

ORIGINAL ARTICLE

Population ecology and spatial synchrony in the abundance of leaf gall wasps within and among populations of valley oak (*Quercus lobata*)

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Abstract

What factors drive population variability through space and time? Here we assess patterns of abundance of seven species of gall wasps in three genera occurring on the leaves of valley oaks (*Quercus lobata*) at 10 sites throughout this species' statewide range in California, from 2000 to 2006. Our primary goals were to understand the factors driving variability in gall abundance and to assess the extent of spatial synchrony in gall wasp communities at both large and small geographic scales. On the large, statewide scale, there was significant site-to-site variation in gall abundance, driven in all cases primarily by differences in mean maximum seasonal temperatures, and lesser year-to-year variation. In contrast, on the small, local scale, differences were more pronounced from year to year than from tree to tree, and were to some extent correlated with differences in acorn production, suggesting an interaction with the reproductive effort of hosts. Significant spatial synchrony was detected, particularly at the statewide scale, but in no case did synchrony decline significantly with distance, despite sites being up to 741 km apart. Variation in spatial synchrony was correlated with a number of exogenous factors, including seasonal weather conditions, the acorn crop at the statewide scale and soil phosphorus availability at the local scale; however, most variation in spatial synchrony in our analyses remained unexplained.

KEYWORDS

Andricus, *Antron*, gall wasps, *Neuroterus*, *Quercus lobata*

1 | INTRODUCTION

Study of patterns of variation in populations of related species through space and time is a central focus of ecology, having motivated population studies for over a century. Nonetheless, for most taxa, we lack a predictive understanding of the drivers of population fluctuations. Nowhere is this lack of knowledge more prevalent than among insects, whose vast diversity and abundance offers a wide range of opportunities to study and test ecological principles.

Among the many insect taxa providing excellent opportunities for studying ecological questions are gall wasps (Hymenoptera: Cynipidae). Gall wasps are common and widespread throughout the world, with approximately 1,000 known species in 41 genera, the majority of which occur on oaks in the Northern Hemisphere (Ronquist, 1999). Gall wasps specialize on virtually all plant parts including stems, leaves, roots, inflorescences and fruits (acorns) (Askew, 1961; Stone, Schonrogge, Atkinson, Bellido, & Pufade-Villar, 2002), with each species producing a gall unique in its structure and

physiology such that they can be used to identify the galling taxon even in the absence of the insect itself (Shorthouse, Wool, & Raman, 2005). With such a broad range and diversity, it is unsurprising that numerous studies have used this taxon to test ecological and evolutionary questions (Cornell & Washburn, 1979; Joseph, Gentles, & Pearse, 2011; Price, Abrahamson, Hunter, & Melika, 2004; Ronquist & Liljeblad, 2001). Nonetheless, in contrast to the considerable amount of work done on galling insects in the Neotropics (Fernandes & Santos, 2014; Santos de Araújo, Scareli-Santos, Guilherme, & Cuevas-Reyes, 2013), relatively less is known concerning the drivers of variation in gall wasp abundance or of the importance of competition, weather or other factors in structuring gall wasp communities in temperate regions (Hayward & Stone, 2005). This is particularly true in the case of spatial synchrony—the extent to which population dynamics, including growth rate, phenology and reproduction are synchronized over space and time (Liebhold, Koenig, & Bjørnstad, 2004; Royama, 1992).

A deeper understanding of the spatiotemporal variation in gall wasp abundance may give insights into long-standing theories about plant–insect interactions. First, the plant vigor hypothesis states that herbivores will tend to attack healthy and fast-growing plant tissues (Price, 1991), and this hypothesis has been particularly relevant to explaining the abundance of galling insects (Cornelissen, Wilson Fernandes, & Vasconcellos-Neto, 2008). The plant vigor hypothesis predicts that the abundance of gall wasps should be greater on trees growing in more resource rich environments, such as high nutrients and high water availability, and in years in which trees have high growth potential, such as wet years and years in which resources are not depleted by mast acorn production. Second, it has long been known that the

abundance of herbivores varies considerably over time due to density-dependent processes, such as the build-up of parasites and predators, as well as density-independent processes, such as mortality due to weather events (Turchin, Lorio Jr., Taylor, & Billings, 1991). Each of these processes may be important to the population dynamics of gall wasps. Gall wasps can experience high levels of parasitism from a diverse group of parasitoids (Joseph et al., 2011; Schönrogge et al., 2012). Much less is known about the degree to which weather events might cause the variation in gall wasp abundance over time. Finally, there is ongoing interest in the degree to which plant resistance to herbivores is heritable and follows gross genetic differences between plant individuals (Fritz & Simms, 1992), and this topic has received considerable attention in oak interactions with specialist herbivores (Pearse, Baty, Herrmann, Sage, & Koenig, 2015). Evidence for genetic determination of gall wasp communities would come from more similar and temporally synchronous gall communities on more related oak trees.

We quantified gall wasp populations occurring on the leaves of valley oak (*Quercus lobata* Née) over a 7-year period across the statewide range of this species in California, with the goal of gaining insight into the ecological factors driving variability of galls through space and time. Specifically, we address the following questions: (a) In what ways and to what extent do total gall mass, abundance and species richness vary within or among years and study locations? (b) What exogenous variables correlate with gall mass, abundance and species richness over time? (c) What is the pattern of spatial synchrony in gall mass, abundance and species richness within and among sites? and (d) What exogenous variables correlate with spatial synchrony of total gall mass, total gall abundance and species richness? We investigated the effect of

TABLE 1 Analysis of variance testing differences in mean site gall abundance across years and sites at the statewide scale, 2000–2006

Dependent variable	Mean square			F-value		p-value	
	Year (df = 6)	Site (df = 9)	Residuals (df = 53)	Year	Site	Year	Site
<i>Andricus kingi</i>	0.08×10^{-2}	1.43×10^{-2}	0.09×10^{-2}	0.97	16.69	.45	<.001
<i>Andricus parmula</i>	1.19×10^{-7}	4.14×10^{-7}	1.03×10^{-7}	1.16	4.03	.34	<.001
<i>Andricus confertus</i>	2.20×10^{-5}	2.47×10^{-5}	0.78×10^{-5}	2.81	3.15	.02	.004
<i>Andricus fullawayi</i>	1.99×10^{-7}	6.70×10^{-7}	1.21×10^{-7}	1.65	5.54	.15	<.001
<i>Neuroterus saltatorius</i>	0.38×10^{-5}	1.72×10^{-5}	0.35×10^{-5}	1.08	4.89	.39	<.001
<i>Antron douglasii</i>	0.21×10^{-3}	1.23×10^{-3}	0.09×10^{-3}	2.47	14.22	.03	<.001
<i>Antron clavula</i>	3.27×10^{-7}	2.61×10^{-7}	1.07×10^{-7}	3.05	2.43	.01	.02
Total gall mass	0.17×10^{-2}	2.55×10^{-2}	0.10×10^{-2}	1.76	26.19	.12	<.001
Total N galls	0.71	8.69	0.14	5.04	61.95	<.001	<.001
N gall species	0.54×10^{-1}	2.63×10^{-1}	0.11×10^{-1}	5.00	24.35	<.001	<.001

Note: All values are *ln*-transformed values per gram of dry leaf weight; significant values are in boldface.

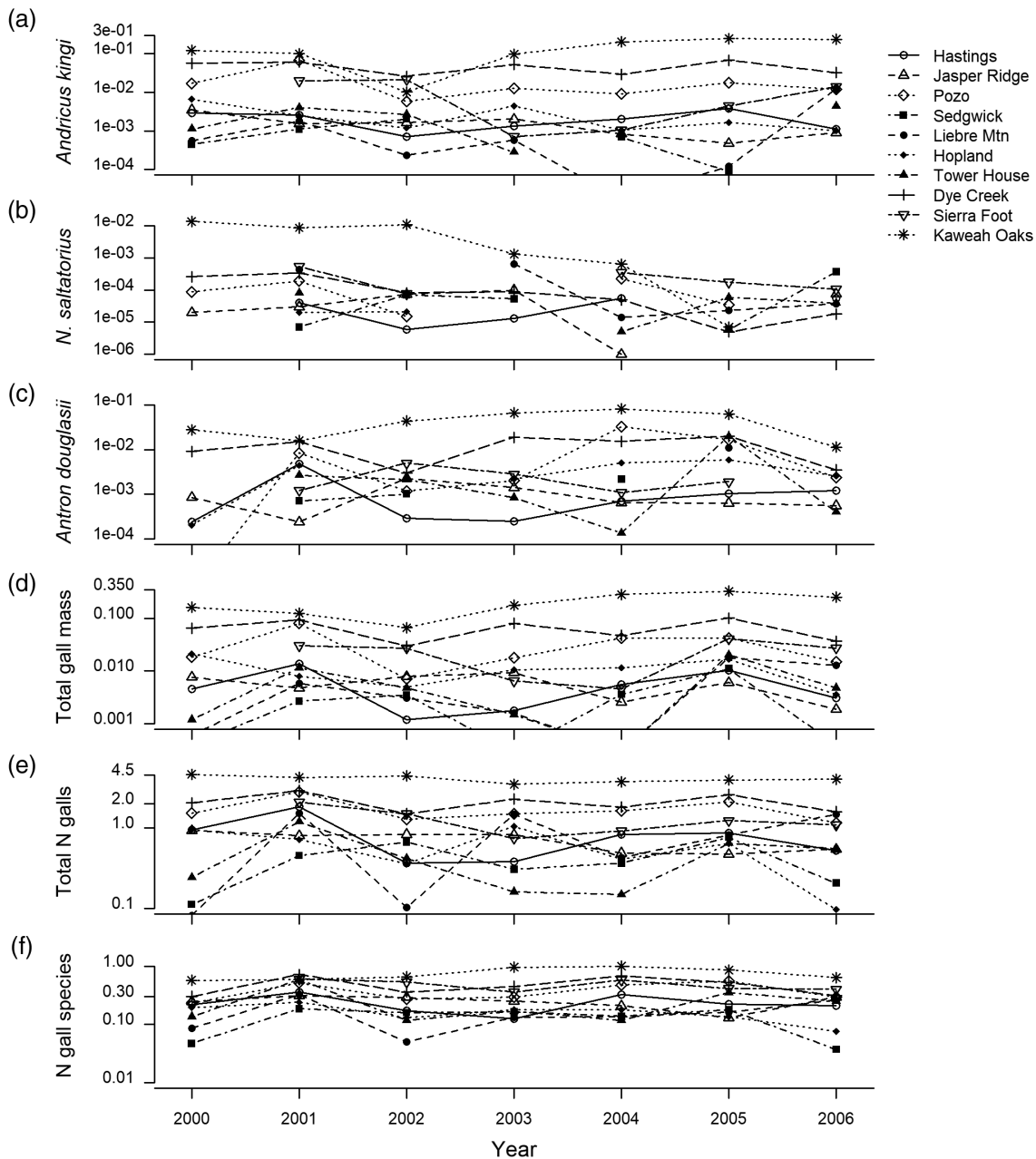


FIGURE 1 Annual means (all *in*-transformed and plotted on a log scale) by site (all per gram of dry leaf mass). (a) *Andricus kingi*; (b) *Neuroterus saltatorius*; (c) *Antron douglasii*; (d) total gall mass; (e) total *N* galls; (f) *N* gall species

geographic scale on each of these processes by conducting analyses at the scale of a single site and at the scale of the statewide range of valley oak.

2 | MATERIALS AND METHODS

Quercus lobata is a deciduous species of white oak (section *Quercus*) endemic to California. Populations of *Q. lobata* can be found throughout much of the state, but the species is most common in the foothills of the coastal and transverse ranges and the Sierra Nevada Mountains

surrounding the Central Valley (Bolsinger, 1988; Griffin & Critchfield, 1972). We conducted analyses at two different spatial scales: (a) an among-population analysis including 10 locations across the geographic range of *Q. lobata* (statewide scale) and (b) a within-population analysis focused on individual trees at Hastings Reservation, which is located near the center of *Q. lobata*'s geographic range (local scale).

Sampling consisted of randomly harvesting leaves from the lower branches of marked trees (20–50 leaves per tree) while conducting acorn surveys at each of 10 sites throughout California (Table S1) during the first

TABLE 2 Results of linear mixed models of environmental variables affecting abundance of *Quercus lobata* leaf galls (all per gram of leaf dry weight) at the statewide scale

Dependent variable	Mean maximum seasonal temperature (<i>df</i> = 60)		Seasonal rainfall (<i>df</i> = 60)		Acorn crop (<i>df</i> = 1,195)	
	Effect size ± <i>SE</i>	<i>t</i> -value (<i>p</i> -value)	Effect size ± <i>SE</i>	<i>t</i> -value (<i>p</i> -value)	Effect size ± <i>SE</i>	<i>t</i> -value (<i>p</i> -value)
<i>Andricus kingi</i> ($\times 10^{-2}$)	3.09 ± 0.45	6.86 (<.001)	-0.18 ± 0.48	-0.38 (.71)	-0.15 ± 0.15	-1.00 (.32)
<i>Andricus parmula</i> ($\times 10^{-5}$)	8.02 ± 3.64	2.20 (.31)	-2.50 ± 3.67	-0.68 (.50)	1.26 ± 1.92	0.65 (.51)
<i>Andricus confertus</i> ($\times 10^{-3}$)	1.08 ± 0.31	3.46 (<.001)	0.06 ± 0.35	0.16 (.87)	-0.06 ± 0.21	-0.29 (.77)
<i>Andricus fullawayi</i> ($\times 10^{-4}$)	1.67 ± 0.37	4.50 (<.001)	-0.25 ± 0.40	-0.62 (.54)	0.13 ± 0.28	0.47 (.64)
<i>Neuroterus saltatorius</i> ($\times 10^{-4}$)	8.75 ± 2.18	4.01 (<.001)	-1.35 ± 2.20	-0.61 (.54)	-1.08 ± 0.53	-2.05 (.04)
<i>Antron douglasii</i> ($\times 10^{-3}$)	7.72 ± 1.21	6.37 (<.001)	-0.56 ± 1.32	-0.42 (.67)	-0.65 ± 0.97	-0.67 (.50)
<i>Antron clavula</i> ($\times 10^{-4}$)	1.24 ± 0.29	4.33 (<.001)	-0.32 ± 0.33	-0.98 (.33)	0.23 ± 0.27	0.84 (.40)
Total gall mass ($\times 10^{-2}$)	4.24 ± 0.57	7.42 (<.001)	-0.44 ± 0.64	-0.70 (.49)	-0.12 ± 0.19	-0.62 (.54)
Total <i>N</i> galls	10.70 ± 1.48	7.22 (<.001)	-0.99 ± 1.50	-0.66 (.51)	-1.03 ± 0.46	-2.23 (.03)
<i>N</i> gall species ($\times 10^{-1}$)	1.29 ± 0.15	8.34 (<.001)	-0.12 ± 0.18	-0.70 (.49)	0.25 ± 0.10	2.43 (.02)

Note: Listed are results from linear mixed models including mean maximum seasonal temperature, seasonal rainfall and the acorn crop of individual trees as fixed effects. In all cases, fixed effects were standardized (mean = 0 and standard deviation = 1) and tree ID within site within year was included as a random effect.

half of September from 2000 to 2006. Galls were identified using Weld (1957) before being removed from leaves, dried in a drying oven and weighed; leaf tissue was also dried and weighed. The number and weight of galls of each species were recorded along with the number of species present in each sample. For statistical analysis, all values were standardized by dividing by the dry weight of all leaves collected from an individual tree.

Seasonal temperature and rainfall (mean maximum temperature and rainfall from April 1 to August 31 of the year samples were collected) were obtained from the PRISM climate group (Oregon State University, Corvallis, Oregon). Acorn crop estimates for the individual trees were obtained via the ongoing California Acorn Survey (Koenig, Knops, Carmen, Stanback, & Mumme, 1994; Koenig, Mumme, Carmen, & Stanback, 1994), in which two observers scanned different parts of the canopy of each tree and counted as many acorns as they could in 15 s. Counts were summed and *ln*-transformed to reduce non-normality. For the analysis of spatial synchrony at the statewide scale, we averaged values across all individuals within each of the 10 sites.

Genetic relatedness among trees was quantified using selectively neutral markers. For the statewide analysis, we used eight microsatellite loci derived from 14–26 individual trees located at each site. For the local-scale analysis of Hastings Reservation, we used six of these microsatellite loci derived from 61 trees. Further details can be found in Abraham, Zaya, Koenig, and

Ashley (2011) and Ashley, Abraham, Backs, and Koenig (2015).

Additional data for individual trees were available for our local-scale analysis. These included estimates of predawn xylem water potential (XWP) measured using a pressure bomb in September 1991 (Barringer, Koenig, & Knops, 2013; Knops & Koenig, 1994) and soil nitrogen and phosphorus availability estimated using ion-exchange resin bags placed under each tree between October 1992 and April 1993 (Knops & Koenig, 1997). Although our estimates of these factors did not overlap the time period of the study, additional work on XWP indicates that this factor, at least, represents differences among trees that are concordant among years (Knops & Koenig, 2000), and thus relevant to the time period considered here.

All statistical analyses were conducted in R 3.3.1 (Development Core Team, 2016). Analysis of variance (procedure “ANOVA”) was used to quantify variability in abundance of galls (*ln*-transformed) in space and time at both the statewide and local scales. Also at both geographic scales, we used linear mixed models to analyze the relationship between gall abundance and environmental factors including mean maximum seasonal temperature, seasonal precipitation, and the acorn crop of the trees. Interaction effects were not included in the models. Significance was set at $p < .05$.

For analyses of variation in and the environmental factors influencing population-level abundance, we analyzed seven of the most abundant species divided among

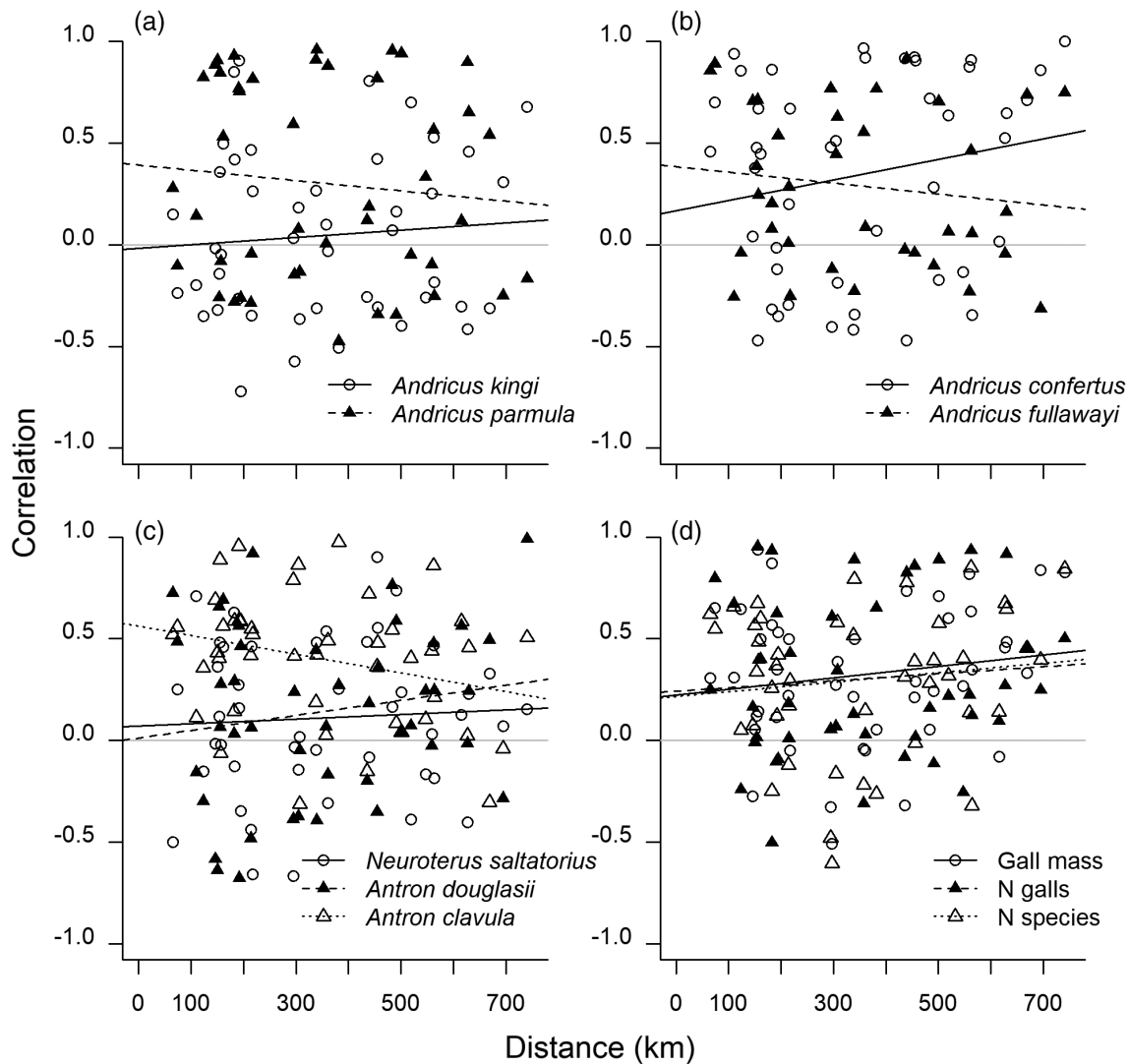


FIGURE 2 Spatial synchrony of gall abundance and species diversity at the statewide scale. (a) *Andricus kingi* and *Andricus parmula*; (b) *Andricus confertus* and *Andricus fullawayi*; (c) *Neuroterus saltatorius*, *Antron douglasii* and *Antron clavula*; (d) Total gall mass, total *N* galls and *N* gall species. Individual values are plotted and regression lines drawn; for reference, gray solid lines are drawn at zero (no spatial synchrony). For statistics, see Table 3

three genera: *Andricus kingi*, *Andricus parmula*, *Andricus confertus*, *Andricus fullawayi*, *Neuroterus saltatorius*, *Antron douglasii* and *Antron clavula*. For analysis of spatial synchrony at the within-site, local scale, only *Andricus kingi* was sufficiently common to warrant analysis. A complete list of species identified and their raw abundance by year is provided in Table S2. More details are available from the authors on request.

In addition to the analyses of individual species, we conducted analyses of three community-level variables: the total dry mass of galls, the total number of galls and the number of gall species (species richness) in the samples. Unidentified galls were excluded from this last analysis. In all cases, we divided the dependent variables (both mass of individual species and the community-level

variables) by leaf dry mass to control for differences in samples and then standardized values to a mean of zero and standard deviation of one. In order to reduce pseudoreplication and focus the analyses on differences among sites and trees, “tree ID within location within year” was treated as a random effect in the statewide-level models, whereas “tree ID within year” was included as a random effect in the local-level models.

At its most basic level, analysis of spatial synchrony involves calculating pairwise correlations of annual values between individuals or sites. Spatial synchrony at the statewide scale, where data were combined within each of the 10 sites, was quantified using the modified correlogram method (Koenig & Knops, 1998). Sample sizes at the within-site individual tree level were

TABLE 3 Overall spatial synchrony in gall abundance and species diversity (mean r value \pm standard error [SE]), MRM coefficients and percent of variance explained attributable to different variables at the statewide scale

Species/ variable	Mean \pm SE spatial synchrony (r)	Proximity	Seasonal temperature	Seasonal rainfall	Acorn crop	Pairwise genetic relatedness	Percent of variance explained
<i>Andricus kingi</i>	0.04 \pm 0.13	-0.20	0.03	-0.15	-0.04	0.28	9.5
<i>Andricus parmula</i>	0.30 \pm 0.15*	-0.04	0.31*	-0.32*	-1.02***	-0.32	41.8**
<i>Andricus confertus</i>	0.35 \pm 0.16*	-0.20	0.11	0.09	0.14	0.21	6.6
<i>Andricus fullawayi</i>	0.29 \pm 0.15*	-0.27	0.26	-0.38	-0.13	-0.19	15.4
<i>Neuroterus saltatorius</i>	0.11 \pm 0.13	-0.08	0.10	0.08	0.20	-0.19	6.5
<i>Antron douglasii</i>	0.14 \pm 0.14	0.16	0.12	-0.28*	-0.23	0.29	17.4
<i>Antron clavula</i>	0.40 \pm 0.10***	0.44	0.12	0.33	-0.54	-0.13	18.7
Total gall mass	0.32 \pm 0.10***	-0.04	0.05	-0.23	-0.10	0.28	12.7
Total N galls	0.30 \pm 0.11**	0.01	0.08	-0.18	-0.04	0.33	12.9
N gall species	0.30 \pm 0.10**	-0.01	0.37**	-0.32*	-0.54	0.20	32.8**

Note: $N = 10$ sites (45 pairwise correlations) up to 741 km apart; mean r values tested by randomizations. Significant values are in boldface. MRM analyses based on models including all factors simultaneously. * $p < .05$; ** $p < .01$; *** $p < .001$; other $p > .05$. Abbreviation: MRM, multiple regression on distance matrices.

TABLE 4 Analysis of variance testing differences in mean site gall abundance across years and individual trees at the local scale, 2000–2006

Dependent variable	Mean square			F value		p-value	
	Year (df = 6)	Tree (df = 77)	Residuals (df = 356)	Year	Tree	Year	Tree
<i>Andricus kingi</i>	4.01×10^{-3}	0.87×10^{-3}	0.60×10^{-3}	6.65	1.45	<.001	.014
<i>Andricus parmula</i>	4.38×10^{-5}	0.40×10^{-5}	0.39×10^{-5}	11.06	1.02	<.001	.42
<i>Andricus confertus</i>	0.98×10^{-3}	1.17×10^{-3}	0.30×10^{-3}	3.29	3.91	.004	<.001
<i>Andricus fullawayi</i>	2.31×10^{-5}	0.53×10^{-5}	0.50×10^{-5}	4.62	1.05	<.001	.38
<i>Neuroterus saltatorius</i>	2.15×10^{-6}	1.36×10^{-6}	1.69×10^{-6}	1.27	0.80	.39	.88
<i>Antron douglasii</i>	2.68×10^{-3}	1.20×10^{-3}	1.09×10^{-3}	2.47	1.11	.024	.27
<i>Antron clavula</i>	3.43×10^{-5}	0.81×10^{-5}	0.84×10^{-5}	4.10	0.97	<.001	.55
Total gall mass	1.23×10^{-3}	0.18×10^{-3}	0.17×10^{-3}	7.42	1.07	<.001	.34
Total N galls	15.00	2.04	0.87	17.27	2.35	<.001	<.001
N gall species	2.33	0.51	0.20	11.57	2.52	<.001	<.001

Note: All values are \ln -transformed values per gram of dry leaf weight; significant values are in boldface.

sufficiently large that we were able to use the *ncf* package (Bjørnstad, 2018). In order to investigate the factors correlating with spatial synchrony, we conducted multiple regression on distance matrices (MRM) analyses (Arnold 2010; Haynes, Bjørnstad, Allstadt, & Liebhold, 2013;

Lichstein, 2007; Manly, 1986) carried out using the *ecodist* package (Goslee & Urban, 2007). MRM analyses explain variation in spatial synchrony attributable to similarity (or differences) in multiple exogenous factors. In our analyses, all variables were similarity matrices

TABLE 5 Results of linear mixed models of environmental variables affecting abundance of *Quercus lobata* leaf galls (all per gram of leaf dry weight) at the local scale

Dependent variable	Mean maximum seasonal temperature (<i>df</i> = 4)		Seasonal rainfall (<i>df</i> = 4)		Acorn crop (<i>df</i> = 432)	
	Effect size ± <i>SE</i>	<i>t</i> -value (<i>p</i> -value)	Effect size ± <i>SE</i>	<i>t</i> -value (<i>p</i> -value)	Effect size ± <i>SE</i>	<i>t</i> -value (<i>p</i> -value)
<i>Andricus kingi</i> ($\times 10^{-3}$)	1.26 ± 0.91	1.39 (.24)	1.12 ± 0.95	1.19 (.30)	0.37 ± 0.28	1.30 (.19)
<i>Andricus parmula</i> ($\times 10^{-4}$)	0.91 ± 1.26	0.72 (.51)	0.60 ± 1.30	0.46 (.67)	0.59 ± 0.25	2.30 (.02)
<i>Andricus confertus</i> ($\times 10^{-4}$)	-1.72 ± 7.32	-0.23 (.83)	-6.85 ± 7.62	-0.90 (.42)	-4.57 ± 2.27	-2.07 (.04)
<i>Andricus fullawayi</i> ($\times 10^{-5}$)	7.04 ± 7.53	-0.94 (.40)	0.79 ± 7.85	0.10 (.93)	0.36 ± 2.49	0.14 (.89)
<i>Neuroterus saltatorius</i> ($\times 10^{-5}$)	-2.05 ± 2.26	-0.91 (.41)	-1.75 ± 2.40	-0.73 (.51)	-0.01 ± 1.00	-0.04 (.97)
<i>Antron douglasii</i> ($\times 10^{-3}$)	0.95 ± 1.69	0.56 (.60)	1.09 ± 1.76	0.62 (.57)	0.78 ± 0.52	1.50 (.13)
<i>Antron clavula</i> ($\times 10^{-4}$)	0.28 ± 1.09	0.25 (.81)	-0.17 ± 1.14	-0.15 (.89)	0.45 ± 0.35	1.30 (.19)
Total gall mass ($\times 10^{-3}$)	3.48 ± 4.06	0.86 (.44)	2.20 ± 4.18	0.53 (.63)	0.27 ± 0.94	0.29 (.77)
Total N galls	1.09 ± 1.30	0.86 (.45)	0.48 ± 1.37	0.35 (.74)	-0.17 ± 0.50	-0.33 (.74)
N gall species ($\times 10^{-2}$)	1.84 ± 7.26	0.25 (.81)	-0.92 ± 7.47	-0.12 (.91)	3.23 ± 1.61	2.00 (.04)

Note: In all cases, the fixed effects were standardized (mean = 0 and standard deviation = 1) and *tree ID within year* was included as a random effect. Significant values are in boldface.

(transformed when necessary), so positive effects translated into positive correlations between the exogenous factors and variation in spatial synchrony.

We determined the pairwise Euclidean distances (proximity) among sites for the statewide analysis and among individual trees for the Hastings Reservation data. We then conducted two sets of analyses. For the statewide analysis, we calculated MRM coefficients and the percent of variance in gall abundance and species richness explained by seasonal temperature, seasonal rainfall, acorn crop and genetic differentiation of trees among sites based on the *F*-statistic analogue D_{Jost} (Jost, 2008). For the Hastings Reservation data, we calculated MRM coefficients and the percent of variance in gall abundance and species richness explained by the mean April temperature, mean annual temperature, acorn crop, XWP, soil nitrogen and phosphorus, and our estimate of the pairwise genetic relatedness between trees.

3 | RESULTS

3.1 | Statewide scale

3.1.1 | Gall abundance and species richness

At the statewide scale, abundance of all species and variables varied significantly among sites, whereas abundance of three of the seven species, the total number of galls and gall species richness varied significantly among

years (Table 1; Figure 1). In the analyses investigating the ecological factors correlating with abundance, mean maximum seasonal temperature was significant in all cases (Table 2; Figure S1). The only other ecological variable that was significant in any of the analyses was the mean acorn crop of host trees, which correlated significantly and negatively with abundance of *Neuroterus saltatorius* and the total number of galls, and positively with gall species richness (Table 2; Figure S1).

3.1.2 | Spatial synchrony

At the statewide scale, we detected significant spatial synchrony in four of the seven species, the total number of galls and gall species richness (Figure 2; Table 3). Based on the nonsignificance of the variable proximity in the MRM analyses, however, spatial synchrony did not decline significantly with distance in any of the analyses (Table 3).

Ecological variables that correlated with variation in spatial synchrony in the MRM analyses included seasonal temperature and/or rainfall (*Andricus parmula*, *Antron douglasii* and gall species richness, all of which correlated positively with seasonal temperature and negatively with rainfall) and the mean acorn crop, which correlated negatively with spatial synchrony of *Andricus parmula* (Table 3). Overall, the ecological variables we included explained a statistically significant 41.8% of variance in spatial synchrony in *Andricus parmula* and 32.8% of variance in spatial synchrony in gall species richness.

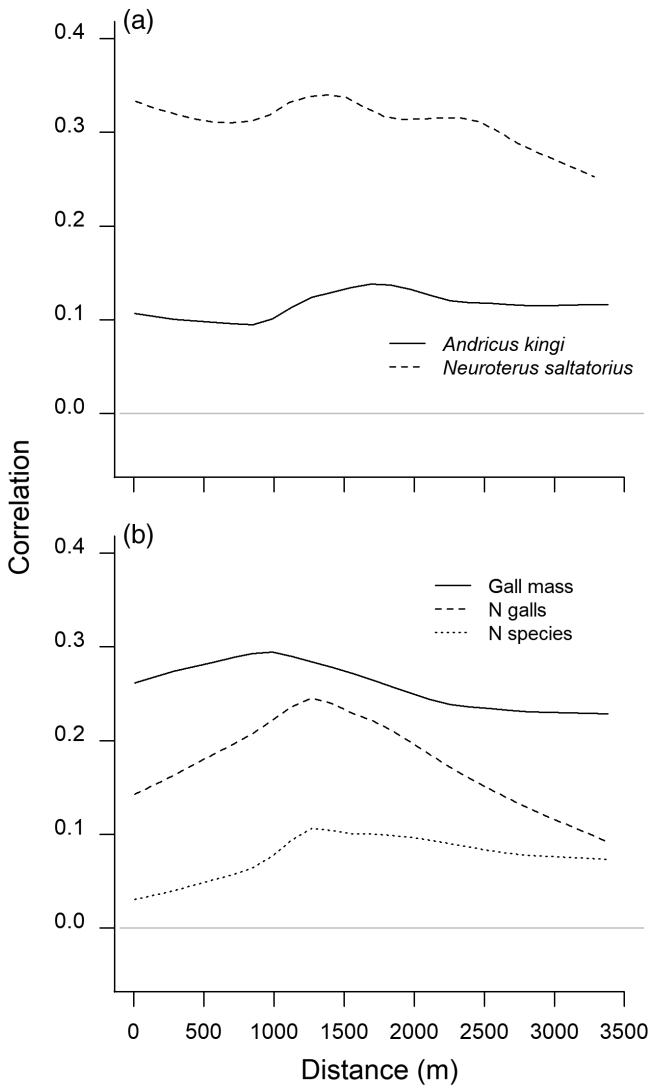


FIGURE 3 Spatial synchrony of gall abundance and species diversity at the local, within-site level. (a) *Andricus* spp., *Neuroterus* spp. and *Antron* spp.; (b) Total gall mass, total N galls and N gall species. For reference, light gray lines are drawn at zero (no spatial synchrony). For statistics, see Table 6

The proportion of variance explained in the other analyses was not significant.

3.2 | Local scale

3.2.1 | Gall abundance and species richness

At the local level, abundance of all but one of the species and all three community variables varied significantly among years, while only two of the species, total number of galls and gall species richness varied significantly among individual trees (Table 4). In the analyses

TABLE 6 Overall spatial synchrony in gall abundance and species diversity (mean *r* value ± standard error [SE]), MRM coefficients and percent of variance explained attributable to different variables at the local level

Variable	Mean ± SE spatial synchrony (<i>r</i>)	Proximity	Mean April temperature	Mean annual temperature	Acorn crop	Xylem water potential	Soil N	Soil P	Pairwise relatedness	Percent of variance explained
<i>Andricus kingi</i>	0.12 ± 0.06*	0.043	-0.186	0.088	0.040	-0.051	-0.156	-0.220	0.028	1.4
Total gall mass	0.27 ± 0.06***	0.004	-0.166	0.228	0.233	-0.086	-0.093	-0.005	0.007	1.5
Total N galls	0.18 ± 0.06**	0.057	0.144	-0.073	0.149	-0.096	0.048	-0.099	-0.047	0.7
N gall species	0.07 ± 0.06	-0.071	0.263	-0.225	0.153	0.088	0.087	0.194*	-0.136	1.4

Note: N = 59 trees (1,711 pairwise correlations) up to 3.38 km apart; mean *r* values tested by randomizations; only the species and variables that could be analyzed by means of the MRM analyses are listed; overall spatial synchrony of the other species (none of which was statistically significant) are listed in Table S3. Significant values are in boldface. MRM analyses based on models including all factors simultaneously. * *p* < .05, ** *p* < .01, *** *p* < .001; other *p* > .05. Abbreviation: MRM, multiple regression on distance matrices.

investigating the ecological factors correlating with abundance, none of the factors was significant in most cases. In two of the species and for gall species richness, however, the acorn crop was significant, positively in the case of *Andricus parmula* and gall species richness and negatively for *Andricus confertus* (Table 5).

Significant spatial synchrony was detected in the local level in two of the seven species along with total gall mass and total number of galls (Figure 3; Table 6). In the MRM analyses, the only variable that was significant in any of the analyses was soil phosphorus content, which had a significant positive correlation with spatial synchrony of gall species richness (Table 6). Overall, the factors we included were able to explain $\leq 1.5\%$ of the variance in spatial synchrony in gall abundance among the individual trees.

4 | DISCUSSION

4.1 | Abundance and diversity

How does gall abundance and species richness vary among sites and across years? Although we found significant variability in gall abundance and diversity both among years and sites at both the statewide and local levels (Tables 1 and 4), variability was generally greater and more widespread among sites at the statewide level and among years at the local level. Thus, at large geographic scales of hundreds of kilometers, there tended to be highly significant differences in gall wasp abundance and communities from place to place, but overall year-to-year differences were relatively small. Conversely, at small geographic scales of a few kilometers, year-to-year differences tended to be greater than differences among individual trees.

What factors correlate with gall abundance and richness? The above results are related, at least in part, to the environmental variables correlating with gall wasp abundance and community composition. The relationship between gall insect abundance and temperature is complex and somewhat contentious (Blanche, 2001; Blanche & Ludwig, 2001; Juliao, Venticinque, Fernandes, & Price, 2014; Veldtman & McGeoch, 2008). However, at the large, statewide scale, mean maximum seasonal temperature was by far the most important variable correlating with gall wasp abundance (Table 2). Other studies have suggested gall wasps are more active and/or more abundant when conditions are warmer (e.g., Fernandes & Price, 1988), and differences in temperature among our study sites appeared to translate into significant site-to-site variation in gall wasp abundance. Such site-to-site variation in weather conditions at this

large geographic scale apparently had a much greater influence on gall wasp abundance than year-to-year variation in weather among the sites.

Of secondary importance in the statewide analyses, including total number of galls and gall species richness, was the acorn crop. Specifically, galls were less numerous but more diverse in years when trees devoted more of their resources to acorn production. This finding is unlikely to be an indirect result of the relationship between temperature on acorn production, since acorn production in *Q. lobata* is positively correlated with seasonal temperatures (Koenig, Knops, Carmen, & Pearse, 2015; Koenig, Mumme, et al., 1994), contrary to what would be predicted given the positive correlation between temperature and gall mass. More likely is that when gall wasps were less numerous, trees had more resources left over for reproduction. Alternatively, trees produced higher-quality leaves more attractive to gall wasp infestation when they were not investing in acorns, a finding requiring a rapid numerical response as demonstrated recently for acorn weevils (*Curculio* spp.) attacking three eastern oak species (Bogdziewicz, Marino, Bonal, Zwolak, & Steele, 2018). The latter interpretation would be consistent with the plant vigor hypothesis (Price, 1991, but see Souza & Fagundes, 2016).

Additional study would clearly be necessary to distinguish between these alternatives. However, consistent with this latter possibility is the finding that valley oaks exhibit significant trade-offs between the energy they invest in reproduction and leaves both within and among years (Barringer et al., 2013), and positive correlations between leaf nutrition and the presence of galls have been found in other systems (Cuevas-Reyes, De Oliveira-Ker, Fernandes, & Bustamante, 2011).

At the local level, few differences among individual trees correlated significantly with gall wasp abundance. In three analyses where a significant result was found, however, among-tree differences correlated with significant differences in the acorn crop of individual trees (Table 5). Consistent with results at the statewide scale, a larger acorn crop correlated with fewer *Andricus confertus* galls but greater gall species diversity. In general, however, there were highly significant differences in gall wasp abundance across years, indicating that at relatively small spatial scales, year-to-year differences in overall environmental conditions had a much greater effect on gall wasp abundance than differences among individual trees (Table 4). The high degree of year-to-year variability in gall wasp abundance that was unrelated to exogenous factors might suggest that endogenous processes, like the interaction between gall wasps and their parasitoids, might be important in the long-term dynamics of gall wasp populations (Turchin et al., 1991).

4.2 | Spatial synchrony

What are the patterns of spatial synchrony? Our analyses suggested significant, but generally low, spatial synchrony in gall abundance of several of the species and in all three community-level variables at the statewide level (Table 3), and in the most abundant species (*Andricus kingi*), total gall mass and the total number of galls at the local level (Table 6). Interestingly, however, spatial synchrony did not decline significantly with distance in any of the analyses either at the local or the statewide levels, a result counter to theoretical expectations (Liebhold et al., 2004), especially given the large geographical scale of the statewide analyses. We are not aware of another organism exhibiting such a distance-independent pattern of spatial synchrony, although the relatively low level of spatial synchrony observed in this taxon clearly makes any distance-related decline more difficult to detect.

What factors correlate with spatial synchrony? At the statewide level, we were able to explain a significant amount of the variation in spatial synchrony based on environmental factors (seasonal temperature and/or rainfall) and, in the case of *Andricus parmula*, the mean acorn crop (Table 3). At the local level, the only significant correlation we found was a positive relationship between soil phosphorus availability and the species diversity of gall wasps (Table 6). Interestingly, this latter result counters the hypothesis that more fertile soils reduce the incidence of gall-forming insects, as has been found in several studies (Blanche & Westoby, 1995; Cuevas-Reyes, Quesada, Siebe, & Oyama, 2004; Cuevas-Reyes, Siebe, Martinez-Ramos, & Oyama, 2003). It is, however, consistent with the expectations of the plant vigor hypothesis that herbivore species feed preferentially on vigorous plants (Price, 1991) and results of gall-inducing insects in the tropical tree *Eremanthus glomerulatus* (Cuevas-Reyes et al., 2011).

We failed to find any evidence that genetic differences among host trees influenced gall wasp abundance or community diversity, despite past studies using zones of hybridization and known introgressed lines of valley oak that have demonstrated complex genetic bases for gall wasp associations (Moorehead, Taper, & Case, 1993; Pearse & Baty, 2012). To the extent this is also true outside of hybrid zones, we would have predicted relatives to produce tissues of similar quality and to have more similar parasite (i.e., gall wasp) loads. The role of genetic relatedness in driving patterns of spatial synchrony clearly warrants further study.

The only previous study of spatial synchrony in this taxon of which we are aware is that of Biedermann (2007), who found that some oak gall-making taxa found on oaks in Germany exhibited synchrony over small

(8 km) spatial scales but that synchrony at the scale of several hundred kilometers was found in only one species, *Neuroterus anthacinus*. In contrast, we found significant, albeit relatively low, spatial synchrony on the scale of 700+ kilometers for four species of galls along with all three community measures, including gall species richness, an index that has not previously been investigated for spatial synchrony.

Most small-scale (within a few kilometers) studies of insects have found relatively high levels of synchrony among populations (Hanski & Woiwod, 1993; Sutcliffe, Thomas, & Moss, 1996; Thomas, 1991), while larger-scale studies (involving distances of tens or hundreds of kilometers) indicate greater variability (Biedermann, 2007; McCullough, 2000; Pollard, 1991; Williams & Liebhold, 2000). Our results found the opposite: in general, spatial synchrony was greater at the statewide scale than at the local scale within a single site a few kilometers in extent.

Broadly speaking, at least three mechanisms can drive spatial synchrony, including dispersal of individuals among populations, synchronized exogenous stochastic effects known as Moran effects, and trophic interactions with other species that are themselves either synchronized or mobile (Bjørnstad, Ims, & Lambin, 1999; Koenig, 1999; Ranta, Kaitala, & Lindstrom, 1999). The relative importance of these processes is not well understood in most cases. Furthermore, the drivers of spatial synchrony may vary depending on the spatial scale being considered (Koenig, Knops, Pesendorfer, Zaya, & Ashley, 2017). For example, stochastic forces such as temperature or rainfall patterns are likely to be more important at larger geographic scales, while dispersal among populations may be more influential at smaller spatial scales (Hanski & Woiwod, 1993; Steen, Ims, & Sonerud, 1996; Sutcliffe et al., 1996). In our case, temperature and rainfall were indeed important drivers of spatial synchrony at the statewide scale, whereas microclimatic differences among trees were not significantly related to spatial synchrony in any of the analyses. In general, however, we were able to explain a significant proportion of variation in spatial synchrony in only a small proportion of analyses at the statewide scale, and in none of the local-level analyses, even where significant spatial synchrony was detected.

Understanding this unexplained variation will likely require a better understanding of gall wasp dispersal and the intrinsic factors that regulate gall wasp populations and communities. For example, dispersal patterns of gall wasps are not well known, although patterns of decreased gall wasp richness on more isolated trees are suggestive of some degree of dispersal limitation even at relatively small spatial scales (Herrmann, Pearse, & Baty, 2012). Likewise, there is considerable evidence that a

diverse suite of hymenopteran parasitoids limit populations of gall wasps (Prior & Hellmann, 2013), but the ability of parasitoids to cause spatial synchrony in gall wasps is unclear. Clearly much work remains to be done on the geography of spatial synchrony in this taxon (Walter et al., 2017).

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AUTHOR CONTRIBUTIONS

The study was conceived and performed by W.D.K. and J.M.H.K. W.D.K. performed the analyses; B.C.B. wrote the initial draft; all authors contributed to framing the paper and helping to revise the manuscript.

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