# HOST PLANT AND SPATIAL INFLUENCES ON THE NATURAL ENEMY COMMUNITY STRUCTURE OF A HOST SPECIFIC INSECT HERBIVORE

by

Robert Waid Busbee, B.S.

A thesis submitted to the Graduate Council of
Texas State University in partial fulfillment
of the requirements for the degree of
Master of Science
with a Major in Population and Conservation Biology
May 2018

Committee Members:

James Ott, Chair

Chris Nice

Noland Martin

**FAIR USE AND AUTHOR'S PERMISSION STATEMENT**

## Fair Use



### Duplication Permission

## ACKNOWLEDGEMENTS

This research project was enriched by the associates of the Population and Conservation Biology Program as well as the Ecology, Evolution, and Behavior Group at Texas State University. This research was funded by awards to Robert W. Busbee from the Howard McCarley Student Research Award from the Southwestern Association of Naturalists, Freeman Center Fellows Award, Thesis Research Fellowship from Texas State University, and a Theodore Roosevelt Memorial Grant from the American Museum of Natural History. I thank the following for help in collections, Dr. Gavin Naylor, Dr. Carmen Hall, Dr. Evan Brasswell, Linyi Zhang, and Dr. Glen Hood. I want to thank Jim Ott for guiding me in my academic pursuits and allowing me to participate and learn in his lab. I appreciate the help and support from fellow colleagues that assisted me and the Ott lab with this project for which it would not be possible without them. I especially want to thank my loving family and caring friends who helped me through my journey for which I am eternally grateful.

## TABLE OF CONTENTS

**Page**

## LIST OF TABLES

**Table** **Page**

## LIST OF FIGURES

**Figure** **Page**

## LIST OF ABBREVIATIONS

| **Abbreviation** | **Description** |
|---|---|

NE- Natural Enemies

RDA-Redundancy Analysis

PCNM- Principal Coordinates of Neighbor Matrices

*Qf - Quercus fusiformis*

*Qv - Quercus virginiana*

*Qg - Quercus geminata*

## ABSTRACT

Both environmental variation and spatial autocorrelation play roles in structuring communities at all spatial scales. However, untangling the respective contributions of these sources of variation represents a long-standing, complex, and methodologically ever-evolving question for community ecology. Here I investigate the structure of the insect natural enemy community centered on galls produced by *Belonocnema treatae* (Hymenoptera: Cynipidae) on the leaves of its host plants across the gall former's geographic range while controlling for spatial autocorrelation among sample sites. *Belonocnema treatae* exhibits regional host plant specialization across the southern US on three live oak species, *Quercus fusiformis (Qf), Quercus virginiana (Qv), and Quercus geminata (Qg)*. I sampled the natural enemy community at 94 sites by rearing natural enemies that emerged from galls collected at each site. I identified 32,722 natural enemies representing ≥30 taxa from 126,812 galls. I hypothesized that richness and diversity on *Qv* would exceed that on *Qf* and *Qg* since the geographic range of *Qv* bridges that of *Qf* to the west and *Qg* to the east. Contrary to my hypothesis one-way ANOVA followed by a Tukey's HSD showed that both richness and Shannon-Wiener diversity was greatest on *Qf*. To disentangle the role of host plant affiliation from spatial autocorrelation among sample sites I conducted a Redundancy Analysis (RDA). I first used Principal Coordinates of Neighbor Matrices (PCNM) to generate explanatory variables representing orthogonal aspects of spatial structure within the sampling frame. The set of PCNM vectors that were significantly correlated with community structure

were then included in a RDA along with the host plant species from which each natural enemy was reared to examine the respective roles of host plant association and spatial structure in determining abundance and species composition of the natural enemy community. This study establishes a significant role for both alternative host plants and geography in structuring the diversity of the natural enemy community of *B. treatae* and illustrates the advantages of the PCNM & RDA approach.

# I. INTRODUCTION

A central goal of ecology is to understand the relationship between the environment and the structure of communities (Boyce and McDonald, 1999) at all spatial scales (Legendre and Fortin, 1989; Legendre, 1993). A major issue in ecology, thus has been to understand the determinants of variation in community structure by appropriately partitioning environmental and spatial components of variation in community structure. Studies that aim to understand the relative importance of spatial and environmental variables as contributors to community structure can improve understanding of both drivers of and patterns of biodiversity (Legendre and Fortin, 1989; Peres-Neto et al., 2006), and enhance prediction (Peterson and Parker, 1998). Communities of organisms are structured by the species that are present along with the abundance of individuals for each species which can vary among different communities. Variation in communities can be attributed to abiotic factors (average temperature, precipitation gradients, and soil types), biotic factors (competition among organisms, parasitism, and host associations) and genetic diversity (host plant genotype) (Willis, 1922; MacArthur, 1972; Stireman III et al., 2005; Janz et al., 2006). The influence of abiotic and biotic factors on community compositions varies depending on regions and trophic levels (Rahbek, 2005; Tuomisto, 2010). For communities that span large geographic areas, determining the relative influence of environmental and spatial variables remains a central issue.

The degree to which spatial structure (autocorrelation) influences community structure across a sampling design makes it difficult to isolate the contribution of environmental variables in understanding patterns in ecological data (Legendre and Fortin, 1989). Thus it is important to employ appropriate statistical testing that includes

spatial components (Legendre and Fortin, 1989; Borcard and Legendre 2002; Borcard et al., 2004; Blanchet et al., 2008; Legendre et al., 2015). In the past, techniques such as the Mantel test (Mantel, 1967) have been used to integrate the spatial component to test significant relationships between space and community structure (Sokal, 1979). The repeated use of this test by ecologists when combining spatial data with ecological data to understand spatial processes has been found to be inappropriate for many ecological studies (Legendre et al., 2015). The Mantel test has been shown through simulation results that using this test does not have enough power to detect spatial autocorrelation (Legendre et al., 2015). Detection of the spatial autocorrelation in community data is essential to access the influence of candidate environmental components on community structure. .

To quantify spatial autocorrelation among samples in an ecological study distributed across space, techniques such as a Principal Coordinates of Neighbor Matrices (PCNM) can be used (Legendre and Borcard, 2002; Borcard et al., 2004; Dray et al., 2006). This technique generates spatial explanatory variables that have structure at all the scales encompassed by the data matrix (spatial component), and calculates to which of these variables the response variables(s) (environmental component) are statistically responding (Legendre and Borcard, 2002; Borcard et al., 2004). Interpretation of the PCNM analysis can then provide insight into course and fine scale spatial autocorrelation among sites following canonical analysis that include the environmental variables of interest (Borcard et al., 2004). Assessing the joint contribution of spatial and environmental components in explaining observed variation in community data can be achieved by conducting a Redundancy Analysis (RDA). By combining PCNM with RDA

one can disentangle the effects of environmental and spatial variables on variation in community structure.

Host specific gall inducing insects have associated with them a diverse natural enemy (NE) community (Askew, 1961; Askew, 1980; Askew, 1984; Stone et al., 2002). This system composed of the host plant, the obligate herbivorous insect, and the natural enemies of the herbivore constitutes a rich tri-trophic system.

Increased geographic ranges of groups of plants have been shown to have a positive influence on the number of herbivorous insect species present in the community (Cornell, 1985). The geographic range of the host plants used by particular herbivorous insects can influence the species richness and diversity of the natural enemies associated with the herbivore (Cornell and Washburn, 1979). Thus both the host plant of host specific gall inducing insects and the geographic range of the plant used by the herbivore can influence the structure of natural enemy communities. This tri-trophic host specific herbivorous insect system provides an opportunity to investigate the influence of spatial structure (geography) and an environmental variable (host plant) that contributes to variation in natural enemy community structure.

Herein, I investigated the relative contribution of regional specialization on three species of alternative host plants by a host specific gall wasp and spatial autocorrelation to variation in community structure of the natural enemies of the gall wasp. This study provides an example of applying recently developed techniques to determine the influence of spatial and environmental components on community structure. For highly specialized host specific insects, the environment (host) could be a key driver in explaining variation in the natural enemy community regardless of the spatial distribution

(Egan et al., 2008). *A priori* knowledge of reproductive isolation and genetic differences within a herbivorous insect species would suggest that the host plant is playing a role in driving the differences in the herbivorous insect populations (Funk 1998; Egan et al., 2008; Nosil et al., 2008). One can thus investigate the next trophic level to see if this relationship can drive community structure differences in their natural enemy community. I hypothesized that host plant contributes significantly to the proportion of explained variation in natural enemy community structure in a host specific insect across its geographic distribution. If host plant explains most of the community structure I expect to see evidence that the spatial components explain significantly less of the variation in the dataset at either a course or fine scale compared to the influence of host plant. I also hypothesized that the diversity of natural enemies is different based on host plant use, thus providing a prediction for host plant use as a key driver in community structure and diversity for a natural enemy community.

## II. MATERIALS AND METHODS

### Biology of the Study System

Cynipid wasps are a diverse group of secondarily phytophagous Hymenoptera (Malyshev, 1968; Quicke, 1997) that are specialized to induce and develop within plant galls (Akew, 1984). Galls are 3-dimensional structures composed of plant tissue whose growth and development is under genetic control of the insect (Malyshev, 1968; Askew, 1984; Tooker and De Moraes, 2008). Cynipids are typically host plant specific, inducing galls on a single, or series of closely related, plant species (Askew, 1984; Stone et al., 2002). The group of plants with the highest diversity of Cynipids are the Oaks, genus *Quercus* (Askew, 1984; Stone et al., 2002) which are broadly distributed throughout the northern hemisphere (Nixon, 2006). The appearance of galls can vary greatly within Cynipids for which the adaptive significance is not fully known but may be advantageous for the reduction in mortality of the gall former (Miller et al., 2009; Stone and Cook, 1998). Galls attract a diverse group of NE which can inflict high mortality among the gall formers (Hayward and Stone, 2005; Hood and Ott, 2010). Cynipids express heterogony in which asexual and sexual generations alternate to complete the life cycle (Crozier 1975; Askew, 1984; Pujade-villar et al., 1999). Because the alternating sexual and asexual generations induce galls on different plant tissues at different times both the diversity of the natural enemy community centered on galls induced by each generation and the magnitude of mortality inflicted by natural enemies can differ between generations (Askew, 1984; Stone et al., 2002; Hood and Ott, 2010; Forbes et al., 2015).

The Cynipid, *Belonocnema treatae* (Mayr, 1881) is restricted to inducing galls on species of live oaks in the series *Virentes* (Lund et al., 1998; Melika and Abrahamson,

2002; Egan et al., 2013). This series includes seven closely related species (*Quercus fusiformis, Q. virginiana, Q. geminata, Q. minima, Q. oleoides, Q. brandegeei, and Q. sagraena*) (Muller 1961; Cavender-Bares et al., 2015). In the southern United States, *B. treatae* is widely distributed across three host plant species: *Q. fusiformis (Qf), Q. virginiana (Qv) and Q. geminata* (*Qg*) (Lund et al., 1998; Egan et al., 2012; Egan et al., 2013; Schuler et al., 2018; Figure S1). Three other oak species in the series, *Q. oleoides* (Mexico and Central America), *Q. brandegeei (*Baja California) and *Q. sagraena* (Cuba) have not been confirmed as host plants of *B. treatae* and *Q. minima* appears to not be differentiated from *Qv* (Cavender-Bares et al., 2015). This study focuses on the diverse insect natural enemy community that attacks *B. treatae* developing within leaf galls on *Qf*, *Qv*, and *Qg* across the geographic range of these host plant species in the southern and southeastern US.

Leaf galls develop on the leaves of live oak following oviposition by sexual generation *B. treatae* which coincides with spring leaf flush (Lund et al., 1998). Upon emergence, sexual females immediately mate and oviposit into lateral veins on the underside of newly flushing immature leaves. Leaf galls become visible in early to mid-May, growing into spheres 0.5 – 9.0 mm in diameter which lignify from late-summer through early fall (Lund et al., 1998). Each leaf gall houses a single asexual female which emerges during the fall and early winter (Lund et al., 1998). Asexuals then oviposit into live oak root tissue and induce the formation of multi-locular root galls housing the sexual generation to complete the life cycle (Lund et al., 1998). Galls induced by *B. treatae* are attacked during all stages of development (Hall 2001) by a diverse group of insect natural enemies (Forbes et al., 2015) that include both parasitoids and inquilines.

Parasitoids feed and complete development within the gall forming larvae from eggs deposited in or on the larvae thus causing direct mortality of the developing gall former. Inquilines develop from eggs laid in or on the gall, consume gall tissue and complete development within the gall. Inquilines are classified as natural enemies as they may indirectly or directly lead to the death of the gall former (Askew, 1984).

Community associates of *B. treatae* were reared directly from galls that produced parasitoids of *B. treatae*, hyperparasitoids, associated inquilines and parasitoids that could be associated with the inquilines (Forbes et al., 2015). The inclusive community of *B. treatae* NE (*sensu stricto*) I refer to as the entire community of associated NE (*sensu lato*) since the relationship of niches inside the galls are not resolved and when NE emerge *B. treatae* individuals from these galls do not survive (Forbes et al., 2015). The natural enemy community associated with galls induced by *B. treatae* has been described for both asexual and sexual generations developing on *Qf and Qv* for populations in central Texas, USA which constitute only a portion of the geographic range. Forbes et al. (2015) reported 24 species of natural enemies associated with the leaf gall generation and four species associated with the root gall generation.

A closer inspection of 1) the geographic distribution of the three host plants used by *B. treatae* across the southern US, 2) niche differences among the host plant species, and 3) evidence of population genetic structure of *B. treatae* across these three host plants motivates my inspection of the possible roles of host plant affiliation and geography as drivers of variation in natural enemy community diversity in this gall former. As shown in Figure S1 the geographic range of the three host plants varies. *Quercus fusiformis* is restricted to central Texas southward, with relict populations in southwestern Oklahoma

while *Qv* is restricted to the southeastern U.S. In contrast, *Qv* is broadly distributed and spans the U.S. gulf coast eastward to the Atlantic coast. Notably, *Qv* and *Qg*. are widely sympatric throughout parts of their range and can occupy immediately adjacent habitats while the range of *Qv* and *Qf* marginally overlap in the west. Sympatric *Qv* and *Qg* exhibit niche differences with *Qv* occupying richer soils, exhibiting faster growth, higher photosynthetic rates, and lower allocation to underground biomass (Cavender-Bares and Pahlich 2009; Cavender-Bares et al., 2015). These patterns of ecological niche differentiation between host plants in sympatry in combination with clear niche differentiation among the three host plants in parapatry and allopatry (Cavender-Bares and Pahlich 2009) indicates that host plant affiliation may serve as a possible driver in influencing natural enemy community variation.

The biogeographic, phylogenetic and phylogenomic history of the three oak hosts of *B. treatae* are well studied. The crown age of the series *Virentes* is 11 Ma consisting of a western clade of *Qf* along with an eastern clade of *Qv* and *Qg* (Cavender-Bares et al., 2015). *Q. fusiformis* is considered more distantly related to *Qv* and *Qg* which represent sister species (Cavender-Bares and Pahlich 2009; Cavender-Bares et al., 2015). RADseq data has indicated that *Q. fusiformis* diverged roughly 8 Ma due to drying periods and promoting adaptation for tree growth, leaf morphology, flowering time, freeze tolerance fire tolerance, and drought tolerance (Cavender-Bares et al., 2015). Divergence within the eastern clade occurred within 8 Ma due to environmental conditions in Florida changing which provided for new niches thus promoting speciation of *Qv* and *Qg*. Pairwise comparison of genetic diversity among the three host plants show they are genetically distinct with introgression evident between *Qf* and *Qv* in parapatry. Introgression is not

evident in sympatric populations of *Qv* and *Qg* which can be attributed to differential flowering times. Interestingly, chloroplast haplotypes across the *Virentes* show that haplotype richness was highest in *Qf* and *Q*v which can be related to range size (Cavender-Bares et al., 2015).

Importantly, the three oak species differ in freeze, fire, and drought tolerance, and phenology (Cavender-Bares and Pahlich 2009; Cavender-Bares et al., 2011; Cavender-Bares et al., 2015) and in the characteristics of leaf galls that develop on each host (Egan et al., 2012). These niche differences among host plants lead to the prediction that sympatric populations of specialized gall-forming insects that feed on these oak species will show evidence of ongoing genetic differentiation. Indeed *B. treatae* populations associated with these oak species are genetically divergent (Schuler et al., 2018) and populations of *B. treatae* on *Qv* and *Qg* exhibit evidence for partial reproductive isolation (Egan et al., 2011; Egan et al., 2012; Egan et al., Egan et al., 2013). Ongoing genomic studies show genetic differentiation based on host plant affiliation and a west-east divide across the geographic range thus further motivating to the hypothesis of possible host plant influence on community structure of associated natural enemies. In total, the phylogenetic divergence among host plants, niche differentiation among host plants, differences in the range-wide geography of the three host plants in combination with the evidence of genetic substructure in the host specific herbivore related in part to host plant affiliation, together create the template for asking whether the community of natural enemies centered on *B. treatae* also shows signs of differentiation based on host plant and geography. I hypothesized that richness and diversity on *Qv* would exceed that on *Qf* and *Qg* since the geographic range of *Qv* bridges that of *Qf* to the west and *Qg* to the east.

## Sample Design

The sampling design for this study spans the entire known geographic range of *B. treatae* in the southern U.S. across its three host plants (Figure 1). Thus, in the west I sampled both the western and north-western terminus of *Qf's* geographic range along the western edge of the Edwards Plateau in central Texas, and at the disjunct quartz mountains site in Oklahoma and found *B. treatae* in both regions. Along the southern Gulf Coast I sampled the western terminus of both *Qg* and *Qv,* and along the Atlantic coast I sampled the northern range of *Qv* to its terminus in coastal southern Virginia. I note that *B. treatae* was not detected north of the sample site at Beaufort, NC (Figure 1) despite an exhaustive search of *Qv* populations extending hundreds of kilometers northward throughout coastal North Carolina and southern Virginia. Importantly, range-wide sampling justifies the decision to not detrend the data in downstream data analysis.

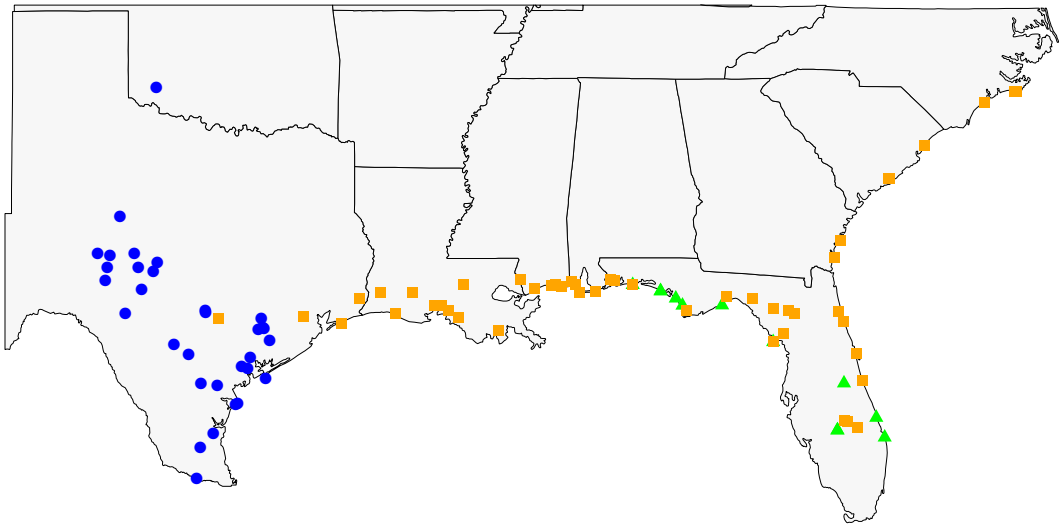


**Figure 1: Sampling of Natural Enemies reared from *B. treatae* leaf galls.** The symbols correspond to study sites (Table S1) distributed across the southern United States from collections made in the Fall of 2015 and 2016. Blue circles indicate *Qf* sites, orange squares indicate *Qv* sites, and green triangles indicate *Qg* sites.

Sample collections

The abundance of *B. treatae* leaf galls varies dramatically among trees within populations of live oaks (Egan and Ott, 2007), and at larger scales occupied sites are patchily distributed. Oak trees populated by moderate to high densities of *B. treatae,* are however readily detected. Thus, to locate sample sites I drove public roadways stopping at intervals to inspect individual, clumps, or scores of live oak trees. From mid-October thru late-November in 2015 and again in 2016 I collected from 50 sites and 68 sites respectively. Some sites were visited in both years to augment samples and for these sites the samples were pooled. Across years a total of 94 independent sites were sampled. I collected a total of 126,812 galls (mean = 1093 ± 103.3; median = 741.5 per site). Details of site locations, collection information, and samples sizes for galls and emergent insects are presented in Table S1. The timing of gall collection was set to coincide with the onset of *B. treatae* maturation/emergence because galls collected at this time are mature enough to allow all gall occupants to complete development post-harvest. As well, by this time galls have had the opportunity to accumulate NE during the entire cycle of growth and development of both the gall and the galler. Moreover, while NE can emerge from leaf galls prior to *B. treatae* emergence (Hall 2001), both the interval of peak emergence and the bulk of NE emergence occurs following *B. treatae* emergence (Lund 1998; Hall 2001). Natural enemies emerge throughout a protracted period that spans up to two years following lignification of the leaf gall (Lund et al., 1998; Hall 2001).

I collected leaf galls primarily by stripping galls from leaves attached to trees. However, periodically live oaks prematurely abscise leaves, which may contain galls. At the subset of sites, where abscised but galled leaves were apparent, I collected galls from leaves that were retained on the tree and from abscised leaves under the host tree.

Comparison of the emergent NE from these two classes of galls allowed me to test whether the number or community composition of NE that emerged differed between these categories. I subsequently pooled the data from these collections at each of these sites as I detected no difference in the numbers of individuals, or the composition of natural enemies emerging from the two types of galls (6 abscised and 6 retained sites; Chi-Square test: $X^2 = 0.1026$: P-value = 0.74). Additionally, four *Qv* sites represent composite sites created by pooling samples of galls collected from two to four sites in close proximity (< 8 km) in order to attain adequate sample sizes. In each case these represented areas of low gall density.

After separating galls from leaves, galls were placed into collection traps that were housed outdoors where they were exposed to daily fluctuations of temperature and humidity but sheltered from direct sunlight. Traps were surveyed daily for emergent *B. treatae* and natural enemies for one year following the collection date. Henceforth, collection traps were surveyed every 6 mo. during the second year. Collected insects were stored by site and month of emergence in 95% ethanol. After removing sites that failed to yield at least 50 natural enemies, I retained a total of 74 sites which were then used for diversity analyses. I reared a total of 32,722 natural enemies from these 74 sites (Table S1). The average number of natural enemies to emerge per site sites was (mean ± SE) 439 ± 49.9 with a median of 312. All *B. treatae* gall samples, plant voucher material, and all emergent insects are archived at Texas State University.

## Identification of Natural Enemies

Natural enemies were identified following Forbes et al. (2015) and/or taxonomic specific keys using a WILD M3Z dissecting scope. Given the difficulty of delineating species within the speciose parasitic hymenoptera on the basis of morphology using keys that for some groups are incomplete, the number of natural enemy taxa I identified likely underestimates the actual number of taxa (Forbes et al., 2015). Where necessary, morphotypes within species were designated. To aid in delineating operational taxonomic units I obtained CO1 data and conducted molecular taxonomy analysis for morphotypes that I distinguished within the genus, *Synergus*, *Ormyrus*, and *Brasema* (Tables 1 and S2).

Parasitic Hymenoptera represented the most common group within the 32,722 insects reared from *B. treatae* leaf galls. However, a small percentage of emergent insects represented Coleoptera, and Lepidoptera, which are known to function as natural enemies of *B. treatae* (Hall 2001). Species of Diptera, Pscocoptera, and Thysanoptera also emerged from the leaf gall collections. These species are not known to parasitize *B. treatae* galls (Forbes et al., 2015). Because I am interested in the natural enemy community associated with *B. treatae* I dropped all Pscocoptera, Diptera, and Thysanoptera from my analysis of natural enemy community composition. After including only taxa known to develop within galls and associated with *B. treatae* mortality I retained a total of 30 taxa for analysis (Tables 1 and S2).

## Natural Enemy Species Range Maps

Broad geographic-scale sampling provided the opportunity to characterize the geographic range of each natural enemy species associated with *B. treatae*. Latitude and longitude coordinates from each collection site were used to create a base map of all collection sites. Presence/absence data across all 94 sites were then used to illustrate the distribution of occupied sites for each natural enemy using the 'maps' and 'mapdata' packages in R (Figure S2). These maps provide a ready means of illustrating differences between widespread and restricted species, and species turnover within and among genera.

## Diversity Analysis

Because the distribution of *Qv* overlaps the eastern portion of the *Qf* range along with the entire range of *Qg* thus linking *Qv* to the other host plants, I hypothesized that *Qv* would have a higher richness and diversity because it overlaps *Qf* and *Qg* ranges, thus it is possible it will contain elements of both communities. To investigate the hypothesis that the diversity of NE is higher in the *Qv* community, I calculated richness and Shannon-index diversity values using the 'vegan' package in R for each of the 74 sites (categorized by host plant). I then conducted an ANOVA to determine if richness and diversity differed based on host plant. A Tukey Honestly Significant Difference post hoc test was then conducted to compare richness and diversity of NE among the host plants. To visualize the diversity patterns within and among hostplants, I then constructed a dendrogram of Beta diversity across all 74 sites using the hclust function in the 'stats' package in R.

To isolate the contribution of host plant and spatial autocorrelation among sample sites inherent to the sampling design to variation in the diversity of natural enemies among sites, I used principal coordinates of neighbor matrices, (PCNM) in conjunction with redundancy analysis, (RDA). This approach allowed me to partition variation explained by use of alternative host plants while controlling for spatial autocorrelation among sample sites (Dray et al., 2006; Legendre et al., 2015). Because the biology of both the host plants and the gall former are such that their distributions are not uniform across the landscape, sites discovered to be occupied by *B. treatae* and included in the sample design for my range-wide study were irregularly spaced both within and among host plant species across the range of all three host plant species. Thus my sampling design is described as irregular two-dimensional sampling (Borcard et al., 2004). Accounting for spatial autocorrelation among sites when partitioning the effects of environmental variables on community diversity protects against inflating explained variation attributable to explanatory variables in RDA analysis (Borcard and Legendre, 2002; Peres-Neto et al., 2006; Legendre et al., 2015).

To reduce the amount of skew in the distribution of abundances of natural enemy species in the data and to address the problem of "double-zero asymmetry" in diversity data (Caceres et al., 2013), I implemented the BCD function (Legendre et al., 2018 *in press*) to determine which transformation is most appropriate for my dataset. Based on this stepwise test (Legendre et al., 2018 *in press*), I used a box-cox-chord transformation with an exponent of 0.7 to transform the raw abundance data. This transformation best normalized the data and yielded the matrix of pairwise Euclidean distances representing

differences in diversity between all paired sites for subsequent comparison to the spatial dissimilarity matrix used for the RDA.

While I used the full transformed dataset as described above to conduct an RDA, sampling effort varied across my 74 collection sites since some sites produced more natural enemies than others. Because sites varied in the number of NE used to estimate community structure, I created three rarefied datasets at varying sample size minimums. I then applied a box-cox-chord transformation, as above, with exponents of 0.5, 0.6, and 0.5 (at sample minimums of 55, 100, and 150 respectively) on these rarefied datasets to determine whether the results of the RDA were robust against variation in sampling effort. To create these rarefied datasets I dropped sites that produced less than the sample number minimums of natural enemies (Table 2).

To investigate the influence of latitude and longitude on the community dissimilarity data, I first constructed a preliminary RDA with latitude and longitude as my predictor variables. I first used the distHaversine function in R to obtain Haversine distances between all pairs of sites. The resulting spatial dissimilarity matrix was then used to conduct a PCNM. I used the pcnm function in the 'vegan' package in R to determine the positive PCNM. To determine the significant spatial components that explain most of the variation in my dataset I constructed an initial RDA using my non-rarefied transformed dataset as my response variable and host plant as my discrete environmental variable, along with the positive PCNM axes as the spatial explanatory variables. A permutational ANOVA, using the 'vegan' package, on the initial RDA indicated five significant PCNM axes (Table S3) which were then selected as the spatial components that explained the most variation on the dataset. I then used the five

significant axes from the PCNM to construct the final RDA with the transformed community dissimilarity data as the response and host plant along with the five significant PCNM axes as explanatory variables. A permutational ANOVA on the final RDA estimated the proportion of variance explained by host plant association and PCNM axes. I used the same protocol for RDA construction for each of the rarefied and non-rarefied datasets. Spatial data were not detrended for the analyses since the sampling design essentially covered the entire host plant range in the southern U.S. which is my only environmental variable.

## III. RESULTS

My widespread sampling adds an additional 11 taxa to the leaf gall natural enemy community previously described by Forbes et al. (2015) (Table 1). Results of the ANOVA conducted to examine species richness and diversity among the three host plants contradicted my hypothesis. Results showed that both species richness and diversity are significantly greater on *Qf* compared to *Qv* and *Qg* (Tables S4, S5, S6, and S7). There were no differences in species richness and diversity between *Qv* and *Qg* (Tables S4, S5, S6, and S7). Box-and-Whisker plots (Figure 2) illustrate the difference in species richness and Shannon-index of diversity among the hosts. A dendrogram of Beta diversity shows a clear clustering of *Qf* sites together with 2 *Qv* sites that were each located in the same geographic region (Figure 3). The other branches show a mix of *Qv* and *Qg* sites clustering together with some sites occurring in close proximity while other sites in the same cluster are hundreds of kilometers away.

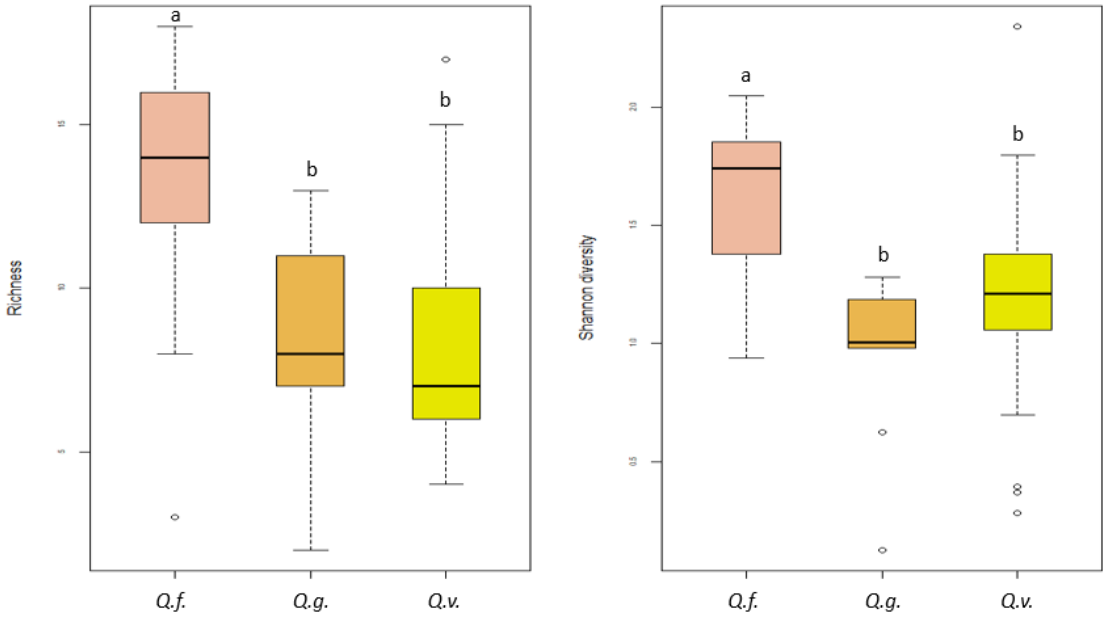



**Figure 2: Species richness and Shannon-Weiner diversity index plot.** Box and whisker plots of species richness and Shannon-Weiner diversity index of insect natural enemies associated with leaf galls housing the asexual generation of the Cynipid, *B. treatae* for each of three species of Live oak. Box and whisker plots depict the distribution of richness and Shannon-Wiener diversity values with each plot being are divided up by 4 25% quartiles containing 25% of the data points within each quartile. Black lines within each plot depict the median value and hollow circles denote outlier site richness and diversity values. Above each plot is a letter denoting a difference/similarity in richness or Shannon-Wiener index: for example a = a and b = b states the values are not different while a ≠ b states the values are different. For both species richness and Shannon-Wiener index *Qf* is significantly higher compared to *Qv* and *Qg* which show no difference in richness and diversity.

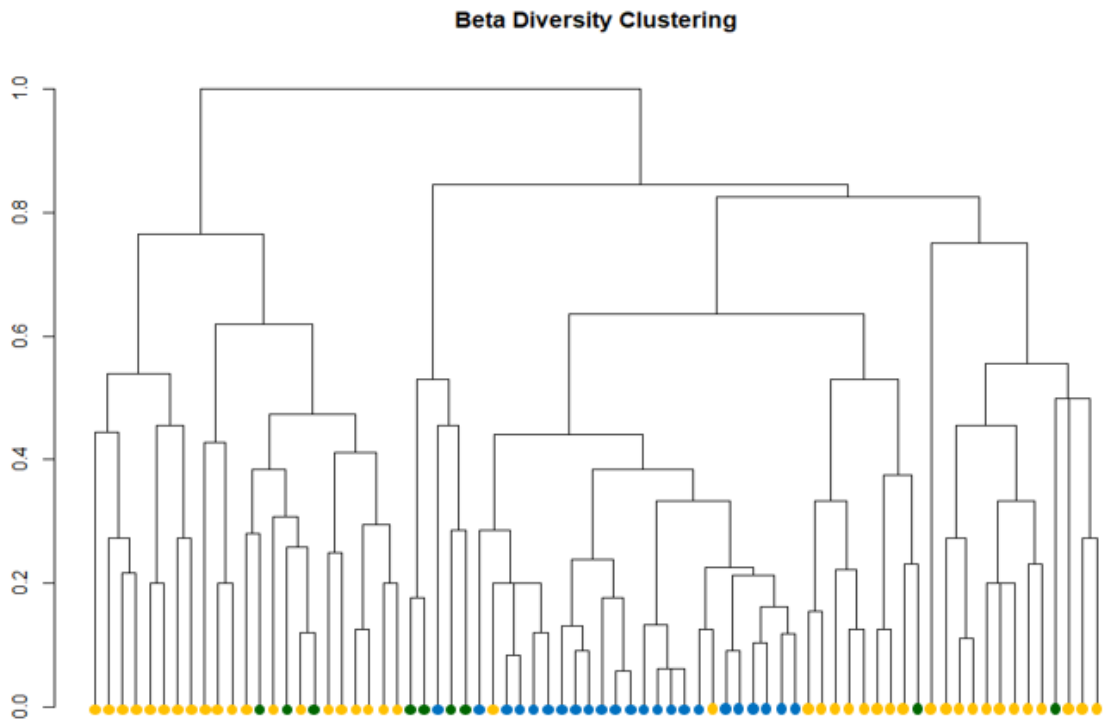



**Figure 3: Dendrogram of Beta diversity across all sites.** Sites are designated by colored circles which indicate host affiliation. Blue circles are *Qf* sites, green circles are *Qg* sites and orange circles are *Qv* sites. The dendrogram depicts 5 main clusters of sites: cluster 1) most *Qf* sites are located in this cluster with 2 *Qv* sites that are also located in Texas, cluster 2) 4 *Qg* and 1 *Qf* site form this cluster, cluster 3,4,5) these are primarily *Qv* sites with the remaining *Qg* sites. These clusters do not show grouping based on geography as sites that are distant from each other occur within the same cluster and other sites close together fall in another cluster.

**Table 1: Natural Enemies of *B. treatae* across three live oak host species.** List of NE present in this study with presence of each taxa denoted by an X across the three host plants (*Q. fusiformis, Q. virginiana,* and *Q. geminata*). Taxa annotated with an * indicates a new taxonomic unit that was previously not a known NE associated with *B. treatae* from Forbes et al. (2015).

| Family within Order | Species or subfamily | Host Plant *Qf* | Host Plant *Qv* | Host Plant *Qg* |
|---|---|---|---|---|
| Hymenoptera | | | | |
| Eulophidae | *Galeopsomyia nigrocyanea* | X | X | X |
| | *Eprhopalotus sp.* | X | X | |
| Eupelmidae | *Brasema sp.1* | X | X | X |
| | *Brasema sp.2* | X | X | X |
| | *Brasema sp.3** | X | X | |
| | *Brasema Males* | X | X | X |
| | *Eupelmus cushmani** | | X | |
| | *Eupelmus sp.** | | X | |
| Eurytomidae | *Eurytoma bugbeei* | X | X | X |
| | *Sycophila texana* | X | X | X |
| | *Sycophila varians* | X | X | |
| | *Sycophila dorsalis* | X | X | X |
| | *Sycophila sp.** | X | X | |
| | *Eurytoma sp.* | X | X | X |
| Ormyridae | *Ormyrus labotus* | X | X | |
| | *Ormyrus sp.** | | X | X |
| | *Orymus dryorhizoxeni** | | X | |
| Pteromalidae | *Acaenacis lausus* | X | X | X |
| Torymidae | *Torymus tubicola* | X | X | X |
| Bethyliidae | *Goniozus sp.* | X | X | X |
| Braconidae | *Allorhogas sp.* | X | X | |
| Chalcididae | *Haltichella xanticles** | | | X |
| Megaspilidae* | | X | X | X |
| Encyrtidae* | | X | X | X |
| Ceraphronidae* | | | X | |
| Cynipidae | *Synergus sp.1* | X | X | X |
| | *Synergus sp.2** | | X | X |
| Coleoptera | | | | |
| Anobiidae | *Tricorynus sp.* | X | X | X |
| Curculionidae | *Conotachelus juglandis* | X | X | X |
| Lepidoptera | | | | |
| Gelechiidae | | X | X | X |

The preliminary RDA, conducted to determine the influence of latitude and longitude, showed that these two explanatory variables explained 21.11% of the total explained variation in community structure. The permutational ANOVA of the initial RDA showed that both latitude and longitude were significant (P-value < 0.01) contributors to the variation explained. RDA 1 axis was explained by longitude and RDA 2 axis was explained by latitude. I then constructed my PCNM and RDA with the full (non-rarefied) dataset. The PCNM indicated 43 positive PCNM axes out of a possible 74, which were then used in the initial RDA to determine the number of axes that contributed significantly to explained variation. The initial RDA summary indicated 43 positive PCNM axes explaining the variation in community structure. Following the permuational ANOVA on the RDA, five significant axes (PCNM: 1,2,3,4,6) were retained as spatial explanatory variables for the final RDA. Results of the RDA show that host plant along with the five axes explains 34.67 % of the variation (Table 2 and S8). Ordination of the RDA (Figure 4) shows host plant contributing to the first RDA axis while the second axis is explained by two spatial axes (PCNM 1 and 4). The first RDA axis explained 66% of the explained variation with host plant contributing the most to the axis biplot score (Table S9). The second RDA axis explained 17% with PCNM1 and PCNM4 contributing the most to the axis (Table S9). The permutational ANOVA of my final RDA included host plant and the 5 PCNM axes showed that host plant explained 5.27% of the variation in NE community structure (Tables 2 and S8). Four PCNM axes were significant (PCNM: 1,2,4,6) with PCNM 1 explaining 4.15% of the variation (Table S8). PCNM 1 shows that there is a clear longitudinal divide west and east of the Mississippi River

divide (Sites 34-40; Figures 5 and S3). Together all PCNM axes (spatial components) constituted 29.4% of explained variation (Table 2).

Because the number of total NE that emerged varied across sample sites, I wanted to test if the results were robust when accounting for sampling effort. Following the process of RDA construction, results of the final RDA using the rarefied datasets showed that host plant along with their significant PCNM axes explained an increased percent of the variation within the datasets (Table 2). The permutational ANOVA on the final RDA using the rarefied datasets (55, 100, 150) showed that variation explained by host plant changed from 5.27% to 5.45%, 5.03%, and 6.43% while the variation explained by the PCNM axes increased from 29.4% to 37.33%, 43.68%, and 40.32% (Table 2). These results show no substantial difference among the three rarefied datasets compared to the non-rarefied dataset (Table 2).

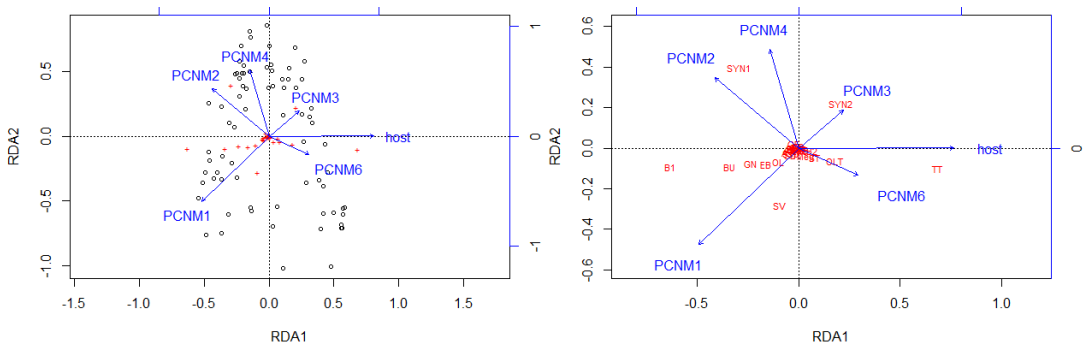



**Figure 4: RDA plot of environmental (Host plant species) and spatial variables.** Both plots depict host and PCNM axes from the RDA and the influence on the first and second RDA axes. Sites are denoted as hollow circles and taxa are represented by red crosses and taxa codes.

**Table 2: Summary table of Permutational ANOVA's on multiple RDA's.** Non-rarefied and Rarefied datasets were used to run multiple RDA's to determine if accounting for sampling effort would result in a different outcome.

| Dataset Type | Sample Number Minimum | Host Plant | Number of Sites | Percent Explained Variation | Total Host Variation | Total PCNM Variation |
|---|---|---|---|---|---|---|
| Non-rarefied | | *Qf* | 23 | | | |
| | | *Qv* | 42 | | | |
| | | *Qg* | 9 | 34.67 | 5.27 | 29.4 |
| Rarefied | 55 | *Qf* | 21 | | | |
| | | *Qv* | 37 | | | |
| | | *Qg* | 8 | 42.79 | 5.45 | 37.33 |
| Rarefied | 100 | *Qf* | 21 | | | |
| | | *Qv* | 30 | | | |
| | | *Qg* | 8 | 48.72 | 5.03 | 43.68 |
| Rarefied | 150 | *Qf* | 20 | | | |
| | | *Qv* | 23 | | | |
| | | *Qg* | 8 | 46.76 | 6.43 | 40.32 |

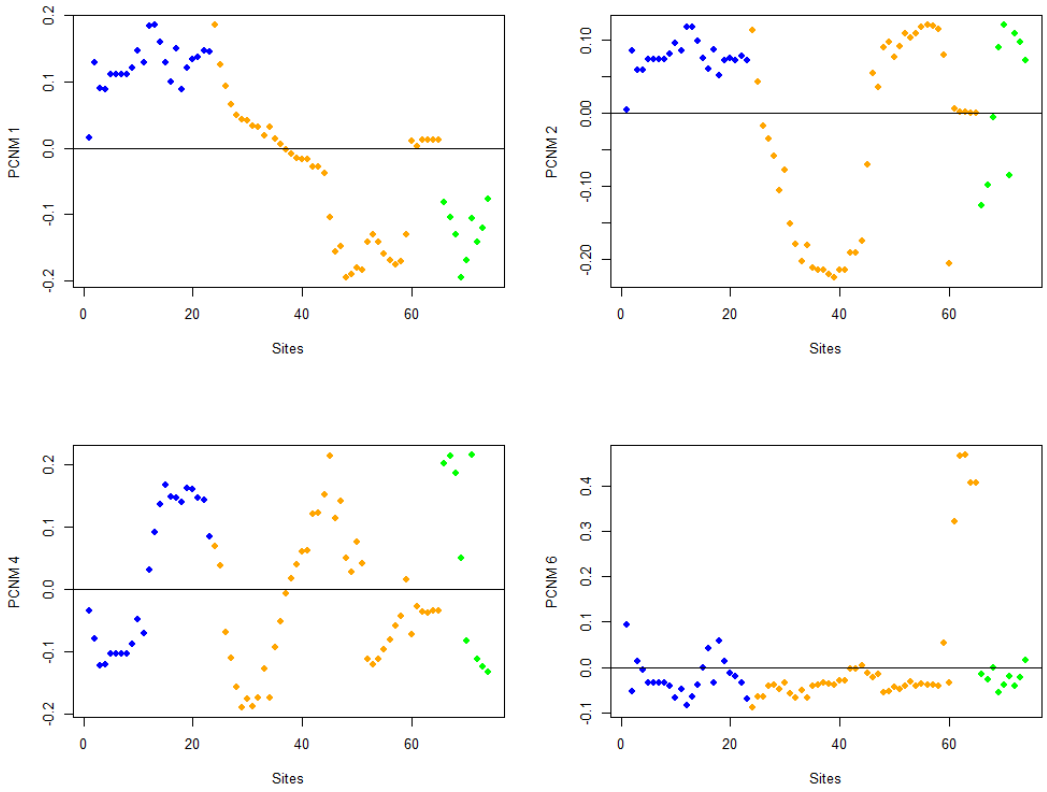



**Figure 5: Significant PCNM axes plots across all sites.** Each plot represents the significant PCNM axes used in the RDA. Sites are color-coded based to indicate host plant affiliation: Blue (*Qf)*, Green (*Qg)* and Orange (*Qv)*. Sites are arranged left to right from 1 through 74 which corresponds geographically from west to east within each host plant. PCNM 1 axis explained the largest percentage of the spatial autocorrelation and depicts an east to west divide at the Mississippi River.

# IV. DISCUSSION

In this study I examined the natural enemy community of the Cynipid gall former *Belonocnema treatae* on three host plant species sampled throughout the geographic ranges of the three host plants spanning the southern U.S. I hypothesized that host plant affiliation contributes to the variation in the natural community structure of *B. treatae* in addition to the spatial autocorrelation among sample sites that is expected from the layout of study. I expected that host plant affiliation would influence community structure of NE because the expansive geographic distribution of the host plants would be expected to cover a diversity of regional pools of natural enemies (Cornell and Lawton, 1992). As well, the broad geographic range of the host plants spans a wide range of biotic and abiotic dimensions of environmental variation that is experienced by the host plants, the host-specific gall former, and the associated natural enemies. This variation is expected to lead to environmental filtering (Lebrija-Trejos et al., 2010) of the natural enemy community. Moreover, while *Qv* and *Qg* occur in sympatry in the southeastern portion of their range, *Qv* is parapatric to *Qf* in the western part of the *Qv* range. Thus I also tested the more specific hypothesis that species richness and diversity would be greater on *Qv* host plants than *Qf* and *Qg* due to the wide range of *Qv* and the overlap with the other two host plants. I found that host plant had a significant effect on the natural community structure while demonstrating that spatial structure also contributes a significantly large proportion of explained variation in natural enemy community structure. However, contrary to my expectation, I found that species richness and diversity of NE were significantly greater on *Qf* host plants. Finally, I learned that my range-wide study which sampled an area at least 10x larger than the previous study of *B. treatae* leaf gall NE

(Forbes et al., 2015) only marginally increased the number of known NE of *B. treatae*. This result suggests that natural enemy community of *B. treatae* is relatively similar across its geographic range in the southern U.S. on three host plants.

This study allowed me to partition and hence evaluate the importance of environmental and spatial components on community structure. While host plant association did significantly affect the community structure (Table S8), the majority of explained variation was due to spatial components (Table 2). The PCNM axes are a key component in interpreting patterns of spatial autocorrelation including where spatial autocorrelation is highest. In my study, PCNM 1 contributed the most to the second RDA axis which the PCNM axis shows more spatial autocorrelation between sites east and west of the Mississippi River (Figures 5 and S3) regardless of host plant affiliation. Sites that are west of the Mississippi River are more spatially autocorrelated than those to the east suggesting a coarse grain interpretation of spatial patterns. Interestingly, it seems that overall spatial influence on community structure is better explained by broad-scale spatial patterns rather than local site-to-site variation (Table 2; Figure 5). The influence of these spatial patterns however does not affect each species in the same manner with the abundance and distribution of some species being better explained by spatial patterns (Table S10; Figure 4). Spatial structure can thus explain the variation in species abundance and distribution such as *Synergus sp.1* (Table S11; Figure 4) which could be attributed to abiotic and or biotic factors not accounted for in my analysis. The influence of host plant is also greater on certain species such as *T. tubicola* which suggests a closer relationship between this species and host plant affiliation (Figure 4) rather than spatial structure. However, for many species neither host plant nor spatial structure appears to

influence their abundance and distribution which indicates other drivers likely influence the patterns of the natural enemy community.

Forbes et al. (2015) identified 24 natural enemy species of *B. treatae* in studies that surveyed *Qf* in south central Texas and *Qv* in southeast Texas. In the current study, I expanded the area surveyed to encompass the entire southeastern U.S. across the geographic range of three host plant species to acquire a more complete picture of the NE community and I recovered 30 natural enemy species. However, the community of NE I identified were relatively consistent across the geographic range of *B. treatae* and across host plant species. This relatively modest increase in NE is counter to what one would expect if geographic regions and or host plants sharply delineated species boundaries or greatly increased the likelihood of adding new NE community members. If host plants played a major influence on community structure of NE an extreme expression of this would be recovering a completely different NE community from each host plant species. In contrast, finding no difference in NE community structure would suggest little to no influence of host plant. It could have been the case that from the western and eastern region of the U.S. there would be 100% species turnover and a completely different NE community. Contrary to this, I saw species still present from the west within the community in the eastern U.S. My finding of increased richness and diversity in *Qf* but no difference in NE diversity on *Qv* and *Qg* host plants suggests that host plants play a role in shaping the NE community structure but are not the sole driver.

Plants can have a direct or indirect effect on the herbivorous insect community associated with them and thus may influence the natural enemy community of those herbivores (Price et al., 1980). Kemp et al. (2017) found that species turnover of

herbivorous insects was positively related to the plant turnover showing a close relationship between these trophic levels. Effects of community structure from one trophic level can influence the structure of another, which one can predict may cascade to the next. Kruess (2003) showed that the influence of habitat type on the herbivores and parasitoids was significant. However, features of plant-insect communities such as species richness of herbivores and host plant abundance can affect each level differently.

Within the natural enemy community of *B. treatae*, the nature of species distributions is such that some are extremely common and widespread such as *Synergus sp.1* and *Torymus tubicola* (Figure S2) while other species are rare and uncommon (Tables 2 and S1: Figure S2). Differences in patterns of abundance and distribution are evident, for example within the genus *Sycophila*. *Sycophila texana* is both common and abundant across all three hosts while congenitor *S. varians* is less abundant and only found on 2 hosts plant species indicating a higher turnover within this species across host plants compared to *S. texana*. Some species such as *O. dryorhizoxeniv* have a limited distribution in a restricted geographic range on 2 sites in North Carolina on *Qv* host plants (Table S1; Figure S2). Two species within the genus *Orymus* are associated with two host plants (*O. labotus* found on *Qf* and *Qv*; *O. sp.1* found on *Qv* and *Qg*) and are distributed in the west and east but overlapped at two sites in Louisiana (Table S1; Figure S2). Abundances vary significantly across taxa (Figures S4 and S5) and show patterns of skew towards the most abundant species (*Synergus*). The genus *Synergus* is an inquiline group which has the ability to emerge with up to 15 *Synergus* individuals produced per *B. treatae* gall (Hall et al., *unpublished*) so multiple individuals have the potential to emerge even in areas with fewer galls. I categorized *Synergus sp.1* and *sp.2* based on

mitochondrial COI sequence data, however preliminary results showed that within a subsample of *Synergus sp.1* individuals there were at least three distinct groups which were lumped into one unit. The resolution of taxonomic certainty within the genus *Synergus* is low due to lack of key information to ID species (Forbes et al., 2015). This lumping of ≥ three taxonomic units can have a large effect on explained variation in community structure due to host plant or spatial structure (Isaac et al., 2004) thus creating a problem to detect accurate signals of variation in community structure since there is evidence of cryptic speciation within at least one taxon (*Synergus*) (Busbee et al., *unpublished*).

The relationship between spatial structure and community composition can be influential as seen in this study, which could be attributed to abiotic factors and overlapping of with other natural enemy guilds. Large-scale spatial patterns have the ability to determine the biodiversity of different regions which can then cause species to respond differently in their structure and distribution (Kruess and Tscharntke, 1994). These effects due to spatial patterns can be due to numerous factors and thus trying to explain them with the spatial component remains a challenge. Each species in a community can experience their respective landscape at a range of spatial scales (Holt, 1996). Fine-scale spatial effects on community structure may be influenced by the rate of parasitism and competition while broad scale effects can be attributed to their distributions and possible fluctuations (Cornell and Lawton, 1992). The genetic structure of *B. treatae* across its geographic range and three host plants has been recently investigated and provides evidence of differentiation based on host plant and within host plant (Driscoe 2018). Populations of *B. treatae* developing on *Qg* are genetically

distinctly from those from *Qf* and *Qv* host plants. Populations of *B. treatae* cluster together west of the Mississippi River reared from both *Qf* and *Qv* hosts, while to the east *B. treatae* reared from *Qv* host plants cluster together. Host plant genetic structure has shown each plant species is genetically different, however ancestral group proportions within *Qf* populations indicate substructure (Cavender-Bares et al., 2015). Based on ancestral proportion, *Qf* populations can be grouped into 2 subunits of a more central Texas unit and a south central Texas unit. Because there is genetic substructure in *B. treatae* collected from *Qv*, this suggests that by strictly adhering to host plant as a taxonomic unit may be misleading to explain the natural enemy community structure due to the close relationship between NE and *B. treatae.* In future research I will construct an RDA using genetic divisions among *B. treatae* populations to partition sites west of the Mississippi River on *Qf* and *Qv* plants, sites on *Qv* plants east of the Mississippi River, and sites on *Qg* plants. This analysis will allow me to test whether the role of host plant in driving variation in NE community structure increases when fine-scale host plant affiliated genetic differentiation among the host-specific galler populations is incorporated into the analysis. Another possibility is that an RDA that incorporates subdivided host plant taxonomic units based on ancestral haplotypes from Cavender-Bares et al. (2015) may also increase the role of host plant affiliation as a driver of variation in NE community structure.

Since I collected varying gall counts across 74 sites which subsequently yielded differing size samples of the NE community per site, I investigated the extent to which variation in sampling effort accounted for the results of the RDA. I accounted for variation in sampling effort by rarefying at three levels based on the number of NE that

emerged (i.e., 55, 100, 150). I then compared total explained variation, explained variation due to host plant and spatial structure between rarefied and non-rarefied analyses and found that the amount of variation in NE community structure explained by host plant decreased (Table 2) compared to the non-rarefied dataset. Through the rarefication process the quality of the data is reduced by discarding the actual data by introducing random error and may affect the results of the RDA (McMurdie and Holmes, 2014). However even accounting for sampling effort by rarefying the dataset host plant still has a significant effect on the natural enemy community structure.

My current taxonomic classification is almost certainly an underestimate of the true number of independent taxonomic units in the natural enemy community. For example, the designated taxon *Synergus sp.1* alone contains possibly ≥3 species. Determining cryptic species within this genus would thus expand the total number of NE taxa within the *B. treatae* community. Future work is directed at uncovering cryptic species of *B. treatae* NE and following this I plan to conduct RDA's using non-rarefied/rarefied datasets on the collapsed and expanded number of NE. Along with these comparisons I will use host plant and the genetic divisions of *B. treatae* populations (Driscoe 2018) to conduct RDA's to compare results of the RDA. By producing a series of RDA's I can obtain a greater understanding of the natural enemy community structure of *B. treatae* while exploring sampling effort effects. While there is a clear signal that richness and diversity are significantly different among the host plants (Tables S4 and S5: Figure 2), results of the RDA that shows small percentage of host plant explaining the variation in the natural enemy community compared to spatial structure does not negate that host plant is influential.

In this study, I have used currently accepted best statistical practices coupled with robust sampling to disentangle the influence of spatial and environmental components of the community structure of NE associated with a host specific gall forming insect. While a large proportion of variation in this community can be attributed to space and environment, a significant amount remains unexplained. The work presented shows a way to tease apart the proportion of variation explained by spatial and environmental variables. I recommend using such appropriate techniques when addressing ecologically relevant questions focused on community ecology which can have a profound influence for conservationists and the field of ecology.

# APPENDIX SECTION

**Table S1: Natural enemies of *B. treatae*: collection site information and species data.** Each row represents a collection site (numbered) with the associated host plant, latitude and longitude, number of galls collected, and number of NE reared in total and by taxa (see Table S2 for Taxa code designation).

| Host | Site Name | Site # | Longitude | Latitude | Galls | GN | EP | B1 | B2 | BU | B3 | EU | EB | Eury | ST | SV | SD | Ssp | OL | OLT | OLB | AL | TT | GO | BA | SYN1 | SYN2 | AT | CJ | GE | Hx | Meg | Enc | Cer | Enu |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Q.f. | QuartzMtsC | 1 | -99.30109167 | 34.890075 | 4276 | 119 | 0 | 483 | 1 | 106 | 0 | 0 | 79 | 3 | 9 | 20 | 3 | 2 | 3 | 0 | 0 | 20 | 181 | 0 | 0 | 303 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | CokeCounty | 2 | -99.26875 | 31.00380833 | 268 | 8 | 0 | 36 | 0 | 18 | 0 | 0 | 2 | 0 | 5 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 27 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | FortChadbourne | 3 | -100.2516111 | 32.04247222 | 1462 | 8 | 0 | 253 | 0 | 77 | 0 | 0 | 17 | 0 | 19 | 103 | 7 | 0 | 0 | 0 | 0 | 0 | 16 | 0 | 0 | 66 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | IrionCounty | 4 | -100.8420889 | 31.21473889 | 2681 | 139 | 0 | 284 | 0 | 132 | 5 | 0 | 48 | 3 | 92 | 4 | 38 | 27 | 1 | 0 | 0 | 1 | 21 | 0 | 0 | 223 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | TomGreenCounty | 5 | -100.5128222 | 31.16408056 | 1168 | 38 | 0 | 143 | 0 | 31 | 1 | 0 | 17 | 1 | 8 | 84 | 4 | 6 | 0 | 0 | 0 | 5 | 46 | 0 | 0 | 66 | 0 | 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | SuttonCounty | 6 | -100.6366028 | 30.617875 | 815 | 18 | 0 | 34 | 1 | 28 | 2 | 0 | 19 | 1 | 2 | 16 | 2 | 3 | 1 | 0 | 0 | 9 | 10 | 0 | 1 | 182 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | SchleikerCounty | 7 | -100.5843889 | 30.89636111 | 1167 | 24 | 0 | 51 | 1 | 21 | 0 | 0 | 19 | 0 | 3 | 26 | 0 | 0 | 20 | 0 | 0 | 13 | 32 | 0 | 0 | 214 | 0 | 37 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | ConchoCountyC | 8 | -99.87218056 | 31.21634167 | 808 | 15 | 0 | 58 | 0 | 30 | 0 | 0 | 44 | 1 | 3 | 48 | 1 | 12 | 6 | 0 | 0 | 0 | 16 | 0 | 1 | 116 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | MenardCountyC | 9 | -99.768675 | 30.88563889 | 704 | 6 | 0 | 63 | 2 | 58 | 1 | 0 | 12 | 0 | 16 | 23 | 5 | 2 | 1 | 0 | 0 | 1 | 5 | 1 | 0 | 113 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | MasonCountyC | 10 | -99.37379167 | 30.81743056 | 1184 | 4 | 0 | 78 | 0 | 73 | 0 | 0 | 4 | 1 | 4 | 3 | 2 | 0 | 8 | 0 | 0 | 1 | 2 | 0 | 0 | 205 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | Rocksprings | 11 | -100.1086111 | 29.87511111 | 2929 | 77 | 0 | 189 | 34 | 95 | 1 | 0 | 34 | 0 | 385 | 1 | 30 | 8 | 181 | 0 | 0 | 1 | 1 | 0 | 0 | 65 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | FreemanRanch | 12 | -97.99458333 | 29.908 | 1498 | 3 | 0 | 25 | 1 | 7 | 0 | 0 | 21 | 0 | 0 | 43 | 0 | 0 | 5 | 0 | 0 | 2 | 22 | 0 | 6 | 71 | 0 | 8 | 0 | 1 | 0 | 1 | 2 | 0 | 0 |
| Q.f. | PleasantonC | 13 | -98.45086111 | 28.95227778 | 1473 | 12 | 0 | 103 | 0 | 65 | 1 | 0 | 10 | 0 | 43 | 2 | 1 | 0 | 2 | 0 | 0 | 1 | 3 | 0 | 2 | 56 | 0 | 4 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | GeorgeWest | 14 | -98.118 | 28.3212 | 121 | 0 | 0 | 10 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | LiveOakPark | 15 | -97.21049444 | 27.85438333 | 2710 | 23 | 1 | 41 | 0 | 8 | 0 | 0 | 3 | 0 | 103 | 14 | 1 | 0 | 12 | 0 | 0 | 11 | 40 | 4 | 2 | 600 | 0 | 8 | 0 | 20 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | SecondEncino | 16 | -98.13519444 | 26.89416667 | 2875 | 14 | 0 | 496 | 0 | 52 | 0 | 0 | 37 | 0 | 7 | 3 | 0 | 0 | 1 | 0 | 0 | 1 | 138 | 0 | 0 | 309 | 0 | 18 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | FlemmingPrairieRdandRt77 | 17 | -97.04711944 | 28.703325 | 148 | 6 | 0 | 16 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 3 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | McAllenC | 18 | -98.23638889 | 26.21638889 | 6044 | 3 | 4 | 21 | 3 | 15 | 0 | 0 | 57 | 0 | 74 | 16 | 3 | 0 | 16 | 0 | 0 | 4 | 37 | 0 | 7 | 817 | 0 | 2 | 0 | 19 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | Ssarita | 19 | -97.79124722 | 27.19641667 | 1387 | 2 | 0 | 38 | 0 | 23 | 0 | 0 | 11 | 1 | 6 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 49 | 0 | 0 | 142 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | AransasPassIngleside | 20 | -97.15677778 | 27.88272222 | 1480 | 0 | 0 | 13 | 1 | 19 | 0 | 0 | 2 | 0 | 4 | 4 | 0 | 0 | 15 | 0 | 0 | 3 | 14 | 0 | 0 | 306 | 0 | 3 | 0 | 5 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | PortOConnorC | 21 | -96.42466667 | 28.44649167 | 3182 | 30 | 0 | 20 | 1 | 5 | 0 | 0 | 25 | 0 | 4 | 52 | 0 | 0 | 22 | 0 | 0 | 0 | 8 | 0 | 2 | 601 | 0 | 6 | 0 | 28 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | InezRestStop | 22 | -96.82483333 | 28.89025 | 614 | 66 | 7 | 33 | 0 | 7 | 0 | 0 | 0 | 0 | 21 | 50 | 1 | 0 | 13 | 0 | 0 | 7 | 24 | 1 | 0 | 214 | 0 | 2 | 0 | 9 | 0 | 0 | 0 | 0 | 0 |
| Q.f. | AltairC | 23 | -96.45806667 | 29.55515833 | 1245 | 40 | 3 | 42 | 1 | 9 | 0 | 0 | 12 | 0 | 89 | 8 | 1 | 0 | 16 | 0 | 0 | 6 | 31 | 6 | 15 | 317 | 0 | 0 | 0 | 33 | 0 | 0 | 0 | 0 | 0 |
| **Q.f.** | **Total** | **.** | **.** | **.** | **40239** | **655** | **15** | **2530** | **46** | **889** | **11** | **0** | **473** | **11** | **901** | **529** | **99** | **60** | **328** | **0** | **0** | **86** | **706** | **12** | **36** | **5030** | **0** | **108** | **5** | **121** | **0** | **1** | **2** | **0** | **0** |
| Q.v. | LulingC | 24 | -97.63497222 | 29.67386111 | 6110 | 234 | 0 | 92 | 77 | 84 | 1 | 0 | 201 | 0 | 233 | 156 | 67 | 159 | 243 | 0 | 0 | 38 | 59 | 3 | 40 | 674 | 0 | 0 | 0 | 14 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | RiceC | 25 | -95.40227778 | 29.71738889 | 6600 | 4 | 0 | 2 | 0 | 3 | 0 | 0 | 8 | 1 | 2 | 6 | 0 | 0 | 57 | 0 | 0 | 0 | 13 | 0 | 0 | 160 | 0 | 4 | 0 | 1 | 0 | 2 | 0 | 0 | 0 |
| Q.v. | HighIsland | 26 | -94.39180556 | 29.56116667 | 1362 | 18 | 11 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 52 | 1 | 3 | 205 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | Vidor | 27 | -93.93197222 | 30.09994444 | 398 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 73 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | Sulpher | 28 | -93.36063889 | 30.23461111 | 1932 | 0 | 0 | 5 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 412 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 179 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | Egan | 29 | -92.52863889 | 30.23513889 | 250 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 |
| Q.v. | OakGrovehwy | 30 | -92.975 | 29.76683333 | 2312 | 0 | 0 | 13 | 1 | 4 | 0 | 0 | 6 | 0 | 66 | 1 | 0 | 0 | 11 | 2 | 0 | 0 | 19 | 0 | 0 | 270 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| Q.v. | Delcambre | 31 | -91.95830556 | 29.95225 | 406 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 36 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| Q.v. | MorganCity | 32 | -91.31158333 | 29.69072222 | 389 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 5 | 1 | 0 | 0 | 15 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | GoldenMeadow | 33 | -90.27286111 | 29.39388889 | 2319 | 0 | 0 | 0 | 15 | 2 | 0 | 0 | 3 | 0 | 106 | 0 | 0 | 0 | 0 | 204 | 0 | 0 | 133 | 0 | 1 | 17 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 |
| Q.v. | BatonRouge | 34 | -91.17683333 | 30.41330556 | 493 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| Q.v. | PicayuneC | 35 | -89.68125278 | 30.52714444 | 3239 | 0 | 1 | 0 | 3 | 2 | 0 | 0 | 19 | 0 | 6 | 30 | 0 | 0 | 0 | 6 | 0 | 4 | 78 | 0 | 0 | 310 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Q.v. | BaySaintLouisC | 36 | -89.32366111 | 30.320025 | 1878 | 0 | 0 | 0 | 5 | 2 | 0 | 0 | 1 | 0 | 0 | 108 | 0 | 0 | 0 | 2 | 0 | 0 | 40 | 0 | 0 | 64 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Q.v. | GokeefeC | 37 | -88.87050278 | 30.393375 | 1434 | 0 | 0 | 0 | 5 | 2 | 0 | 0 | 2 | 0 | 0 | 22 | 0 | 0 | 0 | 0 | 0 | 0 | 61 | 0 | 0 | 113 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | OceanSpringsC | 38 | -88.75572222 | 30.41002778 | 720 | 0 | 0 | 0 | 6 | 0 | 0 | 1 | 6 | 0 | 2 | 64 | 1 | 0 | 0 | 24 | 0 | 0 | 72 | 0 | 0 | 54 | 22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | GautierC | 39 | -88.61033056 | 30.38038611 | 1146 | 0 | 0 | 0 | 9 | 4 | 0 | 0 | 1 | 0 | 0 | 17 | 0 | 0 | 0 | 38 | 0 | 0 | 136 | 0 | 0 | 3 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | GrandBay | 40 | -88.33752778 | 30.49488889 | 323 | 0 | 0 | 0 | 6 | 4 | 0 | 0 | 0 | 0 | 4 | 15 | 0 | 0 | 0 | 10 | 0 | 0 | 43 | 0 | 0 | 0 | 1 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | DauphinIslandC | 41 | -88.132525 | 30.2504 | 1924 | 0 | 0 | 0 | 9 | 5 | 0 | 0 | 43 | 0 | 54 | 11 | 0 | 1 | 0 | 104 | 0 | 12 | 198 | 4 | 6 | 526 | 30 | 0 | 0 | 7 | 0 | 0 | 1 | 0 | 0 |
| Q.v. | GulfShores | 42 | -87.72052778 | 30.25575 | 658 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 77 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | PensecolaC | 43 | -87.22669444 | 30.49975 | 1210 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 46 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| Q.v. | 13BQvN.SantaRosaIsl | 44 | -86.73663889 | 30.41211111 | 220 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 26 | 0 | 0 | 69 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | N.HighlandView | 45 | -85.31655556 | 29.83827778 | 888 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 43 | 1 | 0 | 57 | 12 | 1 | 0 | 0 | 0 | 5 | 0 | 1 | 0 |
| Q.v. | LanarkVillage | 46 | -83.04368611 | 29.88843056 | 321 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 11 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 46 | 1 | 0 | 75 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | Perry | 47 | -83.58954167 | 30.1161 | 2601 | 0 | 0 | 6 | 22 | 26 | 0 | 0 | 6 | 0 | 388 | 0 | 2 | 5 | 0 | 6 | 0 | 0 | 80 | 1 | 0 | 585 | 152 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | 5BCedarKey | 48 | -83.038 | 29.0141 | 55 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 11 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | S.OtterCreekAve | 49 | -82.77191667 | 29.32477778 | 190 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 41 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | HighSpringsC | 50 | -82.63189444 | 29.84375 | 1499 | 0 | 0 | 10 | 5 | 6 | 0 | 0 | 0 | 0 | 308 | 7 | 1 | 0 | 0 | 5 | 0 | 1 | 43 | 0 | 0 | 323 | 91 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Q.v. | ProgressParkC | 51 | -82.47336111 | 29.78122222 | 283 | 0 | 0 | 0 | 9 | 3 | 0 | 0 | 1 | 0 | 10 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 19 | 0 | 0 | 4 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | HickoryHammock | 52 | -81.1685 | 27.40280556 | 368 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 10 | 0 | 0 | 15 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | Okeechobee | 53 | -80.81677778 | 27.244 | 1162 | 0 | 0 | 0 | 2 | 3 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 | 0 | 0 | 214 | 67 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | KissimmeeRiver | 54 | -81.09677778 | 27.37797222 | 1157 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 94 | 0 | 0 | 235 | 297 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | Rockledge | 55 | -80.69666667 | 28.28791667 | 1680 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 2 | 0 | 0 | 147 | 8 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | OakHill | 56 | -80.85463889 | 28.89577778 | 1461 | 1 | 0 | 36 | 0 | 2 | 0 | 0 | 0 | 0 | 22 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 201 | 0 | 1 | 294 | 86 | 0 | 1 | 5 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | PalmCoast | 57 | -81.19502778 | 29.595 | 377 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 34 | 0 | 0 | 11 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | StAugustine | 58 | -81.32258333 | 29.82988889 | 391 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 36 | 0 | 0 | 17 | 34 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | JekyllIsland | 59 | -81.42972222 | 31.01744444 | 3013 | 1 | 0 | 1 | 9 | 8 | 0 | 0 | 2 | 0 | 224 | 4 | 2 | 0 | 0 | 318 | 0 | 2 | 208 | 0 | 0 | 268 | 33 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | SapeloIsland | 60 | -89.68121667 | 31.3975 | 276 | 0 | 0 | 0 | 5 | 7 | 0 | 0 | 0 | 0 | 12 | 0 | 0 | 0 | 0 | 32 | 0 | 0 | 24 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | CharlestonC | 61 | -79.97338889 | 32.76877778 | 1956 | 0 | 0 | 8 | 4 | 0 | 0 | 0 | 0 | 0 | 116 | 0 | 0 | 0 | 0 | 14 | 0 | 0 | 410 | 0 | 0 | 302 | 28 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | PawleysIsland | 62 | -79.0625 | 33.50736111 | 674 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 124 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | Topsail | 63 | -77.47986111 | 34.46427778 | 1153 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 4 | 5 | 0 | 51 | 0 | 0 | 108 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | FortMacon | 64 | -76.68622222 | 34.69508333 | 653 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 90 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.v. | Beaufort | 65 | -76.63219444 | 34.70988889 | 4868 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 146 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 216 | 0 | 0 | 9 | 0 | 3 | 0 | 6 | 0 | 0 | 0 | 0 | 0 |
| **Q.v.** | **Total** | **.** | **.** | **.** | **60349** | **261** | **13** | **184** | **208** | **174** | **1** | **1** | **304** | **1** | **1827** | **928** | **74** | **165** | **322** | **797** | **6** | **63** | **2890** | **11** | **51** | **5428** | **960** | **17** | **1** | **50** | **0** | **20** | **5** | **1** | **1** |
| Q.g. | InletBeachC | 66 | -86.00386944 | 30.27431389 | 1470 | 0 | 0 | 83 | 4 | 4 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 45 | 2 | 0 | 260 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.g. | Parker | 67 | -85.60355556 | 30.11238889 | 999 | 0 | 0 | 11 | 8 | 5 | 0 | 0 | 23 | 0 | 73 | 0 | 0 | 0 | 0 | 22 | 0 | 0 | 127 | 0 | 0 | 515 | 33 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| Q.g. | Ochlocknee | 68 | -84.38511111 | 29.96008333 | 1082 | 0 | 0 | 51 | 6 | 27 | 0 | 0 | 11 | 3 | 2 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 29 | 0 | 0 | 1022 | 7 | 0 | 0 | 8 | 0 | 0 | 1 | 0 | 0 |
| Q.g. | 5ACedarKey | 69 | -83.04222 | 29.14463 | 953 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.g. | LakeLizzie | 70 | -81.17998889 | 28.22767222 | 6079 | 1 | 0 | 167 | 2 | 32 | 0 | 0 | 8 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 11 | 139 | 1 | 0 | 565 | 0 | 0 | 0 | 5 | 1 | 0 | 0 | 0 | 0 |
| Q.g. | OceansideVillage | 71 | -85.42772222 | 29.95422222 | 2459 | 0 | 0 | 64 | 0 | 8 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 31 | 0 | 0 | 206 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.g. | ArchboldC | 72 | -81.35211111 | 27.18461111 | 1842 | 0 | 0 | 54 | 4 | 8 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 42 | 0 | 0 | 249 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Q.g. | FortPierce | 73 | -80.33019444 | 27.46441667 | 1135 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 77 | 0 | 0 | 50 | 11 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| Q.g. | DickinsonStatePark | 74 | -80.10902778 | 27.02611111 | 2935 | 0 | 0 | 463 | 1 | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 252 | 1 | 0 | 43 | 0 | 0 | 5 | 93 | 0 | 0 | 0 | 0 | 0 |
| **Q.g.** | **Total** | **.** | **.** | **.** | **18954** | **1** | **0** | **896** | **25** | **106** | **0** | **0** | **47** | **3** | **76** | **0** | **1** | **0** | **0** | **28** | **0** | **14** | **743** | **4** | **0** | **2945** | **55** | **1** | **6** | **108** | **1** | **2** | **1** | **0** | **0** |
| **.** | **TOTAL** | **.** | **.** | **.** | **119542** | **917** | **28** | **3610** | **279** | **1169** | **12** | **1** | **824** | **15** | **2804** | **1457** | **174** | **225** | **650** | **825** | **6** | **163** | **4339** | **27** | **87** | **13403** | **1015** | **126** | **12** | **279** | **1** | **23** | **8** | **1** | **1** |

**Table S2: List of Taxonomic units and their designated code used in analyses.** The codes for each taxa were shorthand names used for all data tables and RDA analyses. CO1 data on each taxa was used to determine distinct taxonomic units. The taxa were identified to the species level, a morphotype within a genus, to the genus level, or to the family.

| Taxonomic Unit | Taxa Code |
|---|---|
| *G. nigrocyanea* | GN |
| *Eprhopalotus sp.* | EP |
| *Brasema sp.1* | B1 |
| *Brasema sp.2* | B2 |
| *Brasema Males* | BU |
| *Brasema sp.3* | B3 |
| *E. cushmani* | EU |
| *E. bugbeei* | EB |
| *Eurytoma sp.* | Eury |
| *S. texana* | ST |
| *S. varians* | SV |
| *S. dorsalis* | SD |
| *Sycophila sp.* | Ssp |
| *O. labotus* | OL |
| *Ormyrus sp.* | OLT |
| *O. dryorhizoxeniv* | OLB |
| *A. lausus* | AL |
| *T. tubicola* | TT |
| *Goniozus sp.* | GO |
| *Allorhogas sp.* | BA |
| *Synergus sp.1* | SYN1 |
| *Synergus sp.2* | SYN2 |
| *Tricorynus sp.* | AT |
| *C. juglandis* | CJ |
| *Gelechiidae* | GE |
| *H. xanticles* | Hx |
| *Megaspilidae* | Meg |
| *Encyrtidae* | Enc |
| *Ceraphronidae* | Cer |
| *Eupelmus sp.* | Euu |

**Table S3: Summary table of the permutational ANOVA on initial RDA.** This table shows all 43 positive PCNM axes and the results from the permutational ANOVA indicating that PCNM 1, 2, 3, 4, and 6 are significantly explaining the variation in the NE community.

| Axis | P-value |
|---|---|
| PCNM1 | 0.001 |
| PCNM2 | 0.001 |
| PCNM3 | 0.019 |
| PCNM4 | 0.011 |
| PCNM5 | 0.242 |
| PCNM6 | 0.005 |
| PCNM7 | 0.064 |
| PCNM8 | 0.212 |
| PCNM9 | 0.265 |
| PCNM10 | 0.421 |
| PCNM11 | 0.175 |
| PCNM12 | 0.916 |
| PCNM13 | 0.058 |
| PCNM14 | 0.830 |
| PCNM15 | 0.129 |
| PCNM16 | 0.390 |
| PCNM17 | 0.958 |
| PCNM18 | 0.703 |
| PCNM19 | 0.770 |
| PCNM20 | 0.883 |
| PCNM21 | 0.758 |
| PCNM22 | 0.136 |
| PCNM23 | 0.793 |
| PCNM24 | 0.177 |
| PCNM25 | 0.787 |
| PCNM26 | 0.241 |
| PCNM27 | 0.344 |
| PCNM28 | 0.121 |
| PCNM29 | 0.688 |
| PCNM30 | 0.847 |
| PCNM31 | 0.989 |
| PCNM32 | 0.710 |
| PCNM33 | 0.516 |
| PCNM34 | 0.525 |
| PCNM35 | 0.846 |

| **Table S11 Continued.** | |
|---|---|
| **Axis** | **P-value** |
| PCNM36 | 0.530 |
| PCNM37 | 0.341 |
| PCNM38 | 0.158 |
| PCNM39 | 0.657 |
| PCNM40 | 0.629 |
| PCNM41 | 0.778 |
| PCNM42 | 0.722 |
| PCNM43 | 0.907 |

**Table S4: ANOVA table of species richness by host plant.**

| | Df | Sum sq | Mean sq | F-value | P-value | Significance |
|---|---|---|---|---|---|---|
| Host Plant | 2 | 361.96 | 180.98 | 16.571 | 1.242e-06 | *** |
| Residuals | 71 | 775.45 | 10.922 | | | |

**Table S5: ANOVA table of Shannon diversity index by host plant.**

| | Df | Sum sq | Mean sq | F-value | P-value | Significance |
|---|---|---|---|---|---|---|
| Host Plant | 2 | 3.8123 | 1.90617 | 14.002 | 7.482e-06 | *** |
| Residuals | 71 | 9.6657 | 0.13614 | | | |

**Table S6: Tukey's Honest Significant Difference post-hoc test for species richness among the host plants.** Results of this test indicate that *Qf* community is more species rich than *Qv* and *Qg* communities which show no differences between each other.

| Host Plants | Mean Difference | 95 % Lower Bound | 95 % Upper Bound | P adjusted |
|---|---|---|---|---|
| *Qg – Qf* | -4.5797101 | -7.690208 | -1.469212 | 0.0021327 |
| *Qv – Qf* | -4.8178054 | -6.869951 | -2.765660 | 0.0000010 |
| *Qv – Qg* | -0.2380952 | -3.143986 | 2.667795 | 0.9790213 |

**Table S7: Tukey's Honest Significant Difference post-hoc test for Shannon diversity index among the host plants.** Results of this test indicate that *Qf* community is more diverse than *Qv* and *Qg* communities which show no differences between each other.

| Host Plants | Mean Difference | 95 % Lower Bound | 95 % Upper Bound | P adjusted |
|---|---|---|---|---|
| *Qg – Qf* | -0.6650810 | -1.01235449 | -0.3178075 | 0.0000561 |
| *Qv – Qf* | -0.4158818 | -0.64499490 | -0.1867687 | 0.0001335 |
| *Qv – Qg* | 0.2491992 | -0.07523078 | 0.5736292 | 0.1644926 |

**Table S8: Summary table of the permutational ANOVA on the RDA using the Non-rarefied data.** This table shows that host plant explains a significant amount of the variation in community structure along with 4 of the 5 PCNM axes (PCNM 1,2,4,6) used to construct the RDA. PCNM 1 contributed the highest percentage of explained variation among all of the axes.

| | Variance | F | P-value | Significance |
|---|---|---|---|---|
| Host | 0.018096 | 4.4901 | 0.001 | *** |
| PCNM 1 | 0.014250 | 3.5358 | 0.010 | ** |
| PCNM 2 | 0.010054 | 2.4948 | 0.033 | * |
| PCNM 3 | 0.006548 | 1.6249 | 0.155 | |
| PCNM 4 | 0.010528 | 2.6124 | 0.029 | * |
| PCNM 6 | 0.013915 | 3.4529 | 0.011 | * |
| Residual | 0.270018 | | | |

**Table S9: RDA Biplot scores of the explanatory variables from the Non-rarefied data for each RDA axis.** This table shows the contribution of each explanatory variable for each of the RDA axes. For RDA axis 1, host plant is loading the highest thus for the first axis host plant is the largest contributor.

| | RDA1 | RDA2 | RDA3 | RDA4 | RDA5 | RDA6 |
|---|---|---|---|---|---|---|
| host | 0.953723 | 0.000799 | -0.24435 | 0.165235 | -0.05509 | -0.01916 |
| PCNM1 | -0.61501 | -0.59255 | -0.26246 | -0.28823 | 0.334726 | 0.081499 |
| PCNM2 | -0.51657 | 0.434403 | 0.160168 | 0.505702 | 0.443596 | -0.25745 |
| PCNM3 | 0.275518 | 0.232035 | -0.35592 | -0.46103 | 0.390695 | -0.61513 |
| PCNM4 | -0.17774 | 0.606226 | -0.19084 | -0.40688 | 0.094551 | 0.624491 |
| PCNM6 | 0.364676 | -0.16745 | 0.564179 | -0.10379 | 0.660607 | 0.271107 |

**Table S10: RDA species scores arranged in descending order for RDA axis 1 and 2 for all taxa.** The scores for each species show how they are loading onto each axis either positively or negatively. For RDA axis 1, for which host plant explained most of the variation for this axis, TT (*T. tubicola*) has the highest score suggesting that the abundance and distribution of this species is closely associated with host plant.

| Taxa Code | RDA 1 Scores | Taxa Code | RDA 2 Scores |
|---|---|---|---|
| TT | 0.683632 | SYN1 | 0.395554 |
| SYN2 | 0.208671 | SYN2 | 0.219512 |
| OLT | 0.17765 | GE | 0.020642 |
| ST | 0.08052 | GO | 0.007663 |
| B2 | 0.067949 | Cer | 0.002347 |
| Meg | 0.035232 | Euu | 0.000906 |
| OLB | 0.010841 | Hx | 0.000606 |
| Enc | 0.004745 | EP | -0.00082 |
| Cer | 0.001415 | EU | -0.00104 |
| EU | 0.001193 | CJ | -0.00133 |
| Euu | 0.00035 | Eury | -0.00422 |
| Hx | -3.02E-05 | BA | -0.0057 |
| CJ | -0.00325 | OLB | -0.00647 |
| EP | -0.00423 | AL | -0.00714 |
| GO | -0.00428 | B3 | -0.0077 |
| Eury | -0.01014 | Enc | -0.01259 |
| B3 | -0.01156 | B2 | -0.01344 |
| GE | -0.0256 | AT | -0.0219 |
| BA | -0.02579 | Ssp | -0.03146 |
| Ssp | -0.03656 | SD | -0.03166 |
| SD | -0.0429 | Meg | -0.04232 |
| AL | -0.04456 | ST | -0.04456 |
| AT | -0.05331 | OLT | -0.0635 |
| SV | -0.09152 | OL | -0.06613 |
| OL | -0.10026 | GN | -0.07487 |
| EB | -0.16013 | EB | -0.08041 |
| GN | -0.23374 | B1 | -0.09348 |
| SYN1 | -0.29401 | BU | -0.09352 |
| BU | -0.33884 | TT | -0.10137 |
| B1 | -0.62989 | SV | -0.28297 |

**Table S11: RDA site scores arranged in descending order for RDA axis 1 and 2 for all sites.** The scores for each site show how they are loading onto each axis either positively or negatively. For RDA axis 1, for which host plant explained most of the variation, site 43 is loading positively on this axis suggesting that host plant is explaining a significant amount of the community structure.

| Site Number | RDA 1 Scores | Site Number | RDA 2 Scores |
|---|---|---|---|
| 43 | 0.57919 | 53 | 0.856443 |
| 64 | 0.571861 | 55 | 0.805225 |
| 62 | 0.567792 | 69 | 0.763031 |
| 29 | 0.563158 | 68 | 0.698696 |
| 39 | 0.557753 | 42 | 0.696558 |
| 49 | 0.556222 | 54 | 0.680945 |
| 65 | 0.494688 | 20 | 0.576718 |
| 40 | 0.478483 | 52 | 0.576015 |
| 31 | 0.452431 | 67 | 0.548988 |
| 57 | 0.429277 | 18 | 0.544387 |
| 33 | 0.420018 | 26 | 0.532586 |
| 51 | 0.415229 | 63 | 0.525536 |
| 60 | 0.399571 | 47 | 0.502472 |
| 32 | 0.384455 | 30 | 0.500668 |
| 61 | 0.329435 | 72 | 0.486253 |
| 58 | 0.324023 | 71 | 0.485572 |
| 73 | 0.314285 | 15 | 0.483523 |
| 38 | 0.282908 | 21 | 0.479789 |
| 52 | 0.273812 | 66 | 0.446707 |
| 59 | 0.265372 | 56 | 0.441161 |
| 48 | 0.254462 | 45 | 0.438161 |
| 45 | 0.251997 | 44 | 0.437516 |
| 46 | 0.209411 | 70 | 0.384746 |
| 54 | 0.197009 | 50 | 0.38429 |
| 63 | 0.156807 | 46 | 0.375517 |
| 56 | 0.146946 | 41 | 0.374556 |
| 41 | 0.112182 | 35 | 0.373146 |
| 27 | 0.108526 | 25 | 0.364018 |
| 37 | 0.105463 | 23 | 0.304112 |
| 44 | 0.098822 | 10 | 0.255079 |
| 36 | 0.064547 | 6 | 0.229942 |
| 34 | 0.028532 | 58 | 0.217108 |
| 50 | 0.026103 | 19 | 0.210292 |
| 47 | 0.019557 | 48 | 0.168982 |

**Table S11 Continued.**

| Site Number | RDA 1 Scores | Site Number | RDA 2 Scores |
|---|---|---|---|
| 67 | 0.017263 | 37 | 0.164589 |
| 42 | 0.00405 | 73 | 0.151934 |
| 35 | -0.00365 | 61 | 0.105221 |
| 53 | -0.01536 | 7 | 0.100707 |
| 26 | -0.01922 | 22 | 0.071285 |
| 74 | -0.13546 | 59 | -0.04173 |
| 28 | -0.14178 | 57 | -0.06548 |
| 69 | -0.14306 | 9 | -0.12146 |
| 55 | -0.14787 | 16 | -0.15502 |
| 30 | -0.14794 | 17 | -0.18703 |
| 25 | -0.17775 | 24 | -0.20854 |
| 19 | -0.1851 | 31 | -0.27983 |
| 18 | -0.19446 | 8 | -0.28214 |
| 15 | -0.19773 | 4 | -0.28246 |
| 70 | -0.20179 | 12 | -0.31971 |
| 72 | -0.20627 | 2 | -0.32344 |
| 68 | -0.21779 | 1 | -0.33109 |
| 20 | -0.22663 | 32 | -0.33662 |
| 23 | -0.22729 | 13 | -0.35734 |
| 66 | -0.23075 | 38 | -0.3607 |
| 12 | -0.24587 | 51 | -0.38826 |
| 71 | -0.24696 | 14 | -0.48013 |
| 21 | -0.26251 | 36 | -0.54199 |
| 22 | -0.26959 | 28 | -0.55129 |
| 24 | -0.28561 | 43 | -0.55192 |
| 7 | -0.30727 | 62 | -0.55943 |
| 11 | -0.31668 | 74 | -0.57855 |
| 16 | -0.36247 | 65 | -0.59243 |
| 6 | -0.36605 | 33 | -0.59405 |
| 5 | -0.36853 | 64 | -0.60176 |
| 1 | -0.36866 | 11 | -0.60484 |
| 8 | -0.40106 | 39 | -0.68008 |
| 2 | -0.42362 | 34 | -0.69488 |
| 17 | -0.45697 | 29 | -0.70935 |
| 10 | -0.46301 | 49 | -0.71037 |
| 9 | -0.4645 | 60 | -0.71337 |
| 3 | -0.48734 | 5 | -0.75043 |
| 4 | -0.49315 | 3 | -0.76171 |

**Table S11**
**Continued.**

| Site | RDA 1 | Site | RDA 2 |
|---|---|---|---|
| 13 | -0.50853 | 40 | -1.00591 |
| 14 | -0.54335 | 27 | -1.01916 |

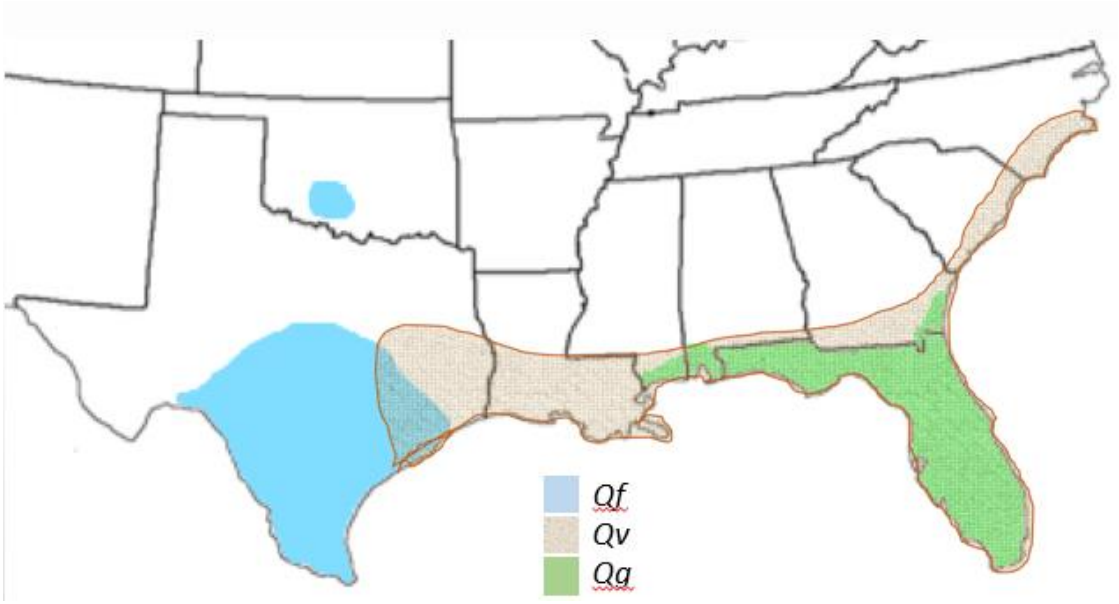
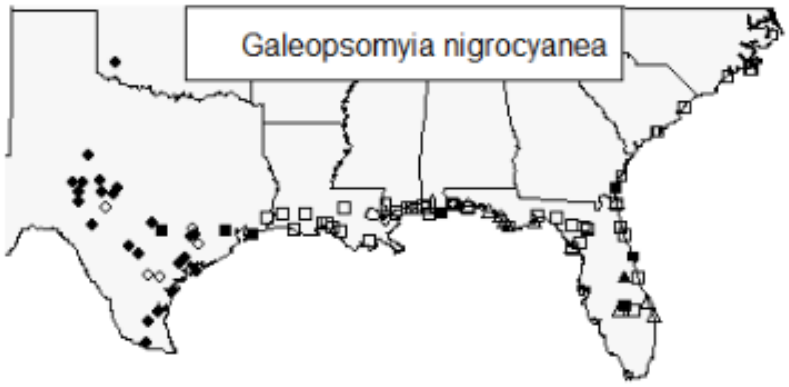
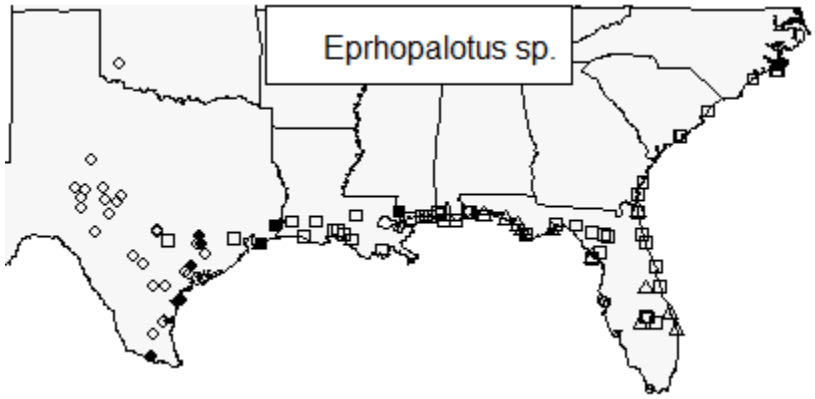
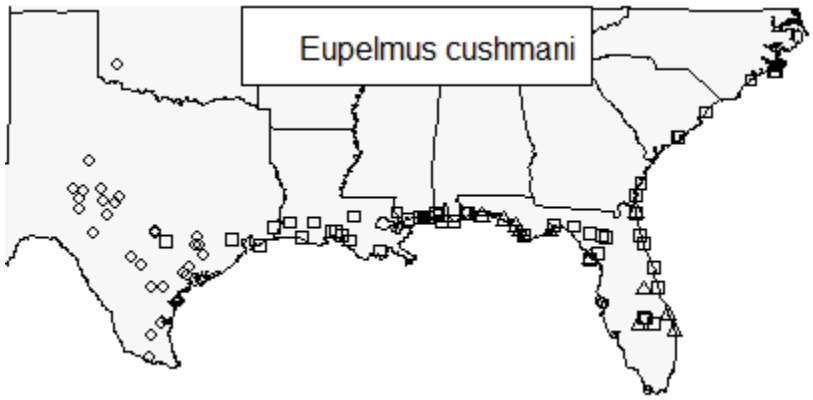
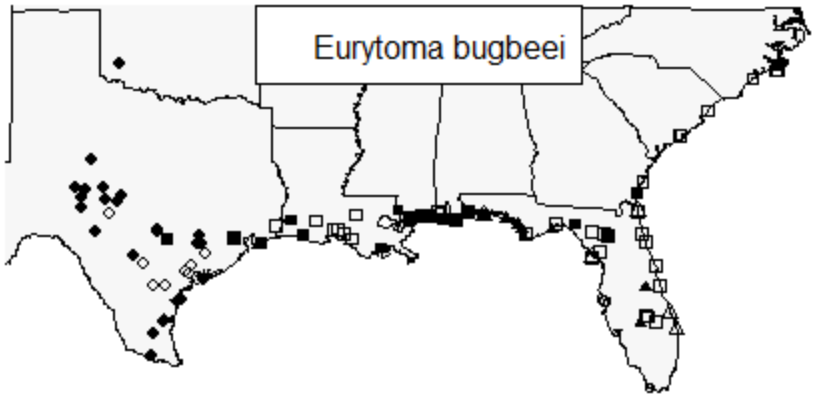


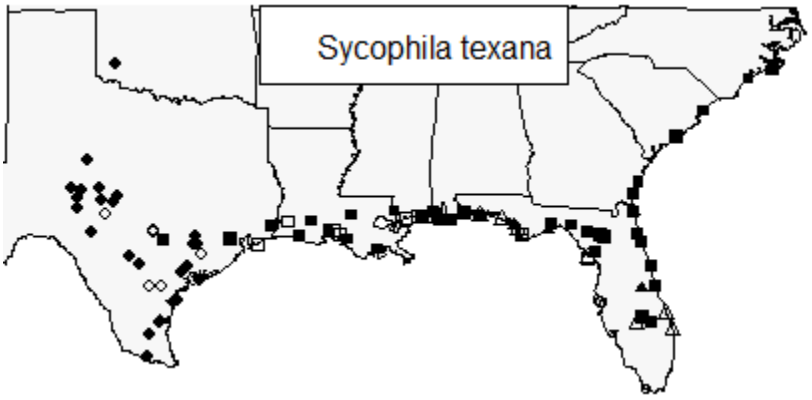

**Figure S1: Range map for three live oak species.** This map shows the ranges of *Q. fusiformis* (*Qf*), *Q. virginiana* (*Qv*), and *Q. geminata* (*Qg*) across the U.S. The western range of *Qv* is in parapatric with *Qf* and *Qv* is sympatric with the entire range of *Qg*. Colors denote the range of each host plant: *Qf* range is in Blue, *Qv* range is checkered Brown, and *Qg* range is in Green.

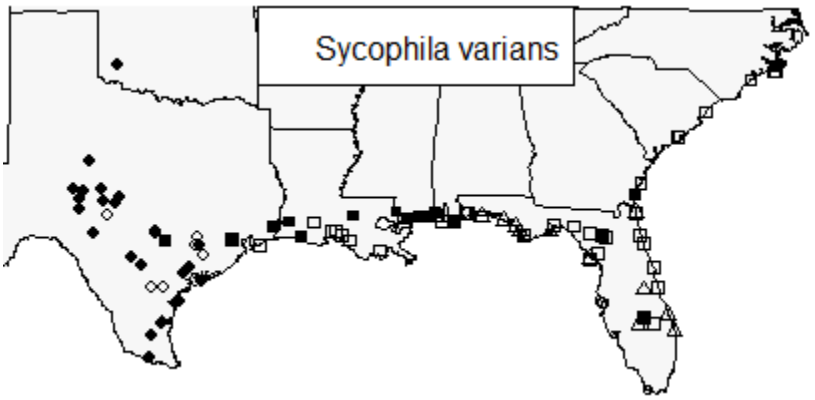

Galeopsomyia nigrocyanea

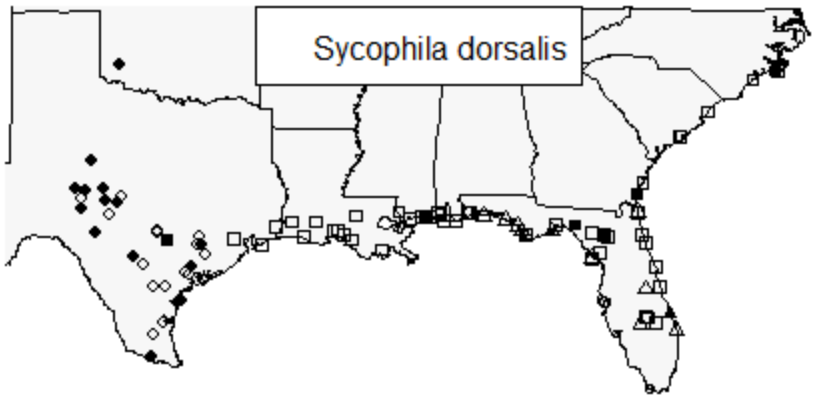

Eprhopalotus sp.

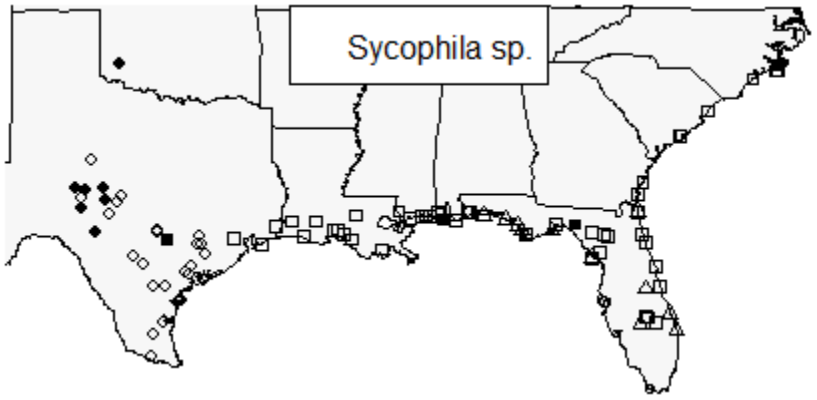

Eupelmus cushmani

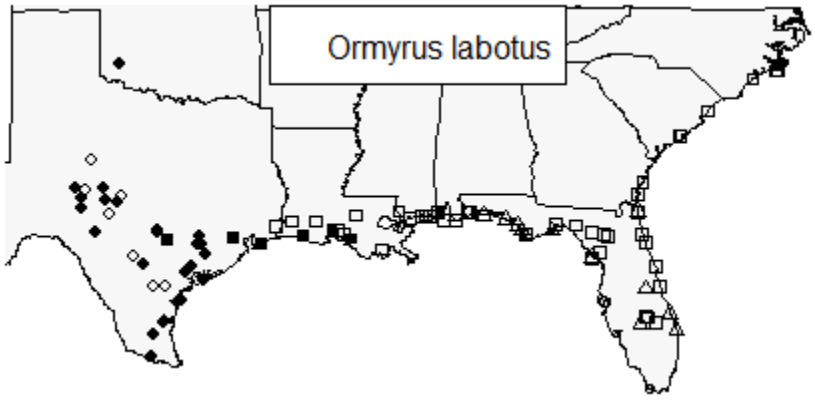

Eurytoma bugbeei

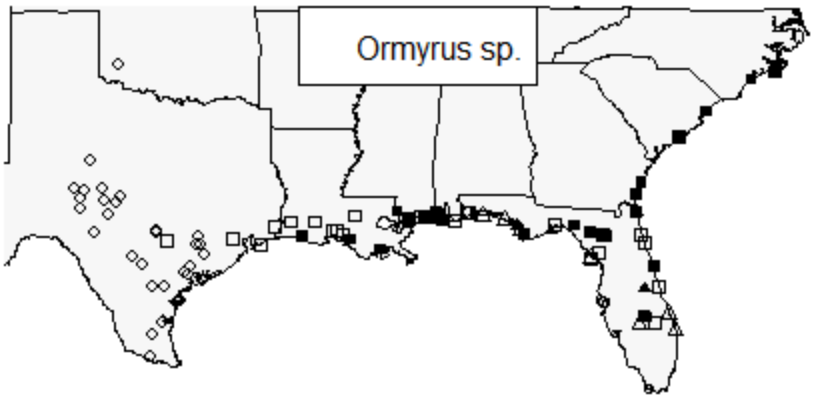

Sycophila texana

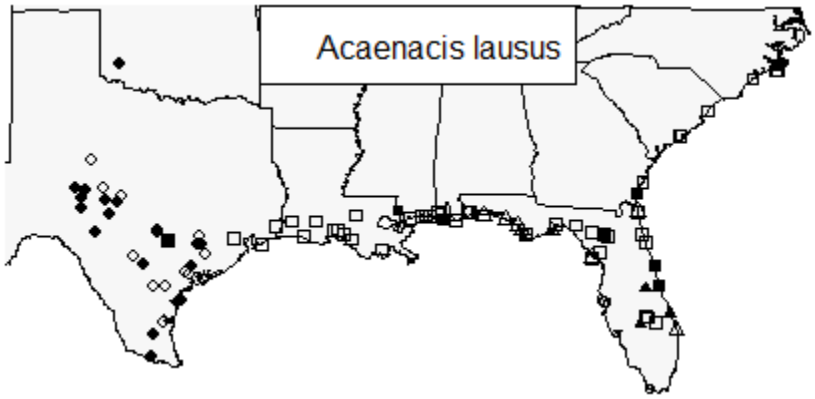

Sycophila varians

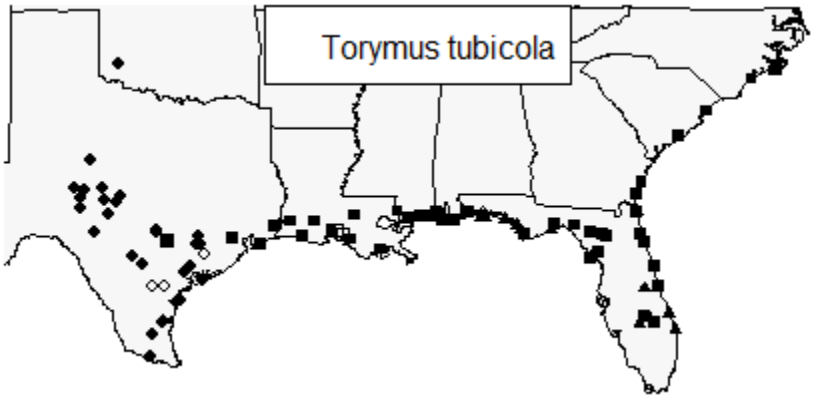

Sycophila dorsalis

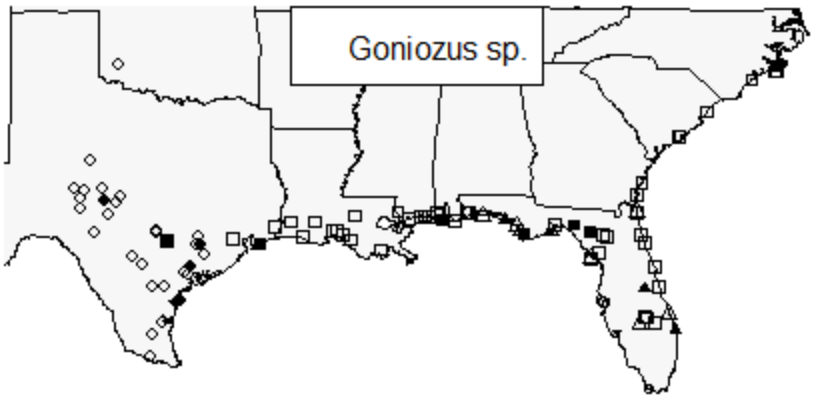

Sycophila sp.

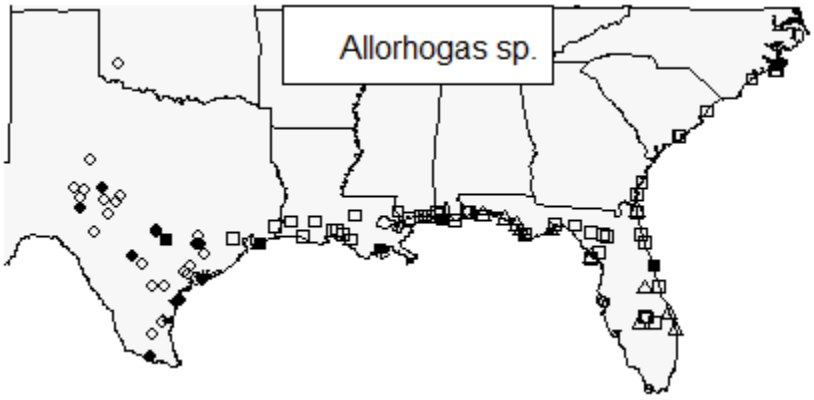

Ormyrus labotus

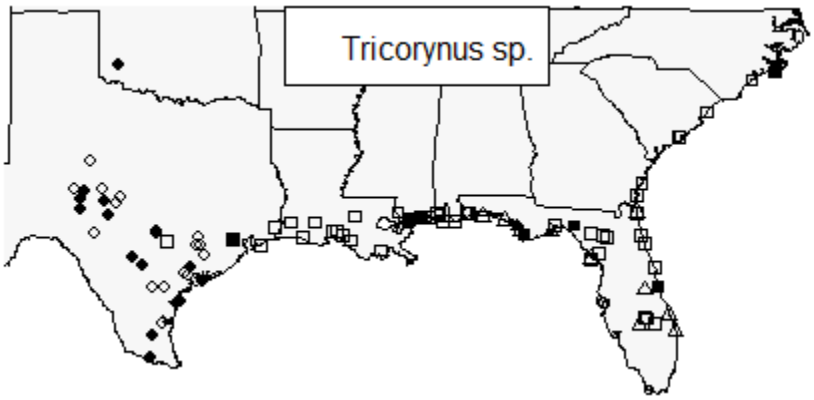

Ormyrus sp.

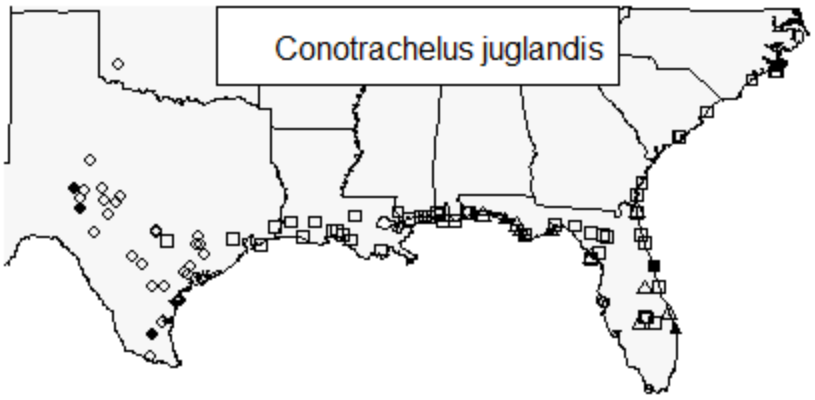

Acaenacis lausus

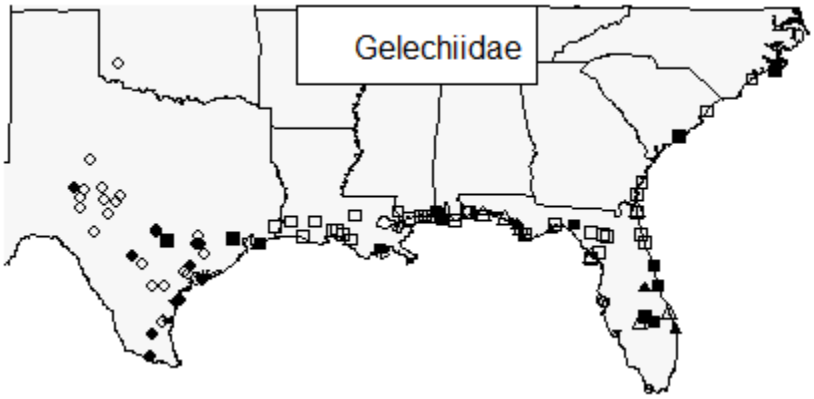

Torymus tubicola

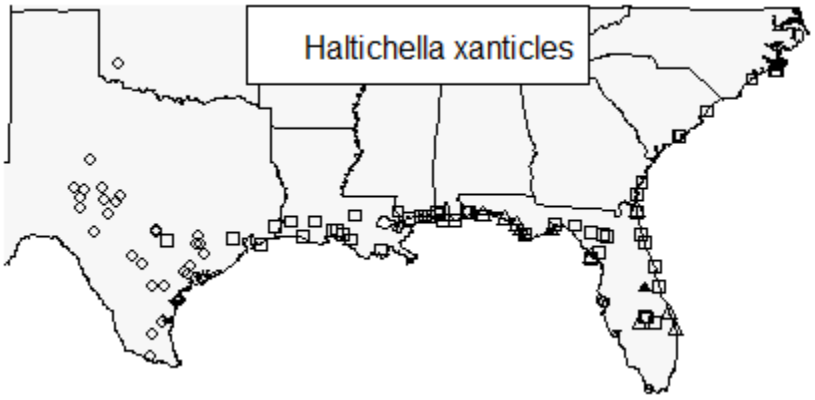

Goniozus sp.

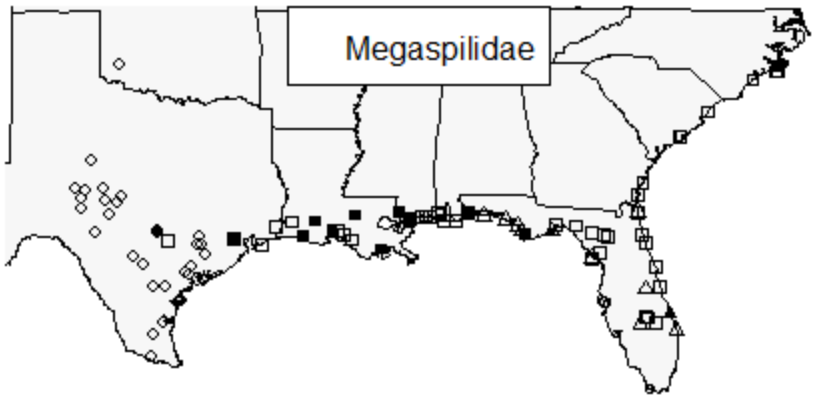

Allorhogas sp.

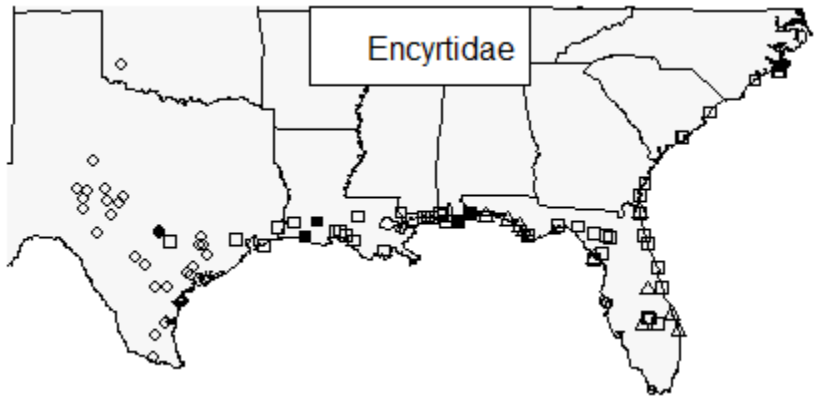

Tricorynus sp.

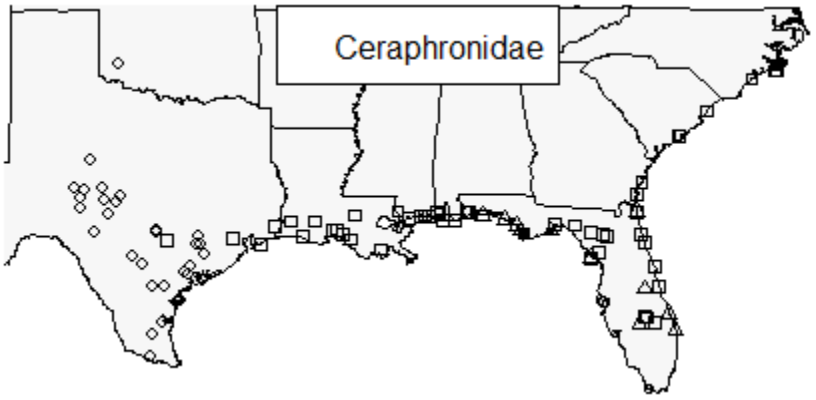

Conotrachelus juglandis

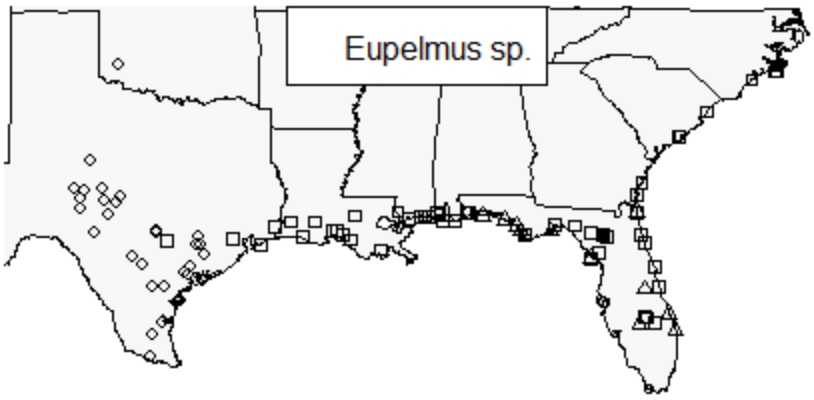

Gelechiidae

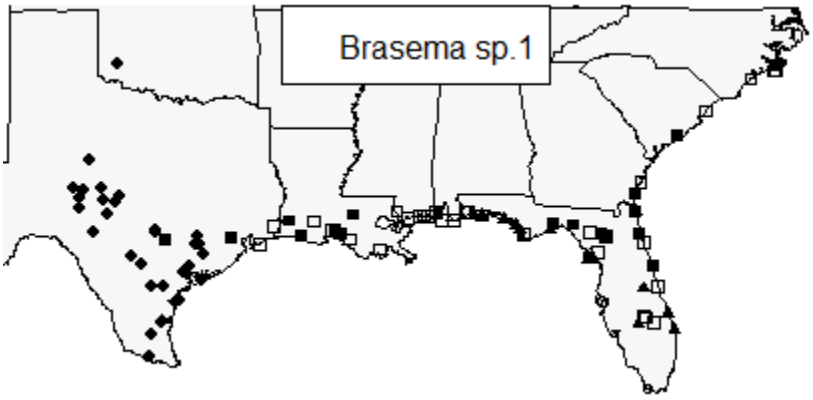

Haltichella xanticles

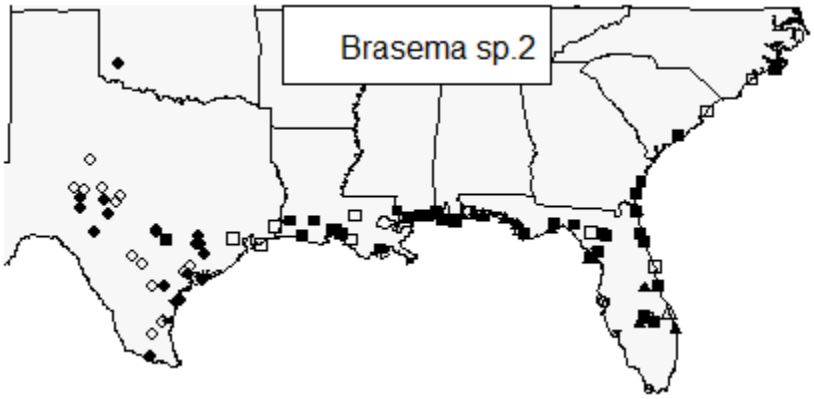

Megaspilidae

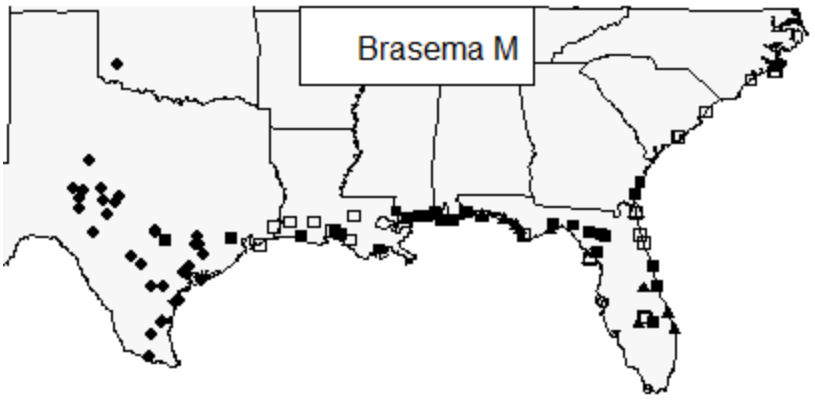

Encyrtidae

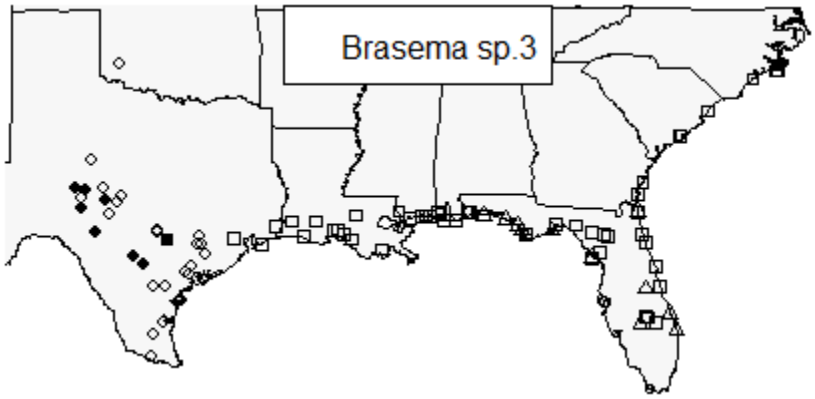

Ceraphronidae

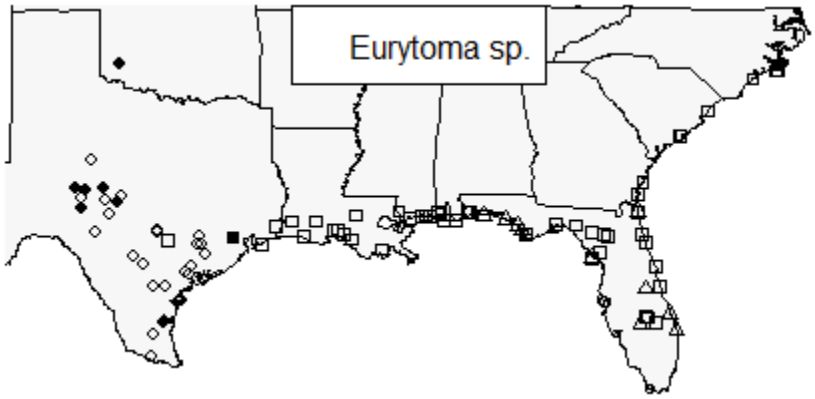

Eupelmus sp.


Brasema sp.1


Brasema sp.2


Brasema M


Brasema sp.3


Eurytoma sp.

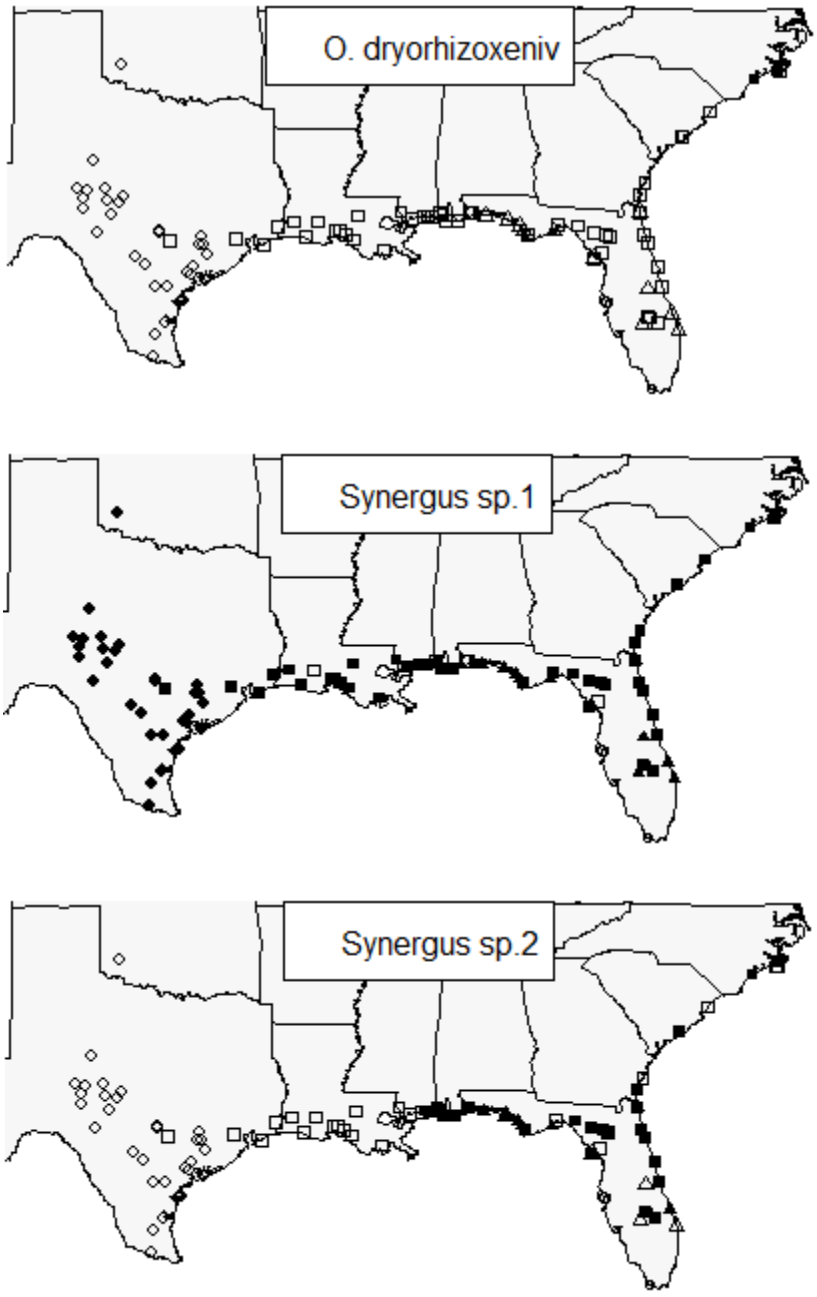



**Figure S2: Range maps for each taxa of NE on 3 live oak species.** Each map represents if the labeled taxa was present (black filled shapes) or absent (hollow shapes). The different shapes represent the host plant the individuals were reared from. Diamond circles are *Qf*, squares are *Qv*, and triangles are *Qg* host plants. The ranges for each taxa may not be their exclusive range since they may be associated with other gallers thus extending their respective ranges. These ranges are their ranges within the 3 live oak species within the clade *Virentes* across the geographic range of the host plants in the U.S.

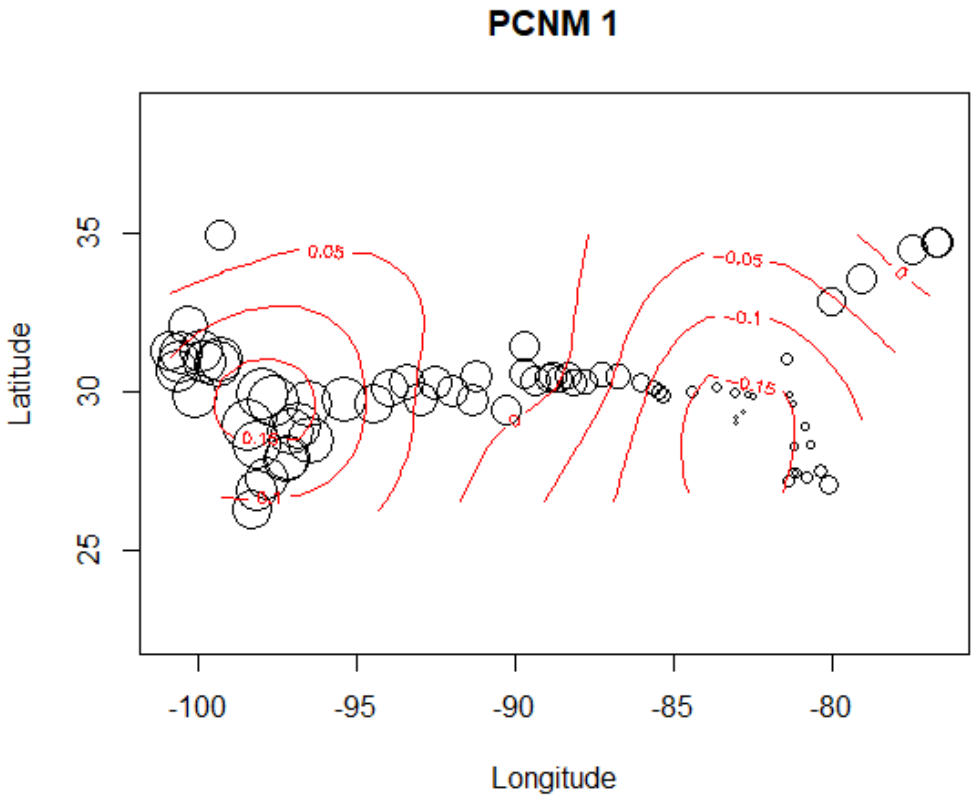
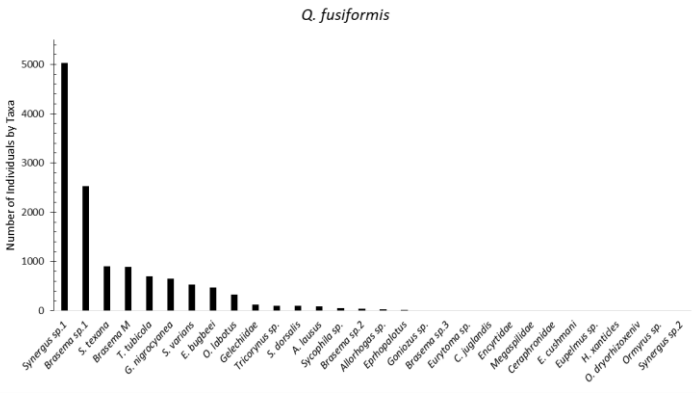
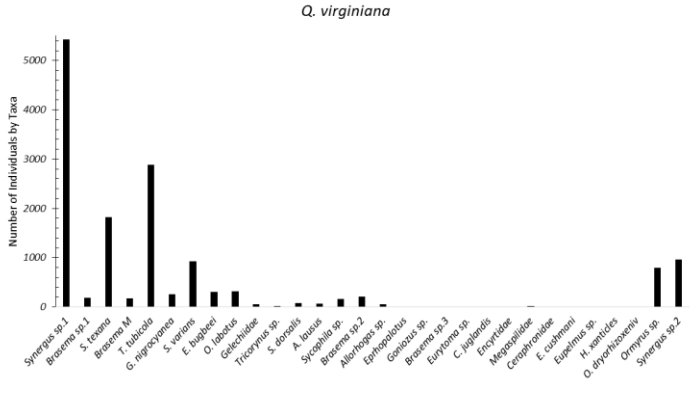



**Figure S3: Ordisurf plot of PCNM 1 axis.** Bubbles represent site locations and the size of the bubbles indicate degrees of spatial autocorrelation. The plot shows a divide in the middle of the range at the Mississippi River creating an west to east division with values to the west of the divide are positively spatially autocorrelated and values east are negatively autocorrelated.

a.




b.




c.

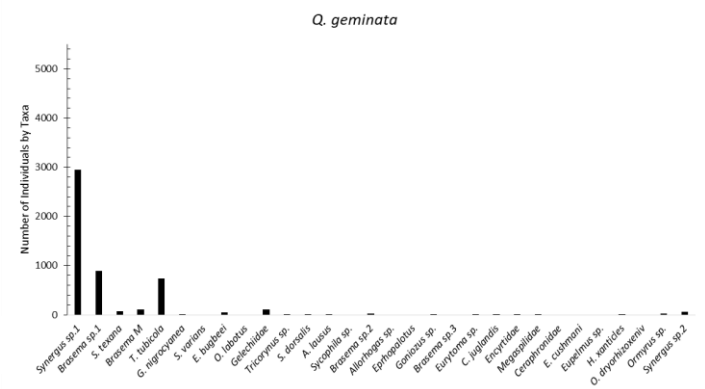
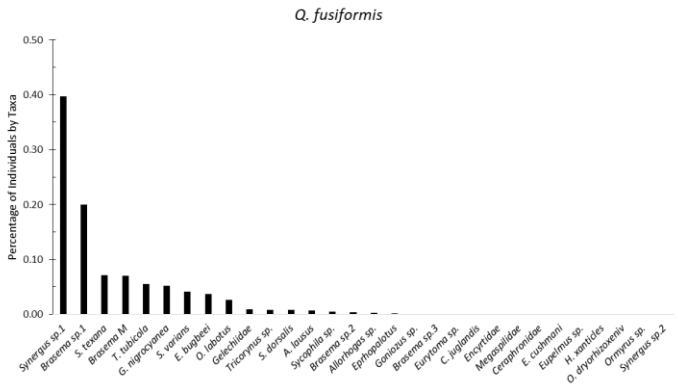
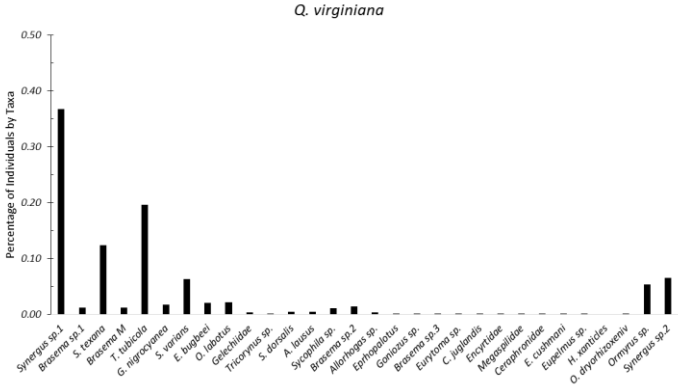



**Figure S4: Relative abundance of insect natural enemies associated with leaf galls housing the asexual generation of the Cynipid, *B. treatae* for each of three species of Live oak.** Bar graphs shows the total number of individuals reared for each taxa summed across sample sites within each of the three host plant species: *Qf* = 23, *Qv* = 42; and *Qg* = 9 sites, respectively. See Table 1 for rare taxa whose abundance was so low as to not be visible in this graph. Note that the order of species in Fig 2b and 2c follow that shown in Fig 2a to facilitate comparison of the abundance of taxa across the host plant species.

a.




b.




c.

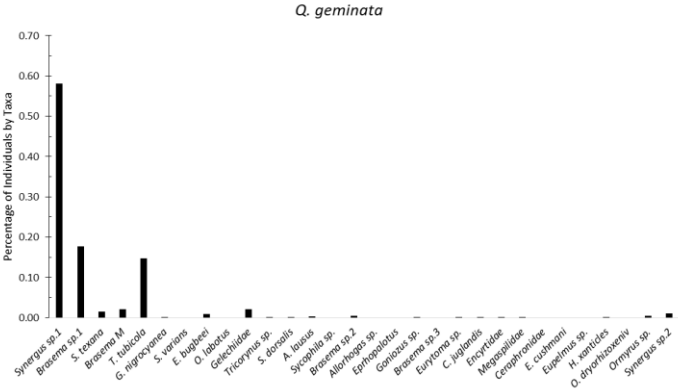



**Figure S5: Relative abundance of insect natural enemies associated with leaf galls housing the asexual generation of the Cynipid, *B. treatae* for each of three species of Live oak.** Bar graphs shows the relative abundance in percent (i.e. the number of NE $taxa_i$ relative to the total number of individual across all NE reared from all sites (*Qf* = 23, *Qv* = 42; and *Qg* = 9 sites, respectively) for each of the three host plants. See Table 1 for rare taxa whose abundance was so low as to not be visible in this graph. Note that the order of species in Fig 2b and 2c follow that shown in Fig 2a to facilitate comparison of the abundance of taxa across the host plant species.

## REFERENCES


Askew, R. R. (1961). On the biology of the inhabitants of oak galls of Cynipidae (Hymenoptera) in Britain. *Trans Soc Bri Entomol*, *14*, 237-268.

Askew, R. R. (1980). The diversity of insect communities in leafmines and plant galls. *The Journal of Animal Ecology*, 817-829.

Askew, R. R. (1984). Biology of gall wasps. *Biology of gall insects/editor TN Ananthakrishnan*.

Blanchet, F. G., Legendre, P., & Borcard, D. (2008). Forward selection of explanatory variables. *Ecology*, *89*(9), 2623-2632.

Borcard, D., & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of principal coordinates of neighbmy matrices. *Ecological Modelling*, *153*(1-2), 51-68.

Borcard, D., Legendre, P., Avois-Jacquet, C., & Tuomisto, H. (2004). Dissecting the spatial structure of ecological data at multiple scales. *Ecology*, *85*(7), 1826-1832.

Boyce, M. S., & McDonald, L. L. (1999). Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution*, *14*(7), 268-272.

Cavender-Bares, J., & Pahlich, A. (2009). Molecular, morphological, and ecological niche differentiation of sympatric sister oak species, Quercus virginiana and Q. geminata (Fagaceae). *American Journal of Botany*, *96*(9), 1690-1702.

Cavender-Bares, J., Gonzalez-Rodriguez, A., Pahlich, A., Koehler, K., & Deacon, N. (2011). Phylogeography and climatic niche evolution in live oaks (Quercus series Virentes) from the tropics to the temperate zone. *Journal of Biogeography*, *38*(5), 962-981.

Cavender-Bares, J., González-Rodríguez, A., Eaton, D. A., Hipp, A. A., Beulke, A., & Manos, P. S. (2015). Phylogeny and biogeography of the American live oaks (Quercus subsection Virentes): a genomic and population genetics approach. *Molecular Ecology*, *24*(14), 3668-3687.

Cornell, H. V., & Washburn, J. O. (1979). EVOLUTION OF THE RICHNESS-AREA CORRELATION FOR CYNIPID GALL WASPS ON OAK TREES: A COMPARISON OF TWO GEOGRAPHIC AREAS. *Evolution*, *33*(1Part2), 257-274.

Cornell, H. V. (1985). Local and regional richness of cynipine gall wasps on California oaks. Ecology, 66(4), 1247-1260.

Cornell, H. V., & Lawton, J. H. (1992). Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of animal ecology*, 1-12.

Crozier, R. H. (1977). Evolutionary genetics of the Hymenoptera. *Annual review of entomology*, *22*(1), 263-288.

Dray, S., Legendre, P., & Peres-Neto, P. R. (2006). Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbmy matrices (PCNM). *ecological modelling*, *196*(3-4), 483-493.

Egan, S. P., & Ott, J. R. (2007). HOST PLANT QUALITY AND LOCAL ADAPTATION DETERMINE THE DISTRIBUTION OF A GALL-FORMING HERBIVORE. *Ecology*, *88*(11), 2868-2879.

Egan, S. P., Nosil, P., & Funk, D. J. (2008). Selection and genomic differentiation during ecological speciation: isolating the contributions of host association via a comparative genome scan of Neochlamisus bebbianae leaf beetles. *Evolution*, *62*(5), 1162-1181.

Egan, S. P., Hood, G. R., & Ott, J. R. (2011). NATURAL SELECTION ON GALL SIZE: VARIABLE CONTRIBUTIONS OF INDIVIDUAL HOST PLANTS TO POPULATION-WIDE PATTERNS. *Evolution*, *65*(12), 3543-3557.

Egan, S. P., Hood, G. R., Feder, J. L., & Ott, J. R. (2012). Divergent host-plant use promotes reproductive isolation among cynipid gall wasp populations. Biology letters, rsbl20111205.

Egan, S. P., Hood, G. R., DeVela, G., & Ott, J. R. (2013). Parallel patterns of morphological and behavioral variation among host-associated populations of two gall wasp species. *PloS one*, *8*(1), e54690.

Forbes, A. A., Hall, M. C., Lund, J., Hood, G. R., Izen, R., Egan, S. P., & Ott, J. R. (2015). Parasitoids, hyperparasitoids, and inquilines associated with the sexual and asexual generations of the gall former, Belonocnema treatae (Hymenoptera: Cynipidae). *Annals of the Entomological Society of America*, *109*(1), 49-63.

Funk, D. J. (1998). Isolating a role for natural selection in speciation: host adaptation and sexual isolation in Neochlamisus bebbianae leaf beetles. *Evolution*, *52*(6), 1744-1759.

Hall, C. 2001. Community structure of parasitoids attacking leaf galls of *Belonocnema treatae* on *Quercus fusiformis*. Thesis. Texas State University, San Marcos, Texas, USA.

Hayward, A., & Stone, G. N. (2005). Oak gall wasp communities: evolution and ecology. *Basic and Applied Ecology*, *6*(5), 435-443.

Holt, R. D. (1996). Food webs in space: an island biogeographic perspective. In *Food webs* (pp. 313-323). Springer, Boston, MA.

Hood, G. R., & Ott, J. R. (2010). Developmental plasticity and reduced susceptibility to natural enemies following host plant defoliation in a specialized herbivore. *Oecologia*, *162*(3), 673-683.

Isaac, N. J., Mallet, J., & Mace, G. M. (2004). Taxonomic inflation: its influence on macroecology and conservation. *Trends in Ecology & Evolution*, *19*(9), 464-469.

Janz, N., Nylin, S., & Wahlberg, N. (2006). Diversity begets diversity: host expansions and the diversification of plant-feeding insects. *BMC Evolutionary Biology*, *6*(1), 4.

Kemp, J. E., Linder, H. P., & Ellis, A. G. (2017). Beta diversity of herbivorous insects is coupled to high species and phylogenetic turnover of plant communities across short spatial scales in the Cape Floristic Region. *Journal of Biogeography*, *44*(8), 1813-1823.

Kruess, A., & Tscharntke, T. (1994). Habitat fragmentation, species loss, and biological control. *Science*, *264*(5165), 1581-1584.

Kruess, A. (2003). Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. *Ecography*, *26*(3), 283-290.

Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Bongers, F., & Poorter, L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology*, *91*(2), 386-398.

Legendre, P., & Fortin, M. J. (1989). Spatial pattern and ecological analysis. *Vegetatio*, *80*(2), 107-138.

Legendre, P. (1993). Spatial autocorrelation: trouble or new paradigm?. *Ecology*, *74*(6), 1659-1673.

Legendre, P., & Cáceres, M. (2013). Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology letters*, *16*(8), 951-963.

Legendre, P., Fortin, M. J., & Borcard, D. (2015). Should the Mantel test be used in spatial analysis?. *Methods in Ecology and Evolution*, *6*(11), 1239-1247.

Lund, J. N. 1998. The biology and ecology of *Belonocnema treatae* (Hymenoptera: Cynipidae) on its host plant, *Quercus fusiformis*. Thesis. Texas State University, San Marcos, Texas, USA.

Lund, J. N., Ott, J. R., & Lyon, R. J. (1998). Heterogony in Belenocnema treatae Mayr (Hymenoptera: Cynipidae). PROCEEDINGS-ENTOMOLOGICAL SOCIETY OF WASHINGTON, 100, 755-763.

MacArthur, R. H. 1972. Geographical ecology. Harper & Row, New York.

Malyshev, S. I. (1968). Genesis of the Lower Hymenoptera (Phytophaga). In *Genesis of the Hymenoptera and the phases of their evolution* (pp. 10-25). Springer, Boston, MA.

Mayr, G. (1881). Die Genera der gallenbewohnenden Cynipiden.–20. *Jahresb. Rossauer Communal-Oberealschule, Wien, Bezirke d*, *1*(20), 1-38.

McMurdie, P. J., & Holmes, S. (2014). Waste not, want not: why rarefying microbiome data is inadmissible. PLoS computational biology, 10(4), e1003531.

Melika, G., & Abrahamson, W. G. (2002). Review of the world genera of oak cynipid wasps. *Parasitic wasps: evolution, systematics, biodiversity and biological control. Agroinform, Budapest*, 150-190.

Miller, D. G., Ivey, C. T., & Shedd, J. D. (2009). Support for the microenvironment hypothesis for adaptive value of gall induction in the California gall wasp, Andricus quercuscalifornicus. *Entomologia Experimentalis et Applicata*, *132*(2), 126-133.

Muller, C. H. (1961). The live oaks of the series Virentes. *American Midland Naturalist*, 17-39.

Nixon, K. C. (2006). Global and neotropical distribution and diversity of oak (genus Quercus) and oak forests. In *Ecology and conservation of neotropical montane oak forests* (pp. 3-13). Springer, Berlin, Heidelberg.

Nosil, P., Egan, S. P., & Funk, D. J. (2008). Heterogeneous genomic differentiation between walking-stick ecotypes:"isolation by adaptation" and multiple roles for divergent selection. *Evolution*, *62*(2), 316-336.

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer research*, *27*(2 Part 1), 209-220.

Peres-Neto, P. R., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, *87*(10), 2614-2625.

Peterson, D. L., & Parker, V. T. (1998). *Ecological scale: theory and applications*. Columbia University Press.

Price, P. W., Bouton, C. E., Gross, P., McPheron, B. A., Thompson, J. N., & Weis, A. E. (1980). Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual review of Ecology and Systematics*, *11*(1), 41-65.

Pujade-Villar J, Bellido D, Segu G, Melika G. 1999, Current state of knowledge of heterogony in Cynipidae (Hymenoptera, Cynipoidea). *Ses. Entomol*. 11: 85-105.

Quicke, D. L. (1997). *Parasitic wasps*. Chapman & Hall Ltd.

Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology letters*, *8*(2), 224-239.

Sokal, R. R. (1979). Testing statistical significance of geographic variation patterns. *Systematic Zoology*, *28*(2), 227-232.

Stireman III, J. O., Nason, J. D., & Heard, S. B. (2005). Host-associated genetic differentiation in phytophagous insects: general phenomenon or isolated exceptions? Evidence from a goldenrod-insect community. *Evolution*, *59*(12), 2573-2587.

Stone, G. N., Schönrogge, K., Atkinson, R. J., Bellido, D., & Pujade-Villar, J. (2002). The population biology of oak gall wasps (Hymenoptera: Cynipidae). *Annual review of entomology*, *47*(1), 633-668.

Tooker, J. F., & De Moraes, C. M. (2008). Gall insects and indirect plant defenses: A case of active manipulation?. *Plant signaling & behavior*, *3*(7), 503-504.

Tuomisto, H. (2010). A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography*, *33*(1), 23-45.

Willis, J. C. (1922). *Age and area*. The University Press; Cambridge.