CHANGING CLIMATES AND THE EVOLUTION OF INSECT HERBIVORY IN WESTERN OAKS

by

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ABSTRACT

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Changing climates and the evolution of insect herbivory in western oaks

Thesis directed by Associate Professor Dena Smith

Studies of insect herbivory in modern ecosystems have shown that climatic shifts can lead to changes in insect feeding behavior. This also has been found to be true for plant communities preserved in the fossil record, but hasn't been examined in a way that takes into account the coevolution of host-herbivore systems. Examining the pattern of feeding in insects that use a restricted group of host plants is important because insects that are highly specialized are thought to have different levels of climatic sensitivity than generalist herbivores. The relative influences of climate and coevolution can only be examined by following specific host taxa and the feeding damage made by their insect herbivores through time.

In this work, I focus on species of oak (*Quercus*) and follow their patterns of leaf herbivory across 25 floras from western North America, with ages ranging from the Eocene to the present. This set of floras captures the evolution of leaf herbivory made by insects across time and through different climatic regimes. I find numerous types of specialized insect damage that recur on the same oak hosts over time, indicating strong specialization and host-fidelity. These results suggest that while there are likely to be effects of climate on herbivory, that the relationship is not a simple one, and that by focusing our studies only at the community level, we miss nuances and risk creating models with limited predictive power.

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DEDICATION

This work is dedicated to my fellow scientist, field assistant and father

David G. Leckey

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INTRODUCTION

Plant-insect interactions represent a dynamic and nuanced system continuously evolving over millions of years (Labandeira et al., 1994; Farrell and Mitter, 1998; Berenbaum, 2001). The diversity and abundance of insects and plants in modern ecosystems is partially a result of their influence on each others' evolutionary histories (Futuyma and Moreno, 1988; Janz et al., 2006), but may also be influenced by climate (Landsberg and Gillieson, 1995; Coley and Barone, 1996; Logan et al., 2003; Adams et al., 2011; Garibaldi et al., 2011). In a world of changing global climates, it is critical to examine these relationships so we can better predict how future plant-insect interactions may be affected (Lewinsohn et al, 2005; Zvereva and Kozlov, 2006; Wolf et al., 2008; Leimu et al., 2012), and understand the consequences for global ecosystems. This understanding may help us identify which ecosystems are most threatened, and which are most in need of further study (Bale et al., 2002).

Fossil insect herbivory is a relatively new field of study, although work on modern plantinsect interactions has a rich history (Ehrlich and Raven, 1964; Farrell and Mitter, 1998; Berenbaum, 2001; Novotny et al., 2006). The discovery and categorization of insect damage on fossil leaves had led to studies seeking to interpret patterns of insect damage on whole floras (*e.g.* Wilf et al., 2001; 2006; Smith, 2008), generally testing whether floras from one climatic type are different from damage on floras from another climatic type. These studies have provided important foundations to establish the importance and validity of fossil floras as a source of information on how plant-insect interactions have evolved. In this dissertation, I use a new approach. Instead of examining broader community-level patterns of insect damage found in whole floras, I focus on the evolutionary history of a specific plant host group to examine how the relationships between insect herbivory and climate develop over time. This allows me to not

only study the effects of climate change, but also gain a greater understanding of how host specialization and coevolutionary history shape plant insect interactions.

To study the evolution of plant-insect interactions, I have focused on oaks and their herbivores. Oaks are an excellent group for this purpose because they are well-preserved and abundant in fossil floras across a wide range of known climatic conditions. Oaks also are host to a variety of insect herbivores in modern system. Oaks are genetically labile, hybridizing easily and changing leaf morphology to fit their climatic situation; they also can adapt their level of chemical defenses to match their environment (Pearse and Hipp, 2012). Yet across time and geography, some of the same herbivores remain faithful to their hosts (Erwin and Schick, 2007; Stone et al., 2009), their damage patterns being found again and again in different Cenozoic floras across the northern hemisphere.

The goal of Chapter 1 is to gain an understanding of the biases that may affect ecological studies that use fossil leaves housed in museum collections. Because museums maintain a wealth of fossil leaves, they are a great data source for large-scale paleoecological studies. However, time limitations of collectors, curatorial constraints of museums, and other potential restrictions may introduce biases that affect our ability to use these collections to study patterns of insect herbivory. In this chapter, I compare insect damage level and feeding guild structure between museum and unbiased field-collected samples. Although taxonomic differences appear, the dominant plants were similar in both samples. Additionally, the field-collected and museum-housed specimens were not significantly different in terms of overall damage patterns and there is little effect of bias on insect-damage patterns. These results are encouraging because they demonstrate that fossil floras housed in natural history collections can be used to examine large-scale leaf-herbivory patterns in deep time.

The goal of Chapter 2 is to understand modern patterns of oak herbivory. Studying modern oaks provides a model for examining the influence of climate on herbivory in this system and allows me to develop a baseline for comparison with fossil data. Chapter 2 analyzes leaf herbivory in four modern oak species from California to examine the relationship between climatic factors (mean annual temperature and precipitation) and oak herbivory levels at multiple scales. In these oaks, temperature and precipitation do not appear to have a significant overall effect on most measures of total herbivore damage, rather the strongest predictor of herbivore damage overall was the identity of the host species. However, increases in precipitation are correlated with an increase in some types of specialized damage indicating that specialist herbivores of oaks may respond differently to climatic variation than generalist herbivores.

Chapter 3 documents the effects of range expansion of highly specialized oak gallwasps on their host taxa across western North America by examining the distinctive leaf galls they induce. Fossil leaf galls are similar to galls made on oaks by modern Cynipini wasps and are present in western floras back to the Oligocene, demonstrating a high degree of host fidelity through time. The distribution of leaf galls occurs in tandem with expansion of their oak hosts across the western United States, which indicates that the radiation of this group of gallwasps occurred more or less simultaneously across a wide geographic area. Also significant is the strength of these relationships, which, once established, continued through to the recent.

Chapter 4, investigates the effects of changing climate and the evolutionary history of oak-herbivore interactions. I examine leaves of oaks whose ages span Eocene to Pliocene (38 to 5 Ma) across a range of mean annual temperature (6.5 to 17.6°C) and average 3-month precipitation levels (9.8 to 78.2 cm) in western North America. Patterns of leaf herbivory in these oaks are used to test whether insect damage on oaks is more intense in floras that grew under

warmer and wetter conditions, and whether specialist and generalist insect herbivores respond similarly to climatic shifts. The results show that neither mean annual temperature nor average precipitation significantly determines insect damage for generalist herbivores, but that both are important predictors of specialist herbivore damage. Additionally, a high degree of host-fidelity through time in gallers and leaf miners, suggests that the interactions between oaks and their insect herbivores are driven strongly by their long-term evolutionary history.

Across western North America for the past 35 million years, fossil oak leaves have recorded a history of insect herbivory. While previous work suggests that temperature and precipitation should have significantly impacted the amount and types of herbivory found on these oaks, the results of this work indicate a more nuanced story. By using floras housed in natural history collections, we can examine broad evolutionary and ecological trends in insect herbivory and compare what we find in the fossil record to modern patterns. Overall herbivory and climate are not always correlated. Strong and sustained host fidelity may be the norm for some insect-herbivore systems. These results from oaks suggest that future climatic change may not affect all host-herbivore systems in the same ways, and instead, we can expect individual host-herbivore systems to have their own individualized responses to shifting climatic conditions.

Future studies should explore the patterns of host use of other Woody Rosid Gallers, beyond the Cynipini, prior to their appearance on oaks to examine whether their host-use is as strongly constrained through time. This study includes some evidence of the beginning of strongly host-constrained relationships, and, based on phylogenetic work in modern rosids (the larger group to which oaks belong), the specialist herbivores of oaks are expected to be phylogenetically similar to specialist herbivores on closely related host-plants (Ronquist and Liljeblad, 2001; Stone et al., 2009). Future work may also investigate whether other strongly

defended host plants (such as the legumes) and their herbivores have insect feeding patterns that are unaffected by climate relative to less strongly defended host plants. Additionally, more work should be done to investigate how other abiotic factors affect herbivory. For example, paleoelevation can be estimated for some floras (McElwain, 2004), and elevation has been demonstrated to affect the size of oak leaves (Qi et al., 2009). Changes in leaf size can affect how patterns of herbivory are interpreted (Chapter 2), and may be correlated with changes that are not easily measured in the fossil record but which may affect insect herbivores, such as differences in leaf chemistry (Erelli et al., 1998) or differences in the predator-pressure that herbivores experience (Reynolds and Crossley, 1997).

<u>CHAPTER 1. FOSSIL PLANTS AND INSECT HERBIVORY: HOW ACCURATELY DO</u> <u>MUSEUM COLLECTIONS PRESERVE ECOLOGICAL PATTERNS?</u>

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ABSTRACT

Fossil floras preserved in natural history collections offer a unique data source for studying insect-feeding damage on leaves across broad spatial and temporal scales. Curatorial constraints of museums, time limitations of collectors and other potential restrictions, however, may introduce biases that affect our ability to use these collections to study patterns of insect herbivory through time. Here we assess the potential biases in a typical museum collection by comparing it to a standardized field collection of leaves from the same source locality. We compare insect damage levels and feeding guild structure and find that overall damage patterns between the field-collected and museum-housed specimens are not significantly different from each other. These results demonstrate that fossil floras housed in natural history collections may be used to examine large-scale leaf-herbivory patterns in deep time.

1. INTRODUCTION

Interactions between plants and insects represent a series of relationships that have been evolving since the Paleozoic (Labandeira and Sepkoski, 1993; Labandeira et al., 1994; Farrell and Mitter, 1998; Berenbaum, 2001; Bethoux et al., 2004; McLoughlin, 2011) and may be influenced by a number of biotic and abiotic factors (Landsberg and Gillieson, 1995; Coley and Barone, 1996; Logan et al., 2003; Adams et al., 2011; Garibaldi et al., 2011). Fossil leaves have been used with great success to study leaf herbivory in past systems (*e.g.* Wilf et al., 2006; Currano et al., 2008; Smith, 2008; Currano et al., 2010) and two common approaches have been used. One is to collect new fossil material, obtaining leaves directly from the strata in which they are preserved. This is often done in floras where a large paleobotanical collection is planned, and insect damage is recorded in the course of collecting plant materials. Some studies have also

made new collections of fossil plants with the primary goal of studying insect herbivory (Smith, 2008; Currano, 2009). Field collections such as these afford the opportunity to examine the insect damage patterns for an entire community and to compare the relative damage levels of different, contemporaneous host plant taxa. However, the time and resources needed to obtain new field collections necessarily limit the number of floras that can be examined and compared.

The second approach to examining insect herbivory in fossil floras is to use previously collection plant fossils that are housed in museums. Museum collections allow a much broader number of floras to be examined in less time. With increased sampling power comes the ability to examine trends at larger spatial and temporal scales, as well as to focus on the herbivory that occurs on specific taxa that are broadly distributed through time. The extent to which these collections represent the same sampling quality as field collected samples, however, is unclear, in particular because they tend not to have been collected with an eye towards inclusion of leaves with insect damage. Generally, paleobotanical collections, especially those made before the late 20th century, were collected with the goal of obtaining the widest diversity of plants possible (S. Wing, pers. comm., 2010).

Systematically excluding damaged or imperfect specimens (*i.e.* high-grading), has been found to affect other types of museum collections including both fossil and modern specimens of other taxa (Donovan 2001; Jeppsson et al., 2010), and this practice could potentially remove insect-damaged leaves from collections and lower apparent rates of herbivory. In this study, we seek to test whether museum collections can be used to study insect herbivory with the level of accuracy expected from newly-collected field samples from which no specimens have been excluded (*i.e.* unbiased). This is accomplished by comparing museum and field collected samples of leaf fossils from the Clarkia flora, Idaho (15.3 Ma). This flora was chosen because of

the quality of preservation of the leaves and the availability of a large museum collection for which specific locations were accessible for re-collection. By collecting a new, unbiased sample of plant fossils from the same locality and horizon as the museum collection, the prevalence of insect herbivory in the two collections can be compared.

In this study we examine the expectation that the museum collected Clarkia flora leaves have been biased by collectors attempting to gain a taxonomically broad and diverse plant sample, and one that maximizes the number of undamaged leaves. A collector bias should result in higher plant diversity in the museum collection relative to an unbiased field sample (Guralnick and VanCleve, 2005). In addition, the museum sample should have fewer leaves with insect damage than the field collection. If the two collections are capturing different host plants, we also expect dissimilarity between the two samples in the types of feeding damage and the distribution of damage on plants due to insect feeding preferences.

To study potential bias in museum collections, we test the following predictions: 1. The proportion of leaves displaying insect-mediated damage will be lower in the museum collection than in the field collection, reflecting a tendency to exclude damaged leaves from the collection; 2. The amount and type of feeding will be significantly different between the collections, reflecting differences in plant host taxa between field and museum collections and the insects that feed on them.

2. MATERIALS AND METHODS

2.1 *Geological setting*

Clarkia Lake is a middle Miocene deposit of fine, silty-claystones from northern Idaho (Figure 1) formed when lava flows of the Columbia River basalts dammed the local St. Maries

River. These fluvio-lacustrine beds preserve plant and animal fossils of exceptional-quality (Smiley and Rember, 1985a; Logan et al., 1995; Lockheart et al., 2000; Otto et al., 2005; McNamara et al., 2012) from which rare ecological data are preserved (Batten et al., 1999; Yang and Huang, 2003). Leaf macrofossils are preserved as carbonaceous compressions, many of which are preserved in overlapping leaf mats, which, along with their excellent preservation, indicates only a small degree of transport (Smiley and Rember, 1985b). The warm-temperate taxa of the Clarkia flora are also found in other Miocene floras of the Pacific Northwest such as the Mascall and Latah floras. The Clarkia flora contains many taxa similar to those currently living in the area, as well as plants of Asia and the southeastern United States (Smiley and Rember, 1985a). Age for the flora is approximately 15.5 Ma based on K/Ar dates from the surrounding volcanics (Schorn et al., 2007).

2.2 Museum sample

The museum collection utilized for this study is housed at the University of Idaho. Collections from multiple localities within the Clarkia flora are available for study. We chose the P37 locality (Figure 1) for its excellent quality of preservation and the availability of the site for recollection, with the assistance of W. Rember, who made most of the identifications for the museum collection. Additionally, the material from this locality represents a "typical" museum collection in that it was collected by numerous professional and amateur paleobotanists over many years. The collectors did not attempt to obtain an unbiased sample, or to collect every leaf encountered; rather, emphasis was placed on obtaining rare taxa and/or exceptionally wellpreserved leaves (W. Rember, pers. comm.).

Of the hundreds of leaf specimens contained in the collection from this locality, we aimed to examine between 150 and 200 dicot leaf specimens, as this number was found to capture the diversity of other Cenozoic floras from similar depositional environments (Burnham, 1994). To obtain our desired number of specimens, we took a subsample by applying a diagonal transect to each drawer of material (drawers are organized taxonomically) and included all specimens that came in contact with our transect. All drawers containing material from the P37 locality were sampled, comprising approximately half of the material in the collection. Drawers generally held between 10–20 leaves, from a single taxon, resulting in samples of between 5–10 sampled leaves per drawer. Some drawers contained specimens from multiple taxa. The taxonomic identity, length, width, and margin-type were recorded for each leaf. Collection of insect herbivory data is described in section 2.4.

2.3 Field sample

New plant specimens were collected on a single day, from the P37 locality, from the same stratigraphic level at which the museum collection was made (Figures 2, 3). Specimens were collected until 200 leaves or partial leaves (all potentially identifiable fragments at least 1 cm^2 in size) were collected, in order to obtain a similar sample size to that taken from the museum collection. Identification of leaves was done in the field at which time the insect herbivory assessment was also made, using the criteria described in section 2.4.



FIGURE 1. Map of Idaho, showing location of Clarkia beds outcrops and position of locality P-37 within the lake boundaries.

FIGURE 2. Field images, 1. Sample site (W. Rember shown obtaining samples), and 2. Claystone unit from which plant samples were obtained





FIGURE 3. Generalized stratigraphy of Clarkia beds, modified and redrawn from Smiley and Rember, 1985b.



2.4 Quantification of herbivory

Insect damage was identified through the presence of reaction tissue (as per Smith, 2008) around missing leaf tissue, and was distinguished from leaf tissue removed by mechanical destruction or decay. Insect damage was quantified in two ways for each leaf: 1) presence or absence of damage; and 2) number of functional feeding groups represented. Many types of insects feed on leaves, and we categorize insect damage into five functional feeding types: hole feeding, margin feeding, skeletonizing, leaf mining and galling, following Smith (2008).

2.5 Statistical analyses

All statistical analyses were performed with the use of JMP, Version 8 (SAS Institute, 1989–2012) with the exception of rarefaction curves, which were generated using Ecosim (Gotelli and Enstminger, 2011). Rarefaction curves were plotted to compare taxonomic richness between the museum and field samples, a lack of significant difference between the two curves is indicated by overlap in their 95% confidence intervals as curves approach their maximal values. Analysis of variance was used to compare the diversity of taxa within samples and logistic regression was used to compare overall herbivore damage between field and museum samples.

3. RESULTS

For overall herbivory, just over half of the leaves in each sample have insect damage (59% for museum, S.E. 5.8; 53% for field, S.E. 7.5) and the two samples are not significantly different in terms of their overall damage ($X_{1,309}^2$ =2.51 P=0.113, Table 1). Both samples have all damage types present (holes, margin feeds, skeletonizing, leaf mines and galls; Figure 4) and no significant differences are seen in the number of feeding types per leaf ($X_{1,311}^2$ =6.17 P=0.187) between the museum and field samples. All taxa from the museum sample have at least one damaged leaf, whereas four of the taxa from the field sample have no damage. Leaf mines and galls are rare in both samples, with three total leaf mines (on *Lithocarpus sp.*, and Ulmaceae.) and four galls (on *Lithocarpus sp.*, *Magnolia sp.* and Platanus) observed between the museum and field samples. However, feeding guild structure was not significantly different between the museum and field samples (X^2 =0.08, P=0.7785, Figure 5).

TABLE 1. Comparison of taxa between field (F) and museum (M) collections. Percent damage is the number of leaves per taxon with any kind of insect damage. Average number of feeding types per leaf is the number of different guilds on a single leaf per taxon and the number of types per taxon is the total number of feeding guilds found on all leaves sampled for each taxon.

Taxon	Tot	Total n		Rank		naged	avg #	feed	#types	/taxon
			abuno	dance	types					
	159	153					/le	af		
	Μ	F	Μ	F	Μ	F	Μ	F	Μ	F
Acer	7	4	6	8	0.80	0.75	1.25	1.67	2	3
Aescalus	5	1	8	11	1.00	0	1.40	0	3	0
Alnus	0	7	0	7	—	0.43		1.00		2
Betula	8	0	5	0	0.38		1.00		2	
Cascara	0	1	0	11	—	1.00		1.00		1
Castanea	10	0	4	0	0.60		1.33		2	
Crataegus	0	1	0	11	—	1.00		1.00		1
										0
Fraxinus	0	1	0	11	—	0		0		
Hydrangea	5	2	8	10	0.40	0	1.50	0	2	0
Jugland	0	1	0	11		1.00		2		2
Laurel	7	14	6	4	0.43	0.71	1.00	1.40	2	2
Legume	15	23	1	2	0.27	0.22	1.33	1.00	2	3
Liquidambar	15	15	1	3	0.73	0.33	1.55	1.20	3	2
Liriodendron	10	2	4	10	0.30	0.50	1.33	1.00	3	1
Lithocarpus	14	10	2	5	0.64	0.60	1.22	1.33	2	4
Magnolia	0	3	0	9		0.67	_	2.00		3
Nyssa	3	0	10	0	0.33		1.00		1	
Philadelphus	0	1	0	11		1.00		2.00		2
Platanus	8	3	5	9	0.88	0.67	1.25	1.00	3	2
Populus	7	2	6	10	0.29	0	1.50	0	3	0
Quercus	12	34	3	1	0.75	0.53	1.89	1.28	3	3
Rhamnus	0	2	0	10	—	1.00		1.00		1
Rosaceae	3	0	10	0	1.00		1.67		2	
Salix	6	0	7	0	0.50		1.00		2	
Simplocus	6	15	7	3	0.83	0.47	1.80	1.00	3	3
Theaceae	0	3	0	9	—	0.33		1.00		1
Tilia	1	0	11	0	1.00		1.00	1.00	1	
Ulmaceae	4	0	9	0	0.50		1.00		1	
Viburnum	6	0	7	0	0.17		1.00		1	
Zeusaphoides	7	8	6	6	0.57	0.38	1.75	1.00	3	3

FIGURE 4. Photos of Clarkia flora leaves with representative damage indicated with arrow (except for photo 1) 1. *Lithocarpus sp.*, with likely gall damage (multiple); 2. *Populus sp.* with margin-feeding damage; 3. *Quercus sp.*, with skeletonizing damage; 4. Indeterminate rosid with hole feeding damage. Scale bars for images 2 and 4 are 5 mm.



FIGURE 5. Distribution of insect damage by feeding guild in museum and field samples. Percentages reflect the number of leaves in each sample with damage in each guild-type. Museum and field samples were not significantly different (X^2 =0.08, P=0.7785) indicating a similar proportion of feeding guilds between the two samples.



The museum and field samples had 13 of the 30 taxa shared between the samples, including three of the four most abundant taxa in each sample (Table 1), and a simple-matching coefficient of 0.43. This low overall similarity with shared dominant taxa suggests that there was little overlap in rare taxa between the two samples. Individual based rarefaction curves for the two samples (Figure 6) show overlap in their 95% confidence intervals at the highest values of both curves, demonstrating a lack of significant difference. Comparison of the shape of the two curves, however, indicates that the field sample has reached its asymptote by 140 leaves, while the museum curve has not. The shape of the museum rarefaction curve suggests, therefore, that additional sampling of the museum collection is necessary to capture the full diversity of the collection.

FIGURE 6. Between-sample comparison of taxon-based rarefaction comparing field (dashed line) and museum (solid line) samples with 95% confidence intervals.



4. DISCUSSION

The museum and field collections are similar overall in terms of their patterns of insect herbivory. The average number of leaves with insect damage and the average number of feeding types per leaf demonstrate that the museum collection is equivalent to the field-collected sample in terms of capturing overall herbivory patterns. The similarity in feeding between the two samples shows that those who curated the original museum collection were not rejecting leaves based on the presence of insect damage, and, when coupled with the high level of damage in the museum collection overall indicate that patterns of insect damage have not been negatively affected by biased collecting.

Damage to leaves of the most abundant plant taxa, those having a rank abundance of 5 or lower in both samples was similar to the damage for the least abundant taxa, those having a rank abundance of 6 or higher (museum sample most abundant 48% damage, least abundant 60% damage; field sample most abundant 57% damage, least abundant 55% damage). The similarity in damage between the most common and least common taxa in each sample indicates that the correspondence in herbivory patterns between the museum and field samples is not simply a function of high damage levels on the most abundant taxa. Additionally, abundance of taxa was a poor predictor of its overall damage level ($F_{1,42} = 0.834$, P = 0.367). The similarity in guild structure of herbivores between the two samples also suggests that differences in plant communities between the museum and field samples did not strongly influence herbivore feeding and that most of the insect feeding damage was produced by insects that were able to utilize a variety of host plants. This lack of host-specificity in herbivore feeding would be expected if insects that were living around Clarkia Lake had fed more or less equally on all available trees.

A second pattern that we would expect, if herbivory is predominantly made by generalist herbivores, is a scarcity of leaf mines and galls in both samples, as these types of damage are made by specialist herbivores (Gaston et al., 1992; Stone and Cook, 1998; Nyman et al., 2006). Leaf mines and galls are both very rare in the Clarkia flora (approximately 2% of leaves have mines or galls), unfortunately, leaf mines and galls are generally rare in fossil and modern floras (Smith, 2008; Winkler et al., 2010; Knor et al., 2013; Leckey et al., *Accepted*), and very large sample sizes are usually required to recover enough mines and galls to perform a robust examination of their distribution patterns. Future studies of Clarkia's insect herbivory may be able to address the role of specialist herbivory with more extensive sampling.

5. CONCLUSIONS

The results of this case study show that the insect damage found on the leaves of museum-housed paleobotanical collections may not be biased by high-grading or other curatorial practices. The results are encouraging for paleobotanists interested in using fossil floras for

studying insect damage preserved on fossil plants. The ability to use museum collections to examine insect herbivory expands the scope of possible questions to include those that would be difficult to address with only newly collected field samples.

<u>CHAPTER 2. OAK-INSECT HERBIVORE INTERACTIONS ALONG A TEMPERATURE</u> <u>AND PRECIPITATION GRADIENT</u>

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ABSTRACT

The interactions between herbivorous insects and their host plants are expected to be influenced by changing climates. Oaks provide an excellent system to examine this assumption because their interactions with herbivores occur over broad climatic and spatial scales, and they vary in their defensive and nutritional investment in leaves by being deciduous or evergreen. Additionally, their insect herbivores range from generalists to highly specialized feeders. In this study, we surveyed leaf-litter samples of four oak species along an elevation gradient, from coastal northern California, USA, to the upper montane woodlands of the Sierra Nevada, to examine the relationship between climatic factors (mean annual temperature and precipitation) and oak herbivory levels at multiple scales; across all oak species pooled, between evergreen and deciduous species, and within species.

Overall, temperature and precipitation did not appear to have a significant effect on most measures of total herbivore damage (percent leaves damaged per tree, actual and percent leaf area removed and average number of feeding damage marks per leaf) and the strongest predictor of herbivore damage overall was the identity of the host species. However, increases in precipitation were correlated with an increase in the leaf area removed, and specialized insects, such as those that make leaf mines and galls, were the most sensitive to differences in precipitation levels. This suggests that the effects of changing climate on some plant-insect interactions is less likely to result in broad level increases in damage with increasing temperatures or changing precipitation levels, but is rather more likely to be dependent on the type of herbivore (specialist vs. generalist) and the scale (species vs. community) over which the effect is examined.

1. INTRODUCTION

Terrestrial ecosystems function through a complex web of interactions between members of different trophic levels and the strength of these interactions are often modified by abiotic factors (Ayres, 1993; Lawton, 1995; Bale et al., 2002; Lewinsohn et al., 2005; Danks, 2007; DeLucia et al., 2012). At the base of these interacting webs lay two diverse and dominate groups, plants and their insect herbivores, whose interactions can be strongly influenced by the prevailing climate of the region, as well as by seasonal changes in temperature and precipitation (Coley, 1998; Adams et al., 2010; Zvereva and Kozlov, 2010; Garibaldi et al., 2011, Pearse and Hipp, 2012). In regards to plants, temperature may affect their developmental rates (Went, 1953; Kramer et al., 2000; Körner and Basler, 2010; Hänninen and Tanino, 2011), and their phenologies and leaf chemistry (both in nutritional quality and defensive compounds) (Reich and Oleksyn, 2004; Reich et al., 2007; Veteli et al., 2007; Asner et al., 2009; Janecke and Smit, 2011) and these changes may directly or indirectly influence their susceptibility to herbivores (Aizen and Patterson, 1995; Dury et al., 1998; Menzel et al., 2008; Wu et al., 2011). In turn, variation in temperature may influence the diversity of insect herbivores in an area, their population sizes, over-wintering survival rates, and thermal budgets for growth and reproduction (Sanderson, 1910; Headlee, 1914; Golightly and Lloyd, 1939; Headlee, 1941; Davidson, 1944; Wagner et al., 1985; Gilbert and Raworth, 1996; Régnière et al., 2012); all important factors that influence the potential impact of insect herbivores on their hosts (Bale et al., 2002; Laws and Belovsky, 2010; Leimu et al., 2012).

While the effects of temperature on plant-insect interactions have received much attention, the effects of precipitation on levels and types of herbivory experienced by plants are less understood (Bale et al., 2002; Ellwood et al., 2012). Many workers investigating the role of

precipitation on herbivore-plant interactions have focused on examining the effects of temporary stressors such as drought (Huberty and Denno, 2004; Mazía et al., 2004; Guarin and Taylor, 2005) rather than comparing herbivory levels associated with areas that have differing levels of annual rainfall (but see Sinclair and Hughes, 2008; Mazía et al., 2012). However, both types of studies have shown that drought stress and naturally occurring precipitation regimes can affect the abundance, development and distribution of plants and insects, while also affecting the nutritional quality and defenses of plants (Ordoñez et al., 2009; Gutbrodt et al., 2012; Mazía et al., 2012). These associated changes in plants and insects may also influence the type and strength of interactions that occur between these two groups. It has been further demonstrated that internal-feeding insects, such as those making galls or leaf mines, are particularly sensitive to variation in precipitation levels. Drier climates tend to have higher survivorship for gall-inducing insects (Fernandes and Price, 1992; Price et al., 1998), while dry conditions decrease survivorship for leaf mining insects (Fernandes et al., 2004; Yarnes and Boecklen, 2005).

The response of plants to changes in climatic factors, and thus their susceptibility to insect herbivores, may be further modified by whether they employ a deciduous or evergreen strategy of leaf permanence (Dirzo et al., 2008; Pringle et al., 2011). Leaf permanence plays a role in plant-insect interactions because the timing of leaf development, the investment in leaf defenses, and differences in the nutritional quality of leaves play a critical role in influencing a plant's susceptibility to insect herbivores (Field and Mooney, 1983; Barone, 2000; Karban, 2007; van Asch et al., 2007; Karban, 2008). Deciduous leaves are relatively short-lived and are associated with a relatively high photosynthetic potential but may be more vulnerable to herbivores because fewer resources are invested in their defenses, both physically and chemically (Coley, 1988). The leaves of evergreen trees, on the other hand, have higher leaf

permanence, which requires a larger allocation of resources to defense (both physically and chemically), leading to an associated reduction in nutritious quality and a lowering of a leaf's photosynthetic potential (Mooney and Gulmon, 1982; Field and Mooney, 1983; Coley and Barone, 1996; Borchard et al., 2011).

Oaks (*Quercus* spp.), members of the Beech family (Fagaceae), are distributed across a wide range of Mediterranean semi-desert and temperate to subtropical forests throughout North and Central America, Europe and Asia (Nixon, 2006). Because of their widespread distributions and, at times, dominance within forests, oaks play a significant ecological role within a variety of communities and are often considered keystone species (Leach and Givnish, 1999; Grivet et al., 2008).

In this study, we use four oak species distributed along a coastal to inland elevational gradient in California to explore how climatic factors and leaf permanence strategies (deciduous vs. evergreen) influence the relationship between oaks and their insect herbivores, both generalist, external feeding insects and internal feeding insects, which are often more specialized (Gaston, 1992). Consistent with the literature on plant-insect herbivore interactions in general, and within oaks specifically, we test the predictions that 1) herbivory will be greatest where temperature and precipitation are highest (Bale et al., 2002; Huberty and Denno, 2004; Adams et al., 2010; Garibaldi et al., 2011). 2) that deciduous oak species will have higher levels of herbivory than evergreen species (Pearse, 2011; Pringle et al., 2011), and 3) that specialized, internal feeding types may be particularly sensitive to changes in climatic conditions, with a higher frequency of galls in more xeric conditions (Fernandes and Price, 1992; Price et al., 1998) and a higher frequency of leaf mines corresponding to areas with higher annual rainfall (Fernandes et al., 2004; Yarnes and Boecklen, 2005; but see Nakamura et al., 2008). Finally, we also measured the
leaf sizes associated with each oak species along the elevational gradient to explore whether climate along the gradients may influence leaf size and to determine whether such a change could influence our measures of herbivore damage (Ackerly et al., 2002; Qi et al., 2009).

2. MATERIALS AND METHODS

To examine the role that climate and leaf development strategies (deciduous vs. evergreen) play in determining insect herbivory in oaks, we examined insect herbivore damage levels associated with four oak species native to California. Of the four species, two were evergreens, Quercus agrifolia (Coast Live Oak) and Q. chrysolepis (Canyon Live Oak), and two were deciduous, Q. kelloggi (California Black Oak) and Q. douglasii (Blue Oak). The gradient encompassed an elevation gain of 1,804 m (from 137 to 1941 m), which was associated with a 6.1 °C range in mean annual temperature (9.7 – 15.8 °C) and a 57 cm range in annual precipitation (28.9-86.3 cm). The sites along this gradient were surveyed in July 2007, and included coastal to inland areas (Figure 1) including the Landels-Hill Big Creek (0 - 1,220 m)elevation; 36°4' N, 121°34 'W) and Hastings Natural History Reserves (467 – 953 m elevation; 36°12.5' N, 121°33.5' W), within the University of California Natural Reserve System, and Sequoia National Forest (305 – 3,658 m elevation; 35°56' N, 118°29' W), which is located in the southern Sierra Nevada. While none of the oak species were found at all sites, each species was found at several elevations within at least two sites (Figure 2). Quercus agrifolia was found at Landels-Hill and Hastings; Q. chrysolepis was found at Landels-Hill, Hastings and Sequoia National Forest; *O. kelloggi* was found at Landels-Hill, Hastings and Sequoia National Forest; and Q. douglasii was found at Hastings and Sequoia National Forest. Each species was sampled over a portion of its elevational range at this latitude: Quercus agrifolia (range from below

1,000m), *Q. chrysolepis* (from 200 to 2600m), *Q. kelloggi* (from 300 to 2,500m), and *Q. douglasii* (below 1200m; elevation data from Knops and Koening 1997).

FIGURE 1. Map of sampling localities.



FIGURE 2. Elevational distribution of oak species, marks represent individual trees sampled within the total elevation range for the species (n=40, 10 trees per species). Circles indicate trees growing in the Coast Ranges, triangles indicate those from the Sierra Nevada. *Quercus kelloggii* and *Q. douglasii* are deciduous species while *Q. chrysolepis* and *Q. agrifolia* are evergreen.



2.1 Herbivory levels and specialized feeding types

The herbivory levels and specialized, internal feeding types associated with ten trees of each species (for a total of 40 sampled trees) along the elevational gradient were estimated by the collection of leaf litter samples as follows. A focal tree that was considered representative of the trees in an elevational zone was selected, and below each focal tree, 20 leaves were sampled from three locations directly beneath the canopy by placing a 1 m² quadrat haphazardly at distances of one-third and two-thirds from the trunk of the tree to the canopy edge and at the canopy edge (60 leaves/tree x 10 trees/species = 600 leaves/species). Leaves were collected in

July 2007 from the upper leaf litter layer to avoid the inclusion of leaves that could be damaged as the result of physical processes or by detritivores (*sensu* Smith and Nufio, 2004). Leaf litter sampling was chosen to gain a better representation of herbivory for the whole tree, as herbivory is not evenly distributed throughout a tree's canopy (Reynolds and Crossley, 1997; Cornelissen and Stiling, 2005) and because higher canopy leaves are difficult to access. In addition, leaf litter samples allow for greater standardization of samples between trees (Adams and Zhang, 2009). It was assumed that the sampled leaves beneath the deciduous trees were shed during the previous fall and winter and that the leaves beneath the evergreens were part of the regular, periodic process of leaf shedding in these species.

Once collected, leaves were brought into the lab where they were photographed and the area of a subsample of leaves (n=10 per tree) was measured using ImageJ (Rasband, 1997–2012) to estimate changes in the average leaf size of each species along the gradient. The potential effect of elevation on leaf size was also explored to evaluate the assumption that leaf sizes stayed the same or changed predictably as elevation increased. If leaf sizes changed with elevation, then similar amounts of area removed along the gradient could result in differences in the percent area removed being detected even though this would not reflect changes in the degree to which climate influences herbivore intensity. Herbivory levels associated with each tree were measured as: 1) the proportion of sampled leaves with herbivore damage; 2) the average actual leaf area removed; 3) percent leaf area removed; and 4) the number of discreet feeding damage marks per leaf, which were further categorized by functional feeding types (*e.g.* hole feeding, margin feeding, skeletonizing, galls and leaf mines, adapted from Smith, 2008). All damage except galls and leaf mines, are known to be made by specialist herbivores, all external

feeding damage (such as holes, margin feeding and skeletonizing) were considered to be associated with generalist herbivores because we were not able to determine the degree of specialization associated with these feeding types.

2.2 Estimating annual temperature and precipitation

To estimate the annual temperature and precipitation associated with each tree along the elevational gradient, the Global Positioning System (GPS) coordinates for each tree were recorded. Temperature and precipitation data were generated based on the latitude/longitude and elevation of each tree using the Parameter-Elevation Regression on Independent Slopes Model (PRISM) developed by the PRISM Group at Oregon State University. This model provides interpolated monthly and annual averages of temperature and precipitation values for a 2.5 minute (~4 km) grid cell associated with the georeference coordinates of each of tree (http://www.prism.oregonstate.edu/; data accessed April 2010, Daly et al., 2008). The average temperature and precipitation associated with each tree was estimated using PRISM's interpolated yearly averages for an eleven-year period (1999–2009). Time-average climate variables were used because leaf defenses in oaks are primarily driven by regional climate trends (Pearse and Hipp 2012).

2.3 Statistical Analyses

We determined whether differences among the proportion of leaves with herbivore damage, the average actual and percent leaf area removed, the average number of feeding instances per leaf and the percent leaves with leaf mines could be detected on different scales. First, we pooled the data within the two deciduous and two evergreen trees and conducted Student t-tests to compare whether the above measures of herbivory differed between the two

groups. Next, we conducted separate ANOVA analyses to determine the degree to which all species (regardless of their leaf types) differed in each of these measures of herbivory and conducted *post-hoc* Tukey-Kramer HSD tests were used to determine which species differed from each other in relation to each measure of herbivory (Table 1).

Generalized Linear Models (GLM) were then used to determine the degree to which climatic variables (mean annual temperature and precipitation, as independent variables), might explain different measures of herbivore damage (the average percent leaves with damage per tree, average total and percent area removed, and average percent leaves with leaf mines damage [as the dependent variables]). In these models, tree species was added as a fixed effect to control for its influence on measured herbivory levels and to determine whether climatic factors and species designation explained levels of herbivore damage. Due to a lack of degrees of freedom, it was not possible to conduct statistical models that included both leaf permanence type and tree species. As galls were uncommon among trees, we simply noted whether galls were present or absent within a tree and conducted two multiple logistic regression analyses to determine whether the effects of temperature and precipitation could be detected when noting whether a given tree was evergreen or deciduous or when we controlled for species. TABLE 1. a) The overall levels of herbivore damage (the average amount of leaf tissue removed per tree and the ratio of damaged to undamaged leaves per tree) and specialized damage (the percent of leaves with either leaf mine or gall damage per tree) was calculated across all trees. b) The amount of herbivore damage on each of the four *Quercus* species was calculated and compared between the two deciduous species (D), *Q. kelloggii* and *Q. douglasii*, and the two evergreen species (E) *Q. agrifolia* and *Q. chrysolepis*. c) For each of the four species, the overall damage and specialized damage were calculated and compared. Tukey-Kramer HSD test performed with logit-transformed data, all other reported values are untransformed.

Species	me leaf	an size	% leaves per	damaged tree	actual l remove	eaf area ed (cm ²)	% lea rem	af area oved	average per	# of feeds leaf	% leav leaf r	es with nines	% trees with galls
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	
a) All Species	17.9	±2.56	81.0	±2.14	1.08	±0.16	6.8	±0.72	3.0	±0.22	17.2	±1.92	40%
b) Evergreen	9.3	±0.87	80.9a	±0.03	0.89a	±0.17	8.6a	±0.01	2.5a	±0.13	17.9a	±0.03	30%
Deciduous	26.5	±4.28	81.2a	±0.04	1.28a	±0.28	4.3b	±0.01	3.5b	±0.39	16.4a	±0.02	50%
c) <i>Q. agrifolia</i>	12.6	±0.76	83.0a,b	±4.21	1.39a	±0.22	10.8a	±1.35	2.8b	±0.20	16.3a	±3.84	10%
Q. chrysolepis	5.9	±0.32	78.7b	±3.19	0.39b	±0.13	6.4b	±1.72	2.1b	±0.07	19.4a	±5.05	50%
Q. douglasii	9.5	±0.71	70.1b	±3.86	0.33b	±0.06	3.6b	±0.57	2.4b	±0.17	12.2a	±2.17	80%
Q. kelloggii	43.6	±3.49	92.2a	±2.90	2.22a	±0.36	5.1b	±0.78	4.7a	±0.57	20.7a	±3.75	20%

(E) evergreen species, (D) deciduous species

Notations a and b indicate results of Tukey-Kramer HSD test, levels not connected by the same letter are significantly different within groups (evergreen/deciduous and species).

Finally, we used a GLM to explore the effect of elevation on the leaf size of trees when controlling for tree species. We then used a *post hoc* GLM analysis to explore how temperature and precipitation influence leaf area when controlling for tree species. To meet the assumptions of normality, the data on percent leaves with leaf damage, percent leaf area removed and percent leaves with leaf mines data were normalized by use of a logit-transformation (Warton and Hui 2011). This logit-transformation effectively normalized the residuals associated with these dependent variables and the different climatic estimates. To meet the assumptions of normality, the actual area removed was also log transformed in all analyses. All statistical analyses were performed using JMP, Version 8 (SAS Institute 1989-2012).

3. RESULTS

Variation in temperature and precipitation with elevation in our sample was within the expected values based on terrestrial lapse rates for California of 3–6 °C for every increase in elevation of 1 km (Meyer, 1992). The varied topography in our sample, including the Coast Range and Sierra Nevada, is reflected in the uneven climate/elevation pattern associated with the sampled trees (Figure 3). In general, an increase in elevation led to a decrease in the average annual temperature for the locations of the forty trees sampled ($r^2 = 0.55$, P < 0.0001), although relatively little directional change in total annual precipitation was detected with elevation ($r^2 = 0.002$, P = 0.81). Still, temperature and precipitation were found to be positively correlated ($r^2 = 0.31$, P = 0.0002).

FIGURE 3. Mean annual temperature (range 9.6-15.6 °C) and average monthly precipitation (range 2.4-7.2 cm/month) estimates for locations at which oaks were sampled at different elevation levels (n=40).



3.1 Overall patterns

In terms of overall herbivory, all trees experienced a high incidence of leaf damage with an average of nearly 81% (range for all species: 70.1–92.2%) of leaves showing some sign of insect damage (Table 1a, percent leaves damaged per tree). This incidence of herbivory did not differ between evergreen and deciduous trees ($t_{1,38}$ = 0.07, P= 0.94; Table 1b) but did differ among species ($F_{1,36}$ = 6.6, P= 0.001; Table 1c) with *Q. kelloggii* having the highest incidence of herbivory and *Q. douglasii* having the lowest. The actual area removed by herbivores averaged 1 cm² per leaf (range of species: 0.33–2.22 cm²) and while these levels did not differ between evergreen and deciduous trees ($t_{1,38}$ = 0.52, P= 0.60) they did differ across tree species ($F_{1,36}$ = 21.08, P= < 0.0001; Table 1c) with the greatest amount of leaf tissue removed again in *Q. kelloggii* and the lowest in *Q. douglasii*. In turn, the 1 cm² of leaf area removed amounted to a removal of 6.8% of leaf area on average (range of species: 3.6–10.8%) and while this percent did differ between evergreen and deciduous trees ($t_{1,38}$ = 3.34, P= 0.002), it was mainly due to a high amount in one evergreen tree (*Q. agrifolia*, 10.8% removed; Table 1c). Finally, the number of feeding damage incidents associated with a given leaf averaged about 3 feeds per leaf (range for all species: 2.1–4.7) and while this value also differed between evergreen and deciduous trees ($t_{1,38}$ = 2.51, P= 0.02), it was mostly attributable to the high number of feeding incidents per leaf associated with the deciduous species *Q. kelloggii* (4.7 feeds/leaf).

In regards to the specialized feeding types, on average 17.2% of leaves across all trees had signs of leaf miners (Table 1a) and this percentage did not differ between evergreen and deciduous trees ($t_{1,38}$ = 0.37, P= 0.71) nor between species ($F_{1,36}$ = 0.98, P= 0.41). Because of the low incidence of leaf galls, only 40% of trees had at least one leaf gall and while the number of trees with galls varied between the evergreen and deciduous trees and across different species, this difference is likely driven by the high incidence of galls in *Q. douglasii*, on which 80% of trees had at least one gall. The low occurrence rates of galls did not allow us to statistically compare these rates.

3.2 The role of climate, leaf type and tree species on levels of herbivory

Overall, we could not detect a significant effect of temperature and precipitation on most measures of herbivory. In GLMs that controlled for whether trees were evergreen or deciduous and that included both temperature and precipitation, an increase in precipitation correlated with an increase in the actual leaf area removed although temperature did not explain any measure of herbivory (Table 2a). The importance of precipitation and herbivory levels was scale dependent, as we did not find this relationship when deciduous and evergreen trees were analyzed separately. Controlling for precipitation and temperature, we again found that the percent leaf area removed

		% leave	% leaves with		actual area		% leaf area		of feed
		dama	age	removed	(cm^2)	remo	ved	types pe	er leaf
Species	df	F	Р	F	Р	F	Р	F	Р
a) All Species									
Temp.	1	3.67	0.06	0.13	0.72	0.72	0.40	0.01	0.93
Ppt.	1	0.09	0.77	6.17	0.02	0.75	0.39	0.06	0.80
Ever/ Decid	1	0.30	0.59	3.57	0.07	5.31	0.001	9.06	0.0002
b) Evergreen Species									
Temp.	1	0.18	0.68	0.82	0.38	0.05	0.83	2.30	0.15
Ppt.	1	0.20	0.89	0.74	0.40	0.11	0.74	3.19	0.09
Sp. (2)	1	0.67	0.43	9.29	0.008	2.46	0.14	1.98	0.18
c) Deciduous Species									
Temp.	1	0.45	0.51	4.14	0.06	1.24	0.28	0.18	0.68
Ppt.	1	0.54	0.47	0.04	0.84	2.08	0.16	0.17	0.69

26.22

Ppt.

Sp. (2)

1

1

8.64

0.009

TABLE 2. Generalized linear mixed models examining the relationship between mean annual temperature (Temp.) and precipitation (Ppt.) on measures of herbivory, a) when all four species are pooled and b) within the evergreen (Q. agrifolia and Q. chrysolepsis) and deciduous species (Q.douglasii and Q. kelloggii). Bolded numbers signify significant effects.

<0.0001

7.04

0.02

7.40

0.02

and average number of feeding instances per leaf differed between the deciduous and evergreen trees. That is, a higher percentage of leaf area was removed in evergreen trees, while deciduous trees were associated with more feeds per leaf. However, these differences between evergreens and deciduous trees appear to be driven by one evergreen species (*Q. agrifolia*) that had a much higher percentage of leaf area removed than all other species and a deciduous tree (*Q. kell*ogii) that had the highest number of feeds per leaf of all trees (Table 1c).

3.3 The role of climate, leaf type and tree species on specialized feeding types

The percentage of leaves with leaf miner damage on a given tree was not correlated with climatic factors (temperature and precipitation) when trees were grouped as being either evergreen or deciduous (Table 3a). However, increases in precipitation were found to be associated with greater levels of leaf mines when the models controlled for a species effect (Table 3b). The probability that galls were present on a tree was strongly species and precipitation dependent, with trees of *Q. chrysolepis* and *Q. douglasii* being more likely to be associated with mines with an increase in precipitation (Table 1c, Table 3b).

3.4 The role of climate and elevation on leaf area

When controlling for tree species (given that leaf area differed between species $[F_{3, 33}=$ 89.84, P= <0.0001]), the average leaf size of a tree significantly declined with elevation (F_{1, 34}= 13.99, P= 0.0007) and there was not a significantly different response between species to the effects of elevation on leaf size (F_{3, 33}= 1.92, P = 0.146). An exploration of the climatic factors that affect leaf size showed that, when controlling for tree species, there was an interactive effect between precipitation and temperature (F_{1, 33}= 4.52, P = 0.04), such that at higher temperatures

increases in precipitation increased leaf area, while at lower temperatures, increases in

precipitation decreased leaf size.

TABLE 3. The effects of climatic factors and leaf permanence or species designation on the proportion of leaves with mines and the probability that galls are present or absent on a given oak tree a) for a model that includes temperature, precipitation and whether the species is evergreen or deciduous and b) for a model that includes temperature, precipitation and species identity. Bold numbers signify significant values.

		% leaves with leaf mines		Presence/abs	ence of galls
	df	F	Р	X^2	Р
a) Leaf permanence					
Temp.	1	0.73	0.39	0.10	0.76
Ppt.	1	2.79	0.10	0.03	0.86
Ever./Decid.	1	0.15	0.69	1.63	0.20
b) Species identity					
Temp.	1	0.38	0.54	0.49	0.49
Ppt.	1	4.45	0.04	4.24	0.04
Sp.	3	0.66	0.58	21.86	<0.0001

4. DISCUSSION

As oak species are broadly distributed across a variety of spatial gradients they have been used to examine the influence of large-scale biotic and abiotic factors on the life history traits of trees, forest dynamics and ecological interactions (Gratani et al., 2003; Gómez, 2004; Romero et al., 2009). In this study, we used four oak species along an elevational gradient to explore the effects of leaf permanence strategies and climatic factors on the incidence and intensity of herbivore damage. While we did find that tree species varied in the incidence and levels of herbivore damage, counter to our expectations, we did not find a consistent difference between evergreen and deciduous trees in each of the different measures of herbivory (incidence of herbivory, percent or actual area removed and number of feeding instances per leaf). We also found that climatic factors, such as precipitation and temperature, were not correlated with most measures of herbivore damage associated with external feeders, except the actual amount of leaf tissue removed which was associated with increases in precipitation. Precipitation also was correlated with damage by specialist feeders such as leaf miners and gallers. In the following, we address the importance of our study for understanding the relationships between plants and their insect herbivores.

4.1 Overall patterns

In terms of overall herbivory, all species experienced a high incidence of leaf damage with nearly 81% of leaves within trees showing signs of insect damage. This incidence of herbivory was associated with a roughly 1 cm² (or 6.8%) loss of leaf area and although the incidence of herbivore damage on leaves and leaf area removed varied significantly between oak species, this pattern was not explained by whether trees were deciduous or evergreen. For example, when it came to the incidence of herbivore damage and leaf area removed, *Q. agrifolia* and *Q. kelloggii*, an evergreen and deciduous species respectively, experienced similar levels of herbivory while they differed from their respective evergreen or deciduous pair. In turn, relative to all other species, *Q. agrifolia*, had a higher percent leaf area removed than all other species and *Q. kelloggii*, had more feeding incidents per leaf than all other species. There also was no difference in the percentage of leaves with leaf mines associated with deciduous and evergreen species.

4.2 The role of climate, leaf type and tree species on levels of herbivory

Among oak trees, temperature and precipitation were not correlated with most measures of herbivory. More specifically, while temperature did not appear to influence any measure of herbivory, when controlling for whether trees were deciduous or evergreen, higher precipitation levels were only associated with an increase in the actual leaf area removed per tree. The relationship between precipitation and actual leaf area removed was scale-dependent as we did not find such a pattern when analyzing the evergreen and deciduous species separately. In turn, within both evergreen and deciduous trees, we found that tree species often explained the difference between different measures of herbivory but climatic variables did not. While we did not find consistent differences between the two evergreen and two deciduous trees, a future analysis across many oak species could be informative in helping us understand the degree to which leaf permanence affects the role of herbivore-plant interactions across climatic gradients. Additional fieldwork conducted along these gradients should add additional replicates (trees) and compare cohorts of trees associated with different elevational belts (low, intermediate and high elevation) to strengthen their ability to detect a climatic signal. Future studies may also build on this work by employing an experimental approach, which would allow examination of the causes leading to the measured correlations between climatic factors and herbivory.

4.3 The role of climate, leaf type and tree species on specialized feeding types

Consistent with our prediction, the percentage of leaves with leaf miner damage on a given tree were correlated with increased precipitation when the models controlled for a potential species effect, but there was no difference in the abundance of leaf mines between deciduous or evergreen species. Leaf miners are thought to become more abundant with increases in

precipitation because of corresponding decreases in larval mortality in more moist conditions (Yarnes and Boecklen, 2005; Nakamura, 2008). In regards to whether galls were likely to be present or absent on a tree, there also was a strong species effect and, counter to our expectation, an increase in precipitation was correlated with increased likelihood that a tree would be associated with leaf galls. While some studies have noted that gall-making insects are most abundant in mesic habitats (Blanche and Ludwig, 2001), most studies have found that galls tend to be more diverse or abundant in more xeric conditions (Fernandes and Price, 1992; Price et al., 1998; Cuevas-Reyes et al., 2004). Future explorations of the relationship between oaks and leaf gallers and miners should examine how the range of oak species (Cornell and Washburn, 1979; Abe et al., 2007), habitat complexity (Yarnes and Boecklen, 2006; Stoepler and Rehill, 2012), and interactions between insect herbivores (Faeth, 1991; Nakamura et al., 2008; Prior and Hellmann, 2010) may also influence the diversity and abundance of these specialized feeding types.

4.4 The role of climate and elevation on leaf area

Along the mountain gradient, oak leaf size declined with increases in elevation, as has been found by others (Qi et al., 2009), although mechanistically, changes in leaf size were influenced by an interaction between temperature and precipitation. That is, at lower temperatures, increases in precipitation were associated with smaller leaf sizes while at higher temperatures, increases in precipitation were associated with an increase in leaf size. In regards to other herbivory studies, this finding suggests that potential changes in leaf sizes should be taken into account when determining the measures of herbivore damage used when comparing species or communities across sites. In this study system, for example, while we found that the

actual leaf area removed was significantly correlated with increases in precipitation, this pattern was not detected when we considered the percent leaf area removed, most likely because changes in leaf area removed may have been obfuscated by changes in leaf sizes when determining the percent area consumed.

It has been suggested that changes in temperature and precipitation should be associated with changes in the levels of herbivory through their effects on herbivore development and abundance (Bale et al., 2002), herbivore diversity (Wilf and Labandeira, 1999), or through their effects on leaf chemistry, plant stress or host plant defenses (Coley and Barone, 1996). Understanding the relationship between climate and herbivore-plant interactions is currently an important issue in climate change biology as it may affect issues associated with conservation, ecosystem function and stability and agricultural systems (Sutherst et al., 2011; Abrol, 1912; DeLucia et al., 2012; Juroszek and von Tiedemann, 2013). However, while numerous studies have found that climate and life history characteristics, such as leaf permanence strategy, often explain herbivory patterns between populations, species, communities and regions (Vanbergen et al., 2003; Huberty and Denno, 2004; Mazía et al., 2004; Guarin and Taylor, 2005; Yarnes and Boecklen, 2005; Pringle et al., 2011), in other studies these relationships have not been detected (Yela and Herrera, 1993; Andrew and Hughes, 2007). Further, these patterns may be difficult to detect because the relationship between plants and their herbivores may be region or taxon specific, may involve complex interactions between biotic and abiotic components of an ecosystem (Yela and Herrera, 1993), or because the effects may only be detectable during extreme weather events (Shure et al., 1997; Brenes-Arguedas et al., 2009; Gutbrodt et al., 2012).

Although differences in climatic conditions did not impact generalized herbivory patterns on oaks within our study, we did find that the abundance of specialized feeding types, leaf

miners and gallers, was influenced by climatic conditions. This relationship between climatic variables and the diversity and abundance of these specialized feeding types has been documented in a variety of studies (Fernandes and Price, 1992; Price et al., 1998; Fernandes et al., 2004; Yarnes and Boecklen, 2005). Our results showed that certain feeding types may be more susceptible to changes in climatic variables than others, as such we may expect that future climate change will continue to differentially impact internal feeding specialists over more generalist external feeding insects. Therefore, we suggest that future analyses of herbivory and climate not only take into account level of host-specificity, but also the distinction between external and internal feeding strategies to explore how one-to-one interactions between herbivores and their host plants may be impacted by changes in climate and extreme weather conditions.

CHAPTER 3. HOST FIDELITY OVER GEOLOGIC TIME: RESTRICTED USE OF OAKS BY OAK GALLWASPS

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ABSTRACT

Oaks and their associated gallwasps are often cited as a classic example of coevolution in a plant-insect system. Therefore, it is expected that these gallwasps should demonstrate a highdegree of host fidelity over their evolutionary history. To test this, we studied 25 fossil floras from the Oligocene through Pliocene of the western United States. Galls were found on the leaves of *Quercus simulata*-type Knowlton, 1898 and *Q. pollardiana*-type (Knowlton) Axelrod, 1940 and match previously reported galls of the form genus *Antronoides* Waggoner and Poteet, 1996. These fossil leaf galls are similar to galls made on oaks by modern Cynipini wasps and were restricted to two oak species. Galls are present on these oaks in western floras for a span of 30 million years, indicative of remarkable host fidelity through time. The distribution of galled leaves from across the western United States indicates that the radiation of this group of gallwasps occurred more or less simultaneously across a wide geographic area.

1. INTRODUCTION

Specialized interactions between insects and plants are often examined though the lens of co-evolution, a mechanism by which each group promotes the evolution of novel traits in the other (Ehrlich and Raven, 1964; Berenbaum and Feeny, 1981). Specialization of insects on their host plants is a successful and recurring evolutionary theme across many lineages (Mitter et al., 1991; Bernays, 1998, Ward et al., 2003). One requirement of specialization is strong host fidelity on the part of the insect, as prolonged association of insect and host allows evolutionary processes to occur (Futuyma and Moreno, 1988; Berenbaum, 2001). Instances of specialized insect feeding have been reported in the fossil record, where fossilized plant tissues with herbivore damage are preserved and are similar to damage made on extant members of those

plant groups (Labandeira et al., 1994; Wilf et al., 2005; Krassilov, 2008; Wappler, 2010). One of the clearest examples of specialized herbivore damage commonly preserved in the fossil record is that made by leaf galling insects. Galls are caused by the induction of abnormal growth in plant tissues for the purpose of feeding and protecting developing larvae and have an extensive fossil record reaching back to the Paleozoic (Larew, 1992; Labandeira and Phillips, 2002).

Many modern insects are known to induce leaf gall formation on their host plants. Here we focus on the galls of Cynipini (Hymenoptera: Cynipidae) gallwasps due to their tightly constrained host use (Ronquist and Liljeblad, 2001; Stone et al., 2009; Hardy and Cook, 2010), diversity of gall forms, and hypothesized long-lived host relationships (Stone et al., 2009). Cynipini have a fossil record that extends back to the Oligocene (Liu et al., 2007) and their galls are often distinct from those of other oak gallers such as aphids or midges, in both their overall shape and the internal structure of their galls (Stone and Schönrogge, 2003, Erwin and Schick, 2007). Gallwasps and their oak hosts also have been shown to be a useful system for examining the evolution of host-plant specificity (Cornell, 1985; Stone and Cook, 1998; Stone and Schönrogge, 2003). The clade Cynipini (Cynipidae) is part of the Woody Rosid Gallers, a group that exclusively galls woody roses and oaks, although the Cynipini are primarily specialized on Quercus Linnaeus, 1758 (Liljeblad et al., 2008; Stone et al., 2009). An extensive body of work on modern gall wasps and oaks has documented strong host fidelity that has been hypothesized to stretch back at least 20 million years (Ronquist and Liljeblad, 2001; Stone et al., 2009). This is supported by the presence of cynipid galls on oak leaves preserved in Miocene floras (Waggoner and Poteet, 1996; Waggoner, 1999; Erwin and Schick, 2007). The shapes of these Miocene galls differ from extant galls primarily in the degree of elongation and tapering at the distal end (Erwin and Schick, 2007) and they all have been assigned to the form-genus Antronoides Waggoner and

Poteet, 1996. *Antronoides* was originally aligned with the modern genus *Antron* Kinsey, 1930, but later found to be more similar morphologically to galls made by wasps of the genera *Cynips* Linneaus, 1758 and *Xanthoteres* Ashmead, 1897 (Erwin and Schick, 2007).

For all the fossil and modern examples of specialization, little is known about what the relationship between specialized insect herbivores and their hosts looks like over geologic time. Specialists have been hypothesized to adopt new hosts when their ancestors are specialists on closely related hosts (Berenbaum, 2001). Once established, the relationship is thought to persist relatively unchanged for millions of years (Moran, 1989) resulting in a tight phylogenetic congruence between the clades of herbivores and their hosts (Farrell and Mitter, 1998; Ronquist and Liljeblad, 2001; Ward et al., 2003; Ramamurthy, 2007). We therefore expect that distribution of fossilized cynipid galls (specifically those of the tribe Cynipini) will be confined to closely related plants throughout time, including oaks and other members of the Fagaceae. Here we study fagaceous leaves from fossil floras that span a broad geographic and temporal range across the western United States to examine host use patterns in oak gallwasps. Specifically, we examine how galls are distributed among leaves of different members of the Fagaceae through time to test the assumption that oaks and oak gallwasps have had a long-lived, co-evolved association, with little host-shifting.

2. MATERIALS AND METHODS

Fossil leaves used in this study come from deposits that consist of fine-grained, lacustrine or floodplain shales and siltstones. The floras from which these leaves were recovered are found across most western states (California, Idaho, Nevada, Oregon, Washington) and span an age range from 5–45 Ma (Figure 1). Tectonic and volcanic activity in western North America during

the late Paleogene and Neogene led to the creation of basins that preserved the abundant fossil floras that are the basis of this study (Schorn et al., 2007). Floras were included in this study if they met the basic criteria of: 1) preservation in fine-grain fluviolacustrine sediments, 2) an age within the range of Oligocene to Pliocene, 3) a large sample of Fagaceae leaves (average N =120) leaves. In order to focus on the same species through time, the geographical focus was limited to floras from the western United States, where many oak species are common to multiple floras (Axelrod, 1983). Several floras were considered for inclusion but were rejected for either poor preservation or too few leaves preserved, including: The Chula Vista and Gold Bluffs floras of California; the Haynes Creek flora of Idaho; the Aldrich Station, Eastgate, Middlegate, Purple Mountain and Verdi floras of Nevada; the Keasey, Pittsburg Bluffs, Sardine and Thomas Creek floras of Oregon; and the Grand Coulee and Keechelus floras of Washington. Precision of age determination varies widely for the included floras. For those interspersed with volcanics, Ar/Ar or K/Ar dates are available. Many other floras have mammalian faunal elements preserved in close proximity for which an age can be estimated. Several of the floras, however, have not yet been well-studied and for these, a taxonomic comparison with geographically proximal floras provides the only age estimate (Retallack et al., 2004; Schorn et al., 2007).

We used museum collections to obtain the largest possible sample of leaves from floras across western North America. We focused on the collections of the University of California Museum of Paleontology, the National Museum of Natural History and the University of Colorado Museum of Natural History, due to their large holdings of western floras. The number of leaves bearing either galls or gall scars was recorded for each flora as well as the taxa on which galls were found and other fagaceous taxa present.

FIGURE 1. Map showing floras with preserved gall structures. Eocene/Oligocene floras (black circles): 1. Chalk Bluffs, CA (Eocene); 2. Grant, MT (Eocene); 3. Bridge Creek, OR (Oligocene); 4. Rujada and Willamette, OR (Oligocene); 5. Ramsey, NV (Oligocene): Miocene floras (grey circles): 6. Cascadia, OR; 7. Tipton, OR; 8. Gilliam Springs, NV; 9. Fingerrock, NV; 10. Buffalo Canyon, NV; 11. Temblor, CA; 12. Mascall, OR; 13. Succor Creek, ID; 14. "Latah" and Almaden, ID; 15. Webber Lake, CA; 16. Stewart Valley, NV; 17. Mint Canyon, CA; 18. Trapper Creek, ID; 19. Stinking Water, OR; 20. Hidden Lake, OR; 21. Mt. Reba, CA: Pliocene floras (open circles): 22. Washoe, NV (Miocene/Pliocene); 23. Turlock Lake CA.



The oaks (Quercus) and beeches (Fagus) Linnaeus, 1753 along with Castanea Miller, 1754 and 'Lithocarpus' are the most common and abundant fagaceous genera in these floras. Many Fagaceae have sclerophylous leaves, which aids in their preservation, although more delicate fagaceous leaves, such as *O. pseudolyrata* (Condit, 1944), also are well represented. Fossil leaves of Fagaceae were identified using shape, tooth morphology, and vein architecture. Oaks vary widely in their leaf morphologies, and species groupings made on the basis of leaf traits correlate poorly with those based on genetic traits (Manos et al., 1999). Because leaves from the same species can have markedly different appearances, previous identifiers have had a tendency to oversplit fagaceous taxa (Jones, 1986). For this reason, we took an inclusive approach to identifying leaves, aiming to unite taxa with general overall similarity. Leaves of both *Quercus pollardiana*-type and *Q. simulata*-type showed variation in morphology in that they could be either toothed or untoothed and more or less elongate. Following the opinions of previous workers, Q. hannibali and Q. dayana are considered to be synonyms of Q. pollardiana (Axelrod, 1983; Fields, 1996), although other authors continue to use the name Q. hannibali (Buechler et al., 2007). Additionally, we did not attempt to resolve some of the nomenclatural discrepancies surrounding Q. simulata, but rather accepted the identification of previous workers and the wide range of morphological variation for this species. We also follow Fields, 1996 inclusion of Q. consimilis (Newberry, 1883) as part of the Q. simulata-type, in light of the difficulties in reliably separating these species (MacGinitie, 1933).

Identification of fossil galls rests on the overall morphology and the position of the galls on the leaf, as microscopic details are often difficult to distinguish (Scott et al., 1994). These galls, attributed to *Antronoides schornii* Waggoner and Poteet, 1996, are elongate and tapered at their distal ends in an obclavate shape. The galls observed share many characteristics, such as the

overall shape, size and disk-like basal expansion (Waggoner and Poteet, 1996; Waggoner, 1999; Erwin and Schick, 2007) with those made by modern members of the tribe Cynipini, and we find this designation to be the most parsimonious, however the precise generic assignment is uncertain and validity of assigning the genus *Antronoides* to a living taxon has been difficult (Erwin and Schick, 2007; Liljeblad et al., 2008). Other potential gall-inducers such as mites of the family Eriophyoidea or midges of the family Cecidomyidae, are unlikely to be the insects responsible for these galls based on modern patterns of association and morphology. For example, mite galls tend to be tiny relative to insect-induced galls (Westphal, 1992) and midge galls on oaks tend to be blister-type galls or leaf rolls (Gagné, 1989). Midges are less common on oaks than on other members of the Fagaceae today (Kampichler and Teschner, 2002), although some species gall live oaks in North America (Gagné and Riley, 1999).

3. RESULTS

A total of ~ 2,980 fossil leaves were examined for this study. The majority of these leaves were oaks, although other genera of Fagaceae were examined if they too were preserved (~ 146 leaves total). Of these, only 39 galled oak leaves were recovered. Galls and gall scars examined in this study included both previously reported and new material (Table 1). New occurrences of galls from the Trapper Creek (OR), and the Fingerrock Wash floras (NV) may be made by the same insect as the previously reported galls from the Gilliam Springs flora (NV).

TABLE 1. Comparison between geographic and temporal distribution of galls on *Quercus pollardiana* type and *Q. simulata* type leaves. The Clarkia flora, ID (Miocene), was also examined but contained neither host plant. Category "other Quercus" may include leaves of *Q. pollardiana* type or *Q. simulata* type that did not have the preservational quality to allow for positive identification. Category "# leaves galled" includes all potential gall structures, including those identified as cynipid galls.

Map Loc. # (Fig 1)	Locality Name	Epoch (Ma)	Taxa	# spp.	# Leaves Galled (# galled leaves/ total examined)	Preserved gall structure
23	Turlock Lake, CA	Pliocene (5.0) ^{1 a}	Q. pollardiana type		1/31	basal disk (?)
			other Quercus	2	9	none
			non-Quercus Fagaceae	0	0	none
22	Washoe, NV	Miocene/Pliocene (5.2) ^{1 a}	Q. pollardiana type		2/41	basal disk
			other Quercus	1	0/46	none
			non-Quercus Fagaceae	0	0	none
21	Mt. Reba, CA	late Miocene (7.0) ^{1 e}	Q. pollardiana type		0/19	none
			other Quercus	0	0	none
			non-Quercus Fagaceae	1	0/14	none
20	Hidden Lake, OR	middle Miocene (11.7) ^{2 b}	Q. pollardiana type		0/27	none
			Q. simulata type		0/9	none
			other Quercus	1	0/11	none
			non-Quercus Fagaceae	2	0/62	none
19	Stinking Water, OR	middle Miocene (12.5) ^{1 e}	Q. pollardiana type		4/34	basal disk (?)
			Q. simulata type		1/7	gall and basal disk*
			other Quercus [#]	3	9/177	gall? and basal disks

			non-Quercus Fagaceae	0	0	none
18	Trapper Creek, ID	middle Miocene (12.5) ^{1 c}	Q. pollardiana type		2/35	gall and basal disks
			Q. simulata type		0/26	none
			other Quercus	1	0/16	none
			non-Quercus Fagaceae	1	0/10	none
17	Mint Canyon, CA	middle Miocene (12.5) ^{1 a, d}	Q. pollardiana type		11/162	basal disks
			other Quercus	1	1/36	basal disk(?)
			non-Quercus Fagaceae	0	0	none
14	Almaden, ID	middle Miocene (14.0) ^{2 b}	Q. pollardiana type		0/16	none
			Q. simulata type		0/34	none
			other Quercus	2	0/94	none
			non-Quercus Fagaceae	0	0	none
16	Stewart Valley, NV	middle Miocene (14.5) ^{1 c}	Q. pollardiana type		0/116	basal disk
			other Quercus	0	0	none
			non-Quercus Fagaceae	0	0	none
15	Webber Lake, CA	middle Miocene (15.1) ^{1 b, d}	Q. simulata type		1/40	basal disk
			other Quercus	1	0/36	none
			non-Quercus Fagaceae	0	0	none

14	"Latah", ID	middle Miocene (15.2) ^{1 e}	Q. pollardiana type		0/44	none
			Q. simulata type		0/19	basal disk
			other Quercus	3	0/3	none
			non-Quercus Fagaceae	0	0	none
13	Succor Creek, ID	middle Miocene (15.2) ^{1 e}	Q. simulata type		1/10	basal disk
			other Quercus	0	0	none
			non-Quercus Fagaceae	0	0	none
12	Mascall, OR	middle Miocene (15.2) ^{1 a, e}	Q. pollardiana type		0/14	basal disk
			other Quercus	2	0/90	none
			non-Quercus Fagaceae	1	0/1	none
11	Temblor, CA	middle Miocene (15.3) ^{1 a, d}	Q. pollardiana type		0/10	none
			Q. simulata type		0/18	none
			other Quercus	3	0/75	none
			non-Quercus Fagaceae	2	0/20	none
10	Buffalo Cyn, NV	middle Miocene (15.4) ^{1 c}	Q. pollardiana type		0/228	basal disk
			other Quercus	1	0/5	none
			non-Quercus Fagaceae	0	0	none
9	Fingerrock, NV	middle Miocene (15.4) ^{1 c, e}	Q. pollardiana type		1/438	gall and basal disk
			Q. simulata type		0/133	none
			other Quercus	2	0/540	none
			non-Quercus Fagaceae	1	0/3	none

8	Gilliam Springs, NV	middle Miocene (15.4) ^{1 c}	Q. pollardiana type		from previous work	galls and basal disks *
7	Tipton, OR	middle Miocene (16-14.7) ⁷	Q. simulata type		from previous work	galls and basal disks**
6	Cascadia, OR	early Miocene (15.8) ^{3 c}	Q. simulata type		2/35	basal disk
			other Quercus	1	0/2	none
			non-Quercus Fagaceae	1	0/4	none
5	Ramsey, NV	Oligocene (27.1) ⁸	Q. simulata type		1/8	basal disk
			other Quercus	0	0	none
			non-Quercus Fagaceae	0	0	none
4	Willamette, OR	Oligocene (30.1) ^{4 c}	Q. simulata type		0/24	none
			other Quercus	1	0/12	none
			non-Quercus Fagaceae	1	0/1	none
4	Rujada, OR	Oligocene (31.3) ^{4 c}	Q. simulata type		0/32	none
			other Quercus	0	0	none
			non-Quercus Fagaceae	0	0	none
3	Bridge Creek, OR	Oligocene (32.9) ^{5 c}	<i>Q. simulata</i> type ^{##}		1/47	basal disk (?)
			other Quercus	1	0/9	none
			non-Quercus Fagaceae	1	0/3	none
2	Grant, MT	Eocene (38.0) ^{6 b}	Q. pollardiana type		0/2	none
			<i>Q. simulata</i> type ^{##}		1/26	basal disk (?)
			other Quercus	0	0	none
			non-Quercus Fagaceae	0	0	none

1	Chalk Bluffs, CA	Eocene (48) ⁹	Q. simulata type ^{##}		0/1	none
			other Quercus	4	0/11	none
			non-Quercus Fagaceae	1	0/4	none

Age data from: 1) Schorn et al., 2007; 2) Wolfe and Tanai 1987; 3) unpublished data, Oregon State University; 4) Retallack et al., 2004; 5) Meyer and Manchester, 1994; 6) Call and Dilcher, 1997; 7) Erwin and Schick, 2007; 8) UCMP, unpublished; 9) Wolfe/USGS, unpublished. Basis of age determination from: a) mammals; b) floral evidence; c)⁴⁰Ar/³⁹Ar; d) stratigraphic position; e) K/Ar.

Galls previously reported from: *Waggoner and Poteet 1996, Stinking Water flora was re-collected for this study; ** Erwin and Schick 2007; [#] Gall-bearing leaves are from *Q. sp* which are likely members of *Q. pollardiana*-type and *Q. simulata*-type that were too fragmentary or poorly preserved to allow for positive identification ^{##} Host is *Q. consimilis*.

Galled leaves displayed either three-dimensional gall structures or gall scars (Figure 2). The number of galls per leaf varied from one or two to up to 20. The galls were located on the leaf surface, often adjacent to major veins as has been found by other authors (Waggoner and Poteet, 1996). Galls tended to be attached to the lower surface of the leaf and corresponded with a disk-like scar with a width of between 1–2 mm on the upper or lower surface. Gall scars, while not diagnostic on their own, are repeatedly found in association with preserved galls and similar structures have been attributed to cynipids by other authors (Scott et al., 1994). Gall scars could be distinguished from hole-feeding damage because holes tended to be more irregular in size and shape. Additionally, the gall scar tissue was often impressed into the leaf surface, forming a slight indentation. These features allowed gall scars to be readily distinguished from holes or other types of insect-feeding damage. Furthermore, the reaction tissue around the gall scars is generally thicker than around hole-feeding damage. Examples of structures (< 5) that are possibly galls with different morphologies than those described were also found, but were not able to be attributed to a known gall maker.

The two species of oaks on which cynipid galls were preserved, *Quercus simulata*-type and *Q. pollardiana*-type, were abundant in most of the floras examined (*Q. simulata*-

FIGURE 2. Photographs of gall structures and gall scars from the middle Miocene of western North America: 1. and 2. Part and counterpart of Quercus simulata-type leaf from the Stinking Water Formation, Oregon (UCMP #168315), previously described in Waggoner (1999); 3. Quercus pollardiana-type leaf from the Trapper Creek Formation, Idaho (UCMP #8605); 4. Quercus pollardiana-type leaf from the Fingerrock Formation, Nevada (UCMP #191949). All scale bars = 5mm. Images courtesy of D. Erwin.



type in 17 floras, *Q. pollardiana*-type in 16 floras, Table 1). *Quercus simulata*-type leaves are present in the oldest flora (Chalk Bluff, CA, Eocene), and the first Q. pollardiana-type leaves are present in the Grant flora (MT, Eocene), although the first unambiguous cynipid galls appeared later (mid-Oligocene for *O. simulata*-type, mid-Miocene for *O. pollardiana*-type), excluding the uncertain gall scars in the Bridge Creek and Grant floras. Galls were found on Q. simulata-type leaves in 8 of 17 floras in which this oak was recorded, and on Q. pollardiana-type leaves in 7 of 16 floras in which that oak was recorded. Although these two oak species xo-occur in eight floras, galls were found on leaves of both species only in the Stinking Water flora had galls on both species, even when both species were present. Seven floras were examined in which no galls were found: Chalk Bluffs (Eocene, CA); Rujada and Willamette (Oligocene, OR); Mt. Reba (Miocene, CA); Almaden and Clarkia (Miocene, ID); and Hidden Lake (Miocene, OR). The stratigraphic distribution of galled floras (Figure 3) shows that once galls were first seen on a host, they remain on that host throughout the rest of the host's stratigraphic range. Gaps in the stratigraphic range reflect a lack of floras of that age, rather than the presence of floras without galls. The age of the flora was a significant predictor of whether or not galls were found $(X_{1.22}^2 =$ 3.98, P = 0.046) as floras with galls tended to be younger, having an average age of 14 million years compared to an average age of 25 million years for floras without galls. The number of fagaceous leaves examined did not significantly affect whether or not galls were found in a flora $(X_{1,22}^2 = 1.68, P = 0.195)$, nor did the number of oak species present $(X_{1,22}^2 = 1.90, P = 0.168)$.

FIGURE 3. Stratigraphic ranges of gall-bearing oak species. Dots indicate ages of floras with gall-bearing leaves of each taxon, lines indicate entire range of each taxon.



4. DISCUSSION

4.1 Highly conserved host associations.

Throughout the range of oaks in western North America, we found no evidence for hostshifting from *Quercus simulata*-type and *Q. pollardiana*-type to either other oaks or other members of the Fagaceae. This finding is consistent with modern oak-gallwasp work (Liljeblad et al., 2008; Stone et al., 2009) and more recent fossil galls (Stone et al.,2008) showing that oak gallwasp host-shifts are exceedingly rare. Only two oak species were host to gallwasps across the floras examined that ranged in age from Eocene to Pliocene, and in the majority of floras where the oaks are found, leaf galls are also found. In both host species, the existence of the host predates the first galls by several million years. Once galls appear on leaves, however, they are found in almost all floras where their hosts are found throughout the rest of the sample, even when other potential hosts are present. This indicates that the gallwasps are moving with and identifying their hosts as their hosts expanded across western North America. The rapidity of this expansion in the Miocene does not seem to have caused a lag in the occurrence of galls and it seems that both host and gall-makers expanded simultaneously into these new areas.

The relationship between modern cynipids and their hosts is tightly constrained, and we find no evidence to suggest that the relationship was different in the past. This suggests that whatever the affinities of *Quercus simulata*-type and *Q. pollardiana*-type might actually be, they are probably closely related. Indeed, some authors have suggested that *Q. pollardiana* is an extinct version of *Q. simulata* (P. Fields pers. comm., 2010). It may be the case that *Q. simulata* and *Q. pollardiana* hybridized, which may have facilitated the shift of Cynipini to the new host *Q. pollardiana*, the later appearing species. This "hybrid bridge" hypothesis (Floate and Whitham, 1993) has been proposed to explain the movement of herbivores between hosts using hybrid species, although host shifting in oak gallwasps may be considerably more complicated (Pearse and Baty, 2012).

4.2 Implications for Models of Specialization.

Models for the development of specialized feeding relationships between herbivorous insects and plants based on examination of modern interactions tend to focus on the fitness benefits for an individual or community of insects (Jaenike, 1990). At their most general, models based on maximizing fitness rewards predict that host plants that are the most abundant and that offer the best nutritional trade-offs are most likely to be targeted by specialists. Although the prediction of these models can be difficult to extrapolate over geologic time, the distribution of galls examined in this study provides a system in which models of specialization may be
examined. *Q. simulata*-type and *Q. pollardiana*-type oaks were the two most common and abundantly preserved fagaceous species, even when other species were also available. Both species are evergreen, a leaf trait that, in oaks, often correlates with higher levels of chemical protection than deciduous leaves (Estiatre, 2007), and therefore lower levels of generalized insect herbivory (Pascual-Alvarado et al., 2008; Pearse, 2011). Evergreen leaves are nevertheless correlated with higher incidence of cynipid galls (Karban, 2007) as they are available to ovipositing insects when deciduous trees are bare and because gall-dwelling larvae are able to feed off of toxin-free leaf tissue within the gall (Kinsey, 1930; Cornell, 1983).

Two common models for specialization in herbivorous insects are: 1) evolution of generalist herbivores to specialization on a host that was already within the herbivores' range (Futuyma and Moreno, 1988) and 2) transfer of already specialized herbivores from one host to another (Bernays, 1998). Specialization in the Cynipini may follow this second path, through a transfer of the gall-making habit from other, herbaceous plant families onto oaks (Ronquist and Liljeblad, 2001). Other members of the Woody Rosid Galler group have non-oak hosts, including roses, but all show strong phylogenetic constraint between host groups and wasp groups (Liljeblad et al., 2008). Although not specifically a part of this study, preliminary observations of rosids in two Miocene floras had possible cynipid gall scars, which is consistent with modern host use patterns. Further examination of rosid materials in future studies may be able to determine the relationship between these potential galls and those of oak galls. We also examined several floras that pre-date the first appearance of galls in this region, we found no evidence of Cynipini-style galls appearing on other fagaceous genera prior to their appearance on Q. simulata. It is not possible, therefore, to interpret based on these data what the history of Cynipini wasp may have been prior to their occurrence on oaks. A more precise identification of

the gall-making wasps responsible for the damage we observed and an expanded examination of other taxa, such as the rosids, would be an important next step to answer these questions.

4.3 Implications for Gall-Maker Identity.

The similarity in morphology between the fossilized galls on western oaks provides a straightforward basis for inferring the close relationship between the gallmaking insects, although exact species identification and placement of those species within the Cynipini are difficult to determine. The affinities of some species within the form genus Antronoides are currently thought to belong with *Cynips* or to *Xanthoteres* Ashmead, 1897 (Erwin and Schick, 2007), although they had previously been assumed to be aligned with the modern genus Antron (Waggoner and Poteet, 1996; Waggoner, 1999). Cynipa and Xanthoteres are hosted by oaks in section Quercus sensu stricto today (Erwin and Schick, 2007; Stone et al., 2009). If modern Q. chrysolepis is the correct modern analog for the fossil species Q. pollardiana, this would indicate that the wasps who induced the galls on the fossil leaves had undergone a major host shift, from section Quercus to section Protobalanus (Trelease) A. Camus, 1938, the clade to which modern Q. chrysolepis belongs. The strong host fidelity between gallwasps and their hosts makes it unlikely that a major host shift, such as would be necessary to move from section *Protobalanus* species, to a section Quercus species, would occur. Shifts of this magnitude have not been found to occur in modern oak-Cynipini relationships (Stone et al., 2009), and there is no fossil evidence thus far that would support such a shift. Therefore, the assignment of gall species of the genus Antronoides to either Cynips or Xanthoteres may be in error.

We suggest that an alternative explanation to a major host shift is at work in the cynipids of western North America and that their affinity lies with modern gall making genera of Q.

chrysolepis of the tribe Cynipini, such as *Andricus* Hartig, 1840 or *Heteroecus* Kinsey, 1922. Gall-inducing insects from closely related species can produce galls of varying morphologies (Stone and Schönrogge, 2003), and modern genera induce a wide range of gall types that encompass the range of morphologies seen in the fossil forms (Figure 4). The galls we observe on *Q. simulata*-type and *Q. pollardiana*-type leaves are consistent with the modern pattern of host-conservatism seen in these wasps. Regardless of which genus these galling insects actually represent, these fossil galls were certainly produced by a member of the Cynipini, those most closely tied with modern oaks in western North America (Liljeblad et al., 2008).

Another area in which galls might give information about their host's identity is with the larger placement of *Q. pollardiana* and *Q. simulata* within the genus *Quercus*. Most authors (Axelrod, 1995; Retallack, 2004; Buechler et al., 2007) consider extant *Q. chrysolepis* Liebmann, 1854 (canyon live oak) an oak in section *Protobalanus*, to be the nearest living relative of *Q. pollardiana*. The relationship of *Q. simulata* to extant oak species is more problematic. The most rigorous treatment of the systematic placement of *Q. simulata* is in Fields (1996), where a wide range of evidence including acorn morphology are considered to place the "*Quercus simulata* morphoplex" somewhere in section *Lobatae* (G. Don) Louden, 1830. Work based solely on morphological characters in oaks, however, has been repeatedly undermined by convergence (Manos et al., 1999), and *Q. simulata* leaves have been attributed to every section within the genus *Quercus* (Bortgard and Pigg, 1999), including section *Protobalanus* (Wolfe, 1964). Therefore, insect herbivory may be usable to help identify different oak species as it has been used in other host plants (Floate and Whitham, 1995).

FIGURE 4. Photographs of fossil and modern gall structures: 1. Galls on *Q. pollardiana* from the Gilliam Springs flora, Miocene, Nevada (UCMP #398561), previously described in Waggoner and Poteet (1996), scale bar = 5mm; 2. Detachable gall of *H. sp.* on *Q. chrysolepis* (section *Protobalanus*), overall gall length approximately 13 mm; 3. and 4. Detachable galls of *X. clavuloides* on valley oak, *Q. lobata* (section *Quercus* s.s.), overall gall lengths approximately 7mm and 8.5mm respectively; 5. Integral gall of *H. flavens* on huckleberry oak, *Q. vaccinifolia* (section *Protobalanus*), overall gall diameter approximately 6mm. Fossil gall image courtesy of D. Erwin, modern gall images courtesy of J. DeMartini.



4.4 Origins of Gallwasps in Western North America.

The biogeographic complexities of the Cynipini make it difficult to infer the area of origin for this group, although they likely have roots in Asia (Abe et al., 2007; Stone et al., 2009). The fossil record of galls has provided evidence for inferring the pattern of diversification of cynipines across western North America (Kinsey, 1930; Kinsey, 1936; Waggoner and Poteet, 1996; Ronquist, 1999; Waggoner, 1999; Erwin and Schick, 2007) and documenting their presence by the Miocene. Fossil gall evidence can therefore augment the scarce record of body fossils, such as the single cynipoid from the Eocene of Colorado (Ronquist, 1999). The pattern of gall distribution underscores the similarity in timing of diversification between the Cynipini and major groups of modern North American oaks, which likely happened more or less in place from the Eocene through the Miocene (Axelrod, 1983; Manos et al., 1999). While other authors also have suggested a concomitant radiation of oaks and oak gallwasps (Stone et al., 2001; Liu et al., 2007; Liljeblade et al., 2008), we find several early floras in which Q. simulata or similar oaks (e.g. *Q. consimilis* Newberry, 1883) are preserved without galls. Although it is possible that there may have been some galls present but not preserved, especially for floras with low numbers of preserved leaves such as the Chalk Bluffs flora, it does leave open the possibility that the radiation of gallwasps into western North America was secondary to the radiation of their hosts. The possible appearance of galls in the Grant flora (38.0 Ma), the Bridge Creek flora (32.7–33.0 Ma) and the Ramsey flora from Nevada (27.1 Ma) followed by a profusion of galls of Miocene age from across the western United States suggests that the radiation of this group of gallwasps occurred more or less simultaneously across a wide geographic area.

5. CONCLUSIONS

Gall structures on *Q. simulata*-type and *Q. pollardiana*-type oaks are abundant and widespread, and are not associated with other oak species. Although this finding might appear to be at odds with the presumed host shift of these gallwasps onto the oak species on which they are found on extant oaks, we believe that this pattern more likely reflects the difficulties in aligning fossil and modern gallwasps, rather than a host-shift.

We find early evidence of galls on floras from both Oregon and Nevada that are of similar age. While the circular gall-like scars on the leaf from the ~38 Ma Grant flora may represent the first occurrence of cynipid galls in the West, the appearance of both galls and gall scars from many locations across the west in the middle Miocene suggests that the radiation of gallwasps occurred nearly simultaneously in many areas. The impressive fossil record of oak leaves from this region clearly demonstrates a relationship with gallwasps that was rapidly established over a broad geographic range and that has been maintained over evolutionary time.

CHAPTER 4. THE EFFECTS OF CLIMATE CHANGE AND HOST-SPECIFICITY ON LEAF HERBIVORY IN WESTERN OAKS

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ABSTRACT

The interaction between plant-eating insects and their hosts are hypothesized to shift dramatically as global temperatures increase. Examination of both modern and fossil leaves has led to generalized predictions of increased herbivory in a warmer world. However, climate induced changes in the relationships between herbivorous insects and their specific host plant taxa may differ from the responses that have been documented for entire plant communities. To examine how climate affects herbivory in a single, ecologically widespread host taxon we studied insect feeding damage on the fossilized leaves of oaks (Quercus), which are host to a diverse group of herbivores and have been broadly distributed in western North America throughout the Cenozoic. Their occurrence across wide climatic zones makes them ideal for evaluating whether intensity of leaf herbivory has had a positive relationship with temperature and precipitation levels through time. We examined leaves of oaks with ages that range from Eocene to Pliocene (38 to 5 Ma) with a range of mean annual temperatures (6.5–17.6°C) and 3month average precipitation levels (9.8-78.2 cm) to test whether insect damage on oaks is more intense in floras that grew under warmer and wetter conditions and whether climatic variation has similar effects on specialist and generalist insect herbivores.

Examination of leaves from thirteen floras shows that neither mean annual temperature nor average precipitation was a significant determinant of overall insect damage. Herbivory made by endophagous insects (*e.g.* gallers and leaf miners) was more prevalent in dry conditions. Temperature was also a significant determinant of gall and leaf mine damage; warmer floras tended to have more galls and less leaf mines. In addition, gallers and leaf miners show a high degree of host-fidelity through time such that the same traces of insect feeding damage are found

on the same oak hosts across many floras over time. This pattern of host-fidelity suggests that the interactions between oaks and their specialized, endophagous insect herbivores are more climatically sensitive than those of their more generalized, exophagous herbivores, and that future climatic change may not affect all host-herbivore systems, nor all herbivores within a single host system, in the same ways.

1. INTRODUCTION

Insect herbivory has a history that began with early terrestrial ecosystems of the Paleozoic (Labandeira et al., 1994; Bethoux et al., 2004; McLoughlin, 2011) and insect feeding has continued to evolve and diversify through time (Ehrlich and Raven, 1964; Labandeira and Sepkoski, 1993; Farrell and Mitter, 1998; Berenbaum, 2001; Klavins et al., 2005; Janz et al., 2006; Brandle et al.,2008). Modern insects and plants are widespread, abundant, and diverse, which may be a result of their influence on each other's evolutionary histories through time (Futuyma and Moreno, 1988; Berenbaum, 2001). Phylogenetic comparisons of insect herbivores and their hosts suggests that several groups have undergone coevolution as evidenced by highly selective feeding strategies in insects and specialized chemical and morphological defenses of their hosts (Ehrlich and Raven, 1964; Bernays and Graham 1988; Berenbaum, 2001; Nyman et al., 2006; Ramamurthy, 2007).

Work on plant-insect interactions in both modern and fossil systems has found that the interactions between insects and their host plants is correlated with climatic variables (Landsberg and Gillieson, 1995; Coley and Barone, 1996; Wilf et al., 2001; Logan et al., 2003; Andrew and Hughes, 2007; Currano et al., 2008; Smith, 2008; Brenes-Arguedas et al., 2009; Winkler et al., 2009; Currano et al., 2010; Adams et al., 2011; Garibaldi et al., 2011). Temperature, in particular,

has been shown to have a strong and generally positive effect on herbivory (Bale et al., 2002; Logan et al., 2003), which may be related to host plant developmental rates, phenology, and leaf chemistry (Went, 1953; Reich and Oleksyn, 2004; Reich et al., 2007; Veteli et al., 2007; Körner and Basler, 2010; Hänninen and Tanino, 2011) as well as insect development and population dynamics (Sanderson, 1910; Headlee, 1941; Davidson, 1944; Wagner et al., 1985; Gilbert and Raworth, 1996; Régnière et al., 2012).

The effect of precipitation on the degree and types of herbivory experienced by plants is less well understood (Bale et al., 2002; Ellwood et al., 2012). Precipitation levels can affect the abundance, development, and distribution of plants and insects, while also affecting the nutritional quality and defenses of plants (Ordoñez et al., 2009; Gutbrodt et al., 2012; Mazía et al., 2012). Average rainfall may directly or indirectly influence the types of insects that can utilize plant hosts and the amount of leaf tissue herbivores consume (Bale et al., 2002; Gutbrodt et al., 2012; Mazía et al., 2012). Thus, changes in precipitation can influence the type and strength of interactions that occur between plants and insects. Work on endophagous (internalfeeding) insects, such as those that make galls or leaf mines, has shown them to be particularly sensitive to variation in precipitation relative to exophagous (external-feeding) insects. Gallinducing insects have higher survivorship in dry climates (Fernandes and Price, 1992; Price et al., 1998), although dry conditions decrease survivorship for leaf mining insects (Fernandes et al., 2004; Yarnes and Boecklen, 2005).

Examining insect herbivory in deep time also can illuminate the longevity of relationships between plants and their specialized herbivores. Specialization of insects on their host plants is a successful and recurring evolutionary theme across many lineages (Mitter et al., 1991; Bernays, 1998, Ward et al., 2003). Insects that are specialists (*i.e.* feed on a restricted set

of host-plants) are thought to have an association with their host that has persisted for millions of years (Futuyma and Moreno, 1988; Berenbaum, 2001). Instances of specialized insect feeding have been reported in the fossil record, where fossilized plant tissues with herbivore damage are preserved, and are similar to damage made on extant members of those plant groups (Labandeira et al., 1994; Wilf et al., 2005; Krassilov, 2008; Smith, 2008; Wappler, 2010). Leaf galling and leaf mining insect damage provide some of the clearest examples of specialized herbivore damage preserved on fossil leaves. These specialist herbivores have relationships with their hosts that are thought to persist relatively unchanged for millions of years (Moran, 1989), resulting in a tight phylogenetic congruence between the clades of herbivores and their hosts (Farrell and Mitter, 1998; Ronquist and Liljeblad, 2001; Ward et al., 2003; Ramamurthy, 2007).

In this study, we examine the unique relationship between one host plant group and its suite of herbivores over evolutionary time. We focus on a single host taxon and follow it through time and across varying climatic regimes, which allows us to determine whether more generalized, exohphagous or specialist, endophagous insect herbivores are most climate-sensitive. The oaks (*Quercus*, Fagaceae) are a modern plant group that has both abundant and well-preserved fossils; making it possible to examine the effects of climate change on oak herbivory over millions of years. In addition, the suite of endophagous and exophagous insects that feed on oaks in modern ecosystems is well known. Modern endophagous herbivores have been found to be sensitive to climatic variation, particularly variation in precipitation (Fernandes and Price, 1992; Price et al., 1998; Fernandes et al., 2004; Yarnes and Boecklen, 2005; Leckey et al., *Accepted*) and in this study we examine whether these patterns occur and can be detected over millions of years. If climate is a primary driver of herbivory, as whole-flora studies have suggested, then we expect to find levels of herbivory increasing in tandem with increasing

temperature and precipitation through time. We also expect that the abundance of insect damage made by specialists will show a positive relationship with precipitation, consistent with modern patterns. Finally, we examine differences in patterns of host-fidelity and document these associations through time. These patterns are not only important to understanding past drivers of plant-insect interactions, but also allow us to better predict how plant-insect interactions may be affected under future climatic change scenarios (Lewinsohn et al, 2005; Zvereva and Kozlov, 2006; Wolf et al., 2008; Leimu et al., 2012).

2. MATERIALS AND METHODS

2.1 Oaks of the western United States

The Fagaceae have been a major component of terrestrial floras in western North America since the mid-Cenozoic (Axelrod, 1983). Their excellent preservation in broadly distributed floras makes them uniquely suited to analyzing the history of their association with insect herbivores. The oaks (*Quercus*) and beeches (*Fagus*) along with *Castanaea* and *Lithocarpus* are common and abundant fagaceous genera in most Neogene western floras. Their abundance may be aided by the high preservation potential of the scelrophylous leaves of many evergreen oak species, although deciduous oaks are also well represented in the fossil record, as are other plant organs (Borgardt and Pigg, 1999). Today, the Fagaceae, and oaks especially, form an integral part of western landscapes as components of major ecosystems such as oak savannas and oak-pine forests. They are host to a wide range of generalist and specialist herbivores (Cornell and Washburn, 1979; Swiecki and Bernhardt, 2006; Pearse and Hipp, 2009), some of which are expected to have been restricted to using oaks as hosts for millions of years (Stone et al., 2009). In western fossil floras, the majority of leaves come from evergreen oak species *Q*. *pollardiana* and *Q. simulata. Quercus pollardiana* has been aligned with the modern species *Q. chrysolepis* (Axelrod, 1995); the affinities of *Q. simulata* are more difficult to determine, although it is also likely closely related to *Q. chrysolepis* (Fields, 1996; Erwin and Schick, 2007). Additionally, many deciduous species are preserved, such as *Q. pseudolyrata* and *Q. prelobata*, species aligned with modern California Black oaks and Valley oaks (*Q. kelloggii* and *Q. lobata*). It is possible that the dominance of *Q. pollardiana* and *Q. simulata* represents a taphonomic bias, as many aspects of preservation can influence the abundance of taxa in a flora (Burnham 1994, Ellis and Johnson, 2013). These two species may be over-represented because, as evergreen oaks, their leaves are thick and tough, giving them increased durability during transport (Spicer and Wolfe, 1987).

This study examines the leaves of the oaks (*Quercus*) preserved in floras with ages ranging from Eocene to the beginning of the Pliocene (38–5 Ma). We used museum collections to obtain the largest possible collection of leaves from across the western United States and to maximize the temporal range of floras. We focused on the collections of the University of California Museum of Paleontology, the National Museum of Natural History, and the University of Colorado Museum of Natural History, due to their large holdings of western floras. Floras were included if they had a minimum of 12 *Quercus* leaves (average n = 156 leaves) and were located in western North America. We included floras that are preserved in similar depositional environments. Most leaves included in our sample were identified by previous workers, but the remainder were identified using shape, tooth morphology, and vein architecture. That leaves from the same species can have distinctly different appearances may have led previous identifiers to over split oak species. For this reason, we took an inclusive approach to

identifying leaves, aiming to unite taxa with general overall similarity and accepting broad species definitions, as other workers have done (Fields, 1996).

The floras we examined span an approximately 25 million year time period, during an interval of global climatic change (Zachos et al., 2001). Previous work using the Climate Leaf Analysis Multivariate Program (CLAMP, Wolfe, 1993; 1995) gives estimates for many of these floras with a range of mean annual temperature (MAT) from approximately 6.5°C to 17.6°C and 3-month average precipitation levels of 9.8 cm to 78.2 cm, obtained by averaging the estimated rainfall of the three wettest and three driest months (data from Yang et al., 2011). Previous studies of the effects of temperature on insect leaf herbivory suggest that this range in temperatures is sufficient for detecting a climatic signal, if present (Currano, 2008; Smith, 2008).

2.2 Paleofloral Regions and Floras

Fossil leaves were preserved in lacustrine or floodplain shales and siltstones from across several western U.S. states (Figure 1). Tectonic and volcanic activity in western North America during the late Paleogene and Neogene formed basins that preserved the abundant fossil floras that are the basis of this study. The floras are categorized within four paleofloral regions that have broad taxonomic similarities: the Great Basin and Southern Oregon; the Columbia Plateau; the Western Cascades; and Central and Southern California (adapted from Schorn et al., 2007). We sought to include floras that had similar depositional environments and an abundance of oaks, although many of the floras initially identified were excluded because they did not have sufficiently well-preserved oak fossils (e.g. the Tehachapi and Alvord Creek floras). Other floras were examined, but excluded from statistical analyses because of a lack of robust climatic estimates (e.g. the Almaden, Cascadia, Latah, Mint Canyon, Ruby and Washoe floras). Paleoclimatic estimates for the discussed floras obtained using the methods described in section

2.3.

FIGURE1. Map of the western United States showing locations of Eocene/Oligocene floras (black circles), Miocene floras (grey circles), and Pliocene floras (open circles) in principal paleofloral regions: Great Basin floras: 1. Buffalo Canyon (Miocene); 2. Fingerrock Wash (Miocene); 3. Stewart Valley (Miocene); 4. Trapper Creek (Miocene); 5. Washoe (Miocene). Columbia Plateau floras: 6. Almaden and Latah (Miocene); 7. Bridge Creek (Oligocene); 8. Clarkia (Miocene); 9. Grant (Eocene); 10. Mascall (Miocene); 11. Stinking Water (Miocene). Western Cascades floras: 12. Cascadia (Miocene); 13. Willamette (Oligocene). 14. Hidden Lake (Miocene) and Southern Central California floras: 15. Mint Canyon (Miocene); 16. Temblor (Miocene); 17. Turlock Lake (Pliocene); 18. Webber Lake (Miocene).



Ages for the floras were obtained from the existing literature (Table 1), which included the use of a variety of methods for dating. For floras interspersed with volcanics, ⁴⁰Ar/³⁹Ar or K/Ar dates are available. Other floras have mammalian faunal elements preserved in close proximity, for which an age can be estimated. Several of the floras have not yet been wellstudied, and, for these, a taxonomic comparison with geographically proximal floras was used to provide a biostratigraphic age estimate (Retallack et al., 2004; Schorn et al., 2007).

2.2.1 Floras of the Great Basin and southern Oregon (Buffalo Canyon, Fingerrock Wash, Stewart Valley, Trapper Creek)

Many of these floras are preserved in broad basins formed by the opening of the Basin and Range province in the Nevada-California area or in fluviolacustrine and back-arc basins in the eastern Cascades of Oregon and southwestern Idaho (Schorn et al., 2007). The influence of magmatic activity is apparent in the depositional setting of many of these floras. The Buffalo Canyon flora (15.4 Ma) of western Nevada is preserved in a depression left after magmatic depletion of a volcanic complex (Axelrod, 1991); Fingerrock Wash (15.4 Ma) and Stewart Valley (14.5 Ma), also of western Nevada, are preserved in a sequence of interbedded shale and fluvial tuff (Wolfe, 1964); and Trapper Creek (12.5 Ma), from southern Idaho, is lacustrine, but in an ashy-shale deposited on a delta within the lake (Axelrod, 1964). Ages for these floras are based on dating of interbedded volcanics (Schorn et al., 2007). The Great Basin floras considered here are primarily of middle Miocene age.

Relatively dry, mesic climates have been interpreted for these floras (Wolfe, 1964), based on the dominance of plant taxa such as live oaks (Wolfe, 1964) as well as deciduous hardwoods

and scrub vegetation (Axelrod, 1991). The Stewart Valley flora (MAT 9.3 °C, 3-month average ppt. 9.8 cm) has more lacustrine taxa than the other floras of this region, (Wolfe, 1964), although the Buffalo Canyon (MAT 6.5 °C, 3-month average ppt. 16.7 cm) and Fingerrock Wash (MAT 8.8 °C, 3-month average ppt. 22.2 cm) floras have similarly cool, dry CLAMP estimates. The presence of a large component of evergreens in some of the floras (particularly the Trapper Creek flora, MAT 7.7 °C, 3-month average ppt. 24.3 cm) indicates that they may have been growing at altitudes greater than floras in other regions (Axelrod, 1964; Axelrod, 1991).

TABLE 1. Ages of examined floras, arranged stratigraphically and numbered corresponding to their position in Figure 1. Floras excluded from statistical analyses due to lack of climatic data indicated with an asterisk.

Flora	Age (Ma)	Basis of Age
Turlock Lake (17)	5.0 ¹	mammalian biostratigraphy
Washoe*(5)	5.2^{-1}	mammalian biostratigraphy
Hidden Lake (14)	$11.7^{\ 2}$	floral evidence
Trapper Creek (4)	12.5^{-1}	40 Ar/ 39 Ar
Mint Canyon*(15)	12.5^{-1}	mammalian biostratigraphy,
• • •		stratigraphic position
Stinking Water (11)	12.5^{-1}	K/Ar
Almaden* (6)	$14.0^{\ 2}$	floral evidence
Stewart Valley (3)	14.5^{1}	40 Ar/ 39 Ar
Webber Lake (18)	15.1^{1}	floral evidence, stratigraphic
		position
Latah*(6)	15.2^{-1}	K/Ar
Mascall (10)	15.2^{-1}	mammalian biostratigraphy, K/Ar
Temblor (16)	15.3^{-1}	mammalian biostratigraphy,
		stratigraphic position
Buffalo Canyon (1)	15.4^{-1}	⁴⁰ År/ ³⁹ År
Fingerrock Wash (2)	15.4^{-1}	40 Ar/ 39 Ar, K/Ar
Clarkia (8)	15.5^{-1}	K/Ar
Cascadia*(12)	15.8 ³	40 Ar/ 39 Ar
Willamette (13)	30.1 4	40 Ar/ 39 Ar
Bridge Creek (Painted Hills) (7)	32.9 ⁵	$^{40}Ar/^{39}Ar$
Grant* (9)	~37.8 ⁶	floral evidence

Age data from: 1) Schorn et al.,2007; 2) Wolfe and Tanai 1987; 3) unpublished data, Oregon State University; 4) Retallack et al.,2004; 5) Meyer and Manchester, 1997; 6) Call and Dilcher 1997.

<u>2.2.2 Floras of the Columbia Plateau</u> (*Bridge Creek [Painted Hills], Clarkia, Mascall, Stinking Water*)

Many of the Columbia Plateau floras are preserved in sedimentary beds deposited by streams blocked by basalts of the Columbia River Basalt flows (CRBs). The lacustrine deposits in which most of the floras of the Columbia Plateau were preserved are generally fine claystones with interbedded ash. The Bridge Creek flora is preserved in a series of relatively contemporaneous lake facies of the John Day Formation from central Oregon, formed by structural depressions made by lava flows and consisting of tufaceous lacustrine shales (Meyer and Manchester, 1997). We examined leaves from one locality within the Painted Hills assemblage (32.7–33.0 Ma, Meyer and Manchester, 1997), part of the Eastern Facies of the John Day Formation. The Clarkia and Mascall floras are lake shales interbedded with CRBs and all, have ages based on adjacent basalts (Prothero et al., 2006; Schorn et al., 2007). The Clarkia beds, in which the Clarkia flora is preserved, are slightly older and contain multiple ash beds within fine silty claystones (Smiley and Rember, 1985a). The Mascall flora is a large and diverse flora from central Oregon of which we examined one locality, White Hills (15.2 Ma, Schorn et al., 2007), which is composed of fine gray tuff in which the leaf-bearing units consist of diatomaceous ash (Chaney and Axelrod, 1959). The Stinking Water flora has been considered part of the Mascall flora (Chaney and Axelrod, 1959) and shares taxonomic similarities with it. The locality we sampled is younger (12.5 Ma, Schorn et al., 2007) and geographically separated from our Mascall flora locality, therefore, we treat them as discreet floras.

In comparison to the Great Basin floras, the Columbia Plateau floras tend to reflect moist, temperate growing climates free from severe shifts in temperature. These floras tend to have cool, moist climatic estimates, as with the Stinking Water (MAT 9.6 °C, 3-month average ppt. 26.7 cm) and Mascall (MAT 8.8 °C, 3-month average ppt. 27.0 cm) floras. The Bridge Creek flora

(MAT 7.8 °C, 3-month average ppt 32.6 cm) is thought to have grown under conditions that correlate most closely with modern temperate hardwood forests of Asia (Meyer and Manchester, 1997). The Clarkia flora (MAT 9.2 °C, 3-month average ppt. 39.0 cm) also has affinities with modern Asian forests, although many of the fossil taxa are similar to those inhabiting northern Idaho today (Smiley and Rember, 1985b).

2.2.3 Floras of the Western Cascades (Hidden Lake, Willamette)

These floras come from western Oregon where, during the upper Oligocene and Miocene, local geology was heavily influenced by the formation of the CRBs and Little Butte Volcanics (Schorn et al., 2007). The floras are preserved in lacustrine shales, interbedded with ash and basalt (Retallack et al., 2004). The Hidden Lake (11.7 Ma, Wolfe and Tanai, 1987) flora is Miocene in age, given its relationship to the CRBs, while the Willamette flora (30.1 Ma, Retallack et al., 2004) has been interpreted as Oligocene.

The floras of the Western Cascades are taxonomically and ecologically similar due to the plentiful rainfall across the area (Schorn et al., 2007). Paleoclimatic estimates for Hidden Lake flora (MAT 8.0 °C, 3-month average ppt. 18.5 cm) are cooler and drier than for the Willamette flora (MAT 13.3 °C, 3-month average ppt. 53.9 cm), yet both represent a moist and mild climate, dominated by broad-leaved deciduous trees. Although these floras have not been monographed, they have received attention from paleobotanists for their diversity and ecological importance (Wolfe and Tanai, 1987).

2.2.4 Floras of Central and Southern California (Temblor, Turlock Lake, Webber Lake)

The wide range of depositional environments represented by these floras reflects the diversity of terranes found between central and coastal California during the Neogene. These floras are located in terrestrial deposits interbedded with marine sediments (Temblor, 15.3 Ma and Turlock Lake, 5.0 Ma), and lakes formed by debris flows acting as dams (Webber Lake, 15.1 Ma). Ages for the floras are based primarily on associated mammal fossils and their inferred stratigraphic relationship with other floras (Schorn et al., 2007). The floras of this region are preserved in fine-grained, shallow lacustrine deposits.

The Temblor flora (MAT 17.6 °C, 3-month average ppt. 78.2 cm) has not been well studied, although interpretations of its ecology have been made based on its geographic position and the inferred low elevation growing conditions of the plants (Axelrod, 1956; 1995). The Temblor flora is most similar taxonomically to mesic floras from the northern California/Nevada border and shares many warm-temperate elements with Oregon Miocene floras such as Succor Creek (Axelrod, 1956). This is also true for the Webber Lake flora (MAT 12.8 °C, 3-month average ppt. 31.4 cm), which also has affinities with mesic floras that have a large component of temperate evergreen species and the Turlock Lake flora (MAT 14.4 °C, 3-month average ppt. 33.0 cm) which has many scrub species, indicating an environment similar to, but wetter than today's climate in central California (Axelrod, 1980).

2.3 Paleoclimate Estimation

Paleoclimatic estimates for all study floras were obtained using the Climate-Leaf Analysis Multivariate Program (Wolfe, 1993; 1995), published by Yang et al. (2011, Table 2). We use MAT as our temperature parameter because MAT has been found to be the most robust

of the temperature parameters provided by CLAMP (Wilf, 1997), especially for floras with a large number of taxa (Green, 2006). For precipitation, we average the precipitation estimated for the three wettest and three driest months. This estimate of precipitation allows us to mitigate the tendency of the CLAMP method to overestimate annual precipitation (Wilf, 1997; Wilf et al., 1998). Although CLAMP analyses have been criticized because standardizing analyses between workers is difficult (Wilf, 1997; Peppe et al., 2011), we use estimates compiled by Yang et al, (2011) a single group of workers whose estimates use a simplified coding system to ensure greater accuracy.

Many potential sources of uncertainty exist for paleoclimatic reconstruction using fossil floras. Difficulties range from incomplete preservation of leaves whose characters are used to infer past climates, to calibration complications that arise from the differences between modern, open-vegetational sites where the climatic data used to calibrate paleoclimatic estimates and the forest environments represented in most fossil floras. These difficulties lead to uncertainty in paleoclimatic estimates, some of which can be approximated, and others of which are unknown. These methods are, therefore, constantly being revised. Estimated errors for MAT using the CLAMP method are generally within 1.5 °C, and yield estimates comparable to other leaf physiognomic methods (Uhl et al., 2007; Yang et al., 2007). Estimates were available for most floras, but floras that were not included in Yang et al. (2011) were not included in the statistical analyses.

<u>TABLE 2.</u> Estimated values for paleoclimatic parameters of included floras obtained using CLAMP methods and the grid-adjusted Physg3brc dataset (data from Yang et al., 2011). Mean annual temperature and 3-month average precipitation (derived from averaging the CLAMP scores for the 3-wettest and 3-driest months) and their estimated uncertainties are given.

Flora	Number of	MAT (°C)	MAT	3 month	Precip.
	Taxa		estimated	average	estimated
			uncertain.	Precip.	uncertain.
			(2.1 °C)	(cm)	(2.3 cm)
Turlock Lake	15	14.4	12.3–16.5	33.0	30.7–35.3
Hidden Lake	20	8.0	5.9–10.1	18.5	16.2-20.8
Trapper Creek	14	7.7	5.6–9.8	24.3	22.0-26.6
Stinking Water	16	9.6	7.5–11.7	26.7	24.4-29.0
Stewart Valley	32	9.3	7.2–11.4	9.8	7.45-12.1
Webber Lake	32	12.8	10.7 - 14.9	31.4	29.1-33.7
Mascall	28	8.8	6.7–10.9	27.0	24.7-29.3
Temblor	22	17.6	15.5–19.7	78.2	75.9-80.5
Buffalo Canyon	23	6.5	4.4-8.6	16.7	14.4–19.0
Fingerrock Wash	25	8.8	6.7–10.9	22.2	19.9–24.5
Clarkia	26	9.2	7.1–11.3	39.0	36.7-41.3
Willamette	18	13.3	11.2–15.4	53.9	51.6-56.2
Bridge Creek*	19	7.8	5.7–9.9	32.6	30.3–34.9
	1 D 1 C				

*estimate from Gray's Ranch flora

FIGURE 2. Range of 1. Mean annual temperatures and 2. 3-month average precipitation levels for all floras. Error bars show one standard deviation of the calibration data of the Physg3brc dataset (Yang et al., 2011).



2.4 Assessment of herbivory

To study the evolutionary history and effects of climate change on insect feeding on oaks, we examined the traces of insect feeding damage left on fossilized leaves. Both exo- and endophagous insects are responsible for leaf damage, and the types of leaf damage associated with exophagous insects (hole feeders, margin feeders and skeletonizers) are distinct from those of endophagous insects (Labandeira, 1998), with endophagous insects tending to be more host restricted (Gaston, 1992). To capture feeding differences between insect groups, we categorize insect damage into five functional feeding types following Smith (2008), including both exophagous (hole feeders, margin feeders and skeletonizers) and endophagous (leaf miners and gallers) types. These feeding categories allow us to distinguish between insects that are host specific and only feed on one to a few hosts and insects that may feed on a range of hosts. For example, endophagous insects such as leaf miners and gall-inducing insects are generally specialized to feed only on a single type of host plant (Jaenike, 1990; Gaston et al., 1992; Stone and Cook, 1998; Nyman et al., 2006; Yamazaki, 2010), whereas many insects that are exophagous (resulting in damage such as holes or margin removal), can move among hosts (Bernays, 1998).

Insect damage was identified by the presence of reaction tissue (as per Smith, 2008) around missing leaf tissue, and was, in this way, distinguished from leaf tissue removed by mechanical destruction or decay. Insect damage was quantified in four ways for each leaf: 1) presence or absence of damage; 2) average amount in cm²; 3) percentage of leaf tissue removed (estimated within increments of 5%); and 4) number of functional feeding groups present in each flora. We used these multiple measures to capture different aspects of insect feeding. Presence or absence of damage gives an overall sense of the abundance of herbivores in the local insect

community, with the expectation that larger communities of herbivores will lead to a larger number of damaged leaves. The average amount of leaf tissue removed and percent leaf tissue removed quantify the amount consumed by herbivores. This allows us to look at the amount of tissue that individual insects are removing from leaves. The difference between amount and percent of leaf tissue removed to capture potential differences in leaf size within host species. Percent area removed allows us to compare herbivory levels between large leaves and small leaves while average amount of leaf tissue removed (measured in cm²), allows us to examine the volume of leaf tissue being consumed. The number of functional feeding groups represented gives a conservative estimate of the diversity of herbivores and the number of different feeding guilds that are using oaks as hosts, which allows us to examine whether patterns of herbivory in some guilds of insects are more sensitive than others to climatic variation.

2.5 Statistical analyses

All statistical analyses were performed using JMP, Version 8 (SAS Institute, 1989-2012). To examine the effects of temperature and precipitation on overall herbivory, we included MAT, average precipitation, and the number of leaves in the sample in a general linear model (GLM). Temperature, precipitation and sample size were then compared with each of the three herbivory metrics in a multiple regression: the percentage of leaves with herbivore damage present per flora; the approximate amount of leaf tissue removed per flora; and the number of functional feeding groups represented in each flora. Herbivory measurements that were calculated as a percentage (percent of leaves in a flora with insect damage and average amount of leaf tissue removed) were normalized by use of a logit-transformation (Warton and Hui, 2011). To meet the assumptions of normality, the actual area removed was also log transformed in all analyses. In

each of these models, we also tested for interactions between temperature and precipitation in explaining different metrics of herbivory.

To examine the relationship between specialized (endophagous) leaf damage and climate, incidence of leaf mining and gall damage were recorded and the number of different gall and mine types were determined for each flora. Where possible, the identity of leaf mining and galling insects was determined by comparison with fossil and modern leaf damage. Leaf mines and galls were expected to be rare in all floras, so we used presence/absence data to compare their distribution among floras. Logistic regression analyses were run separately for gall inducing and leaf mining insects, and tests for potential interaction between temperature and precipitation were included.

3. RESULTS

The fifteen sampled floras include 2,756 oak leaves from 20 oak species with an average of 145 leaves per flora, and the number of oak leaves available for each flora varies widely (*e.g.* 12 leaves at Clarkia compared to 1,112 at Fingerrock Wash; Table 3). Insect damage is found on almost half of the leaves sampled (46.8%, SD \pm 16.2%, range 23.1–75.5%), although the actual amount of leaf tissue removed and percent leaf tissue removed per leaf are low (actual removed: 0.69 cm², SD \pm 0.71, range 0.1–2.5 cm²; percent removed: 4.4%, SD \pm 2.2%, range 1.5%–8.3%). Exophagous feeding damage is common, with all floras exhibiting hole and margin feeding damage and almost all floras preserving skeletonizing damage. Endophagous damage is found in several floras, although the number of leaves in any one flora with these types of damage are rare (average of one mined leaf and four galled leaves per flora), which is consistent with other studies of fossil leaf herbivory (Smith, 2008; Winkler et al., 2010).

3.1 Effects of climate on overall patterns of herbivory

The floras examined display a range of mean annual temperature (6.5–17.6°C) and average 3-month precipitation (9.8–78.2 cm), and no significant interactions between MAT and average precipitation are found in GLMs for any damage variables. In GLMs that include temperature, precipitation and the number of leaves in the flora, temperature has no significant effect on overall herbivory across oak species (Table 4), in terms of the percentage of leaves in a flora with damage ($F_{1, 12} = 0.03$, P = 0.877), the actual amount of leaf area removed ($F_{1, 12} = 2.62$, P = 0.140), the percent of leaf area removed ($F_{1, 12} = 0.88$, P = 0.373), or the number of feeding types present ($F_{1, 12} = 1.16$, P = 0.310). Similarly, models that control for temperature and the number of leaves in a flora with damage of leaves in a flora with damage of leaves in the flora show no significant correlation between precipitation and overall herbivory: percentage of leaves in a flora with damage ($F_{1, 12} = 0.02$, P = 0.895); actual area removed ($F_{1, 12} = 4.15$, P = 0.072); percent area removed ($F_{1, 12} = 0.53$, P = 0.485); and number of feeding types present in these models ($F_{1, 12} = 0.37$, P = 0.559).

TABLE 3. Amount and types of herbivore damage on oak leaves in each flora. Damage made by insects is categorized by functional feeding groups: H=Hole feed, M=Margin feed, S=Skeletonizing, LM=Leaf Mine and G=Gall. Endophagous insect damage (leaf mines and galls) emphasized in bold. Temperature and precipitation estimates from Yang et al. (2011)

Flora	Number of	% leaves	Average	Average %	Functional	Mean Annual	3-Month
	Oak Leaves	with	leaf area	leaf area	Feeding groups	Temperature	Average Ppt.
		damage	removed	removed	present	^{(o} C)	(cm)
			(cm^2)				
Turlock Lake	39	30.8	0.10	3.33	H, M, G	14.4	33.0
Washoe*	91	36.3	0.17	3.85	H, M, S, LM , G		
Hidden Lake	46	41.3	0.50	2.75	H, M, S	8.0	18.5
Trapper Creek	74	24.3	0.17	2.50	H, M, S, LM , G	7.7	24.3
Mint Canyon*	198	31.9	0.47	2.69	H, M, S, LM , G		
Stinking Water	218	48.3	0.85	5.30	H, M, S, LM , G	9.6	26.7
Almaden*	144	35.7	0.11	1.58	H, M, S		
Stewart Valley	116	57.0	0.39	7.70	H, M, S, LM	9.3	9.8
Webber Lake	76	76.9	0.18	1.50	H, M, S, G	12.8	31.4
Latah*	63	46.0	0.74	8.28	H, M, S, LM , G		
Mascall	104	53.8	0.93	3.17	H, M, S, G	8.8	27.0
Temblor	103	42.7	0.94	3.75	H, M, S, G	17.6	78.2
Buffalo Canyon	233	42.9	0.18	5.05	H, M, S, G	6.5	16.7
Fingerrock Wash	1,112	75.5	1.91	8.18	H, M, S, LM , G	8.8	22.2
Clarkia	12	75.0	2.12	7.78	H, M, S, LM	9.2	39.0
Cascadia*	37	59.5	0.23	2.05	H, M. S. G		
Willamette	36	42.3	0.80	5.00	H, M, S	13.3	53.9
Bridge Creek	114	45.8	0.46	5.00	H, M, S, LM	7.8	32.6
(Painted Hills)							
Grant*	26	23.1	0.29	5.00	Н, М, G		

* floras excluded from statistical analyses

TABLE 4. General linear models examining the relationship between mean annual temperature and precipitation on measures of herbivory. Paleoclimatic estimates (MAT and 3-month average precipitation) are from Yang et al. (2011).

		% leav dan	b leaves with damage removed (cm ²)		% leaf area removed		# of feeding types present in flora		
	df	F	Р	F	Р	F	Р	F	Р
Temperature	1	0.03	0.877	2.62	0.140	0.88	0.373	1.16	0.310
Precipitation	1	0.02	0.895	4.15	0.072	0.53	0.485	0.37	0.559
# of Leaves	1	1.95	0.196	2.45	0.152	1.99	0.192	3.31	0.102

3.2 Specialized endophagous herbivores, climate and host fidelity

Both galls and leaf mines are present in cool and dry floras such as Mint Canyon as well as in relatively warm and moist floras such as Stinking Water. For floras with galls, average MAT is 10.6 °C, while for those without galls it is 9.6 °C (Figure 3.1). Floras with galls are drier, on average than those without, as average 3-month precipitation for those with galls is 29.9 cm and for those without it is 36.0 cm (Figure 3.2). In logistic regression analyses controlling for precipitation, the presence of galls is significantly correlated with temperature (Table 5, $X_{1,12}^2$ = 6.51, P = 0.011, Figure 2), and precipitation has a negative correlation with the presence of galls in models controlling for temperature ($X_{1,12}^2$ = 4.34, P = 0.037, Table 5). FIGURE 3. Differences in 1. Mean annual temperature (no galls mean = 9.6, SE = 1.3; with galls mean = 10.6, SE = 1.2) and 2. Average 3-month precipitation (no galls mean = 36.0, SE = 7.3; with galls mean = 29.9, SE = 6.5) levels between those floras with and without galls.



FIGURE 4. Differences in 1. Mean annual temperature (no leaf mines mean = 11.3, SE = 1.3; with leaf mines mean = 8.6, SE = 0.4) and 2. Average 3-month precipitation (no leaf mines mean = 33.5, SE = 7.9; with leaf mines mean = 29.0, SE = 3.1) levels between those floras with and without leaf mines.



TABLE 5. Logistic regression models examining the relationship between mean annual temperature and precipitation and the presence of leaf mines and galls, paleoclimatic estimates from CLAMP analysis (Yang et al., 2011).

		presence/a	presence/absence galls		nce leaf mines
	df	X^2	Р	X^2	Р
Temperature	1	6.51	0.011	6.36	0.012
Precipitation	1	4.34	0.037	4.29	0.038
# of Leaves	1	6.49	0.011	3.75	0.053

Floras with leaf mines are cooler than those without, as average MAT is 8.6 °C for those with mines, while for those without leaf mines it is 11.3 °C, (Figure 4.1). Floras with leaf mines are also drier, on average, than those without, as average 3-month precipitation for those with leaf mines is 29.0 cm and for those without it is 33.5 cm (Figure 4.2). Although mean values for these categories appear similar, in logistic regression analyses controlling for the effects of temperature and precipitation on each other, both temperature and precipitation are negatively correlated with the presence of leaf mines in a flora (MAT $X^2_{1,12} = 6.36$, P = 0.012; average 3-month precipitation $X^2_{1,12} = 4.29$, P = 0.038).

Twenty-one galled leaves are observed across 13 floras, comprising five different gall types based on size, shape and placement on the leaf surface. The number of galls per leaf varies, from one or two up to 20. Galls are more common in floras with higher numbers of leaves (mean number of leaves for floras with galls = 221, without galls = 52) and this is largely due to one flora with a high sample size (Fingerrock Wash, n = 1,112 leaves), although we do find a significant correlation between sample size and the presence of galls ($F_{1, 12} = 6.49$, P= 0.011, Figure 5).

Galls are attached to the lower surface of leaves and corresponded with a disk-like scar visible on both sides of leaves, with a width of between 1–2 mm. Gall scars are distinct from hole-feeding damage because of the irregularity of hole size and shape, and the thick reaction tissue around gall scars. Additionally, the gall scar tissue commonly forms a slight indentation where the gall is impressed into the leaf surface. The majority of galls and gall scars can be attributed to *Antronoides schornii* and are elongate and tapered at their distal ends in an obclavate shape as are those made by modern members of the tribe Cynipini (Leckey and Smith, *Accepted*).

FIGURE 5. Difference in average leaf number per floras with and without galls, for floras without galls, mean leaf number = 52.0, SE = 21.9; for floras with galls, mean leaf number = 221, SE = 112.7.



Leaf mines are rare and found on only 23 leaves (less than 1%) across only five of the 13 floras. Although leaf mines are more common in floras with higher numbers of leaves (mean number of leaves for floras with mines = 306, without mines = 83), these data are also heavily influenced by the high number of leaves from the Fingerrock Wash flora, and we find a near-significant correlation between sample size and the presence of leaf mines ($F_{1, 12} = 3.75$, P= 0.053). Of the leaf mines preserved, six were made by identifiable genera of Lepidoptera (Table 6). Several of the mines were produced by groups of extant leaf miners that are oak specialists (Figure 6), including those belonging to *Cameraria* (Opler and Davis, 1981), *Caloptilia* (Shibata et al., 2001; Nakamura et al., 2008), and *Nepticula* sp. (Lindquis and Harden, 1970). The presence of the same mines on the same species of oaks, over 15 million years, demonstrates a long-lived

TABLE 6. Identified leaf mine damage, primarily from *Quercus pollardiana* (analog to modern *Q. chrysolepis*), including the floras in which the mined leaves were preserved and the families of Lepidoptera from which the mine-creating insects belong. Identifications provided by P. Opler.

Host plant	Flora	Genus	Family	on modern
				Q. chrysolepis?
Q. pollardiana	Fingerrock	Nepticula sp.	Nepticulidae	no
	Trapper Creek	Nepticula sp.	Nepticulidae	no
	Fingerrock	?Acrocercops sp.	Gracilleriidae	yes
	Fingerrock	Caloptilia sp.	Gracilleriidae	yes
	Fingerrock	?Cameraria sp.	Gracilleriidae	yes
	Washoe	?Phyllonorycter sp.	Gracillariidae	yes
	Stinking Water	Bucculatrix sp.	Bucculatricidae	yes
0 1 1		9.01 11		
Q. sımulata	Fingerrock	?Phyllonorycter sp.	Gracilleriidae	yes

FIGURE 6. Photographs of exceptional leaf mine damage on *Quercus pollardiana (Q. hanniballi)* from the Fingerrock Wash flora (Miocene, NV). 1. UCMP# 192950, *Cameraria sp.* mine; 2. UCMP# 192269, *Nepticula sp.* mine; 3. UCMP, uncataloged, *Caloptilia sp.* mine; 4. UCMP# 192272, *Acrocercops sp.* mine. All scale bars 5 mm.



relationship with a high degree of host fidelity, as in the case of leaf miners on *Quercus chrysolepis* (the modern analog of *Q. pollardiana*), which today hosts both *Cameraria* and *Caloptilia* leaf-miners. Another common leaf-miner in these fossil floras, *Nepticula*, does not occur on *Q. chrysolepis* but does occur on other North American oak species (Braun, 1914; Freeman, 1966). Other modern oaks with fossil counterparts represented in our sample, such as California Black Oaks, *Q. kelloggii*, the modern analog of the fossil form *Q. pseudolyrata*, also have leaf mines, although the mines are poorly preserved and thus unidentifiable. This species is less common in the overall pool of fossil leaves, and the number of mines on this host is low (two potential mines across all floras).

4. DISCUSSION

Across western North America for the past 35 million years, fossil oak leaves record a history of use by endophagous and exophagous insect herbivores. While much work has been done to suggest that temperature and precipitation should have impacted the amount and types of herbivory found on these oaks, the leaves record a more nuanced story than has been found in previous work that used whole-flora approaches. We find that overall herbivory has not been influenced by climatic variation, a pattern that has also been found in modern oaks (Adams et al., 2010; Leckey et al., *Accepted*). The lack of correlation between temperature and overall levels of herbivory suggests that biotic changes hypothesized to be climate driven such as changes in leaf chemistry (Reich and Oleksyn, 2004; Veteli et al., 2007) or insect herbivore development (Davidson, 1944; Gilbert and Raworth, 1996; Régnière et al., 2012) have less of an effect on oaks than in other host-herbivore systems, or that other temperature variables are more important

to oaks than mean annual temperature such as the degree of temperature seasonality (Pearse and Hipp, 2012).

In comparison with other studies that have used similar measures of herbivory and found a strong correlation between insect damage and temperature (e.g. Smith, 2008), our findings suggest that oak herbivores, as a group, may not respond to changes in climate in the same way as herbivores that feed more broadly or on other host plants in the community. Differences between oak species' herbivory patterns and herbivory at the community level (*i.e.* across many host plant types) have been found by others working with modern oaks (Adams et al., 2010; Leckey et al., Accepted). For modern oaks, even generalist herbivores can have strong host plant preferences (Pearse, 2011). Realizing that individual members of a community may respond differently to climatic change than the community as a whole may help resolve conflicting predictions about anticipated future warming (Cox et al., 2000). It is unknown whether warming will lead to greater herbivory (Wolf et al., 2008); have some effect, but be secondary to other factors such as biotic interactions (Lewinsohn et al., 2005; Leimu et al., 2012); or have little effect at all (Zvereva and Kozlov, 2006). There also may be effects of abiotic factors such as increased CO_2 levels, that can work in tandem with temperature increases to boost herbivore feeding (Currano et al., 2008). For an environment in which oaks are a large component, overall herbivory levels may not change as climates continue to warm.

We also find that overall herbivory is unaffected by levels of precipitation. This is surprising, because increased precipitation has been found to have a positive effect on many insect herbivores, either through increased survivorship of the insects (Fernandes et al., 2004; Yarnes and Boecklen, 2005), or through changes in leaf chemistry and leaf size (Coley and Barone, 1996; Mazía et al., 2004; Guarin and Taylor, 2005). Under wetter conditions, leaves tend

to grow larger (Wilf et al., 1998), diluting the leaf nutrients and defensive compounds (Ordoñez et al., 2009) and herbivores must, therefore, consume more leaf tissue to gain the same amount of nutrients. A positive relationship between feeding and precipitation is implied, however, for one of our measures of overall herbivory. This influence is seen in the near-significant values for the correlation between actual amount of leaf tissue removed and increased precipitation. Increasing leaf size would not necessarily affect the percent leaf area removed, however, as leaves tend to be larger size in wetter climates. Therefore, an increase in feeding on leaves that are large due to growing in an area with high precipitation could appear to have the same percentage of leaf tissue removed as leaves with less herbivory that grew in a drier area.

Endophagous herbivory on oaks provides another lens through which to examine the relationship between insect herbivory and climate. In modern systems, endophagous herbivores such as gall forming and leaf-mining insects have been found to be highly sensitive to variation in temperature and precipitation (Fernandes and Price, 1992; Connor and Traverner, 1997; Dury et al., 1998; Blanche and Ludwig, 2001; Bairstow et al., 2010; Winkler et al., 2010). Galls and leaf mines are more likely to be found in dry floras, possibly due to the predicted decrease in parasitoids (Fernandes and Price, 1992). Although our data indicate a strong influence of climate on endophagous herbivores, a larger sample of both galls and leaf mines would be required to more fully examine these findings. Endophagous damage such as galls and leaf mines are rare, possibly aided by preservation bias against them (Smith, 2004), however, these types of damage are generally rare in modern litter samples as well (Smith and Nufio, 2004; Leckey et al., *Accepted*). The effects of temperature were also important to both gall and leaf mining damage prevalence, although interpreting the effects of temperature is made more difficult by the fact that temperature had a positive effect on galls and a negative effect on leaf miners.

Differential effects of temperature on gall and leaf-mining insects has been found in some modern ecosystems, as changes in leaf toughness and chemistry that accompany variation in temperature have been found to have different effects on the distribution of gall-inducing insects relative to those that produce leaf mines (Bairstow et al., 2010). Some gallers thrive in warm conditions due to the persistence of vegetation for longer during the year (Price et al., 1998). An increase in galls with warming temperatures has also been found in some fossil floras (Currano et al., 2008). For leaf mining insects, however, their relationship to temperature variation in modern ecosystems is complex and can change from year to year (Kozlov et al., 2013), however, some modern leaf miners show an increase in larval mortality with increased temperatures (Pincebourde et al., 2007).

The damage made by gall and leaf mine inducing insect damage found on western fossil oaks demonstrates relationships stretching back millions of years. We find that the same gall and leaf mine inducing insects are found on the same host species across floras and into modern ecosystems. A high degree of host fidelity is to be expected in a group of plants with strong herbivore defenses, such as the oaks (Pearse and Hipp, 2012). Endophagous herbivores, such as gall-inducing and leaf mining larvae, may be more susceptible to changes in climatic variables than exophagous herbivores. Therefore, we suggest that future analyses of herbivory and climate not only take into account the diversity of feeding guilds, but also the distinction between external and internal feeding strategies within individual host-herbivore systems.
BIBLIOGRAPHY

- Abe, Y., Melika, G., Stone, G.N., 2007. The difersity and phylogeography of cynipid gallwasps (Hymenoptera: Cynipidae) of the Oriental and eastern Palearctic regions, and their associated communities. Orient. Insects 41, 169–212.
- Abrahamson, W.G., Hunter, M.D, Melika, G., Price, P.W., 2003. Cynipid gall-wasp communities correlate with oak chemistry. J. Chem. Ecol. 29, 209–223.
- Abrol, D.P., 2012. Climate change and pollinators. In: Pollination Biology. Springer, Netherlands, pp. 479–508.
- Ackerly, D.D., Knight, C.A., Weiss, S.B., Barton, K., Starmer, K.P., 2002. Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. Oecologia 130, 449–457.
- Adams, J.M., Ahn, S., Ainuddin, N., Lee, M., 2011. A further test of a palaeoecological thermometer: tropical rainforests have more herbivore damage diversity than temperate forests. Rev. Palaeobot. Palynol. 164, 60–66.
- Adams, J.M., Brusa, A., Soyeong, A., Ainuddin, A.N., 2010. Present-day testing of a paleoecological pattern: is there really a latitudinal difference in leaf-feeding insect-damage diversity? Rev. Palaeobot. Palynol. 162, 63–70.
- Adams, J.M., Zhang, Y., 2009. Is there more insect folivory in warmer temperate climates? A latitudinal comparison of insect folivory in eastern North America. J. Ecol. 97, 933–940.
- Agrawal, A.A., Fishbein, M., 2008. Phylogenetic escalation and decline of plant defense strategies. Proc. Natl. Acad. Sci. 105, 10057–10060.
- Aizen, M.A., Patterson, W.A., 1995. Leaf phenology and herbivory along a temperature gradient—a spatial test of the phenological window hypothesis. J. Veg. Sci. 6, 543–550.
- Andow, D.A., Imura, O., 1994. Specialization of phytophagous arthropod communities on introduced plants. Ecology, 75, 296–300.
- Andrew, N.R., Hughes, L., 2007. Potential host colonization by insect herbivores in a warmer climate: a transplant experiment. Global Change Biol. 13, 1539–1549.

- Araújo, M.B., Luoto, M., 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecol. Biogeogr. 16, 743–753.
- Arellano-Gil, J., Velasco-de Léon, P., Silva-Pineda, A., Salvador-Flores, Rosalba, Beltrán-Romero, F., 2005. Origen y características geológicas del paleo-Lago de Amajac, Hidalgo. Rev. Mex. Cienc. Geol. 22, 199–211.
- Armstrong, R.L., 1975. The geochronometry of Idaho: isochron. West 14, 1–50.
- Ashmead, W.H., 1897. Description of five new genera in the family Cynipidae. Can. Entomol. 29, 260–263.
- Asner, G.P., Martin, R.E., Ford, A.J., Metcalfe, D.J., Liddell, M.J., 2009. Leaf chemical and spectral diversity in Australian tropical forests. Ecol. Appl. 19, 236–253.
- Axelrod, D.I., 1940. The Mint Canyon flora of southern California; a preliminary statement. Am. J. Sci. 238, 577–585.
- Axelrod, D.I., 1956. Mio-Pliocene floras from west-central Nevada. Univ. Calif. Pub. Geol. Sci. 33, 1–315.
- Axelrod, D.I., 1964. The Miocene Trapper Creek flora of southern Idaho. Univ. Calif. Pub. Geol. Sci. 51, 1–161.
- Axelrod, D.I., 1980. Contributions to the Neogene paleobotany of central California. Univ. Calif. Pub. Geol. Sci. 121, 1–212.
- Axelrod, D.I., 1983. Biogeography of oaks in the Arcto-Tertiary Province. Ann. Mo. Bot. Gard. 70, 629–657. Axelrod, D.I., 1983. Biogeography of oaks in the Arcto-Tertiary Province. Ann. Mo. Bot. Gard. 70, 629–657.
- Axelrod, D.I., 1986. Cenozoic History of some western American pines. Ann. Mo. Bot. Gard. 73, 565–641.
- Axelrod, D.I., 1991. The Early Miocene Buffalo Canyon flora, western Nevada. Univ. Calif. Pub. Geol. Sci. 135, 1–76.
- Axelrod, D.I., 1995. The Miocene Purple Mountain flora of Western Nevada. Univ. Calif. Pub. Geol. Sci. 139, 1–62.
- Ayres, MP., 1993. Plant defense, herbivory, and climate change. In: Kareiva, P.M., Kingsolver, J.G., Huey, R.B. (eds.), Biotic Interactions and Global Change. Sinauer Associates, Sunderland, pp. 75–94.

- Bairstow, K.A., Clarke, K.L., McGeoch, M.A., Andrew, N.R., 2010. Leaf miner and plant galler species richness on *Acacia*: relative importance of plant traits and climate. Oecologia 163, 437–448.
- Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D., Whittaker, J.B., 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biol. 8, 1–16.
- Barone, J.A., 2000. Comparison of herbivores and herbivory in the canopy and understory for two tropical tree species. Biotropica 32, 307–317.
- Batten, D.J., Gray, J., Harland, R., 1999. Palaeoenvironmental significance of a monospecific assemblage of dinoflagellate cysts from the Miocene Clarkia Beds, Idaho, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 153, 161–177.
- Becerra, J.X., Venable, D.L., 1999. Macroevolution of insect-plant associations: the relevance of host biogeography to host affiliation. Proc. Natl. Acad. Sci. 96, 12626–12631.
- Becker, H.F., 1969. Fossil plants of the Tertiary Beaverhead basins in southwestern Montana. Palaeontogr. Abt. B. 127, 1–142.
- Berenbaum, M., 2001. Chemical mediation of coevolution: phylogenetic evidence for Apiaceae and associates. Ann. Mo. Bot. Gard. 88, 45–59.
- Berenbaum, M., Feeny, P., 1981. Toxicity of angular furanocoumarins to swallowtail butterflies: escalation in a coevolutionary arms race? Science 212,927–929.
- Bernays, E., 1998. Evolution of feeding behavior in insect herbivores: success seen as different ways to eat without being eaten. Bioscience 48, 35–44.
- Bernays, E., Graham, M., 1988. On the evolution of host specificity in phytophagous arthropods. Ecology 69, 886–892.
- Béthoux, O., Galtier, J., Nel, A., 2004. Earliest evidence of insect endophytic oviposition. Palaios 19, 408–413.
- Blanche, K.R., Ludwig, J.A., 2001. Species richness of gall-inducing insects and host plants along an altitudinal gradient in Big Bend National Park, Texas. Am. Midl. Nat. 145, 219–232.

- Blüthgen, N., Metzner, A., 2007. Contrasting leaf age preferences of specialist and generalist stick insects (Phasmida). Oikos 116, 1853–1862.
- Borchard, F., Berger, H., Bunzel-Drueke, M., Fartmann, T., 2011. Diversity of plantanimal interactions: possibilities for a new plant defense indicator value? Ecol. Ind. 11, 1311–1318.
- Borgardt, S.J., Nixon, K.C., 2003. A comparative flower and fruit anatomical study of *Quercus acutissima*, a biennial-fruiting oak from the *Cerris* group (Fagaceae). Am. J. Bot. 90, 1567–1584.
- Borgardt, S., Pigg, K., 1999. Anatomical and developmental study of petrified *Quercus* (Fagaceae) fruits from the middle Miocene, Yakima Canyon, Washington, USA. Am. J. Bot. 86, 307–325.
- Brändle, M., Kühn, I., Klotz, S., Belle, C., Brandl, R. 2008. Species richness of herbivores on exotic host plants increases with time since introduction of the host. Diversity Distrib. 14, 905–912.
- Braun, A.F., 1914. Notes on North American species of Nepticula with descriptions of new species. Can. Entomol. 46, 17–24.
- Brenes-Arguedas, T., Coley, P.D., Kursar, T.A., 2009. Pests vs. drought as determinants of plant distribution along a tropical rainfall gradient. Ecology 90, 1751–1761.
- Buechler, W.K., Dunn, M.T., Rember, W.C., 2007. Late Miocene Pickett Creek Flora of Owyhee County, Idaho. Contrib. Mus. Paleontol. 31, 305–362.
- Burnham, R.J., 1994. Paleoecolgical and floristic heterogeneity in the plant-fossil record; an analysis based on the Eocene of Washington, U.S. Geol. Surv. Bull, 2085B, 1–36.
- Call, V.B., Dilcher, D.L., 1997. The fossil record of *Eucommia* (Eucommiaceae) in North America. Am. J. Bot. 84, 798–814.
- Camus, A. 1934–1954. Les chénes. Monographie du genre *Quercus* (et *Lithocarpus*), Volume 6–8. Académiedes Sciences, Paris, France.
- Chaney, R.W., Axelrod, D. I., 1959. Miocene floras of the Columbia Plateau Oregon— Part 1, Composition and interpretation; Part 2, Systematic considerations. Carnegie I. Wash. Pub. 237 p.
- Coley, P.D., 1988. Effects of plant-growth rate and leaf lifetime on the amount and type of anti-herbivore defense. Oecologia 74, 531–536.

- Coley, P.D., 1998. Possible effects of climate change on plant/herbivore interactions in moist tropical forests. Clim. Change 39, 455–472.
- Coley, P.D., Barone, J.A., 1996. Herbivory and plant defenses in tropical forests. Annu. Rev. Ecol. Syst. 27, 305–335.
- Condit, C. 1944. The Remington Hill flora. In: Chaney, R.W. (ed.), Pliocene floras of California and Oregon. Carnegie I. Wash. Pub. 2, 21–55.
- Connor, E., Taverner, M., 1997. The evolution and adaptive significance of the leafmining habit. Oikos 79, 6–25.
- Cornelissen, T., Stiling, P., 2005. Perfect is best: low leaf fluctuating asymmetry reduces herbivory by leaf miners. Oecologia 142, 46–56.
- Cornell, H.V., 1983. The secondary chemistry and complex morphology of galls formed by the Cynipinae (Hymenoptera): why and how? Am. Midl. Nat. 110, 225–234.
- Cornell, H.V., 1985. Local and regional richness of cynipine gall wasps on California oaks. Ecology 66, 1247–1260.
- 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, 257–274.
- Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184–187.
- Crepet, W.L., Nixon, K.C., 1989. Extinct transitional Fagaceae from the Oligocene and their phylogenetic implications. Am. J. Bot. 76, 1493–1505.
- Cuevas-Reyes, P., Quesada, M., Hanson, P., Dirzo, R., Oyama, K., 2004. Diversity of gall-inducing insects in a Mexican tropical dry forest: the importance of plant species richness, life-forms, host plant age and plant density. J. Ecol. 92, 707–716.
- Currano, E.D., 2009. Patchiness and long-term change in early Eocene insect feeding damage. Paleobiology, 35, 484–498.
- Currano, E.D., Labandeira, C.C., Wilf, P., 2010. Fossil insect folivory tracks paleotemperature for six million years. Ecol. Monogr. 80, 547–567.

- Currano, E.D., Wilf, P., Wing, S.L., Labandeira, C.C., Lovelock, E.C., Royer, D.L., 2008. Sharply increased insect herbivory during the Paleocene-Eocene thermal maximum. Proc. Natl. Acad. Sci. 105, 1960–1964.
- Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., Pasteris, P.P., 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. Int. J. Climatol. 28, 2031–2064.
- Danks, H.V., 2007. The elements of seasonal adaptation in insects. Can. Entomol. 139, 1–44.
- Davidson, J., 1944. The relationship between temperature and rate of development of insects at constant temperatures. J. Anim. Ecol. 13, 26–38.
- DeLucia, E.H., Nabity, P.D., Zavala, J.A., Berenbaum, M.R., 2012. Climate change: resetting plant-insect interactions. Plant Physiol. 160, 1677–1685.
- Desprez-Loustau, M.-L., Vitasse, Y., Delzon, S., Capdeville, X., Marçais, B., Kremer, A., 2009. Are plant pathogen populations adapted for encounter with their host? A case study of phenological synchrony between oak and an obligate fungal parasite along an altitudinal gradient. J. Evol. Biol. 23, 87–97.
- Dirzo, R., Boege, K., Carson, W., Schnitzer, S., 2008. Patterns of herbivory and defense in tropical dry and rain forests. In: Carson, W.P., Schnitzer, S.A. (eds.), Tropical Forest Community Ecology. Wiley-Blackwell Pub, Chichester, pp. 63–78.
- Donovan, S.K., 2001. Evolution of Caribbean echinoderms during the Cenozoic: moving towards a complete picture using all of the fossils. Palaeogeogr. Palaeoclimatol. Palaeoecol. 166, 177–192.
- Dury, S.J., Good, J.E.G., Perrins, C.M., Buse, A., Kaye, T., 1998. The effects of increasing CO₂ and temperature on oak leaf palatability and the implications for herbivorous insects. Glob. Chang. Biol. 4, 55–61.
- Ehrlich, P., Raven, P., 1964. Butterflies and plants a study in coevolution. Evolution 18, 586–608.
- Ellis, B., Johnson, K.R., 2013. Comparison of leaf samples from mapped tropical and temperate forests: implications for interpretations of the diversity of fossil assemblages. Palaios, 28, 163–177.
- Ellwood, E.R., Diez, J.M., Ibanez, I., Primack, R.B., Kobori, H., Higuchi, H., Silander, J.A., 2012. Disentangling the paradox of insect phenology: are temporal trends reflecting the response to warming? Oecologia 168, 1161–1171.

- Erelli, M.C., Ayres, M.P., Eaton, G.K., 1998. Altitudinal patterns in host suitability for forest insects. Oecologia 117, 133–142.
- Erwin, D.M., Schick, K.N., 2007. New Miocene oak galls (Cynipini) and their bearing on the history of cynipid wasps in western North America. J. Paleontol. 81, 568– 580.
- Estiatre, M. 2007. Effects of resource availability on condensed tannins and nitrogen in two *Quercus* species differing in leaf life span. Ann. For. Sci. 64, 439–445.
- Faeth, S.H., 1991. Effect of oak leaf size on abundance, dispersion, and survival of the leafminer *Cameraria* sp. (Lepidoptera, Gracillariidae). Environ. Entomol. 20, 196–204.
- Farrell, B., Mitter, C., 1998. The timing of insect/plant diversification: might *Tetraopes* (Coleoptera : Cerambycidae) and *Asclepias* (Asclepiadaceae) have co-evolved? Biol. J. Linn. Soc. 63, 553–577.
- Fernandes, G., Castro, F., Faria, M., Marques, E., Greco, M., 2004. Effects of hygrothermal stress, plant richness, and architecture on mining insect diversity. Biotropica 36, 240–247.
- Fernandes, G., Price, P., 1992. The adaptive significance of insect gall distribution survivorship of species in xeric and mesic habitats. Oecologia 90, 14–20.
- Field, C., Mooney, H., 1983. Leaf age and seasonal effects on light, water, and nitrogen use efficiency in a California shrub. Oecologia 56, 348–355.
- Fields, P.F., 1996. The Succor Creek flora of the middle Miocene Sucker Creek Formation, southwestern Idaho and eastern Oregon; systematics and paleoecology. Unpublished Ph.D. dissertation, Michigan State University, 674 p.
- Fine, P.V.A., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H., Sääksjärvi, I., Schultz, J.C., Coley, P.D., 2006. The growth-defense trade-off and habitat specialization by plants in Amazonian forests. Ecology, 87, S150–S162.
- Floate, K.D., Whitham, T.G., 1995. Insects as traits in plant systematics: their use in discriminating between hybrid cottonwoods. Can. J. Bot. 73, 1–13.
- Franklin, A.J., Liebhold, A.M., Murray, K., Donahue, C., 2003. Canopy herbivore community structure: large-scale geographical variation and relation to forest composition. Ecol. Entomol. 28, 278–290.
- Freeman, T.N., 1966. A new species of *Nepticula* on bur oak in Ontario (Nepticulidae). J. Res. Lepidoptera 6, 19–21.

- Frenzel, M., Brandl, R., 2000. Phytophagous insect assemblages and the regional species pool: patterns and asymmetries. Global Ecol. Biogeogr. 9, 293–303.
- Friis, E.M., Pedersen, K.R., Crane, P.R., 1999. Early Angiosperm diversification: the diversity of pollen associated with Angiosperm reproductive structures in Early Cretaceous floras from Portugal. Ann. Missouri Bot. Gard. 86, 259–296.
- Funk, D.J., 2010. Does strong selection promote host specialization and ecological speciation in insect herbivores? Evidence from *Neochlamisus* leaf beetles. Ecol. Entomol. 35, 41–53.
- Futuyama, D., Moreno, G., 1988 The evolution of ecological specialization. Annu. Rev. Ecol. Syst. 19, 207–233.
- Gagné, R.J. 1989. The plant-feeding gall midges of North America. Cornell University Press, Ithaca, New York, 355 p.
- Gagné, R.J., Riley, E.G., 1999. A new gall midge (Diptera: Cecidomyiidae) pest of live oak in Texas. Southwest. Entomol. 24, 159–165.
- Garibaldi, L.A., Kitzberger, T., Ruggiero, A., 2011. Latitudinal decrease in folivory within *Nothofagus pumilio* forests: dual effect of climate on insect density and leaf traits? Global Ecol. Biogeogr. 20, 609–619.
- Gaston, K.J., Reavey, D., Valladares, G.R., 1992. Intimacy and fidelity- internal and external feeding by the British microlepidoptera. Ecol. Entomol. 17, 86–88.
- Giannasi, D.E. 1986. Phytochemical aspects of phylogeny in Hamamelidae. Ann. Missouri Bot. Gard. 73, 417–437.
- Gilbert, N., Raworth, D., 1996. Insects and temperature a general theory. Can. Entomol. 128, 1–13.
- Golightly, W., Lloyd, L., 1939. Insect size and temperature. Nature 144, 155–156.
- Gómez, J., 2004. Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. Evolution 58, 71–80.
- Gotelli, N.J., Enstminger, G.L., 2004. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465.

- Graham, A., 1963. Systematic revision of the Sucker Creek and Trout Creek Miocene floras of Southern Oregon. Am. J. Bot. 50, 921–936.
- Graham, C.H., Ferrier, S., Huettman, F., Moritz, C., Townsend Peterson, A., 2004. New developments in museum-based informatics and applications in biodiversity analysis. Trends Ecol. Evol. 19, 497–503.
- Gratani, L., Meneghini, M., Pesoli, P., Crescente, M., 2003. Structural and functional plasticity of *Quercus ilex* seedlings of different provenances in Italy. Trees-Struct. Funct. 17, 515–521.
- Greenwood, D., Wilf, P., Wing, S.L., Christophel, D.C., 2004. Paleotemperature estimation using leaf-margin analysis; is Australia different? Palaios 19, 129–142.
- Grivet, D., Sork, V.L., Westfall, R.D., Davis, F.W., 2008. Conserving the evolutionary potential of California valley oak (*Quercus lobata* Née): a multivariate genetic approach to conservation planning. Mol. Ecol. 17, 139–156.
- Guarin, A., Taylor, A.H., 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. For. Ecol. Manage. 218, 229–244.
- Guralnick, R. Van Cleve, J., 2005. Strengths and weaknesses of museum and national survey data sets for predicting regional species richness: comparative and combined approaches. Diversity Distrib. 11, 349–359.
- Gutbrodt, B., Dorn, S., Mody, K., 2012. Drought stress affects constitutive but not induced herbivore resistance in apple plants. Arthropod-Plant Inte. 6, 171–179.
- Hall, M.C., Stiling, P. Moon, D.C., Drake, B.G., Hunter, M.D., 2006. Elevated CO₂ increases the long-term decomposition rate of *Quercus myrtifolia* leaf litter. Glob. Chang. Biol. 12, 568–577.
- Hänninen, H., Tanino, K., 2011. Tree seasonality in a warming climate. Trends Plant Sci. 16, 412–416.
- Hardy, N.B., Cook, L.G., 2010. Gall-induction in insects: evolutionary dead-end or speciation driver? BMC Evol. Biol. 10, 257.
- Hartig, T., 1840. Ueber die familie der gallwespen, III. Z. Entomol. 2, 176–209.
- Hattori, K., Ishida, T.A., Miki, K., Suzuki, M., Kimura, M.T., 2004. Differences in response to simulated herbivory between *Quercus crispula* and *Quercus dentata*. Ecol. Res. 19, 323–329.

- Headlee, T., 1914. Some data on the effect of temperature and moisture on the rate of insect metabolism. J. Econ. Entomol. 7, 413–417.
- Headlee, T., 1941. Further studies of the relative effects on insect metabolism of temperatures derived from constant and variable sources. J. Econ. Entomol. 34, 171–174.
- Hickey, L.J., Hodges, R.W., 1975. Lepidopteran leaf mine from the Early Eocene Wind River Formation of northwestern Wyoming. Science 189, 718–720.
- Hilker, M., Meiners, T., 2002. Induction of plant responses to oviposition and feeding by herbivorous arthropods: a comparison. Entomol. Exp. Appl. 104, 181–192.
- Hinz, H.L., Schwarzlaender, M., 2004. Comparing invasive plants from their native and exotic range: what can we learn for biological control? Weed Technol. 18, 1533–1541.
- Huberty, A.F., Denno, R.F., 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. Ecology 85, 1383–1398.
- Jactel, H., Brockerhoff, E.G., 2007. Tree diversity reduces herbivory by forest insects. Ecol. Lett. 10, 835–848.
- Jaenike, J., 1990. Host specialization in phytophagous insects. Annu. Rev. Ecol. Syst. 21, 243–273.
- Janecke, B.B., Smit, G.N., 2011. Phenology of woody plants in riverine thicket and its impact on browse availability to game species. Afr. J. Range Forage. Sci. 28, 139–148.
- Janz, N., Nylin, S., Wahlberg, N., 2006. Diversity begets diversity: host expansions and the diversification of plant-feeding insects. BMC Evol. Biol. 6, 1–10.
- Jeppsson, T., Lindhe, A., Gärdenfors, Forslund, P., 2010. The use of historical collections to estimate population trends; a case study using Swedish longhorn beetles (Coleoptera: Cerambycidae). Biol. Conserv. 143, 1940–1950.
- Jones, J.H., 1986. Evolution of the Fagaceae: the implications of foliar features. Ann. Mo. Bot. Gard. 73, 228–275.
- Jones, M.E., Paine, T.D., Fenn, M.E., 2008. The effect of nitrogen additions on oak foliage and herbivore communities at sites with high and low atmospheric pollution. Environ. Pollut. 151, 434–442.
- Juroszek, P., von Tiedemann, A., 2013. Plant pathogens, insect pests and weeds in a changing global climate: a review of approaches, challenges, research gaps, key studies and concepts. J. Agr. Sci. 151, 163–188.

- Kampichler, C., Teschner, M., 2002. The spatial distribution of leaf galls of *Mikiola fage* (Diptera: Cecidomyiidae) and *Neuroterus quercusbaccarum* (Hymenoptera: Cynipidae) in the canopy of a Central European mixed forest. Eur. J. Entomol. 99, 79–84.
- Kang, H., Xin, Z., Berg, B., Burgess, P., Liu, Q., Liu, Z., Li, Z., Liu C., 2010. Global pattern of leaf litter nitrogen and phosphorus in woody plants. Ann. For. Sci. 67, 811–818.
- Karban, R., 2007. Deciduous leaf drop reduces insect herbivory. Oecologia 153, 81-88.
- Karban, R., 2008. Leaf drop in evergreen *Ceanothus velutinus* as a means of reducing herbivory. Ecology 89, 2446–2452.
- Kinsey, A.C. 1930. The gall wasp genus *Cynips*: a study in the origin of the species. Indiana University Studies, 16, 1–577.
- Kinsey, A.C., 1922. Studies of some new and described Cynipidae (Hymenoptera). Indiana University Studies, 9, 3–141.
- Kinsey, A.C., 1936. The origin of higher categories in *Cynips*. Indiana University Publications in Science Series, 4, 1–334.
- Klavins, S., Kellogg, D., Krings, M., Taylor, E., Taylor, T., 2005. Coprolites in a Middle Triassic cycad pollen cone: evidence for insect pollination in early cycads? Evol. Ecol. Res. 7, 479–488.
- Knops, J.M.H., Koenig, W.D., 1994. Water use strategies of five sympatric species of *Quercus* in central coastal California. Madrono 41, 290–301.
- Knops, J.M.H., Koenig, W.D., 1997. Site fertility and leaf nutrients of sympatric evergreen and deciduous species of *Quercus* in central coastal California. Plant Ecol. 130, 121–131.
- Knor, S., Skuhravá, M., Wappler, T., Prokop, J., 2013. Galls and gall makers on plant leaves from the lower Miocene (Burdigalian) of the Czech Republic: systematic and palaeoecological implications. Rev. Palaeobot. Palynol. 188, 38–51.
- Knowlton, F.H., 1898. The fossil plants of the Payette Formation. In: Lindgren, W. (ed.), The Mining Districts of the Idaho Basin and the Boise Ridge, Idaho. U.S. Geol. Surv. Annu. Rep. 18, 721–744.
- Körner, C., Basler, D., 2010. Phenology under global warming. Science 327, 1461– 1462.

- Kramer, K., Leinonen, I., Loustau, D., 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and mediterranean forests ecosystems: an overview. Int. J. Biometeorol. 44, 67–75.
- Krassilov, V., 2008. Mine and gall predation as top down regulation in the plant-insect systems from the Cretaceous of Negev, Israel. Palaeogeogr. Palaeoclimatol. Palaeoecol. 261, 261–269.
- Labandeira, C.C., Sepkoski, J., 1993. Insect diversity in the fossil record. Science 261, 310–315.
- Labandeira, C.C., 1998. Early history of arthropod and vascular plant associations. Annu. Rev. Earth Planet. Sci. 26, 329–377.
- Labandeira, C.C., Dilcher, D., Davis, D., Wagner, D., 1994. 97-million years of angiosperm-insect association paleobiological insights into the meaning of coevolution. Proc. Natl. Acad. Sci. 91, 12278–12282.
- Labandeira, C.C., Phillips, T.L., 2002. Stem borings and petiole galls from Pennsylvanian tree ferns of Illinois, USA: implications for the origin of the borer and galler functional-feeding groups and holometabolous insects. Palaeontogr. Abt. A 264, 1–84.
- Labandeira, C.C., Wilf, P., Johnson, K, Marsh, F., 2007. Guide to insect (and other) damage types on compressed plant fossils. Version 3.0. Smithsonian Institution.
- Landsberg, J., Gillieson, D.S., 1995. Regional and local variation in insect herbivory, vegetation and soils of eucalypt associations in contrasted landscape positions along a climatic gradient. Aust. J. Ecol. 20, 299–315.
- Larew, H.G., 1992. Fossil galls. In: Shorthouse, J.D., Rohfritsch, O. (eds.), The Biology of Insect-Induced Galls. Oxford University Press, New York. pp. 50–59.
- Laws, A.N., Belovsky, G.E., 2010. How will species respond to climate change? Examining the effects of temperature and population density on an herbivorous insect. Environ. Entomol. 39, 312–319.
- Lawton, J., 1995. The response of insects to environmental change. In: Harrington, R., Stork, N.E. (eds.), Insects in a Changing Environment. Academic Press, London, pp. 3–26.
- Leach, M., Givnish, T., 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. Ecol. Monogr. 69, 353–374.

- Le Brenton, J., Jourdan, H., Chazeau, J., Orivel, J., Dejean, A., 2005. Niche opportunity and ant invasion: the case of *Wasmannia auropunctata* in a New Caledonian rain forest. J. Trop. Ecol. 21, 93–98.
- Leckey, E.H., Smith, D.M., Accepted. Host fidelity over geologic time: restricted use of oaks by oak gallwasps. J. Paleontol.
- Leckey, E.H., Smith, D.M., Nufio, C.R., Fornash, K.F., *Accepted*. Oak-insect herbivore interactions along a temperature and precipitation gradient. Acta Oecol.
- Leimu, R., Muola, A., Laukkanen, L., Kalske, A., Prill, N., Mutikainen, P., 2012. Plantherbivore coevolution in a changing world. Entomol. Exp. Appl. 144, 3–13.
- Lewinsohn, T.M., Novotny, V., Basset, Y., 2005. Insects on plants: diversity of herbivore assemblages revisited. Annu. Rev. Ecol. Evol. Syst. 36, 597–620.
- Liebmann, F. 1854. Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger og dets Midlemmers Arbeider, Copenhagen, 173 p.
- Liljeblad, J., Ronquist, F., Nieves-Aldrey, J., Fontal-Cazalla, F., Ros-Farre, P., Gaitros, D., Pujade-Villar, J., 2008. A fully web–illustrated morphological phylogenetic study of relationships among oak gall wasps and their closest relatives (Hymenoptera: Cynipidae). Zootaxa 1796, 1–73.
- Lill, J.T., Marquis, R.J., Ricklefs, R.E., 2002. Host plants influence parasitism of forest caterpillars. Nature 417, 170–173.
- Lindquis, O.H., Harden, A.A., 1970. A biological study of *Nepticula macrocarpae* (Lepidoptera: Nepticulidae) on oak in Ontario. Can. Entomol. 102, 1290–1293.
- Linnaeus, C., 1753. Species Plantarum, 997 p.
- Linnaeus, C., 1758. Systema Naturae. Laurentii Salvii, Holmiae, 824 p.
- Liu, Z., Engel, M.S., Grimaldi, D.A., 2007. Phylogeny and geological history of the cynipoid wasps (Hymenoptera: Cynipoidea). Am. Mus. Novit. 3583, 1–48.
- Lockheart, M.J., van Bergen, P.F., Evershed, R.P., 2000. Chemotaxonomic classification of fossil leaves from the Miocene Clarkia lake deposit, Idaho, USA based on n-alkyl lipid distributions and principal component analyses. Org. Geochem. 31, 1223–1246.

- Logan, G.A., Eglington, G., 1994. Geochemistry of the Miocene lacustrine deposit, at Clarkia, northern Idaho, USA. Org. Geochem. 21, 857–870.
- Logan, J.A., Regniere, J., Powell, J.A., 2003. Assessing the impacts of global warming on forest pest dynamics. Front. Ecol. Environ. 1, 130–137.
- Louden, J.C., 1830. Hortus Britanicus (Loudon) a catalogue, p. 385.
- MacGinitie, H.D., 1933. The Trout Creek flora of southeastern Oregon. Carnegie Institute of Washington Publications, 416, 21–68.
- Manos, P., Doyle, J., Nixon, K., 1999. Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subgenus *Quercus* (Fagaceae). Mol. Phylogenet. Evol. 12, 333–349.
- Manos, P., Zhou, Z., Cannon, C.H., 2001. Systematics of Fagaceae: phylogenetic tests of reproductive trait evolution. Int. J. Plant. Sci. 162, 1361–1379.
- Maron, J.L., Crone, E., 2006. Herbivory: effects on plant abundance, distribution and population growth. Proc. R. Soc. B. 273, 2575–2584.
- Marques, E.S.A., Price, P.W., Cobb, N.S., 2000. Resource abundance an insect herbivore diversity on woody fabaceous desert plants. Environ. Entomol. 29, 696–703.
- Mazía, C.N., Chaneton, E.J., Dellacanonica, C., Dipaolo, L., Kitzberger, T., 2012. Seasonal patterns of herbivory, leaf traits and productivity consumption in dry and wet Patagonian forests. Ecol. Entomol. 37, 193–203.
- Mazía, C.N., Kitzberger, T., Chaneton, E., 2004. Interannual changes in folivory and bird insectivory along a natural productivity gradient in northern Patagonian forests. Ecography 27, 29–40.
- McDonald, P.M., Tappeiner, J.C., 1996. Silviculture-ecology of forest-zone hardwoods in the Sierra Nevada. In: Sierra Nevada Ecosystems Project: Final Report to Congress. University of California, Davis, pp. 1–18.
- McElwain, J.C., 2004. Climate-independent paleoaltimetry using stomatal density in fossil leaves as a proxy for CO₂ partial pressure. Geology 32, 1017–1020.
- McLoughin, S., 2011. A new record of leaf galls and arthropod oviposition scars in Permian-Triassic Gondwanan gymnopserms. Aust. J. Bot. 59, 156–169.
- McNamara, M.E., Briggs, D.E.G., Orr, P.J., 2012. The controls on the preservation of structural color in fossil insects. Palaios 27, 443–454.

- Meiners, S.J., Handel, S.N., 2000. Additive and nonadditive effects of herbivory and competition on tree seeding mortality, growth and allocation. Am. J. Bot. 87, 1821–1826.
- Meiners, S.J., Martinkovic, 2002. Survival of and herbivore damage to a cohort of *Quercus rubra* planted across a forest-old-field edge. Am. Midl. Nat. 147, 247–256.
- Menzel, A., Estrella, N., Heitland, W., Susnik, A., Schleip, C., Dose, V., 2008. Bayesian analysis of the species-specific lengthening of the growing season in two European countries and the influence of an insect pest. Int. J. Biometeorol. 52, 209–218.
- Mérian, P., Bontemps, J.-D., Bergès, L., Lebourgeois, F., 2011. Spatial variation and temporal instability in climate-growth relationships of sessile oak (*Quercus petraea* [Matt.] Liebl.) under temperate conditions. Plant Ecol. 212, 1855–1871.
- Meyer, H.W., 1992. Lapse rates and other variables applied to estimating paleoaltitudes from fossil floras. Palaeogeogr. Palaeoclimatol. Palaeoecol. 99, 71–99.
- Meyer, H.W., Manchester, S.R., 1997. The Oligocene Bridge Creek flora of the John Day Formation, Oregon. Univ. Calif. Pub. Geol. Sci. 141, 1–195.
- Miller, P., 1754. Gardeners Dictionary, The Abridged 4th Edition. London, 615 p.
- Mitter, C., Farrell, B., 1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? Am. Nat. 132, 107–128.
- Mitter, C., Farrell, B., Futuyama, D., 1991. Phylogenetic studies of insect plant interactions—insights into the genesis of diversity. Trends Ecol. Evol. 6, 290–293.
- Moe, A.P., Smith, D.M., 2005. Using pre-Quaternary Diptera as indicators of paleoclimate. Palaeogeogr. Palaeoclimatol. Palaeoecol. 221, 203–214.
- Mooney, H.A., Gulmon, S.L., 1982. Constraints on leaf structure and function in reference to herbivory. BioScience 32, 198–206.
- Mopper, S., Simberloff, D., 1995. Differential herbivory in an oak population: the role of plant phenology and insect performance. Ecology 76, 1233–1241.
- Moran, N.A., 1989. A 48-million-year-old aphid host plant-association and complex life-cycle—biogeographic evidence. Science, 245, 173–175.

- Morath, S.U., Pratt, P.D., Silvers, C.S., Center, T.D., 2006. Herbivory by *Boreioglycaspis melaleucae* (Hemiptera: Psillidae) accelerates foliar senescence and abscission in the invasive tree *Melaleuca quinquenervia*. Environ. Entomol. 35, 1372–1378.
- Nabeshima, E. Murakami, M., Hiura, T., 2011. Effects of herbivory and light conditions on induced defense in *Quercus crispula*. J. Plant Res. 114, 403–409.
- Nakamura, T., Hattori, K., Ishida, T.A., Sato, H., Kimura, M.T., 2008. Population dynamics of leafminers on a deciduous oak *Quercus dentata*. Acta Oecol 34, 259–265.
- Newberry, J.S., 1883. Brief descriptions of fossil plants, chiefly Tertiary, from western North America. Proceedings of the United States National Museum, 1883, 502– 514.
- Niesenbaum, R.A., Kluger, E.C., 2006. When studying the effects of light on herbivory, should one consider temperature? The case of *Epimecis hortaria* L. (Lepidoptera: Geometridae) feeding on *Lindera benzoin* L. (Lauraceae). Environ. Entomol. 35, 600–606.
- Nixon, K., 2006. Global and neotropical distribution and diversity of oak (genus *Quercus*) and oak forests. In: Kappelle, M. (ed.), Ecology and Conservation of Neotropical Montane Oak Forests. Springer, New York, pp. 1–13.
- Novotny, V., Drozd, P., Miller, S.E., Kulfan, M., Janda, M., Basset, Y., Weiblen, G.D., 2006. Why are there so many species of herbivorous insects in tropical rainforests? Science, 313, 1115–1118.
- Nyman, T., Farrell, B.D., Zinovjev, A.G., Vikberg, V., 2006. Larval habits, host-plant associations, and speciation in nematine sawflies (Hymenoptera: Tenthredinidae). Evolution 60, 1622–1637.
- Opler, P.A., Davis, D.R., 1981. The leafmining moths of the Genus *Cameraria* associated with Fagaceae in California (Lepidoptera: Gracillariidae). Smithson. Contrib. Zool. 333, 1–58.
- Opler, P.A., 1973. Fossil lepidopterous leaf mines demonstrate the age of some insectplant relationships. Science 179, 1321–1323.
- Ordoñez, J.C., van Bodegom, P.M., Witte, J.M., Wright, I.J., Reich, P.B., Aerts, R., 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. Global Ecol. Biogeogr. 18, 137–149.

- Otto, A., Simoneit, B.R.T., Rember, W.C., 2005. Conifer and angiosperm biomarkers in clay sediments and fossil plants from the Miocene Clarkia Formation, Idaho, USA. Org. Geochem., 36, 907–922.
- Pascual-Alvarado, E., Cuevas-Reyes, P., Quesada, M., Oyama, K., 2008. Interactions between galling insects and leaf–feeding insects: the role of plant phenolic compounds and their possible interference with herbivores. J. Trop. Ecol. 24:329–336.
- Pearse, I.S., 2011. The role of leaf defensive traits in oaks on the preference and performance of a polyphagous herbivore, *Orgyia vetusta*. Ecol. Entomol. 36, 635–642.
- Pearse, I.S., Baty, J.H., 2012. The predictability of traits and ecological interactions on 17 different crosses of hybrid oaks. Oecologia, 169:489–497.
- Pearse, I.S., Hipp, A.L., 2009. Phylogenetic and trait similarity to a native species predict herbivory on non-native oaks. Proc. Natl. Acad. Sci. 106, 18097–18102.
- Pearse, I.S., Hipp, A.L., 2012. Global patterns of leaf defenses in oak species. Evolution 66, 2272–2286.
- Peppe, D.J., Royer, D.L., Cariglino, B., Oliver, S.Y., Newman, S., Leight, E., Enikolopov, G., Fernandez-Burgos, M., Herrera, F., Adams, J.M., Correa, E., Currano, E.D., Erickson, J.M., Hinojosa, L.F., Hoganson, J.W., Iglesias, A., Jaramillo, C.A., Johnson, K.R., Jordan, G.J., Kraft, N.J.B., Lovelock, E.C., Lusk, C.H., Niinemets, Ü, Peñuelas, J., Rapson, G., Wing, S.L., Wright, I.J., 2011. Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications. New Phytol. 190, 724–739.
- Pincebourde, S., Sinoquet, H., Combes, D., Casas, J., 2007. Regional climate modulates the canopy mosaic of favourable and risky microclimates for insects. J. Animal. Ecol. 76, 424–438.
- Price, P.W., Abrahamson, W.G., Hunter, M.D., Melika, G., 2004. Using gall wasps on oaks to test broad ecological concepts. Conserv. Biol. 18, 1405–1416.
- Price, P.W., Fernandes, G.W., Lara, A.C.F., Brawn, J., Barrios, H., Wright, M.G., Ribeiro, S.P., Rothcliff, N., 1998. Global patterns in local number of insect galling species. J. Biogeogr. 25, 581–591.
- Pringle, E.G., Adams, R.I., Broadbent, E., Busby, P.E., Donatti, C.I., Kurten, E.L., Renton, K., Dirzo, R., 2011. Distinct leaf-trait syndromes of evergreen and deciduous trees in a seasonally dry tropical forest. Biotropica 43, 299–308.

- Prior, K.M., Hellmann, J.J., 2010. Impact of an invasive oak gall wasp on a native butterfly: a test of plant-mediated competition. Ecology 91, 3284–3293.
- Prothero, D.R., Draus, E., Foss, S.E., 2006. Magnetic stratigraphy of the lower portion of the middle Miocene Mascall Formation, central Oregon. PaleoBios 26, 37–42.
- Qi, J., Ma, K.M., Zang, Y.X., 2009. Leaf-trait relationships of *Quercus liotungensis* along an altitudinal gradient in Dongling Mountain, Beijing. Ecol. Res. 24, 1243–1250.
- Ramamurthy, V.V., 2007. Faunistic, ecological, biogeographical and phylogenetic aspects of Coleoptera as gall-inducers and associates in plant galls in the Orient and eastern Palearctic. Orient. Insects 41, 93–119.
- Rasband, W., 1997–2012. ImageJ. Bethesda, MD: US National Institutes of Health.
- Régnière, J., Powell, J., Bentz, B., Nealis, V., 2012. Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. J. Insect Physiol. 58, 634–647.
- Reich, P.B., Oleksyn, J., 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. Proc. Natl. Acad. Sci. 101, 11001–11006.
- Reich, P.B., Wright, I.J., Lusk, C.H., 2007. Predicting leaf physiology from simple plant and climate attributes: A global GLOPNET analysis. Ecol. Appl. 17, 1982–1988.
- Retallack, G.J., 2004. Eocene-Oligocene extinction and paleoclimatic change near Eugene, Oregon. Geol. Soc. Am. Bull. 116, 817–1839.
- Retallack, G.J., 2004. Late Miocene climate and life on land in Oregon within a context of Neogene global change. Palaeogeogr. Palaeoclimatol. Palaeoecol. 214, 97–123.
- Retallack, G.J., Orr, W.N., Prothero, D.R., Duncan, R.A., Kester, P.R., Ambers, C.P., 2004. Eocene–Oligocene extinction and paleoclimatic change near Eugene, Oregon. Geol. Soc. Am. Bull. 116, 817–839.
- Reynolds, B.C., Crossley, D.A., 1997. Spatial variation in herbivory by forest canopy arthropods along an elevation gradient. Environ. Entomol. 26, 1232–1239.
- Romero, C., Bolker, B.M., Edwards, C.E., 2009. Stem responses to damage: The evolutionary ecology of *Quercus* species in contrasting fire regimes. New Phytol. 182, 261–271.

- Ronquist, F., 1999. Phylogeny, classification and evolution of the Cynipoidea. Zool. Scr. 28, 139–164.
- Ronquist, F., Liljeblad, J., 2001. Evolution of the gall wasp-host plant association. Evolution 55, 2503–2522.
- Roslin, T., Salminen, J.P., 2009. A tree in the jaws of a moth—temporal variation in oak leaf quality and leaf-chewer performance. Oikos 118, 1212–1218.
- Royer, D.L., Sack, L., Wilf, P., Lusk, C.H., Jordan, G.J., Niinemets, Ü., Wright, I.J., Westoby, M., Cariglino, B., Coley, P.D., Cutter, A.D., Johnson, K.R., Labandeira, C.C., Moles, A.T., Palmer, M.B., Vallardes, F., 2007. Fossil leaf economics quantified: calibration, Eocene case study, and implications. Paleobiology 33, 574–589.
- Sanders, N.J., Belote, R.T., Weltzin, J.F., 2004. Multitrophic effects of elevated atmospheric CO₂ on understory plant and arthropod communities. Envirn. Entomol. 33, 1609–1616.
- Sanderson, E., 1910. The relation of temperature to the growth of insects. J. Econ. Entomol. 3, 113–140.
- SAS Institute Inc., 1989–2012. JMP, Version 8. Cary, NC.
- Schorn, H.E., Meyers, J.A., Erwin, D.M., 2007. Navigating the Neogene: an updated chronology of Neogene paleofloras from the western United States. Cour. Forsch. Senck. 258, 139–146.
- Scott, A.C., Stephenson, J., Collinson, M.E., 1994. The fossil record of leaves with galls. In: Willimas, M.A.J. (ed.), Plant Galls. Systematics Association Special Volume, Clarendon Press, Oxford, 49, 44–70.
- Shibata, S., Ishida, T.A., Soeya, F., Morino, N., Yoshida, K., Sato, H., Kimura, M.T., 2001. Within-tree variation in density and survival of leafminers on oak *Quercus dentata*. Ecol. Res. 16, 135–143.
- Shure, D.J., Mooreside, P.D., Ogle, S.M., 1998. Rainfall effects on plant-herbivore processes in an upland oak forest. Ecology 79, 604–617.
- Singer, M.C., Parmesan, C., 1993. Sources of variation in patterns of plant-insect association. Nature 361, 251–253.
- Sinclair, R.J., Hughes, L., 2008. Incidence of leaf mining in different vegetation types across rainfall, canopy cover and latitudinal gradients. Austral Ecol. 33, 353–360.

- Smiley, C.J., Rember, W.C., 1985a. Composition of the Miocene Clarkia flora. In: Smiley, C.J. (ed.), Late Cenozoic History of the Pacific Northwest; Interdisciplinary Studies on the Clarkia Fossil Beds of Northern Idaho. Pacific Division of the American Association for the Advancement of Science, San Francisco, 95, 95–112.
- Smiley, C.J., Rember, W.C., 1985b. Physical setting of the Miocene Clarkia fossil beds, northern Idaho. In: Smiley, C.J. (ed.), Late Cenozoic History of the Pacific Northwest; Interdisciplinary Studies on the Clarkia Fossil Beds of Northern Idaho. Pacific Division of the American Association for the Advancement of Science, San Francisco, 95, 11–32.
- Smith, D.M., 2004. Using insect herbivory as a proxy for insect diversity: cautions from a modern tropical forest assemblage. Geol. Soc. of Am. Ann. Meet. 36, p. 381.
- Smith, D.M., 2008. A comparison of plant-insect associations in the middle Eocene Green River Formation and the Upper Eocene Florissant Formation and their climatic implications. Geol. Soc. Am. Spec. Pap. 435, 89–103.
- Smith, D.M., Nufio, C.R., 2004. Levels of herbivory in two Costa Rican rain forests: implications for studies of fossil herbivory. Biotropica 36, 318–326.
- Speer, J.H., Grissino-Mayer, H.D., Orvis, K.H., Greenberg, C.H., Climate response of five oak species in the eastern deciduous forest of the southern Appalachian Mountains, USA. Can. J. For. Res. 39, 507–518.
- Spicer, R.A., Wolfe, J.A., 1987. Plant taphonomy of late Holocene deposits in Trinity (Clair Engle) Lake, Northern California. Paleobiology 13, 227–245.
- Stoepler, T.M., Rehill, B., 2012. Forest habitat, not leaf phenotype, predicts late-season folivory of *Quercus alba* seedlings. Funct. Ecol. 26, 1205–1213.
- Stone, G.N., Atkinson, R., Rokas, A., Csóka, G., Nieves-Aldrey, J.L., 2001. Differential success in northwards range expansion between ecotypes of the marble gallwasp Andricus kollari: a tale of two lifecycles. Mol. Ecol. 10, 761–778.
- Stone, G.N., Cook, J.M., 1998. The structure of cynipid oak galls: patterns in the evolution of an extended phenotype. P. Roy. Soc. Lond. B. Bio. 265, 979–988.
- Stone, G.N., Hernandez-Lopez, A., Nicholls, J.A., di Pierro, E., Pujade-Villar, J., Melika, G., Cook, J.M., 2009. Extreme host plant conservatism during at least 20 million years of host plant pursuit by oak gallwasps. Evolution 63, 854–869.
- Stone, G.N., Schönrogge, K., 2003. The adaptive significance of insect gall morphology. Trends Ecol. Evol. 18, 512–522.

- Stone, G.N., Van der Ham, R.W.J.M., Brewer, J.G., 2008. Fossil oak galls preserve ancient multitrophic interactions. P. Roy. Soc. Lond. B. Bio. 275, 2213–2219.
- Strong, D.R., Sanderson, M., 2006. Cenozoidc insect-plant diversification in the tropics. Proc. Natl. Acad. Sci. 103, 10827–10828.
- Sutherst, R.W., Constable, F., Finlay, K.J., Harrington, R., Luck, J., Zalucki, M.P., 2011. Adapting to crop pest and pathogen risks under a changing climate. Clim. Change 2, 220–237.
- Swiecki, T.J., Bernhardt, E.A., 2006. A field guide to insects and diseases of California oaks. US Department of Agriculture 151, 1–158.
- Toju, H., 2008. Fine-scale local adaptation of weevil mouthparts length and *Camellia* pericarp thickness: altitudinal gradient of a putative arms race. Evolution 65, 1086–1102.
- Uhl, D., Traiser, C., Greisser, U., Denk, T., 2007. Fossil leaves as palaeoclimate proxies in the Palaeogene of Spitsbergen (Svalbard). Acta Palaeobot. 47, 89–107.
- van Asch, M., van Tienderen, P.H., Holleman, L.J.M., Visser, M.E., 2007. Predicting adaptation of phenology in response to climate change, an insect herbivore example. Glob. Chang. Biol. 13, 1596–1604.
- Vanderklein, D.W., Wilkens, R.T., Cartier, A., Lemke, R.W., 2004. Plant architecture and leaf damage in bear oak. 1: physiological responses. Northeast. Nat. 11, 343–356.
- Vanbergen, A.J., Raymond, B., Pearce, I.S.K, Watt, A.D., Hails, R.S., Hartley, S.E., 2003. Host shifting by Operophtera brumata into novel environments leads to population differentiation in life-history traits. Ecol. Entomol. 28, 604–612.
- Van Zandt, P.A., Mopper, S., 1998. A meta-analysis of adaptive deme formation in phytophagous insect populations. Am. Nat. 152, 595–604.
- Vehviläinen, H., Koricheva, J., Ruohomäki, K., 2007. Tree species diversity influences herbivore abundance and damage: meta-analysis of long-term forest experiments. Oecologia 152, 287–298.
- Veteli, T.O., Mattson, W.J., Niemela, P., Julkunen-Tiitto, R., Kellomaki, S., Kuokkanen, K., Lavola, A., 2007. Do elevated temperature and CO₂ generally have counteracting effects on phenolic phytochemistry of boreal trees? J. Chem. Ecol. 33, 287–296.

- Waggoner, B.M., 1999. Fossil oak leaf galls from the Stinking Water paleoflora of Oregon (middle Miocene). PaleoBios 19, 8–14.
- Waggoner, B.M., Poteet, M., 1996. Unusual oak leaf galls from the middle Miocene of northwestern Nevada. J. Paleontol. 70, 1080–1084.
- Wagner, T., Wu, H., Feldman, R., Sharpe, P., Coulson, R., 1985. Multiple-cohort approach for simulating development of insect populations under variable temperatures. Ann. Entomol. Soc. Am. 78, 691–704.
- Wappler, T., 2010. Insect herbivory close to the Oligocene–Miocene transition— a quantitative analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 292, 540–550.
- Wappler, T., Currano, E.D., Wilf, P., Rust, J., Labandeira, C.C., 2009. No post-Cretaceous ecosystem depression in European forests? Rich insect-feeding damage on diverse middle Palaeocene plants, Menat, France. Proc. R. Soc. B. 276, 4271–4277.
- Ward, L., Hackshaw, A., Clarke, R., 2003. Do food–plant preferences of modern families of phytophagous insects and mites reflect past evolution with plants? Biol. J. Linn. Soc. 78, 51–83.
- Warton, D.I., Hui, F.K.C., 2011. The arcsine is asinine: the analysis of proportions in ecology. Ecology 92, 2–10.
- Wedmann, S., Bradler, S., Rust, J., 2007. The first fossil leaf insect: 47 million years of specialized cryptic morphology and behavior. Proc. Natl. Acad. Sci. 104, 565–569.
- Went, F., 1953. The effect of temperature on plant growth. Annu. Rev. Plant Physiol. Plant Mol. Biol. 4, 347–362.
- Westphal, E., 1992. Cecidogenesis and resistance phenomena in mite-induced galls. In: Shorthouse, J.D., Rohfritsch, O. (eds.), The Biology of Insect-Induced Galls. Oxford University Press, New York, pp. 141–156.
- Wilf, P., 1997. When are leaves good thermometers? A new case for Leaf Margin Analysis. Paleobiology 23, 373–390.
- Wilf, P., Labandeira, C.C., 1999. Response of plant-insect associations to Paleocene-Eocene warming. Science 284, 2153–2156.
- Wilf, P., Labandeira, C.C., Johnson, K.R., Coley, P., Cutter, A., 2001. Insect herbivory, plant defense, and early Cenozoic climate change. Proc. Natl. Acad. Sci. 98, 6221–6226.

- Wilf, P., Labandeira, C.C. Johnson, K.R., Cúneo, N.R., 2005. Richness of plant-insect associations in Eocene Patagonia: a legacy for South American biodiversity. Proc. Natl. Acad. Sci. 102, 8944–8948.
- Wilf, P., Labandeira, C.C., Johnson, K.R., Ellis, B., 2006. Decoupled plant and insect diversity after the end-Cretaceous extinction. Science 313, 1112–1115.
- Wilf, P., Wing, S.L., Greenwood, D.R., Greenwood, C.L., 1998. Using fossil leaves as paleoprecipitation indicators: an Eocene example. Geology 26, 203–206.
- Wilkens, R.T., Vanderklein, D.W., Lemke, R.W., 2005. Plant architecture and leaf damage in bear oak 2: insect usage patterns. Northeast. Nat. 12, 153–168.
- Winkler, I.S., Labandeira, C.C., Wappler, T., Wilf, P., 2010. Distinguishing Agromyzidae (Diptera) leaf mines in the fossil record: new taxa from the Paleogene of North America and Germany and their evolutionary implications. J. Paleontol. 84, 935–954.
- Winkler, I.S., Mitter, C., Scheffer, S.J., 2009. Repeated climate-linked host shifts have promoted diversification in a temperate clade of leaf-mining flies. Proc. Natl. Acad. Sci. 106, 18103–18108.
- Wolf, A., Kozlov, M.V., Callaghan, T.V., 2008. Impact of non-outbreak insect damage on vegetation in northern Europe will be greater than expected during a changing climate. Clim. Change 87, 91–106.
- Wolfe, J.A., 1964. Miocene floras from Fingerrock Wash, southwestern Nevada. U.S. Geol. Surv. Prof. Paper 454N, 1–36.
- Wolfe, J.A., 1993. A method of obtaining climatic parameters from leaf assemblages. U.S. Geol. Surv. Bull. 2040, 1–71.
- Wolfe, J.A., 1995. Paleoclimatic Estimates from Tertiary Leaf Assemblages. Annu. Rev. Earth Planet. Sci. 23, 119–142.
- Wolfe, J.A., Tanai, T., 1987. Systematics, Phylogeny, and Distribution of *Acer* (Maples) in the Cenozoic of Western North America. J. Fac. Sci. Hokkaido University, Series 4, Geology and Minerology 22, 1–246.
- Wu, Z., Dijkstra, P., Koch, G.W., Peñuelas, J., Hungate, B.A., 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Glob. Chang. Biol. 17, 927–942.
- Yamazaki, K., 2010. Leaf mines as visual defensive signals to herbivores. Oikos 119, 796–801.

- Yang, H., Huang, Y., 2003. Preservation of lipid hydrogen isotope ratios in Miocene lacustrine sediments and plant fossils at Clarkia, northern Idaho, USA. Org. Geochem. 34, 413–423.
- Yang, J., Wang, Y.F., Spicer, R.A., Mosbrugger, V., Li, C.S., Sun, Q.C., 2007. Climatic reconstruction of Miocene Shanwang Basin, China, by using Leaf Margin Analysis, CLAMP, Co-existence approach and Overlapping Distribution Analysis. Am. J. Bot. 94, 599–608.
- Yang, J., Wang, Y.F., Spicer, R.A., Spicer, T.E.V., Li, C.S., 2011. CLAMP Online: a new web-based palaeoclimate tool and its application to the terrestrial Paleogene and Neogene of North America. Palaeoio. Palaeoenv. 91, 163–183.
- Yarnes, C., Boecklen, W., 2005. Abiotic factors promote plant heterogeneity and influence herbivore performance and mortality in Gambel's oak (*Quercus gambelii*). Entomol. Exp. Appl. 114, 87–95.
- Yarnes, C., Boecklen, W., 2006. Abiotic mosaics affect seasonal variation of plant resources and influence the performance and mortality of a leaf-miner in Gambel's oak (*Quercus gambelii*, Nutt.). Ecol. Res. 21, 157–163.
- Yarnes, C., Boecklen, W., 2008. No simple sum: seasonal variation in tannin phenotypes and leaf-miners in hybrid oaks. Chemoecology 18, 39–51.
- Yela, J.E., Herrera, C., 1993. Seasonality and life cycles of woody plant-feeding noctuid moths (Lepidoptera: Noctuidae) in Mediterranean habitats. Ecol. Entom. 18, 259–269.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292, 686–693.
- Zehnder, C.B., Stodola, K.W., Cooper, R.J., Hunter, M.D., 2010. Spatial heterogeneity in the relative impacts of foliar quality and predation pressure on red oak, *Quercus rubra*, arthropod communities. Oecologia 164, 1017–1027.
- Zvereva, E.L., Kozlov, M.V., 2006. Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a meta-analysis. Global Change Biol. 12, 27–41.
- Zvereva, E.L., Kozlov, M.V., 2010. Responses of terrestrial arthropods to air pollution: a meta-analysis. Environ. Sci. Pollut. Res. 17, 297–311.