Ground-dwelling Arthropod Community Responses to Extreme Drought

Brianne M. Roxbrough

ABSTRACT

Due to anthropogenic climate change, severe droughts are presenting damaging effects to ecosystems across the globe. Arthropods, as important bioindicators of ecosystems, are important to look at in the context of drought to understand how communities are being altered and what cascading effects this may have. In this study, I examined the effects of drought on ground-dwelling arthropod community activity, composition, and abundance as well as the effects on a single species' body size. Using 60 pitfall traps each month from the beginning of a drought period in 2014 until 2 years after the drought's end in 2017, 2612 specimens were collected and identified to 122 different taxa. I analyzed differences of species activity patterns, richness, Shannon diversity, and abundance between drought and non-drought years. I took the pinned Pterostichus californicus specimens and measured median pronotum length, half of the widest pronotum width, and length of the left elytron to get an estimate of body size. I used one-way ANOVAs to test differences between years where appropriate. Species composition, richness, and activity differed between drought and non-drought years. However, the years were the same in abundance and Shannon diversity. These findings suggest that drought does alter arthropod communities, but the effects and directionality are species-specific, likely dependent on life history traits. As there are many interactions taking place in this community that are not fully understood, it is essential to further develop our understanding of terrestrial, grounddwelling arthropods in the face of drought in order to monitor California ecosystems.

KEYWORDS

California, body size, climate change, Pterostichus, community ecology

INTRODUCTION

Anthropogenic climate change is increasing the length and intensity of droughts, which can greatly alter the structure and function of ecosystems. Climate change has further accelerated hydrological processes, which facilitates intense, prolonged droughts that are expected to increase in severity (Cook et al. 2018, Mukherjee et al. 2018). Visible repercussions have already been observed such as major forest die-off reported in every forested continent, which has had cascading effects on the microclimate, carbon cycle, fire regimes, and nutrient balance of these habitats (Cobb et al. 2017, Hopkins et al. 2018). Further, droughts are amid the most expensive natural disasters across the world due to their devastating effects on ecosystems, agriculture, and human societies (Cook et al. 2018).

In California specifically, the lack of water availability threatens the growing population and one of the largest economies in the world by restricting food production, industrial and urban use, as well as hydropower from reservoirs (Mann and Gleick 2015, Forrest et al. 2018). Like other Mediterranean climates, California continues to warm and become increasingly arid, which has led to recent drought extremes (Stocker et al. 2013). Separate from these economic impacts, hydrological extremes hit biological communities directly with abiotic stressors and indirectly by altering organism interactions (Hung et al. 2021). This unprecedented era of climate change promises droughts of increased frequency, magnitude, and duration, making the threat of irreversible changes to crucial ecosystems a major concern (Mann and Gleick 2015).

The impacts of severe drought events on ecosystems can be monitored through bioindicator species. To monitor ecosystem changes and biodiversity, bioindicator species are a cost-effective method as they are easily identifiable, eco-functionally important, and have sensitivities such that they respond differently to disturbance regimes (Pearce and Venier 2006). Additionally, for a bioindicator species to be effective, it must be specific to habitat requirements as well as have direct and indirect relationships with other organisms (Ferris and Humphrey 1999, Rainio and Niemelä 2003). Arthropods serve as useful bioindicators of habitat change and modification because of their small body size, short generation time (Kremen et al. 1993), high sensitivity to temperature and moisture changes (Schowalter et al. 2003), and provision of ecosystem services (Longcore 2003). They also play a key role in

nutrient cycling and influence other trophic levels, indicating that trophic structures can be affected where arthropods are impacted (Seastedt and Crossley Jr 1984). Therefore, arthropods can be used as a tool to understand both how drought impacts terrestrial arthropod assemblages and the recovery trajectory after the drought ends.

Arthropods may respond differently to drought, depending on life history traits. The majority of research on arthropods in response to drought in Mediterranean climates has focused on aquatic habitats because drought can place substantial ecological pressure on small freshwater water bodies by drying up streams. The changes to streams sever hydrological connectivity, worsens water quality, and leaves taxa vulnerable to predators (Boulton et al. 2008, Rosset et al. 2010). However, research on Mediterranean terrestrial ground-dwelling arthropods experiencing drought is more limited. Moisture stress can directly lower arthropod fitness by promoting desiccation (Block 1996, Haile 2000) and, given that many soil-inhabiting arthropods are adapted to moist and humid environments, it leaves vulnerable life stages at risk in drought conditions. Furthermore, drought can indirectly affect ground-dwelling arthropods through alteration of microenvironments by altering abiotic factors and growth of plants that may serve as habitat or a food source (Haile 2000, Prather et al. 2020). Despite these constraints, organisms living in a Mediterranean climate with multi-year droughts presumably have life history adaptations that allow some resilience to drought conditions. However, it is unclear how the life histories of these ground-dwelling arthropods will be affected by an extended period of severe drought and how community structure is likewise affected.

In this study, I aim to understand how drought affects ground-dwelling arthropod communities over an extended period in a Mediterranean climate using a 5-year long dataset. My objectives are to examine differences between drought and non-drought years and (1) determine how arthropod species activity shifts, (2) evaluate differences in richness, abundance, and diversity of the community, and (3) assess if body size is affected for a single species.

METHODS

Study Site Description

This study takes place in Perkins Canyon in Mount Diablo State Park, which lies just outside the town of Perkins Canyon in Contra Costa County (vicinity of N37.89587, W121.87486). The habitat is an oak woodland of primarily Blue Oak (*Quercus douglasii*),

Grey Pine (*Pinus sabiniana*), and Interior Live Oak (*Quercus wislizeni*). This canyon was burned during the Morgan Fire on September 8th, 2013, which burned 3,100 acres in Mount Diablo State Park (Cuff and Nardi 2013). In the following year, the entire state of California experienced a significant multi-year drought beginning in 2014. According to the U.S Drought Monitor, nearly 60% of California, including the specific area of Perkins Canyon, was in the most severe drought category ("D4-Exceptional Drought") at the time this study began in July 2014 (National Integrated Drought Information System 2021). An official end to the drought was declared on April 7th, 2017 (CBS News 2017). This data collection period ended in July 2019, by which the area was no longer experiencing any drought.

Environmental Data

To quantify the period of drought, I used precipitation data that was collected by a rain gauge at the Marsh Creek Fire Station in Contra Costa County (37.8949°N,-121.8635°W). The data was downloaded from the California Data Exchange Center (California Department of Resources 2020) on February 10th, 2020 for the date range of January 1st, 2014 to December 31st, 2019.

Arthropod Sampling

To determine the effects of drought on arthropods, I used arthropod data collected by Professor Kipling Will and Dr. Patina Mendez from July 2014 to July 2019. They established 6 sites in the canyon, each with a transect line that included 10 traps along it with 5 meters in between each trap, giving a total of 60 traps. Pitfall traps were made from 16 oz. polyethylene terephthalate (PET) cups with 95mm diameter and 121 mm height. To protect each trap, a 27 x 178 mm galvanized steel shingle served as a rain cover and a 40 x 40 cm piece of chicken wire excluded small mammals (Zhang 2015). Once a month, within a few days of the new moon, the traps were buried in 150 mm long PVC pipes and left open for 3 consecutive nights. Propylene

glycol was placed in each cup to kill and preserve the specimens, after which they were sorted, identified, and pinned in a laboratory at the University of California, Berkeley (Will and Mendez 2021).

Temporal Data

To understand the patterns of presence of arthropod taxa throughout the years, I created a table of the 20 most abundant taxa of the 5-year sampling period, which had total abundances ranging from 27 to 295 individuals. For each taxon, I plotted monthly abundance by year and used color intensity going from light to dark to code as (1) absent, (2) present but low abundance, and (3) present at the highest abundances of the entire sampling period relative to that taxon's total abundance. This table was used to determine the activity period of each taxon.

To look at phenology over the 5 years, I took taxa that displayed different activity patterns and plotted counts in order to create a temporal profile for each. I did this in order to compare activity period changes throughout the 5 years with a smaller subset of the community that showed similar or different responses. As not all individuals were identified to species level, in some cases I used morphospecies designations by K. Will. Looking between declared drought and non-drought years, I visually analyzed patterns of disappearance or emergence between the different taxa.

Community Response

To examine community composition, I calculated species richness and species accumulation curves for each cohort year. Due to the timing of sampling, I separated samples into cohort years, which I defined as July of each year to June the following year, in order to create equal sample sizes. For example, the 2014 cohort year is from July 2014 until June 2015. Although a typical water year is considered October to October, California experiences virtually no rainfall in July, August, or September, which results in a cohort year closely resembling the typical water year. To compare diversity, I used the Shannon Diversity Index, which is a measure of entropy or disorder of a community that also considers uncertainty in the outcome of the sampling process' (Daly et al. 2018). It has been used to measure both insect and beetle diversity

(Lencinas et al. 2019, Ghani and Maalik 2020). I also created species accumulation curves that show the aggregation of species richness of each year to compare the total number of species present as time went on. I tested differences of species richness, Shannon diversity, and total arthropod abundance between years using one-way ANOVAs. To understand shifts in taxa dominance, I created rank abundance profiles for each cohort year. All community analysis was completed using Rstudio and BiodiveristyR (RStudio Team 2022).

Body Size Measurements

Pterostichus californicus beetle specimens were pinned and stored in the Will lab at the University of California, Berkeley. To determine if body size changed annually in response to drought conditions, I measured median pronotum length, half of the widest pronotum width, and length of the left elytron to the nearest unit by using a microscope reticle of a Wild M-5 Stereomicroscope at 6x magnification. For each measurement, I secured a pinned specimen under a microscope by sticking the pin in a ball of polymer clay, with the aim to orient the body part I was measuring in one level visible plane. Measuring the elytron first, I ensured the scutellum and the apex of the abdomen were in focus. I measured the left elytron unless there was obvious damage to that side. Moving to the pronotum, I tipped the specimen slightly diagonal, then visually confirmed that the lateral edge of the pronotum was parallel with the microscope stage and all 4 corners together in focus. Using the mid-ecdysial suture as a guide, I measured the pronotum length and then, perpendicular to that line, I measured the width of the right side at the widest point (Figure 1).

To account for sex-based response differences, I separated specimen measurements by sex. To determine if body size changed with drought conditions, I used one-way ANOVAs. To inspect patterns between different cohort years, I created color coded scatterplots of elytron length as a function of pronotal length. All statistical analysis was completed using R statistical software and differences with p-values< 0.05 were considered significant.



Figure 1: Measurements taken on each *Pterostichus californicus* **specimen.** The measurements correspond to: (1) length of the left elytron, (2) median pronotum length, and (3) half of the widest pronotum width.

RESULTS

Environmental Conditions

The average yearly rainfall over the 5-year sampling period was 671.22 mm with a standard deviation of 249.45 mm. The cohort year with the lowest total rainfall was 2017 with a total of 434.086 mm, although 2016 had the highest total rainfall at 1021.65 mm (Figure 2). Each year followed roughly the same pattern with the highest rainfall occurring in winter to early spring months and no rainfall in July or August (Figure 3).

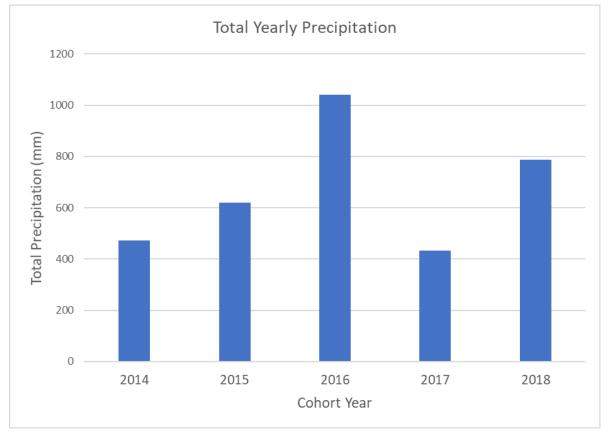


Figure 2: Total precipitation by cohort year in mm.

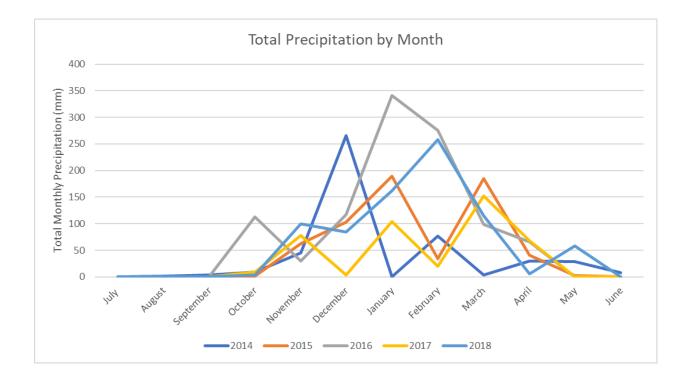


Figure 3: Total precipitation by month for the 2014 (A), 2015 (B), 2016 (C), 2017 (D), and 2018 (E) sampling years.

Arthropod Activity

A total of 122 different taxa were collected and identified across the 6 sites over 5 years. The most abundant species over the period was *Pterostichus californicus*, with a total of 295 individuals recorded. Activity varied across years for the 20 most abundant species of the 5-year sampling period. The 20 taxa were divided into autumn, winter, spring, and summer groups dependent on when they emerged and were most active. 7 taxa fell into the autumn active category (Figure 4A), 4 in the winter (Figure 4B), 4 in the spring (Figure 4C), and 5 in the summer (Figure 4D).

Different taxa showed varying activity patterns between drought and non-drought years. For example, taxa such as *Pterostichus* species, *Coelocnemis magma*, *Eleodes dentipes*, and *Prionus californicus* showed shifts to higher abundances in non-drought years (Figure 4A,C, &D, Figure 5, Figure 6, Figure 7, Figure 8). *Hylurgops porosus* was highly abundant in early drought years, but largely disappeared well before the end of the drought (Figure 4D, Figure 9). Scolytinae had an extreme peak in 2015, but was nearly absent from all other sampling events (Figure 10). Other species, such as *Forficula auricularia* and *Serradigitus gertschi striatus* showed little change between years (Figure 4A,D, Figure 11, Figure 12).

Species_Year	- Jul	- Aug	✓ Sept	- Oct -	Nov 👻	Dec 👻	Jan 👻	Feb 🔻	Mar 👻	Apr 🖃	May 👻	June 🗔
Autumn			•						. L			
Pterostichus vicinus 2014-2015												
Pterostichus vicinus 2014-2015												
Pterostichus vicinus 2016-2017												
Pterostichus vicinus 2017-2018												
Pterostichus vicinus 2018-2019												
Pterostichus californicus 2014-2015												
Pterostichus californicus 2015-2016												
Pterostichus californicus 2016-2017												
Pterostichus californicus 2017-2018												
Pterostichus californicus 2018-2019							_					
Pterostichus protensiformis 2014-2015	5											
Pterostichus protensiformis 2015-2016												
Pterostichus protensiformis 2016-2017												
Pterostichus protensiformis 2017-2018												
Pterostichus protensiformis 2018-2019												
Pterostichus angustus 2014-2015												
Pterostichus angustus 2015-2016											1	
Pterostichus angustus 2016-2017												
Pterostichus angustus 2017-2018												
Pterostichus angustus 2018-2019												
Ptomaphagus sp. 2014-2015												
Ptomaphagus sp. 2015-2016					•							
Ptomaphagus sp. 2016-2017												
Ptomaphagus sp. 2017-2018												
Ptomaphagus sp. 2018-2019												
Forficula auricularia 2014-2015												
Forficula auricularia 2015-2016												
Forficula auricularia 2016-2017												
Forficula auricularia 2017-2018												
Forficula auricularia 2018-2019												
Tachy. sp. 1 2014-2015												
Tachy. sp. 1 2015-2016												
Tachy. sp. 1 2016-2017												
Tachy. sp. 1 2017-2018												
Tachy. sp. 1 2018-2019												
Species_Year	- Jul	- Aug	- Sept	v Oct v	Nov 👻	Dec 🔻	Jan 👻	Feb 🔻	Mar 👻	Apr 👻	May 🚽	June 🗔
Winter												
	5											
Promecognathus laevissimus 2014-201												
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201	16											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201	L6 L7											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015 Leiod. sp. 1 2015-2016	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015 Leiod. sp. 1 2015-2016 Leiod. sp. 1 2016-2017	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015 Leiod. sp. 1 2015-2016 Leiod. sp. 1 2016-2017 Leiod. sp. 1 2017-2018	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015 Leiod. sp. 1 2015-2016 Leiod. sp. 1 2015-2017 Leiod. sp. 1 2017-2018 Leiod. sp. 1 2018-2019	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015 Leiod. sp. 1 2015-2016 Leiod. sp. 1 2016-2017 Leiod. sp. 1 2017-2018 Leiod. sp. 1 2018-2019 Amara conflata 2014-2015	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015 Leiod. sp. 1 2015-2016 Leiod. sp. 1 2016-2017 Leiod. sp. 1 2017-2018 Leiod. sp. 1 2018-2019 Amara conflata 2014-2015 Amara conflata 2015-2016	L6 L7 L8							_				
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015 Leiod. sp. 1 2015-2016 Leiod. sp. 1 2016-2017 Leiod. sp. 1 2017-2018 Leiod. sp. 1 2017-2018 Leiod. sp. 1 2018-2019 Amara conflata 2014-2015 Amara conflata 2015-2016 Amara conflata 2016-2017	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015 Leiod. sp. 1 2015-2016 Leiod. sp. 1 2016-2017 Leiod. sp. 1 2018-2019 Amara conflata 2014-2015 Amara conflata 2015-2016 Amara conflata 2016-2017 Amara conflata 2017-2018	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015 Leiod. sp. 1 2015-2016 Leiod. sp. 1 2016-2017 Leiod. sp. 1 2017-2018 Leiod. sp. 1 2018-2019 Amara conflata 2014-2015 Amara conflata 2015-2016 Amara conflata 2015-2016 Amara conflata 2017-2018 Amara conflata 2017-2018 Amara conflata 2017-2018	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015 Leiod. sp. 1 2015-2016 Leiod. sp. 1 2016-2017 Leiod. sp. 1 2017-2018 Leiod. sp. 1 2018-2019 Amara conflata 2014-2015 Amara conflata 2015-2016 Amara conflata 2015-2016 Amara conflata 2016-2017 Amara conflata 2017-2018 Amara conflata 2017-2018 Amara conflata 2018-2019 Prionus californicus 2014-2015	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015 Leiod. sp. 1 2015-2016 Leiod. sp. 1 2015-2016 Leiod. sp. 1 2017-2018 Leiod. sp. 1 2017-2018 Leiod. sp. 1 2018-2019 Amara conflata 2015-2016 Amara conflata 2015-2016 Amara conflata 2017-2018 Amara conflata 2018-2019 Prionus californicus 2014-2015 Prionus californicus 2015-2016	L6 L7 L8											
Promecognathus laevissimus 2014-201 Promecognathus laevissimus 2015-201 Promecognathus laevissimus 2016-201 Promecognathus laevissimus 2017-201 Promecognathus laevissimus 2018-201 Leiod. sp. 1 2014-2015 Leiod. sp. 1 2015-2016 Leiod. sp. 1 2017-2018 Leiod. sp. 1 2017-2018 Leiod. sp. 1 2018-2019 Amara conflata 2014-2015 Amara conflata 2015-2016 Amara conflata 2015-2016 Amara conflata 2016-2017 Amara conflata 2017-2018 Amara conflata 2018-2019 Prionus californicus 2014-2015	L6 L7 L8											

B. Prionus californicus 2018-2019

Species_Year	🚽 Jul	- Aug	- Sept	- Oct -	Nov 🚽 Dec	- Jan -	Feb 👻 Mar	- Apr -	May 🚽 Ju	ın
Spring										
Scolytinae 2014-2015										-
Scolytinae 2015-2016										
Scolytinae 2016-2017										
Scolytinae 2017-2018										
Scolytinae 2018-2019										
Coelocnemis magma 2014-2015										
Coelocnemis magma 2015-2016										
Coelocnemis magma 2016-2017										
Coelocnemis magma 2017-2018										
Coelocnemis magma 2018-2019										
Eleodes constrictus 2014-2015										
Eleodes constrictus 2015-2016										
Eleodes constrictus 2016-2017										
Eleodes constrictus 2017-2018										
Eleodes constrictus 2018-2019										
Nyctoporis aequicollis 2014-2015										
Nyctoporis aequicollis 2015-2016										
Nyctoporis aequicollis 2016-2017										
Nyctoporis aequicollis 2017-2018										
Nyctoporis aequicollis 2018-2019										
										_
Species_Year	🚽 Jul	- Aug	 Sept 	▼ Oct ▼	Nov 🚽 Dec	- Jan -	Feb 🖃 Mar	- Apr -	May 👻 Ju	r
Summer										

					_
Summer					
Apocrypha anthicoides 2014-2015					
Apocrypha anthicoides 2015-2016					
Apocrypha anthicoides 2016-2017					
Apocrypha anthicoides 2017-2018					
Apocrypha anthicoides 2018-2019					
Eleodes dentipes 2014-2015					
Eleodes dentipes 2015-2016					
Eleodes dentipes 2016-2017					
Eleodes dentipes 2017-2018					
Eleodes dentipes 2018-2019					
Coniontus sp. 2014-2015					
Coniontus sp. 2015-2016					
Coniontus sp. 2016-2017					
Coniontus sp. 2017-2018					
Coniontus sp. 2018-2019					
Serradigitus gertschi striatus 2014-2015					
Serradigitus gertschi striatus 2015-2016					
Serradigitus gertschi striatus 2016-2017					
Serradigitus gertschi striatus 2017-2018					
Serradigitus gertschi striatus 2018-2019					
Hylurgops porosus 2014-2015					
Hylurgops porosus 2015-2016					
Hylurgops porosus 2016-2017					
Hylurgops porosus 2017-2018					
Hylurgops porosus 2018-2019					

Figure 4: Activity tables for the 20 most abundant taxa of the sampling period divided into (A) autumn, (B) winter, (C) spring, and (D) summer active groups. White squares indicate absence, while light, medium, and dark blue squares represent low, medium, and high abundances, respectively.

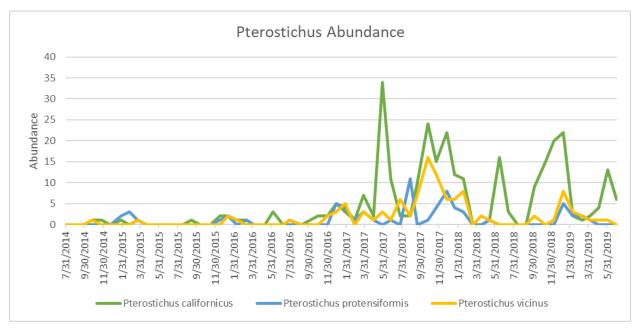


Figure 5: *Pterostichus* species abundances throughout the sampling period.

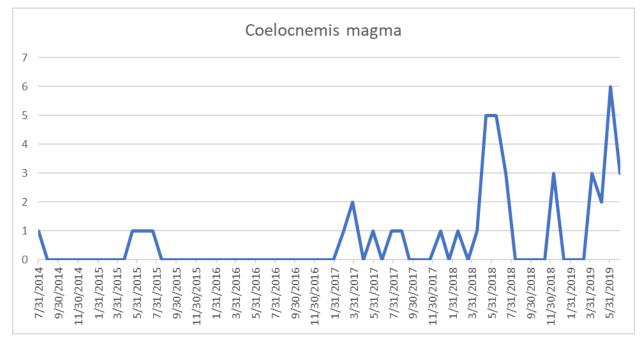


Figure 6: Coelocnemis magma abundance throughout the sampling period.

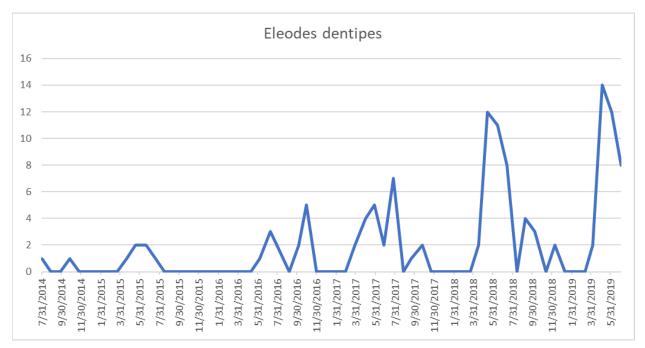


Figure 7: *Eleodes dentipes* abundance throughout the sampling period.

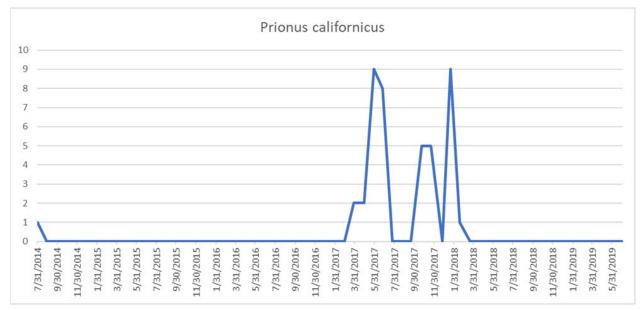


Figure 8: Prionus californicus abundance throughout the sampling period.

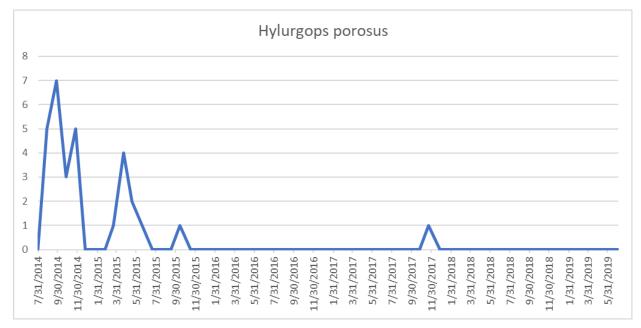


Figure 9: Hylurgops porosus abundance throughout the sampling period.

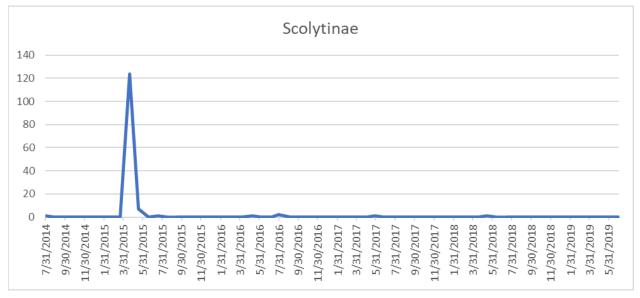


Figure 10: Scolytinae species abundances throughout the sampling period.

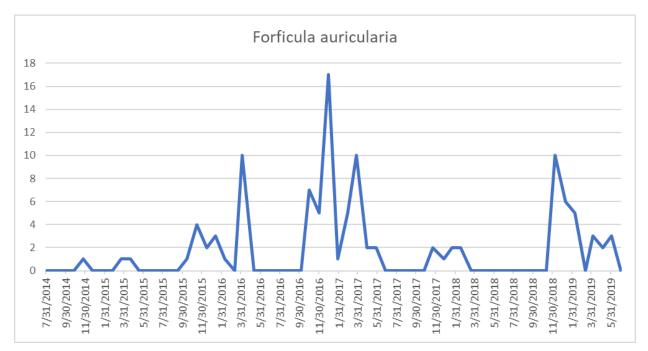


Figure 11: Forficula auricularia abundance throughout the sampling period.

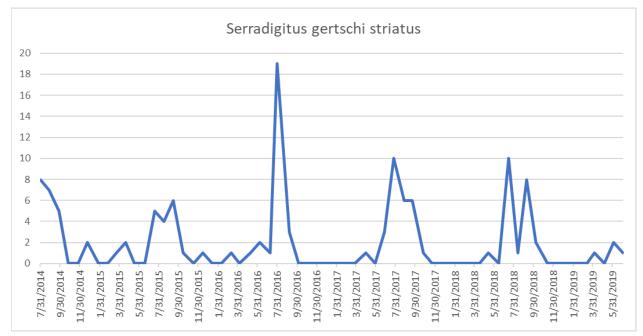


Figure 12: Serradigitus gertschi striatus abundance throughout the sampling period.

Community Response

Drought intensification resulted in staggered changes in community composition. Annual species richness was lower in non-drought years, with a large drop off of species in the 2016 cohort year (Figure 13). In drought years, a species richness of 75 and 78 was recorded for the 2014 and 2015 cohort year, respectively. This number nearly halved in 2016 when the species richness was 47. A gradual decrease continued, with 35 species in 2017 and 26 species in 2018.

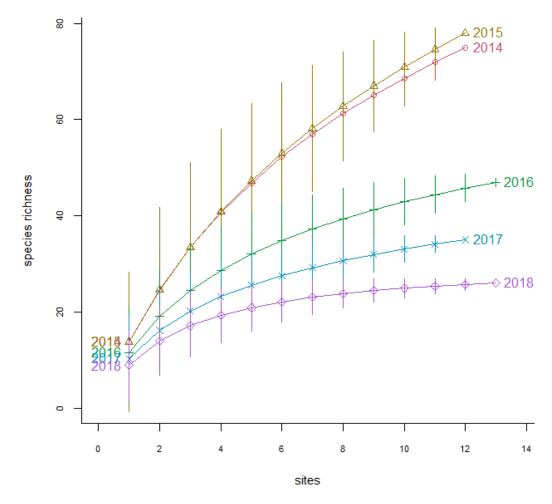


Figure 13: Species accumulation curves for each cohort year. Cohort year is defined as July of each year to June the following year. Each site on the x-axis corresponds to a monthly sampling event.

Species ranks were also different between years, with the major shift in rankings also happening in the 2016 cohort year (Figure 14). Bark beetles of the subfamily Scolytinae and fungus beetles belonging to the family Leiodidae ranked highest in drought years. *Pterostichus californicus* was not ranked in the top 3 in either drought years, but became the first ranked species in 2016 and stayed in that rank for the remainder of the sampling period. Other species

that became prevalent in non-drought years included the darkling beetle *Nyctoporis aequicollis* and the ground beetle *Pterostichus vicinus*. *Coniontus* species were consistently high, ranking in the top 3 in the 2014, 2016, and 2018 cohort years.

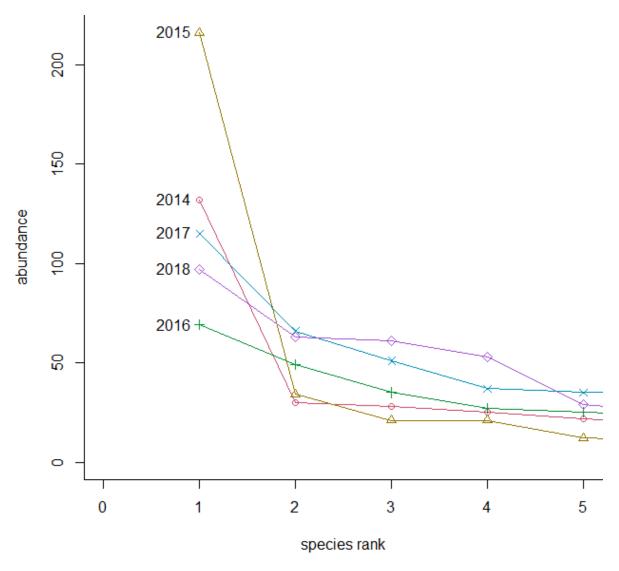
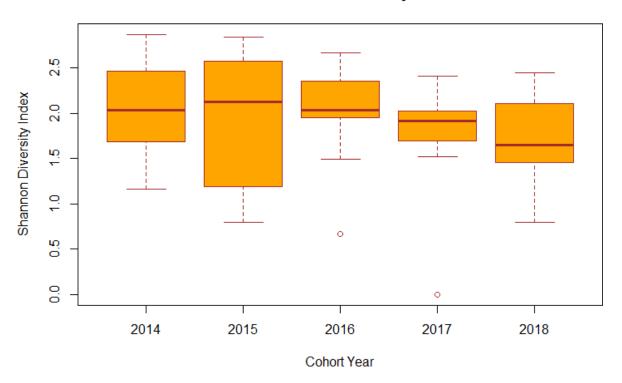


Figure 14: Rank abundance of each cohort year. Cohort year is defined as July of each year to June the following year. Ranks are as follows: 2014: (1) Scolytinae (2) *Coniontus* species and (3) *Hylurgops porosus*, 2015: (1) Leiodidae species (2) Tachy species (3) *Serradigitus gertschi striatus*, 2016: (1) *Pterostichus californicus* (2) *Forficula auricularia* (3) *Coniontus* species, 2017: (1) *Pterostichus californicus* (2) *Pterostichus vicinus* (3) *Nyctoporis aequicollis*, 2018: (1) *Pterostichus californicus*, (2) *Coniontus* species (3) *Nyctoporis aequicollis*.

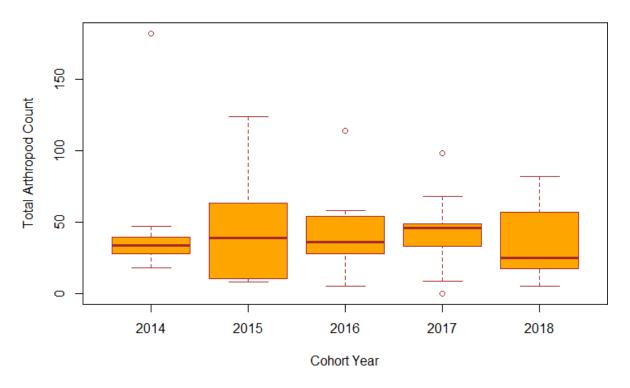
Shannon diversity, however, was not different between years (Figure 15, F= 2.57, P=0.11). Across sampling events, it ranged from 1.17 to 2.87 in 2014, 0.79 to 2.84 in 2015, 0.67 to 2.66 in 2016, 0 to 2.41 in 2017 and 0.80 to 2.44 in 2018. Average Shannon indices for each year were 2.07 in 2014, 1.92 in 2015, 2.02 in 2016, 1.78 in 2017, and 1.74 in 2018. The year 2015 had the most diversity variability between sampling events.



Shannon Diversity

Figure 15: Shannon diversity across cohort years (F= 2.57, P=0.11). Cohort year is defined as July of each year to June the following year.

Abundance also did not fluctuate between years (Figure 16, F=0.493, P=0.485). Total arthropod abundance across sampling events ranged from 18 to 182 in 2014, 8 to 124 in 2015, 5 to 114 in 2016, 0 to 98 in 2017, and 5 to 82 in 2018. The average total abundance was 45.25 in 2014, 44.75 in 2015, 40.23 in 2016, 43.17 in 2017, and 35.83 in 2018. Again, 2015 had the most variability between sampling events.

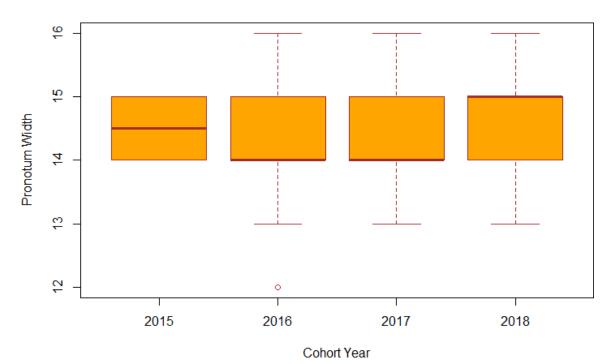


Abundance Across Years

Figure 16: Abundance across cohort years (P= 0.485, F=0.493). Cohort year is defined as July of each year to June the following year.

Beetle Body Size Relationship to Drought

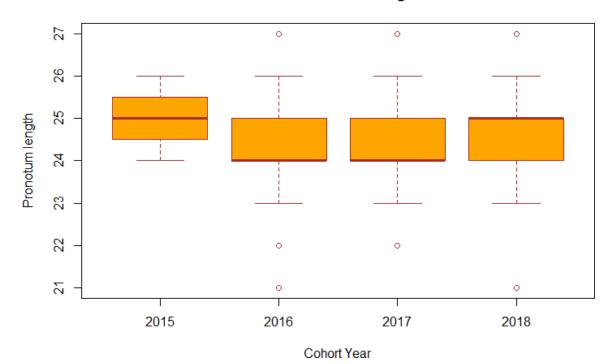
Body size of *Pterostichus californicus* did not change between years. Male specimens showed no difference in pronotum width (Figure 17A, P= 0.554, F= 0.7), pronotum length (Figure 17B, P= 0.263, F= 1.345), or elytron length (Figure 17C, P= 0.945, F= 0.126). Female specimens also were not different by year in terms of pronotum width (Figure 18A, P= 0.22, F= 1.521) or pronotum length (Figure 18B, P= 0.789, F= 0.072). Female elytron length showed a marginal change between years (Figure 18C, P= 0.0534, F= 3.802). Body length measurement plots reveal no trends or groupings by year for either male (Figure 19) or female (Figure 20) specimens.



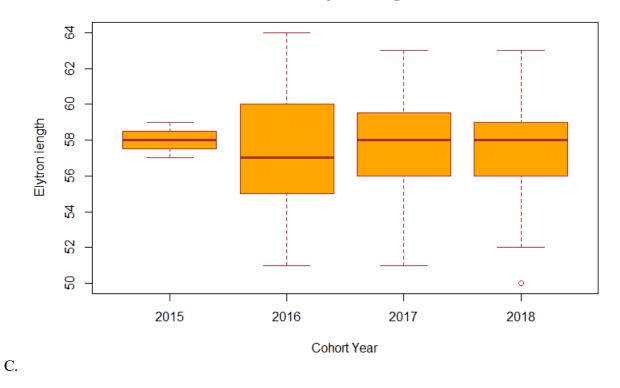
Male Pronotum Width

A.

Male Pronotum length

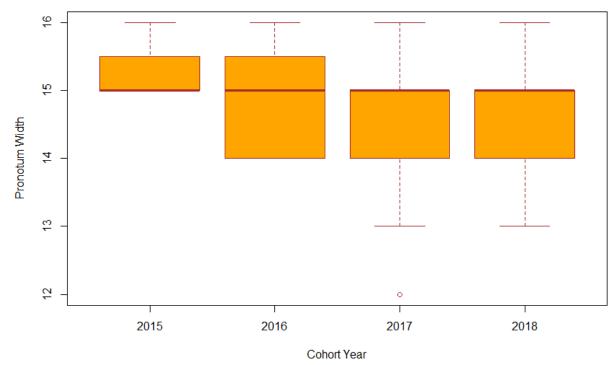


В.



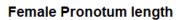
Male Elytron length

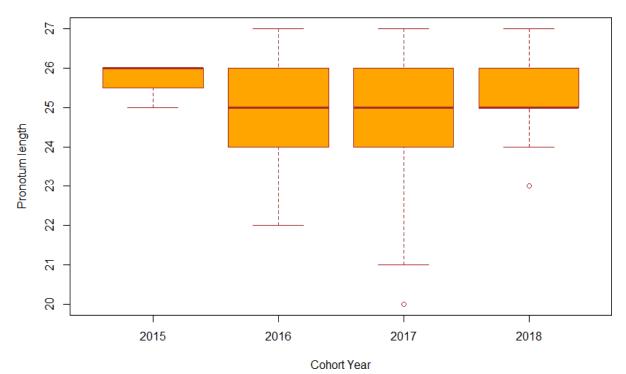
Figure 17: Male *Pterostichus californicus* specimen body sizes across the years including (A) pronotum width (P= 0.554, F= 0.7), (B) pronotum length (P= 0.263, F= 1.345), and (C) elytron length measurements (P= 0.945, F= 0.126). Cohort year is defined as July of each year to June the following year.



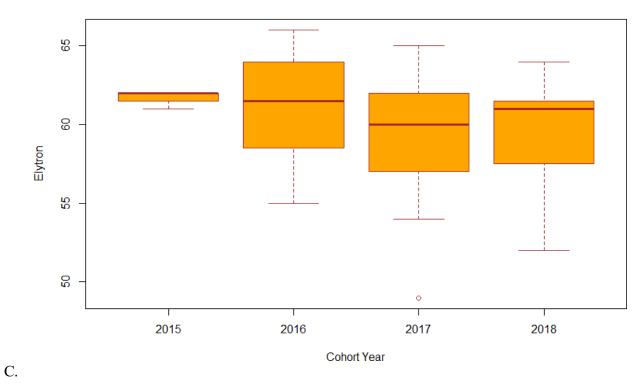
Female Pronotum Width

A.





B.



Female Elytron Length

Figure 18: Female *Pterostichus californicus* specimen body sizes across the years including (A) pronotum width (P= 0.22, F= 1.521), (B) pronotum length (P= 0.789, F= 0.072), and (C) elytron length measurements (P= 0.0534, F= 3.802). Cohort year is defined as July of each year to June the following year.

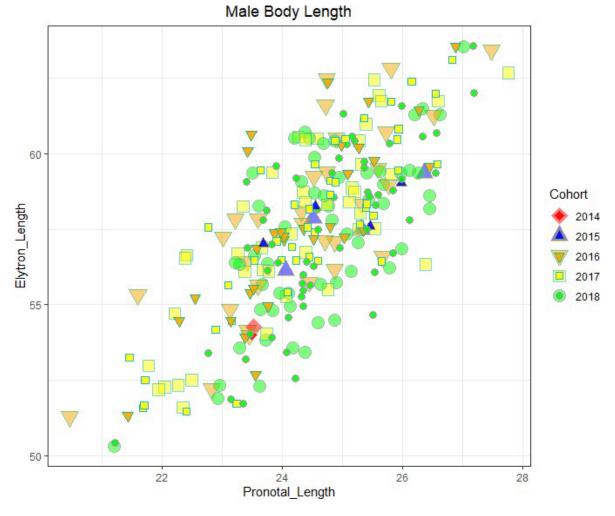


Figure 19: A plot of elytron length as a function of pronotal length of male specimens by year.

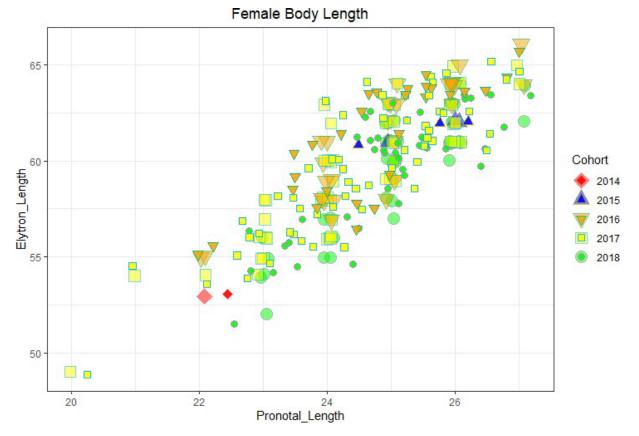


Figure 20: A plot of elytron length as a function of pronotal length of female specimens by year.

DISCUSSION

Drought years differed from non-drought years in terms of species composition, richness, and activity. However, drought and non-drought years did not differ in abundance or Shannon diversity. Richness was high in early drought years, but dramatically drops partially into the drought in the 2016 cohort year. The most abundantly ranked species also changed in the 2016 cohort year. Despite my expectations, I found no difference in body length measurements between years. Overall, I found that drought likely affects ground-dwelling arthropod communities most by affecting their composition and phenology, rather than overall abundance or body size.

Spring 2022

Arthropod activity

Arthropod activity patterns differed between years, but these patterns were species dependent. Activity and abundance appeared unchanged for some species between drought and non-drought years, which could be due to their resilience or differing sensitivities to xeric conditions. Terrestrial arthropod survival is interconnected with their ability to a water balance (Kharboutli and Mack 1993). For example, the earwig *Forficula auricularia* had a consistent presence and abundance throughout the sampling period and may be reasonably resistant to dessication. In an experimental study, another earwig species, *Labidura riparia*, was able to withstand substantial desiccation, losing nearly 50% of its total body water before perishing, compared to a usual lethal average of 25-50% water loss in other insects (Kharboutli and Mack 1993). *Serradigitus gertschi striatus* is another species more adapted to dry conditions that showed little changes among sampling years. This unaffected phenology is not surprising since this is a scorpion species, which are nocturnal burrowers with transpiration rates much lower than arthropods in their habitat (Cloudsley-Thompson 1975).

Along with desiccation risk, food availability may have been a contributor to the lower abundance of some taxa in drought years. For example, *Pterostichus* species, including *P. vicinus, P. californicus, and P. protensiformus,* had similar trends with quite dramatic increases in early 2017 right after the end of the drought, but *P. angustus* generally had the same presence patterns throughout all years. Similar to most *Pterostichus* species, *Prionus californicus* was almost absent in early sampling years, but finally appeared in early 2017. *Pterostichus* species are often generalist feeders that prey on invertebrates and the occasional plant matter (Fawki et al. 2005). It is possible that the arthropods that appeared reduced during drought years primarily rely on prey like soft-bodied invertebrates as their food source. During periods of drought, soil moisture is reduced, which can drive some invertebrate species, such as earthworms, to take shelter deep into the soil, which also makes them harder to reach (Joschko et al. 1989). When total monthly precipitation increased in early 2017, prey may have become easier to locate once again, which may have contributed to increases in predator species. Conversely, one study found

a potential increase in food source for carabid beetles specifically. Dry conditions pushed aphids to reside on lower parts of their host plant or even below the soil, which allowed one of their key predators, carabid beetles, to reach them easier and thus raise predation rates. Carabids as a group were generally diminished in drought years with a rise beginning with precipitation increases, suggesting that food availability may not be the main driver of reduced species abundances.

For arthropods that feed partially or primarily on plant matter, drought can result in reduced vegetation vigor, decreased net primary productivity, delayed seed germination, reduced plant cover, and increased plant mortality (Cady et al. 2019). All these effects can greatly reduce a major food source for grassland arthropods as well as reduce their protection from other predators.

Some taxa had earlier abundance peaks with dramatic drop offs. For example, *Hylurgops porosus*, a bark beetle, showed high abundances in early years, then nearly disappeared before the drought's end. A possible explanation could be the feeding ecology of *H. porosus*, which are bark beetles attracted to plants in stress (Safranyik et al. 1999). Dry conditions can cause plants to produce stress compounds that certain insects are attracted to. This species may have been attracted to these compounds yet was unable to handle the dry conditions or their woody food source became too dry, and they quickly disappeared. Additionally, one study found that plant chemical defenses may increase initially with moderate drought, but, after extended severe drought like this area experienced, their defenses diminish, leading to a benefit to the species that feed on them (Gely et al. 2020). Because the drought began in Spring 2014, plant defenses may have begun to drop before the actual end of the drought, which could explain earlier peaks or abundance boosts of species such as *Eleodes dentipes*, which feeds exclusively on plant matter (Dale and Frank 2017).

Few taxa showed alternate responses where reasons aren't entirely clear. This could simply be a factor of the sampling method. For example, bark beetles in the subfamily Scolytinae were extremely abundant, yet the bulk of its abundance was from a single sampling day where a total of 124 individuals were sampled. It could be that something fell into the pitfall trap that they were highly attracted to, such as woody debris, and produced aggregation pheromones that led to unnaturally high numbers (Miller and Borden 1990). Additionally, the carrion beetles of the *Ptomaphagus* genus had just 2 large peaks in October 2014 and November 2015, then is basically absent from all other sampling events. There are many possible explanations, including the nature of pitfall trap sampling and the possibility of a dead organism near the trap.

Community response

Overall, species richness was greatly reduced as time went on, yet abundance and diversity stayed relatively the same. Species richness was most likely reduced due to certain species succumbing to drought and disappearing from the area (Kemp and Cigliano 1994). Species richness was nearly cut in half in 2016, which indicates there may be a sort of threshold that some taxa can handle. With each subsequent year starting with a reduced species pool and the lack of recruitment, species richness is unlikely to bounce back following drought (Tilman and El Haddi 1992). This is in line with what I observed since richness continually decreased in the post drought years. There was also a large shift of the top ranking species in 2016, which further demonstrates the reorganization of the entire community at that point.

However, Shannon diversity did not differ between years. The Shannon diversity index quantifies both the abundance and evenness. It takes the proportion of a single species compared to the total number of species, and then multiples that by the logarithm of that proportion. This function is summed across species then multiplied by -1, which results in a higher final number representing higher species diversity (Zaimes et al. 2019). I observed similar Shannon diversity indices across years, which could be due to unevenness in the distribution of individuals. For example, the 2014 cohort year had a total abundance of 555, in which a quarter of that was made up from a single taxon, Scolytinae, on one sampling day. Abundance of just a few species in the early years , resulting in high variation in the distribution of all species may be the reason for the lower Shannon diversity although richness is higher (Pirithiraj et al. 2021)

Abundance was likely not reduced greatly because, in the earlier sampling years, richness was still high, but with low abundances for many species. In the later years, when richness was greatly reduced, there were fewer species present, yet the abundance of most of those resilient species were increased after the drought. These findings are in line with a rangeland study that found extreme drought led to a reduction in grasshopper species richness in the following years, indicating a single year of drought can result in long-term richness reduction (Kemp and Cigliano 1994). Post-drought aquatic community composition also reflects the intensity and duration of a drought as well as the accessibility of refuges (Villada-Bedoya et al. 2019). This decreasing richness in response to drought could be what is happening with terrestrial, ground dwelling communities as well. Further monitoring during the post-drought years may give the most insight for long-lasting impacts and implications for the community long-term.

Beetle Body Size Changes

Body size of a single abundant species, *Pterostichus californicus*, did not change between drought and non-drought years. This lack of difference was not what I expected to find given existing literature on relationships with body size and drought. Body size is important in ecology because of its role in life history and the physiological processes of an organism, which then influence its reproduction and survival (Winne et al. 2010). The environment imposes a profound effect on body size and larvae reared at high temperatures or on lower quality diets, both of which are associated with drought periods, produce adults with stunted growth (Nijhout 2003). In vertebrates, a drought-induced body size reduction has been observed in snakes (Winne et al. 2010), marsupials (Rhind and Bradley 2002), and bison (Martin and Barboza 2020). In insects, Carabid beetles respond to disturbance through body length; the carabid species *Carabus nemoralis* has a shorter body length in response to disturbance in the form of proximity to a city center in Germany (Weller and Ganzhorn 2004).

One reason for my conflicting findings could be simply the chosen species. *Pterostichus californicus*, which was first found in California and described from a Californian specimen, may not show a response as it is already resilient to drought conditions given the arid environment it originates from. I did observe lower abundances of it during drought years, but, again, that is likely a function of food sources diminishing in drought conditions. Other species may display variation in body length. The response of *P. californicus* agrees with those of Baar et

al (2018), who noted no changes in body sizes in response to precipitation, net primary productivity, or temperature in herbivorous beetles, concluding that findings of other papers must be due to species-specific responses.

Another possibility could be the timing of sampling. The sampling period ranged from exactly the beginning of the drought, July 2014, to July 2019, which was just over 2 years after the declared end of the drought. Most studies that report changes in body size in vertebrates or arthropods are comparing pre- and post- drought measurements. Since my sampling covered only during drought and 2 years post drought, I may not have been able to capture the initial body size reduction I had expected. Perhaps measuring pre-drought specimens would show a different pattern. If this is the case, there could be broader implications for the post drought recovery time of insect body size being greater than the 2 years I examined.

Measurement methods are likely playing a large role in this result. How a specimen is preserved and pinned may affect how accurate a measurement can be. For example, some specimens were more distorted in ways that made it challenging to view it in a single plane. Additionally, the body length measurements that I chose to take may provide little evidence for the status of a specimen's fitness. Body size or body condition are terms often used by studies that can represent numerous types of measurements, which can make studies hard to directly compare depending on the employed method (Knapp and Knappová 2013). Multiple studies have suggested that dry weight or even fat content are most suitable in assessing a carabid beetle's body condition or fitness (Knapp and Knappová 2013, Tseng et al. 2018). Although there is new research confirming the correlation of body length to body mass, measuring this myself would have been most ideal to gain insight on body condition (Weiss and Lind 2022).

Drought Effects on Terrestrial Arthropod Communities

Overall, drought affects ground-dwelling arthropods by altering their community composition. Activity periods of some species were changed over time dependent on species, which means that some taxa are not present at times they usually are. This, in combination with a decreased species richness, implies that taxa that presumably influence the trophic structure,

contribute ecosystem functioning, and perhaps serve as essential rare species in the community are disappearing, which greatly affects the entire ecosystem (Gascon et al 2015). These findings also highlight that drought affects ground-dwelling in a species specific way likely dependent on life history aspects. Therefore, the way in which drought affects ground-dwelling arthropods is not simple, but it is clear that there are worrisome alterations to the community as well as select species.

Limitations & Future Directions

Although this study demonstrated changes between drought and non-drought years, there are many interactions not taken into account that are necessary to fully understand what is happening within these communities. Pre- and post- drought data would have been more ideal to monitor changes. Sampling for this study began in July 2014, which was right at the beginning of the drought period. Although the aftermath of drought was able to be analyzed, major changes may have occurred at the beginning of the drought. Looking at richness, presence, and abundance of prior years would help provide a more complete picture of what changes are actually occurring.

Another major limitation to this study is the dataset being partially incomplete. Myriapoda taxa, including Chilopoda and Diplopoda, were not included in the final data due to sampling errors as well as Formicidae. These groups are major contributors to ground-dwelling arthropod richness and diversity that would have been important to include into community analysis. As this is an observational study, I cannot assign drought as the direct cause for these shifts. Other possible drivers, such as NDVI (Elliott 2020), degree days, or solar index were not analyzed in this study.

Furthermore, as I looked at overall differences between years labeled "drought" and "non-drought," I did not directly correlate precipitation with the community metrics I analyzed, but rather grouped years based on drought status. This categorical approach is likely ignoring many interactions within the community that could be analyzed. Controlled experimental studies would be the only way to confidently pin point rainfall alone as the main driving factor, but there

are multiple other drought-associated drivers of community change that are likely playing a role in this study. As there are limited studies on drought in relation to ground-dwelling arthropod community abundance, diversity, and body size, there is much more to be studied in order to fully understand the mechanisms by which drought could have caused these shifts I observed.

Broader Implications

Although we can't conclude drought is the only driver of these community shifts, it is clear that there are changes taking place within the community related to drought periods that will likely have rippling effects on the rest of the ecosystem. As these ground-dwelling arthropods are essential to the trophic structure and nutrient cycling of their habitat, we can infer that other organisms are likely affected where we see arthropods affected (Seastedt and Crossley Jr 1984). Similar to previous studies on drought effects, my research demonstrates the importance of examining community wide effects, rather than a few select species, due to species-specific responses of different organisms (Baar et al. 2018, Cady et al. 2019). Not all species have the same life history traits and therefore have different sensitivities to disturbance that can affect how useful they are as bioindicators. Although some species may appear to benefit or be unaffected by drought, the shift in the community as a whole, as seen from the dramatic decrease in species richness, is what is altering the natural balance of taxa, therefore affecting ecological niches, ecosystem processes, and other essential interactions (Gascon et al 2015). This, presumably drought adapted, Californian arthropod community was altered by the extended severe period of drought, and, as anthropogenic climate change promises longer, more intense droughts, it will likely be altered again by the next drought (Cook et al. 2018). Because of this, it is important to continually develop this area of study, as has been done for aquatic arthropods, to understand and manage the effects extreme droughts will have on California ecosystems.

ACKNOWLEDGEMENTS

A big thank you to Patina Mendez, my mentor, instructor, and one of the providers of this data, for helping me through every step of this process. Thank you to Kip Will, who also provided this data and the lab specimens, and all of my ESPM 175 classmates for their feedback, support, and sense of community they provided. Last, thank you to my parents, Jamie and Michael Roxbrough, who encourage me in any and all of my endeavors, as well as my friends, Jasmin Wyatt, Izzy Vinyard, and Christian Ellwood, for continually being there for me throughout my time at UC Berkeley.

REFERENCES

- Baar, Y., A. L. L. Friedman, S. Meiri, and I. Scharf. 2018. Little effect of climate change on body size of herbivorous beetles: Climate change and beetle body size. Insect Science 25:309– 316.
- Block, W. 1996. Cold or drought-The lesser of two evils for terrestrial arthropods? European Journal of Entomology 93:325–340.
- Boulton, A. J., P. S. Lake, and others. 2008. Effects of drought on stream insects and its ecological consequences. Aquatic insects: Challenges to populations 2008:81–102.
- Cady, S. M., T. J. O'Connell, S. R. Loss, N. E. Jaffe, and C. A. Davis. 2019. Species-specific and temporal scale-dependent responses of birds to drought. Global Change Biology 25:2691–2702.
- California Department of Resources. 2020. California Data Exchange Center. URL http://cdec.water.ca.gov/index.html
- CBS News. 2017. California's drought is officially over, Gov. Jerry Brown says <u>https://www.cbsnews.com/news/calif-gov-jerry-brown-declares-an-end-to-drought/</u>. Accessed 12/13/2021.
- Cloudsley-Thompson, J. L. 1975. Adaptations of Arthropoda to arid environments. Annual review of entomology 20:261–283.
- Cobb, R. C., K. X. Ruthrof, D. D. Breshears, F. Lloret, T. Aakala, H. D. Adams, W. R. L.
 Anderegg, B. E. Ewers, L. Galiano, J. M. Grünzweig, H. Hartmann, C. Huang, T. Klein, N. Kunert, T. Kitzberger, S. M. Landhäusser, S. Levick, Y. Preisler, M. L. Suarez, V.
 Trotsiuk, and M. J. B. Zeppel. 2017. Ecosystem dynamics and management after forest die-off: a global synthesis with conceptual state-and-transition models. Ecosphere

8:e02034.

- Cook, B. I., J. S. Mankin, and K. J. Anchukaitis. 2018. Climate Change and Drought: From Past to Future. Current Climate Change Reports 4:164–179.
- Cuff, D., and E. Nardi. 2013, October 1. Mount Diablo fire revives debate over cattle grazing limits in state park.
- Dale, A. G., and S. D. Frank. 2017. Warming and drought combine to increase pest insect fitness on urban trees. PLOS ONE 12:e0173844
- Daly, A., J. Baetens, and B. De Baets. 2018. Ecological Diversity: Measuring the Unmeasurable. Mathematics 6:119.
- Elliott, S. 2020. Evaluating the Effects of Drought, Wildfire, and Habitat on Beetle Assemblages in a Mediterranean Oak Woodland. UC Berkeley, Environmental Sciences Senior Thesis. <u>https://nature.berkeley.edu/classes/es196/projects/2020final/ElliottS_2020.pdf</u>
- Fawki, S., S. Smerup, S. Toft, and others. 2005. Food preferences and food value for the carabid beetles Pterostichus melanarius, P. versicolor and Carabus nemoralis. Pages 99–109 Proceedings of the 11th European Carabidologist Meeting.
- Ferris, R., and J. Humphrey. 1999. A review of potential biodiversity indicators for application in British forests. Forestry 72:313–328.
- Forrest, K., B. Tarroja, F. Chiang, A. AghaKouchak, and S. Samuelsen. 2018. Assessing climate change impacts on California hydropower generation and ancillary services provision. Climatic Change 151:395–412.
- Gascon, C., T. M. Brooks, T. Contreras-MacBeath, N. Heard, W. Konstant, J. Lamoreux, F. Launay, M. Maunder, R. A. Mittermeier, S. Molur, R. K. Al Mubarak, M. J. Parr, A. G. J. Rhodin, A. B. Rylands, P. Soorae, J. G. Sanderson, and J.-C. Vié. 2015. The Importance and Benefits of Species. Current Biology 25:R431–R438.
- Gely, C., S. G. W. Laurance, and N. E. Stork. 2020. How do herbivorous insects respond to drought stress in trees? Biological Reviews 95:434–448.
- Ghani, A., and S. Maalik. 2020. Assessment of diversity and relative abundance of insect fauna associated with Triticum aestivum from district Sialkot, Pakistan. Journal of King Saud University-Science 32:986–995.
- Haile, F. J. 2000. Drought stress, insects, and yield loss. Pages 131–148 Biotic stress and yield loss. CRC press.
- Hopkins, A. J. M., K. X. Ruthrof, J. B. Fontaine, G. Matusick, S. J. Dundas, and G. Es. Hardy. 2018. Forest die-off following global-change-type drought alters rhizosphere fungal communities. Environmental Research Letters 13:095006.

- Hung, K.-L. J., S. S. Sandoval, J. S. Ascher, and D. A. Holway. 2021. Joint Impacts of Drought and Habitat Fragmentation on Native Bee Assemblages in a California Biodiversity Hotspot. Insects 12:135.
- Joschko, M., H. Diestel, and O. Larink. 1989. Assessment of earthworm burrowing efficiency in compacted soil with a combination of morphological and soil physical measurements. Biology and Fertility of Soils 8:191–196.
- Kemp, W., and M. Cigliano. 1994. Drought and rangeland grasshopper species diversity. The Canadian Entomologist 126:1075–1092.
- Kharboutli, M. S., and T. Mack. 1993. Tolerance of the striped earwig (Dermaptera: Labiduridae) to hot and dry conditions. Environmental entomology 22:663–668.
- Knapp, M., and J. Knappová. 2013. Measurement of Body Condition in a Common Carabid Beetle, Poecilus cupreus: A comparison of Fresh Weight, Dry Weight, and Fat Content. Journal of Insect Science 13:1–10.
- Kremen, C., R. Colwell, T. Erwin, D. Murphy, R. Noss, and M. and Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. Conservation biology:796–808.
- Lencinas, M. V., F. J. Sola, J. M. Cellini, P. L. Peri, and G. M. Pastur. 2019. Land sharing in South Patagonia: Conservation of above-ground beetle diversity in forests and non-forest ecosystems. Science of The Total Environment 690:132–139.
- Longcore, T. 2003. Terrestrial Arthropods as Indicators of Ecological Restoration Success in Coastal Sage Scrub (California, U.S.A.). Restoration Ecology 11:397–409.
- Mann, M. E., and P. H. Gleick. 2015. Climate change and California drought in the 21st century. Proceedings of the National Academy of Sciences 112:3858–3859.
- Martin, J. M., and P. S. Barboza. 2020. Decadal heat and drought drive body size of North American bison (*Bison bison*) along the Great Plains. Ecology and Evolution 10:336– 349.
- Miller, D. R., and J. H. Borden. 1990. β-Phellandrene: kairomone for pine engraver, Ips pini (Say)(Coleoptera: Scolytidae). Journal of Chemical Ecology 16:2519–2531.
- Mukherjee, S., A. Mishra, and K. E. Trenberth. 2018. Climate Change and Drought: a Perspective on Drought Indices. Current Climate Change Reports 4:145–163.
- National Integrated Drought Information System. 2021. Current U.S. Drought Monitor Conditions for California. <u>https://www.drought.gov/states/california</u>. Accessed 12/2/2021.
- Nijhout, H. F. 2003. The control of body size in insects. Developmental Biology 261:1–9.

- Pearce, J. L., and L. A. Venier. 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. Ecological Indicators 6:780–793.
- Pirithiraj, U., R. Soundararajan, C. Justin, and V. Lakshmanan. 2021. Studies on insect diversity in jasmine (Jasminum sambac L.) ecosystem. Journal of Environmental Biology 42:1470–1477.
- Prather, R. M., K. Castillioni, E. A. Welti, M. Kaspari, and L. Souza. 2020. Abiotic factors and plant biomass, not plant diversity, strongly shape grassland arthropods under drought conditions. Wiley Online Library.
- Rainio, J., and J. Niemelä. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodiversity & Conservation 12:487–506.
- Rhind, S. G., and J. S. Bradley. 2002. The effect of drought on body size, growth and abundance of wild brush-tailed phascogales (Phascogale tapoatafa) in south-western Australia. Wildlife Research 29:235.
- Rosset, V., A. Lehmann, and B. Oertli. 2010. Warmer and richer? Predicting the impact of climate warming on species richness in small temperate waterbodies. Global Change Biology 16:2376–2387.
- RStudio Team (2022). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.
- Safranyik, L., D. A. Linton, and T. L. Shore. 1999. Emergence of Ips pini and Hylurgops porosus (Coleoptera: Scolytidate) from duff at the base of lodgepole pines (Pinaceae) killed by mountain pine beetle (Coleoptera: Scolytidate). The Canadian Entomologist 131:825–827.
- Schowalter, T., Y. Zhang, and J. Rykken. 2003. Litter invertebrate responses to variable density thinning in western Washington forest. Ecological Applications 13:1204–1211.
- Seastedt, T., and D. Crossley Jr. 1984. The influence of arthropods on ecosystems. Bioscience 34:157–161.
- Stocker, T. and others. 2013. Close Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.
- Tilman, D., and A. El Haddi. 1992. Drought and biodiversity in grasslands. Oecologia 89:257–264.
- Tseng, M., K. M. Kaur, S. Soleimani Pari, K. Sarai, D. Chan, C. H. Yao, P. Porto, A. Toor, H. S. Toor, and K. Fograscher. 2018. Decreases in beetle body size linked to climate change and warming temperatures. Journal of Animal Ecology 87:647–659.
- Villada-Bedoya, S., A. Córdoba-Aguilar, F. Escobar, I. Martínez-Morales, and D. González-

Tokman. 2019. Dung Beetle Body Condition: A Tool for Disturbance Evaluation in Contaminated Pastures. Environmental Toxicology and Chemistry 38:2392–2404.

- Weiss, F., and A. Linde. 2022. How to estimate carabid biomass?—an evaluation of size-weight models for ground beetles (Coleoptera: Carabidae) and perspectives for further improvement. Journal of Insect Conservation.
- Weller, B., and J. U. Ganzhorn. 2004. Carabid beetle community composition, body size, and fluctuating asymmetry along an urban-rural gradient. Basic and Applied Ecology 5:193– 201.
- Will, K., and P. Mendez. 2021. Mating marks on museum specimens reveal breeding patterns in species of Pterostichus Bonelli (Carabidae, Pterostichini). Biodiversity Data Journal 9:e70897.
- Winne, C. T., J. D. Willson, and J. Whitfield Gibbons. 2010. Drought survival and reproduction impose contrasting selection pressures on maximum body size and sexual size dimorphism in a snake, Seminatrix pygaea. Oecologia 162:913–922.
- Zaimes, G. N., P. Loisios, P. Fytopoulos, C. Mersina, N. Fyllas, V. Iakovoglou, and D. Avtzis. 2019. Ground dwelling insects as environmental indicators of riparian habitats in agricultural mediterranean landscapes. Environmental Engineering & Management Journal (EEMJ) 18.
- Zhang, A. 2015. Terrestrial arthropod community responses to wildfire in Mediterranean forest ecosystems. UC Berkeley, Environmental Sciences Senior Thesis. <u>https://nature.berkeley.edu/classes/es196/projects/2015final/ZhangA_2015.pdf</u>