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Climate-Driven Insect Herbivory in Mixed Coast Live Oak Woodlands Within the Mt. Hamilton Range, Santa Clara County

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CLIMATE-DRIVEN INSECT HERBIVORY IN MIXED COAST LIVE OAK
WOODLANDS WITHIN THE MT. HAMILTON RANGE,
SANTA CLARA COUNTY

A Thesis

Presented to

The Faculty of the Department of Environmental Studies

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Michelle Domocol

December 2019

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The Designated Thesis Committee Approves the Thesis Titled

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by

Michelle Domocol

APPROVED FOR THE DEPARTMENT OF ENVIRONMENTAL STUDIES

SAN JOSÉ STATE UNIVERSITY

December 2019

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ABSTRACT

CLIMATE-DRIVEN INSECT HERBIVORY IN MIXED COAST LIVE OAK WOODLANDS WITHIN THE MT. HAMILTON RANGE, SANTA CLARA COUNTY

by Michelle Domocol

Climate change is expected to dramatically alter and destabilize critical functions of oak woodlands (*Quercus spp.*) in California. Oak woodlands support hundreds of vertebrate species and thousands of native insect species. Climate-driven changes in annual temperature, annual rainfall, and spatial climatic variability may increase insect herbivore pressures on mixed coast live oak (*Quercus agrifolia*) woodlands. The Mt. Hamilton Range of Santa Clara County, California offers a unique matrix to study oak-insect herbivore relationship using elevation as a proxy for climate change. This thesis research assessed the relationship between lepidopteran herbivory and coast live oak with insect surveys and the laboratory analysis of phenolic compound concentrations. Results were evaluated under two plant-herbivore theories, Resource Availability Hypothesis (RAH) and Plant-Size Apparency Hypothesis (PSAH). Results indicate elevation increased as mean annual temperature declined, confirming that elevation in this system is a suitable proxy for climate change. Relationships between herbivory, elevation and plant defense chemicals showed larger plant size correlated with higher herbivory. Overall, the results did not support RAH and partially supported PSAH. Results suggest managers should use alternate hypotheses in combination with an elevational framework. As the climate changes, future elevational surveys may help managers understand how to best preserve Mt. Hamilton's oak woodlands.

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Introduction

The ecological functioning of terrestrial ecosystems depends on a complex web of multiple trophic levels, biotic interactions (Anstett, Nunes, Baskett, & Kotanen, 2016; González-Zurdo et al. 2016; Pellissier et al., 2012) and abiotic factors (Jamieson, Trowbridge, Raffa, & Lindroth, 2012; Voelckel & Jander, 2014). Vegetation and insect communities, the foundation of most terrestrial trophic complexes, (Abdala-Roberts et al., 2016; Buckley, Widmer, Mescher, & De Moraes, 2019) are strongly influenced by regional climate, seasonal temperature and precipitation (Leckey, Smith, Nufio, & Fornash, 2014; Rasmann et al., 2014; Voelckel & Jander, 2014). Understanding multitrophic responses (i.e. diverse plant-insect interactions) to climate change will be essential to managing plant communities (Jamieson et al., 2012; Moreira, Petry, Mooney, Rasmann, & Abdala-Roberts, 2017). Analyses that explain how herbivores mediate plants' response to climate change are necessary. Additionally, data from plant-insect surveys are needed to describe how plants mediate insect herbivores' response to climate change (Jamieson et al., 2012; Moreira et al., 2017). For example, researchers observe that, with climate warming, plants' phenological processes such as budbreak and leaf expansion can occur sooner than historic patterns (Jamieson et al., 2012). Simultaneously, climate warming can cause higher rates of insects' larval development and overwinter survival (Jamieson et al., 2012; Haavik, Flint, Coleman, Venette, & Seybold, 2019; Mclaughlin, Morozumi, MacKenzie, Cole, & Gennet, 2014). Jamieson, Trowbridge, Raffa, and Lindroth (2012) observed that unseasonable warming during dry periods can result in heightened insect herbivory, vegetation mortalities, and impaired

leaf development (Jamieson et al., 2012). However, these observed trends lack a complete analysis of mechanisms that mediate both plants' and insects' responses to climate change (Jamieson et al., 2012). With more plant-insect herbivore studies, researchers and managers can fully assess multitrophic responses associated with spatial climatic variability in local and regional areas (McLaughlin et al., 2014).

Despite increasing evidence that climate change is altering composition and multitrophic interactions, surveys on species' adaptations and responses remain limited (Buckley et al., 2019). The assessment of climate change consequences on insect herbivory and defense patterns in oak woodlands is increasingly imperative as oak habitat shrinks in biodiversity hotspots such as California (Brooks & Merenlender, 2001). Mixed oak woodlands in Santa Clara County, California are particularly vulnerable to change as temperatures continue to rise over this century (Brown, 2018; Maizlish, English, Chan, Dervin, & English, 2017). Climate-driven changes in annual temperature, rainfall, and spatial climatic variability are predicted to increase herbivore pressures on coast live oak woodlands in California (Hardy, Vreeland, & Tietje, 2013).

To examine local and regional oak-herbivore relationships, researchers can employ elevational surveys as a proxy for climate change (Körner, 2000). Santa Clara County provides an excellent location to study elevational insect herbivory and plant defense concentrations. Resident oaks are distributed over elevations from sea level to 1050 m (Calflora, 2019). Lepidoptera larvae are primary foliar feeders of Santa Clara County oaks. Further, Lepidoptera such as *Adelpha californica*, *Erynnis propertius*, and *Erynnis tritius*, support higher trophic levels in Santa Clara County's oak woodlands (Shapiro,

2007). As pollinators and prey for birds, bats and other insectivores in the county's oak woodlands, Lepidoptera significant ecological roles (Shapiro, 2007). Oak woodlands in Santa Clara County clearly offer suitable elevational characteristics and multitrophic relationships for elevational oak herbivory studies.

Several hypotheses predict how climate-driven herbivory impacts on plants, including the Resource Availability Hypothesis. However, current elevational surveys on oak defenses, insect herbivory rates and herbivore pressure are inconclusive, driving the need for additional studies (McClaughlin et al., 2014; Peters, Schwartz, & Lubell, 2018; Rasmann et al., 2014; Voelckel & Jander, 2014). California is a biodiversity hotspot at risk of significant species loss due to climate change. The results from this thesis research on elevational oak-lepidopteran interactions can inform local and regional climate adaptation as well as biodiversity conservation in Santa Clara County (Abdala-Roberts et al., 2016; González-Zurdo, Escudero, Nuñez, & Mediavilla, 2016; Pearse, 2011).

Literature Review

Climate Impacts and Plant-Insect Herbivore Relationships

Climate change is predicted to impact ecosystems at the organism, population and community level (González-Zurdo et al., 2016; Pardikes, Shapiro, Lee, & Forister, 2015; Rasmann et al., 2014). At the organismal level, climate change may alter individual physiological processes such as growth, phenology and mortality rates of host vegetation and insect herbivores (Bale et al., 2002; Kingsolver & Buckley, 2018) (Figure 1). These interacting ecological processes are known as multitrophic responses.

Figure 1. Expected multitrophic responses to climate change. Hollow arrows within the figure point to direct effects of climate change on species traits. Black arrows indicate direct effects resulting from altered trophic interactions. Traits are identified inside the black arrows. The bottom box highlights indirect effects that can influence species interactions between and across trophic levels. Adapted from Jamieson et al., 2012.

Host-plants and insect herbivores are the foundation of higher trophic levels and their interactions drive community-level dynamics. (Voelckel & Jander, 2014; Zehnder & Hunter, 2008). Insect herbivory plays a major role in shaping plant community diversity and composition (Gallou, Baillet, Ficetola, & Després, 2017; Kergunteuil, Descombes, Glauser, Pellissier, & Rasmann, 2018; Pardikes et al., 2015). As climate becomes less favorable for insect development, these herbivores may become progressively less successful at completing their life cycle on specific host-plants (Bale et al., 2002; Leingärtner, Hoiss, Krauss, & Steffan-Dewenter, 2014).

In addition, climatic events such as advanced or delayed snowmelt can lead to phenological desynchronization. Phenological desynchronization occurs when plant or insect growth becomes out-of-phase with other aspects of the ecological environment (Kessler, Poveda, & Poelman, 2012; Kergunteuil et al., 2018; Leingärtner et al., 2014).

Plant and insect phenology are cued by temperature, climate and photoperiods, all of which can be disrupted by climate change. Studies show insect herbivores and their associated host-plants respond to unseasonable warming with phenological desynchronization. Moreover, Bale et al. (2002) reported insects can produce unexpected colonies when cued by recent unstable climate and unseasonable temperature increases. As a result, host-plants may not develop the defenses to counter early upsurges in herbivore colonies (Bale et al., 2002).

Studies of European and southern California oak woodlands indicate that extreme thermal changes can directly influence insect herbivore development, reproduction, and survival (Voelckel & Jander, 2014). Several cases that highlight Lepidoptera with limited distributions indicate their host-plants were vulnerable to climate impacts (Gallou et al., 2017; Kergunttil et al., 2018; Kingsolver & Buckley, 2018; Pardikes et al., 2015). Gallou, Baillet, Ficetola, and Després (2017) suggest the decrease in plant diversity was associated with lowered butterfly species richness. This decline in plant diversity was specifically due to stressful climatic conditions such as novel low temperatures. As a result, specialist butterfly larvae were unable to find their preferred host-plants. In addition, Gallou et al. (2017) found abnormally low temperatures inhibited complete larval life cycles.

Other investigations emphasize that, unlike their sessile host-plants, some insect populations can respond to climatic variability with new migratory patterns and quick range shifts (Abdala-Roberts et al., 2016; de Sassi, Lewis, & Tylianaki, 2012; Moreira et al., 2017). Novel migrations and immediate range shifts produced rapid trophic

mismatches between insect herbivores and host-plants (Abdala-Roberts et al., 2016; de Sassi et al., 2012). Trophic mismatches are closely tied with phenological desynchronization. Since insect herbivores are more sensitive to thermal changes, their development, reproduction and population dynamics are directly influenced by climate change. Bale et al. (2002) found certain Lepidoptera such as *Pieris brassicae* will disperse to new habitats and shift their demographic range. In turn, insect herbivores might defoliate different host-plants unable to resist new colonies of herbivores (Bale et al., 2002). In northern California, oak woodlands with increased climate-related herbivore pressure exhibited lower host-plant productivity, higher mortality rates, and severe leaf damage rates (Leckey et al., 2014; Pearse, 2011).

Moreover, related research predicts unseasonable oscillations in herbivore population density may lead to herbivore population increases and rapid host-plant declines (Pellissier, Aurélien, Bilat, & Rasmann, 2014). These predictions suggest climate-induced insect defoliations may lead to modified oak canopy development, and higher mortalities in oak overstory and associated understory host-plants (Kessler et al., 2012). Compared to insects, vulnerable, sessile host-plants may slowly adapt their geographic range to the new climate stressors (Forister et al., 2010). These novel migration rates will result in trophic mismatches or reshuffled plant and insect communities (Casner, et al., 2018). Changes in herbivore populations can negatively affect plant community composition and community-level functional traits (de-Dios-García, Manso, Calama, Mathieu, & Pardos, 2018; de Sassi et al., 2012; McLaughlin et al., 2014).

Ecological Relationships in Californian Oak Woodlands

Regional and local taxa-specific analyses are necessary to understand and manage climate impacts on oak woodland ecosystems in central California (Machuca, Ferreira, Martinez, & Santos, 2011; Voelckel & Jander, 2014). Elevational surveys investigate how abiotic conditions and climate change may degrade or disrupt vital multitrophic relationships (Rasmann et al., 2014) in Californian oak woodlands. In California, oak woodlands are widespread and support approximately 300 species of terrestrial vertebrate wildlife, 370 fungi, and approximately 5,000 insect species (Barry et al., 2005; SFEI, 2017; Zack, Chase, Geupel & Stralberg, 2005). At least 169 terrestrial mammal species depend on oak woodlands for food, shelter, or cover (Barry et al., 2005).

Coast live oak woodlands (*Quercus agrifolia*) provide significant host-plants, food sources, protective cover, nesting sites, and corridors for a diversity of native invertebrates, avian species, reptiles and amphibians, and mammals (Barry et al., 2005; SFEI, 2017). The oak woodland understory assemblage includes endemic shrubs, such as manzanita species (*Arctostaphylos spp.*), and trees like buckeye (*Aesculus californica*), madrone (*Arbutus menziesii*), wild cherry (*Prunus ilicifolia*), and California bay laurel (*Umbellularia californica*) (SFEI, 2017). Oak communities also include several keystone terrestrial species like mountain lions (*Puma concolor*) and predators such as coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) (Costello, Hagen, & Jones, 2012).

Wildlife and floristic communities rely on stable ecological functions of oak woodlands (Costello et al., 2012). For instance, Californian oak woodlands provide the production high volumes of biomass and uptake significant amounts of nitrogen and

carbon to resident flora and fauna (Coleman et al., 2011; Scott, Turner, Washington, & Corella, 2015). Resident predators, herbivores, understory vegetation and decomposers depend on oak woodland litter decomposition, soil stabilization, and water quality regulation (Rasman et al., 2014; SFEI, 2017). Biodiverse coast live oak woodlands support productive soil and protect the integrity of regional watersheds (Tietje, Purcell, & Drill, 2005). Oak canopy layers produce high volumes of biomass, take up nitrogen and carbon, and decompose litter (Hardy et al., 2013). Biomass production and leaf litter decomposition increase soil organic matter and fertility of woodland soils (Costello et al., 2012; Tietje et al., 2005).

Unstable temperature and climate are forecasted to threaten the stability of oak woodland vegetation. Average maximum and minimum temperatures in regions of central California are projected to be higher than historic average maximum temperatures (Cal-Adapt, 2019; Langridge, 2018). With average temperature increases, principal multitrophic interactions and ecological functions of oak woodlands may deteriorate (Coleman et al., 2011; Kingsolver & Buckley, 2018; SFEI, 2017).

Estimating the Impact of Climate in Oak-Insect Herbivore Relationships

Multitrophic plant-insect herbivore responses to climate factors still require thorough, systematic analysis of oak-insect relationships (Pardikes et al., 2017). Elevation gradients can be optimal tools to infer climate change dynamics (Boscutti et al., 2018). Since air temperature can decrease by 5.5 C° per vertical kilometer, many studies use elevation as a proxy for temperature and climate change conditions (Körner, 2007). The spatial variation in climatic factors such as temperature represent strong environmental

pressures on ecosystems that mirror climate change conditions (Dunne, Saleska, Fischer, & Harte, 2004; Pfennigwerth, Bailey, & Schweitzer, 2017). The use of elevation gradients to infer climate change responses can minimize the confounding effects of historical and biogeographical differences in plant responses (Andrew, Roberts, & Hill, 2012; Kershaw, Ducey, Beers, & Husch, 2016; Pellissier et al., 2014; Rasmann et al., 2014).

Numerous hypotheses predict specific plant defense trends and multitrophic responses to abiotic factors, such as climate change. The Resource Availability Hypothesis (RAH) is one such well-known theoretical approach (Körner, 2007; McLaughlin et al., 2014; Pellissier et al., 2012). RAH suggests that multitrophic trends are driven by ecological gradients such as elevation, temperature, and precipitation (Rasmann et al., 2014; Voelckel & Jander, 2014). Using elevation as a proxy for temperature, researchers have employed the RAH framework to investigate climate change responses of plant-insect population dynamics (de Sassi et al., 2012), herbivore pressure, herbivore assembly, and host-plants' defensive trait expression (de-Dios-García et al., 2018; Hahn & Maron, 2016). Essentially, the RAH framework can be used to assess the degree of influence climate may have over plant-insect herbivore relationships (Kessler et al., 2012; Galmán et al., 2018; Moreira et al., 2017). RAH posits that plant defense traits, such as foliar nitrogen, defensive chemistry, structural compounds, and leaf morphology traits, will change with climate stress and with other varying elevational conditions (Galmán et al., 2018; Rasmann et al., 2014). Plant defenses are anticipated to

change according temperature stressors, biotic impacts, and degrees of herbivore pressure (Descombes et al., 2017; Kergunteuil et al., 2018).

At lower elevations, RAH predicts that limiting abiotic conditions are reduced. Lower elevations are characterized with less resource stress, warmer conditions, and less wind (Buckley et al., 2019; Moreira et al., 2017). As a response to favorable conditions, lower elevation habitats should exhibit higher levels of growth, abundance and diversity than higher elevations (Moreira et al., 2017). At lower elevations, tree species more successfully counter insect herbivory with potent foliar defensive compounds (Anstett et al., 2016; Hahn & Maron, 2016). In response, to the higher herbivory, increased leaf area loss and frequent insect outbreaks, lower elevation plants use chemical defense to maintain abundance and fitness (Abdala-Roberts et al., 2016; Pearse, 2011). At lower elevations, plant chemical defenses include secondary metabolites, induced defenses, direct and indirect defenses (e.g. volatile organic compounds and glucosinolates) (Defosezz, Pellissier, & Rasmann, 2018; Tietje et al., 2005; Rasmann et al., 2014; Voelckel & Jander, 2014). Foliar defensive compounds also include tannins, phenolics, and terpenoids (Anstett et al., 2016; Kessler et al., 2012; Mizumachi, Mori, Akiyama, Tokuchi, & Osawa, 2012). Since they depend more on defensive compounds, lower elevation vegetation is expected to express fewer physical resistance traits and resource allocation strategies (Abdala-Roberts et al., 2016; Defosezz et al., 2018; Rasmann et al., 2014; Tschardtke & Hawkins, 2002; Voelckel & Jander, 2014).

At higher elevations, plants are predicted to adapt to resource stress and harsh conditions with slow growth (Kessler et al., 2012). Slow-growing vegetation is expected

to defend against lower insect diversity and decreased herbivory (Anstett et al., 2016; Defosezz et al., 2018; Hahn & Maron, 2016). High elevation plants can also resist defoliation with enhanced physical defense traits and morphological resource allocation strategies (Copolovici et al., 2017; Leckey et al., 2014; Rasmann et al., 2014). Morphological defenses include the development of protective leaf shapes, increased leaf thickness, protective epicuticular wax layer or increased plant size (Hahn & Maron, 2016; Jamieson et al., 2012; Kergunteuil et al., 2018; Pellissier, et al., 2014). These physical strategies protect and regulate leaf development, leaf's photosynthetic potential, and leaf permanence (Descombes et al., 2017). High elevation vegetation also expresses resource allocation strategies that redirect resources away from herbivore-damaged sites, decrease leaves' palatability and lower leaves' nutritive value (Defosezz et al., 2018).

A survey of elevational RAH studies indicated that over 60% provided evidence supporting the predictive trends of RAH (Moreira et al., 2017). These studies' findings supported elevational changes in herbivory plant defense investment (Pellissier, et al., 2014; McLaughlin et al., 2014; Voelckel & Jander, 2014). However, many other studies have not confirmed the expected relationships (Casner et al., 2014; Espeset et al., 2016). For example, two community-level examinations of plot surveys and meta-analyses reported elevation lacked any influence over woodland plant-herbivore relationships (Pellissier et al., 2012; Rasmann et al., 2014). In addition, recent analyses report high herbivory levels in upper elevations, rather than lower levels as predicted by RAH (McClaughlin et al., 2014; Peters et al., 2018; Rasmann et al., 2014; Voelckel & Jander, 2014). A recent review by Moreira et al. (2017) refuted the expected elevational trends in

chemical defense investment (Abdala-Roberts et al., 2016; Buckley, Pashalidou, et al., 2019; De Long et al., 2015; Koptur, 1985; Pellissier et al., 2014; Rasmann et al., 2014;). Other inquiries report non-linear or the absence of associations with elevation (Dostálek, Rokaya, & Münzbergová, 2018; Louda & Rodman, 1983; Pellissier et al., 2014). Since plant defense mechanisms may have drivers other than, or in addition to, elevation, researchers suggest it is important to consider selective biotic and abiotic forces that can shape the patterns of defense investment along elevation gradients (Buckley et al., 2019). RAH predictions related to the influence and mediation of population size, predator to herbivore ratios, chemical defense diversity is largely untested in various montane, woodland ecosystems (Leingärtner et al., 2014). Consequently, the influence of elevation on herbivore pressure and other biotic interactions is highly debated (Agne et al., 2018; Leingärtner et al., 2014; Moreira et al., 2017).

Beyond the Resource Availability Hypothesis, there are additional theories and explanatory models for plant-insect herbivore relationships and plant defense mechanisms. One popular and well-tested hypothesis focuses on morphological plant defense strategy of increased plant size (Pellissier, et al., 2014). This framework is called the Plant-Size Apparency Hypothesis (PSAH). Other plant defense explanatory models include the Optimal Defense Theory and the Feeding Specialization Hypothesis. The Plant-Size Apparency Hypothesis (PSAH) predicts larger plants are apparent or easily found by herbivores and other associated organisms (Blanckenhorn, 2000; Hemptinne, Magro, Evans, & Dixon, 2012). This morphological trait to higher plant palatability, higher vigor and lower chemical resistance than smaller, less visible plants (Feeny,

1976). PSAH posits chemical defenses from apparent and unapparent plants differ (Schlinkert et al., 2012). Moreover, the hypothesis emphasizes a plant's morphological investment in larger size often relates to greater dispersal ability, enhanced competitiveness for resources, and higher attractiveness to both beneficial organisms and insect defoliators (Rommel & Tammaru, 2009; Schlinkert et al., 2012). The attractiveness of larger plants may also be higher as they can offer large microhabitat for insects (Schlinkert et al., 2012). Several case studies support the PSAH. One study showed the large host-plants increased their leaf digestibility to larvae when signaled by the oviposition by female winter moths (Schlinkert et al., 2012). The plants' digestibility increased with heightened leaf tannins and lowered proteins (Rommel & Tammaru, 2009). Other cases report the effects of unapparent plants displayed a different multitrophic and phenological relationship to herbivores. For instance, cruciferous plants such as *Pieris rapae* avoid specialist insect herbivores with decrease plant size (Schlinkert et al., 2012). Additionally, generalist insect herbivores are deterred by the cruciferous plant's emission of volatile foliar chemical defenses.

The Feeding Specialization Hypothesis presents an alternative, nuanced perspective to PSAH (Termonia, Hsiao, Pasteels, & Milinkovitch, 2001). This hypothesis asserts specialist herbivore species prefer unapparent plants rather than apparent plants (Termonia et al., 2001). Studies that support this theory indicate specialist butterfly species prefer unapparent herb hosts, while moth species feed on apparent tree and larger understory species (Gómez-Zurita, Juan, & Petitpierre, 2000).

An alternate plant defense explanatory model is the Optimal Defense theory (ODT) (Alba, Bowers, & Hufbauer, 2012). ODT posits that vegetation with limited resources use chemical defenses to increase the fitness of their plant tissues and prevent attacks from insect defoliators, pathogens, and other types of herbivores (Cates, 1980). ODT asserts that herbivores are the main mediators of plants' evolutionary selection of toxic or deterrent chemical defenses (Buschmann, Edwards, & Dietz, 2005). As a result, insect herbivores contribute to the host-plant's fitness and population dynamics (Buschmann, et al., 2005).

Oak Herbivory Response to Temperature and Precipitation

Researchers emphasize the importance of monitoring elevational temperatures and the effects on host oak defenses, insect herbivore interaction, oak life-history characteristics and distributions. The direct effects of temperature and precipitation on insects are likely to differ among oak and associated host species (Casner et al., 2014; Gallou et al., 2017; Kerguntill et al., 2018). Woodland management and oak's potential adaptive capacities may help oaks resist deleterious effects of changing temperature conditions (Tscharntke & Hawkins, 2002; Voelckel & Jander, 2014).

Changes in annual temperature and precipitation may drive the altered migratory patterns and range distribution of oak herbivores (Moreira et al., 2017; Rasmann et al., 2014). Findings already suggest regional temperature rise is likely to affect insect morphology and demographic patterns (Bale et al., 2002; Speed, Austrheim, Hester & Mysterud, 2012). Altered insect colonization, increased herbivore attacks and decreased host-plant fitness are direct multitrophic responses (Tscharntke & Hawkins, 2002;

Voelckel & Jander, 2014). A study by Leckey, Smith, Nufio, & Fornash (2014) indicated that climate change impacts on annual temperature in California may destabilize populations of specialists and generalist feeding insects, such as Lepidoptera. In contrast, Galmán et al. (2018) found, with four European oak species, temperature was not correlated with most measures of herbivory. The contrast in findings may indicate the effects of herbivory may vary with location and specific regional abiotic conditions (Leckey et al., 2014). Many case studies have demonstrated that drought stress and precipitation regimes can affect the abundance, development, and distribution of plants and insects, while also affecting the nutritional quality and defenses of plants (de Sassi et al., 2012; Jamieson et al., 2012; Körner, 2007). Foliar feeders such as gall formers or leaf miners are increase their feeding rates and actual leaf area loss during high precipitation (Galmán et al., 2018). Precipitation-associated changes in plants and insects may influence the type and strength of interactions that occur between these two groups (Coleman et al., 2011; Galmán et al., 2018).

Elevational insect herbivory research shows that shifts in precipitation, temperature, climate, and biotic conditions impact to oak woodland defensive chemistry (Haavik et al., 2015; Jamieson et al., 2012; McLaughlin et al., 2014). Researchers suggest some host-plant species that historically relied on physical defenses will produce novel defensive chemistry (Rasmann et al., 2014; Voelckel & Jander, 2014). Vegetation is expected to respond to climate stress with higher levels of constitutive direct defenses such as glucosinolates (de-Dios-García et al., 2018; de Sassi et al., 2012; Descombes et al.,

2017). Glucosinolates are secondary metabolites synthesized in plant tissue (Barba et al., 2016) that deter insect defoliators (Barba et al., 2016).

An elevational study found European mediterranean oak species in lower elevations exhibited a novel increase of herbivore-induced phenolic compound concentrations to resist novel lepidopteran attacks (Rasmann et al., 2012). Similarly, Leckey et al., (2014) observed that northern California oaks, at lower elevations, produced increased concentrations of total phenolics and proanthocyanins (condensed tannins) to resist an unseasonable upsurge in lepidopteran herbivory. Similarly, Mizumachi, Mori, Akiyama, Tokuchi, & Osawa (2012) found that at upper elevations in Japan, oaks (*Quercus serrata*) adjusted their physiological and morphological properties as a response to novel herbivore attacks. These studies reveal oaks can respond with phenotypic plasticity and induce stronger foliar defensive compounds to adapt to new herbivory patterns (Leckey et al., 2014; Mizumachi et al., 2012). The development of stronger herbivore resistance may show how plants can mitigate novel herbivore outbreaks and increased defoliation in future periods of unseasonable climate warming (Tschardtke & Hawkins, 2002; Voelckel & Jander, 2014). Locally focused studies of oak responses to climate change using elevational studies can be used to assess whether hosts can effectively defend against novel herbivore pressures (Descombes et al., 2017; Mizumachi et al., 2012). Given the variability in oak community responses, managers need local studies that assess oak-herbivory interactions under different climate, temperature and precipitation regimes (Descombes et al., 2017).

Research Objectives

Santa Clara County oak woodlands provide an opportunity to study oaks and their lepidopteran herbivores under a range of elevational conditions. Santa Clara County is located at the southern end of the San Francisco Bay in California (SFEI, 2017). The county encompasses 1,312 square miles which includes Santa Clara Valley (SFEI, 2017). The Mt. Hamilton Range is a belt of mountains that lie east of the Santa Clara Valley. Mixed coast live oak woodlands cover approximately 11,696 hectares of the Mt. Hamilton Range (Figure 2). The range's elevation extends from sea level to 1,399 m (Barry et al., 2005; Grossinger, Striplen, Askvold, Brewster, & Beller, 2007; SFEI, 2017). Oak communities within the Mt. Hamilton Range include coast live oaks, oak hybrids, blue oak (*Quercus douglasii*) woodlands, valley oak (*Quercus lobata*) woodlands, foothill pine-oak woodlands (*Pinus sabiniana*), interior oak (*Quercus wislizeni*) chaparral, leather oak (*Quercus durata*) chaparral and black oak (*Quercus kelloggii*) woodlands. Many of the communities overlap and lack sharp boundaries.

Figure 2. Coast live oak distribution in Santa Clara County. Solid, green patches indicate areas with coast live oaks. Adapted from “Observation Hotline: *Quercus agrifolia*,” by Calflora, 2019.

Understanding the oak-lepidopteran responses to changing temperature and precipitation patterns can provide guidance for managing oak woodlands in Santa Clara County as the climate changes (Brooks & Merenlender, 2001; Grossinger, et al., 2007). Researchers and oak woodland managers in Santa Clara County should monitor patterns of phenological disruption, trophic mismatches and biogeographical shifts in oak defoliators such as Lepidoptera (Brooks & Merenlender, 2001; Grossinger, et al., 2007). Studies on lepidopteran responses to climate change will help managers predict and possibly mitigate the occurrence of outbreaks. These plant-herbivore studies may also reveal oaks’ defense and response to unseasonable lepidopteran upsurges. California

coast live oaks in Santa Clara County are projected to experience rising temperatures by the end of this century (Maizlish et al., 2017). Average maximum temperatures in Santa Clara County are projected to be 3.8° C higher than historic maximum temperatures (Cal-Adapt, 2019; Langridge, 2018). High carbon emissions models foresee increased average temperatures, more frequent extreme heat events, flooding and extreme storms in Santa Clara County (Langridge, 2018). Thirty-year averages of annual rainfall in Santa Clara County are projected to increase from 38.6 centimeters to 45.2 centimeters by the end of the century (Cal-Adapt, 2019; Langridge, 2018).

Elevational plant-herbivore and plant defense studies can assess how herbivore pressures on coast live oak woodlands may change with increasing temperature and precipitation (Rasmann et al., 2014; Voelckel & Jander). The Resource Availability Hypothesis and Plant-Size Apparency Hypothesis are possible theoretical frameworks to evaluate herbivory rates, defense patterns and abiotic influences (McClaughlin et al., 2014; Peters et al., 2018). Studies have found variability in the temperature-mediated responses to herbivores highlight the need for local, climate-driven elevational herbivory studies (Casner et al., 2014; Leckey et al., 2014). Local studies will ensure effective conservation and management of local ecosystems (McClaughlin et al., 2014; Peters et al., 2018; Rasmann et al., 2014; Voelckel & Jander, 2014).

This case study addresses the following research questions and hypotheses to assess climatic variability, using elevational change, on oak-lepidopteran interactions in the Mt. Hamilton Range of Santa Clara County oak woodlands.

Research Questions

1. Do rates of observed native lepidopteran larvae herbivory support the expected patterns of elevational herbivory and plant chemical defense concentrations as predicted by the Resource Availability Hypothesis or the Plant-Size Apparency Hypothesis?
2. To what extent are abiotic factors such as mean annual temperature associated with elevational insect herbivory? Given the results, what are the implications for oak woodland management practices?

Null Hypotheses:

1. In the Mt. Hamilton range, mean annual temperature and elevation are not significantly related.
2. Native lepidopteran (Nymphalidae) larvae herbivory rates, as measured in percentages of leaf area removed, in coast live oak clusters do not differ along elevations from 350 m to 1050 m.
3. Concentrations of these phenolic compounds, kaempferol, quercetin, gallic acid, ellagic acid, do not differ by elevation from 350 - 1050 m in coast live oak leaves.
4. Lepidopteran herbivory rates are not related to coast live oak diameter at breast height (DBH) or height.
5. Concentrations of these phenolic compounds, kaempferol, quercetin, gallic acid, ellagic acid, are not related to coast live oak diameter at breast height (DBH) or height.

Study Area

Data were collected from September to December 2018 and March to May 2019 in the Mt. Hamilton Range, Santa Clara County, California. The data collection sites of this study are Lick Observatory, Grant Ranch County Park, Blue Oak Ranch Reserve, and Cañada de los Osos Ecological Reserve (Figure 3).

Figure 3. Oak sample sites and weather station locations. Hollow circles indicate sampling areas and diamond symbols represent weather station sites. Elevation is indicated next to sample site. Adapted from “Mt. Hamilton, San Jose, CA” by Google, 2019.

The Mt. Hamilton Range, with its summit at 1,399 m, is part of the Diablo Range and lies on the east side of Santa Clara County. Within each sampling site is a variety of grasslands, mixed oak woodlands, chamise chaparral, riparian vegetation and abundant faunal diversity.

The elevation and temperature gradient at Mt. Hamilton Range was expected to act as a proxy for climate variation and the region's predicted climate increase. Average annual temperatures in lower elevations of the Mt Hamilton are 33°C, while high elevations average 25°C (Langridge, 2018). Average maximum and minimum temperatures in Santa Clara County are projected to be 3.8°C and 3.9°C higher, respectively, than historic temperatures (Cal-Adapt, 2019; Langridge, 2018). These projections are according to two climate model climate model simulations called HadGEM2-ES and MIROC5 (Cal-Adapt, 2019). The HadGEM2-ES is simulation model that forecasts warmer and drier years in the Mt. Hamilton area. The MIROC5 model provides alternate climate scenarios beyond warm/dry, cool/wetter and average simulation models (Cal-Adapt, 2019). Table 1 lists the 30-year annual average maximum and minimum temperatures in an 8.5 Representative Concentration Pathway (RCP) scenario (Cal-Adapt, 2019; Langridge, 2018). RCPs describe alternative trajectories for carbon dioxide emissions and the resulting atmospheric concentration from 2000 to 2100 (Cal-Adapt, 2019).

Table 1

Historic and Projected Annual Temperature Averages in Santa Clara County

	Historic 30-year Annual Average	Projected 30-year average the end of century
Maximum Temperature (°C)	21.9	25.8
Minimum Temperature (°C)	10.2	14.1

Note. Temperatures represent historic and project annual temperatures averages in Santa Clara County under an 8.5 RCP Scenario. This Representative Concentration Pathway (RCP) scenario assumes greenhouse gas emissions will rise through 2015 and plateau around 2100. Adapted from “Annual Averages” by Cal-Adapt, 2019.

Methods

Data were collected from September to December 2018 and March to May 2019 in the Mt. Hamilton Range of Santa Clara County, CA (Figure 3). Data collection methods included three components: 1) standing herbivory surveys; 2) plant defense chemical laboratory analysis; and 3) vegetation community surveys. The data collection sites of this study are Lick Observatory, Grant County Park, Blue Oak Ranch Reserve and Cañada de los Osos Ecological Reserve. Lick Observatory sits atop Mt. Hamilton while mid to lower elevation sites such as Blue Oak Ranch Reserve and Joseph Grant County Park sit on the slopes of the Mt. Hamilton Range. All sampling sites had northerly aspects. Blue Oak Ranch Reserve's elevation range is 454 m to 870 m above sea level adjacent to Grant County park. Grant County park's elevation ranges from 427 m to 853 m above sea level. The lowest elevation sites are in Cañada de los Osos Ecological Reserve. This site sits east of Gilroy in the southern portion Santa Clara County. The Mt. Hamilton Range was also selected for its vulnerable habitats, protected wildlife corridors, resident live oak community composition, structure, and habitat value (SFEI, 2017; Tietje et al., 2005).

Site selection was modeled after the experimental design of Leckey et al. (2014). Individual oaks were sampled at 100-meter intervals between elevations of 350 m to 1050 m in order to provide a gradient in temperature conditions. Herbivory rates of native lepidopteran larvae were collected from March to May 2019. The target individuals were mature coast live oaks and saplings of at least 1.2 m in height and a total

of 502 individual specimens were sampled over the different elevations at the four sites (Table 2).

Table 2

Location of Oak Samples

Data Collection Site	Total Number of Individual Specimens Sampled (n)	Elevation (m)
Cañada de los Osos Ecological Reserve	65	350
Cañada de los Osos Ecological Reserve	76	450
Joseph Grant County Park	64	550
Joseph Grant County Park	64	650
Joseph Grant County Park	68	750
Lick Observatory	61	850
Lick Observatory	39	950
Lick Observatory	64	1050

Note. Data collection sites of oak samples with corresponding elevation and total number of individual specimens.

Vegetation assessments recorded specimens' DBH, canopy cover, and height class.

Height class refers to the category of average plant height at the time of observation.

Examples of height intervals for average height trees are $1 \leq 1/2$ m, $5=5-10$ m, $10 \geq 50$.

Shrub cover and associated tree species were estimated with a Rapid Assessment/Releve (CNPS, 2018). Tree coordinates were recorded with Global Positioning System (GPS) units. GPS measurements were accurate to within 3 meters.

From March 2019 to May 2019, standing lepidopteran herbivory rates and oak community characteristics were recorded for each sampling site along the elevation gradient. Standing lepidopteran herbivory recorded leaf damage from Nymphalidae foliar feeders such as *Adelpha californica* larvae (Figure 4).

Figure 4. Target species and insect feeding pattern in herbivory surveys. Left-hand image shows coast live oak leaves and *Adelpha californica* larvae are target specimens in surveys. Right-hand image shows common marginal leaf feeding pattern. Right-hand image adapted from “Butterflies and Moths of North America,” by Metalmark Web & Data, 2019.

The specific herbivory scoring criteria were guided by protocols from Rasmann et al. (2014) and Leckey et al. (2014) and used these metrics:

- the average actual leaf area removed;
- percent leaf area removed;
- number of discrete feeding damage marks per leaf;
- foliar feeding type.

As part of the standing herbivory survey, two lower branches of each oak specimen with at least 10 leaves were surveyed for feeding damage (de Sassi et al., 2012). Leaf damage

was measured through a square-centimeter grid. Each search was at least one minute for consistency in effort (Leckey et al., 2014).

To determine the elevational difference in foliar defense concentrations, leaf samples from the oak sampling site were collected and analyzed for their phenolic compound concentrations. The analyzed phenolic compounds were kaempferol, quercetin, gallic acid, ellagic acid. These phenolic compounds are related to defense responses in coast live oaks. Oak phenolic compounds can act as leaves' defensive coloring for camouflage, insect deterrents, and antibacterial protection (Voelckel & Jander, 2014). Leaf samples were 5 grams in fresh weight. Samples were sent to Brookside Laboratories in New Brennan, Ohio. The laboratory used liquid chromatography (LC-MS/MS) to test the mg/kg phenolic compound concentrations of quercetin and kaempferol. LC-MS/MS uses liquid chromatography with highly sensitive and selective mass analysis capability of triple quadrupole mass spectrometry (Voelckel & Jander, 2014). High performance liquid chromatography (HPLC) was used to test the phenolic compound concentration of gallic and ellagic acid. HPLC separates the phenolic compounds by dissolving the sample in suitable solvents (Voelckel & Jander, 2014).

Mean annual temperatures and historical weather data was collected from online weather station archives. Weather stations were located in Lick Observatory, Blue Oak Ranch Reserve and Cañada de los Osos Ecological Reserve.

Data Analysis

All statistical analysis was conducted using IBM® SPSS® Statistics Version 25. The following analyses tested the predictions of Resource Availability Hypothesis. Mean

annual temperature was tested to determine temperature's correlation with each sampling site's elevation. Spearman's rank order correlation was used to assess whether a relationship existed between mean annual temperature and elevation. The r_s value in Spearman's correlation refers to the correlation coefficient for variables that were converted into ranked scores.

Herbivory rates were represented by the percentages of leaf area removed from each specimen at each sampling site. Herbivory rates at each site were compared to assess a significant difference per elevation. A Kolmogorov-Smirnov normality test found herbivory rates were not normally distributed. As a result, a Kruskal-Wallis H-test was conducted. The Kruskal-Wallis H-test is a rank-based nonparametric test to assess if herbivory rates were significantly different at each elevation. Since variables were not normally distributed, a Spearman's rank-order correlation was used to assess relationships between lepidopteran herbivory rates and elevation. The mean annual temperatures and the corresponding herbivory rates were compared to assess a significant temperature difference between elevations. A Kolmogorov-Smirnov normality test determined herbivory rates were not normally distributed; therefore, a Kruskal-Wallis H test was used. Dunn-Bonferroni's post hoc tests identified the significant difference between pairs of mean annual temperatures. To address variables' non-normal distribution, a Spearman's rank-order correlation measured the relationship between lepidopteran herbivory rates and mean annual temperature.

Phenolic concentrations were mean concentrations of kaempferol, quercetin, gallic acid and ellagic acid. A relationship between mean kaempferol concentrations and

elevation was determined using the Spearman's rank order-correlation. A one-way analysis of variance (ANOVA) compared the quercetin levels at different elevations, as these data were normal. One-way ANOVA tests also determined the significant difference of gallic acid and ellagic concentrations per elevation.

Results

A total of 502 oak specimens were sampled at elevations from 350 m to 1050 m at all sites (Table 3). Mt. Hamilton has an elevational temperature gradient of approximately 4°C, a suitable proxy (Rasmann et al., 2018) for climate variability as predicted in Santa Clara County climate change scenarios (Cal-Adapt, 2019; Langridge, 2018). The following results describe the analyses of the Resource Availability Hypothesis (RAH) predictions.

Table 3

Oak Specimens and Temperature Per Elevation

Elevation (m)	Number of Oak specimens per elevation	Mean Annual Temperature (C°)	Standard Error for Leaf Area Loss (SE)
350	65	14.58	0.882
450	76	14.33	0.815
550	64	13.11	0.889
650	64	13.92	0.889
750	68	12.67	0.862
850	61	13.66	0.91
950	39	10.8	1.138
1050	64	7.23	0.882

Note. Number of oaks sampled, temperature, and standard error for leaf area loss per elevation.

Mean annual temperature was strongly and inversely correlated to elevation ($r_s = -0.90$, $n = 502$, $p < 0.001$; Figure 5), demonstrating an expected RAH relationship.

Figure 5. Relationship between mean annual temperature and elevation interval. Error bars represent standard errors (mean $\pm$ SE).

Herbivory rates, as measured by percent of leaf area removed, varied greatly between elevation ($H(2) = 227.243$, $p < 0.001$; Figure 6), which was a proxy for temperature.

There was a weak positive relationship between area removed and elevation ($r_s = 0.388$, $n = 502$, $p < 0.001$). Herbivory was significantly higher in individual trees located at the highest sampled elevations (850 m, 950 m and 1050 m) (Figure 6). The sites in the highest elevations also had the lowest temperatures. Individual trees in the lower elevations (350 m, 450 m, and 550 m) and higher temperatures had lower rates of leaf area loss (Figure 6).

Figure 6. Leaf area loss per elevation and mean annual temperature. The symbols **a** and **b** above box plots indicate elevation groups with significantly different herbivory rates. Error bars represent standard errors (mean $\pm$ SE).

The percentage of leaf area removed ($n=502$) significantly differed between different mean annual temperatures ($H(2) = 227.243$, $p < 0.001$; Figure 6). Leaf area removed was much greater at the mean annual temperatures of higher elevations (950 m and 1050 m) than mean annual temperatures of mid- (650 m and 750 m) or low elevations (350 m and 450 m). Leaf herbivory rates at 450 m were significantly lower than herbivory rates at mean annual temperatures of mid and high elevations (650 m, 750 m and 950 m). There was a weak negative relationship between temperature and leaf area removed ($r_s = -0.40$, $n = 502$, $p < 0.001$).

There were no strong linear relationships with any phenolic compound concentrations and elevation (Table 4). There was no significant mean difference for any phenolic compound concentrations except quercetin (Table 4). There was a significant mean

difference in quercetin concentrations ($n=24$) between elevations ($F(7,16)=3.849$, $p = 0.012$; Figure 7), with concentrations at 650 m being greater than those at 450 m ($p=0.047$) or 950 m elevation ($p=0.043$).

Table 4

No Relationships Between Oak Compounds and Elevation

	Quercetin	Kaempferol	Gallic Acid	Ellagic Acid
Elevation	$R=.030$; $p= 0.002$	$r_s= -0.13$, $p<0.001$	$R=.048$; $p= 0.824$	$R=.219$; $p= 0.304$

Note. No strong linear relationships exist between oak phenolic compounds and elevation. R , r_s , and p -values show the absence of relationships.

Figure 7. Mean quercetin levels per elevation. Line graph shows significant higher quercetin concentrations in 650 m elevation than concentrations in 450 m and 950 m elevations.

The following results describe the analyses of the Plant-Size Availability Hypothesis predictions. Individual tree diameter (DBH) and herbivory rates were strongly correlated ($r=0.455$; $n=502$; $p<0.001$; Figure 8). Individual plant height and leaf herbivory rates

were also positively correlated, but the relationship was relatively weak relationship ($r=0.291$; $n=502$; $p<0.001$; Figure 9). There was no relationship between DBH at each elevation for any phenolic concentrations (Table 5). Table 5 also shows no linear relationships between phenolic concentrations and plant height.

Figure 8. Individual oak diameter (DBH) versus leaf area removed. $n=502$.

Figure 9. Individual oak height versus leaf area removed. $n=502$.

Table 5

No Relationships Between Oak Compounds, Diameter and Height

	Quercetin	Kaempferol	Gallic Acid	Ellagic Acid
Oak Diameter (DBH)	R=0.067; p= .754	r= -0.13, p=0.550	R =.230 p =.288	R=.07 p=.746
Oak Height (m)	R=0.183; p=0.392.	r _s = -.12; p=0.570	R=.241 p =.256	R=.086 p =.690

Note. No strong linear relationships between oak phenolic compounds, diameter and height. R, r_s, and p-values show the absence of relationships.

Discussion

This study examined the relationship between temperature and oak herbivory rates in Santa Clara County, CA, using elevation as a proxy for climate change conditions. I postulated that elevation would provide a suitable temperature range to test the effects of temperature variability. Results indicated the Mt. Hamilton Range is indeed a good system to perform elevational plant-herbivore research. Numerous studies confirm the use of elevational gradients can successfully infer species' responses to climate change (Boscutti et al., 2018; Moreira et al., 2017; Pfennigwerth et al., 2017). Rasmann et al. (2014) referred to elevational gradients as 'optimal ecological surrogates' for predicting climate-driven dynamics. Elevational studies have multiple advantages that may improve climate change research in Santa Clara County. Elevation gradients incorporate local climatic variation that can identify the mechanisms underlying oak-lepidopteran interactions sensitive to climate change impacts (Abdala-Roberts et al., 2016). Through elevational analysis, researchers can also compare interspecific patterns of insect

herbivores and plant communities at the same scale and climatic range (Abdala-Roberts et al., 2016; Anstett et al. 2016; Moreira et al., 2017, Pfennigwerth et al., 2017).

Moreover, fieldwork along natural climatic gradients associated with elevation can assess long term and short-term plant-insect relationships over multiple generations (Johnson & Pfennigwerth et al., 2017; Rasmann et al., 2011).

Herbivory rates and phenolic compound concentrations were used to compare the validity of two competing hypotheses predicting the effects of climate change on plant herbivory. The Resource Availability Hypothesis (RAH) proposes that multitrophic trends are driven by ecological gradients such as elevation, temperature, and precipitation (Rasmann et al., 2014; Voelckel & Jander, 2014). In contrast, the Plant-Size Apparency Hypothesis suggests that a plant will invest morphological defenses such as larger plant growth to increase visibility, dispersal rates and fitness. (Feeny, 1976; Schlinkert et al., 2012;).

Consistent with previous research, this study in Santa Clara County confirmed mean annual temperature was strongly related to both elevation and herbivory rates. This association of temperature with elevation and herbivory suggest elevation may substitute temperature to potentially predict climate-driven impacts in Santa Clara County. Future surveys in other systems of Santa Clara County should test and confirm elevational temperature relationships to ensure an elevational framework is appropriate.

The Resource Availability Hypothesis (RAH) already predicts that rates of insect herbivory, upsurges and species richness will be higher in lower elevations than at higher elevations. (Abdala-Roberts et al., 2016; Anstett et al., 2016; Hahn & Maron, 2016;

Pearse, 2011). Contrary to these predictions, this study in the Mt. Hamilton Range found herbivory was significantly greater in the highest sampled elevations compared to lower elevations. Previous elevational studies have also found herbivory patterns to be variable with opposing trends and nonlinear responses (Adams et al., 2011; Zhang, Adams et al., 2011; Pellissier et al., 2012). An analysis of forest herbivores along 24 elevation gradients in Europe confirm an inconsistent effect of elevation and variable herbivory rates among four sampled tree species (Pellissier et al., 2012). Moreover, responses from different insect herbivores such as generalist herbivores, leaf chewers, miners, and sap feeders contradicted RAH expectations (Pellissier et al., 2012)

Galmán et al. (2018) suggest insect herbivory rates were dependent on host-plants' growth form and leaf habit. Their results showed no herbivory trends with non-woody species and evergreen woody species along elevational gradients (Galmán et al., 2018). Herbivory increased with deciduous woody species at lower elevations.

RAH posits that plant defense traits and defensive chemistry will change with climate stress and with other varying elevational conditions (Galmán et al., 2018; Rasmann et al., 2014). At lower elevations, plant chemical defenses include foliar defensive compounds such as secondary metabolites, induced defenses, direct and indirect defenses (Defosezz et al., 2018; Voelckel & Jander, 2014). High elevation plants resist with morphological resource allocation strategies (Copolovici et al., 2017; Leckey et al., 2014). This study in Santa Clara County was largely inconsistent with expected plant defense patterns in the Resource Availability Hypothesis. Three phenolic compounds showed no differences in concentration with elevation in the Mt. Hamilton Range. A fourth compound, quercetin,

showed highest concentrations at mid-elevations and lower concentrations at both low and high elevations. Quercetin is an anti-herbivore plant chemical that can be toxic to herbivores and increase their mortality (Voelckel & Jander, 2014). When consumed by generalist herbivores, quercetin can reduce larval masses (Bale et al., 2002). In addition, quercetin in *Pinus sp.* can inhibit the development of a gypsy moth, *Lymantria dispar*, while, studies on peanuts showed quercetin increased mortality rates of tobacco army worms (*Spodoptera litura*) (Bale et al., 2002).

Recent work in elevational plant-insect studies contradict or partially refute the classical expectations of the Resource Availability Hypothesis. Descombes et al. (2017) and Callis-Duehl et al. (2017) confirm physical and chemical defensive traits were not consistently correlated with elevation. Researchers explain that plant defense patterns may change with the level of ecological organization examined (Callis-Duehl et al., 2017; Descombes et al., 2017). With analyses of singular plant-herbivore interactions, Callis-Duehl et al. (2017) found chemical defensive traits and elevations showed nonlinear relationships. However, in community-level studies, chemical defensive traits declined with increasing elevation (Callis Duehl et al., 2017). Similarly, community-weighted analyses from Descombes et al. (2017) reported increased concentrations of plant palatability chemicals at higher elevations. At the individual species level, there was no effect of elevation on plant palatability chemicals (Descombes et al., 2017). Rasmann et al. (2014) assert the expression of chemical defenses may be contingent on both climatic factors and elevational herbivory. Severe climate, drought (Gutbrodt et al., 2011), and delayed snowmelt might inhibit phenolic concentrations (Torp, Witzell,

Baxter, & Olofsson, 2010), secondary metabolism (Jactel et al., 2012), and plant palatability traits (Wright et al., 2007).

Herbivory rates in this study align more closely with predictions in the Plant-Size Apparency Hypothesis. This hypothesis predicts larger plant size may lead to increased visibility, plant palatability, high vigor and lower plant resistance than small plants (Schlinkert et al., 2012). Indeed, this study found a positive relationship between DBH, although a weaker relationship with height and no association with any phenolic compounds. De Sassi, Lewis, & Tylianaki (2012) found defoliation of woody species and associated insect species richness increased with taller specimens. Although other studies indicate plant height may be significant predictor for leaf area loss, this thesis work found DBH to be a more important indicator.

Understanding and predicting the impacts of climate change in Santa Clara County oak woodlands offers management challenges and research opportunities. Elevational surveys are potentially effective methods to monitor and predict the impacts of climate change on oak woodlands' species ranges (Chen, Flint, & Seybold, 2011; Colwell, Brehm, Cardelús, Gilman, & Longino, 2008), species traits (Franks, Weber, & Aitken, 2013; Moreira et al., 2017), and multitrophic relationships (Moreira et al., 2017). By monitoring how insect herbivory and plant defense along elevational gradients change over time in oak woodlands, researchers and managers can understand abiotic drivers in novel climates. For instance, multi-decadal elevational surveys of chemical defenses (i.e. terpenes) observed wild *Thymus vulgaris* colonized higher elevations and exhibited novel decreases in palatability (Moreira et al., 2017). The new shift in distribution and

palatability traits are responses to higher elevations that no longer exhibit former freezing conditions (Amiot, Georgé, Brat, & Alter, 2005; Thompson, Schwind, Paulo, Guimarães, & Friberg, 2013). Likewise, long term elevational studies in the oligophagous butterfly *Aporia crataegi* exhibit critical findings for range-shifted herbivores (Moreira et al., 2017). The elevation range of this herbivore was historically limited to the distribution range of its host-plants (Moreira et al., 2017). However, temperature increases over the past several decades have reduced larval survival (Moreira et al., 2017). The decrease in larvae was caused by climate-induced changes in population density, phenology and habitat use at low elevations (Moreira et al., 2017). With new climate stressors, the butterfly only feeds on host-plants in the lower 300 m of its former range (Merrill, et al., 2008; Moreira et al., 2017). As a result, range-shifted insect herbivores may also encounter species mismatches, novel host species and new plant defense levels (Moreira et al., 2017; Rasmann et al., 2014).

Phenological desynchronization, range shifts and species mismatches need to be monitored in oakwood lands. Some studies suggest oaks may respond to novel climate warming and excessive drought with decreased defenses against herbivores (Moreira et al., 2017). If oak ecosystems are met with new insect outbreaks, they may lack the defenses and risk higher mortalities or defoliation (Mizumachi, Mori, Osawa, Akiyama, & Tokuchi, 2006). Still, further studies are required to understand if oaks may adapt to climate stressors with decreased plant palatability and higher defenses against new herbivore attacks (Mizumachi, 2006).

Recommendations

With current and future climate change impacts on Californian oak woodlands, comprehensive research and progressive open space management is vital (Bedsworth & Hanak, 2013; Moore, Seavy, & Gerhart, 2013). Vegetation biologists and resource managers can use elevational plant-herbivore evaluations in concert with other plant-insect frameworks to monitor and predict ecological responses to climate change (Pellisier et al., 2014). Results from elevational surveys can improve multiple aspects of oak woodland management. These aspects include a) restoration planning (Abdala-Roberts et al., 2016; Pearse & Hipp, 2012) b) the management of local extinctions and novel recolonizations (Defosezz et al., 2018) c) selection of areas for preserve acquisition (Boscutti et al., 2018), and d) the management of new disturbance regimes in current and future climate change scenarios (Rasmann et al., 2014). In turn, managers may be more equipped to understand how climate-related disturbances may impact oaks and dependent herbivores' life histories (Moreira, Petry, Mooney, Rasmann & Abdala-Roberts, 2018). In addition, elevational assessments of potential climate-related changes to disturbance regimes can greatly improve managers' abilities to adaptively manage oak woodlands ecological functioning and critical ecosystem services (Agne et al., 2018).

Future Research

The method design, number of target species, and duration of this study were limited by budget and time constraints. Subsequent field surveys using alternate hypotheses in combination with an elevational framework may provide more information. More surveys of Mt. Hamilton's oak-lepidopteran relationships may provide a more robust

baseline and elevational framework for predicting patterns of climate change impacts (Pfennigwerth et al., 2017; Moreira et al., 2018). Ideally, elevational analyses in Santa Clara County may be more substantive when researchers examine multiple oak-lepidopteran relationships across several elevation gradients over two or more years. Long-term studies can better examine the association between elevational herbivory and other abiotic and climatic variabilities such as precipitation, soil characteristics and herbivory (Galmán et al., 2018).

This study was limited by restricting phenolic compound data collection to field surveys. To better understand the relationship between elevation, herbivore pressure and plant defenses, researchers should incorporate common garden experiments (Casner et al., 2014; Rasmann et al., 2014). Researchers could plant corresponding gardens in the same elevation as their native field sites (Rasmann et al., 2014). These garden experiments would be planted with the same target species in field elevational surveys. Herbivory would be observed in both native field sites and common gardens (Casner et al., 2014; Rasmann et al., 2014). Comprehensive and robust elevational studies on multitrophic responses to climate change will be essential to the effective preservation of oak woodlands.

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