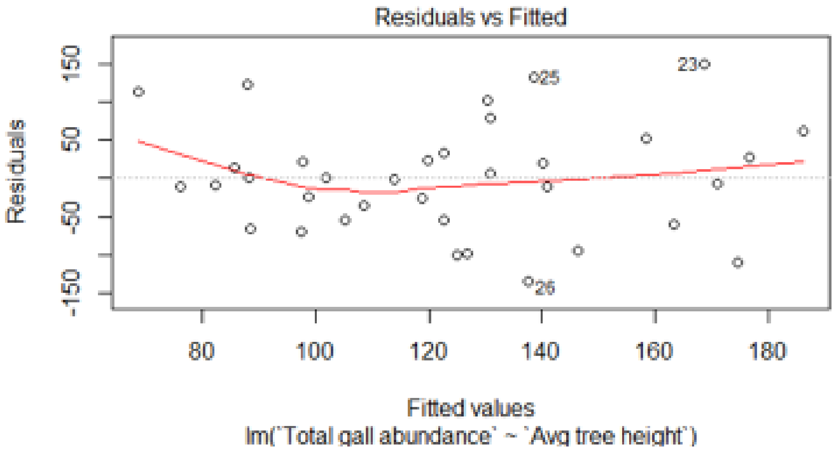


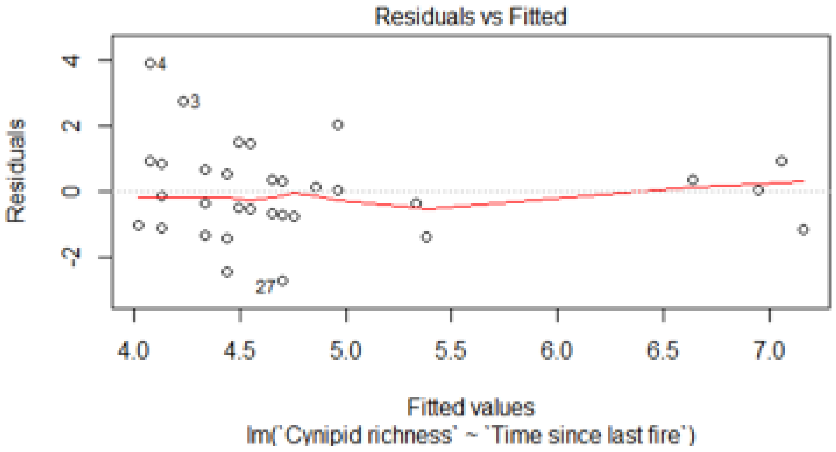


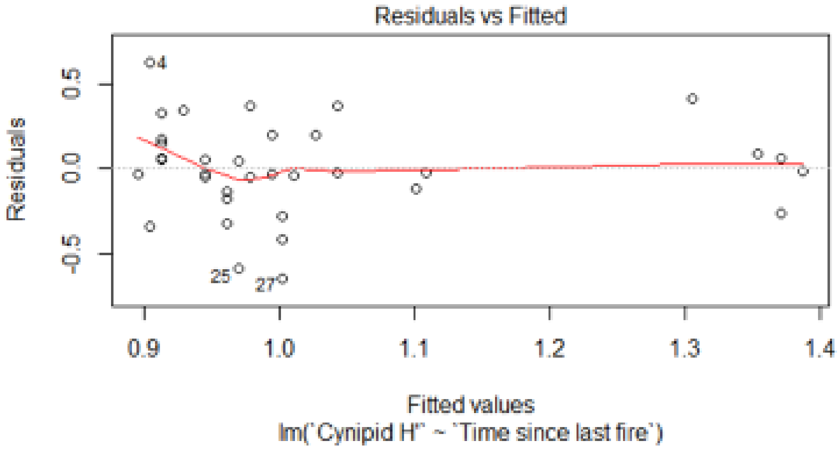

Distribution of Total Gall Abundance per Tree
Frequency
250
200
150
100
50
0
0
50
100
150
200
Total galls per tree

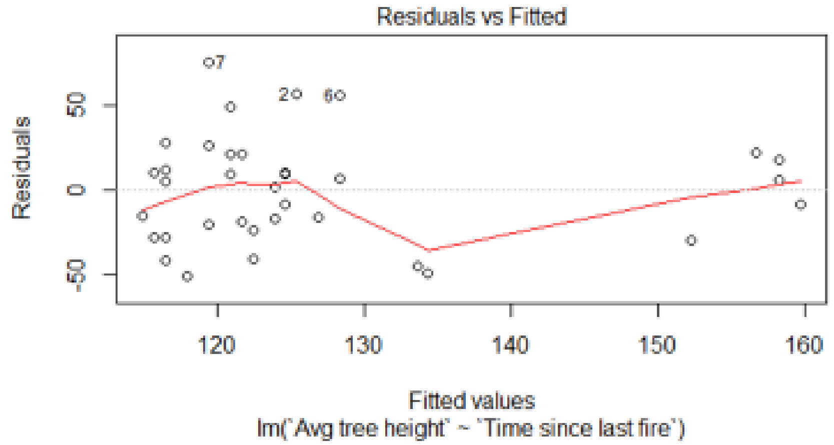

Distribution of Cynipid Species Richness per Tree
Frequency
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
Cynipid species per tree

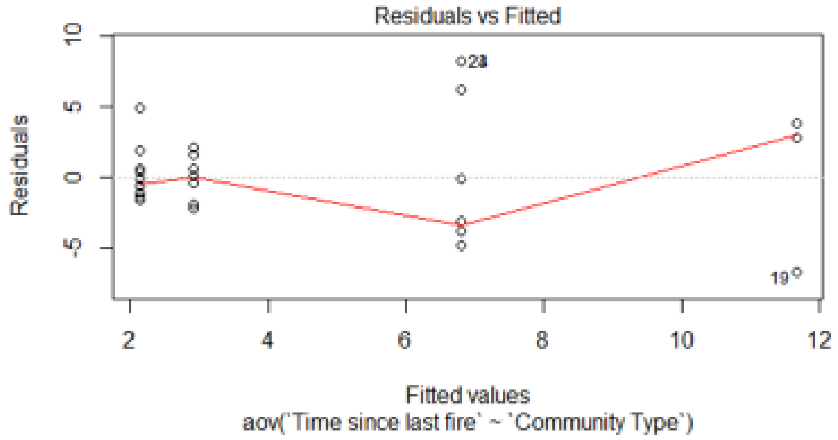
Residuals vs. fitted values plots.

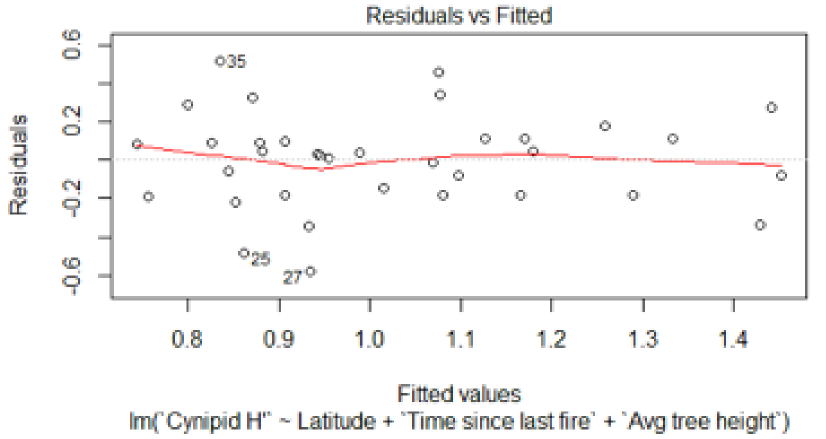




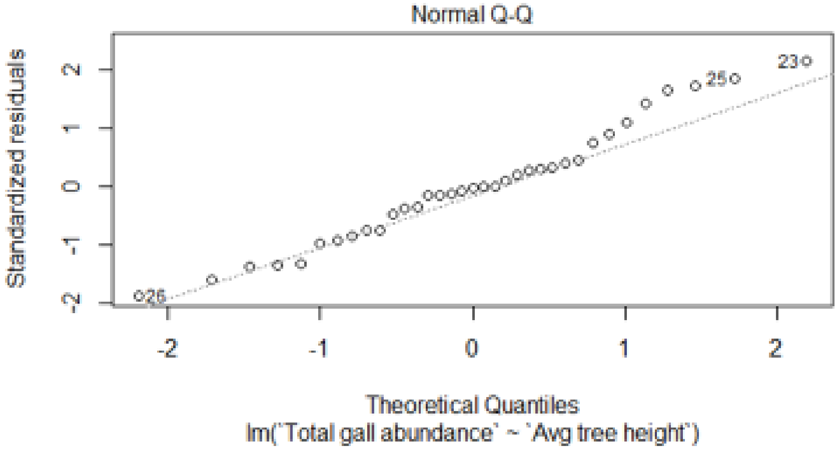


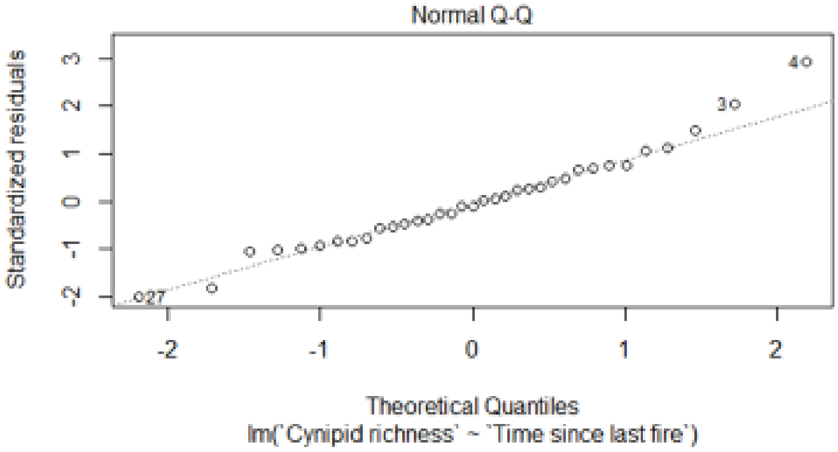

Residuals vs Fitted
Residuals
50
0
-50
7
2
6
120
130
140
150
160
Fitted values
lm(`Avg tree height` ~ `Time since last fire`)

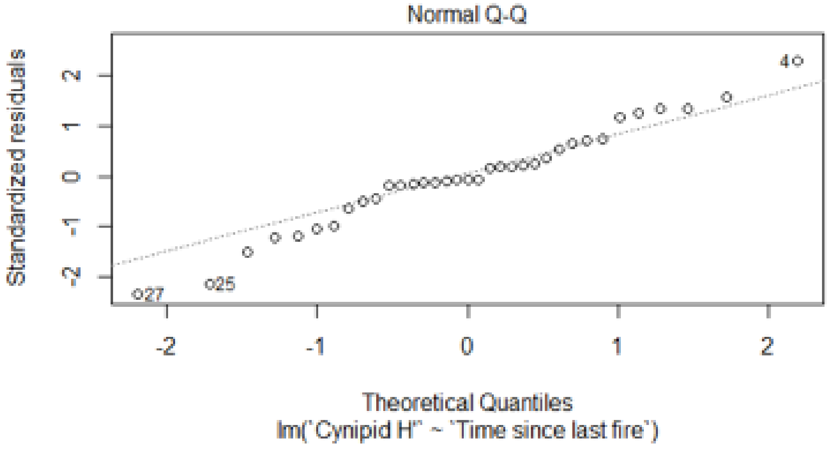

Residuals vs Fitted
Residuals
10
5
0
-5
23
19
2
4
6
8
10
12
Fitted values
aov(`Time since last fire` ~ `Community Type`)

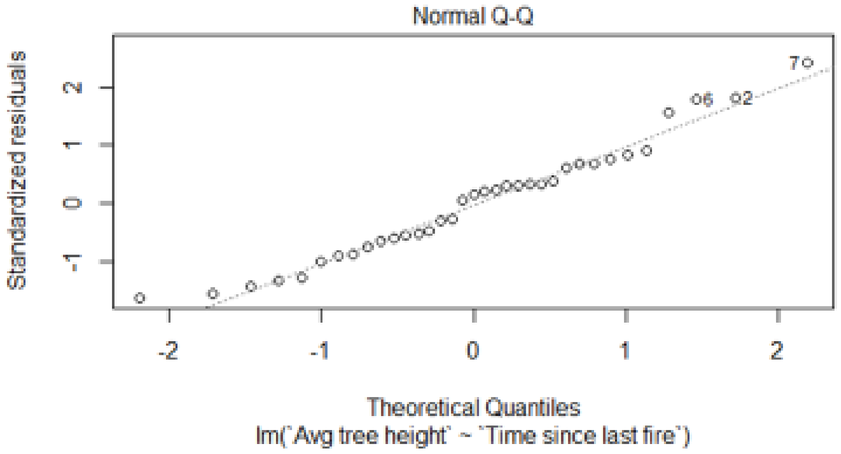

Residuals vs Fitted
Residuals
0.6
0.2
-0.2
-0.6
35
25
27
0.8
0.9
1.0
1.1
1.2
1.3
1.4
Fitted values
lm(`Cynipid H'` ~ Latitude + `Time since last fire` + `Avg tree height`)

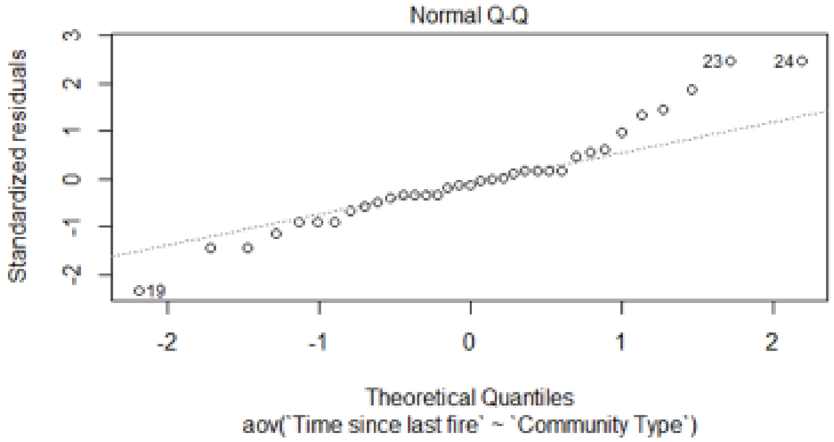
Normal Q-Q probability plots.

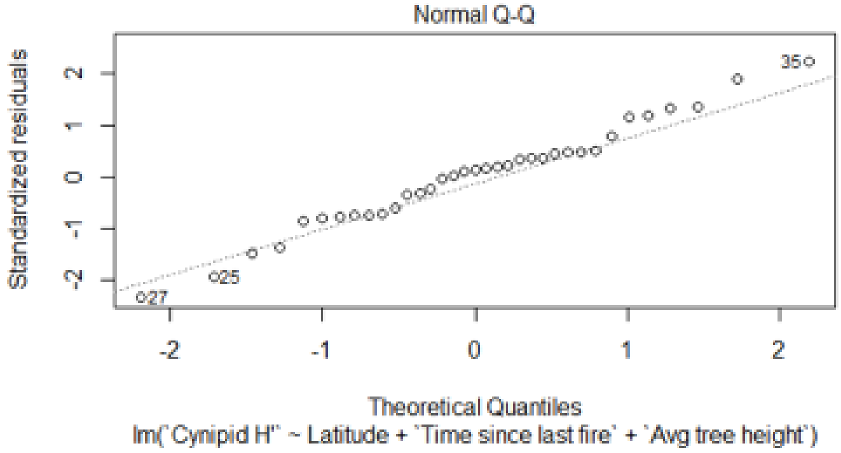




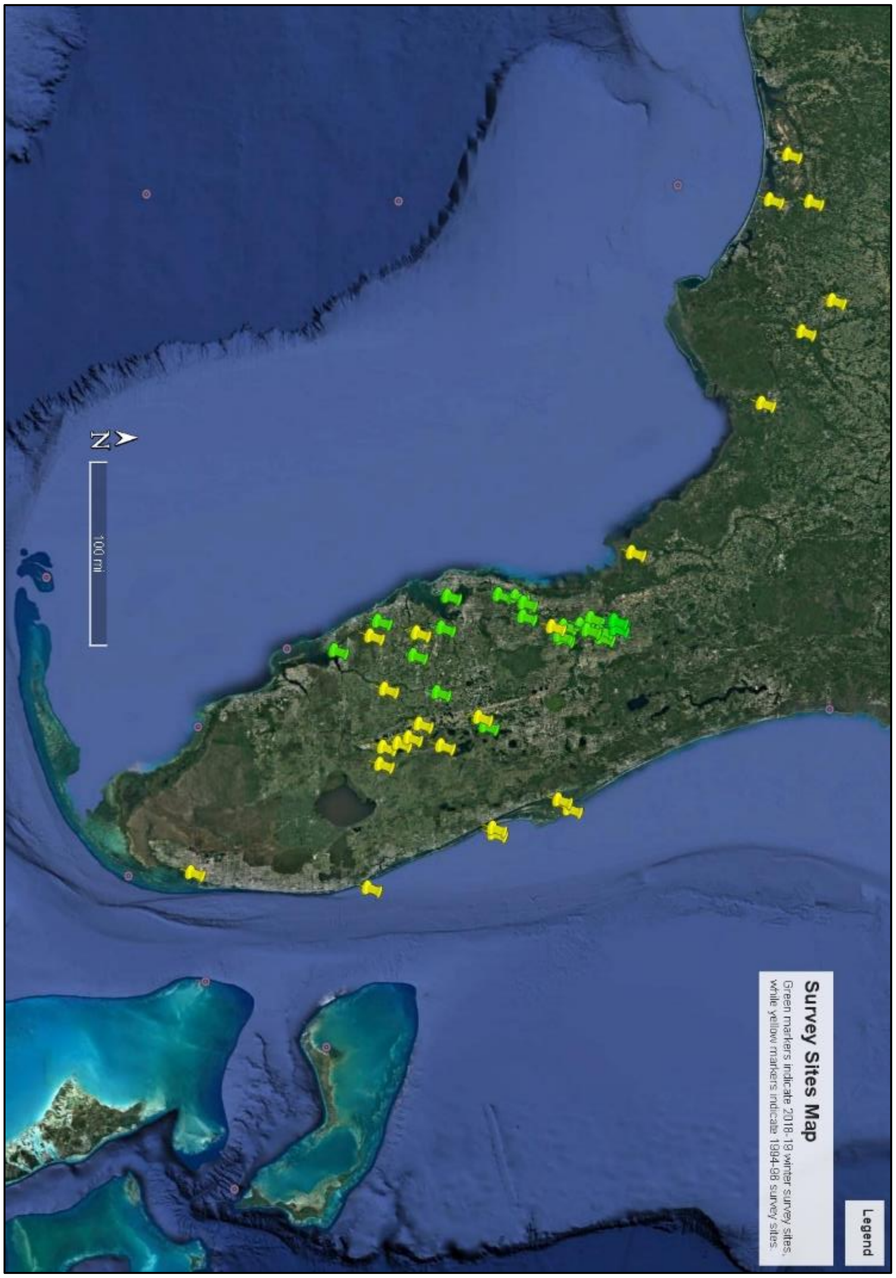



Normal Q-Q
Standardized residuals
Theoretical Quantiles
lm(`Avg tree height` ~ `Time since last fire`)
-1
0
1
2
-2
-1
0
1
2
7
6
2


Normal Q-Q
Standardized residuals
Theoretical Quantiles
aov(`Time since last fire` ~ `Community Type`)
-2
-1
0
1
2
3
-2
-1
0
1
2
23
24
19


Normal Q-Q
Standardized residuals
Theoretical Quantiles
lm(`Cynipid H'` ~ Latitude + `Time since last fire` + `Avg tree height`)
-2
-1
0
1
2
-2
-1
0
1
2
35
25
27

Appendix B: Reference Map with Sample Sites from Price et al (2004)



Sample sites from the 1994-1995 survey conducted by Price et al (2004) are shown in yellow. Sample sites from this survey during the 2018-2019 winter season are shown in green. The only shared site was Bok Tower Gardens in Polk County.