Post-fire succession of plants and soils in chaparral shrublands: the role of ephemeral herbs and mammalian herbivores

By

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Abstract

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Understanding the drivers of ecological succession requires linking ecological interactions and biodiversity to ecosystem soil processes. California's widespread chaparral shrublands provide an ideal setting to investigate mechanisms linking plant and soil dynamics during succession. Periodic crown-fire in chaparral temporarily removes all living shrub cover, deposits mineral N on soils, and allows functionally diverse herbaceous communities to dominate the landscape for 3-5 years. In many areas, chaparral stands are bordered by non-native grasslands and fire can facilitate invasion of chaparral by grasses. Herbivorous small mammals in chaparral have been previously demonstrated to impact the composition of the chaparral understory and consume non-native grasses at the grassland-chaparral border. Herbivory may also impact soil N and C cycling through changes to plant community composition and direct additions of herbivore feces and urine. The composition of post-fire herbaceous communities, whether influenced by herbivory or another factor, may itself impact soil nutrient cycling. In particular, N-fixing and non-N-fixing herbs can have functionally distinct effects on ecological and ecosystem processes, influencing herbivore feeding preferences, competitive or facilitation relationships between plants, and litter decomposition rates.

In this dissertation, I conducted three field experiments in Northern California chaparral. In Chapter 1, I established an herbivore-exclosure experiment at chaparral-grassland borders to investigate how mammalian herbivores impact invasive grasses and general understory herb composition, as well as how this effect was mediated by wildfire. In Chapters 2 and 3, respectively, I manipulated herbivore abundance and the biomass of N-fixing and non-N-fixing herbs to investigate how these factors influence soil C and N cycling in post-fire chaparral during the first two years after fire.

Mammalian herbivory reduced herbaceous abundance post-fire, particularly non-native grasses, suggesting herbivores limit grassland invasion into chaparral. However, herbivore exclosures did not measurably impact N and C cycling during the first two post-fire seasons. Removing N-fixing and non-N-fixings herbs dramatically influenced soil N and C dynamics in the same system. Two years after fire, plots with all herbs removed had significantly lower soil N and C than any treatment with herbs. Post-fire herbs do appear to enrich soil in C and N, which may benefit recovering shrubs even after herbaceous communities die back.

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PREFACE

Background

Elucidating patterns and mechanisms of ecological succession following disturbance has been a central goal of the fields of community and ecosystem ecology since the turn of the 20th century (Cowles 1899, Clements 1916, McIntosh 1981). While community ecologists have focused primarily on species interactions as the drivers of species replacements and biodiversity following disturbance (Connell and Slatyer 1977, Pickett et al. 1987), the efforts of ecosystem ecologists have been directed towards testing predictions concerning patterns of nutrient retention and productivity (Odum 1969, Vitousek and Reiners 1975). The false dichotomy between these lines of inquiry belies the interdependence of biotic and abiotic change at both population and ecosystem scales (Loreau 2010). Linking patterns of biodiversity and ecological interactions to ecosystem processes is essential to understanding mechanisms of ecological succession, making predictions about the effects of non-random extinctions in a changing world (Díaz et al. 2003), and achieving restoration and conservation goals (Heneghan et al. 2008, Kardol and Wardle 2010). In this dissertation, I investigate in chaparral shrublands (1) how herbivory by small mammals impacts herbaceous functional composition and invasion by non-native grasses, (2) how the effects of herbivores are mediated by fire, (3) how herbivory impacts post-fire chaparral N and C cycling, and (4) how experimental manipulations of herbaceous assemblages of N-fixers and non-N-fixers impact N and C cycling.

Chaparral ecosystems, the fire-prone shrublands that cover over 7% of California's land area (Keeley and Davis 2007) have been a common study system for botanists, ecologists, and resource managers over the past eighty years. Comprised mainly of *Adenostoma fasciculatum*, as well as interspersed *Ceanothus spp.*, *Arctostaphylos spp.*, and other taxa, chaparral is susceptible to high-intensity fires, typically occurring in the late summer and early fall dry season (Keeley et al. 2012). Nutrient dynamics following fire (e.g. Christensen 1973, Hanan et al. 2016) and patterns of species replacement during chaparral succession (Hanes 1971, Keeley et al. 1981, Keeley et al. 2005) have been well-characterized. Mature *Adenostoma* chaparral is considered nitrogen-limited (Wier 1950, Hellmers et al. 1955, Vlamis and Gowans 1961, Christensen and Muller 1975, McMaster et al. 1982) and hosts almost no herbaceous understory beneath its dense shrub canopy (Sampson 1944, Went et al. 1952, Horton and Kraebel 1955, Hellmers et al. 1955, Muller et al. 1968, Chou and Muller 1972, Christensen and Muller 1975, Shmida and Whittaker 1981). Disturbance by fire temporarily eliminates canopy cover, liberates nitrogen, and stimulates the germination of fast-growing herbs, resulting in accelerated N-cycling in recently burned stands (Hanan et al. 2016). During fire, large net losses of N occur through volatilization from shrub biomass, litter, and soils (Debano and Conrad 1978, Debano and Conrad 1979). Despite net losses to total N, soil mineral nitrogen is elevated after fire. The ash layer deposited on chaparral soils is rich in ammonium (NH_4^+) (Christensen 1973, Debano and Conrad 1978), which is available for immediate uptake by plants. Within two to three months after fire, the onset of winter rains stimulates rapid nitrification, which is the conversion of NH_4^+ to nitrate (NO_3^-) (Christensen 1973). While both NH_4^+ and NO_3^- are available for plant uptake, NO_3^- is highly soluble and vulnerable to leaching if not taken up immediately by plants (Debano and Conrad 1978). Thus, post-fire assemblages, and herbivore interactions that mediate their composition, have an important influence on nitrogen cycling in recently burned chaparral.

There is a growing appreciation that herbivory—already known to be a biotic interaction that can limit plant biomass, mediate species coexistence (Lubchenco 1978, Crawley 1983, Huntly 1991, Hulme 1996, Maron and Crone 2006) and influence successional dynamics (Sousa 1979, Brown 1985, Davidson 1993)—can also have important effects on nutrient cycling in ecosystems (Pastor et al. 2006, Sitters and Olde Venterink 2015, Metcalfe et al. 2016). Current theory predicts that herbivore preferences and grazing intensity will change plant functional diversity with implications for soil N cycling. In N-poor systems, herbivores are predicted to selectively consume high-N plants (low C:N ratio), facilitating dominance by low-N plant species (high C:N ratio). Thus, low-quality litter is supplied to decomposers, slowing N cycling and decreasing N availability. In high-N systems, herbivores stimulate the growth of fast-growing N-rich species that can tolerate defoliation (*sensu* McNaughton 1983). This effect accelerates N cycling by increasing rates of plant N uptake, N content of litter, and dung/urine N (Ritchie et al. 1998, Sitters and Olde Venterink 2015). However, experimental tests of these theories have been limited to a few studies systems (e.g. Augustine and McNaughton 1998, Olofsson et al. 2004), and results have been contradictory (Hawkes and Sullivan 2001, Bakker et al. 2009, Sitters and Olde Venterink 2015). Disentangling the complex effects of herbivory on soil nutrient cycling requires tests in natural communities that address the influence of plant functional diversity on soil nutrient cycling, herbivore-mediated shifts in plant composition, and most importantly, the integrated effect of these two processes. This dissertation addresses these questions in Northern California chaparral shrublands.

Historically chaparral has resisted grassland invasion (Davis and Mooney 1985, Keeley et al. 2005b), which may be influenced in part by small-mammal herbivory (Park and Jenerette 2019). The grasslands that typically occur adjacent to chaparral shrublands are usually dominated by non-native annuals (Bossard and Randall 2007). In mature stands of chaparral, mammalian herbivores can provide effective biotic resistance to alien grass invasion, consuming non-natives in the understory (Kruger et al. 1989, Lambrinos 2002, 2006). In fact, the feeding activity of small mammals is well-established to maintain a devegetated “bare zone” immediately outside of chaparral cover (Bartholomew 1970, Halligan 1973). Small mammals dwelling in the chaparral understory venture out just far enough to feed on grasses, while minimizing the risk of predator attack (Bartholomew 1970). However, there is increased evidence of type conversion to non-native grasslands (Park et al. 2018, Syphard et al. 2019), particularly after short-return-interval fires (Zedler et al. 1983, Keeley and Brennan 2012), in masticated areas (Potts and Stephens 2009), and in areas of decreased moisture (Park et al. 2018). In the first few years after fire, chaparral persistence depends on shrubs successfully competing with invading grasses (Keeley et al. 2005a). Intense rodent herbivory can facilitate the exclusion of exotic grasses from shrublands (Park and Jenerette 2019), indirectly benefitting shrubs and limiting exotic grass invasion. In all chapters, I examine the implications of my findings for understanding grassland invasion of chaparral.

Dissertation

In Chapter 1, I use an herbivore-exclosure experiment to test the role of mammalian herbivores in maintaining chaparral-grassland boundaries and limiting grassland invasion of chaparral, both in mature and recently-burned areas at Mt. Diablo State Park (Contra Costa County, CA). Although previous investigations have demonstrated the role of small mammalian herbivores in maintaining a “bare zone” between chaparral and grassland vegetation (Bartholomew 1970, Halligan 1973), no previous investigation has tested the impact of small mammals on the bare zone after fire. I placed herbivore exclosures in the bare zone and inside of the chaparral, which also allowed me to explore patterns of herb abundance and functional diversity. I found that herbivores concentrate their feeding on non-native grasses in the bare zone in both non-burned and burned areas, although the burned bare zone was no longer bare. In non-burned chaparral, mammalian herbivores consumed almost all seedlings emerging in the herbaceous understory, including many non-native grasses, suggesting herbivores play a role in limiting grassland invasion of mature chaparral. Non-native grasses were not abundant in post-fire chaparral, but herbivores did substantially reduce densities and cover of non-native and native N-fixers.

A key focus of this dissertation is how herbivores mediate the post-fire composition of N-fixing and non-N-fixing herb assemblages (Chapters 1 and 2), and how this composition impacts soil N and C cycling (Chapters 2 and 3). In Chapter 1, only N-fixers were significantly reduced by herbivores in both cover and density during the growing season in post-fire chaparral. While the immediate post-fire environment is characterized by high soil mineral N (Christensen 1973, Hanan et al. 2016) and high tissue N of fire-following plants, plant tissue N can drop considerably by the second year post-fire (Rundel and Parsons 1984), when this study took place. The reduction of N-fixers by herbivores in this study suggests lower soil N availability, although it was not measured.

In Chapter 2, I implemented another herbivore-exclosure experiment, this time within post-fire chaparral at Hopland Research and Extension Center (Mendocino County, CA). Over the first two years after fire, I monitored the effect of herbivore exclosures on herbaceous plant assemblages and soil N and C cycling. By the second season after fire, excluding mammalian herbivores increased overall herb standing biomass by 54%, with the effect concentrated on non-native annual non-N-fixers (increased 48%) and native annual N-fixers (increased 54%). However, herbivory did not change the relative abundance of N-fixing vs. non-N-fixing herbs, nor annuals vs. perennials. Surprisingly, I detected no significant effects on any measure of N or C cycling by herbivore exclosure treatment throughout the study. In contrast to the findings of Chapter 1 (Mt. Diablo), non-native grasses were a substantial component post-fire chaparral at Hopland, and excluding herbivores increased the standing biomass of non-native herbs. However, while mammalian herbivores concentrated their feeding particularly on non-native annual non-N-fixers (typically invasive grasses), these species were still abundant where grazed. Herbivory reduced, but was not sufficient to prevent, grassland invasion into chaparral over the first two years after fire.

Chapter 3 uses an herb-removal experiment to evaluate the impact of N-fixing and non-N-fixing herbs on post-fire soil N and C cycling in chaparral at Hopland. Investigations that link plant functional diversity to ecosystem processes and services have often used experimentally-assembled, rather than natural, communities (e.g. Naeem et al. 1994, Tilman et al. 1997, Nicklaus et al. 2006). While such synthetic systems may be more experimentally tractable, allowing tighter control over environmental conditions, they cannot answer the key question of whether these predictions apply to natural ecosystems (Diaz et al. 2003, Wardle 2016). It has been suggested that the abundant herbs in post-fire chaparral influence soil processes by immobilizing ash-derived mineral N, preventing N losses due to leaching and runoff, and contributing N from symbiotic root fixation. I implemented a two-year herb-removal experiment in which I weeded plots to include (1) all herbs (unmanipulated control), (2) only non-N-fixing species, (3) only N-fixing species, and (4) no herbs, then measured the response of herbaceous biomass and N and C cycling. No-herb plots had lower soil respiration rates and bulk soil C and N than all herb treatments. Two treatments, no-herb and N-fixer plots, had elevated mineral N concentrations and N mineralization rates in the second year of the experiment. Rapid N cycling

in N-fixing plots may have been driven by the decomposition of N-rich litter and N rhizodeposition. All-herb plots, occupied by both N-fixers and non-N-fixers, maximized immobilization of mineral N for storage in soils and built soil organic C, which may influence soil fertility during chaparral succession.

Conclusion

Mammalian herbivory clearly influenced the composition of the herbaceous assemblages in non-burned and burned chaparral. Where non-native grasses were found, like the bare zone or in some post-fire chaparral stands, herbivores selectively consumed these species. This suggests a role for herbivores in limiting grassland invasion into chaparral. Despite a large impact of herbivores on overall herb abundance and composition, herbivore exclosures did not measurably impact N and C cycling over the first two years after fire. However, directly manipulating the composition of N-fixing and non-N-fixings herbs did dramatically influence soil N and C dynamics in the same system. It is possible that the effect of herbivores may influence herb composition and vegetation succession after fire, but that these changes are not dramatic enough to alter N and C cycling. Plots containing both N-fixing and non-N-fixing herbs had the highest soil N and C two years after fire. The presence and composition of post-fire herbs in chaparral influence soil ecosystem processes, potentially impacting soil fertility during shrub regrowth.

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CHAPTER 1

Small mammal herbivory concentrated at the chaparral-grassland ecotone in mature and recently-burned vegetation.

ABSTRACT

California chaparral shrublands frequently occur adjacent to non-native grasslands, with a border that is distinguishable as a striking “bare zone”, devoid of vegetative cover. Small mammalian herbivores dwelling inside of the chaparral are responsible for these devegetated edges, venturing out of the shrub cover to feed on nearby grasses. Although this pattern is well-established in mature stands of chaparral, it is unknown if herbivores continue to maintain the bare zone after chaparral wildfire, which temporarily removes the shrub cover for 3-5 years. As California chaparral continues to face the risk of grassland invasion, particularly after fire, it is very important to understand how disturbance and herbivory interact at chaparral borders. I conducted an herbivore-exclosure experiment at Mt. Diablo State Park, Contra Costa Co., CA (USA) following the 2013 Morgan Fire at clearly-defined chaparral-grassland borders in burned and mature (non-burned) chaparral. Exclosures were positioned immediately inside of the chaparral and just outside in the bare zone. Burning increased seedling density and cover in both chaparral and the bare zone. In non-burned stands of chaparral, mammalian herbivores maintained a bare chaparral understory and limited the density and cover of herbs in the bare zone, particularly non-native grasses. After fire, herb abundance was much higher than in non-burned stands and not significantly different between chaparral and bare zone. Despite the similar plant resource abundance, the impact of herbivores was still concentrated in the bare zone, principally resulting in the reduction of non-native grasses. In post-fire chaparral, herbivores reduced cover of herbs throughout the whole growing season, but densities were reduced only at the onset of summer drought and for only some herb functional groups. Eurasian grasses were not a substantial component of post-fire chaparral community, but herbivores did limit the density and cover of a non-native annual N-fixer, likely a preferred food for rabbits. Despite a reduced relative impact of mammalian herbivory on post-fire chaparral herbaceous communities, the impact remained concentrated in the bare zone and largely limited the abundance of non-native species in and near chaparral.

INTRODUCTION

The maintenance and function of ecological boundaries have been the subject of extensive research over the past century (Ries et al. 2004). The edges between terrestrial habitat types often exhibit diversity patterns and ecosystem properties influenced by, but distinct from, their adjacent habitats (Cadenasso et al. 2003). It is well-established that patterns of herbivory can change at habitat edges, with an increased presence of folivorous and seed predatory animals frequently denuding vegetation edges (Ries et al. 2004). Furthermore, herbivores can dramatically influence the competitive relationship between plants (Whittaker 1979) and may be responsible for the vegetation structure that unfolds over succession (Sousa 1979, Whittaker 1979, McNaughton 1983, Louda et al. 1990). However, few investigations have addressed how the persistence and biological characteristics of edge species assemblages are influenced by disturbance, which can temporarily change the vegetation structures and resources that define edges. Elucidating the interaction between disturbance and edge dynamics is essential for predicting landscape changes in a world where disturbance patterns are changing globally. In particular, wildfire regimes are predicted to change dramatically, with 82% percent of globe's land projected to experience an alteration of fire patterns by the end of the twenty-first century (Moritz et al. 2012). Specifically, the western United States are predicted to experience changes in seasonality and an increase in the intensity and frequency of wildfires (Westerling 2016). Most climate change models predict that Mediterranean-type vegetation, such as shrubs, will have a high probability of increased burning over the next decades (Moritz et al. 2012).

California's fire-prone chaparral shrublands, which cover 7% of the state's land (Keeley and Davis 2007), provide an ideal setting to investigate how shifting habitat structure and resource conditions influence the character of herbivore-mediated edge effects. Chaparral is dense, medium-stature shrubland typically dominated by *Adenostoma fasciculatum* (chamise) and frequently bordered by non-native grasslands (Keeley and Davis 2007). Chaparral has been the subject of several investigations into biotically-mediated edge effects (Bartholomew 1970, Halligan 1973, Larson 1985). The chaparral-grassland border is typically defined by a striking transitional "bare zone" devoid of herbaceous cover (**Figure 1**). It is well established that small mammalian herbivores are responsible for maintaining this devegetated edge. Dwelling under the protective cover of chaparral, they venture out only far enough to feed on the abundant nearby grassland resources. When herbivore exclosures are placed in the bare zone outside of chaparral cover, herbaceous cover returns within a growing season (Bartholomew 1970, Halligan 1973). However, no study has examined vegetation dynamics following a fire to determine if the chaparral-grassland border remains bare through the fire recovery, or if the small mammalian herbivore effect is diminished.

Herbivory in the bare zone is closely linked to the structure and processes immediately inside of the chaparral shrublands, where small mammals seek refuge. Herbivory has been shown to significantly reduce seedling emergence, survivorship, or growth in mature chamise chaparral (McPherson and Muller 1969, Christensen and Muller 1975a, Swank and Oechel 1991) as well as in maritime chaparral (Tyler 1995). A comprehensive manipulative study of the controls on the chaparral understory found that competition with adult shrubs, water, and nutrients all limit chaparral understory herbs, but only in plots caged from mammalian herbivores. When natural grazing is allowed, herb survivorship is driven to such low levels that other limiting factors are no longer significant (Swank and Oechel 1991). Even when herbs germinate in wet understory microsites, they quickly disappear if not protected from mammalian herbivory (Larson 1985, Swank and Oechel 1991, Tyler 1995). Even though herbivory alone is not sufficient to explain the low emergence of herbs under mature chaparral, small mammal grazing does significantly impact seedling survivorship throughout the growing season (Tyler 1995).

Chaparral shrublands are subject to periodic high-intensity, late-summer and fall fire (Keeley et al. 2012), which leads to drastic changes to habitat structure and plant composition (Keeley et al. 1981). While mature chaparral stands are typically dominated by a few large shrubs species, with almost no herbaceous understory (Sampson 1944, Went et al. 1952, Horton and Kraebel 1955, Hellmers et al. 1955, Muller et al. 1968, Chou and Muller 1972, Christensen and Muller 1975b, Shmida and Whittaker 1981) or shrub recruitment (Sampson 1944, Horton and Kraebel 1955, Hanes 1971, Christensen and Muller 1975a), the post-fire environment in chaparral is characterized by a flush of herbaceous species, mainly from a large dormant seedbank (Brandegee 1891, Cooper 1922, Sampson 1944, Horton and Kraebel 1955, Sweeney 1956, 1956, Hanes 1971, Keeley et al. 1981, 2005b, Keeley and Keeley 1988, Potts and Stephens 2009). Herbaceous dominance may persist for 3-5 years before the shrub canopy closes over, primarily effected by the growth of basal resprouts of *Adenostoma fasciculatum* (Keeley et al. 2005a, 2005b, Potts et al. 2010). The removal of protective shrub cover has the potential to change patterns of small mammal foraging, potentially dispersing them to other areas, precluding concentrated feeding at the bare zone.

Of all the vertebrates, mammals undergo the most short-term change in response to fire. During the fire, most of the animals that die are small immobile animals, often mammals, and many others die in the immediate post-fire environment, exposed to predation by removal of protective cover. The succession of animal populations is largely driven by resource-availability changes related to plant community shifts, specifically in California chaparral (Quinn 1979, 1983, 1990) and in other Mediterranean systems (Taber and Dasmann 1958, Biswell 1961, Quinn 1983, Fox et al. 1985). Although it has been suggested that reduction in small mammals reduces post-fire herbivory in chaparral (Mooney and Dunn 1970, Christensen and Muller 1975b), there is conflicting evidence as to how small mammals are affected by fire, with some species increasing and others decreasing in densities (Lawrence 1966, Wirtz 1977, Nichols and Menke 1984, Griffiths and Brook 2014). Multiple investigations have demonstrated that the effect of herbivores on post-fire chaparral plant cover, biomass, or density decreases or disappears after fire (Tyler 1995, 1996), likely due to displacement or death of herbivores (Christensen and Muller 1975b). However, specific plants, such as the common soap root, *Chlorogalum pomeridianum*, suffered sufficient post-fire herbivory that it suppressed flower and fruit formation (Borchert and Tyler 2009), and multiple studies have shown that N-fixing *Ceanothus spp.* seedlings are browed more intensively post-fire than co-occurring *Adenostoma fasciculatum* seedlings (Mills 1983, Quinn 1994). Thus, while the overall effect of mammalian herbivory inside chaparral may be reduced, specific groups of plants may be especially impacted, possibly mediating plant competition at an early successional stage.

Finally, the question of herbivore impacts on chaparral-grassland edges has particular importance in light of the combined threats of alien grassland invasion into chaparral and increased frequency of fires due to climate change. The grasslands occurring directly adjacent to chaparral shrublands are typically dominated by non-native annuals, as are 98% of the grasslands in California (Bossard and Randall 2007). Although chaparral has largely resisted invasion by grasses (Davis and Mooney 1985, Keeley et al. 2005b), there is increased evidence of type conversion to non-native grasslands (Park et al. 2018, Syphard et al. 2019), particularly after short-return-interval fires (Zedler et al. 1983, Keeley and Brennan 2012), in masticated areas (Potts and Stephens 2009), and in areas of decreased moisture (Park et al. 2018). The most critical factor in driving chaparral persistence after fire is the speed of shrub canopy closure over grasses (Keeley et al. 2005a). Additionally, intense rodent herbivory can facilitate the exclusion of exotic grasses from shrublands (Park and Jenerette 2019) and other investigations demonstrate that mammalian herbivores can provide effective biotic resistance to alien grass invasion, at least in mature chaparral (Kruger et al. 1989, Lambrinos 2002, 2006). As fire return intervals and seasonality are predicted to change (Westerling 2016), more chaparral could become sensitive to grassland invasion, suggesting increased importance of biotic resistance.

The present study examines the role of mammalian herbivores at the chaparral-grassland ecotone in both mature and recently-burned vegetation. In the summer of 2014, one year after the 2013 Morgan Fire at Mt. Diablo State Park (Contra Costa Co., CA), I installed herbivore exclosures along the bare zone and immediately inside burned and non-burned stands on the same mountain. I hypothesized that mammalian herbivores living inside mature chaparral would limit the establishment and growth of all herbaceous species under the chaparral canopy and in the bare zone adjacent to non-burned patches, resulting in higher densities and cover inside exclosures. This would also limit the abundance of non-native grasses and herbs in the chaparral. In contrast, the population of mammalian herbivores in post-fire chaparral would decrease due to the temporary removal of protective chaparral canopy. Therefore, the herbivore effect on post-fire seedling establishment would decrease or disappear. As a result, I predicted that in burned stands herbivores would not limit the chaparral herb understory, maintain a bare zone, nor limit invasion by non-native plants. This research examines a basic relationship between edge effects and disturbance, while also demonstrating patterns of non-native grass invasion in Northern California chaparral, which is less researched than in the southern part of the state. To my knowledge, this is the first investigation to quantify the interaction of disturbance by fire and herbivory both in chaparral and at the bare ecotone zone.

METHODS

Study Location

I conducted this study from winter 2014 to summer 2015 at Mount Diablo State Park (Contra Costa County, California) near and within the perimeter of the Morgan Fire (September 8-14, 2013, 1259 ha in extent). Mount Diablo (37.88, -121.91, max. elevation 1,173 m) is an isolated peak located at the north end of the Diablo Mountain Range, nestled between the North and South Coast Ranges of California (Taff 1935), thus hosting a high plant diversity containing representatives of northern and southern floras (Ertter and Bowerman 2002). The vegetation of the mountain is a mosaic typical of Mediterranean California, including grasslands, chaparral shrublands, coastal sage scrub, and oak woodlands. Chaparral general occurs on slightly steeper slopes (Ertter and Bowerman 2002) and rockier soils (Soil Survey Staff 2018) than grasslands, but this delineation is not strict. The climate at Mt. Diablo follows the typical pattern of a Mediterranean-type ecosystem, with relatively hot arid summers and rainy winters (Ertter and Bowerman 2002). The years preceding and succeeding the Morgan fire (2013-2015) were substantially drier than 30-year averages (1981-2010) (National Oceanic and Atmospheric Administration 2018) (**Figure 2a**). Fall 2011 to fall 2015 was the driest period on record throughout California, with 2014-2015 the two hottest years recorded on instrumental records (Hanak et al. 2016) and 2012-2014 the most severe drought years recorded in 1200 years of tree ring chronologies (Griffin and Anchukaitis 2014). At Mt. Diablo, the winters of 2014 and 2015 were unseasonable warm (**Figure 2b**). Mt. Diablo is home to several herbivorous small mammals, including desert cottontail (*Sylvilagus audubon*), brush rabbit (*Sylvilagus bachmani*), black-tailed jackrabbit (*Lepus californicus)*, Botta's pocket gopher (*Thomomys bottae*), fox squirrel (*Sciurus niger*), and California ground squirrel (*Spermophilus beecheyi*). Major predators of these small mammal herbivores include the gray fox (*Urocyon cinereoargenteus californicus*), coyote (*Canis latrans*), mountain lion (*Felis concolor*), bobcat (*Lynx rufus californicus*), and red-tailed hawk (*Buteo jamaicensis*) (Pelonio 2019).

Site Selection

I used aerial imagery to identify sites based on a clearly-defined ecotone between grassland and chamise chaparral, selecting two sites inside and two outside the burn perimeter.

Sites were at approximately the same elevation (**Figure 3**, **Table 1**). All chaparral sites were south facing. Chaparral shrub vegetation was comprised mainly of *Adenostoma fasciculatum* (chamise), with occasional *Ceanothus cuneatus*, *Quercus* spp., and *Arctostaphylos* spp. The adjacent grasslands were dominated by non-native grasses, particularly *Avena barbata*, *Avena fatua*, *Bromus diandrus*, and *Bromus madritensis ssp. rubens*. In March 2014, during the first season following the fire, I defined the grassland-bare zone border by noting where the first grass seedlings emerged. Grasses germinated in high densities at the location of the pre-fire grassland, allowing me to clearly view and mark a bare zone between chaparral and grassland, likely because on a depleted grass seedbank in the bare zone. I marked chaparral edge as the border of the standing woody canopy or the skeletal burnt trunk left by the fire.

Experimental Design

In July and August 2014, approximately one year after the Morgan Fire, I installed an herbivore-exclosure experiment along the four defined chaparral-grassland ecotones. I arranged herbivore-exclosure treatments in arrays of six blocks at each of the four ecotones, with all chaparral plots positioned parallel to the chaparral edge at exactly 5 m into the canopy and the parallel bare zone plots at a distance halfway between the grassland and chaparral edges (**Figure 4**). A block comprised one full-exclosure, a half-exclosure control, and an open unmanipulated control. I placed treatments within each block 5 m apart in a random order. I spaced the blocks 5 m from the nearest block unless there was a major obstruction, such as a rocky outcrop. In this case, I skipped the barrier and continued the placement pattern of the next block along the ecotone on the other side. I constructed full exclosures from ¼ in. (0.635 cm) hardware mesh, with a circular 1 m diameter footprint at 90 cm height, enclosing an area of 0.785 m^2. Full exclosures were sealed at the base with a 15 cm wide strip of window screen to prevent burrowing mammal entry and covered with a hardware mesh roof to exclude climbing animals. I installed half-exclosure controls forming a semi-circular half wall on the southern side and a full roof. These half exclosures controlled for growth reduction due to shading or increase due to dew accumulation. I marked and labeled all plots, including the open control, with a galvanized steel nail and washer.

Vegetation Sampling

I measured pre-treatment seedling density in June 2014 before installing the exclosures in July and August 2014 (144 plots total). I monitored plots for seedling density and percent canopy cover during the rainy growing season (March 2015, May 2015) and after the onset of summer drought (July 2015). Thus, these results document the effect of herbivory in the mature chaparral understory in the second growing season after fire only. All seedlings of fire-following plants were sampled in a 0.25 m^2 quadrat located in the center of each plot. I counted and identified all seedlings and made visual estimates of cover. Although potentially affected by subjective bias, visual cover estimates of sessile organisms can be more accurate than the objective point-intercept method and have a greater capacity to detect rare species (Meese and Tomich 1992, Dethier et al. 1993). Species percent cover estimates were summed within each plot to reflect overlapping plants, allowing for total cover values over 100%.

Statistical Analyses

Pre-treatment Vegetation Patterns

I examined pre-treatment data (June 2014) to ensure that plots assigned to different exclosure treatments had similar vegetation characteristics at the start of the experiment. For the mature bare zone, I dropped three blocks from the analyses which I determined did not qualify as bare ground, despite their proximity to the chaparral. Due to isolated patches of grass in the bare zone, these blocks contained plots with pre-treatment seedling densities over 150 seedings/m^2, in contrast to an average of 27.6 seedlings/m^2 in the remaining plots.

To test whether there were significant differences among the plots assigned to each treatment prior to the exclosure installation, I created a model of all possible interactions of fixed effects, including a random effect for block within Site. All factors and levels are defined in **Table 2**.

$$Y = Exc * Veg * Burn * Site(Burn) + random(Block(Site)) \quad \text{Eqn. 1}$$

A lack of exclosure main effect or interaction would indicate that June 2014 plot starting conditions were appropriately similar. I fit this and all mixed models in *R* (*R* Core Team 2018) with the package *lme4* (Bates et al. 2015), using a restricted maximum likelihood estimation procedure (REML) and analyzed the Type III ANOVA output using the *lmerTest* package (Kuznetsova et al. 2017). Data were square-root transformed to reduce unequal variance between treatments. I conducted any posthoc tests based on marginal means estimates using the *emmeans* package (Lenth 2018), adjusting p-values with the semi-conservative Benjamini-Hochberg false discovery rate procedure (Benjamini and Hochberg 1995). Block(Site) was included as a significant random factor by likelihood ratio test (LRT) comparison to the fixed-factor model. I ran the model for the density of total seedlings, herbs, and shrubs to confirm no differences between plot treatment types before building exclosures.

This mixed-model ANOVA revealed no significant main effects of exclosure treatment assignment in the June 2014 pre-treatment sampling for herbs, shrubs, or total seedlings (**Table 3**). There was a significant interaction of Exclosure x Site(Burn) only for shrubs, but the effect was small. Post-hoc exclosure treatment contrasts found that the only significant treatment difference within any site was between the control and half-cage control plots in the bare zone of one burned site (*P* = 0.016). However, there was no significant difference between plot treatments when results were averaged across Site(Burn) (*P* = 0.254). Given this relatively isolated result, along with the small contribution of shrubs to overall bare zone composition, I did not consider this result to indicate overall pre-treatment differences in plots before exclosure installation; therefore, subsequent analyses only examine post-treatment samples.

Test for Cage Artifacts

To assess whether there was an artifactual effect of caging on seedling density and cover, I ran a model comparing open and half-control exclosures across all possible vegetation, burn and site interactions at all post-treatment dates (March, May, July 2015).

$$Y = Exc * Veg * Burn * Date * Site(Burn) + random(Plot(Block(Site))) \quad \text{Eqn. 2}$$

Plot(Block(Site)) was included as a significant random factor by likelihood ratio test (LRT) comparison to the fixed-factor model (*P* <0.001 for all tested groups). For total seedling and herb density and cover, I found no significant main or interactive effects of Exclosure; however, for shrub density and cover the Exclosure x Vegetation x Burn interaction was significant (**Table 4**). Post-hoc analysis of densities at each date showed that when averaged across Site(Burn), there were no significant differences between open controls and half-cage controls. Although there was a marginal difference in March 2015 at the burned bare zone (*P* = 0.094), this actually reflected lower densities in the half-cage than the control, opposite the expected artifact of the cages. March 2015 cover at the burned bare zone followed the same pattern, with the half-cage lower than the control (*P* = 0.003). Only in the burned chaparral, the half-cage was systematically higher in cover than the open controls by a significant, but minuscule, margin of less than 1.5% cover (Mar *P* = 0.010, May *P* = 0.037, July *P* = 0.037), with these differences appearing at one site only. The relative infrequency, low magnitude, and inconsistent direction of these Exclosure treatment differences suggest random plot-to-plot variation, not a systematic artifact of cage structure. Thus, I deemed that there was no significant cage artifact over the course of the experiment. I combined half-cage and open control treatments as general controls for forthcoming analyses of density and cover to double replication, thus adding statistical power.

Post-treatment Vegetation Response

A separate model was fit for each dependent variable, including total density and summed percent cover, as well as for functional subgroups of density and cover totals: shrubs and herbs. Herbs were further divided into three dichotomous paired groups: annual/perennial, native/non-native, and N-fixing/non-N-fixing.

$$Y = Exc * Veg * Burn * Date * Site(Burn) + random\Big(Plot\big(Block(Site)\big)\Big) \text{ Eqn. 3}$$

The random factor Plot(Block(Site)) was demonstrated as significant for most functional groups by likelihood ratio test (LRT) comparison to the fixed-factor model. The effect of herbivore treatment on each group at each date was determined by *a priori* planned contrasts of estimated marginal means, with no p-penalization procedure (Day and Quinn 1989). Estimates of the impact of vegetation type were also estimated from marginal means within the same models. To estimate the impact of burning, I used a model with a random block instead of fixed Site(Burn):

$$Y = Exc * Veg * Burn * Date + random(Block) + random(Plot(Block)) \text{ Eqn. 4}$$

All density and cover values given are estimated marginal means based on linear mixed models for each plant functional group, averaged across Site(Burn). In contrast to the simple arithmetic means plotted on Figures 5-7, these model mean estimates give the isolated effect of a given tested factor, controlling for variation from other variables (Martinez and Bartholomew 2017).

RESULTS

In general, excluding mammalian herbivores significantly increased seedling density and cover throughout the 2015 growing season, but the magnitude and seasonality of these effects differed by plant functional group, vegetation and burn. I will examine the results by first analyzing the effect of fire in the absence of herbivory (i.e. comparing caged plots between burn treatments). I will then analyze the effect of herbivory in each vegetation and burn condition: (1)

mature chaparral, (2) burned chaparral, (3) mature bare zone, and (4) burned bare zone. Finally, I examine the results holistically through the lens of the Fire x Herbivore interactions. All density and cover values are reported as estimated marginal means of treatment groups, based on linear mixed models (**Table 5**, **Table 6** and **Table 7**) for each plant functional group, averaged across vegetation type, burn and site(burn).

Burned vs. Non-burned Sites

Comparisons of herbivore-excluded plots between burned and non-burned areas provide a test of the effect of burning on seedling density and cover, in the absence of herbivory ("caged") (**Figure 5**, **Figure 6**, **Figure 7** dashed line only). Here I assume that non-burned sites are representative of the pre-burn condition of burned sites. Burned sites were substantially higher in total seedling density and cover than non-burned sites.

Chaparral

In mature chaparral, exclosure plots were relatively bare at all points (<15.0 seedlings/m^2 and <2.9% cover) (**Figure 5a,g**), while burn effect increased the seedling understory significantly ($P < 0.001$), as high as 153.1 seedlings/m^2 and 161.3% cover in March (**Figure 5d,j**). Burned areas had higher densities of caged herbs than non-burned areas in March and May ($P < 0.05$), and higher herb cover in all months ($P < 0.01$) (**Figure 5b,h** vs. **e,k**). In March, the burn effect increased herb density ($P < 0.05$) and cover ($P < 0.001$) for all functional groups (**Figure 6a-l**). For perennial, native, and N-fixing herbs, burn effects increased canopy cover all the way through May ($P < 0.001$) and July ($P < 0.01$). A few herb species were responsible for these increases, most of them N-fixers: *Trifolium hirtum* (invasive annual), *Acmispon glaber* and *Lupinus bicolor* (native perennials), and several other *Acmispon* species (native annuals). For native non-N-fixers, the annual *Emmenanthe penduliflora* was high in density and cover all season and the perennial *Solanum umbelliferum* was low in density but high in cover. Density and cover of caged shrubs were higher in burned sites at every time point (**Figure 5c,i** vs. **f,l**, $P < 0.001$), with most of this increase accounted for by *Adenostoma fasciculatum*, whose seedlings covered around 20% of the canopy for the whole 2015 season. Seedlings of the shrub *Ceanothus cuneatus* covered 5% of plots during the same period.

Bare Zone

In the bare zone, the burn effect also increased density and cover, but this effect varied considerably throughout the season. In March, burned bare zone total density was 565.4 compared to 240.6 seedlings/m^2 in the non-burned and cover 161.3 compared to 57.3% (**Figure 5m,s** vs. **p,v**, $P < 0.001$). However, there was no significant effect of burn on caged bare zone density or cover by May and July, except for a very small increase in July cover from 2.0 to 10.5% ($P = 0.035$). Burned areas had higher density and cover of herbs in March only ($P < 0.001$, **Figure 5n,t** vs. **q,w**). Burned areas developed higher (compared to non-burned areas) density and cover of all herb functional groups except for N-fixers, with the most dramatic differences in three groups. Caged annual, non-native, non-N-fixers were most dramatically higher in density and cover at burned sites (**Figure 7a,d,f,g,j,l** vs. **m,p,r,s,v,x**). In March, burn effect increased the density of these groups from 173.9-188.5 to 474.2-498.0 seedlings/m^2 and cover from 38.4-52.1% and 105.5-132.2% ($P < 0.001$). The vast majority of this increase was represented by the non-native *Avena* grass species, followed by *Centaurea melitensis* and *Lysimachia arvensis*. Burned bare zone was higher in native density in March (39.8 vs. 10.1

seedlings/m^2, $P = 0.002$, **Figure 7c** vs. **o**), mainly from annual *Acmispon* species and the perennials *Dichelostemma capitatum*, *Eschscholzia californica* (non-N-fixers) and *Lupinus bicolor*. Burned native cover was higher throughout the season (March 13.3 vs. 6.1%, July 7.1 vs. 0.1%, $P < 0.05$, **Figure 7i** vs. **u**). Burned bare zone perennials were significantly but only slightly higher in density and cover in March only ($P < 0.01$, **Figure 7h** vs. **t**). The native perennials comprising this cover were mainly *Acmispon glaber*, *Eschscholzia californica, Galium andrewsii*, *Lomatium dasycarpum*, *Lupinus bicolor*, and *Solanum umbelliferum*. The common native geophyte *Chlorogalum pomeridianum* was actually lower in burned than non-burned areas.

The burn effect did not change bare zone shrub densities or cover, except for a slight increase from 1.0 to 6.6% in March only ($P = 0.033$, **Figure 5u** vs. **x**), comprised mainly from *Adenostoma fasciculatum*. Actually, in June 2014 seedling densities of *A. fasciculatum* and *Artemisia californica* were quite high in the burned bare zone, each at over 30 seedlings/m^2. By March and May of 2015, *A. californica* seedlings almost disappeared from the burned bare zone, but were present at high densities at non-burned sites. *A. fasciculatum* seedlings at burned sites decreased to non-burned levels throughout 2015.

Burning generally increased the density and cover or herbs in the bare zone and chaparral in the absence of herbivores. Shrub seedling densities were higher in the chaparral understory after burning, but not in the bare zone. Burning in chaparral resulted in increases in a wide variety of seedling functional groups, while increases in the bare zone mainly resulted from non-native, non-N-fixing, annual herbs.

Herbivore Impacts

Mature Chaparral

The mature chaparral understory was nearly bare in control plots, even throughout the rainy growing season (density ≤ 0.1 seedlings/m^2; cover < 1% in March/May/July). In exclosures, seedling density increased significantly to 11.2 and 15.0 seedling/m^2 in March and May, respectively (**Figure 5a**), while cover increased only modestly to 2.9 and 2.1% (**Figure 5g**). Increases in seedling density and cover in exclosures were comprised almost exclusively of herbaceous species (**Figure 5b,h**). Although shrub seedling increases were not significant (**Figure 5c,i**), it is notable the seedlings of the fire-germinated species *A. fasciculatum* did emerge when herbivores were excluded and persisted through July. The effect of herbivory was diffuse across herb functional groups (**Figure 6a**-l). The densities of annuals, non-natives, and non-N-fixers were most impacted by exclosures, with significant increases in May only to 7.2-12.2 seedling/m^2. These key species in this group were *Avena spp.*, *Bromus diandrus*, and *Centaurea melitensis*. Of these three groups, only the cover of non-N-fixers was significantly increased by exclosures in March and May, although annuals and non-natives increased marginally in cover in May. Of all the species in the chaparral understory, only *Marah fabacea* increased appreciably in cover to over 5% when herbivores were excluded. Density of perennials slightly but significantly increased in exclosures to 2.2 seedling/m^2 in May, with no significant increase in cover. N-fixing species were unaffected by herbivore exclosures. In all functional groups, the exclosure effect disappeared by the onset of summer drought in July, with density and cover returning to nearly zero.

Burned Chaparral

Exclosure effects persisted in burned chaparral plots, although with altered seasonal patterns and functional group responses from mature stands. Again, there was no exclosure effect on shrub seedling density or cover at any time point (**Figure 5f,l**). Unlike in mature chaparral, total seedling and herb densities were unaffected by exclosures in March, at the peak of the growing season. By May, an exclosure effect on herbaceous and total seedling density appeared, increasing total seedlings by 76% over controls from 54.3 to 95.3 seedlings/m^2 and total herbs by 122% from 60.0 to 123.4 seedlings/m^2. Total percent cover increased in March from 92.4% in controls to 125% exclosures and in May from 42.0 to 79.0%. Herbaceous cover increased from 69.1 to 91.4% in March and 19.0 to 42.4% in May.

Relatively few herb functional groups were significantly impacted in density by exclosures, even though all groups were present at relatively high densities throughout the growing season (**Figure 6m-r**). The only functional groups that increased in density in May were annual (marginal increase), non-native, N-fixers, almost exclusively because of the growth of *Trifolium hirtum*. In contrast, herbivore exclosures increased the total cover of most herb groups at some point during the growing season (**Figure 6s-x**), with contributions from several different species. In March, exclosures increased cover of annuals, non-natives, and N-fixers (marginally), with the biggest contributor again being *Trifolium hirtum*. The May cover of annual, perennial (marginal), natives, and N-fixers, with the largest contributors being *Acmispon glaber* (perennial native N-fixer) and *Emmenanthe penduliflora* (annual native non-N-fixer). Overall, exclosures in burned chaparral increased herbaceous cover more than density, primarily in May as overall living plant abundance decreased.

Mature (Non-burned) Bare zone

The mature bare zone was denser in vegetation than the adjacent grassland (Hendricks-Franco observation) but more vegetated than the chaparral understory. Control total density and cover peaked in March at 98.6 seedlings/m^2 and 23.8% cover. The exclosure effect was significant and substantial for total density and cover. In March, herbivore exclosure increased seedling density from 98.6 to 258.9 seedlings/m^2 (163% increase) and cover from 23.8 to 63.0% (165% increase). Significant exclosure effect persisted in May, albeit at a lower magnitude, and disappeared by July when total seedling density and cover return nearly to zero (**Figure 5m,s**). The effect was almost totally accounted for by herbs (**Figure 5n,t**), except for slight exclosure effect on shrub densities in May only (**Figure 5o,u**), when exclosures increased shrub densities from 2.3 to 13.8 seedlings/m^2, mainly from *Artemisia californica*, but also including seedlings of the fire-stimulated *Adenostoma fasciculatum*. This was the only date and vegetation/burn condition at which shrubs were affected by herbivores.

The mature bare zones showed a clear pattern of functional group dominance by annual, non-native, and non-N-fixing herbs (**Figure 7a,d,f,g,j,l**), such as *Centaurea melitensis*, *Logfia gallica*, *Brassica nigra*, and *Bromus madritensis* ssp. *rubens*, and *Avena spp.* These three groups were dominant in control plots where herbivores were allowed, peaking in March densities between 67.7 and 77.6 seedlings/m^2. Exclosure effects on densities of these groups were dramatic, with increases of 176-198% to 201.8-214.4 seedlings/m^2 in March, mainly from contributions by *L. gallica*, *B. madritensis* ssp. *rubens*, and *Avena spp*. Herbivore exclosure effects decreased but remained significant on these group densities in May and disappeared by July. In May, *L. gallica* densities remained elevated in exclosure plots, while *B. nigra* was actually less dense when herbivores were excluded. Cover followed a similar pattern; March control cover ranged 16.6-21.4% for these dominant groups and significantly increased in exclosures to 46.6-53.3% The main contributors were *B. madritensis* ssp. *rubens*, and *Avena spp*., with smaller contributions by *L. gallica* and *Carduus pycnocephalus*. May exclosure effects were also significant for annuals, non-natives, and non-N-fixers, although less substantial. *Chlorogalum pomeridianum* (native, perennial, non-N-fixer) increased substantially in cover in exclosures, even though its densities were unaffected. Grouped perennial, native, and N-fixing herbs never reached densities of over 7.6 seedlings/m^2. Herbivore exclosure resulted in a small, but significant increase in March densities of N-fixers, almost exclusively from *Acmispon glaber*. Cover of perennials, natives, and N-fixers remained low, never exceeding 4.6%, and were not affected by herbivore exclosure.

In summary, the bare zone immediately adjacent to non-burned, mature chaparral was generally maintained at low densities and cover of herbs by herbivores. Those herbs that did live in the bare zone were principally non-native, non-N-fixing annuals, usually Eurasian invaders.

Burned Bare Zone

After burning, the bare zone was generally much higher in seedling density and cover than the mature non-burned areas. Control total density and cover peaked in March at 391.8 seedlings/m^2 and 100.7% total cover. Herbivore exclosure significantly increased total seedling density in March only from 391.8 to 565.4 seedlings/m^2 (44% increase). Total cover followed the same pattern, increasing significantly in exclosures in March only from 100.7 to 161.3% (**Figure 5p,v**) and marginally in May and July. Patterns in total density and cover are accounted for by herbaceous species (**Figure 5q,w**). Exclosure substantially increased the cover of herbs in March (91.9 to 147.8%) and slightly in May (22.4 to 33.6%) and July (4.4 to 10.5%). There was no exclosure effect on shrubs, which remained low throughout the entire growing season (maximum of 10.3 seedlings/m^2 and 6.6% cover, **Figure 5r,x**).

Patterns in herb functional-group dominance at the burned bare zone closely mirrored those in the mature stands (**Figure 7m-x**). The densities of annual, non-native, and non-N-fixing herbs, mainly grasses, were far higher than the other groups. In March, control densities of these three groups ranged from 336.0-360.8 seedlings/m^2, increasing significantly to 474.2-498.0 seedlings/m^2 when herbivores were excluded. Three species contributed the majority of the density increase in exclosures: *Centaurea melitensis* (which was not affected by exclosures in non-burned bare zone), *Avena spp.,* and *Lysimachia arvensis*. Densities of perennials, natives, and N-fixers were comparatively much lower, never exceeding 39.8 seedlings/m^2. Densities of perennials and natives were very slightly increased by herbivore exclosure at different time points: perennials significantly in March and marginally in May, and natives significantly in May. Cover mirrored density measurements in annual, non-native, non-N-fixers and the aforementioned species, peaking in March and showing a significant exclosure effect of herbivores only at that time point. The cover of perennial, native, non-N-fixing herbs was significantly increased by exclosure in March and throughout the later growing season, mainly because of increases in *Eschscholzia californica* and *Galium andrewsii*. There was no effect of herbivore manipulation on N-fixer density or cover.

Similar to mature non-burned areas, the zone immediately outside of burned chaparral was dominated by non-native, annual, and non-N-fixing herb species. However, after burning this zone was no longer “bare”. Herbivore exclosures generally increased density and cover of these species at the peak of the growing season (March), but exposure to herbivores in open controls did not drive herb densities to low levels.

Fire and Herbivore Interactions

The goal of this study was to investigate how plant-herbivore interactions are modified by fire disturbance in chaparral, and how these changes affect vegetation patterns across a landscape. A fundamental question was whether herbivore maintenance of a bare chaparral understory and grassland border (bare zone) remains strong during post-fire succession.

At non-burned sites, control herb density and cover were higher in the bare zone than the chaparral throughout the whole growing season (density: March $P < 0.001$, May $P < 0.001$, July $P = 0.048$; cover: March $P < 0.001$, May $P < 0.001$, July $P = 0.071$). When herbivores were excluded, differences were more extreme, with bare zone gaining much more seedling density and cover inside of exclosures than the adjacent chaparral.

After disturbance by fire, the bare zone was still higher in seedling density than chaparral during the rainy portion of the growing season (March, May $P < 0.001$), for both open and exclosure plots. Cover showed a different pattern: there was no difference in total canopy cover between bare zone and chaparral in March and in May and July chaparral was actually higher in cover (May $P < 0.001$, July $P = 0.001$). This reflects the functional group composition of post-fire chaparral. The post-fire bare zone remained dominated by non-native annuals, mainly Eurasian grasses, which almost totally die back by May. On the other hand, native perennials, such as *Acmispon glaber* and *Solanum umbelliferum*, had high cover in chaparral that persisted into May and June, after the onset of seasonal drying, which accounts for the higher cover in the chaparral than bare zone at these time points.

When herbivores were excluded, a similar pattern emerged between chaparral and bare zone, but differences were more exaggerated. In March, herbivore exclusion increased total density in the bare zone but not in chaparral (**Figure 5**). Thus, densities were much higher in the bare zone than chaparral in March ($P < 0.001$). Interestingly, the functional groups that dominated the bare zone (annual, non-native non-N-fixers) were affected differently by herbivores in the chaparral and bare zone. They were significantly reduced by herbivores in March in the bare zone (**Figure 7**c), but not in the chaparral (**Figure 6m,p,r,s,v,x**), despite their direct proximity. By May, herbivore exclusion increased total densities in the chaparral but not in the bare zone, and there was no difference in total density between the adjacent vegetation types in May and June when herbivores were excluded.

DISCUSSION

The goal of this study was to determine the role of small mammalian herbivores in limiting seedling density and cover in chaparral vegetation and the adjacent bare zone, as well as how this effect is mediated by wildfire disturbance. I predicted that herbivores would limit the chaparral understory in mature stands, but not in post-fire chaparral, due to the loss of protective shrub cover. I also predicted that the effect of herbivores at the bare zone would diminish after fire, due to the displacement of herbivores out of the shrublands.

Burned vs. Non-burned Sites

Comparison of mature and post-fire chaparral exclosure plots revealed drastic increases in seedling density and cover as a result of burning. The mature chaparral understory was essentially bare throughout the entire spring growing season. After fire, however, chaparral plots hosted extremely high density and cover, particularly in March, for all herb functional groups. Cover and densities in burned sites remained higher in burn plots into even the dry season (July).

This result is consistent with many other investigations demonstrating an extremely limited chaparral understory (Sampson 1944, Went et al. 1952, Horton and Kraebel 1955, Hellmers et al. 1955, Muller et al. 1968, Christensen and Muller 1975b, Keeley et al. 1981, Shmida and Whittaker 1981, Swank and Oechel 1991, Tyler 1995, 1996) and flushes of seedlings following fire, coming from long-dormant soil seedbanks collected after the previous fire (Cooper 1922, Sampson 1944, Horton and Kraebel 1955, Sweeney 1956, Hanes 1971, Keeley et al. 1981, Keeley and Keeley 1988, Potts and Stephens 2009). A soil seed bank is an important factor in determining vegetation successional dynamics and floristic composition after disturbance (Pakeman and Small 2005). Burning increased shrub seedling density and cover at all time points, which is unsurprising. Seeding density was principally comprised on *Adenostoma fasciculatum*, the facultative seeding shrub that dominate the chaparral canopy. The seeds of *A. fasciculatum* are abundant in the chaparral seedbank and germinate readily by fire or post-fire conditions (Stone and Juhren 1953, Keeley 1987). They recruit mainly in the first year after fire, and many persist at least into the second year (Keeley et al. 2006). Densities of *A. fasciculatum* seedlings have been found to tightly correlate with pre-fire densities of adults (Keeley et al. 2006). *Acmispon* spp. and *Emmenanthe penduliflora* are typical fire-followers (Keeley et al. 1981), with *Acmispon* being particularly common in the second year post-fire (Rundel and Parsons 1984).

The dominant plant species in the bare zone were similar in non-burned sites: invasive non-N-fixing annuals such as *Avena* spp. and *Centaurea melitensis*, but their density and cover are much increased after a fire. These species are typical of the California grassland (Bartolome 1987) and demonstrate the advancement of the grassland into the chaparral-grassland border. The majority of the native perennials that increase after fire are representative grassland species (Harrison 1999). Seedlings of the shrubs *A. fasciculatum* and *A. californica* were initially high in post-fire bare zone density and cover, but decreased quickly, much more so than in the adjacent chaparral. This could be due to several factors, including competition with grasses and higher temperatures. Davis and Mooney (1985) demonstrated that at non-burned chaparral ecotones, the grassland and bare zone experience seasonal soil drying before the chaparral. These results suggest that chaparral shrubs do initially recruit outside of existing shrubland boundaries, but experience high seedling mortality due to conditions other than herbivory.

Herbivore Impacts

Mature Chaparral

Exclosures in mature chaparral led to small but significant increases in herb density and cover at the peak of the growing season, with contributions across most herb functional groups. This finding is in line with the work of several other investigations that find small mammal herbivory to be an important limiting factor in the chaparral understory; in fact, in other studies, herbivory has been found to over-ride such factors as soil moisture or light availability (Swank and Oechel 1991, Tyler 1995, 1996). It is noteworthy that the species most limited in density by herbivores were invasive, non-native, annuals such as *Avena spp.*, *Bromus diandrus*, and *Centaurea melitensis*, the same species that dominate the bare zone when herbivore are excluded. This finding suggests that small mammalian herbivores play a role in preventing the non-native grassland invasion of mature chaparral. The fact that N-fixers were not affected was surprising. In nitrogen-limited environments, such as mature chaparral (Hellmers et al. 1955), N-fixers are often disproportionately limited by herbivores compared to non-N-fixers, due to large differences in their tissue quality (Ritchie et al. 1998). By the end of the season, all herbivore effects had disappeared, consistent with the findings of other investigators (McPherson and Muller 1969, Christensen and Muller 1975a); thus, it is unclear whether these effects would magnify over the following years as seeds produced during the growing season accumulated in the soil seedbank. Seed predation can be an important factor limiting seedbank density and emergence (Mayor et al. 2003). Specifically, rodents are known to be voracious seed predators in California grasslands, consuming 37-75% of available seeds (Borchert and Jain 1978).

Burned Chaparral

In post-fire chaparral, the seasonality and functional group effects of herbivory changed considerably. As previously mentioned, all functional groups were higher in density and cover in the burned than non-burned chaparral at the peak of the growing season (March). However, there was no effect of herbivores on the density of any functional group in March. Multiple explanations could account for this discrepancy between burned and non-burned stands. It is possible that, as I predicted, herbivores were simply displaced from the chaparral after burning, leading to a reduced effect of herbivory. Additionally, the plants dominating this post-fire landscape may be less palatable. By May, herbs in the annual, non-native, N-fixer category had increased in density in exclosures, mainly due to increases in the clover *Trifolium hirtum*. Notably, the common grassland invaders in the mature chaparral, *Avena spp.*, *Bromus diandrus*, and *Centaurea melitensis*, were not reduced in density by herbivores, and they were generally low in abundance in post-fire chaparral. Grass seeds, often shallowly buried in shrublands, are vulnerable to rodent herbivory (Borchert and Jain 1978) and the high heat (Ditomaso et al. 2006) of summer shrub fire, minimizing their presence in the chaparral seedbank when both controlling factors are present. Brush rabbits (*Sylvilagus bachmani*) are important herbivores in the chaparral understory (Connell 1954), are known to feed heavily and preferentially on a green clover when it is present, although they usually rely on edible grasses, including *Avena* and *Bromus spp* (Chapman 1974). Thus, the pattern of reduction in a clover species and grasses is consistent with rabbit feeding.

It is also possible that all plants became more tolerant of defoliation, perhaps due to the high available nitrogen to support compensatory growth. This idea is supported by the fact that herbivory reduced cover slightly across most functional groups while densities mostly remained constant. Very few plants died as a result of post-fire herbivory, tolerating some consumption, but their growth may have been limited.

Mature (Non-burned) Bare zone

Herbivore exclosures in the mature bare zone led to substantial increases in species typical of the adjacent grassland, consistent with the findings of others (Bartholomew 1970, Halligan 1974). It is noteworthy that the bare zone was not always completely bare, reaching total cover of 23% at the peak of the growing season. However, this was still much lower than the adjacent grassland and half of total cover as when herbivores were excluded, implying a strong effect on chaparral-dwelling mammals. A few important native herbs did respond to herbivore exclosure. Individuals of the common geophyte *Chlorogalum pomeridianum* dramatically increased their leafy cover when released from herbivores. Overall, these results support the idea that mammalian herbivores prevent the advance of non-natives into the chaparral understory.

The emergence of *Adenostoma fasciculatum* shrub seedlings in the bare zone was a curious result, as these seeds typically only germinate after fire. However, others have noted that the seedbank of *A. fasciculatum* is polymorphic and can germinate at low rates without post-fire conditions. The emergence of these seedlings in exclosures could suggest a role for herbivores in limiting the spread of chaparral shrubs into grasslands in non-fire years. *A. fasciculatum* seedlings remained present at low levels in July in the exclosures, while they were completely absent from exposed controls. More years of data collection would be necessary to observe whether shrubs persist in the bare zone through the summer dry season.

One species actually decreased in the mature bare zone exclosures: *Brassica nigra*. This species is from a family known to resist seed and leaf consumption by herbivores (Feeny 1977) more so than co-occurring grass species. It is possible that when more palatable competitors were allowed to grow in the absence of herbivores, *B. nigra*'s cover and density were decreased by competition with these grasses.

Burned Bare Zone

Similar to mature non-burned areas, the zone immediately outside of chaparral was dominated by non-native, annual, and non-N-fixing herb species. However, two years after burning, this zone was no longer "bare". Herbivore exclosures generally increased density and cover of this species at the peak of the growing season (March), but exposure to herbivores in open controls did not drive herb densities to low levels. A curious result was that the density of *Centaurea melitensis* increased dramatically in exclosures compared to controls in the burned bare zone, which it did not in the non-burned areas.

Fire and Herbivore Interactions

The goal of this study was to investigate how plant-herbivore interactions are modified by fire disturbance in chaparral, and how these changes affect vegetation patterns across a landscape. A fundamental question was whether herbivore maintenance of the chaparral understory and grassland border (bare zone) remain strong during post-fire succession. With the typically high cover of herbs and removal of protective shrub cover in post-fire chaparral, I hypothesized that herbivory pressure would be diluted as they dispersed to other parts of the landscape, reducing pressure on the chaparral-grassland border.

In non-burned conditions, these results demonstrate a concentration of feeding immediately outside the chaparral with a higher abundance of food resources in the bare zone than chaparral understory. In control plots, the bare zone had higher densities of herbs than the chaparral and recovered higher density cover when herbivores were excluded. After fire, there is not a clear difference in the general abundance of herbaceous and shrub seedling food resources between chaparral and bare zone. Total seedling canopy cover was the same throughout most of the 2015 growing season. However, the impact of herbivores was still concentrated in the bare zone, principally consuming non-natives. Herbivore effect was strongest in the bare zone in March, when non-native grasses would have been at peak biomass there. Later in May and July, the impact of herbivory was more significant in the post-fire chaparral than in the adjacent bare zone. It is possible that herbivores concentrated their feeding in the chaparral after bare zone resources were less abundant.

Southern California chaparral is increasingly falling victim to grassland and herbaceous invasion, with one estimate finding that 34% of historical chaparral vegetation is now covered with herbs (Park et al. 2018); a reduction in rodent grazing may be to contributing to this phenomenon, along with increased fire frequency (Park and Jenerette 2019). This landscape-scale change underscores the importance of the question posed above. Overall, these findings demonstrate that herbivores at non-burned chaparral stands play an important role in limiting the densities and cover of non-native herbs, especially in the bare zone. Eurasian grasses were not a substantial component of the post-fire chaparral environment, with or without herbivores. However, herbivores did limit the spread of a non-native annual N-fixer in the chaparral understory.

Conclusion

Small mammalian herbivores influenced herbaceous density, cover, and community composition in the chaparral and bare zone, in burned and non-burned areas. Herbivores maintained a nearly bare chaparral understory in mature stands and reduced cover of invasive grasses in the bare zone. Burning led to higher herb cover in both vegetation types, with or without herbivores present. The post-fire bare zone remained a site of intense herbivory at the peak of the growing season, particularly on non-native grassland species in the bare zone. However, the bare zone was no longer bare; despite some limitation by herbivores, herb cover was high in the post-fire chaparral-grassland ecotone, which could suggest an advancing front of grassland invasion into chaparral in subsequent years. In burned chaparral, there was a small reduction in the high herb cover and density due to herbivores but only concentrated on a few species. Eurasian grasses were not a substantial component of the post-fire chaparral understory, with or without exclosures. Although herbivory was not the primary factor limiting grass invasion in burned chaparral at this early post-fire timepoint, there was evidence the herbivores were still present in post-fire chaparral. The relative impact of mammalian herbivory was reduced, but not removed, after chaparral fire, and was still concentrated more in the bare zone than the chaparral understory.

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TABLES

Table 1. Characteristics of chaparral-grassland ecotone at each selected site at Mt. Diablo.

Site	Burn	Length (m)	Elevation (m)	Longitude	Latitude
1	Y	216	495-562	37°51'57.27"N	121°54'09.80"W
2	Y	294	605-771	37°52'00.66"N	121°54'42.40"W
3	N	315	621-710	37°51'40.94"N	121°55'38.67"W
4	N	486	765-823	37°52'26.40"N	121°55'59.96"W

Table 2. Factors and levels/replicates used in all statistical models.

Crossed Fixed Factors	**Levels**			
Exclosure (Exc)	Open Control	Half-cage Control	Exclosure	
Vegetation (Veg)	Bare zone	Chaparral		
Date	June 2014	March 2015	May 2015	July 2015
Nested Fixed Factors				
Burn	Yes		No	
Site(Burn)	Site 1	Site 2	Site 3	Site 4
Nested Random Factors	**Replicates**			
Block(Site)	6	6	6	3
Plot(Block(Site))	3	3	3	3

Table 3. Effects of fixed factors on seedling density before the introduction of exclosure treatments. ANOVA results of pre-treatment (June 2014) density sampling. Bold indicates a significant effect. Significance levels: ≤0.10., ≤0.05*, ≤0.01**, ≤0.001***.

Factor	**Total Seedlings**	**Herbs**	**Shrubs**
		P(F)	
Exc	0.13 (0.875)	0.59 (0.556)	0.21 (0.813)
Veg	4.89 (0.033*)	18.24 (<0.001***)	0.57 (0.457)
Burn	34.32 (<0.001***)	17.47 (<0.001***)	13.59 (<0.001***)
Exc x Veg	0.45 (0.640)	0.01 (0.992)	0.48 (0.624)
Exc x Burn	0.58 (0.564)	0.94 (0.395)	0.66 (0.518)
Veg x Burn	0.55 (0.462)	2.42 (0.128)	0.29 (0.593)
Site(Burn)	13.27 (<0.001***)	5.72 (0.007**)	15.60 (<0.001***)
Exc x Veg x Burn	0.93 (0.398)	1.14 (0.326)	0.39 (0.678)
Exc x Site(Burn)	1.61 (0.181	0.31 (0.871)	3.07 (0.021*)
Veg x Site(Burn)	2.50 (0.096.)	3.49 (0.041*)	0.12 (0.887)
Exc x Veg x Site(Burn)	0.35 (0.845)	0.98 (0.424)	0.05 (0.995)
Random Factor		LRT (P_{ChiSq})	
Block(Site)	0.85 (0.356)	9.32 (0.002**)	2.60 (0.107)

Table 4. Test of half-cage effect on seedling density and canopy cover during the 2015 growing season (March, May, July 2015). ANOVA results only include controls and half-cage control treatments. Significance levels: *P* ≤0.10., ≤0.05*, ≤0.01**, ≤0.001***.

	F(p)					
	Density			**Cover**		
Factor	Total	Herb	Shrub	Total	Herb	Shrub
Burn	121.61 (<0.001***)	134.04 (<0.001***)	4.046 (0.048*)	166.61 (<0.001***)	148.97 (<0.001***)	18.99 (<0.001***)
Exc	1.71 (0.196)	0.92 (0.342)	0.33 (0.568)	1.82 (0.182)	1.38 (0.245)	0.3 (0.588)
Date	214.61 (<0.001***)	258.25 (<0.001***)	1.047 (0.354)	315.33 (<0.001***)	335.33 (<0.001***)	1.99 (0.14)
Veg	109.74 (<0.001***)	149.62 (<0.001***)	2.8 (0.098.)	9.42 (0.003**)	22.86 (<0.001***)	12.78 (0.001***)
Burn(Site)	9.69 (<0.001***)	17.45 (<0.001***)	10.529 (<0.001***)	8.16 (0.001***)	15.09 (<0.001***)	9.12 (<0.001***)
Burn x Exc	0.05 (0.823)	0.68 (0.411)	0.08 (0.778)	0.03 (0.866)	0.00 (0.953)	0.53 (0.467)
Burn x Date	40.51 (<0.001***)	60.00 (<0.001***)	6.467 (0.002**)	85.33 (<0.001***)	89.93 (<0.001***)	0.07 (0.929)
Exc x Date	0.46 (0.632)	0.48 (0.618)	0.095 (0.909)	0.93 (0.397)	1.3 (0.275)	0.84 (0.433)
Burn x Veg	6.76 (0.011*)	27.43 (<0.001***)	16.522 (<0.001***)	5.74 (0.019*)	0.8 (0.375)	15.24 (<0.001***)
Exc x Veg	0.54 (0.466)	0.42 (0.519)	0.246 (0.622)	0.1 (0.751)	1.03 (0.314)	3.25 (0.076.)
Date x Veg	82.99 (<0.001***)	68.01 (<0.001***)	1.511 (0.224)	48.89 (<0.001***)	35.04 (<0.001***)	0.44 (0.646)
Burn(Site) x Exc	1.43 (0.245)	0.92 (0.402)	2.993 (0.056.)	0.2 (0.819)	0.56 (0.574)	1.93 (0.152)
Burn(Site) x Date	5.59 (<0.001***)	7.58 (<0.001***)	1.478 (0.212)	9.32 (<0.001***)	9.85 (<0.001***)	0.82 (0.513)
Burn x Exc x Date	0.99 (0.375)	0.90 (0.407)	0.035 (0.966)	0.41 (0.666)	0.02 (0.984)	1.63 (0.199)
Burn(Site) x Veg	25.48 (<0.001***)	32.03 (<0.001***)	2.297 (0.108)	8.4 (0.001**)	10.61 (<0.001***)	0.46 (0.634)
Burn x Exc x Veg	3.04 (0.085.)	0.020 (0.888)	8.944 (0.004**)	1.67 (0.2)	0 (0.988)	5.94 (0.017*)
Burn x Date x Veg	18.94 (<0.001***)	24.48 (<0.001***)	4.777 (0.010**)	15.49 (<0.001***)	12.22 (<0.001***)	1.58 (0.209)
Exc x Date x Veg	1.15 (0.319)	0.43 (0.651)	0.853 (0.428)	1.7 (0.186)	0.88 (0.417)	2.18 (0.117)
Burn(Site) x Exc x Date	1.65 (0.165)	1.07 (0.376)	1.353 (0.253)	1.86 (0.12)	1.1 (0.359)	1.33 (0.263)
Burn(Site) x Exc x Veg	1.38 (0.257)	0.84 (0.438)	1.889 (0.158)	0.6 (0.552)	0.32 (0.728)	0.47 (0.629)
Burn(Site) x Date x Veg	13.02 (<0.001***)	17.76 (<0.001***)	2.104 (0.083.)	18.42 (<0.001***)	19.5 (<0.001***)	1 (0.409)
Burn x Exc x Date x Veg	0.72 (0.491)	0.87 (0.422)	0.278 (0.758)	0.75 (0.475)	0.25 (0.782)	1.33 (0.268)
Burn(Site) x Exc x Date x Veg	0.74 (0.569)	1.07 (0.376)	0.276 (0.893)	1.33 (0.26)	1.17 (0.326)	0.25 (0.909)

Table 5. Full-effects models for density and cover of total, herb, and shrub seedlings during the 2015 growing season (March, May, July 2015). The reported values are from a linear mixed model with a random plot and a square-root transformed response variable.

	F(p)					
	Density			**Cover**		
Factor	Total	Herb	Shrub	Total	Herb	Shrub
Exc	26.30 (<0.001)	24.22 (<0.001)	5.01 (0.027)	32.43 (<0.001)	31.13 (<0.001)	2.02 (0.158)
Veg	163.07 (<0.001)	209.83 (<0.001)	0.94 (0.334)	17.96 (<0.001)	43.49 (<0.001)	11.17 (0.001)
Date	351.32 (<0.001)	407.95 (<0.001)	5.06 (0.007)	460.69 (<0.001)	504.98 (<0.001)	7.14 (0.001)
Burn	110.86 (<0.001)	110.05 (<0.001)	6.37 (0.013)	224.52 (<0.001)	175.26 (<0.001)	26.54 (<0.001)
Exc x Veg	0.91 (0.342)	1.23 (0.269)	0.39 (0.532)	0.35 (0.553)	1.18 (0.279)	0.02 (0.885)
Exc x Date	9.04 (<0.001)	9.46 (<0.001)	1.71 (0.184)	10.99 (<0.001)	10.26 (<0.001)	1.00 (0.369)
Veg x Date	135.64 (<0.001)	118.46 (<0.001)	2.20 (0.113)	71.75 (<0.001)	56.72 (<0.001)	0.33 (0.722)
Burn(Site)	7.81 (0.001)	11.20 (<0.001)	5.74 (0.004)	7.91 (0.001)	11.64 (<0.001)	5.19 (0.007)
Exc x Burn	2.11 (0.149)	3.25 (0.074)	0.36 (0.547)	0.12 (0.735)	0.68 (0.412)	0.81 (0.369)
Veg x Burn	5.83 (0.017)	17.37 (<0.001)	6.50 (0.012)	21.05 (<0.001)	12.31 (0.001)	6.28 (0.014)
Date x Burn	41.40 (<0.001)	61.50 (<0.001)	5.77 (0.004)	84.73 (<0.001)	92.06 (<0.001)	2.11 (0.123)
Exc x Veg x Date	5.07 (0.007)	5.26 (0.006)	0.01 (0.986)	3.64 (0.028)	2.95 (0.054)	1.21 (0.299)
Exc x Burn(Site)	0.18 (0.833)	0.73 (0.485)	0.99 (0.373)	0.48 (0.618)	1.14 (0.324)	0.62 (0.540)
Veg x Burn(Site)	25.30 (<0.001)	17.68 (<0.001)	9.72 (<0.001)	4.55 (0.012)	3.74 (0.026)	5.86 (0.004)
Exc x Veg x Burn	1.30 (0.257)	3.81 (0.053)	1.77 (0.186)	3.04 (0.084)	6.15 (0.015)	1.70 (0.195)
Date x Burn(Site)	5.66 (<0.001)	6.00 (<0.001)	1.22 (0.303)	13.09 (<0.001)	12.79 (<0.001)	0.50 (0.733)
Exc x Date x Burn	2.68 (0.071)	2.45 (0.088)	0.23 (0.794)	0.09 (0.917)	0.24 (0.789)	2.46 (0.088)
Veg x Date x Burn	13.39 (<0.001)	18.47 (<0.001)	8.04 (<0.001)	10.44 (<0.001)	7.69 (0.001)	2.37 (0.096)
Exc x Veg x Burn(Site)	2.23 (0.112)	3.11 (0.048)	5.03 (0.008)	2.70 (0.071)	4.44 (0.014)	4.31 (0.016)
Exc x Date x Burn(Site)	1.21 (0.309)	1.21 (0.309)	1.53 (0.194)	1.31 (0.267)	1.24 (0.297)	1.90 (0.110)
Veg x Date x Burn(Site)	5.67 (<0.001)	11.83 (<0.001)	4.11 (0.003)	7.29 (<0.001)	10.14 (<0.001)	0.91 (0.457)
Exc x Veg x Date x Burn	3.03 (0.050)	2.43 (0.090)	0.67 (0.512)	5.13 (0.007)	5.81 (0.003)	1.46 (0.235)
Exc x Veg x Date x Burn(Site)	2.00 (0.095)	1.04 (0.389)	0.38 (0.821)	3.71 (0.006)	2.98 (0.020)	0.28 (0.892)

Table 6. Full-effects model for density of herb functional groups during the 2015 growing season (March, May, July 2015). The reported values are from a linear mixed model with a random plot and a square-root transformed response variable.

	F(p)					
Factor	**Annual**	**Perennial**	**Native**	**Non-Native**	**N-Fixer**	**Non-N-Fixer**
Exc	14.43 (<0.001)	12.17 (0.001)	8.24 (0.005)	14.30 (<0.001)	8.10 (0.005)	12.87 (<0.001)
Veg	216.58 (<0.001)	0.36 (0.549)	0.34 (0.558)	250.60 (<0.001)	8.64 (0.004)	251.64 (<0.001)
Date	405.62 (<0.001)	62.61 (<0.001)	112.26 (<0.001)	310.29 (<0.001)	69.04 (<0.001)	361.49 (<0.001)
Burn	90.28 (<0.001)	8.39 (0.004)	29.34 (<0.001)	60.35 (<0.001)	3.35 (0.070)	92.55 (<0.001)
Exc x Veg	1.43 (0.234)	0.29 (0.592)	0.05 (0.817)	0.62 (0.431)	0.24 (0.627)	2.72 (0.102)
Exc x Date	10.00 (<0.001)	1.94 (0.147)	2.17 (0.116)	11.32 (<0.001)	2.74 (0.066)	8.34 (<0.001)
Veg x Date	116.46 (<0.001)	2.51 (0.084)	0.10 (0.907)	144.31 (<0.001)	1.94 (0.145)	137.08 (<0.001)
Burn(Site)	13.08 (<0.001)	4.77 (0.010)	7.54 (0.001)	13.72 (<0.001)	23.10 (<0.001)	17.20 (<0.001)
Exc x Burn	0.91 (0.341)	4.93 (0.028)	1.67 (0.199)	1.45 (0.231)	3.33 (0.071)	1.84 (0.178)
Veg x Burn	20.73 (<0.001)	3.22 (0.075)	7.82 (0.006)	33.80 (<0.001)	8.11 (0.005)	21.84 (<0.001)
Date x Burn	71.87 (<0.001)	1.57 (0.210)	11.09 (<0.001)	48.14 (<0.001)	2.96 (0.053)	62.63 (<0.001)
Exc x Veg x Date	4.54 (0.012)	0.85 (0.429)	0.16 (0.852)	5.05 (0.007)	0.05 (0.952)	5.00 (0.007)
Exc x Burn(Site)	0.35 (0.706)	4.10 (0.019)	2.35 (0.099)	0.13 (0.877)	2.38 (0.097)	1.05 (0.353)
Veg x Burn(Site)	16.56 (<0.001)	0.68 (0.510)	0.14 (0.869)	17.56 (<0.001)	4.02 (0.020)	10.35 (<0.001)
Exc x Veg x Burn	4.93 (0.028)	0.11 (0.740)	1.00 (0.318)	3.38 (0.068)	1.62 (0.205)	3.35 (0.070)
Date x Burn(Site)	6.18 (<0.001)	18.26 (<0.001)	10.17 (<0.001)	5.36 (<0.001)	15.97 (<0.001)	9.24 (<0.001)
Exc x Date x Burn	1.62 (0.201)	2.33 (0.100)	1.00 (0.369)	1.60 (0.204)	1.22 (0.296)	2.28 (0.104)
Veg x Date x Burn	16.69 (<0.001)	0.01 (0.989)	2.41 (0.092)	25.03 (<0.001)	1.45 (0.236)	18.93 (<0.001)
Exc x Veg x Burn(Site)	2.91 (0.059)	1.23 (0.296)	1.85 (0.161)	1.96 (0.145)	1.55 (0.217)	3.71 (0.027)
Exc x Date x Burn(Site)	0.93 (0.448)	2.31 (0.058)	2.03 (0.091)	0.69 (0.597)	1.70 (0.150)	1.71 (0.148)
Veg x Date x Burn(Site)	9.74 (<0.001)	2.54 (0.040)	1.69 (0.153)	7.90 (<0.001)	3.13 (0.016)	8.18 (<0.001)
Exc x Veg x Date x Burn	2.85 (0.060)	0.21 (0.813)	1.39 (0.251)	1.96 (0.144)	1.32 (0.268)	2.32 (0.100)
Exc x Veg x Date x Burn(Site)	1.55 (0.189)	0.15 (0.963)	1.01 (0.406)	1.19 (0.318)	1.23 (0.298)	1.13 (0.343)

Table 7. Full-effects model for cover of herb functional groups during the 2015 growing season (March, May, July 2015). The reported values are from a linear mixed model with a random plot and a square-root transformed response variable.

	F(p)					
Factor	**Annual**	**Perennial**	**Native**	**Non-Native**	**N-Fixer**	**Non-N-Fixer**
Exc	19.22 (<0.001)	7.21 (0.008)	10.47 (0.002)	18.36 (<0.001)	3.79 (0.054)	18.55 (<0.001)
Veg	134.60 (<0.001)	1.08 (0.302)	6.16 (0.014)	272.11 (<0.001)	19.56 (<0.001)	115.68 (<0.001)
Date	531.42 (<0.001)	79.28 (<0.001)	133.69 (<0.001)	396.03 (<0.001)	89.51 (<0.001)	433.92 (<0.001)
Burn	143.54 (<0.001)	29.01 (<0.001)	67.97 (<0.001)	65.55 (<0.001)	11.62 (0.001)	141.06 (<0.001)
Exc x Veg	0.94 (0.335)	0.19 (0.662)	0.05 (0.820)	1.17 (0.282)	0.28 (0.600)	4.26 (0.041)
Exc x Date	12.03 (<0.001)	2.40 (0.093)	3.43 (0.034)	12.98 (<0.001)	1.08 (0.341)	10.26 (<0.001)
Veg x Date	78.69 (<0.001)	0.32 (0.725)	2.35 (0.098)	148.71 (<0.001)	7.77 (0.001)	81.96 (<0.001)
Burn(Site)	24.98 (<0.001)	0.06 (0.938)	0.27 (0.763)	24.65 (<0.001)	8.62 (<0.001)	27.92 (<0.001)
Exc x Burn	0.01 (0.903)	0.19 (0.663)	0.03 (0.854)	2.58 (0.111)	0.63 (0.429)	0.36 (0.548)
Veg x Burn	0.02 (0.897)	10.65 (0.001)	29.48 (<0.001)	20.82 (<0.001)	16.35 (<0.001)	2.26 (0.135)
Date x Burn	128.61 (<0.001)	7.56 (0.001)	26.62 (<0.001)	71.93 (<0.001)	6.46 (0.002)	94.51 (<0.001)
Exc x Veg x Date	3.95 (0.021)	0.14 (0.869)	0.05 (0.954)	4.19 (0.016)	0.27 (0.764)	2.29 (0.104)
Exc x Burn(Site)	1.98 (0.142)	1.33 (0.267)	0.56 (0.574)	0.82 (0.444)	1.62 (0.203)	1.07 (0.347)
Veg x Burn(Site)	13.40 (<0.001)	1.39 (0.253)	3.97 (0.021)	24.70 (<0.001)	0.35 (0.705)	6.85 (0.002)
Exc x Veg x Burn	12.23 (0.001)	0.18 (0.673)	1.42 (0.236)	5.50 (0.021)	0.30 (0.585)	6.17 (0.014)
Date x Burn(Site)	13.30 (<0.001)	8.95 (<0.001)	9.00 (<0.001)	8.23 (<0.001)	21.85 (<0.001)	15.66 (<0.001)
Exc x Date x Burn	0.13 (0.876)	0.42 (0.660)	0.09 (0.915)	0.68 (0.507)	0.32 (0.724)	0.04 (0.960)
Veg x Date x Burn	9.37 (<0.001)	1.89 (0.154)	11.79 (<0.001)	24.86 (<0.001)	6.63 (0.002)	7.04 (0.001)
Exc x Veg x Burn(Site)	5.60 (0.005)	0.87 (0.422)	1.92 (0.151)	2.46 (0.090)	1.00 (0.372)	7.63 (0.001)
Exc x Date x Burn(Site)	0.78 (0.542)	0.56 (0.695)	1.53 (0.195)	1.03 (0.391)	0.16 (0.956)	2.19 (0.071)
Veg x Date x Burn(Site)	9.08 (<0.001)	3.34 (0.011)	2.62 (0.036)	10.82 (<0.001)	1.47 (0.212)	5.47 (<0.001)
Exc x Veg x Date x Burn	5.65 (0.004)	0.86 (0.423)	3.29 (0.039)	1.86 (0.158)	0.65 (0.524)	6.69 (0.001)
Exc x Veg x Date x Burn(Site)	3.07 (0.017)	1.24 (0.294)	2.84 (0.025)	0.72 (0.576)	0.64 (0.637)	3.65 (0.007)

FIGURES

Figure 1. Example of chaparral-grassland bare zone at Mt. Diablo State Park (site 4). Photo by Lindsey Hendricks-Franco, June 2014.

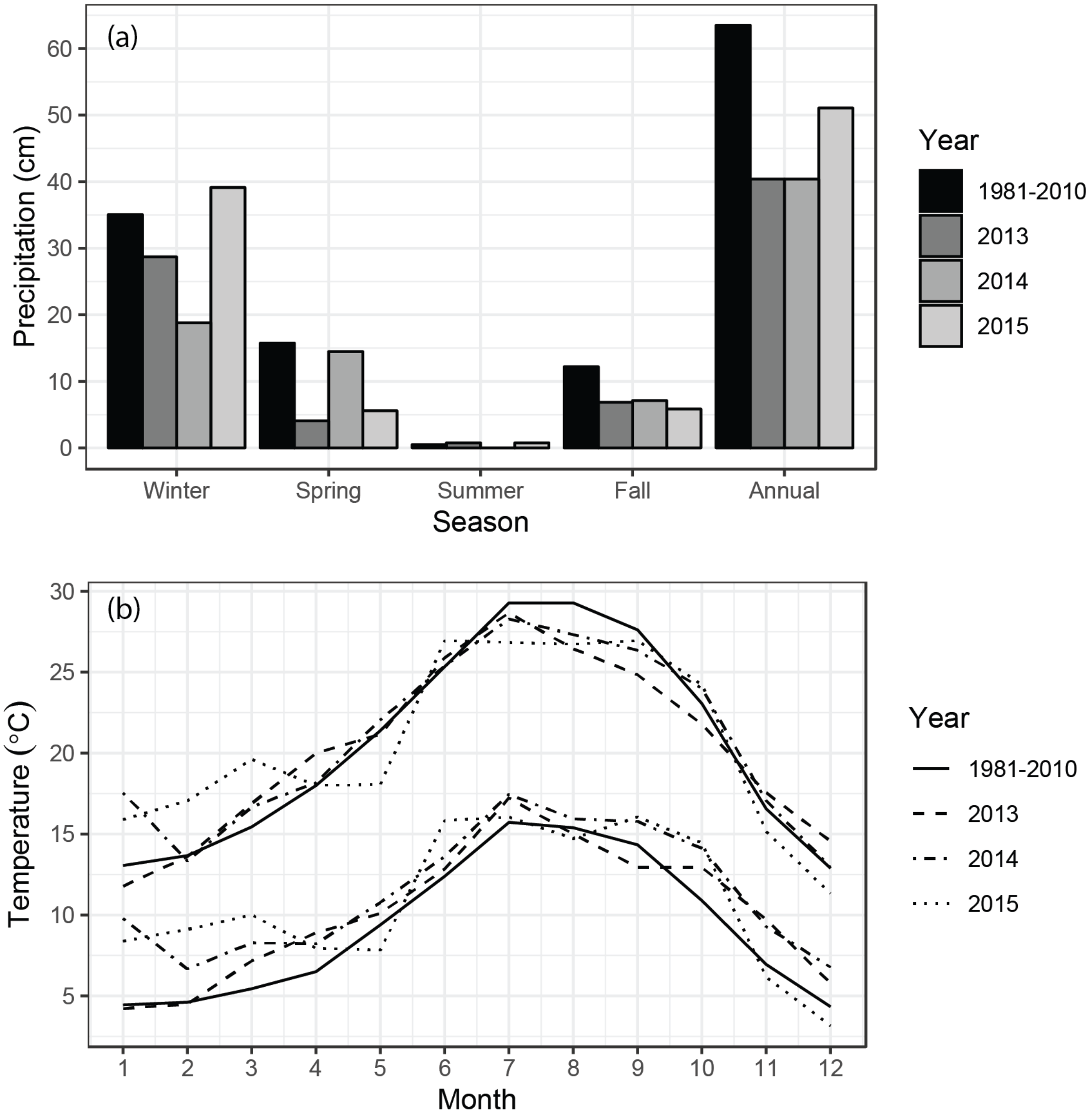

Figure 2. Annual weather data at Mt. Diablo Junction Station (Elev: 2170 ft. Lat: 37.8792° N Lon: -121.9303° W), including (a) monthly means of minimum and maximum daily temperature and (b) seasonal total precipitation.

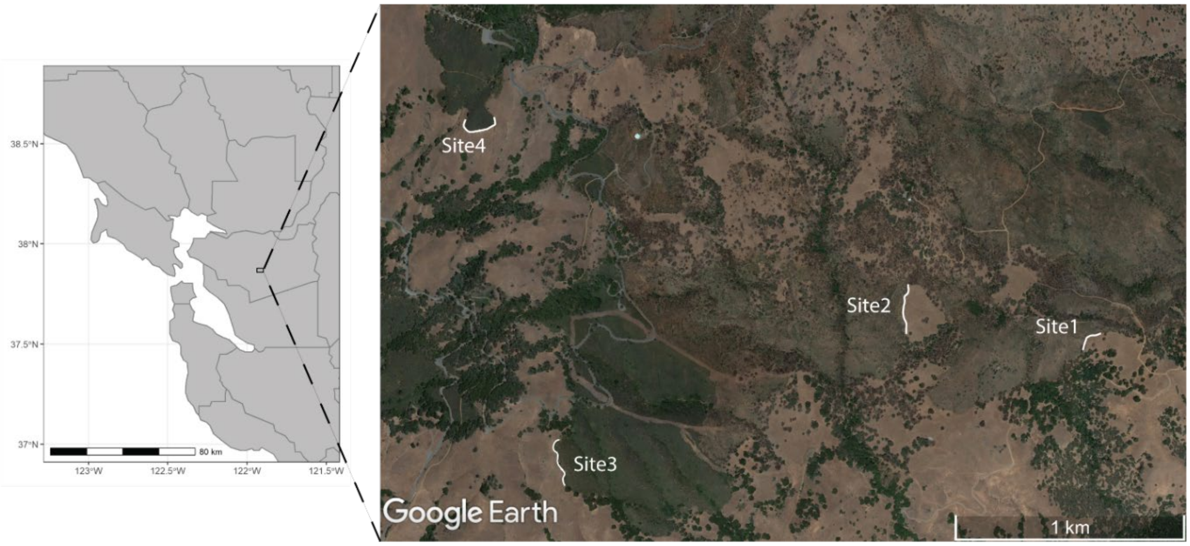

Figure 3. Map of selected chaparral-grassland ecotone sites at Mt. Diablo State Park. Site1 and Site2 were in the Morgan Fire perimeter, while Site3 and Site4 were unaffected. Imagery Date June 2014.

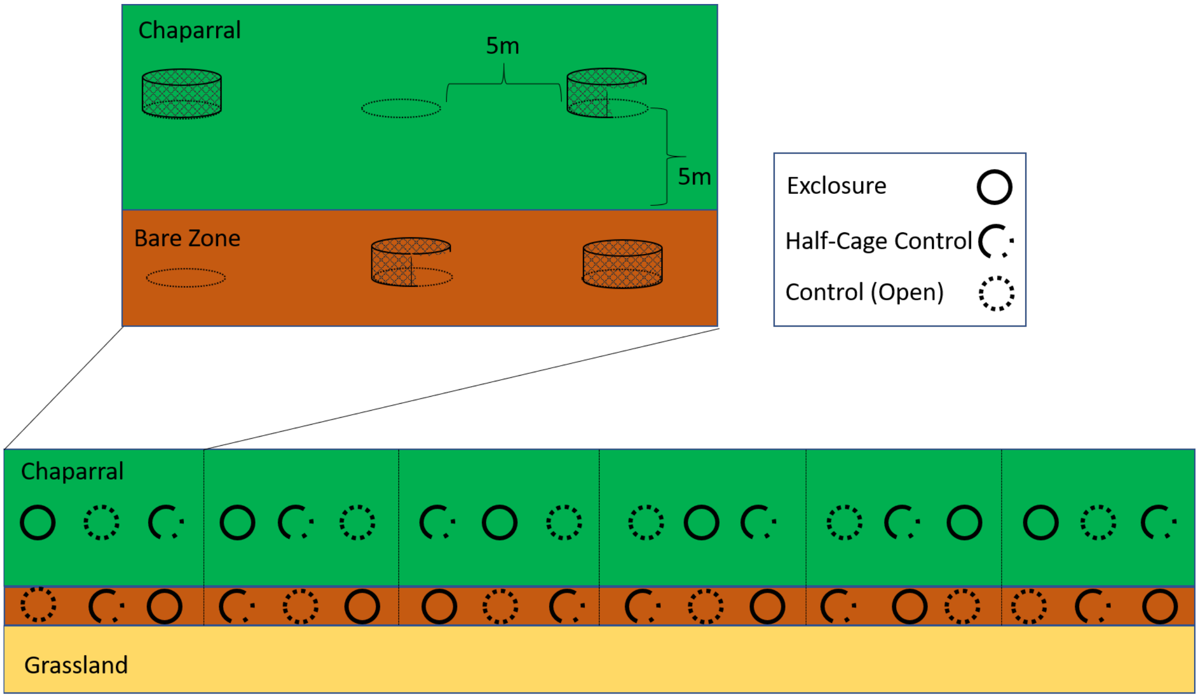

Figure 4. Layout of exclosure treatments in blocks at each chaparral-grassland border.

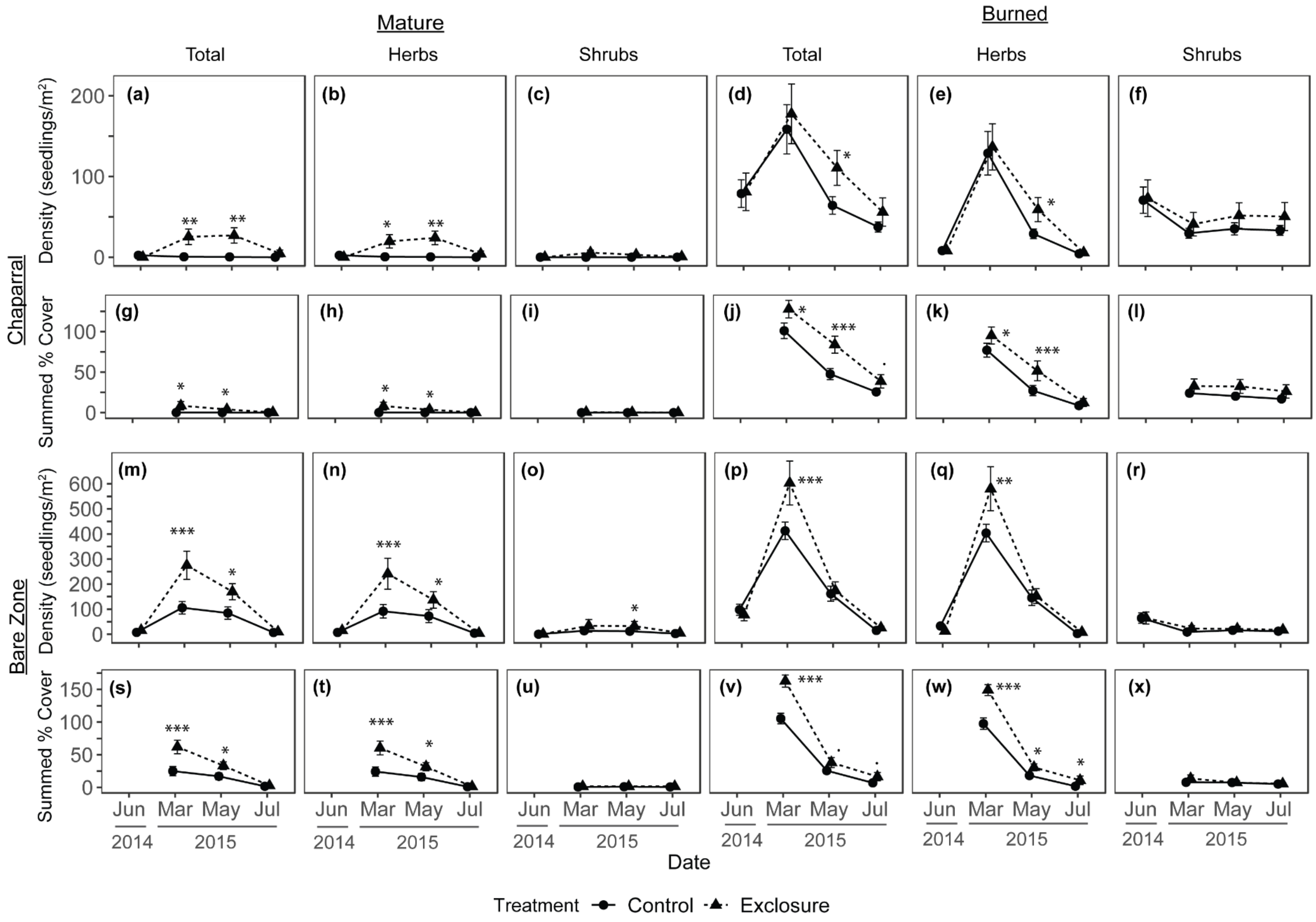

Figure 5. Effect of herbivore exclosures on total seedlings, herbs, and shrubs. Error bars represent S.E.M. Significance levels: $P \leq 0.10$., ≤ 0.05*, ≤ 0.01**, ≤ 0.001***.

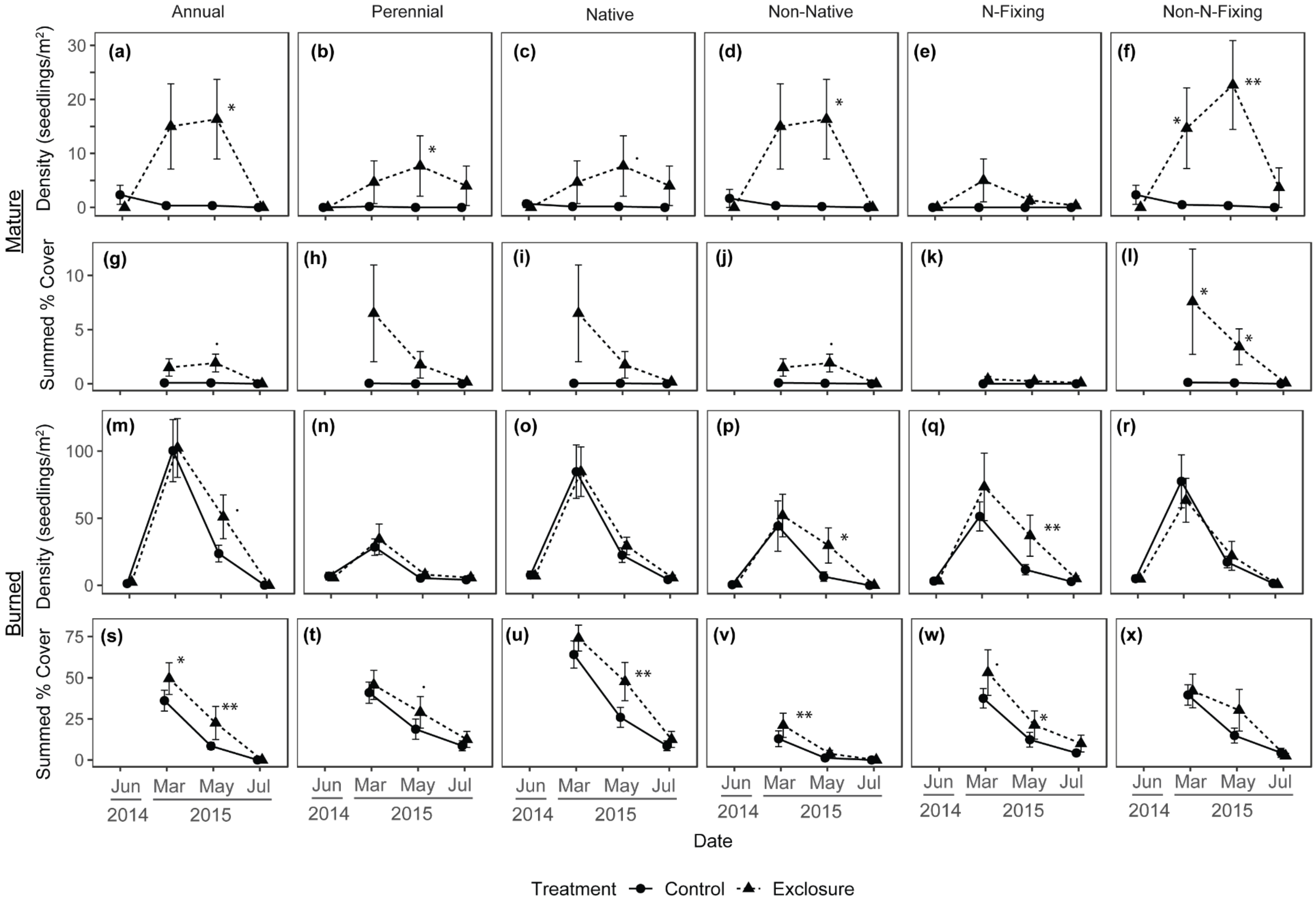

Figure 6. Effect of herbivore exclosures on chaparral herb functional groups. Error bars represent S.E.M. Significance levels: *P* ≤0.10., ≤0.05*, ≤0.01**, ≤0.001***.

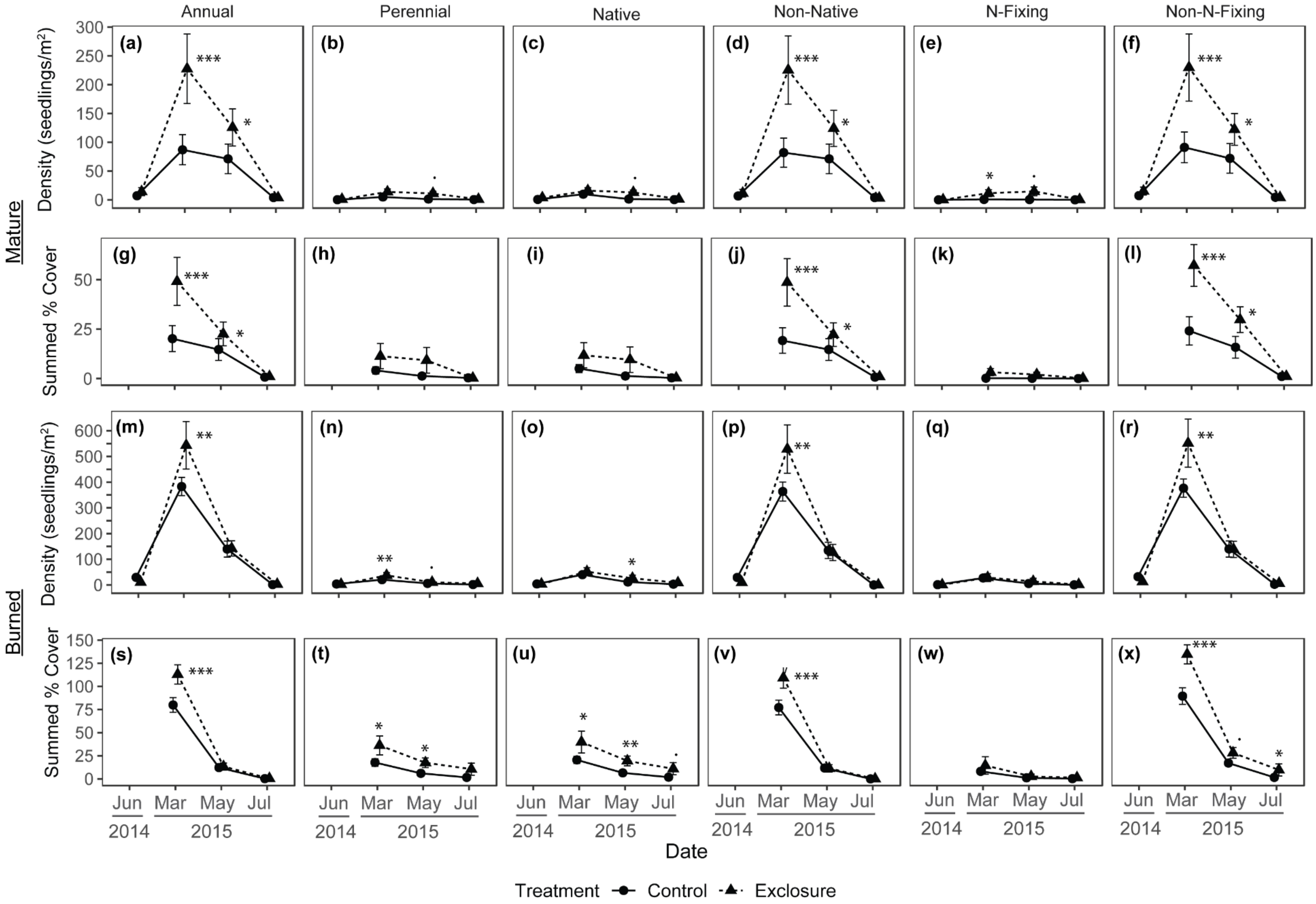

Figure 7. Effect of herbivore exclosures on bare zone herb functional groups. Error bars represent S.E.M. Significance levels: *P* ≤0.10., ≤0.05*, ≤0.01**, ≤0.001***.

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CHAPTER 2

Mammalian herbivory in post-fire chaparral impacts herbaceous composition, but not N or C cycling.

ABSTRACT

Classical theories predict that herbivores impact soil nitrogen (N) cycling through selective consumption of high-quality plants and the deposition of N-rich waste, with the effect dependent on ecosystem N availability. Herbivores are predicted to accelerate N cycling when N availability is high and decelerate cycling when availability is low. However, experimental tests of these theories are limited and yield contradictory results. Recently-burned chaparral shrublands provide a tractable system in which to test these theories, with implications for post-fire land management strategies. California's widespread chaparral shrublands are prone to periodic crown-fire, which temporarily removes all living shrub cover, deposits mineral N on soils, and allows herbaceous communities to dominate the landscape for 3-5 years. In this project, I implemented an exclosure experiment to assess the impact of mammalian herbivory during early post-fire chaparral succession, both on herbaceous plant communities and soil N and C cycling. By the second season after fire, excluding mammalian herbivores increased overall herb standing biomass by 54%, with the effect concentrated on non-native annual non-N-fixers (increased 48%) and native annual N-fixers (increased 54%). However, herbivory did not change the relative abundance of N-fixing vs. non-N-fixing herbs, nor annuals vs. perennials. Despite substantial changes to overall herbaceous abundance, I detected no significant effects on any measure of N or C cycling by herbivore exclosure treatment over the course of the study. It is possible that herbivore impacts on nutrient cycling are not significant over the short two-year time scale of the experiment, that physical effects of herbivore presence counteract the effect of plant litter or animal dung/urine inputs, or that my sampling regime was not sufficient to detect real effects. Herbivore exclosures slightly increased the relative abundance of non-native herbs, and non-natives also increased substantially between the two years of sampling, regardless of treatment. Mammalian herbivores concentrated their feeding on non-native annual non-N-fixers in post-fire chaparral (typically invasive grassland species), but these species were still abundant where grazed. Despite community-level impacts on herb abundance and composition, mammalian herbivory was not sufficient to stem the increase in grassland invasion of chaparral or alter C and N cycling over the first two years after fire.

INTRODUCTION

Community ecologists have long appreciated the role of herbivory in limiting plant biomass and abundance, mediating species coexistence (Harper 1977, Lubchenco 1978, Whittaker 1979, Crawley 1983, Huntly 1991, Hulme 1996, Maron and Crone 2006) and influencing successional change (Sousa 1979, Whittaker 1979, McNaughton 1983a, Brown 1985, Davidson 1993). In the previous chapter, I explored such effects of herbivory on plant communities at the chaparral-grassland ecotone. Herbivores can also have important effects on nutrient cycling in ecosystems (Pastor et al. 2006, van der Putten et al. 2013, Sitters and Olde Venterink 2015, Metcalfe et al. 2016). The effect of herbivores on ecosystem nutrient cycling depends on both top-down and bottom-up effects, namely the preferences and nutritional needs of grazers and the nutritional quality (C:N ratio) of plants (Hobbs 1996, Bardgett and Wardle

2003, Hobbie and Villóeger 2015). Classic theory predicts that herbivory's effect on nitrogen (N) cycling depended on the N availability of a given ecosystem. Herbivory is thought to accelerate N cycling in high-N systems and decelerate cycling in low-N systems (Ritchie et al. 1998, Wardle et al. 2004, Bardgett and Wardle 2010). However, experimental tests of these theories have been limited to a few study systems, namely grassland systems with ungulate grazers (e.g Augustine and McNaughton 1998, Olofsson et al. 2001) and geese grazing in salt marshes (e.g Wilson and Jefferies 1996), and results have been contradictory (Hawkes and Sullivan 2001, Bakker et al. 2009, Sitters and Olde Venterink 2015). Testing this prediction in a natural setting provides evidence that can support the development of context-specific frameworks relating herbivory to N cycling; an updated framework will increase the generalizability of this ecological theory (Sitters and Olde Venterink 2015).

In terrestrial systems, grazing is predicted to accelerate or decelerate nutrient cycling through consumptive and non-consumptive mechanisms. Herbivore preferences and grazing intensity will change plant functional diversity, influencing litter quality supplied to decomposers and ultimately N cycling rates, which are primarily controlled by plant traits (Cornwell et al. 2008). N fixers generally have higher tissue N content (lower C:N ratio) than non-N fixers (Wright et al. 2004, Scherer-Lorenzen 2008). In N-limited systems, herbivores are predicted to selectively consume plants with low C:N ratios, such as legumes, facilitating dominance by higher C:N ratio species. Thus, the low-quality litter of the surviving plants is supplied to decomposers, slowing N cycling and decreasing N availability to growing plants. These conditions may even promote the growth of nutrient-poor plants that can tolerate low-N soils, further decelerating N cycling (Ritchie et al. 1998, Bardgett and Wardle 2003, 2010, Wardle et al. 2004). In high-N systems, non-N-fixers may have higher tissue N than in low-N systems, decreasing the herbivore preference for N-fixers. Herbivores may actually stimulate compensatory growth of fast-growing N-rich species that can tolerate defoliation (*sensu* McNaughton 1983b). This effect may accelerate N cycling by increasing rates of plant N uptake, N content of litter, and dung/urine N (Hobbs 1996, Ritchie et al. 1998, Sitters and Olde Venterink 2015).

Chaparral ecosystems, the fire-prone shrublands that cover over 7% of California's land area (Keeley and Davis 2007), have been a popular study system for botanists, ecologists, and resource managers over the past eighty years. Comprised mainly of *Adenostoma fasciculatum*, as well as interspersed *Ceanothus spp.*, *Arctostaphylos spp.*, and other taxa, chaparral is susceptible to high-intensity crown fires, typically occurring in the late-summer and fall dry seasons (Keeley et al. 2012). Nutrient dynamics following fire (Christensen 1973, Hanan et al. 2016a) and patterns of species replacement during chaparral succession (Hanes 1971, Keeley et al. 1981, 2005b) have been well-characterized. Mature *Adenostoma* chaparral is considered N-limited (Wier 1950, Hellmers et al. 1955, Vlamis and Gowans 1961, Christensen and Muller 1975, McMaster et al. 1982) and hosts almost no herbaceous understory beneath its dense shrub canopy (Sampson 1944, Went et al. 1952, Horton and Kraebel 1955, Hellmers et al. 1955, Muller et al. 1968, Chou and Muller 1972, Christensen and Muller 1975, Shmida and Whittaker 1981).

Disturbance by fire temporarily eliminates canopy cover, liberates N, and stimulates the germination of fast-growing herbs, resulting in accelerated N-cycling in recently burned stands (Hanan et al. 2016a). During fire, large net losses of N occur through volatilization from shrub biomass, litter, and soils (Debano and Conrad 1978, DeBano et al. 1979). Despite net losses of total N, labile N is highly elevated after fire. The ash layer deposited on chaparral soils is rich in ammonium (NH_4^+) (Christensen 1973, Debano and Conrad 1978), which is available for immediate uptake by plants. Within 2-3 months after fire, the onset of winter rains stimulates rapid nitrification, conversion of ammonium (NH_4^+) to nitrate (NO_3^-) (Christensen 1973). While both NH_4^+ and NO_3^- are available for plant uptake, NO_3^- is highly soluble and vulnerable to leaching if not taken up immediately by plants (Debano and Conrad 1978). Thus, the post-fire plant community, and herbivore interactions that mediate its composition, have an important influence on N cycling in recently burned chaparral. Post-fire chaparral is characterized by a flush of herbaceous species (Brandegee 1891, Cooper 1922, Sampson 1944, Horton and Kraebel 1955, Sweeney 1956, 1956, Hanes 1971, Keeley et al. 1981, Keeley and Keeley 1988, Keeley et al. 2005c, Potts and Stephens 2009), which may dominate for 3-5 years before the shrub canopy closes over, primarily driven by the basal regrowth of *Adenostoma* (Keeley et al. 2005a, 2005c, Potts et al. 2010).

Herbivory is theorized to impact soil N cycling through differential impacts on plant functional groups (Ritchie et al. 1998, Sitters and Olde Venterink 2015). Several herbivore-exclosure experiments in post-fire chaparral have demonstrated effects of mammalian herbivory on shrub growth and survivorship (Mills 1986, Tyler 1995, Potts et al. 2010). A common finding is that herbivores demonstrate a preference for N-fixing shrubs, such as *Ceanothus ssp*. (Mills 1986). Fewer investigations have addressed herbivore effects on post-fire herbaceous communities (Tyler 1995). The previous chapter demonstrated that mammalian herbivores exert a large effect on herbaceous cover and density at the end of the second growing season after fire. While both N-fixing and non-N-fixing herbs were abundant in post-fire chaparral, only N-fixers were significantly reduced by herbivores during the second growing season. While the immediate post-fire environment is characterized by high soil mineral N (Christensen 1973, Hanan et al. 2016a) and high tissue N of fire-following plants, plant tissue N can drop considerably by the second year post-fire (Rundel and Parsons 1984), when the experiment in the previous chapter took place. The reduction of N-fixers by herbivores in this study suggests lower N conditions in the second year but does not give information about the effect of herbivores during the first year post-fire.

In the present study, I established an herbivore-exclosure experiment immediately after chaparral fire in northern California to test the effect of mammalian herbivores on chaparral herb community composition and soil N cycling. I hypothesized that herbivores would accelerate N cycling in the first year when N availability was high, but slow cycling in the second year as N availability declined. I also expected the consumption of N-fixers to vary between years. Herbivory of N-fixers in year two should be more intense due to N limitation.

METHODS

Study Location and Site Selection

I conducted this study at the Hopland Research and Extension Center (Mendocino County, California, 39.00, -123.08, **Figure 1**). Hopland is located in the North Coast Mountain Range of California. The vegetation is a mosaic typical of Mediterranean California, including grasslands, chaparral shrublands, oak woodlands, and mixed evergreen forests. Hopland experiences a typical Mediterranean-type climate with a warm dry spring through summer (1981-2010: 11.2 cm precip.) and a mild rainy fall through winter (83.7 cm precip.). The first season of monitoring had a particularly rainy fall and winter (2016-2017: 117.0 cm), while the second was comparatively dry (2017-2018: 18.3 cm, **Figure 2A**). Temperatures were fairly consistent between years of sampling, with mean lows–highs of 10.2–20.5°C in 2016, 10.4–21.0°C in 2017, and 10.7–21.1°C in 2018 (**Figure 2B**).

Herbivore exclosures were placed in the footprint of four prescribed fires: two conducted in spring (April 21) and two in fall (October 23) 2016. Each burn area ranged from 1-2 ha in extent. The California Department of Forestry (CalFire) set upslope prescribed fire (headfire) using a combination of drip torches with a gasoline/diesel mixture and mounted terra torches with gelled aviation fuel. To prevent fire escape, the borders of each site were cleared by bulldozer and the uphill side of the fire was backburned. The elevation of these sites ranges from 556 to 907 m. All except for one were south-facing. Chaparral prescribed fires conducted outside of the typical summer burn window (June – November; after spring drying and before first fall rain) are typically much less intense than wildfires (Beyers and Wakeman 1997, Stephens et al. 2008) and may favor a different suite of species (Knapp et al. 2009, Wilkin et al. 2017). Before fire, shrub vegetation was thick and continues (**Figure 3A**); after fire, almost all living aboveground plant biomass was consumed, leaving only woody skeletons (**Figure 3B**).

Several species of small herbivorous mammals have been observed in the early post-fire chaparral at Hopland, including brush rabbit (*Sylvilagus bachmani*), black-tailed jackrabbit (*Lepus californicus)*, Botta's pocket gopher (*Thomomys bottae*), Townsend chipmunk (*Neotamias townsendii)*, Heermann's kangaroo rat (*Dipodomys heermanni*), deer mice (*Peromyscus spp.*), and the dusky footed woodrat (*Neotoma fuscipes*). Black-tailed deer (*Odocoileus hemionus*) are also common (Longhurst 1978).

Experimental Design

I placed six experimental blocks within each of the four sites, with a minimum of 20 m between blocks. Each of the blocks in a site included an open control plot, paired with an herbivore-exclusion treatment (installed Dec. 2016-Jan. 2017). The herbivore exclosures were rectangular plots of 3 x 4 m staked at the corners with rebar stakes. The plots in a block were arranged side by side along the hillside, so that no plot within a block was uphill of another. The fencing material was a heavy UV-resistance plastic mesh with 0.64 cm openings. Fences were approximately 130 cm high. The mesh was installed flush to the ground, but was not buried (**Figure 3C,D**). Thus, some small mammals may have been able to burrow underneath the fence. However, small mammal entry was likely substantially reduced and deer should not have been able to enter. I did not find deer droppings inside of exclosures. I monitored regularly for damage to the fences , which only occurred during one snowstorm in early 2017.

To evaluate potential artifacts due to cage installation and presence, I included half-cage controls in three of the six experimental blocks per site. Half-cage controls consisted of rebar stakes in the four corners of the plot as well as fencing on the upper and lower edge. This was intended to control for fencing effects, including sediment capture, shading, and dew collection, while allowing for mammal entry. These half cages were monitored for the first season only.

Great care was used to place plots in regions dominated by chamise (*Adenostoma*) chaparral. Regions with apparent N-fixing shrubs (*Ceanothus* spp. and *Pickeringia montana*) were rejected. After one year of the experiment, some plots contained an unexpectedly high component of recovering non-chamise shrubs, including *Quercus* spp. These blocks were dropped from the analyses. Vegetation sampling (described below) confirmed dominance by *Adenostoma*, with a standing dry biomass of 107±16 g/m^2 in 2017 and 202±19 g/m^2 in 2018. No other shrub exceeded average standing biomass of 4.4 g/m^2 in either year. In 40-year-old chaparral vegetation, standing living biomass of approximately 50 kg/m^2 has been recorded (Oechel and Reid 1984), over ten times the post-fire shrub biomass reported here.

Vegetation Sampling

I monitored vegetation at peak biomass at the end of each growing season (June-July 2017 and May 2018). Because a July 2018 wildfire burned the experimental plots, it was not possible to conduct a third year of vegetation sampling. I estimated biomass using the point intercept method with a pin-frame sampler. In each 3 x 4 m plot, I subsampled three 0.5 x 0.5 m quadrats, one in the center of the plot, one in the top left, and one in the bottom right. The top and bottom plots were always placed 0.5 m inside of the plot, measured from the top and the side. The pin-frame quadrat held twenty pins vertically over the shrub and herbaceous vegetation growing in the plot. The pins were placed so that 5 pins were in each quarter of the quadrat. I counted how many times each pin hit each plant species.

I used the total number of pin hits as a proxy for plant dry biomass (Jonasson 1988). To relate this value to standing biomass, I collected and dried plants that were sampled using this method. I sampled 32 quadrats using the pin frame, principally outside of the experimental plots to minimize vegetation disturbance. I then clipped aboveground growth of plants and sorted it by plant functional group: shrubs, N-fixing herbs, and non-N-fixing herbs. In the lab, I thoroughly rinsed these herbs in water to remove all soil and dried them at 65°C for at least 48 hours before weighing their dry biomass. I estimated equations relating pin hits in each of these groups to biomass using a linear regression for each group. In order to avoid regression estimates of negative biomass values, I set the y-intercept to zero:

$$biomass = \ 0 + \ \beta_1 \times hits \qquad \text{Eqn. 1}$$

where *biomass* is dry mass of plants (g^{-1}m^2) and *hits* is the total number of pit hits per group in a plot. R^2 was over 0.9 in all cases, demonstrating a strong relationship between biomass and pin hits (**Figure 4**).

Soil Physical and Chemical Properties

Soil Collection

For all soil measurements in this project, I collected soils to a depth of 10 cm to capture the dynamics most likely driven by herbaceous growth and litter decay. Throughout the 2017 and 2018 spring growing seasons, I collected soil samples monthly from each plot (March-June 2017 and February-May 2018). Generally, I collected four 2.5 cm-diameter, 10 cm-deep soil cores at each plot and pooled the soil to minimize plot level variation. The exception was a collection in late January 2017, during which I pooled soil from cores across the whole block in order to capture seasonal conditions and block-level characteristics, without respect to a specific treatment. At each sampling, the soil cores to be pooled were first collected into a common plastic bag, and then immediately homogenized by gently massaging the bag contents to break up large aggregates and passing the soils through a 4 mm sieve. I refrigerated soils at 4°C soon after collection and processed soils for analysis (described below) within 48 hours.

Bulk Density and Texture

I collected separate soil cores for bulk density analysis during late January 2017 block-level sampling. At each block, I collected one soil core (5 cm diameter x 10 cm deep) for bulk density analysis. I carefully scraped off soil from the bottom of the core to ensure that the exact volume of the core was collected. In the lab, I sieved soil cores to 4 mm and used a water displacement method to measure the volume of the removed rocks and roots. The total volume of soil was $\text{volume}_{\text{core}} - \text{volume}_{\text{rocks}}$. The remaining soil was dried at 105°C for 72 hours and weighed. Bulk density was the dry mass of soil divided by the total volume. I determined soil texture on soils collected from every block using the hydrometer method (Gee and Bauder 1986), abbreviated with readings at 40 s and 2 h.

Total Soil C and N

Total soil carbon (TC) and nitrogen (TN) were determined from air-dried soils. First, I tested soils for the presence of inorganic C. I gently ground soil samples and moistened with one drop deionized water. I added one drop of 4M HCl. As there was no fizzing or effervescence, I determined that no significant inorganic C was present. Thus, TC is an appropriate measure of organic C. I determined TC and TN on a Flash 2000 Elemental Analyzer (Thermo Scientific, Germany). I analyzed duplicate samples and repeated the analysis of soils for which duplicates differed by more than 10%. I performed this analysis on soils collected from every plot at pre-treatment (March 2017) and post-treatment (May 2018) times. Although the pre-treatment date was actually shortly after exclosure installation, this was the earliest point at which plot-level soils were collected and thus the best indication of pre-treatment conditions available. Post-treatment soils were analyzed at the end of two growing seasons in May 2018.

Soil Mineral Nitrogen

I extracted soils in 2M KCl for analysis of mineral N: ammonium (NH_4^+) and nitrate (NO_3^-). I mixed 10.0 g soil samples with 40 ml of 2M KCl in an acid-washed 50 ml centrifuge tube. Samples were shaken for 1 hour at 200 RPM. The soil slurry was then gravity filtered through KCl soaked Whatman #1 filters and acid-washed funnels into separate new clean centrifuge tubes. Samples were stored at -20°C until analysis.

Soil gravimetric percent water was determined for every collected soil. I measured 10.0 g subsamples into metal tins and dried the soils at 105°C for 24h hours and then weighed the dry soil. Soil gravimetric water content was calculated as: $(\text{mass}_{\text{wet}} - \text{mass}_{\text{dry}})/\text{mass}_{\text{dry}}$.

Nitrogen Mineralization

I determined the rate of soil net N mineralization and nitrification using a laboratory dark incubation. This setup was combined with a soil C mineralization (respiration) incubation described below. After measuring soil subsamples for mineral N at collection (above), soils were incubated in 495 ml glass mason jars. A subsample of approximately 30 g of wet soil was packed into a tared 30 ml medicine cup and weighed. The medicine cup was placed carefully into the base of the jar, which was sealed and allowed to incubate in the dark for one week. After the 7 days, I removed each incubated soil sample from its jar, mixed it thoroughly, then measured out a 10.0 g subsample for a 2M KCl extraction. This subsample was extracted using the same procedure described above. The resulting extract samples were analyzed for $NH\text{-}^+$ and $NO\text{-}^-$ concentrations using Lachat Flow Injection Analyzer (Hofer 2003, Knepel 2003) or the microplate method (Wu et al. 2016).

Carbon Mineralization (Respiration)

During the most active months of the second year of soil collection (March-May 2018), I used the soil mineral N incubations to also collect data on soil respiration over a 48 h period. Samples were collected in plastic syringes with O-ring seals and medical grade stopcocks. I took three initial 5 ml samples from ambient air above the jars prior to sealing them with gas-tight lids fitted with septa (T_1). After a 48 h dark incubation, I injected 5 ml of CO_2-free air into each jar, pumped the syringe slowly to mix the headspace, and then withdrew a 5 ml sample for analysis (T_2). Samples were analyzed on an FoxBox IRMS Flow Analyzer. I calculated the total headspace carbon at T_1 and T_2, adjusting for the temperature and pressure in the jars, and the small dilution from injecting CO2-free air at T_2. I calculated respiration as (T_2 - T_1) / T (days). Data are reported as µgCO2-C/g dry soil/d.

Statistical Analysis

I fit all models in *R* (*R* Core Team 2018) with the package *lme4* (Bates et al. 2015), using a restricted maximum likelihood estimation procedure (REML) and performed a Type III ANOVA using the *lmerTest* package (Kuznetsova et al. 2017). Planned contrasts on the model were made using the *emmeans* package (Lenth 2018). The effects of treatments on each group at each date were determined by *a priori* planned contrasts of estimated marginal means, with no p-penalization procedure (Day and Quinn 1989).

Half-Cage Control

At each site, there were three blocks containing a half-cage control in addition to the fully open control and an exclosure. At both sites J and L, one of the half-cages was excluded from the analysis due to emergent non-*Adenostoma* shrubs, leaving 10 replicate blocks across 4 sites. I fit a linear mixed-effects model with Exclosure (half-cage vs. open control) as a fixed factor and Site, Block, and Plot as random effects. I fit separate models for each response variable: total herbs and 7 functional groups. There was no difference between open and half-cage controls at the conclusion of the 2017 growing season for any of the herb functional groups tested (**Table 1**); therefore, I stopped maintaining half-cage controls after 2017 and dropped them from all subsequent data/sample collection and analysis.

Because gravimetric moisture was measured with every sample, it was also used to assess the half-cage effect through 2017. I fit a linear mixed-effects model with Month x Exclosure as fixed factors and Site, Block, and Plot as random effects. There was an effect of month on percent moisture ($F = 275.35$, $P < 0.001$), but no effect of Exclosure treatment ($F = 1.14$, $P = 0.314$) or Exclosure*Month ($F = 0.98$, $P = 0.410$). This provides additional evidence that there was no detectable artifact of exclosure installation and presence.

Effect of Herbivore Exclosures

After excluding half-cage plots, I fit a linear mixed-effect model to evaluate the main and interactive effects of Exclosure (*Exc*) and Date on all measured variables in the experiment:

$$Y = Exc + Date + Exc * Date + Random(Site + Block + Plot) \qquad \text{Eqn. 2}$$

The response variables (Y) for vegetation sampling were square-root-transformed biomass for total herbs and functional groups N-fixers and non-N-fixers. These groups were further divided into subgroups based on life-history (annual vs. perennial) and origin (native vs. non-native).

Response variables for soil were gravimetric percent water, total C, total N, C:N ratio, ammonium-N, nitrate-N, or total mineral N, and carbon mineralization (respiration). This chapter addresses the impact of herbivore exclosures across all sites, regardless of the date burning took place at each site (spring or fall prescribed fire); thus, Site was treated as a simple random effect. A forthcoming publication will address the impact of prescribed fire season on soil characteristics. Individual bulk density and texture measurements were reported as pre-treatment descriptive site conditions.

Carbon Mineralization (Respiration)

After Exclosure was determined not to be a significant predictor of soil heterotrophic respiration, I performed a follow-up analysis to test the hypotheses that soil gravimetric percent moisture (*Wat*) influences respiration rates (*Resp*):

$$Resp = Wat + Date + Wat * Date + Random(Site + Block + Plot) \qquad \text{Eqn. 3}$$

The percent variance explained by the model variables was determined using a modified marginal and condition R^2 appropriate for mixed-effects models, calculated with the *MuMIn* package in *R* (Nakagawa and Schielzeth 2013). I considered $P < 0.1$ as the threshold for a significant effect, a typical threshold for marginal significance that avoids unnecessary risk of Type II error in ecological models with relatively low samples size (Hurlbert and Lombardi 2009).

RESULTS

Block-level pre-treatment bulk density values ranges from 1.0 – 1.5 g.m^2 in the blocks used, and most soils were clay or clay loam. There were wide ranges in soil chemical characteristics: TC (16.4 - 40.9 mg/g), TN (1.2 – 2.5 mg/g), NH_4^+-N (2.9 – 23.9 µg/g), and NO_3^--N (0.5 – 2.6 µg/g) (**Table 2**). For all variables, we analyzed the interactive effects of Exclosure and Date using linear mixed-effects models to assess (**Table 3**). Planned contrasts are indicated on the graphs and reported in the text.

Vegetation Monitoring

I measured the response of herbaceous biomass to the exclusion of herbivores and time after fire (annual sampling of peak biomass in 2017 and 2018). Herbivore exclosures significantly increased the biomass of total herbs, N-fixers and non-N-fixers, but only by 2018 (**Figure 5**). All three of these groups increased in biomass from 2017 to 2018 in both treatments ($P < 0.05$). Of the N-fixers subgroups (**Figure 6**), native annuals were the most abundant, and were comprised almost completely of two closely related species *Acmison brachycarpus* and *Acmispon parviflorus*. Native annual N-fixers were significantly increased by herbivore exclosures in 2018 only (**Figure 6B**). The one native perennial N-fixer (*Acmispon glaber*) was comparatively low in abundance, but increased significantly in exclosures in 2018 (**Figure 6C**). Native annuals increased between 2017 and 2018 in both treatments ($P < 0.1$), while native perennials increased only in the Exclosure treatment ($P < 0.05$). The one non-native annual N-fixer (*Trifolium hirtum*) was not significantly affected by year or Exclosure (**Figure 6C**).

The non-N-fixers were further divided into four groups based on life history and origin (**Figure 7**). Of these groups, only non-native annuals were impacted by Exclosure, with dramatically higher standing biomass in exclosures than controls in both 2017 and 2018 (**Figure**

7A). The species most enhanced in herbivore exclosures were the common invasive grasses *Bromus diandrus*, *Bromus madritensis ssp. rubens*, *Festuca myuros,* and *Gastridium phleoides*, along with common invasive forbs *Centaurea melitensis* and *Torilis arvensis.* Non-native annual non-N-fixers increased dramatically between year 2017 and 2018 in both treatments ($P < 0.001$), mainly comprising increases in *Aira caryophyllea*, *Bromus diandrus*, *Gastridium phleoides*, *Festuca myuros*, *Hypochaeris glabra, and Logfia gallica*. Interestingly, *Logfia gallica* was only half as abundant in exclosures as open controls. Native annual non-N-fixers actually decreased between 2017 and 2018 ($P < 0.1$, **Figure 7C**); fire followers *Emmenanthe penduliflora* and *Gilia capitata* were abundant in 2017 and almost totally disappeared by 2018. A few individual native annual non-N-fixers were actually negatively impacted by exclosures (*Calandrinia breweri*, *Logfia filaginoides* and *Navarretia melitta*), while a few were enhanced (*Cryptantha muricata*, *Galium californicum*). The perennial non-N-fixers were not significantly affected by Exclosure or Year (**Figure 7B,D**).

I analyzed the relative abundance of three broad herb functional categories (life history, origin, and N-fixation) in response to herbivore exclosures and time since fire (**Figure 8**). Most herb biomass was from annuals, at over 79-90% for all treatments and time points. There was a weak effect of year only, due to increasing relative annual abundance in exclosures only between 2017 and 2018 ($P = 0.035$). N-fixers comprised on average 38.2% of herb biomass and there was no effect of Exclosure or Year on their relative abundance. Non-natives were relatively low in abundance, but were significantly increased by both time since fire and herbivore exclosures. In herbivore exclosures, non-native herb relative abundance was about 5 percentage points higher than in open controls ($P = 0.06$), although there were no significant differences in individual years based on planned contrasts. Non-native relative biomass also increased significantly from 2017 (16.2%) to 2018 (36.4%).

Soil Physical and Chemical Properties

Gravimetric Percent Moisture

The gravimetric percent moisture of the soil samples was measured at each time point (**Figure 9**). Across all sites and dates, I found a minuscule significant effect of Exclosure treatment on gravimetric moisture (**Table 3**). Planned contrasts demonstrate that exclosures were only slightly moister than controls in May 2017 ($P = 0.084$), by a small trivial margin of 1.3 percentage points (14.1% vs. 12.8% water). Soil moisture varied significantly by date, ranging from 5.9% to 21.9%.

Soil Mineral Nitrogen and Mineralization Rates

I measured plot-level soil mineral N pools and rates of net N mineralization and nitrification monthly during the 2017 and 2018 spring seasons (**Figure 10A-B**). There was no effect of Exclosure on NH_4^+-N, NO_3^--N, or total mineral N. When the monthly values were averaged across each year, all mineral N pools were significantly lower in 2018 than 2017 ($P < 0.001$). For rates of net N mineralization and nitrification, there was an idiosyncratic effect of exclosure in the first month of sampling only (**Figure 10C-D**); however, the overall results fail to support the effect of treatment on nitrification or N mineralization rates. Nitrification rates were significantly higher in 2017 than 2018 ($P < 0.001$) and were highly correlated with soil ammonium concentrations ($F = 31.93$, $P < 0.001$), Date ($F = 1.77$, $P = 0.095$), and their interaction ($F = 4.56$, $P < 0.001$). The modified marginal R^2 for Ammonium x Date alone was

0.50, and the conditional R^2 (including random site, block, and plot) was 0.65. Overall, there was no major difference in net N mineralization between years 2017 and 2018 ($P = 0.340$).

Carbon Mineralization (Respiration)

I measured soil respiration in a lab incubation of soils collected during three months of 2018, the second season after fire. There was no effect of Exclosure treatment on respiration; only Month was a significant predictor (**Figure 11A**, $P < 0.001$), with respiration values decreasing from March through May. I analyzed C mineralization as a function of gravimetric percent soil moisture and month (**Figure 11B**). When Percent moisture was included in the model, Month was no longer a significant predictor, either as a main effect (F = 0.89, $P = 0.417$) or interaction (F = 0.58, $P = 0.563$), but Percent moisture was highly significant (F = 100.72, $P < 0.001$). The modified marginal R^2 for Percent moisture alone was 0.51, and the conditional R^2 (including random site, block, and plot) was 0.75. Including month in the models improved the marginal R^2 only slightly to 0.54 and the conditional R^2 to 0.83.

Total Soil C and N

Total soil C and N were measured at the earliest sampling point (March 2017) and the last point (May 2018) (**Figure 12**). At neither time point were there significant differences between exclosures and open controls in bulk soil C and N. Between March 2017 and May 2018, exclosure treatments decreased significantly ($P < 0.05$), but very slightly, in bulk soil C (-4.0 mg/g) and N (-0.22 mg/g), but open control plots did not.

DISCUSSION

In this study, I established herbivore exclosures in post-fire chaparral to investigate the effect of mammalian herbivores on herb composition and nutrient cycling. I hypothesized that the exclusion of herbivores would impact N cycling, with an effect dependent upon N availability. I predicted that (1) available soil N would be higher in the first year rather than the second year, (2) herbivores would preferentially consume N-fixers more in the second year than the first, and (3) the presence of herbivores would accelerate N cycling, particularly in the first year.

Effect of Time Since Fire and Season of Burning

My first prediction, of elevated soil available N in the first year post-fire, was supported by the results. Levels of NH_4^+-N, NO_3^--N, and total mineral N were higher in the first year after fire than the second. Ammonium is the form of N deposited directly on soils after fire (Christensen 1973, Debano and Conrad 1978) and thus it is logical that it should be higher initially and then decrease with time since fire as seen here. Hanan et al. (2016a) found that NH_4^+-N was lower in the second year after fire in other chaparral watersheds and Fenn, Poth, Dunn, & Barro (1993) found no difference in NH_4^+-N concentrations between two-year and eighty-year old stands.

Nitrification rates are often dependent upon levels of soil NH_4^+-N. This is noteworthy because mechanism for rapid loss of ammonium post-fire is nitrification (Christensen 1973), the oxidation of ammonium to nitrate, which is mobile and vulnerable to leaching. Ammonium substrate availability is known to be a key driver of post-fire nitrification in chaparral (Fenn et al. 1993, Homyak et al. 2014, Hanan et al. 2016b). The rate of net N mineralization, which suggests the ongoing supply of soil available N for plants (Schimel and Bennett 2004), did not differ between years. Thus, any difference in available N between 2017 and 2018 likely resulted from the direct deposition of ammonium on soils during fire.

A forthcoming publication will discuss these results in the context of the direct effects of burning and season of prescribed fire on soil N cycling (Hendricks-Franco, in prep). In this unpublished project, soil mineral N pools and cycling rates were measured at the same post-fire sites in October and November 2016, along with a non-burned control. The burned sites were several times higher than the non-burned sites in mineral N pools (NH_4^+-N and NO_3^-–N), but not in net N mineralization. The present chapter shows a gradual decline of mineral N over spring 2017 and 2018, but unfortunately lacked a non-burned control at each time point. However, the extreme effect of burning on mineral N pools in October/November 2016 suggests that patterns in mineral pools seen here are likely the result of time since fire.

Herbivore Vegetation Effects

My second hypothesis was that the exclusion of herbivores would impact the abundance and composition of post-fire herbs. I predicted that as available soil N dropped in the second year after fire, mammalian herbivores would preferentially consume N-fixers and lead to a reduction of their relative abundance in the open controls. My vegetation surveys did not support this prediction: the fraction of standing plant biomass found in N-fixers did not differ between exclosure treatments or years. However, I found that herbivores did reduce overall herb biomass, particularly in year two, with consumption acutely concentrated on a few functional groups. The most abundant herb group, non-native non-N-fixing annuals, was also the most affected by herbivory. Brush rabbits (*Sylvilagus bachmani*) are important herbivores in the chaparral understory (Connell 1954), and they typically rely on edible grasses, including *Bromus spp.* (Chapman 1974). Curiously, the biomass of two clover species (*Trifolium spp.*) was not affected by herbivore exclosures, despite members of this group being a preferred food source for rabbits (Chapman 1974). It is also possible that plant defensive compounds decreased the overall intensity of herbivory on N-fixers; plant defensive chemicals are often N rich, so N-fixing plants might be generally more defended (Vitousek and Field 1999).

Multiple investigations have demonstrated that herbivore effects on plant abundance are not significant in post-fire chaparral, (e.g. Tyler 1995), plausibly due to displacement or death of herbivores (Christensen and Muller 1975). The present study contradicts those findings, with herbivore effects being particularly pronounced in the second year after fire. The relatively small size of these prescribed fires could be responsible for these different findings. Although some animal death occurred in these fires (Hendricks-Franco, personal observation), the small 1-2 ha burns could have been quickly recolonized by animals from nearby non-burned patches. I found no difference in *Adenostoma* shrub biomass between Exclosure treatments, in either year. This is consistent with a similar investigation at the same reserve (Potts et al. 2010), which found no exclosure effect two years after fire; however, they did see an effect by year three. A wildfire in the summer of 2018 burned my experimental plots before third-year measurements would have been possible for comparison.

A few herbaceous species were negatively impacted by exclosure treatment: *Logfia gallica* (non-native non-N-fixing annual) and three native non-N-fixing annuals: *Calandrinia breweri*, *Logfia filaginoides*, and *Navarretia melitta*. A likely explanation for this effect is that these species were outcompeted by other herb species that performed especially well in exclosures. Notably, these species negatively impacted by exclosures are low-growing plants, which could be easily covered by a larger competitor. *Navarretia melitta* in particular is probably resistant to herbivory, and thus would not have benefited directly from exclosures. The plant is sticky, strongly odored, and defended by spiny leaves, sepals and bracts. Although I did not detect modified competitive relationships of the level of the functional groups tested, these species-specific results demonstrate indirect competitive effects on the species level, which are important in structuring a variety of communities (Wootton 1994).

Grassland Invasion

Historically, chaparral has been considered relatively resistant to grassland invasion, despite its typical proximity to invasive grasslands. Southern California chaparral is increasingly falling victim to grassland and herbaceous invasion, with one estimate finding that 34% of historical chaparral vegetation is now covered with herbs (Park et al. 2018). The drivers of grassland invasion of chaparral remain uncertain, but Park and Jenerette (2019) suggest that mammalian herbivores may consume non-native grasses and limit their success in chaparral. In this study, non-natives were abundant; I found non-natives representing over a third of the herbaceous biomass, consistent with a similar study in the same reserve, three years after prescribed fires (Potts and Stephens 2009). The present study does demonstrate the role of mammalian herbivores in limiting the spread of non-native grassland species; however, mammalian herbivory was not sufficient to stop the increase in non-natives in the years after fire.

Herbivore Effects on N and C Cycling

Overall, the exclusion of small- and medium-sized mammalian herbivores resulted in changes to herbaceous vegetation communities that did not translate to detectable changes in soil N or C cycling. I hypothesized that herbivores would accelerate N cycling in the first year when nutrient resources were high, but slow cycling in the second year as N availability dropped due to leaching. There was no effect of Exclosure treatment on any mineral N pool, N mineralization rate, or C mineralization rate. The one possible exception is the interaction between date and soil C and N. Although there was no Exclosure treatment effect on total soil C and N at pre- or post-treatment sampling, exclosures did significantly decrease soil C and N over the course of the experiment; open plots did not. This very slight effect could suggest that herbivore presence contributes to soil C and N storage over time. However, comparing two sampling points is likely insufficient evidence to draw this inference and further investigation would be required.

Classical theories predict that herbivores impact soil N cycling through changes in resource inputs: the addition of dung/urine and changes to plant litter composition (Bardgett and Wardle 2003, Schrama et al. 2013b), which has been demonstrated in several other studies (Pastor et al. 1993, Ritchie et al. 1998, Wardle et al. 2002, Harrison and Bardgett 2004). Indeed, plant litter quality is the primary determinant of the soil net N mineralization rate (Parton et al. 2007, Cornwell et al. 2008); deer and rabbit dung/urine can add substantial C and N and could be a major source of soil enrichment (Clark et al. 2005, Karberg and Lilleskov 2009).

In this experiment, herbivores decreased the total abundance of herbs, but not the balance between N-fixers and non-N-fixers: the fraction of total herbs that were N-fixing was unaffected by Exclosure treatment or Year. In a laboratory litter-soil incubation, Rossignol et al. (2011) demonstrated that litter from plants selected by herbivores did accelerate N cycling, while the litter from plants selected against slowed it. However, natural plant composition never reached these extremes. Likewise, I found no effect of Exclosure or Date on the relative biomass of N-fixers. The overall quality (C:N ratio) of plant litter may have not shifted enough to impact N cycling, even if the abundance of litter did.

The physical (non-consumptive) effects of herbivores can impact N cycling (Schrama et al. 2013b), potentially counteracting the effects of changing litter supply. Larger herbivores, like deer, can compact soil, leading to lower soil moisture, decreased rates of N cycling (Schrama et al. 2013a), and losses of soil C and N (Asner et al. 2004, Gass and Binkley 2011). Although it was not explicitly measured in this experiment, it is possible that herbivore trampling exerted a physical effect that counter-acted the increases in N cycling potentially caused by dung/urine inputs.

It is worth noting that this was a short-term experiment. Effects of herbivore exclosures on nutrient cycling might have presented themselves after a decade-scale exclosure experiment. In other short-term exclosure experiments (less than 10 years), effects on soil properties were not detected (Andrioli et al. 2010, Lu et al. 2015). After a three-year rodent-exclosure experiment in a post-fire grassland, herb biomass was higher in exclosures than open plots, but N-mineralization was not significantly different (Moorhead et al. 2017). A study in the Canary Islands showed no change to soil chemical characteristics four years after goat grazing removal (Fernández-Lugo et al. 2009). Relva et al. (2014) found no effect of deer exclosure on soil nutrient cycling in a Patagonia conifer forest, despite changes to plant composition.

At the same time, other studies have demonstrated effects of short-term herbivore exclosure. While a test of short-term grazing in Swiss grasslands found an effect on soil temperature, but none on soil total N, C, or P (Haynes et al. 2014), general mammalian herbivore exclosure in the same study increased net-N-mineralization after five years (Risch et al. 2015). Stritar et al. (2010) found that elk decreased soil total N and organic C in the first two years after fire, but increased nitrate concentration. In other short-term experiments, the impacts to C cycling (Chang et al. 2018) and N cycling (Liu et al. 2018) depended on the diversity of herbs and/or herbivores.

Conclusion

In post-fire chaparral, the exclusion of herbivores resulted in an increase in herb biomass but did not result in a dramatic change in relative N-fixer composition or in monthly nutrient-cycling measurements. Non-native invasive annual herbs were the most abundant functional group and the most heavily grazed by herbivores; this finding suggests mammalian herbivores may play a role in limiting grassland invasion of chaparral after fire. Investigations that connect patterns of herbivory to N and C cycling have shown varying and contradictory results. This experiment adds to the pool of findings that will contribute to an evolving predictive framework of herbivore impacts on nutrient cycling.

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TABLES

Table 1. Test of half-cage exclosure effect. Results of Type III ANOVA on linear mixed effects models of herb vegetation biomass (square root-transformed). Random effects are *plot*, *block*, and *site*. There are no significant effects.

Response Variable	**F (p)**
	Exclosure
Vegetation	
Total herbs	0.04(0.846)
N-fixing herbs	
All N-fixing herbs	1.25(0.291)
Non-native annuals	0.52(0.476)
Native annuals	0.71(0.421)
Native perennials	0.10(0.748)
Non-N-fixing herbs	
All Non-N-fixing herbs	0.96(0.354)
Non-native annuals	1.57(0.241)
Non-native perennials	0.10(0.754)
Native annuals	0.85(0.360)
Native perennials	1.37(0.258)

Table 2. Soil block-level pre-treatment characteristics.

Season (Site)	Block	Bulk Density (g/cm^3)	Model Used	Sand/Silt/Clay (%)	Soil Type	Total C (mg g^{-1})	Total N (mg g^{-1})	NH$_4^+$-N (µg g^{-1})	NO$_3^-$-N (µg g^{-1})
Spring	J1	1.4	E	30 / 30 / 40	C	28.7	1.7	8.8	2.6
	J2	1.5	E, H	28 / 31 / 41	C	28.5	1.8	2.9	0.9
	J3	1.3	D	36 / 27 / 36	CL	27.4	1.6	2.9	1.7
Site J	J4	1.3	E	20 / 28 / 52	C	26.5	1.8	5.0	1.8
	J5	1.3	E, H	31 / 18 / 51	C	16.4	1.2	8.4	1.3
	J6	1.1	E	30 / 28 / 42	C	29.3	1.8	10.6	2.3
	T1	1.4	E	36 / 25 / 39	CL	24.2	1.4	4.8	0.4
	T2	1.2	D	30 / 29 / 41	C	29.1	1.6	4.9	0.5
Site T	T3	1.1	E	35 / 24 / 41	C	23.6	1.5	4.5	0.2
	T4	1.2	E, H	31 / 30 / 40	C	30.8	1.8	5.5	0.8
	T5	1.1	E, H	29 / 31 / 41	C	30.3	1.7	6.4	0.5
	T6	1.0	E, H	31 / 25 / 44	C	40.9	2.5	5.9	1.5
Fall	K1	1.3	E, H	30 / 34 / 37	CL	35.3	1.8	11.4	0.5
	K2	0.9	D	36 / 32 / 31	CL	39.4	2.4	23.9	2.5
	K3	1.3	E	36 / 26 / 37	CL	31.0	1.9	11.2	0.6
Site K	K4	1.3	H	29 / 31 / 40	C	37.7	1.9	8.9	1.5
	K5	1.4	E, H	37 / 27 / 36	CL	31.6	1.9	14.6	0.8
	K6	1.3	D	24 / 29 / 47	C	32.4	1.9	13.0	1.0
	L1	1.0	E	32 / 28 / 40	C	38.6	2.1	10.3	1.0
	L2	1.1	H	32 / 29 / 39	CL	25.2	1.5	23.2	2.5
Site L	L3	**1.4**	E	35 / 32 / 33	CL	33.5	1.8	8.3	2.6
	L4	1.2	D	27 / 34 / 39	CL	29.0	1.6	10.3	2.2
	L5	1.4	E	24 / 30 / 46	C	28.4	1.7	6.0	0.6
	L6	1.5	E, H	28 / 29 / 44	C	21.9	1.3	5.0	2.4

Model Used: E = Full model exclosure effect, H = Test of half-cage artifact, D = Dropped from analysis.
Soil Type: C = Clay, CL = Clay Loam Bolded bulk density value measure at later date (October 2018)

Table 3. Results of Type III ANOVA on linear mixed effects models of herb vegetation biomass and soil characteristics. Random effects are *plot*, *block*, and *site*. **Bold** indicates significant effects ($p \leq 0.10$). $^{\surd}$variable square-root-transformed.

Response Variable	**F (p)**		
	Exclosure	***Date***	***Exclosure* x *Date***
Vegetation			
Total herbs$^{\surd}$	**7.42(0.015)**	**33.33(<0.001)**	2.48(0.117)
N-fixing herbs			
All N-fixing herbs$^{\surd}$	1.73(0.207)	**17.73(<0.001)**	1.29(0.257)
Non-native annuals$^{\surd}$	0.59(0.443)	0.33(0.565)	1.71(0.192)
Native annuals$^{\surd}$	1.69(0.211)	**13.39(<0.001)**	0.97(0.326)
Native perennials$^{\surd}$	2.85(0.110)	2.61(0.108)	2.70(0.102)
Non-N-fixing herbs			
All non-N-fixing herbs$^{\surd}$	**7.06(0.018)**	**24.74(<0.001)**	1.00(0.318)
Non-native annuals$^{\surd}$	**8.45(0.010)**	**93.32(<0.001)**	0.18(0.669)
Non-native perennials$^{\surd}$	0.94(0.346)	1.16(0.282)	0.42(0.519)
Native annuals$^{\surd}$	0.50(0.490)	**7.84(0.006)**	0.01(0.904)
Native perennials$^{\surd}$	0.38(0.547)	0.81(0.370)	0.32(0.574)
Relative abundance			
% Annuals	0.30(0.585)	**3.47(0.064)**	1.32(0.252)
% N-fixers	1.31(0.269)	1.77(0.185)	0.53(0.4675)
% Non-natives	**3.90(0.066)**	**54.68(<0.001)**	0.04(0.851)
Soil Characteristics			
Gravimetric Water	**4.34(0.054)**	**203.67(<0.001)**	0.54(0.807)
NH_4^+-N$^{\surd}$	0.38(0.544)	**101.53(<0.001)**	0.80(0.586)
NO_3^--N$^{\surd}$	0.22(0.647)	**31.3(<0.001)**	0.68(0.689)
Net-N-Mineralization$^{\surd}$	**6.74(0.020)**	**18.87(<0.001)**	0.80(0.586)
Nitrification$^{\surd}$	**4.92(0.027)**	**45.19(<0.001)**	1.44(0.190)
Respiration	0.009(0.927)	**26.20(<0.001)**	0.09(0.913)
TC	0.08(0.777)	**3.42(0.074)**	**3.27(0.080)**
TN	0.05(0.818)	**5.43(0.026)**	1.07(0.309)

FIGURES

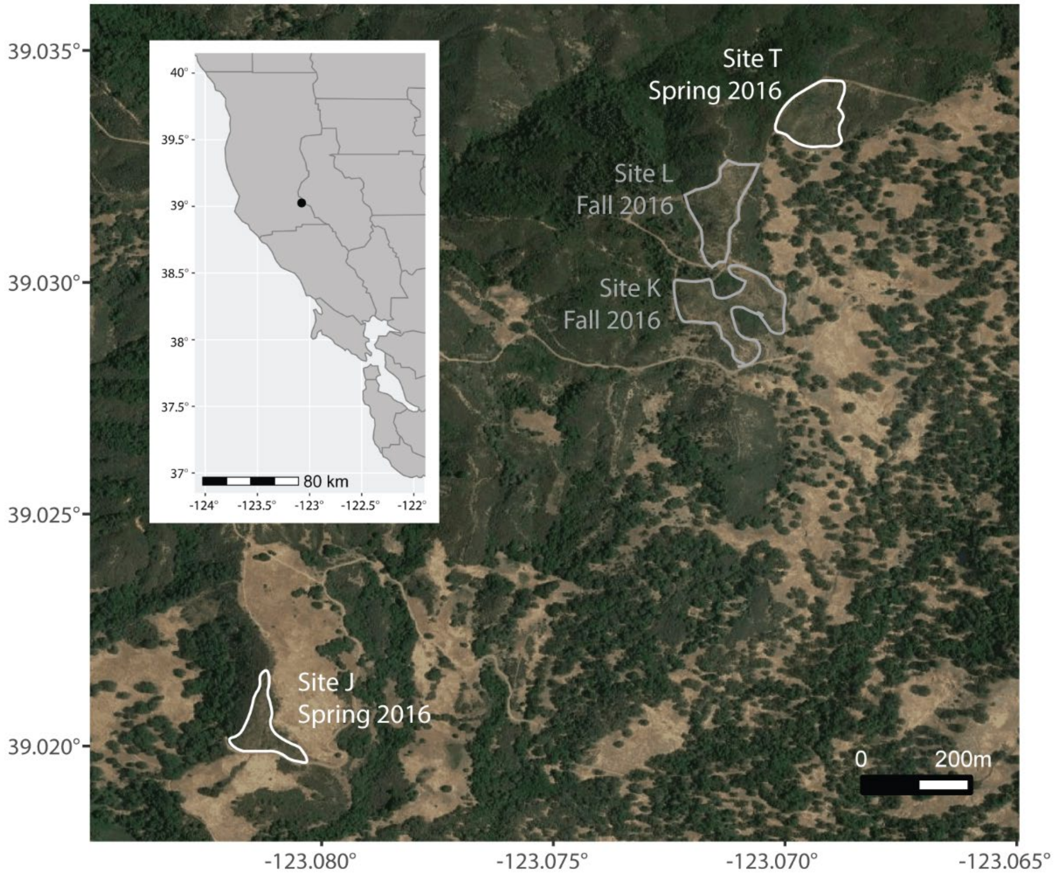

Figure 1. Location of research sites within the Northern California region and perimeters of each prescribed fire. Basemap was built with Google Maps from imagery captured in 2018 and copyrighted (2019) by Mazar Technologies, USDA Farm Service Agency. Black dot in inset map identifies project location.

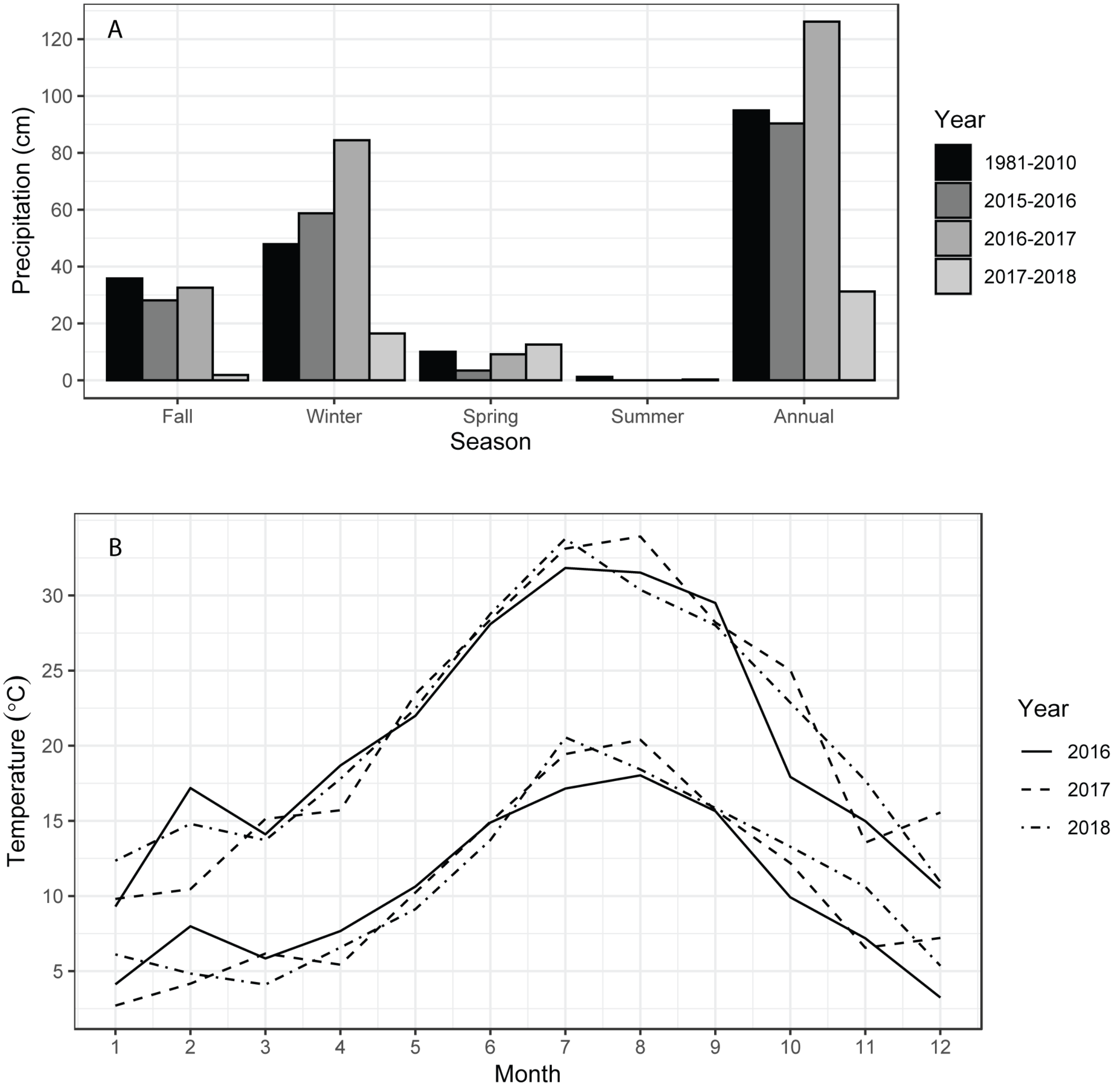

Figure 2. Annual weather data at Hopland Research and Extension Center (HREC). (a) Seasonal total precipitation from two nearby stations; Data from 2015-2018 are from Hopland Station (Elev. 817 m;39.031,-123.081) and 30-year normal are from HREC Headquarters (Elev. 263 m; 39.001,-123.080). (b) Monthly means of minimum and maximum daily temperature are from HREC Headquarters only.

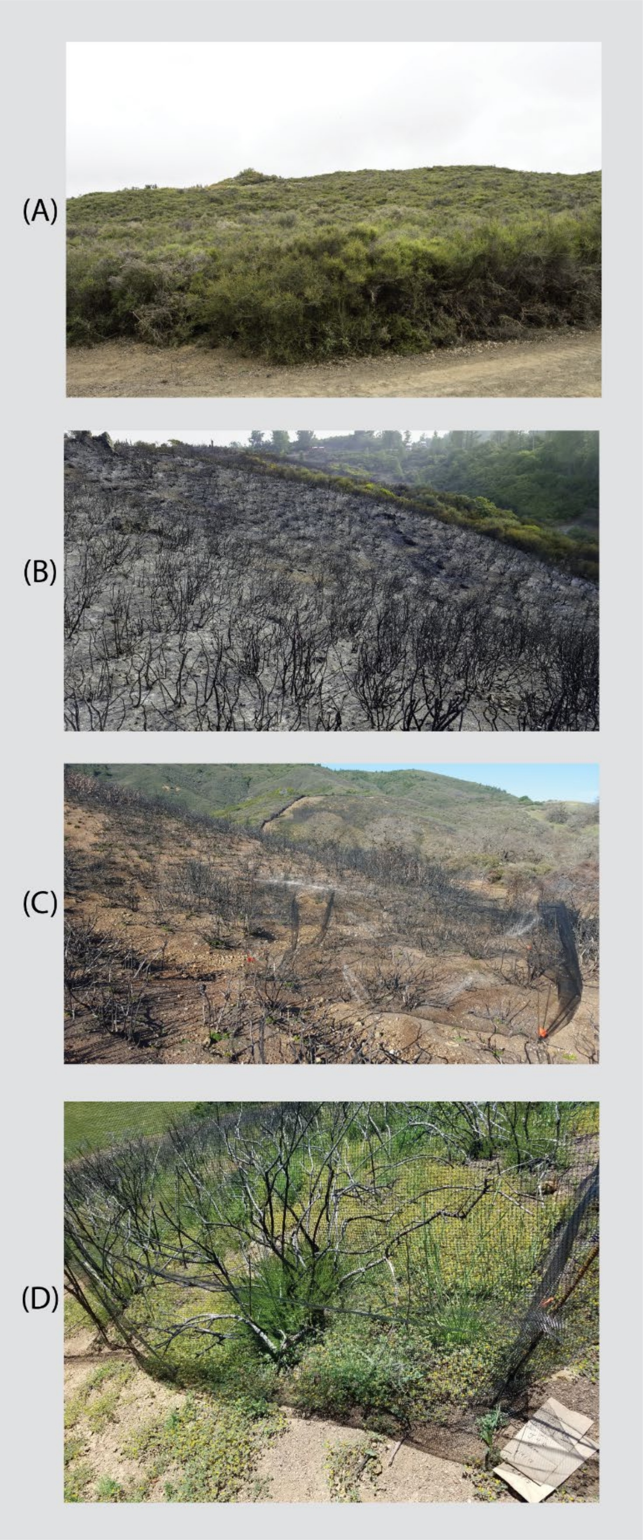

Figure 3. Photos of vegetation and setup, including: (A) mature pre-burn chaparral (Site T, April 21, 2016), (B) immediate post-fire chaparral (Site K, October 23, 2016), (C) herbivore exclosure before herb growth (Site L, March 28, 2017) and (D) herbivore exclosure after one year of growth (Site J, May 9, 2017). Photo credit: Lindsey Hendricks-Franco.

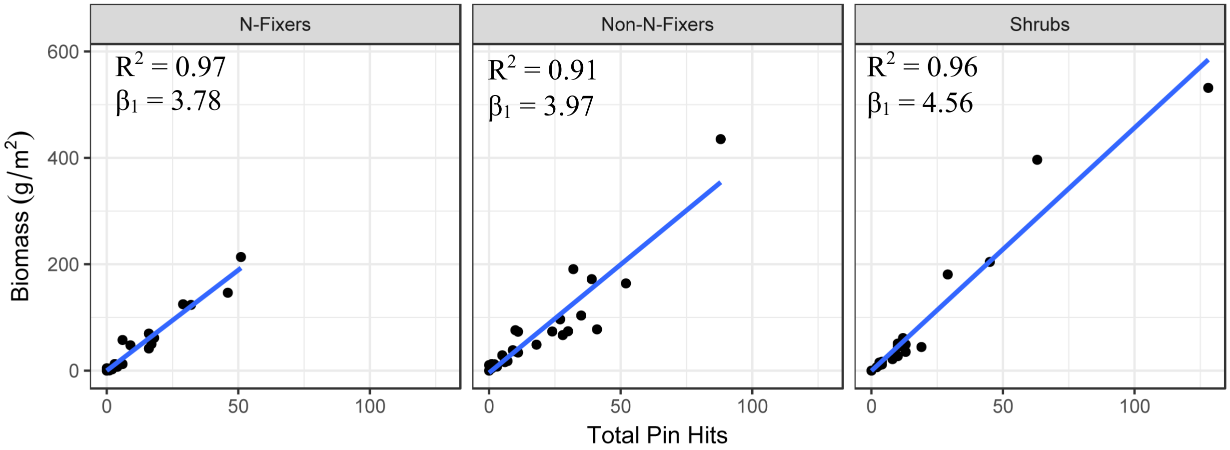

Figure 4. Relationship of dry plant biomass to pin hits using a 0.5mx0.5m pin frame with 20 pins. Plots were sampled at the end of the first post-fire growing season (June/July 2017).

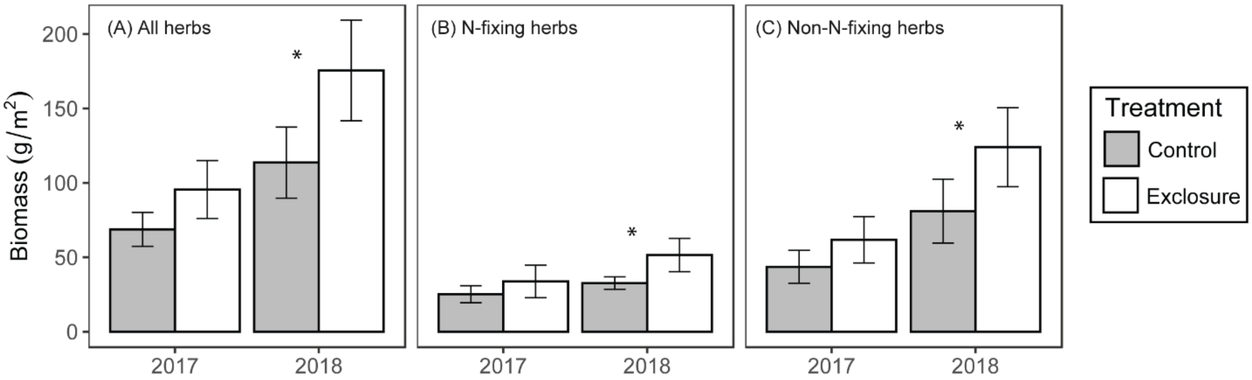

Figure 5. Response of broad herb functional groups to herbivore exclosures. Error bars represent S.E.M. *significant effect of exclosure (p ≤0.10) in planned contrasts of treatment within year.

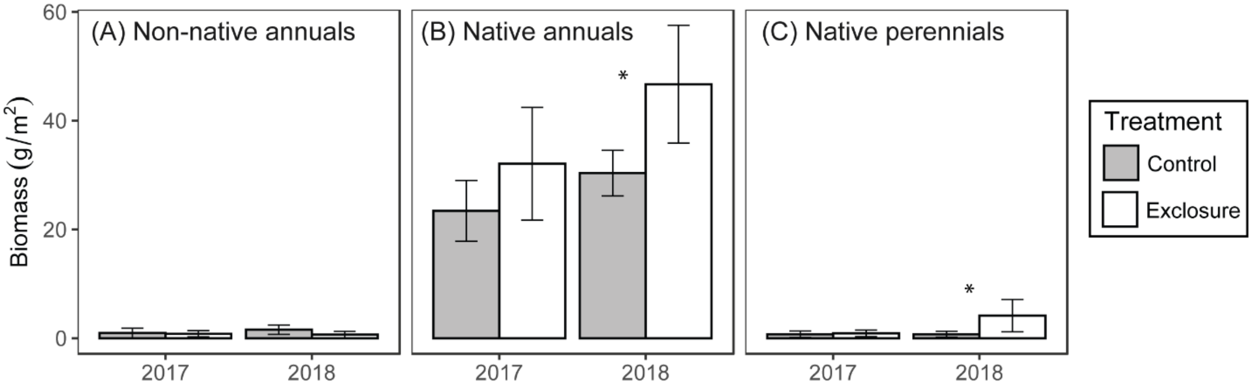

Figure 6. Response of N-fixing herb functional groups to herbivore exclosures. Error bars represent S.E.M. *significant effect of exclosure (p ≤0.10) in planned contrasts of treatment within year.

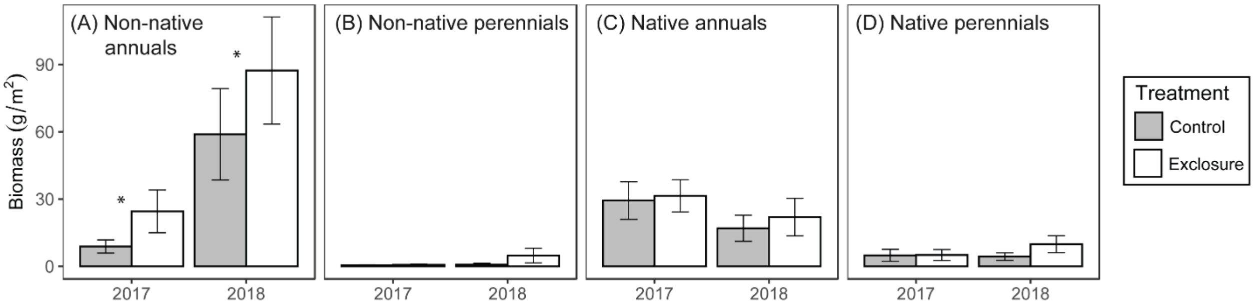

Figure 7. Response of non-N-fixing herb functional groups to herbivore exclosures. Error bars represent S.E.M. *Significant effect of exclosure (p ≤0.10) in planned contrasts of treatment within year.

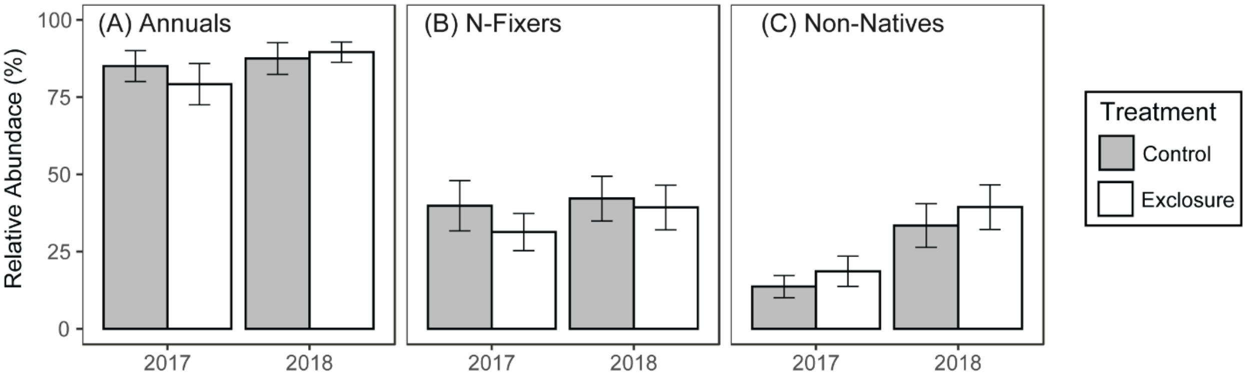

Figure 8. Relative abundance of herb functional groups in response to herbivore exclosures. Error bars represent S.E.M. *Significant effect of exclosure (p ≤0.10) in planned contrasts of treatment within year.

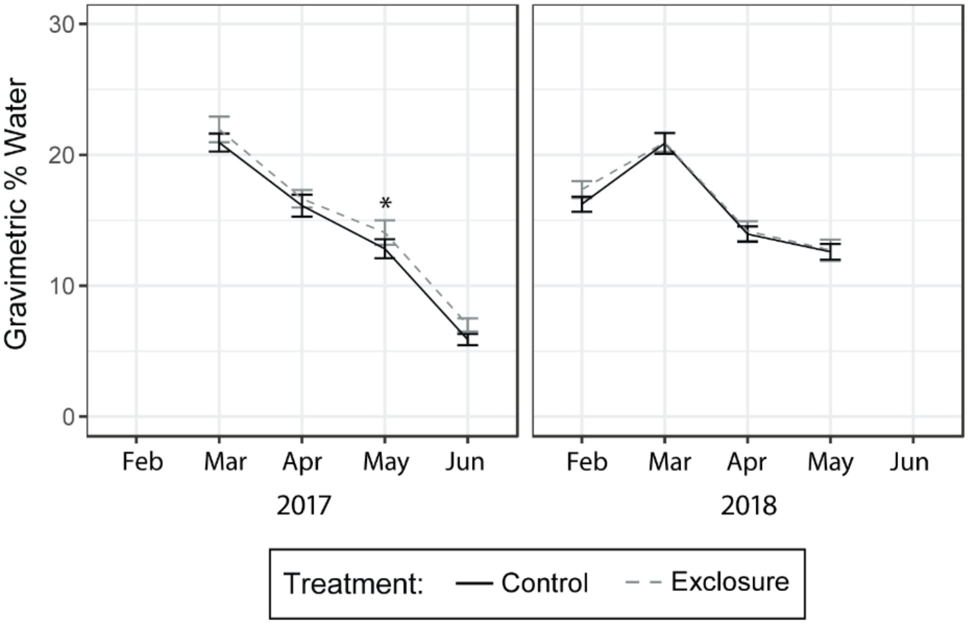

Figure 9. Gravimetric soil moisture over the course of the experiment. Error bars represent S.E.M. *Significant effect of exclosure (p ≤0.10) in planned contrasts of treatment within date.

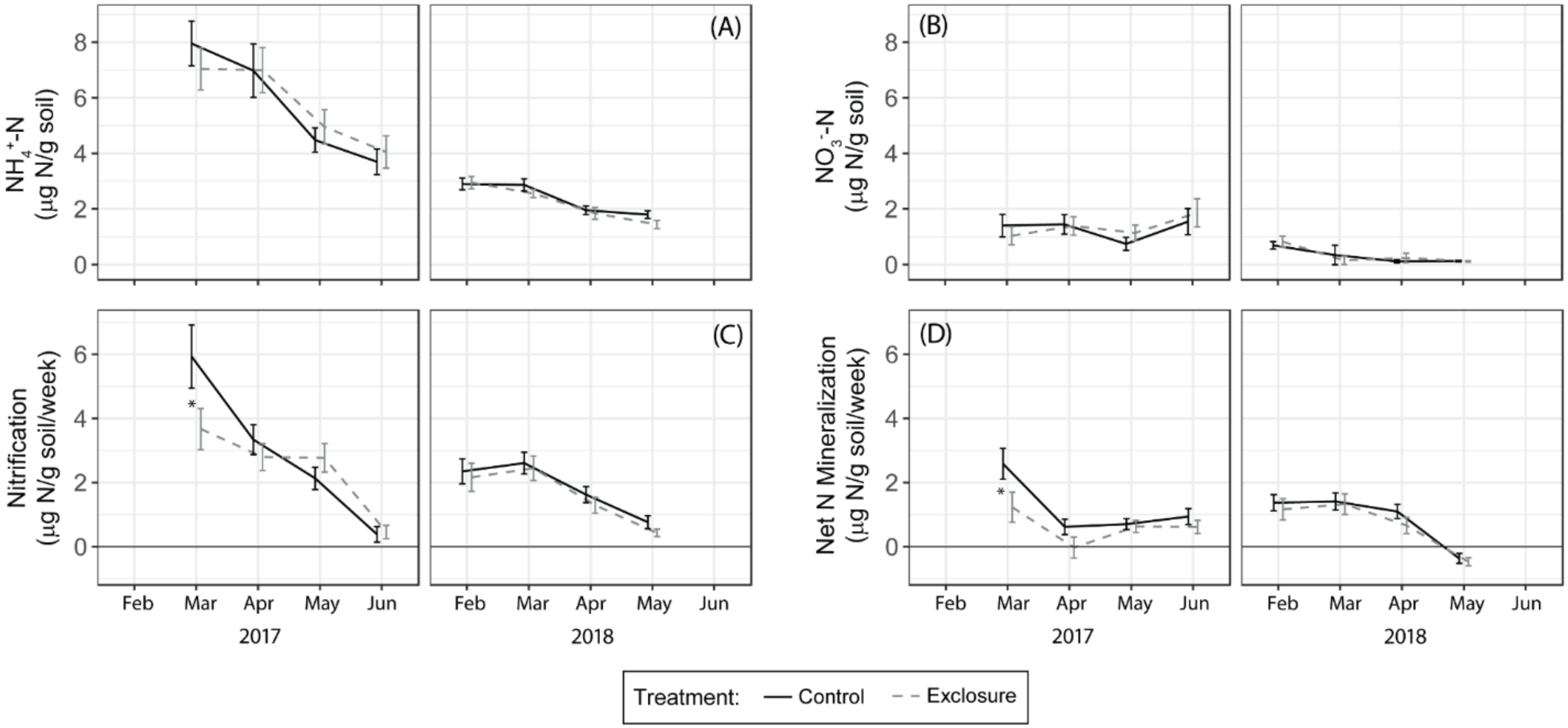

Figure 10. Soil mineral N pools and mineralization rates throughout the course of the experiment. Error bars represent S.E.M. *Significant effect of exclosure ($p \leq 0.10$) in planned contrasts of treatment within date.

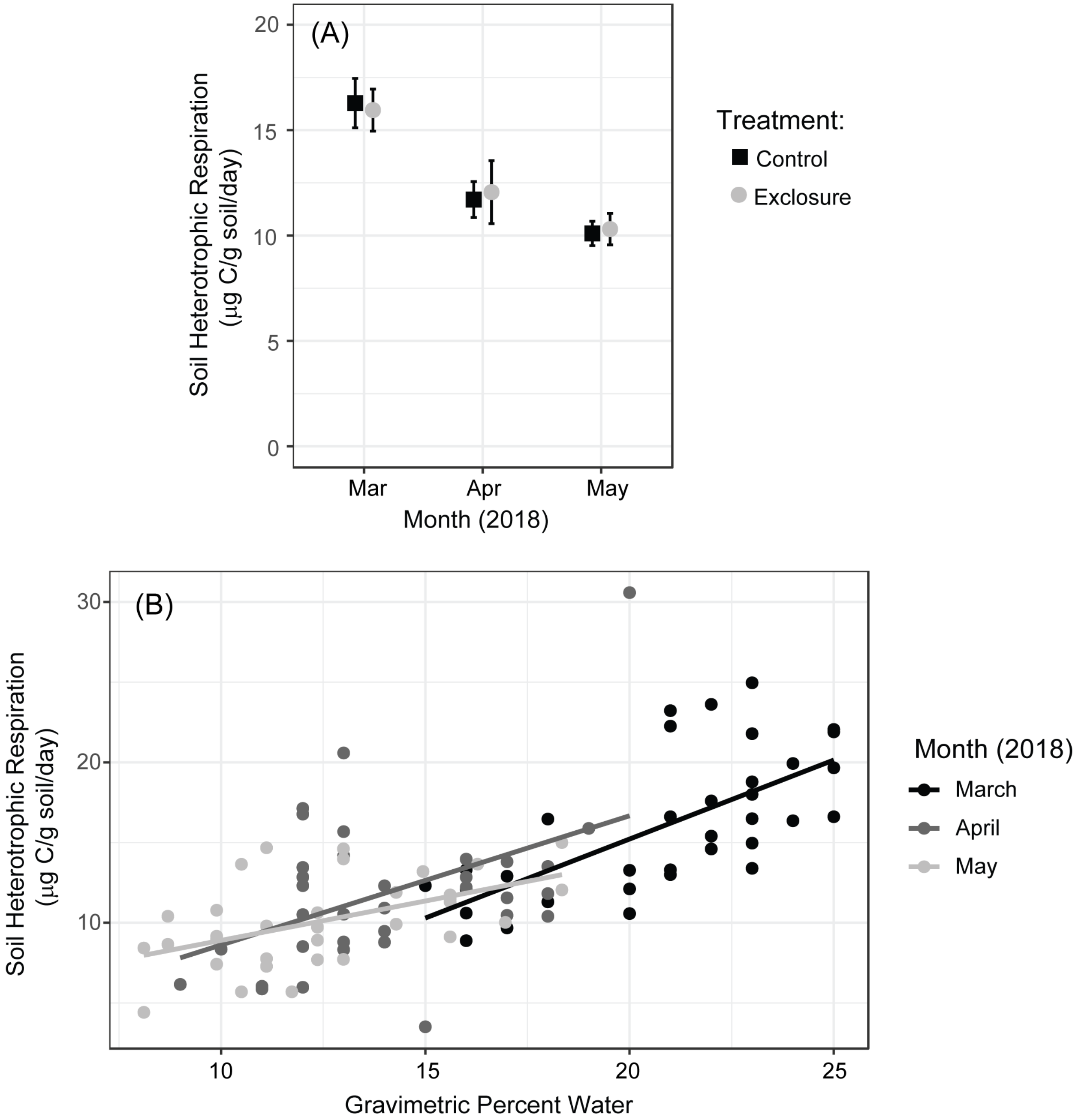

Figure 11. (A) Monthly soil respiration in the second growing season post-fire and (B) soil respiration as a function of gravimetric percent water. Error bars represent S.E.M.

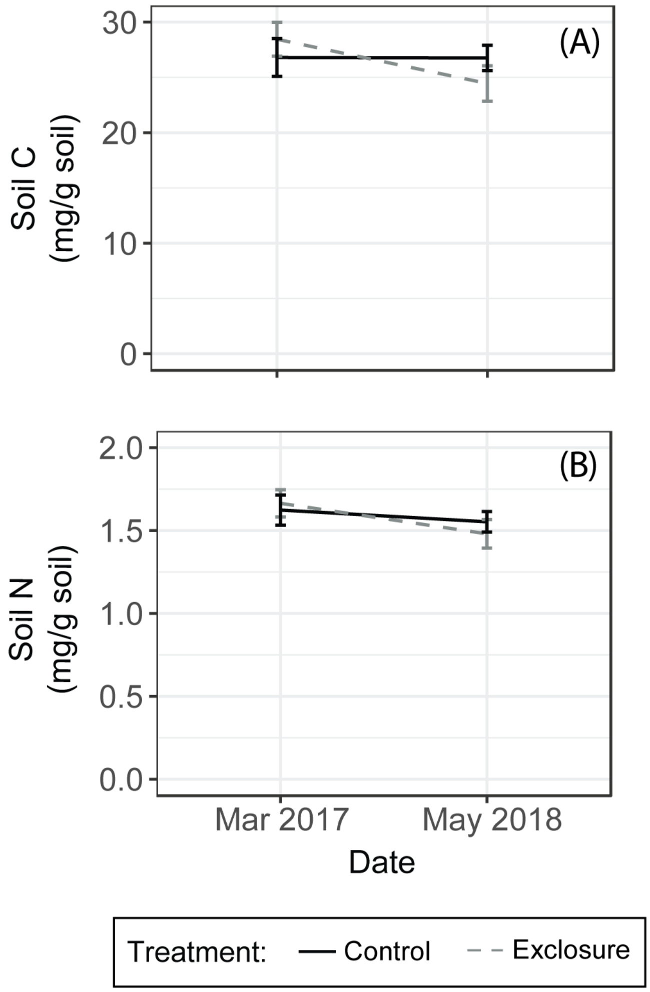

Figure 12. Total soil C and N at beginning and end of experiment. Error bars represent S.E.M.

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CHAPTER 3

Post-fire herbaceous assemblages impact chaparral soil N and C cycling.

ABSTRACT

Nitrogen (N) is often limiting to plant growth and can be an important driver of ecological succession. Herbaceous plants can influence soil N dynamics through a variety of mechanisms, including root uptake, decomposition of dead tissue, and rhizodeposition (root exudate); these are all processes that are influenced by plant abundance and tissue C:N. Experimental manipulations of wild plant assemblages are a powerful tool to demonstrate how plant traits influence belowground ecosystem processes. This study focused on the impact of N-fixing and non-N-fixing herbs on soil ecosystem processes in California's widespread chaparral shrublands. Periodic crown-fire in chaparral temporarily removes all living shrub cover, deposits ammonium on soils, and allows functionally diverse herbaceous assemblages to dominate the landscape for 3-5 years. It has been suggested that these herbs play an important role in immobilizing ash-derived mineral N, preventing N losses due to leaching and runoff, and contributing N from symbiotic root fixation. I implemented a two-year herb-removal experiment to test the impact of herb functional group on post-fire chaparral soil N and C cycling. I weeded plots to include (1) all herbs, (2) only non-N-fixing species, (3) only N-fixing species, and (4) no herbs. In each plot, herbaceous biomass, mineral N concentrations, N and C mineralization rates, and bulk soil N and C were measured to assess responses. At the end of two years, plots with no herbs had lower soil respiration rates and bulk soil C and N than all herb treatments. Two treatments, no-herb and N-fixer plots, had elevated mineral N concentrations and N mineralization rates in the second year of the experiment. Decomposition of N-rich litter and N rhizodeposition are proposed as mechanisms for rapid N cycling in N-fixer plots. A lack of plant uptake or release from microbial-suppressing phytochemicals could have influenced nutrient dynamics in no-herb plots. These results demonstrate that a combination of N-fixing and non-N-fixing species in post-fire herb assemblages maximized immobilization of mineral N for storage in soils and built soil organic C, all essential for soil health and N supply during chaparral succession. Additionally, these results provide a unique dataset that links plant functional diversity and aboveground interactions to belowground ecosystem processes in a natural context.

INTRODUCTION

As the frequency and intensity of wildfires increase with changing climate (Westerling 2016), it is urgent to elucidate the mechanisms that drive post-fire ecosystem recovery. Nitrogen (N) availability can be an important driver of plant succession after disturbance (Parrish and Bazzaz 1982, Tilman 1986, Wilson and Tilman 1991, McLendon and Redente 1992). At the same time, plants themselves influence soil ecosystem processes through patterns of growth, symbiotic N-fixation, interspecific competition, and decomposition patterns, all processes heavily mediated by plant functional group (Díaz and Cabido 2001). There is a growing appreciation for the need to link ecological patterns in aboveground communities to soil nutrient cycling (Naeem and Wright 2003, Díaz et al. 2003), particularly to achieve restoration and conservation goals (Heneghan et al. 2008, Kardol and Wardle 2010). California chaparral shrublands cover 7% of the state's land area and are susceptible to high-intensity summer and fall fires (Keeley and Davis 2007). Nitrogen is often limiting to plant growth in chaparral ecosystems (Wier 1950, Hellmers et al. 1955, Vlamis and Gowans 1961, Christensen and Muller 1975a, McMaster et al. 1982) and N availability can influence shrub and herb succession after fire (Guo 2001, Pasquini and Vourlitis 2010, Kimball et al. 2014). This study addresses the effects of early successional herbaceous assemblages, particularly the N-fixing and non-N-fixing herbs, on chaparral soil N and C cycling.

During chaparral fire, large net losses of N, particularly organic N, occur through volatilization from shrub biomass, litter, and soils (Debano and Conrad 1978, DeBano et al. 1979). Residual mineral N tends to be highly elevated after fire. The ash layer deposited on chaparral soils is often rich in ammonium (NH_4^+) (Christensen 1973, Debano and Conrad 1978), the form commonly utilized by microbes and most plants (Bloom 1997). Within 2-3 months after fire, the onset of winter rains can stimulate rapid nitrification, which is the conversion of NH_4^+ to nitrate (NO_3^-) (Christensen 1973). Some plant species can take up NO_3^- although NO_3^- uptake requires energy expenditure in the plant for the reduction to NH_4^+ in tissues (Salsac et al. 1987). However, NO_3^- is more soluble and vulnerable to leaching than NH_4^+ in most soils, and thus nitrification and subsequent leaching can contribute to even greater soil N losses (Debano and Conrad 1978). The plants that immediately colonize after fire may play an essential role in immobilizing ash-derived N, influencing soil nutrient cycling, and preventing N losses that would slow shrub recovery and threaten water quality in adjacent aquatic habitats. Internal cycling of this retained N through subsequent litter decomposition provides a supply of N to support plant productivity (Parton et al. 2007) during succession, particularly in the case of chaparral which tends to leak nutrients (Miller 1981).

Sequences of post-fire plant succession in chaparral have been well-characterized. At maturity, stands contain dense assemblages of native shrubs, mainly *Adenostoma fasciculatum* with interspersed *Ceanothus spp., Arctostaphylos spp.*, *Quercus spp*., and other taxa (Keeley and Davis 2007). Mature *Adenostoma* chaparral hosts almost no herbaceous understory beneath its dense shrub canopy (Sampson 1944, Went et al. 1952, Horton and Kraebel 1955, Hellmers et al. 1955, Muller et al. 1968, Chou and Muller 1972, Christensen and Muller 1975b, Shmida and Whittaker 1981, see Chapter 1). Periodic wildfire, typically every 30 – 90 years (Water and Safford 2011), temporarily eliminates shrub cover and initiates a transient change in plant assemblages. Soon after fire, shrubs re-establish from either a fire-stimulated seed bank or resprouting burls of burned adults (Keeley et al. 2005). At the same time, bare soil is rapidly colonized by a flush of herbaceous plants (Brandegee 1891, Cooper 1922, Sampson 1944, Horton and Kraebel 1955, Sweeney 1956, Hanes 1971, Keeley et al. 1981, 2005, Keeley and Keeley 1988, Potts and Stephens 2009), which dominate for 3-5 years before the recovering shrub canopy closes (Keeley et al. 2005, Potts et al. 2010). These herbs are functionally diverse, including non-N-fixing annual herbs (e.g. *Emmenanthe penduliflora ssp. penduliflora*, *Calandrinia breweri*), non-N-fixing perennials (e.g. *Chlorogalum pomeridianum*), N-fixing perennials (e.g. *Acmismon glaber*), and N-fixing annuals (e.g. *Acmismon spp.* and *Trifolium spp.*). These ephemeral herbs can dominate recently-burned chaparral for the first two years after fire, with total summed cover of herbaceous species at 100% or higher at the peak growing season (see Chapter 1). It has been repeatedly suggested that short-lived post-fire herbs play an important role in immobilizing ash-derived N and (Rundel and Parsons 1984, Hanan et al. 2016, Goodridge et al. 2018) and increasing soil N availability through inputs from N-fixing herbs (Rundel and Parsons 1984, Guo 2001); however, no experimental approach has directly tested the impact of these ephemeral plant assemblages, and their functional diversity, on post-fire N or C cycling.

Post-fire herb assemblages contain a mix of N-fixing and non-N-fixing species (Sampson 1944, Keeley et al. 1981). These two functional groups are predicted to exert distinct effects on soil N and C cycling, based on their plant tissue chemistry and the energetic costs associated with their resource acquisition strategies. N-fixers, which host root bacterial symbionts that convert atmospheric nitrogen to NH_4^+, tend to have higher tissue N content (lower C:N ratio) than non-N-fixers (Wright et al. 2004, Scherer-Lorenzen 2008). When N-fixers die or senesce, they deposit N-rich litter, which can rapidly decompose (Moro and Domingo 2000, Hobbie 2005, Parton et al. 2007, Scherer-Lorenzen 2008) and increase rates of soil N mineralization (Robertson and Groffman 2007). Litter with lower C:N ratio also generally favors the accumulation of soil organic carbon (Zhou et al. 2019), a process critical for drawing down atmospheric CO_2 concentrations (Rumpel et al. 2018). Plant litter with comparatively high C:N ratio, such as that from non-N-fixers, may decompose more slowly and even lead to the immobilization of mineral N during early decomposition (Parton et al. 2007).

At the same time, soil N and C cycling depend not only on the C:N ratio, but also the presence or abundance of plants and decomposing litter. The N-rich post-fire conditions may not favor the growth of N-fixers, which are generally poor competitors in an environment with high available N (Vitousek et al. 2002). Symbiotic N fixation is costly for host plants, in terms of energy, C, and mineral resources, which can limit their growth rate (Gutschick 1981, Vitousek and Howarth 1991). Non-N-fixers can grow quickly in high-N conditions, absorbing available soil mineral N and ultimately producing more biomass and plant litter. Increased litter mass is generally associated with increased soil C accumulation and soil heterotrophic respiration (Xu et al. 2013). When Non-N-fixers and N-fixers grow together, as they typically do after chaparral fire, N-fixers may facilitate the growth of non-N-fixers through the addition of the their high N litter (Maron and Connors 1996, Menge et al. 2008) and root N exudates (Paynel et al. 2008); although the enhanced growth of non-N-fixers may competitively inhibit the N-fixers themselves, their co-occurance may lead to enhanced biomass production.

In this two-year study, I implemented a field herb-removal experiment to test the impact of herb functional diversity on post-fire chaparral soil N and C cycling. Herb removal experiments are a powerful tool to aid in our understanding of ecosystem effects of local functional plant diversity in natural ecosystems (Díaz et al. 2003). By weeding plants as they emerged from recently burned chaparral, I manipulated the presence of N-fixers and non-N-fixers in post-fire herb assemblages. Treatments were: (1) all herbs, (2) only non-N-fixing species, (3) only N-fixing species, or (4) no herbs. As response variables, I measured herbaceous biomass and soil N and C dynamics. This experiment provides an *in situ* test of competition and facilitation between N-fixing and non-N-fixing herbs in post-fire chaparral. I predicted that N-fixers would be poor competitors against non-N fixers where soil available N is high due to energetic costs associated with maintaining N-fixing bacterial symbionts. I also expected non-N-fixers to be facilitated by N-fixers, resulting in greater growth of non-N-fixers where the two groups grew together, resulting in the highest biomass in plots containing all herbs, followed by non-N-fixers and N-fixers. I predicted the highest levels of mineral N and rates of N mineralization would occur in plots with exclusively N-fixing plants, due to inputs of N-rich plant litter. However, I predicted the highest rate of total soil N (TN) and C (TC) accumulation from all-herb plots and the lowest from bare plots, following plant biomass trends.

METHODS

Study Location and Site Selection

I conducted this study at the Hopland Research and Extension Center (Mendocino County, California, 39.00, -123.08, **Figure 1**). Hopland is located in the inner North Coast Range of California. The vegetation is a mosaic typical of Mediterranean California, including grasslands, chaparral shrublands, oak woodlands, and mixed evergreen forests. Hopland experiences a typical mediterranean-type climate with a warm dry spring through summer (1981-2010: 11.2 cm precip.) and a mild rainy fall through winter (83.7 cm precip.). The first season of monitoring had a particularly rainy fall and winter (2016-2017: 117.0 cm), while the second was comparatively dry (2017-2018: 18.3 cm, **Figure 2A**). Temperatures were fairly consistent between years of sampling, with mean lows–highs of 10.2–20.5°C in 2016, 10.4–21.0°C in 2017, and 10.7–21.1°C in 2018 (**Figure 2B**).

Plots were all located in the perimeter of a ~1ha prescribed fire burned on April 21, 2016. The California Department of Forestry and Fire Protection (CalFire) set upslope prescribed fire (headfire) using a combination of drip torches with a gasoline/diesel mixture and mounted terra torches with gelled aviation fuel. To prevent fire escape, the borders of the site were cleared by bulldozer and the uphill side of the fire was backburned. The site contained mature chaparral vegetation dominated by chamise (*Adenostoma fasciculatum*) shrubs. Elevation ranged from 565 to 635m and hill slope was south-facing and steep (75% maximum, 25% average). Chaparral prescribed fires conducted outside of the typical summer burn window (June – November; after spring drying and before first fall rain) are typically much less intense than wildfires (Beyers and Wakeman 1997, Stephens et al. 2008) and may favor a different suite of species (Knapp et al. 2009, Wilkin et al. 2017). However, a changing precipitiation patterns, may lead to a lengthened or altered wildfire season in the coming decades (Molinari et al. 2018). A risk of fire escape and wildfire make is difficult to conduct prescribe fires during the typical summer and fall dry season.

Experimental Design

I placed six experimental blocks within the site, with a minimum of 20 m between blocks. Each of the blocks contained four plots of 2x3 m. The plots in a block were arranged side by side along the hillside with a minimum of 1 m between them so that no plot within a block was uphill of another.

There were four treatments, randomly assigned to each of the plots in a block. I selectively weeded herbs so that plots included: (1) all herbs (no removal), (2) only non-N-fixing species (removal of N-fixers), (3) only N-fixing species (removal of non-N-fixers), or (4) no herbs (full removal) (**Figure 3**). Plots were monitored weekly or biweekly during the growing season (December through May) so that herbs could be weeded as soon as they emerged, minimizing soil disturbance. Roots were typically 1 cm or less in length when plants were removed. Where possible, I weeded by reaching from outside the plots to avoid trampling the interior. To control for the ground disturbance due to weeding, I shallowly penetrated the soil surface with a stick at multiple locations within the all-herb (no-removal) plots at each weeding session.

Great care was used to place plots in regions dominated by chamise (*Adenostoma fasciculatum*) chaparral. Vegetation sampling (described below) confirmed dominance by *A. fasciculatum*, with an average standing dry biomass of 49 ±15 g/m^2 in 2017 and 78 ± 14 g/m^2 in

2018. No other shrub exceeded average standing biomass of 1.8 g/m^2 in either year (see vegetation sampling below). In 40-year-old chaparral vegetation, standing living biomass of approximately 5 kg/m^2 has been recorded (Oechel and Reid 1984), approximately 100 times the post-fire shrub biomass reported here.

Vegetation Sampling

I monitored vegetation at peak biomass at the end of each growing season (June-July 2017 and May 2018). Because a July 2018 wildfire burned the experimental plots, it was not possible to conduct a third year of vegetation sampling. I estimated biomass using the point intercept method with a pin-frame sampler. In each 2x3 m plot, I subsampled three 0.5x0.5 m quadrats, one in the center of the plot, one in the top left, and one in the bottom right. The top and bottom plots were always placed 0.5 m inside of the plot, measured from the top and the side. The pin-frame quadrat held twenty pins vertically over the shrub and herbaceous vegetation growing in the plot. The pins were placed so that 5 pins were in each quarter of the quadrat. I counted how many times each pin hit each plant species.

I used the total number of pin hits as a proxy for plant dry biomass (Jonasson 1988). To relate this value to standing biomass, I collected and dried plants within some sampled quadrats. I sampled 32 quadrats using the pin frame, principally outside of the experimental plots to minimize vegetation disturbance. I then clipped aboveground growth of plants and sorted it by plant functional group: shrubs, N-fixing herbs, non-N-fixing herbs. In the lab, I thoroughly rinsed these herbs in water to remove all soil and dried them at 65°C for at least 48 hours before weighing their dry biomass. I related pin hits in each of these groups to biomass using a linear regression for each group. To avoid regression estimates of negative biomass values, I set the y-intercept to zero:

$$biomass = 0 + \beta_1 \times hits \qquad \text{Eqn. 1}$$

where *biomass* is the dry mass of plants (g/m^2) and *hits* are the total number of pins hit/group in plot. R^2 was over 0.9 in all cases, demonstrating a strong relationship between biomass and pin hits (Figure 4 in Chapter 2).

Soil Physical and Chemical Properties

Soil Collection

For all soil measurements in this project, I collected soils to a depth of 10 cm to capture the dynamics most likely driven by herbaceous growth and litter decay. Throughout the 2017 and 2018 spring growing seasons, I collected soil samples monthly from each plot (March-June 2017 and February-May 2018). Generally, I collected four 2.5 cm-diameter, 10 cm-deep soil cores at each plot and pooled the soil to minimize plot level variation. The exception was a collection on February 1, 2017, during which I pooled soil from cores across the whole block to capture seasonal conditions and block-level characteristics before the start of the experiment, without respect to a specific treatment (**Table 1**). At each sampling, the soil cores to be pooled were first collected into a common plastic bag, and then immediately homogenized by gently massaging the bag contents to break up large aggregates and passing the soils through a 4 mm sieve. I refrigerated soils at 4°C soon after collection and processed soils for analysis (described below) within 48 hours.

Bulk Density and Texture

I collected separate soil cores for bulk density analysis during February 1, 2017 block-level sampling. At each block, I collected one soil core (5 cm diameter x 10 cm deep) for bulk density analysis. I carefully scraped off soil from the bottom of the core to ensure that the exact volume of the core was collected. In the lab, I sieved soil cores to 4 mm and used a water displacement method to measure the volume of the removed rocks and roots. The total volume of soil was $volume_{core}$ –$volume_{rocks}$. The remaining soil was dried at 105°C for 72 hours and weighed. Bulk density was the dry mass of soil divided by the total volume. I determined soil texture on soils collected from every block using the hydrometer method (Gee and Bauder 1986), abbreviated with readings at 40 s and 2 h.

Total Soil C and N

Total soil carbon (TC) and nitrogen (TN) were determined from air-dried soils. First, I tested soils for the presence of inorganic C. I gently ground soil samples and moistened with one drop deionized water, then added one drop of 4M HCl. As there was no fizzing or effervescence, I determined that no significant inorganic C was present. Thus, TC is an appropriate measure of organic C. I determined TC and TN on a Flash 2000 Elemental Analyzer (Thermo Scientific, Germany). I analyzed duplicate samples and repeated the analysis of soils for which duplicates differed by more than 10%. I performed this analysis on soils collected from every plot at pre-treatment (March 2017) and post-treatment (May 2018) times. Although the pre-treatment date was actually shortly after exclosure installation, this was the earliest point at which plot-level soils were collected and thus the best indication of pre-treatment conditions available. Post-treatment soils were analyzed at the end of two growing seasons in May 2018.

Soil Mineral Nitrogen and Nitrogen Mineralization

I extracted soils in 2M KCl for analysis of mineral N: NH_4^+ and NO_3^-. I mixed 10.0 g soil samples with 40 ml of 2M KCl in an acid-washed 50 ml centrifuge tube. Samples were shaken for 1 hour at 200 RPM. The soil slurry was then gravity filtered through KCl soaked Whatman #1 filters and acid-washed funnels into separate new clean centrifuge tubes. Samples were stored at -20°C until analysis.

I determined the rate of soil net N mineralization and nitrification using a laboratory dark incubation. This setup was combined with a soil C mineralization (respiration) incubation described below. After measuring soil subsamples for mineral N at collection (above), soils were incubated in 495 ml glass mason jars. A subsample of approximately 30 g of wet soil was packed into a tared 30 ml medicine cup and weighed. The medicine cup was placed carefully into the base of the jar, which was sealed and allowed to incubate in the dark for one week. After the 7 days, I removed each incubated soil sample from its jar, mixed it thoroughly, then measured out a 10.0 g subsample for a 2M KCl extraction. This subsample was extracted using the same procedure described above. The resulting extract samples were analyzed for NH-$^{+}$ and NO-$^{-}$ concentrations using Lachat Flow Injection Analyzer (Hofer 2003, Knepel 2003) or the microplate method (Wu et al. 2016).

Soil gravimetric percent moisture was determined for every collected soil. I measured 10.0 g subsamples into metal tins and dried the soils at 105°C for 24h hours and then weighed the dry soil. Soil gravimetric moisture content was calculated as: $(mass_{wet} – mass_{dry})/mass_{dry}$. All soil measurements were normalized by dry mass.

Carbon Mineralization (Heterotrophic Respiration)

During the most active months of the second year of soil collection (March-May 2018), I used the soil mineral N incubations to also collect data on soil respiration over a 48 h period. Samples were collected in plastic syringes with O-ring seals and medical grade stopcocks. I took three initial 5 ml samples from ambient air above the jars prior to sealing them with gas-tight lids fitted with septa (T_1). After a 48 h dark incubation, I injected 5 ml of CO_2-free air into each jar, pumped the syringe slowly to mix the headspace, and then withdrew a 5 ml sample for analysis (T_2). Samples were analyzed on an FoxBox IRMS Flow Analyzer. I calculated the total headspace carbon at T_1 and T_2, adjusting for the temperature and pressure in the jars, and the small dilution from injecting CO2-free air at T_2. I calculated respiration as (T_2 - T_1) / T (days). Data are reported as µgCO2-C/g dry soil/d.

Statistical Analysis

I fit all models in *R* (R Core Team 2018) with the package *lme4* (Bates et al. 2015), using a restricted maximum likelihood estimation procedure (REML) and performed a Type III ANOVA analysis using the *lmerTest* package (Kuznetsova et al. 2017). Planned contrasts on the model were made using the *emmeans* package (Lenth 2018). I fit the following linear mixed-effect model to evaluate the main and interactive effects of Treatment (*Trt*) and Date on all measured variables in the experiment:

$$Y = Trt + Date + Trt * Date + Random(Block + Plot) \qquad \text{Eqn. 2}$$

The effects of treatments on each group at each date were determined by *a priori* planned contrasts of estimated marginal means, with no p-penalization procedure (Day and Quinn 1989). I considered $p < 0.1$ as the threshold for a significant effect, a typical threshold for marginal significance that avoids unnecessary risk of Type II error in ecological models with relatively low samples size (Hurlbert and Lombardi 2009). I describe below additional details regarding analyses of specific response variables.

Vegetation Analysis

The removal of select herb functional groups provided a de facto test of competition between N-fixing and non-N-fixing herbs. To test the impact of competitor removal on each functional group, I compared only the relevant treatments (e.g. non-N-fixer biomass in all-herb vs. non-N-fixer plots, to test the impact of N-fixer removal on non-N-fixers). Total herb biomass was analyzed in a model including only treatments with herbs (i.e. not including full-removal plots).

Soil Characteristics

Ammonium-N, NO_3^--N, net N mineralization, and nitrification were measured during four months of the growing season each year (March-June 2017 and February-May 2018). For these measurements, values were pooled into early- and late-season two-month increments of Date for statistical analysis. The other response variables of gravimetric moisture content, TC, TN, and C mineralization (heterotrophic respiration) were also analyzed in the model above (Eqn. 2).

RESULTS

Herb Composition Effects

Total herb biomass was influenced by removal treatment (F = 8.24, $P = 0.008$), year (F = 25.88, $P < 0.001$), and their interaction (F = 5.66, $P = 0.005$). At the end of the first growing season, there was no significant difference in the total biomass in any treatment where herbs were allowed to grow, i.e. excluding the removal (all herbs vs. N-fixers, p = 0.333; all herbs vs. non-N-fixers, p = 0.388; N-fixers vs. non-N-fixers, p = 0.915). By the end of the second year, all herb removal treatments were significantly different in biomass, in descending order from all-herb, to non-N-fixer only, to N-fixer only plots ($p < 0.05$, **Figure 4A-B**).

I compared the partial-removal and all-herb plots as a test of the effect of neighbor removal. N-fixer biomass was influenced by non-N-fixer removal (F = 12.99, $P = 0.005$), but not year (F =1.76, $P = 0.190$) or their interaction (F = 0.06, $P = 0.805$). N-fixers had nearly twice as much biomass in plots where they grew without non-N-fixers (**Figure 4C-D**, grey bars). On the other hand, the removal of N-fixers did not affect the biomass of non-N-fixers (**Figure 4C-D**, white bars, F = 0.55, $P = 0.491$). Non-N-fixer biomass was much higher in year two than year one (F = 22.86, $P < 0.001$), with no interaction of neighbor removal and year (F = 1.56, $P = 0.216$).

Mineral N Pools and Rates

Soil NH_4^+-N and NO_3^--N were measured over the two-year study. In general, NH_4^+-N decreased across all treatments over time (F = 87.57, $P < 0.001$, **Figure 5A-B**), with significant effects of treatmeant (F = 2.57, $P = 0.065$) and the treatment x date interaction (F = 2.51, $P = 0.010$). Although there was a great deal of variation in NH_4^+-N in the initial months of sampling, a clear pattern of treatment effects emerged by the end of 2017 and throughout all of 2018. Both N-fixer and full-removal (no-herb) plots were elevated in NH_4^+-N compared to all-herb and non-N-fixer plots. NO_3^--N also varied over time (F = 5.58, $P = 0.001$), treatment (F = 3.16, $P = 0.038$), and the treatment x time interaction (F = 2.01, $P = 0.042$, **Figure 5C-D**). At the beginning of sampling in early 2017, there was no difference in NO_3^--N between treatments. At the end of both sampling years, NO_3^--N was significantly higher in no-herb plots than all other treatments.

Net N mineralization varied in response to date (F = 19.92, $P < 0.001$), treatment (F = 5.49, $P = 0.002$), and the date x treatment interaction (F = 2.05, $P = 0.037$, **Figure 6A,B**). Nitrification was influenced by the same variables, date (F = 37.86, $P < 0.001$), treatment (F = 3.14, $P = 0.030$), and the date x treatment interaction (F = 2.57, $P = 0.009$, **Figure 6C,D**). Both net N mineralization and net nitrification rates similar across treatments throughout 2017, except for early 2017, when rates of both processes were higher in all-herb and N-fixer plots. Throughout 2018, N-fixer plots were elevated in both net N mineralization and nitrification compared to all other treatments with herbs. By the end of 2018, bare no-herb plots were significantly higher in net N mineralization and nitrification than all-herb and non-N-fixer plots. Throughout the whole experiment, net nitrification rates and net N mineralization rates were correlated ($R^2 = 0.68$, $P < 0.001$), with net nitrification rates almost always higher than net N mineralization rates across sampling points and treatments (**Figure 7**).

Soil gravimetric moisture content varied by date (F = 263.39, $P < 0.001$), but not by treatment (F = 0.65, $P = 0.590$) or treatment x date interaction (F = 0.75, $P = 0.774$, **Figure 8**).

Soil Carbon Mineralization (Heterotrophic Respiration)

Soil heterotrophic respiration was measured in a lab incubation at three sampling times (March-May) of the 2018 growing season (**Figure 9**). Both month (F = 29.40, $P < 0.001$) and treatment (F = 3.22, $P = 0.054$) were significant predictors of soil respiration, with no interaction of the two (F = 0.06, $P = 0.999$). Overall, respiration rates were highest in March ($P < 0.001$), with no difference between rates in April and May. Across all timepoints, the no-herb plots were significantly lower in respiration than all plots with herbs, which were not significantly different from each other. The largest effect was between no-herb and all-herb plots, with an estimated difference of 5.1 μg C/g soil/day at any month; thus, the effect of full herb removal was 29% decrease in soil respiration in March and 42% in April and May.

Bulk Soil C and N

Although there were no significant main effects of treatments on soil TC (F = 0.51, $P = 0.683$), TN (F = 0.62, $P = 0.614$), or C:N ratio (F = 0.37, $P = 0.773$), there was a significant treatment x year interaction influencing all these measurements: TC (F = 3.98, $P = 0.022$), TN (F = 2.93, $P = 0.058$), C:N ratio (F = 3.07, $P = 0.051$). The mian effect of date did not significantly impact TC (F = 0.83, $P = 0.374$) or C:N (F = 1.14, $P = 0.299$), but did impact TN (F = 3.91, $P = 0.062$). At the beginning of the experiment (March 2017) there were no statistically significant treatment differences in bulk soil TC, TN, or C:N ratio (**Figure 10**). By the end of the experiment (May 2018), all-herb plots were significantly higher than no-herb plots in all three metrics. Partial-removal plots, with either N-fixers or non-N-fixers only, were intermediate to the two other treatments, and not significantly different from either one. The effect of full-removal of herbs was substantial, with no-herbs plots 31% lower in C, 22% lower in N, and 13% lower in C:N ratio than all-herb plots.

DISCUSSION

I selectively weeded post-fire chaparral plots to test the effect of herb composition on soil N and C cycling. I predicted that the tissue C:N ratio of herbs would impact soil nutrient processes and that herb removal would demonstrate interactions between N-fixing and non-N-fixing herbs, described below.

Herb Functional Group Interactions

The removal of select herb functional groups before they were allowed to grow provided a *de facto* test of competition and facilitation between N-fixing and non-N-fixing herbs. I hypothesized that N-fixers would be competitively suppressed by the presence of non-N-fixing herbs. In both years of sampling, N-fixers grew to greater abundance when non-N-fixing competitors were removed, implying that their growth was limited by competition with non-N-fixers (**Figure 4C,D**). This is unsurprising, as N-fixers are predicted to be poor competitors in an environment with high available N, such as post-fire chaparral, where the ability to fix N is less advantageous (Vitousek et al. 2002). Symbiotic N fixation is costly for host plants, in terms of energy, C, and mineral resources (Gutschick 1981, Vitousek and Howarth 1991), and there is a cost of N-fixation ability even when the plant symbiont is a facultative N-fixer (Menge et al. 2009). On the other hand, non-N-fixer abundance was unaffected by N-fixer removal, implying that the former was neither competitively inhibited or facilitated by the latter. Non-N-fixers can facilitate non-N-fixers through the addition of low C:N litter (Maron and Connors 1996, Menge et al. 2008) and exudate from their roots (Paynel et al. 2008) which may ultimately competitively inhibit the N-fixers themselves. It is possible that in the high-N post-fire environment, non-N-fixers are not N-limited enough to be facilitated by N-fixers. By the end of year two, when available soil N was lower, there was a slight trend of increased non-N-fixers where N-fixers were present (**Figure 4D**). Perhaps in an additional year of sampling this trend might have continued, showing facilitation of N-fixers for non-fixers later in succession. Because a July 2018 wildfire burned the experimental plots, it was not possible to conduct a third year of vegetation sampling.

Mineral N Pools and Rates

Patterns in mineral N fluxes and pools differed between the first two years after fire, likely driven by distinct processes. Across all treatments, NH_4^+-N gradually decreased over the course of the experiment, with time since fire, consistent with the findings of others (e.g. Hanan et al. 2016a). Ammonium is initially deposited on soils via ash after fire (Christensen 1973, Debano and Conrad 1978) and rapidly lost through plant and microbial uptake, oxidation (nitrification) to NO_3^- and leaching (Christensen 1973). The effect of specific herb manipulation treatments on these processes also differed by year, discussed separately below.

First season after fire

Those treatments initially highest in NH_4^+-N were also those that had initially high rates of nitrification (**Figure 5**, **Figure 6**), as NH_4^+-N substrate availability is known to be a key driver of post-fire nitrification in chaparral (Fenn et al. 1993, Homyak et al. 2014, Hanan et al. 2016b). However, throughout the rest of 2017, both net nitrification rates and net N mineralization rates were similar between treatments, except the highly variable first sampling point (**Figure 6A,C**). Net N mineralization and nitrification rates are heavily influenced by the quality of existing organic matter (Robertson and Groffman 2007) and NH_4^+ substrate supply (Robertson and Vitousek 1981, Donaldson and Henderson 1990, Carreira et al. 1994), respectively. Theoretically, these experimental plots were chosen to have similar starting conditions across all treatments, and plant litter inputs in the first year would have been minimal. Thus, it is predictable that first-year mineralization rates did not differ between treatments.

Despite similar rates of net N mineralization throughout 2017, two treatment types were elevated in mineral N by the end of that first season: N-fixer and no-herb plots. N-fixer plots, which contained higher N-fixer biomass than even the all-herb plots, had elevated NH_4^+ concentrations (**Figure 5**). This elevated soil NH_4^+, not accompanied by elevated mineralization rates, was possibly the result of direct NH_4^+ rhizodeposition (Fustec et al. 2010) from the root nodules of abundant legumes. Although all-herb plots also contained N-fixers, albeit at lower abundance, they had the lowest mineral N levels in 2017. This could reflect the direct transfer of rhizodeposited NH_4^+ from N-fixers to non-N-fixers, which has been demonstrated in other systems (Paynel et al. 2008).

By the end of 2017, bare (no-herb) plots had the highest concentrations of total mineral N of all treatments; they were elevated in NO_3^- compared to all other treatments and had NH_4^+ concentrations similar to N-fixer plots. In fact, over the course of 2017, NO_3^- steadily increased in bare plots, while decreasing or holding steady in all others. It is likely that NO_3^- and NH_4^+ accumulated in bare plots due to a lack of herb uptake. The decreasing precipitation at the end of the growing season might have contributed to the accumulation of NO_3^-, by preventing NO_3^- losses due to leaching, runoff, or dentrification, all N export processes that depend on rainfall

(Allison 1973, Valeron and Meixner 2010, Homyak et al. 2014). Plots with herbs would have continued to immobilize NO_3^- through plant uptake even as rains stopped, and these all had significantly lower NO_3^- than bare no-herb plots. Furthermore, clay soils such as those found at this site (**Table 1**) typically have lower rates of NO_3^- leaching (longer soil residence time) then other soil types (Vinten et al. 1994) supporting the idea that NO_3^- not absorbed by plants would be detectable at the end of a growing season. Plant uptake of NH_4^+ would have also removed substrate for nitrification, further decreasing NO_3^- in plots with herbs.

Second Season After Fire

By 2018, clear differences in mineral N pools and cycling rates had emerged among herb-manipulations treatments (**Figure 5**, **Figure 6**). Similar to 2017, N-fixer plots were higher than all other herb treatments in soil NH_4^+, which could have resulted from ongoing rhizodeposition of N. However, in this second year after fire N-fixer plots were also elevated in net N mineralization and nitrification rates. Between 2017 and 2018, there was no difference in living herb biomass in these N-fixer plots, but 2018 plots contained the litter of the previous year's growth. N-fixers generally have higher tissue N content (lower C:N ratio) than non-N-fixers (Wright et al. 2004, Scherer-Lorenzen 2008), which can promote rapid decomposition of their litter (Moro and Domingo 2000, Hobbie 2005, Parton et al. 2007, Scherer-Lorenzen 2008). In turn, net N mineralization rates are controlled mainly by the C:N ratio of decomposing organic matter (Robertson and Groffman 2007). I hypothesized that the elevated mineralization rates in N-fixer plots were a function of the low C:N ratio of litter, potentially resulting from rapid decomposition, which is not directly measured in this experiment. A recent litterbag decomposition study post-fire chaparral corroborated this pattern (Wahl et al. in prep.), finding that the N-fixer (*Acmispon glaber*) decayed more rapidly than two non-N-fixers (*Emmenanthe penduliflora* and *Chlorogalum pomeridianum*) in the second year after fire. Maron and Connors (1996) found highly elevated NH_4^+ and NO_3^- concentrations in grassland soils where a legume had grown, even when that legume had been recently killed, suggesting the influence of decomposing litter and not just root exudate on soil mineral N concentrations.

Interestingly, the presence of N-fixers was not sufficient to increase mineralization rates when non-N-fixers were present. Even though N-fixers were present in all-herbs plots, rates of net N mineralization were indistinguishable between plots with all herbs or non-N-fixers alone. The common factor between these plots is the presence of high C:N litter. The abundance and low-quality of non-N-fixer litter may more strongly determine net N mineralization rates than the presence of low C:N litter does. It could also be that the presence of non-N-fixers suppressed N mineralization rates through the leaching of a plant secondary metabolite. Several groups of plant compounds have been demonstrated to slow decomposition, net N mineralization, and nitrification (Chomel et al. 2016).

Similar to the end of 2017, no-herb plots were elevated in soil NO_3^- and NH_4^+, particularly in the later months of the year (**Figure 5B,D**), likely due to lower N losses and a lack of plant uptake. The high 2018 net N mineralization and nitrification rates in no-herb plots are a curious result that is difficult to interpret with certainty (**Figure 6 B,D**). In litterfall manipulation studies, the removal of litter general decreased net N mineralization rates (Xu et al. 2013). Higher rates of net N mineralization here could be a result of low C:N ratio of soil organic matter being mineralized. With no new litter inputs to the bare plots in 2017, the resident soil organic matter could have decomposed, leading to a decreased C:N ratio and accelerating net N mineralization. As previously discussed, it is possible that plants (particularly non-N-fixers) were leaching a secondary compound that inhibited net N mineralization. It is also possible that high soil temperatures on bare soils could be primed microbes responsible for this activity. A future investigation could tests these hypothesis directly.

Across all time points and treatments, nitrification was correlated with and generally higher than net N mineralization (**Figure 7**), suggesting that mineralized N was quickly converted (nitrified) from NH_4^+ to NO_3^-, and likely also NH_4^+ deposited with ash. Others ((Hanan et al. 2016b) also found that NH_4^+ substrate supply and alkalinity stimulated nitrification in laboratory incubations of chaparral soils from different post-fire successional stages. Soils typically increase in pH in the post-fire environment. Gross rates of nitrification could have been much higher (Stark and Hart 1997, Verchot et al. 2001), potentially masking temporary NO_3^- pools that could lead to undetected N 'leaking' through leaching and denitrification, which were not measured here.

Overall, I propose that patterns in NH_4^+ and NO_3^- concentrations in year one were determined by the deposition of NH_4^+ after fire, influenced heavily by N rhizodeposition from N-fixers and herb uptake. In year two, mineral N concentrations were likely additionally influenced by the quality and chemical composition of decaying litter, as well as uptake and immobilization. Treatment differences in net N mineralization and nitrification rates didn't occur until the second year, suggesting the influence of plant litter on these processes.

Soil Carbon Mineralization (Heterotrophic Respiration)

I measured soil respiration in laboratory incubation in March through May 2018, the last three months of sampling (**Figure 9**). All treatments with herbs were significantly higher than no-herb treatments in soil heterotrophic respiration, with respiration values decreasing from March to May 2018. Month-to-month variation in respiration was likely driven by soil moisture effects, rather than temperature, as these were laboratory incubated at field moisture levels. Soil drying can decrease soil microbial and enzymatic activity (Linn and Doran 1984, Or et al. 2007, Šnajdr et al. 2008, Moyano et al. 2013). Differences in treatments were notable, especially between all-herb and no-herb plots. Given the identical conditions between incubations, it is likely that treatment differences in respiration are influenced by either difference in respiring soil microbe abundance or difference in soil organic C substrates. A possible explanation is that the lack of litter inputs from 2017 contributed to lower respiration rates in bare plots in 2018, by reducing C inputs. A high availability of plant litter can stimulate microbial activity and increase microbial biomass (Plante and Parton 2007).

Bulk Soil C and N

Bulk soil C and N were lower in removal plots than all other treatments, with the largest difference from all-herb plots (**Figure 10**). This finding supports the hypothesis that the presence of herbs in either functional group helps retain N in soils or creates conditions that facilitate fixation or other N inputs. The reduction in soil C in removal plots was dramatic, with no-herb plots more than 30% lower in soil C than all-herb plots. This result indicates that post-fire herbs play a key short-term role in building soil organic matter.

It is noteworthy that the C:N ratio fell in herb removal plots compared to all-herb plots. It is possible that this reduced C:N ratio could be partially responsible for the increased rates of N mineralization in no-herb plots in 2018, but it is difficult to draw this connection with certainty.

Grassland Invasion

It must be noted that the majority of the non-N-fixing herb biomass I measured was from typical non-native grassland species. There is increasing concern over the conversion of chaparral to non-native grassland. One estimate found that 34% of Southern California historical chaparral vegetation had been converted to herbaceous cover, including grasses (Park et al. 2018), which often follows shrub losses due to repeated fires at short intervals (Zedler et al. 1983, Smith et al. 2019). More research is needed to understand how grassland invasion impacts chaparral N and C cycling (Park and Jenerette 2019). In another post-fire chaparral herb-manipulation study, the presence of invasive grasses altered nutrient cycling, including increasing total soil C and N storage over plots with natives only (Dickens and Allen 2014). In coastal sage scrub, grassland invasion can increase N and C storage within two years (Wolkovich et al. 2010), similar to the findings in the present investigation.

Conclusions

Plots with no herbs growing after fire resulted in lower soil C and N than those with any type of herb cover, especially unmanipulated all-herb plots. In bare plots, there were also lower rates of C mineralization, but higher rates of N mineralization, potentially due to a shifting C:N ratio in soil organic matter or release from inhibition by plant secondary compounds. Plots with N-fixers only had higher N mineralization rates in year 2, likely due to low C:N litter inputs from year 1. However, while N-fixers drove higher rates of net N mineralization, this did not lead to greater N storage in soils than in the other herb treatments. The presence and identity of post-fire herb assemblages impacted soil C and N dynamics, even over the fairly short two-year time scale of this study. An assemblage of both N-fixing and non-N-fixing herbs leads to the greatest accumulation of soil C and N; this elevated soil nutrient availability may contribute to the long-term recovery of shrubs even after herbs are no longer dominant.

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TABLES

Table 1. Pre-treatment block-level soil characteristics (February 01, 2017). Averages from 6 pooled soil samples to 10 cm depth. Mean values ± S.E.M.

Bulk Density (g cm^{-3})	Sand/Silt/ Clay (%)	Soil Type	Total C (mg g^{-1})	Total N (mg g^{-1})	NH_4^+-N (µg g^{-1})	NO_3^--N (µg g^{-1})	Soil Moisture (%)
1.32 ± 0.05	29 ± 2/ 27 ± 2/ 44 ± 3	Clay	26.1 ± 2.0	1.7 ± 0.1	6.4 ± 1.3	1.77 ± 0.3	17.7 ± 1.1

FIGURES

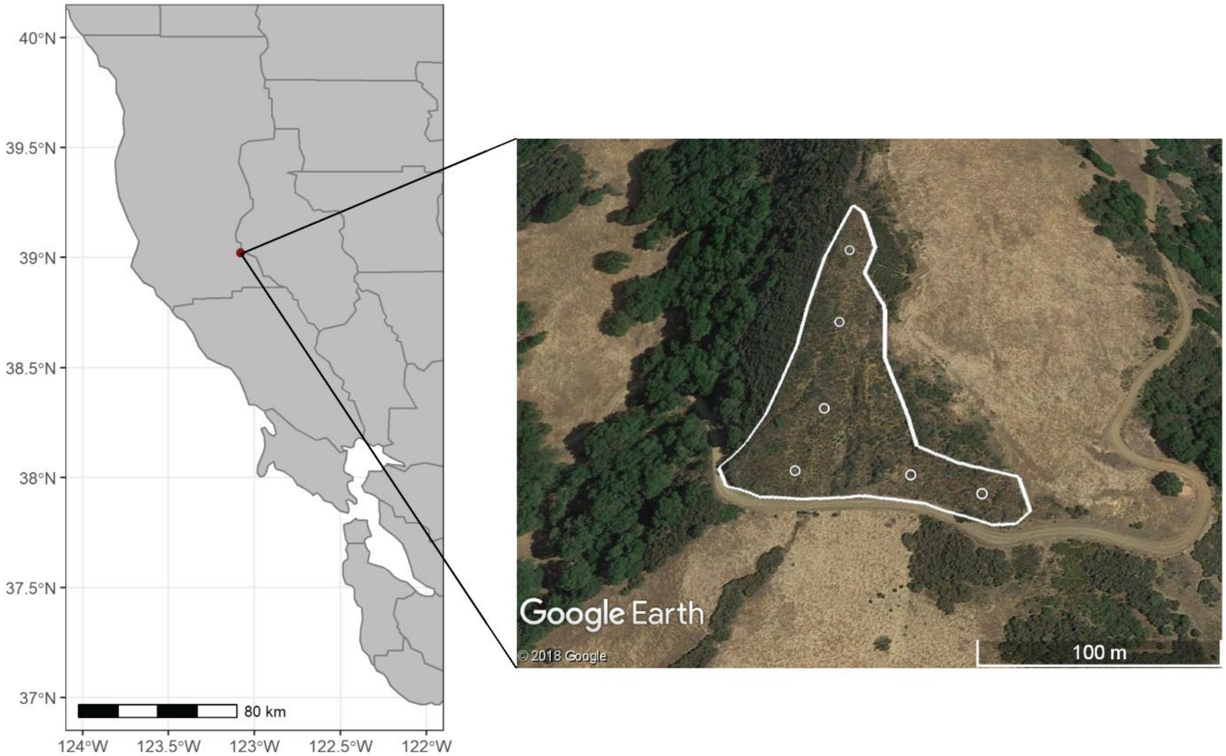

Figure 1. Location of field site, perimeter of prescribed fire (burned April 21, 2016), and location of experimental blocks within site. Imagery date July 02, 2018. Red dot in inset map identifies project location.

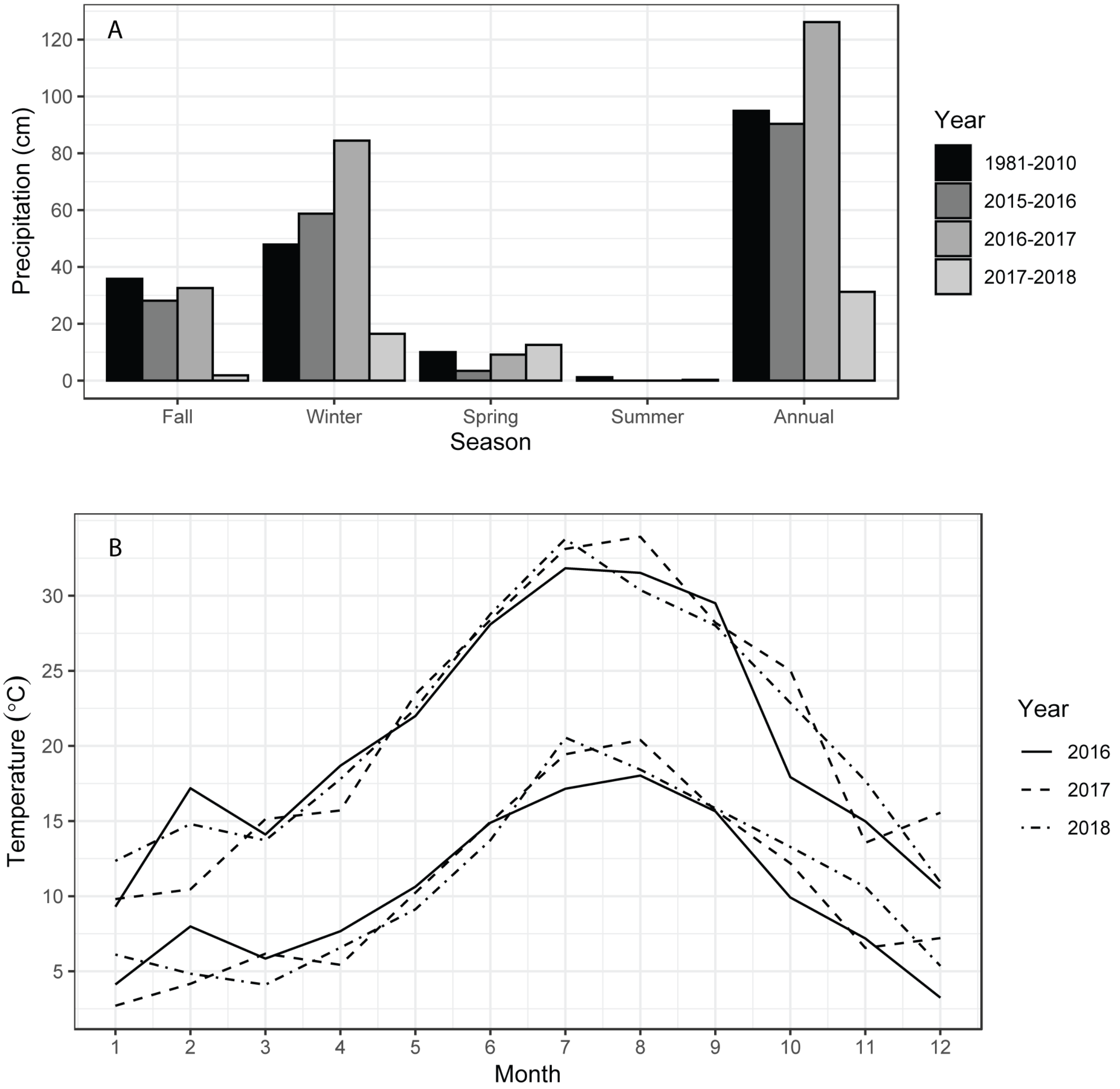

Figure 2. Annual weather data at Hopland Research and Extension Center (HREC). (a) Seasonal total precipitation from two nearby stations; Data from 2015-2018 are from Hopland Station (Elev. 817 m; 39.031, -123.081) and 30-year normals are from HREC Headquarters (Elev. 263 m; 39.001, -123.080). (b) Monthly means of minimum and maximum daily temperature are from HREC Headquarters only.

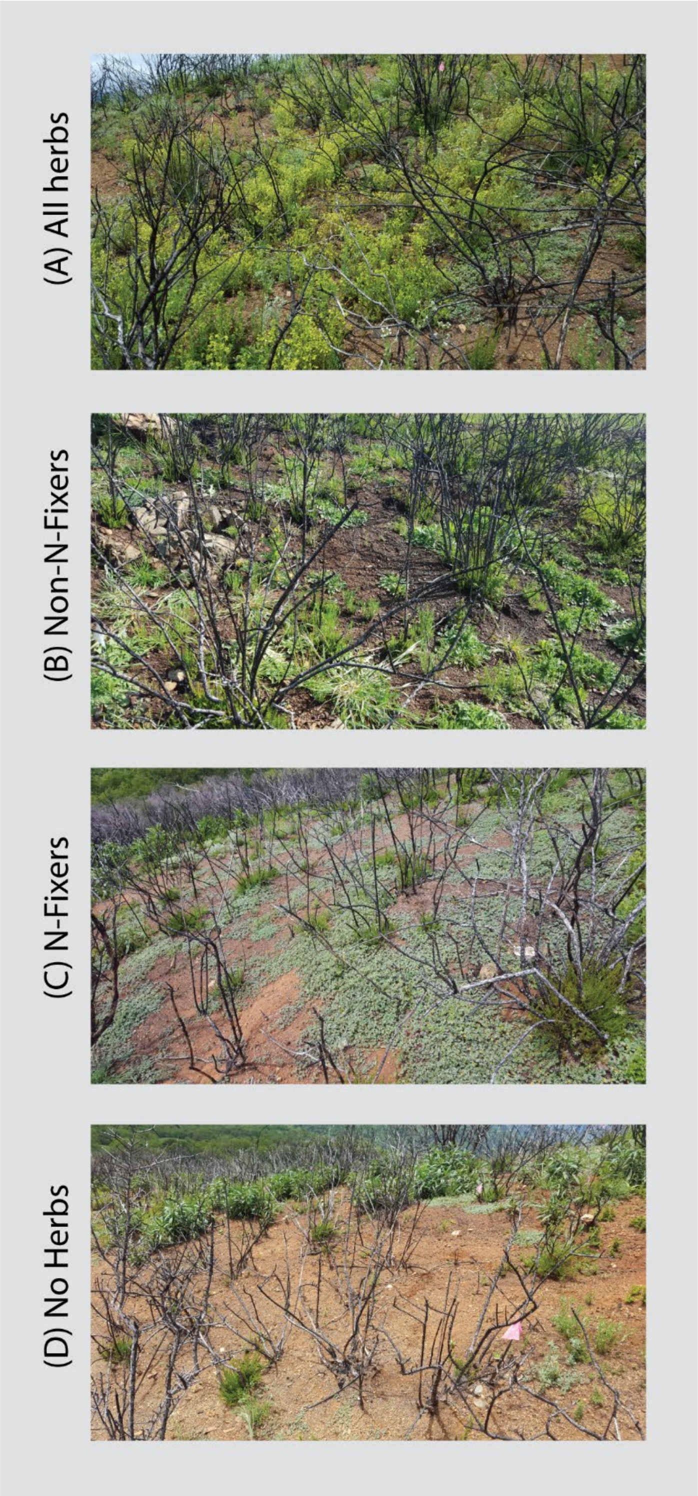

Figure 3. Examples of each herb-manipulation treatment. Photo credit: L. Hendricks-Franco March 2017.

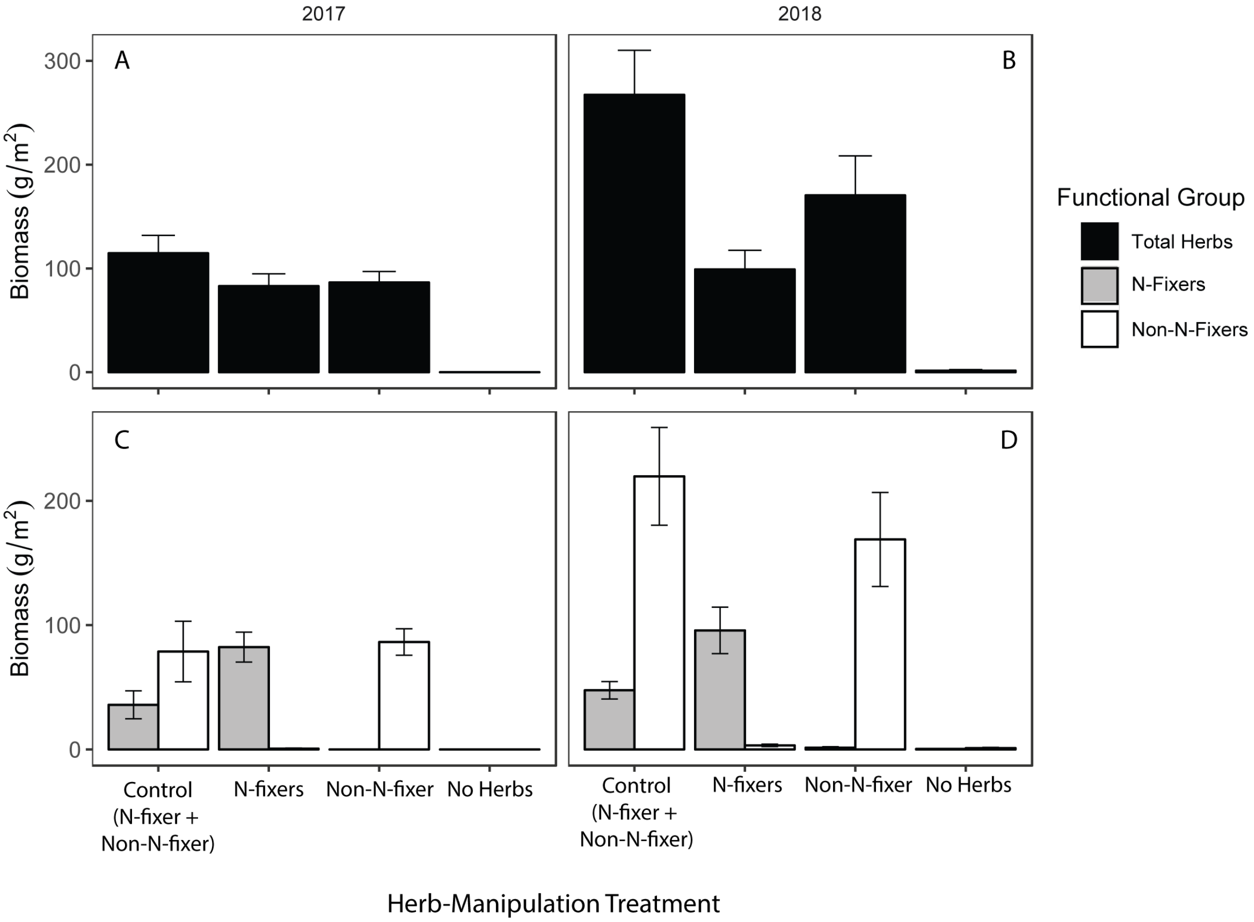

Figure 4. Herb biomass by functional group at each herb manipulation treatment. The x-axis indicates the groups of herbs that were allowed to grow (i.e. not removed). Herbs were measured at peak biomass (June 2017 and late May 2018). Error bars represent S.E.M. Significance levels are described in the results.

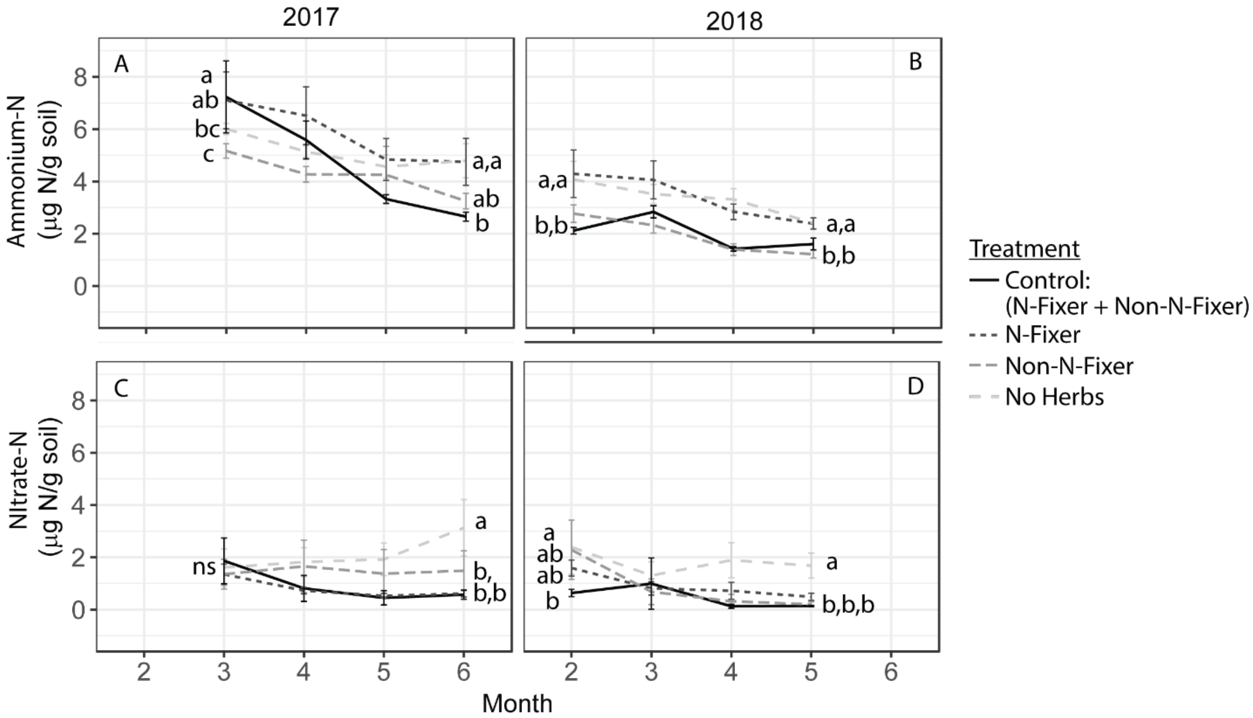

Figure 5. Mineral N pools over the two years of sampling. Error bars represent S.E.M. Lowercase letters indicate groups with significantly different means ($p < 0.10$) or no difference between groups (ns). Dates are pooled into early and late season for significance testing.

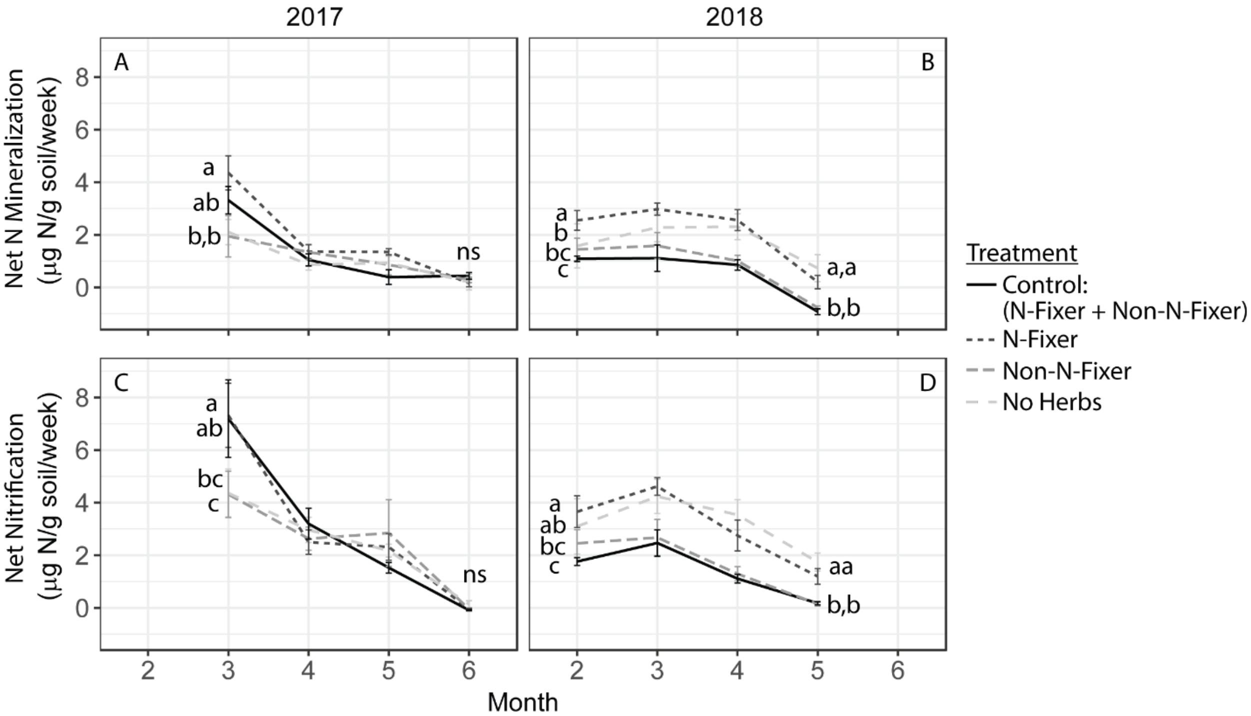

Figure 6. Net-N-mineralization and nitrification rates over the two years of sampling. Error bars represent S.E.M. Lowercase letters indicate groups with significantly different means ($p < 0.10$) or no difference between groups (ns). Dates are pooled into early and late season for significance testing.

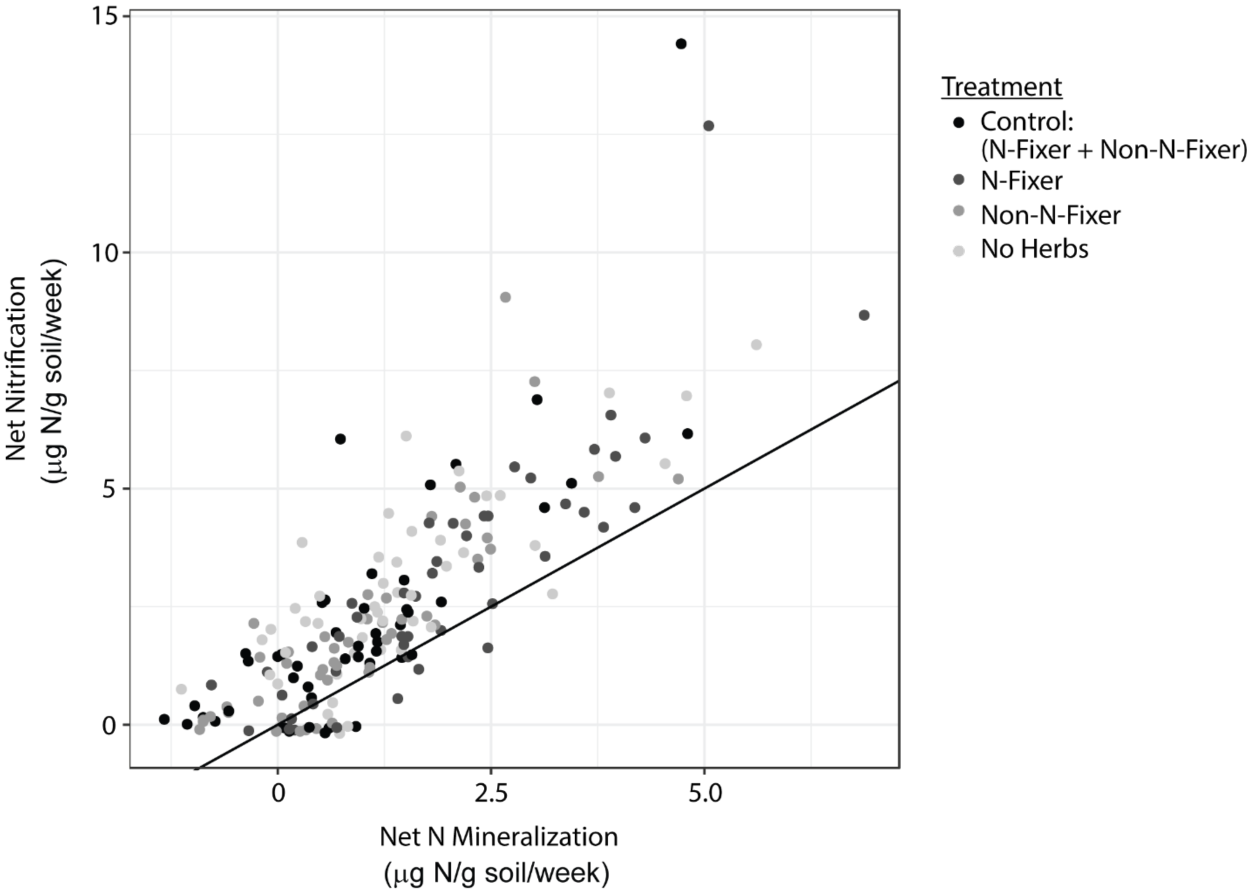

Figure 7. Relationship between net nitrification net N mineralization rates at all sampled timepoints. Solid line shows 1:1 correspondence.

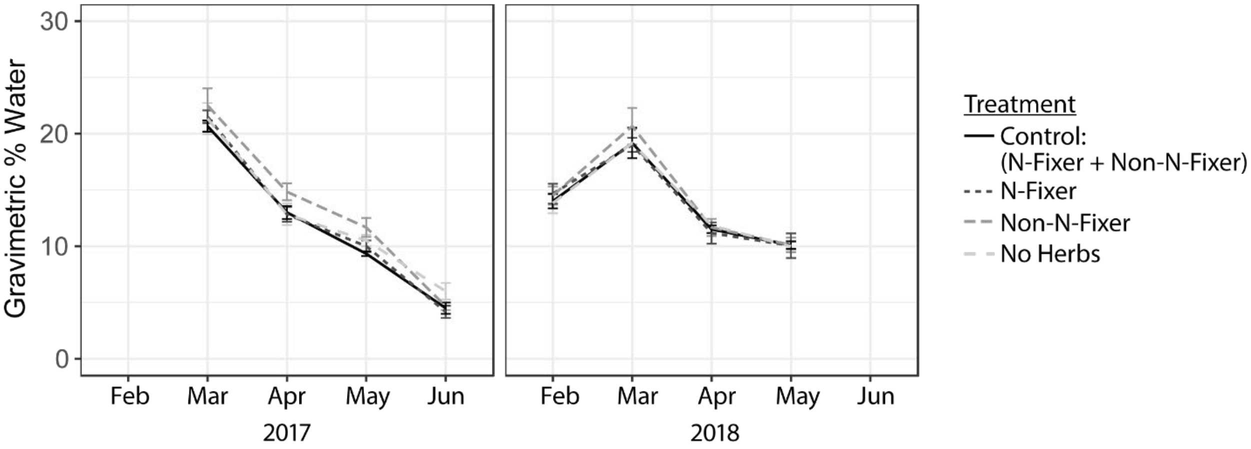

Figure 8. Gravimetric soil moisture content throughout sampling. Error bars represent S.E.M. There was no significant effect of treatment.

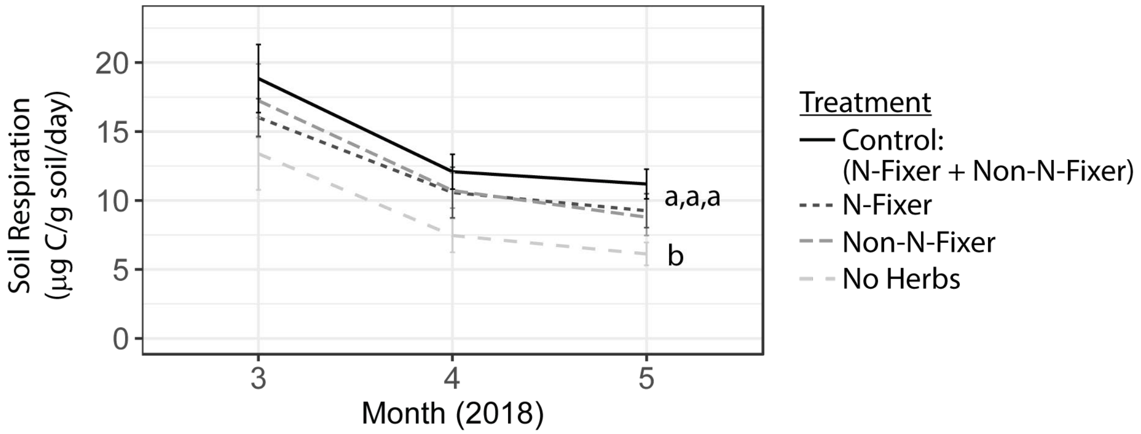

Figure 9. Soil respiration over the three months of the 2018 growing season. Lowercase letters indicate significantly different means ($p < 0.10$) averaged over the three months of sampling. Error bars represent S.E.M.

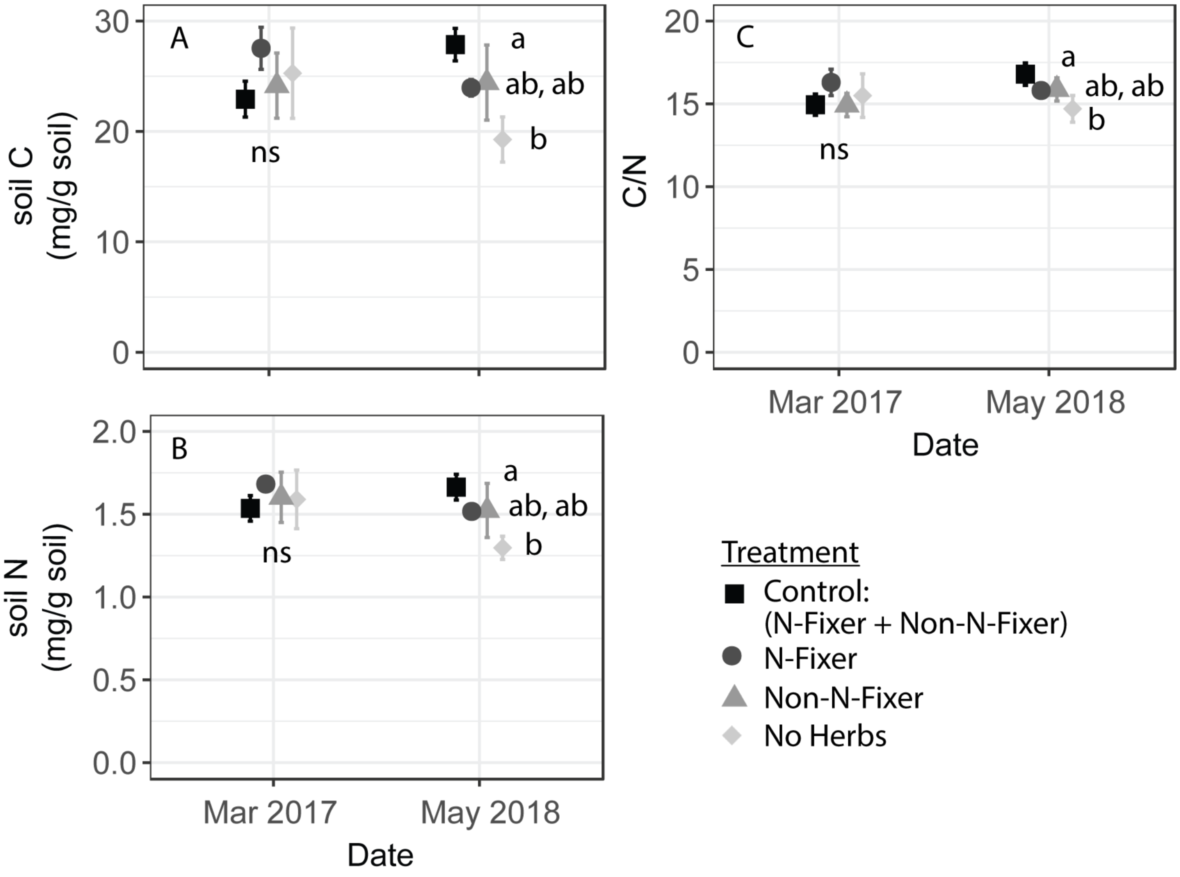

Figure 10. Bulk Soil C and N. Lowercase letters indicate significantly different means ($p < 0.10$) averaged over the three months of sampling. Error bars represent S.E.M.

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