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# Invasive Plant-Soil Feedbacks and Ecosystem Resistance and Resilience: A Comparison of Three Vegetation Types in California

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ABSTRACT OF THE DISSERTATION

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by

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Ecosystem processes are strongly dependant on plant-soil feedbacks. The invasion of exotic plant species can result in the introduction of novel traits capable of de-coupling native plant-soil feedbacks and leading to altered nutrient cycling and availability and microbial community composition. In general the degree to which an invading species will impact the system it invades is dependant on how much it differs from plant species native to that system. However, there are examples in which invasion of an exotic plant similar to natives has led to significant alterations of ecosystem processes. The objective of this work was to examine the impacts of a single suite of exotic annual plants invading three very different vegetation types in southern California, grasslands, coastal sage scrub and chaparral. I predicted that invasion of exotic annuals would have greater impacts on shrubland systems than grasslands due to the greater disparity in plant traits between the exotic annuals and the shrub species. Comparisons of invasion impacts, however must consider factors other than vegetation type such as soil parent material, pH and soil moisture as mechanisms by which a native system may be more or less resistant to

changes associated with invasion and recover following native vegetation re-establishment. In order to examine vegetation type resistance to invasion and soil resilience of these systems, I analyzed soils for total carbon and nitrogen, extractable phosphorus and nitrogen, nitrogen mineralization, soil respiration and microbial community composition using phospholipid fatty acid analysis. Long and short-term restorations were sampled concurrently with the invaded and native vegetation types to assess resilience of soils. Regardless of vegetation type nitrate was reduced by invasion, seasonality of sampling was a greater driver of microbial community composition than invasion or restoration and abiotic factors proved to be important to microbial species composition and soil nutrient availability. Individual chemical pools and functional groups of microbes responded differently in each vegetation type. However, the degree to which invading species differed from natives did not predict the level to which invasion would impact the system.

Table of Contents

List of Figures

List of Tables

# Introduction

Invasive species are now recognized as one of the leading threats to biodiversity world wide (Pimentel et al. 2005). California is recognized as a global biodiversity hot spot (Myers et al. 2000), yet exotic plant species are leading to type conversion of grasslands and coastal sage scrub and altering fire regimes such that the diversity of California flora and fauna is at risk (D'Antonio & Vitousek 1992; Keeley et al. 2005; Klopatek et al. 1979; Minnich 2008; Minnich & Dezzani 1998). Understanding the impacts of exotic plants and the ability of native California ecosystems to resist or recover from the impacts of exotic plants is essential in developing management strategies to protect the biodiversity of California wildlands.

Previous research has found species and site specific interactions associated with invasion. This suggests that invaders have mechanisms by which they affect ecosystems differently or that ecosystems have differing mechanisms by which they resist or recover from invasion. Ecosystem concepts of nutrient rich versus poor sites predict that species of poor sites produce litter of poor quality and slow decomposition while those of fertile systems produce litter of high quality that is easily decomposable (Berendse 1998; Penuelas et al. 2010; Wardle et al. 2004). Invasion by species that produce high quality litter into sites dominated by litter of low quality would promote more rapid decomposition rates that would alter nutrient cycling rates. The level of change caused by an exotic species is considered to be directly related to how much it differs from native species (Ehrenfeld 2003). Shifts in plant-soil feedbacks have occurred following the invasion of exotic plant species, but this is not always the case. Both abiotic and biotic

factors of native systems may promote resistance to such alterations, i.e. in the case of functional redundancy of microbes. Microbes may not change in response to altered vegetative inputs and instead incorporate the new litter along with the original litter mixture. It is unknown by what means or if all native soil systems can resist exotic plant induced changes and recover from invasion.

Non-native plant species can have negative impacts in their new environments, including displacement of native plants, cause decrease in forage of native animals, choking water ways, and more (Pimentel et al. 2000). More specifically they have been found to alter soil characteristics that can lead to reduced success of natives. Exotic plant species are known to alter soil characteristics such as soil fluxes in carbon, nitrogen, and other nutrients, microbial communities and water cycles (Ehrenfeld 2003; Yoshida & Allen 2004). Furthermore, exotic plants may cause changes in soil conditions that promote their own growth. These affects on soil may be capable of persisting in soils even after the removal of exotics.

The effect that invasive plant-mediated changes in soil processes have on native plant species, the reversibility of these changes and the potential for reversing impacts of invasive plants to soils is not well understood. Several studies have shown that soils can be naturally restored with reintroductions of native plant species or inoculations of the soils after disturbances such as mining (Graham & Haynes 2004; Izquierdo et al. 2005), agriculture (Bhojvaid & Timmer 1998; Ros et al. 2003; Zhao et al. 2005) and anthropogenic disturbances (DeGrood et al. 2005). However, little work has been done to

determine if native plant reintroductions alone can promote the re-establishment of microflora and nutrient cycling or if soil amendment aimed at restoring natural soil characteristics would be necessary to reverse the affects of invasion.

The objective of this dissertation was to examine the impacts of a suite of exotic species invading three ecosystems in southern California: grasslands, coastal sage scrub and chaparral. By focusing on a suite of invaders, I was able to test whether introduction of the same plant-soil inputs affect systems of differing vegetation types and soil characteristics differently. The goal of my research was to examine how the presence of non-native plant species changes soil chemical and biological characteristics and whether soils are resilient enough to recover once exotic plant species are removed and native plant species restored. Hypotheses were 1) The presence of exotic plant species changes the biological and chemical characteristics of the soils by altering soil inputs. 2) If exotic plants are controlled and native plant species restored, soil biological and chemical characteristics will return to pre-invaded conditions because native plant inputs would be restored. 3) The resistance and resilience to invasion will depend upon the traits of the invaders and the traits of the native plant community.

In the first three chapters, soil characteristics were held constant within each site so I could assess the impacts of the exotic annual plant species on soil chemical and biological characteristics without confounding factors of differing soil types and climate. In addition, I utilized long-term, pre-established restoration sites and implemented my own short-term restoration treatment to determine whether soils were resistant to the impacts of invasion. Chapter one, "Southern California grassland soil chemical and

biological characteristics are altered by exotic plant invasion", showed that while the annual invaders were similar in traits to many of the native plant species, invasion led to altered microbial communities. In chapter two "Exotic annuals alter the distribution of coastal sage scrub soil chemistry and biological characteristics" and chapter three "Exotic plant invasion alters chaparral ecosystem resistance, resilience and succession", the invaded shrublands experienced shifts in root distribution that led to a loss of soil heterogeneity that explained altered carbon and nitrogen concentrations, nitrogen mineralization, soil respiration and fungal:bacterial ratios.

In the final chapter, I assessed whether the impacts of invasion differ across ecosystems. Based on the degree to which the exotic plant species differed from natives, I expected chaparral vegetation to be most affected by invasion. Results of this final chapter indicated the opposite response, which contradicts the commonly accepted idea that exotic species with the most novel traits in comparison with the native community will cause the greatest impacts to the systems they invade. Instead, the results of this study suggest that abiotic factors are important regulators of soil chemical and biological resistance and resilience to exotic plant invasion, and the different rooting structure of grasses vs. shrubs can account for the high resistance of shrubland soils.

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**Southern California grassland soil chemical and biological characteristics are altered by exotic plant invasion**


## Abstract

Exotic plant invasions are capable of altering biological and chemical characteristics of soil through introduction of novel traits to the plant-soil feedback loop. Exotic annuals have a long history of invasion into California grasslands and their litter quality and biomass turnover traits give them the potential to alter microbial communities and nutrient cycling. The objective of this study was to determine whether soils of California grasslands are resilient enough to recover following exotic plant invasion. Microbial biomass, fungal : bacterial ratio (F:B) and microbial community structure of invaded soils were found to be different from restored soils. Total soil carbon and nitrogen, and potential soil respiration were unchanged by invasion, but the rate of extractable nitrogen cycling was increased and nitrogen immobilization decreased. Restoration of native vegetation produced soil microbial communities and chemistry that are different from that of invaded sites which suggests these soils are responsive to changes in vegetation type and therefore may be resilient.

## Introduction

The impacts of exotic plant invasion can range in scale from competition between individual plants to altered ecosystem-level processes such as nitrogen cycling. When invasions result in ecosystem-level changes, this indicates shifts in linkages between above ground plant communities and below ground abiotic and biotic soil components (Bever et al. 1997; Ehrenfeld 2003; Wolfe & Klironomos 2005). The existence of tight relationships between plants and microbes, points to the importance of understanding the role of feedbacks between these organisms and could be useful in predicting ecosystem-level responses to exotic plant invasion.

Plant-soil feedback loops describe how organisms alter processes such as rates of nutrient cycling and soil nutrient availability, which themselves have a selective pressure on the traits of species that will be most successful in a given environment (Santiago 2007; Santiago et al. 2005). In the case of plant invasion, a new species may migrate into an existing community and alter the microbial community, leading to further modifications of belowground processes such as nutrient availability or the introduction of pathogens, that in turn impact the new plant community (Bever et al. 1997). The common observation that nutrient cycling is altered with shifts in plant species composition suggests that the soil microbial community also changes (Ehrenfeld 2003), and creates a feedback to the new plant community. When feedbacks such as these are altered, the end result can be inhibition of native plant species and/or the facilitation of exotic invading plant species.

Introduction of new plant traits that play vital roles in decomposition, such as litter quality or root biomass, have the potential to change microbial community and soil function through an altered microbial substrate. The extent to which exotic plant invasions may introduce new traits depends on how different they are from native species. The level of dissimilarity between exotic and native plants combined with the capacity of soil to resist perturbation determine the level of impact the invading species (Ehrenfeld 2003). Plants can create positive feedbacks to nutrient cycling through nutrient uptake and loss via litter or rhizodeposition (i.e. root exudates or leaking). By changing plant inputs into soils, exotic plants produce substrate that differs from that of native plants and can promote microbial communities unlike those of native soils (Ehrenfeld 2003; Wardle et al. 2004). Exotic species with novel nutrient uptake or deposition traits could create positive feedbacks with the soil microbial community and facilitate their persistence as the dominant plant species. Batten et al. (2006) found that soils under *Aegilops triuncialis* (goat grass) and *Centaurea solstitialis* (yellow star thistle) contain significantly higher concentrations of sulfur oxidizing and reducing microbes than under native plant species. Grayston and others (1998) found different carbon substrate use by microbial communities under the exotic species. They interpret these findings as an indication that exotic plant exudates differ from native plant exudates and thereby attract a different microbial community or alter which species are active.

In addition to impacting microbial community structure, exotic plant invasion has changed cycling and availability of carbon, nitrogen, and other nutrients (Christian & Wilson 1999; Ehrenfeld 2003; Yoshida & Allen 2004). This occurs when plants produce

litter of a different quantity and/or quality than native species (Hobbie 1992). Litter with high C:N will lead to the immobilization of nitrogen by microbes and a reduction of soil available nitrogen (Brady & Weil 1996; Grayston et al. 1998). Exotic plants can increase leaching of $NO_3^-$, as well as decrease carbon storage in grasslands (Seabloom et al. 2003b) and alter hydrological cycles (Ehrenfeld 2003; Sigüenza et al. 2006; Yoshida & Allen 2004). These alterations may have a negative impact on native plant species and be capable of persisting in soils even after the removal of exotics. It is unknown whether reintroduction of native plants and the removal of exotics alone can aid in soil recovery following invasion.

Soils are resilient to severe impacts such as mining and agriculture when active restoration efforts are used to ensure the appropriate microbial community and plant species are restored (Allen 1988; Allen et al. 2001; Christian 2001). However, recovery may require decades. Studies on the impacts of exotic plant invasion on soils are more recent, and there are many unknowns still to be investigated. Beard and Kulmatiski (2008) observed shifts in microbial community within a few years of plant species community compositional changes and microbial abundances that remain affected by land-use legacies for 50 years, but few studies have examined resilience. The use of BACI (before and after) designs in which a restored system would be compared to adjacent invaded areas presents an opportunity to determine if soils are as resilient to invasion as they have proven to be with anthropogenic disturbances. The key assumptions are that by removing the disturbance, i.e. exotic plants, and re-establishing the native soil inputs, i.e. native litter, restoration efforts facilitate recovery of the native

soil microbial community, biogeochemical cycles and native plant-soil feedbacks. If soils are not resilient, restoration of vegetation and removal of the disturbance will not lead to soil recovery.

The California grasslands are an ideal study systems for plant-soil feedbacks because they turn over annually and are therefore likely to respond to altered plant inputs over a relatively short time scale (Eviner et al. 2006; Jackson et al. 1988; Jones & Woodmansee 1979; Woodmansee & Duncan 1980). A limiting feature of this system is that there are no true relic grasslands to use as reference sites. However, even without relic grasslands, differences in soil microbial community structure and function between invaded and restored soils can be used to evaluate the capacity of grassland soils to respond to altered vegetation type as an indication of the soils potential for resilience.

Two hundred and fifty years of exotic annual plant invasion into California grasslands has created controversy about the historical plant species composition of these grasslands (Minnich 2008). Whether they were dominated by perennial bunch grass, annual forbs or some intermediate mixture, it is clear that the current exotic annual grass domination is an altered and stable state (Bartolome & Klukkert 1986; Biswell 1956; Hamilton 1997; Hatch et al. 1999; Seabloom et al. 2003a; Seabloom et al. 2003b). Exotic species in California grasslands tend to germinate earlier in the growing season than do natives. The combination of an early start, large seed banks and fast growth rates make exotic grasses and some exotic forbs successful at establishing in new areas and maintaining their dominance in areas they have invaded (DiVittorio et al. 2007). Exotic grasses are known to limit germination and establishment of native species through direct

and indirect competition for light, water and nutrients (Biswell 1956; Cione et al. 2002; Dyer & Rice 1997; Eliason & Allen 1997; Hamilton et al. 1999; Moyes et al. 2005; Seabloom et al. 2003a).

Exotic annuals can alter grassland systems by altering nutrient cycles, changing microbial composition and activity, increasing fire intensity and frequency, altering litter quality and quantity, displacing natives, decreasing biodiversity, causing decrease of forage for native animals, choking waterways, and altering hydrologic and disturbance regimes (Cook 1959; D'Antonio & Vitousek 1992; Ehrenfeld 2003; Hobbs & Mooney 1998; Hughes et al. 1991; Jackson et al. 1989; Jackson et al. 1988; Jones & Woodmansee 1979; McNaughton 1968; Moyes et al. 2005; Smith & Tunison 1992; Wardle et al. 2004; Wood et al. 2006; Woodmansee & Duncan 1980). In addition, biomass and nutrient cycling rates are more rapid in annual dominated grasslands than in a native perennial systems (Jackson et al. 1989; Jackson et al. 1988; Jones & Woodmansee 1979; McNaughton 1968; Woodmansee & Duncan 1980). The quality and intensity of change that occurs in an ecosystem is influenced by both the identity and dominance-level of an exotic species (Ehrenfeld 2003). If one species dominates the site, it likely also strongly influences any soil processes affected by the plant community. Exotic annual grasses and forbs dominate California grasslands and thus likely dominate plant to soil feedbacks.

Exotic species invasion threaten native species diversity and ecosystem processes, therefore, it is imperative that research concerning effective control and management strategies become established. There is much to learn about soil resilience following invasion because the potential impacts of invasions are great. Due to the almost complete conversion

from native perennial grassland with annual forbs to exotic annual grassland with annual forbs that has occurred over the past 200 years (Biswell 1956; Hatch et al. 1999; Minnich 2008), it is not possible to study the resistance of native California grasslands to exotic plant invasion. Therefore, the objective of this study was to assess the capacity of California grassland soils for resilience following exotic plant control and native re-vegetation. I hypothesized that: 1) restored grassland plots would differ from exotic grassland plots in soil microbial structure, as a result of altered litter inputs: 2) differences in soil microbial communities would lead to altered nutrient cycling and feedback to the plant community as changes in levels of available nutrients: and 3) exotic plant removal would have immediate positive impacts on native plant success and microbial nutrient cycling that would not equal that of long-term restoration but be an intermediate between invaded and restored systems.

## Methods

Two grasslands were used for this research, each utilizing a different method of exotic plant control, one inland grassland, Santa Rosa Plateau Ecological Reserve, and a coastal grassland at White Point Preserve. Both are invaded by Mediterranean annual grasses and forbs with sparse native bunchgrasses and forbs. The inland grassland is a 4047 ha multi-use reserve located in Murrieta, CA. Soils are basaltic in origin (Gillespie & Allen 2004). Mean annual temperatures are 1-37$^{o}$C and annual precipitation is approximately 48cm with the majority falling between November and April. Restoration consists of exotic grass control through prescribed spring burns (Gillespie & Allen 2004). Restored and invaded sites were last treated with fire in 1997. However, the burn did not effectively reduce the exotic grass cover in the invaded area. While restored areas experienced significant reduction of

exotic grass cover that was maintained over the 9 years, restored areas still have a high proportion of exotic grasses. The coastal grassland is located in San Pedro, Los Angeles County and receives an average of 30cm precipitation annually and experiences mean temperatures of 8-26$^{o}$C. . Soils are classified as a clay loam of Diablo Clay Adobe series (Nelson et al. 1919). The coastal grassland is a 121 ha reclaimed Department of Defense missile facility in which restoration began in 2000. Restoration consisted of exotic plant control using mowing and hand weeding, seeding of native grasses and irrigation.

To examine the effects of invasion on grassland ecosystem structure and function, I utilized previously established long-term restorations and established nine replicate 1m$^2$ plots per treatment (invaded or restored) at each site. Structural data included plant and microbial community composition and soil chemical pools. Functional variables included cycling of nitrogen and carbon. Restored areas were defined as those having exotic plant species cover less than 30 percent and experienced active restoration, while invaded areas contained 50 percent or greater exotic plant species cover.

To understand the immediate impacts of altered vegetation cover on soil characteristics, I established nine additional 1m$^2$ plots in the invaded areas of the inland grassland in which I weeded exotic plant species and planted native seed. These plots will henceforth be referred to as the weed/seed treatment while the long-term restoration treatments mentioned above will be referred to as restored followed by their corresponding exotic plant control method. For the short-term restoration, hand weeding of exotic species was maintained up to 3 weeks prior to data collection and seeding occurred following the first rains in the fall of 2007. However, seeding was unsuccessful during the 2007-2008

season due to high granivory following the 2007 drought, so seed was applied again in the fall of 2008. Seeds of five native species, *Dichelostemma capitatum* (100 seed/ $m^2$), *Nassella pulchra* (100 seed/ $m^2$), *Lasthenia californica* (200 seed/$m^2$), *Cryptantha intermedia* (200 seed/ $m^2$) and *Sidalcea malviflora* (75 seed/$m^2$) were evenly distributed over the entire plot and raked into the soil. *N. pulchra* seed was collected on site between 2006-2007 and *D. capitatum*, *L californica*, *C. intermedia* and *S. malviflora* seed was donated by S&S Seed Company.

## Ecosystem Structure

Individual plot-level species percent cover and richness and litter percent cover were measured annually at the peak of the growing season 2007-09 to quantify plant species composition in each treatment. Net annual productivity of annuals was determined by collection of biomass for four plant functional groups (native forb, native grass, exotic forb and exotic grass) clipped at soil level from 0.25$m^2$ sub-plots and scaled up to the 1$m^2$ using regression models of mass and percent cover. Additional biomass was collected for vegetative plant tissue chemical analysis at peak plant growth. All biomass was oven dried at 60°C and weighed. Biomass for tissue analysis was ground and analyzed for total C and N on a Thermo-Finnigan model: Flash AlllZ soil combustion analyzer system.

To determine the effects of exotic invasion on soil biological and chemical characteristics, soil cores of 2.5 cm diameter and 10 cm depth were collected and transported on ice to be stored at -20°C for chemical analysis in 2006 and -80°C for

microbial analysis in 2007-08. Soils are classified as a clay loam of Diablo Clay Adobe series (Nelson et al. 1919). Soils were analyzed for total carbon and nitrogen by combustion, KCL-extractable $NO_3$ and $NH_4$, and bicarbonate-extractable phosphorus (Olsen P) by the University of California Division of Agriculture and Natural Resources Analytical Laboratory at UC Davis (danranlab.ucdavis.edu). Soil pH was measured with 2:1 soil: water slurry. Soil cores were also collected once annually in 2007 and 2009 at peak growth, and three times annually (at germination, peak plant growth and plant senescence) during the 2007-08 growing season to be analyzed for KCL-extractable nitrogen ($NH_4^+$ and $NO_3^-$). Soil texture was also analyzed at University of California Division of Agriculture and Natural Resources Analytical Laboratory at UC Davis in soil suspension by hydrometer from three composite soil samples per sampling site.

Phospholipid fatty acid (PLFA) analysis was used to determine whether microbial community structure was affected by exotic invasion. Omitting archaea, all other living organisms contain PLFAs as a component of their cellular membranes (Hedrick et al. 2000; White et al. 1996). These compounds, once extracted from the organisms, can be used as biomarkers to identify functional groups of microbes such as gram positive bacteria or arbuscular mycorrhizal fungi (Hedrick et al. 2000; White et al. 1996; Zelles & Bai 1994). PLFAs are preferable to the use of fatty acids alone as fatty acids can persist in soils for long periods of time representing a legacy of past microbial communities. PLFA represent living organisms (White et al. 1996), thus ensuring capture of the current microbial community response to a disturbance such as exotic plant invasion or restoration activities. Samples were collected within 24 hours of rainfall or wetting of

soils to a 10 year average rainfall volume. Soil samples were passed through a 2 mm sieve and lyophilized prior to extraction. PLFAs were extracted from 6 g of soil following the modified Bligh–Dyer method (Frostegard et al. 1991). Quantification of fatty acids was obtained using a gas chromatograph (HP6980; Hewlett Packard, Palo Alto, CA) with flame ionization detector and HP3365 ChemStation Software. PLFA peaks were converted to PLFA identities and abundances using MIDI Sherlock Microbial Identification System (MIDI Inc., Newark, NJ, USA) followed by comparison of peak areas with a known internal standard 19:0 of known concentration. PLFA was not conducted on the short-term, weeded/seeded treatments of the inland grassland due to extremely high proportions of bare ground in these treatments. Bacterial biomarkers included: 14:0, 15:0 iso, 15:0 antiso, 16:0 iso, 16:0 iso G, 16:1 w9c, 16:1 w7c, 16:0, 16:1 2OH, 17:1 Alcohol, 17:0 iso, 17:0 antiso, 17:0 cyclo, 17:1 w8c, 18:1 w5c, 18:0, 19:0 cyclo c11-12, 22:0, and 24:0 and fungi: 18:2 w6c, 18 1w9c, and 17:0 and AM fungi: 16:1 w5c. Nomenclature for PLFAs follow Lechevalier and Lechevalier (1988), Vestal and White (1989), Zelles (1999), Myers et al (2001), and Hebel et al (2009).

## Ecosystem Function

Laboratory incubations for nitrogen mineralization were performed over a 30 day period maintaining 25$^{\circ}$C and 60% humidity. $NH_4^+$ and $NO_3^-$ were extracted with a 2 M KCL 4:1 solution (Riley & Vitousek 1995) and shipped on dry ice for analysis at University of California Division of Agriculture and Natural Resources Analytical Laboratory at UC Davis. Net mineralization was calculated as the change in $NH_4^+$ minus

the change in $NO_3^-$ over time and net nitrification was calculated as the change of $NO_3^-$ over time following Riley and Vitousek (1995). Potential soil respiration rates were determined with laboratory incubations. Soils were maintained at 20% soil moisture and 25°C in sealed mason jars for 10 days. Jar headspace concentrations of $CO_2$ (ppm) were determined using a LiCor 800 infrared gas analyzer (Lincoln, USA) and converted to a rate function of μmol $CO_2$-C/ g soil *day (Chatterjee et al. 2008).

Data were tested for normality using the Shapiro-Wilk W test and non-normal data log (x+1) or square root transformed when appropriate. Plant biomass and litter, soil chemistry, soil extractable nitrogen, potential soil respiration and nitrogen mineralization data were analyzed with ANOVA followed by Tukey's HSD test to establish differences between treatments. Kruskal Wallis was used when data could not be transformed to normality. Plant species percent cover and richness were analyzed using repeated measures MANOVA. Microbial biomass and F:B were also analyzed using ANOVA to determine coarse microbial community compositional shifts between treatments. Principal Components Analysis was used to create PC's to represent microbial community composition throughout PLFA profiles which were then analyzed with ANOVA to determine if community composition differed between treatments and across sampling dates. The above analyses were conducted using JMP9 (SAS Institute 2009) with an alpha level of $P \leq 0.1$ to determine significance. High levels of heterogeneity in soils commonly lead to correspondingly high variation in data, especially soil microbial variables. For this reason, a P-value of $P \leq 0.1$ is considered acceptable for soil analyses (Klironomos et al. 1999).

## Results

The inland site had similar native forb and exotic species percent cover in both the invaded and restored plots, but had greater native grass cover in the restored treatment ($P < 0.001$; Table 1). Weed/seed treatments of the inland plots increased native ($P= 0.015$) and exotic forb cover ($P = 0.073$; Table 1). The coastal site had greater exotic cover of forbs and grasses in the invaded treatment ($P < 0.001$; $P = 0.0661$) and lower native grass cover in invaded than restored plots ($P < 0.001$; Table 2). Percent cover of litter did not differ between invaded and restored plots at the coastal site and was only higher in restored plots at the inland site during germination ($P < 0.001$; Fig. 1). Weeded/ seeded plots had lower litter percent cover than both invaded and restored treatments ($P < 0.001$ for all sample dates in the 2007-08 season; Fig. 1a). Exotic forb and grass and native forb biomass did not differ between treatments at the inland site, but native grass biomass was greater in the native treatment ($P < 0.001$; Fig 2). Biomass data for the coastal site is not available because plots were accidentally destroyed during management practices prior to biomass collection. Exotic forb ($P < 0.001$) and grass biomass ($P = 0.021$) was reduced in weed/seed treatments while native grass ($P < 0.001$) and forb biomass ($P = 0.001$) increased. However, native grass biomass in weed/seed treatments did not reach equivalent levels to the native treatments during the duration of this experiment (Fig. 2). Plant tissue percent carbon was similar across all species tested. *Erodium brachycarpum* and *Avena barbata* had the lowest leaf tissue nitrogen, whereas *Brachypodium distans*

and *Bromus rubens* had the highest. The native grass, *Nassella pulchra* was intermediate to all tested species in its percent nitrogen. The highest and lowest C:N were among the exotic species (Table 3).

Soils of the inland site were 31% sand, 57% silt and 12% clay, whereas those of the coastal site were 29% sand, 35% silt and 36% clay. Neither site differed in soil total carbon or nitrogen, pH, $NH_4$-N or C:N in summer of 2006. The inland site had higher available phosphorus in the invaded treatments ($P = 0.086$; Table 4) and the coastal site had higher levels of $NO_3$-N ($P = 0.001$) in the restored treatments but lower total extractable nitrogen in those same plots ($P = 0.007$; Table 5) from summer-sampled soils. Invaded soils of the inland site had higher $NH_4$-N during germination ($P = 0.004$) in the 2007-08 season but were the lowest at peak season ($P = 0.009$) (Fig. 3a). Soil $NH_4$-N had the opposite pattern during senescence ($P = 0.020$) at the coastal site and showed no difference between treatments earlier in the season (Fig.3 b). Soil $NO_3$-N did not differ between treatments at either site during germination, but was lower the remainder of the year in invaded treatments (inland: peak $P = 0.058$, senescence $P = 0.005$; coastal: peak $P = 0.085$, senescence $P = 0.005$; Figure 3a,b). Total extractable nitrogen was the same in invaded and restored plots at the coastal site, as well as during germination at the inland site, but lower in invaded treatments for the remainder of the season (peak $P = 0.002$; senescence $P = 0.099$; Fig. 3a). Season peak extractable nitrogen patterns were consistent across the three years of 2007-09 at the inland site where $NO_3$-N (2007 $P = 0.041$, 2008 $P = 0.058$, 2009 $P < 0.001$) and total extractable nitrogen (2007 $P = 0.040$, 2008 $P = 0.002$, 2009 $P = 0.001$) were lower in the invaded treatments (Fig. 4a). The coastal site had

lower total extractable nitrogen but higher $NO_3$-N in invaded plots in 2007, but no differences in any form of extractable nitrogen in 2008 (Fig. 4b). Total extractable nitrogen, $NH_4$-N and $NO_3$-N concentrations of the weed/seed treatments were similar to those of the native treatment through out the 2007-08 season and during the peak of 2007 and 2008, but were higher than both invaded and restored treatments in 2009 ($P<0.001$; Fig 3, 4a).

Microbial biomass was higher in invaded soils at the inland site during germination only ($P = 0.050$; Fig. 5a) and more than twice the mass in restored plots compared to invaded plots during senescence at the coastal site ($P = 0.013$; Fig. 5b). Fungal to bacterial ratios, while not different between invaded and restored treatments at the inland site, were lower in invaded treatments during season peak ($P = 0.050$) and higher in invaded soils during plant senescence ($P = 0.050$; Fig. 5c). The greatest number of PLFA biomarkers from the inland site were represented by bacterial functional groups with markers for fungi, microeukaryotes, protozoa, proteobacteria and pseudomonas found in lower abundance (Table. 6). Biomarkers from all functional groups except microeukaryotes and pseudomonas were present at significantly different concentrations between invaded and restored plots during plant germination, whereas the bacterial biomarker 15:0 3OH differed during peak and senescence of the growing season and biomarker 18:1 w5c during plant senescence. The coastal site soils were also dominated by bacterial biomarkers with markers for fungi, proteobacteria and protozoa in smaller numbers (Table 7). The PLFA biomarkers representing bacteria 19:1 (w8) alcohol and 17:1 alcohol (8w) differed during germination and only marker 16:1 w5c representing

AM fungi differed during the season peak. Soils for season senescence had differences in bacterial markers 19:1 (w8) alcohol, 18:0, 16:0 ISO, 17:0 ISO, 17:0 anteiso, 17:0 cyclo, 18:1 w5c, fungal marker 18:2 w6c, and AM fungal marker 16:1 w5c.

The first two PC's described 90.7 percent of microbial community variance at the inland site and ANOVA of the PC values differentiated between invaded and restored treatments along PC1 ($P = 0.009$) and between sample dates along both PC 1 ($P = 0.029$) and PC2 ($P = 0.022$; Figure 6 a,c). PC1 was composed of markers from bacterial, fungal, proteobacterial, protozoan, microeukaryotic and general functional groups while PC2 was primarily composed of gram positive bacteria, proteobacteria, microeukaryotes, and general functional groups (Fig. 8). Microbial communities of coastal site soils were differentiated by treatment along PC2 ($P = 0.041$) and by time along PC2 ($P = 0.077$) and PC3 ($P = 0.022$). The first 3 PC's explained 80 percent cumulative variance at the coastal site (Fig. 6b,c) and were composed to the same microbial functional groups: bacteria, proteobacteria, AM fungi, and protozoa (Fig.6; Table 8)

Soil potential respiration was not different between invaded and restored inland grassland soils (Fig. 7). Potential soil respiration of the weed/seed treatment was significantly reduced by the weeding treatment ($P < 0.001$; Fig 7). Plots at the coastal site had been unintentionally destroyed before soil respiration sampling was conducted so potential soil respiration data was not available for that site. At the inland site potential nitrogen mineralization rates of invaded and restored plots did not differ in April (Fig. 8a), but were lower in restored plots in August collected soils ($P = 0.017$; Fig. 8c). Potential nitrification rates were similar between invaded and restored plots in the April

soils (P = 0.061; Fig. 8a) and lowest in the invaded plots in soils collected in August (P = 0.013; Fig 8c). The coastal site had higher rates of potential nitrogen mineralization in invaded plots (P = 0.067) and lower rates of potential nitrification (P = 0.011; Fig. 8b) in the March collected soils, but no differences between treatments for either potential nitrogen mineralization or nitrification in August collected soils.

## Discussion

Invaded and restored soils differed in extractable nitrogen availability of both $NO_3^-$ and $NH_4^+$, nitrogen mineralization, nitrification and soil microbial community composition at both sites indicating grassland soils respond to altered vegetation types. The timing of sampling was an important factor in identifying changes as shifts in microbial communities and nitrogen cycling occurred on differing schedules at the two sites. This could be a reflection of the inherent difference in available soil moisture between the sites. That carbon and nitrogen pools did not change with vegetation may be due to the longer time scale on which these pools function. Alternatively, carbon and nitrogen pools may be showing resistance to vegetation type induced change or the incomplete nature of the restoration and annual variation of species composition of the annual dominated grasslands I used may be leaving a legacy that confounds carbon and nitrogen pool responses.

Due to high annual variability of annual plant species composition in semi-arid, annual dominated grasslands (Heady 1958; Hervey 1949; Talbot et al. 1939), the original composition used to select plots of invaded vs. restored treatments did not persist within

the selected plots beyond the 2006 season at either location. Exotic grass cover increased in the restored treatments in both grasslands between 2006-08. These natural fluctuations in species composition could expand the impact of exotics beyond a single year as a legacy of the previous year's composition. If legacy effects are important, patterns between invaded and restored treatments may not be detectable, and restored plots may reflect soil impacts from exotic annuals more than aboveground species percent cover would have predicted (Kulmatiski & Beard 2008).

Plant inputs to soil in the form of biomass were altered by invasion of exotic annual plants. Biomass of coastal sites had higher quality and greater C:N in general with one species, *Brassica nigra*, having lower C:N. Biomass of invaded plots at the inland site was dominated by exotics with higher C/N, *Avena barbata*, *Erodioum brachycarpum* and *Vulpia myuros. Vulpia myuros* was not tested for chemical composition in this study, but had a C/N=50:1 in previous work (Chapter 3). About 30% of the biomass input into the inland restored plots had lower C/N ratio than the inputs of invaded plots, yet carbon pools were unaffected by invasion in terms of total percent soil carbon, organic matter and potential soil respiration rates. Carbon pools are slow to cycle and are composed of several fraction of carbon with differing decomposition rates (Schlesinger 1997). Slower cycling of carbon pools may require a longer period of time to experience impacts of vegetation type change than used in this study. Alternatively, the shifts in litter input may not have been great enough to lead to altered carbon pools suggesting carbon pools of

grasslands could be resistant to impacts of exotic annual invasion. Long-term observation of restorations with more successful exotic plant removal is necessary to determine which explanation correctly describes carbon pool responses.

In addition, total nitrogen pools at both sites remained unchanged by restoration although nitrogen cycling was altered. Potential nitrogen mineralization rates were about 25 percent greater in invaded than in restored plots at the inland site from August-collected soils. August is near the end of the dry season, which is when soils have the highest levels of available nitrogen of the season (Jackson et al. 1988; Padgett et al. 1999). Increases in mineralization are found in other grasslands invaded by exotic grass species and are attributed to greater abundance of ammonia-oxidizing bacteria (Hawkes et al. 2005). Biomass of bacteria increased in invaded soils, but without DNA based techniques, I am unable to determine if increased bacterial biomass was associated with increased ammonia-oxidizing bacteria.

Nitrogen immobilization was reduced by invasion at the coastal site. Negative values of potential nitrogen mineralization indicated greater quantities of $NO_3^-$ were taken up than produced by microbes or present at initiation of soil incubations. Increased nitrogen immobilization combined with high potential nitrification suggests that nitrogen cycling rates were higher in restored plots and that soil microbes were immobilizing nitrogen at higher rates. Microbial community biomass was higher in restored plots at the peak season by late March, whereas total carbon and organic matter were similar between treatments. The ideal growth conditions of mineralization incubation could have initiated turnover of the microbial community, and led to higher activity, such as nitrogen cycling

and immobilization in the restored treatment with higher microbial biomass. Immobilization may have occurred at the coastal site and not the inland site because the soil C/N ratio was 15 percent lower and percent soil organic matter 5% less at the inland site. Higher organic matter in conjunction with high C/N soil values would allow for higher rates of nitrogen mineralization while also leading to increased immobilization overall in restored plots of the coastal site.

Soil total extractable nitrogen and $NO_3$-N were reduced by invasion during peak and senescence periods of the growing season. $NO_3$-N is a more mobile nutrient and thus easier for plant roots to obtain than $NH_4^+$ (Nye & Tinker 1977), which may explain the reduced impact of invasion on soil $NH_4$-N. Jackson et al (1989; 1988) also found that $NH_4^+$ remains higher in invaded soils while $NO_3^-$ fluctuates with plant growth rates. In addition, plants can take up as much $NO_3^-$ as becomes available. More interesting was that extractable nitrogen concentrations of the inland site were higher in invaded soils at plant germination but quickly became significantly lower within 2-3 months, suggesting increased rates of extractable nitrogen use in invaded sites. During germination, plant uptake of nitrogen was still low, but began to increase rapidly as plant growth reached its maximum rates. The sampling dates of peak and senescence at these sites correspond to the periods of maximum annual growth and transition to reproduction phases during which their nitrogen use would be highest. The natives, on the other hand, germinated later and began maximum uptake closer to my senescence sampling date. *Nassella pulchra* recycles about half its annual nitrogen internally and thus may not take up nitrogen as soon or at rates as high as exotic annuals (Clark 1977; Hooper & Vitousek

1998; Jackson et al. 1988). In addition, microbial biomass (indicated by concentrations of PLFA biomarkers) was higher in invaded soils during germination indicating a stronger response of soil microbes in invaded soils following the first rains, likely due to higher root activity of germinating exotics or decomposition of the previous year's microbial biomass.

Soil microbial communities were altered by invasion at both sites as indicated by PCA analysis and individual biomarkers. Further differentiation occurred at the inland site evident by lower F:B of invaded soils at the peak of the season, but higher F:B at senescence when larger inputs of root biomass of annuals would be deposited providing substrate for fungal decomposition. Native bunchgrasses continue to grow longer into the season and thus would produce rhizosphere input at a later date but likely at a lower rate than early-senescing annuals (Jackson et al. 1988).

Microbial biomass, F:B and individual biomarkers changed over time and between treatments. Microbial community shifts over time may be a response to dominant plant species and seasonally changing environmental conditions. Shifts in microbial community in response to changes in temperature and moisture through the season are to be expected because different species require different conditions for growth (Pommerville 2007). Differences in microbial community biomass, F:B and individual markers between invaded and restored soils support my hypothesis that restoration of the native plant community produces a shift in the microbial community and that these grassland soils may be resilient to invasion when considering microbial communities. Hawkes and others (2006) found *Glomus* species of mycorrhizal fungi

decline in soils of exotic annual grasses compared to native bunch grasses in California grasslands. The grasslands of this experiment showed fungal biomarkers, 18:2 w6c, 18:1w9c, and 16:1 w5c to be in concentrations that differed in invaded soils across the growing the season. Similar to Hawkes' (2006) findings, my coastal grassland site had lower AM fungi PLFA markers in soils invaded by exotic annuals, but this did not occur until late in the growing season (i.e. plant senescence) when exotic annuals were beginning to move into reproductive phase and native plant species were at peak growth rates.

## Weeding and Seeding Restoration

Seeding of native species at the inland site was unsuccessful. This may be the result of increased seed predation following the drought of 2007 or that the microclimate created by weeding may have been too harsh for seed germination. Initial weeding of the plots created large patches of bare soil that would have experienced higher irradiance at the soil surface and decreased soil moisture. On the other hand, weeding of exotic plant species led to an increase in non-seeded native forb species and percent cover of exotic annuals, thus poor seed response is most likely due to seed predation. Successful germination of non-seeded species following weeding is likely the result of release from direct competition from the exotic species removed. Gillespie and Allen (2004) found that exotic grasses reduce native species success and that in the absence of this more competitive functional group, exotic forb species increase along with natives.

The effects of weeding on soils were to produce extractable nitrogen levels similar to that of restored burned plots. This along with the fact that potential nitrogen mineralization rates of the weeded plots matched restored plots further suggests that differences in extractable nitrogen between invaded and restored treatments was due to plant uptake. Jackson et al (1988) found similar accumulation of $NO_3$-N in soils where plants are absent. The only measure that did not follow suit with restored treatments was potential soil respiration where weed/seed plots had greatly reduced rates. This is most likely due to reduced carbon input into soils since weeded species biomass was not integrated into the plots during the two years of weeding.

## Conclusions

Invaded and restored treatments in both coastal and inland California grasslands differed in soil microbial community composition, extractable nitrogen concentrations, potential nitrogen mineralization and nitrogen immobilization. These differences in soil characteristics were site and season dependant. The results of this study indicate that the soils of these systems are dynamic and change in response to vegetation type and seasonal variation in soil moisture. Semiarid grasslands in general are known to be unstable systems reliant on seasonal precipitation (George et al. 1992). The timing and volume of precipitation are strong determinants of the above ground plant community composition (Biswell 1956; Talbot et al. 1939). In a vegetation type with drastic shifts in plant species compositions and microbial communities that appear reliant on the vegetation type, it is difficult to determine if soils are resilient. The fact that soil chemical

and biological characteristics changed in response to altered vegetation type shows that grassland soils are not resistant to the impacts of exotic plant invasion. Without a reference site, I can not conclude that changes that occurred in the restored soils have put these grasslands on a trajectory towards that of native grasslands soils. However, once native plants and their soil inputs were restored, many soil characteristics diverged from that of the soil characteristics found in invaded soils regardless of the method of exotic plant control (i.e. prescribed burn, mowing and weeding). Results such as these indicate that the method of exotic plant removal is not important in these grasslands, but that the removal of exotic plants themselves and thus their direct impacts is required for grassland soils to recover.

The lack of difference in total carbon and nitrogen and potential soil respiration may be an indication that for some soil characteristics these grasslands are resistant to invasion or that the impact on these characteristics occurred long ago and the soil resilience does not extend to these variables or will require a more complete restoration and more time for recovery. Soil carbon pools change slowly and thus it is more likely the soils have been impacted and would require more extensive vegetative restoration and several years of maintained restoration. Kindscher and Tieszen (1998) found that tall grass prairie soils can require more than 35 years to recover from agricultural use following restoration. While there are no reference sites to compare the restored plots to in order to assess recovery trajectory and success, the presence of differences between soil chemical and biological variables of invaded and restored soils supports the hypothesis that exotic plants facilitate different microbial communities and alter the soils

they invade. That increasing native plant species percent cover and reducing exotic percent cover leads to microbial community and soil chemistry shifts suggests that grassland soils may have the capacity for resilience. In addition, hand removal of exotics followed by recovery of non-seeded native species produced nitrogen cycling rates similar to that of long-term restored soils while other soil properties were different from invaded and restored soils. This illustrates that the effects of invasion on soils may vary in their timescales of impact. Cycling of nutrients like $NO_3^-$ may respond to the restoration of native vegetation quickly, but pools such as carbon may require more time to show a response.

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Table 1.1. Common species mean percent cover of inland grassland dominant plant species during the peak of the 2007-08 season. Repeated measures MANOVA were conducted to assess differences in plant composition between treatments of invaded and restored grasslands over three years during the 2006-09 growing seasons.

| | Invaded | Weed/Seed | Restored-Burned | P values | | |
|---|---|---|---|---|---|---|
| | 2007-08 | 2007-08 | 2007-08 | Treatment | Time | Time x treatment |
| Native Grass | 8.3 | 16 | 40.1 | <.0001 | <.0001 | 0.0713 |
| *Nassella pulchra* | 8.3 | 16.0 | 40.1 | | | |
| Native Forb | 4.1 | 15.5 | 3.2 | 0.0153 | <.0001 | 0.0467 |
| *Asclepias eriocarpa* | 0.2 | 0.0 | 0.1 | | | |
| *Clarkia purpurea* | 0.3 | 5.0 | 1.4 | | | |
| *Conyza canedensis* | 0.0 | 0.6 | 0.0 | | | |
| *Crassula connata* | 0.9 | 6.5 | 0.0 | | | |
| *Gnaphalium canescens* | 0.1 | 0.2 | 0.0 | | | |
| *Holocarpha virgata ssp elongata* | 1.2 | 0.9 | 0.0 | | | |
| *Lotus purshianus* | 0.0 | 1.0 | 0.1 | | | |
| *Lupinus bicolor* | 0.0 | 1.2 | 0.0 | | | |
| *Sidalcea malvaeflora* | 1.2 | 0.0 | 1.3 | | | |
| 4 Combined uncommon spp. | 0.2 | 0.1 | 0.4 | | | |
| Exotic Forb | 59.6 | 8.3 | 24.7 | 0.0734 | <.0001 | <.0001 |
| *Anagallis arvensis* | 3.3 | 0.9 | 0.4 | | | |
| *Cerastium glomeratum* | 0.6 | 0.1 | 2.7 | | | |
| *Erodium brachycarpum* | 41.6 | 0.3 | 20.4 | | | |
| *Erodium cicutarium* | 5.2 | 0.1 | 0.0 | | | |
| *Filago gallica* | 2.6 | 4.1 | 0.0 | | | |
| *Hypochaeris glabra* | 5.8 | 0.7 | 1.1 | | | |
| *Lactuca serriola* | 0.4 | 0.0 | 0.0 | | | |
| *Silene gallica* | 0.2 | 0.4 | 0.0 | | | |
| *Tragopogon dubius* | 0.0 | 0.0 | 0.4 | | | |
| *Trifolium hirtum* | 0.0 | 1.7 | 0.0 | | | |
| Exotic Grass | 47.0 | 24.9 | 39.7 | 0.3718 | <.0001 | 0.0086 |
| *Avena fatua/barbata* | 6.1 | 1.1 | 12.6 | | | |
| *Bromus diandrus* | 1.0 | 0.3 | 1.8 | | | |
| *Bromus hordeaceus* | 12.6 | 2.7 | 10.3 | | | |
| *Bromus madritensis ssp. rubens* | 3.1 | 0.0 | 0.0 | | | |
| *Vulpia myuros* | 24.2 | 20.8 | 15.0 | | | |

Table 1.2. Coastal grassland percent cover of the most common species at the peak of the 2007-08 season. Means are shown for plant species percent cover. Repeated measures MANOVA were conducted to assess differences in plant composition between treatments of invaded and restored grasslands over three years during the 2006-09 growing seasons.

| | Invaded | Restored-Weeded | P-values | | |
|---|---|---|---|---|---|
| | 2007-08 | 2007-08 | Treatment | Time | Time x treatment |
| Native Shrubs | 2.4 | 0.0 | 0.362 | 0.67 | 0.67 |
| *Isocoma menziesii* | 2.4 | 0.0 | | | |
| Native Grasses | 3.0 | 41.5 | < .001 | 0.074 | 0.048 |
| *Nassella pulchra* | 3.0 | 41.5 | | | |
| Exotic Forbs | 50.8 | 12.9 | < .001 | < .001 | 0.01 |
| *Brassica nigra* | 33.7 | 0.3 | | | |
| *Malva parviflora* | 0.0 | 18.0 | | | |
| *Medicago polymorpha* | 1.1 | 0.0 | | | |
| *Melilotus indicus* | 12.9 | 12.3 | | | |
| *Picris echiodies* | 0.3 | 5.3 | | | |
| *Sonchus oleraceus* | 2.8 | 0.0 | | | |
| Exotic Grasses | 67.8 | 41.5 | 0.066 | < .001 | 0.196 |
| *Avena fatua* | 0.2 | 7.6 | | | |
| *Brachypodium distachyon* | 67.6 | 36.8 | | | |

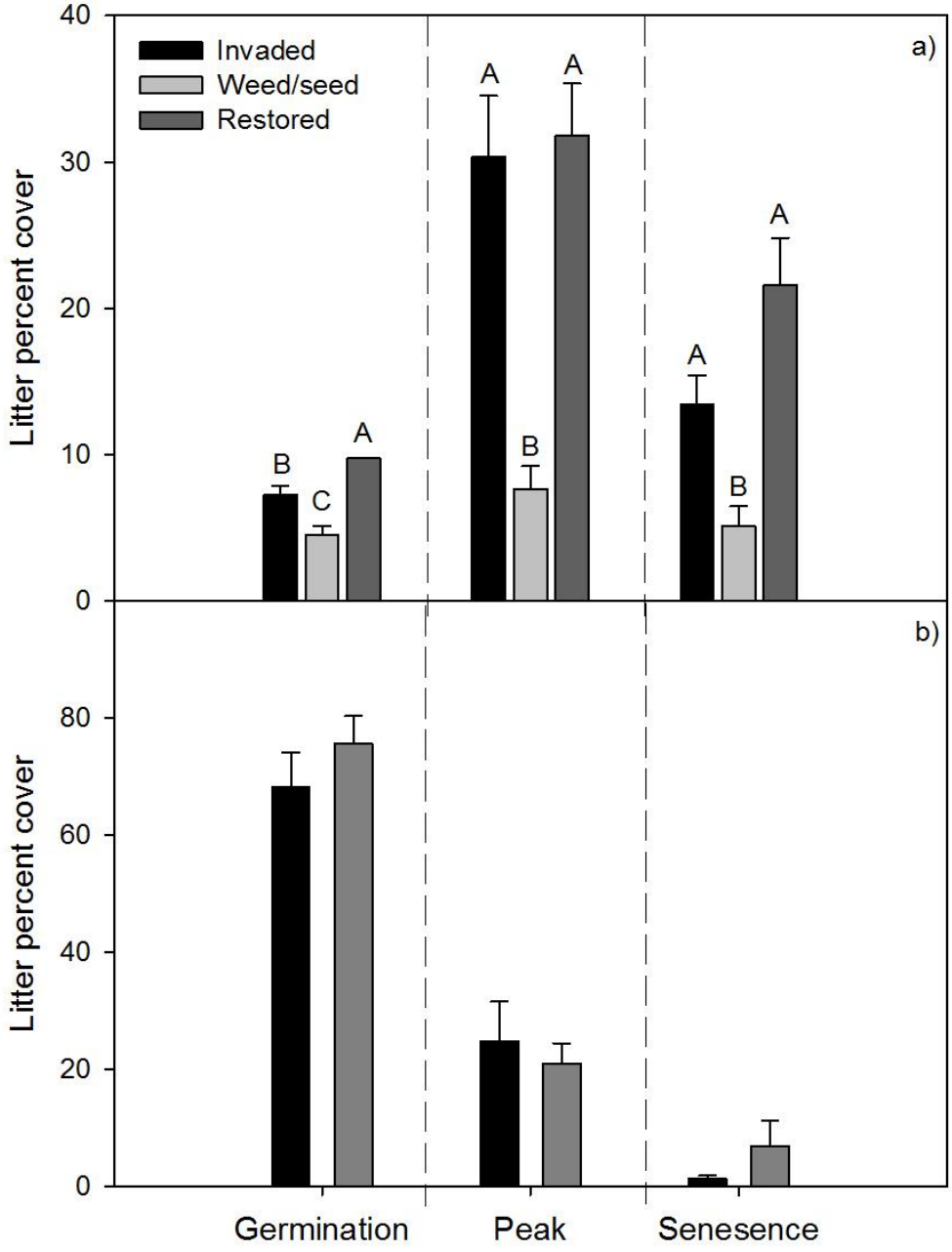


Figure 1.1. Percent litter cover collected at plant senescence of the 2007-08 growing season inland (a) site and coastal site (b) from the 2007-08 season. Restored treatment of graph a) refer to restored-burned treatments of the inland site and those of graph b) refer to restored-weeded treatments of the coastal site. Bars indicate standard error and letters significant differences ($P \leq 0.05$) determined by ANOVA.

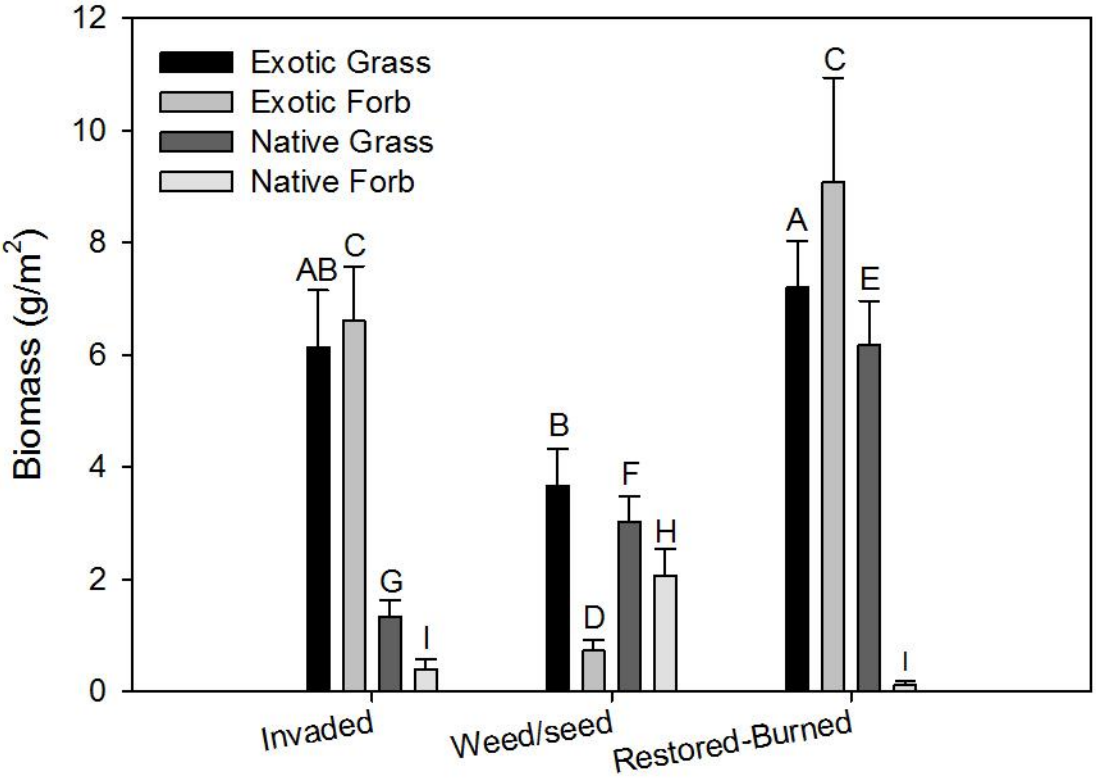


Figure 1.2. Plant biomass clipped at ground level during plant senescence of the 2007-08 growing season at the inland site in invaded, weed/seed, and restored-burn treatments. Bars indicate standard error and letters significant differences ($P \leq 0.05$) determined by ANOVA comparisons within plant functional groups exotic forb, exotic grass, native forb and native grass.

Table 1.3. Nitrogen and carbon composition of leaf tissue from composite samples at both experimental sites. *Brachypodium distans* was found only at the coastal site while the remaining species are found in both locations. Means are shown for dominant plant species. Due to limited tissue, composite samples were used to characterize plant tissue so replication was insufficient for statistical analysis.

| | N (%) | C (%) | C/N |
|---|---|---|---|
| **Natives** | | | |
| *Nassella pulchra* | 1.0 | 42.7 | 42.1 |
| **Exotics** | | | |
| *Avena barbata* | 0.7 | 41.2 | 62.0 |
| *Brachypodium distans* | 1.3 | 42.3 | 31.3 |
| *Brassica nigra* | 0.9 | 41.2 | 56.5 |
| *Bromus madritensis ssp. rubens* | 1.7 | 42.5 | 25.5 |
| *Erodium brachycarpum* | 0.6 | 42.7 | 67.4 |

Table 1.4. Soil chemical data (means and standard errors) for the burned site collected pre-and post-fire. ANOVA was conducted to assess differences in soil chemical characteristics between treatments of invaded and restored inland grasslands during the 2006-07 growing season.

| | Invaded | SE | Weed/Seed | SE | Restored-Burned | SE | P-value |
|---|---|---|---|---|---|---|---|
| Total N (%) | 0.2 | 0.0 | 0.2 | 0.0 | 0.2 | 0.0 | 0.739 |
| Total C (%) | 2.2 | 0.1 | 2.1 | 0.1 | 2.2 | 0.1 | 0.789 |
| Soil organic matter (%) | 8.5 | 0.3 | 7.7 | 0.4 | 8.0 | 0.2 | 0.152 |
| C/N | 13.4 | 0.1 | 13.5 | 0.2 | 13.3 | 0.1 | 0.826 |
| NH4 (ug/g) | 6.5 | 0.3 | 6.5 | 0.3 | 9.2 | 2.4 | 0.601 |
| NO3 (ug/g) | 3.6 | 1.7 | 2.4 | 0.5 | 1.8 | 0.5 | 0.564 |
| Total extractable N (ug/g) | 10.1 | 1.8 | 8.9 | 0.8 | 11.0 | 2.4 | 0.826 |
| Olsen-P (ug/g) | 5.1 | 0.7 | 4.0 | 0.5 | 4.1 | 0.8 | **0.086** |
| pH | 5.9 | 0.1 | 5.9 | 0.0 | 5.9 | 0.0 | 0.999 |

Table 1.5. Soil chemical data (means and standard errors) for the unburned site collected summer 2006. ANOVA was conducted to assess differences in soil chemical characteristics between treatments of invaded and restored coastal grasslands during the 2006-07 growing season.

| | Invaded | SE | Restored-Weeded | SE | P-value |
|---|---|---|---|---|---|
| Total N (%) | 0.2 | <0.1 | 0.2 | <0.1 | 0.162 |
| Total C (%) | 3.2 | 0.2 | 3.1 | 0.2 | 0.727 |
| Soil organic matter (%) | 13.3 | 0.3 | 13.0 | 0.2 | 0.541 |
| C/N | 14.0 | 0.5 | 15.7 | 0.8 | 0.105 |
| NH4 (ug/g) | 7.4 | 0.3 | 8.3 | 0.6 | 0.308 |
| NO3 (ug/g) | 5.8 | 1.3 | 31.9 | 8.3 | **0.001** |
| Total extractable N (ug/g) | 13.1 | 1.5 | 40.2 | 8.6 | **0.007** |
| Olsen-P (ug/g) | 18.8 | 1.1 | 22.1 | 3.6 | 0.401 |
| pH | 8.0 | <0.1 | 8.0 | 0.1 | 0.537 |

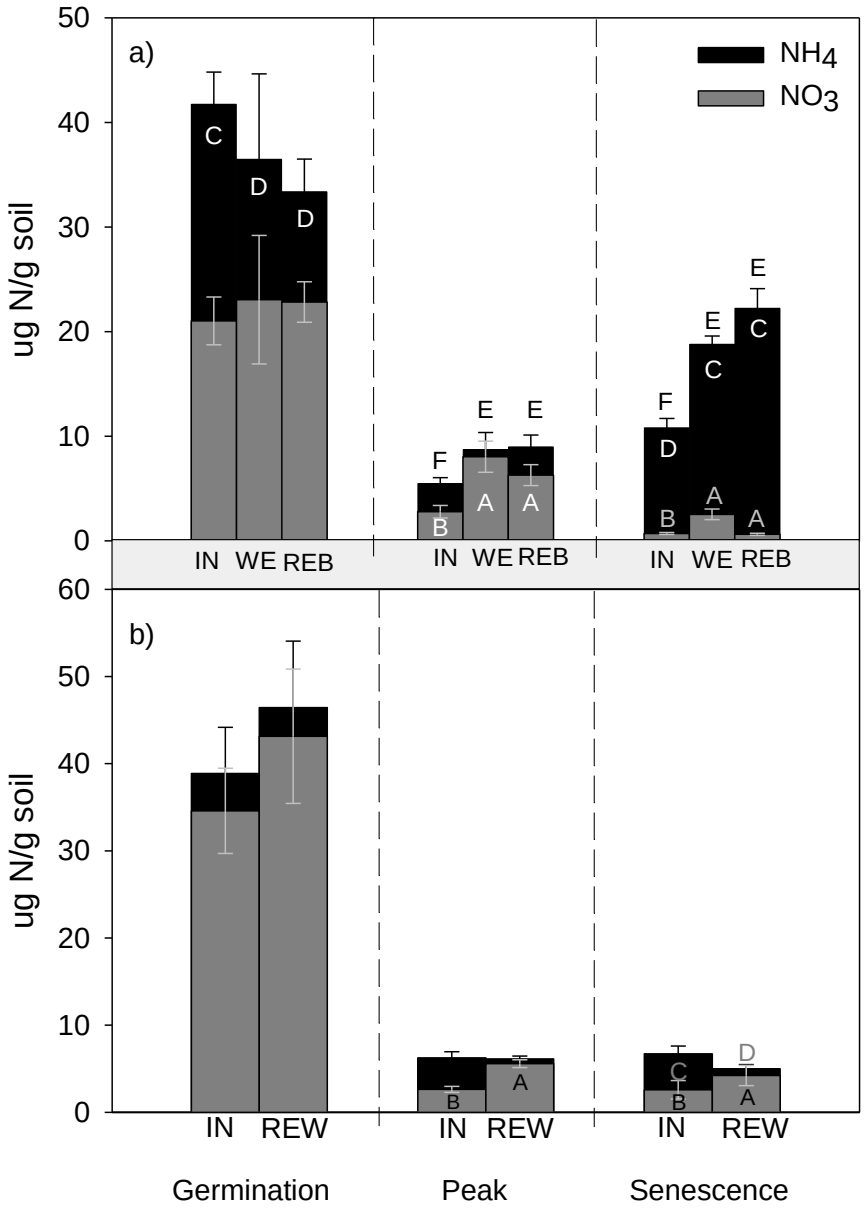


Figure 1.3. Soil extractable nitrogen during the 2007-08 season at the inland site (a) and coastal site (b). Treatments are: IN = invaded, WE = weeded/seeded and REB = restored by burning at the inland site and REW = restored by weeding and mowing at the coastal site. Letters indicate significant differences using ANOVA followed by Tukey-Kramer HSD test: $NO_3$ = A-B, $NH_4$ = C-D and total extractable nitrogen = E-F. Bars indicate standard error and letters significant differences ($P \leq 0.1$).

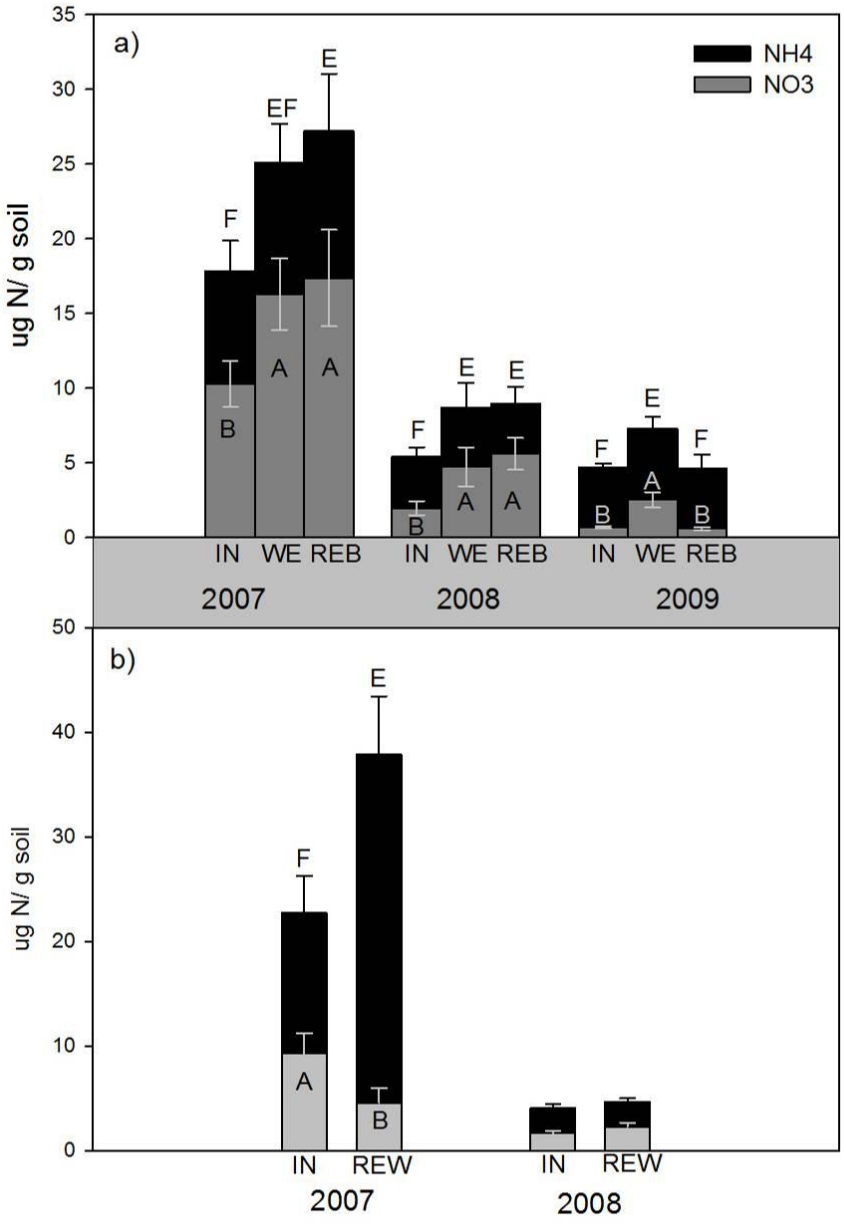


Figure 1.4. Soil extractable nitrogen from the peak of the 2007 and 2008 seasons at the inland site (a) and coastal site (b). Treatments are: IN = invaded, WE = weeded/seeded and REB = restored by burning at the inland site and REW = restored by weeding and mowing at the coastal site. Letters indicate significant differences using Tukey-Kramer test: $NO_3$ = A-B, $NH_4$ = C-D and total extractable nitrogen = E-F. Bars indicate standard error and letters significant differences ($P \leq 0.1$).

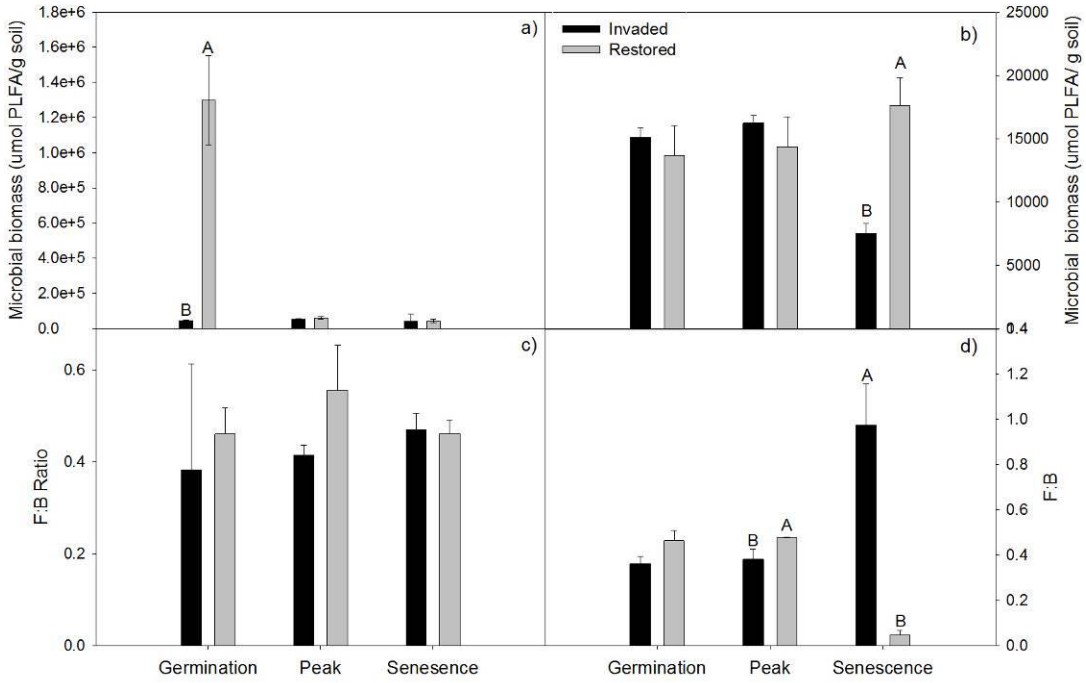


Figure 1.5. Phospholipid fatty acid profiles (umol/PLFA/g soil) and fungal:bacterial (F:B) ratios representing soil microbial community biomass and composition at the inland site (a,c) and coastal site (b,d) for soils collected between fall 2007 and spring 2008. Restored bars of graph a) refer to restored-burned treatments of the inland site and those of graph b) refer to restored-weeded treatments of the coastal site. Bars indicate standard error and letters significant differences ($P \leq 0.1$) for within sampling dates and not across dates.

Table 1.6. The common PLFA biomarkers (µmol PLFA/ g soil) and corresponding microbial functional groups from the inland site during the 2007-08 season. Means are shown for biomarkers making up grater than two percent of total PLFA abundance. Asterisks indicate level of significance between treatments. * P≤ 0.1 determined with ANOVA.

| Inland Site | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | Germination | | Peak | | Senescence | |
| | Biomarker | Invaded | Restored-Burned | Invaded | Restored-Burned | Invaded | Restored-Burned |
| General | ISO 17:1 G | 13987 | 1772 * | 1502 | 1514 | 1288 | 1067 |
| | 15:0 3OH | 5441 | 634 * | 290 | 574 * | 461 | 189 * |
| | 19:1 (w 8?) Alcohol | 0 | 325 | 349 | 435 | 313 | 303 |
| | 19:0 CYCLO 11-12 2OH | 0 | 233 * | 276 | 280 | 168 | 173 |
| | 21:1 w3c | 0 | 81 | 43 | 0 | 40 | 0 |
| Bacteria | 14:0 | 2264 | 174 * | 180 | 245 | 150 | 229 |
| | 18:0 | 12167 | 846 * | 1047 | 1210 | 963 | 859 |
| Gram + | 16:1 ISO G | 0 | 0 | 68 | 78 | 58 | 59 |
| | 15:0 ISO | 9508 | 967 * | 1112 | 1381 | 1188 | 963 |
| | 15:0 ANTEISO | 6541 | 651 * | 725 | 858 | 773 | 678 |
| | 16:0 ISO | 7250 | 595 * | 690 | 856 | 622 | 563 |
| | 16:1 w9c | 3950 | 281 * | 388 | 437 | 321 | 308 |
| | 16:0 | 32211 | 2486 * | 3045 | 3597 | 2844 | 2959 |
| | 17:0 ISO | 4699 | 357 * | 358 | 435 | 332 | 296 |
| | 17:0 ANTEISO | 6305 | 514 * | 561 | 677 | 508 | 468 |
| | 22:0 | 0 | 331 * | 352 | 296 | 142 | 0 |
| | 24:0 | 9631 | 283 * | 343 | 314 | 164 | 59 |
| Gram - | 16:1 w7c | 12589 | 1155 * | 1527 | 1945 | 1354 | 1181 |
| | 17:0 CYCLO | 7374 | 735 * | 841 | 963 | 753 | 648 |
| | 18:1 w5c | 13749 | 942 * | 1342 | 1641 | 1110 | 1052 * |
| | 17:1 w8c | 0 | 0 | 76 | 241 | 0 | 46 |
| Fungi | 18:2 w6c | 12581 | 520 * | 1181 | 1294 | 755 | 1041 |
| | 18:1 w9c | 54220 | 3394 * | 4765 | 5577 | 3866 | 4245 |
| AM Fungi | 16:1 w5c | 11961 | 985 * | 1408 | 1600 | 1273 | 1042 |
| Microeukaryote | 20:0 | 0 | 174 | 256 | 255 | 173 | 0 |
| Protazoa | 20:4 w6c | 497682 | 0 * | 87 | 93 | 94 | 99 |
| Proteobacteria | 19:0 cyclo c11-12 | 0 | 2257 * | 2749 | 2919 | 2301 | 2226 |
| Pseudomonas | 18:1 w9t Alcohol | 944 | 182 | 200 | 264 | 136 | 146 |

Table 1.7. The common PLFA biomarkers (μmol/g soil) and corresponding microbial functional groups from the coastal site during the 2007-08 season. Means are shown for biomarkers making up grater than two percent of total PLFA abundance. Asterisks indicate level of significance between treatments within a sample period. **P≤0.001, * P≤ 0.05.

| Coastal Site | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Germination | | | Peak | | | Senescence | | |
| | Biomarker | Invaded | Restored | | Invaded | Restored | | Invaded | Restored | |
| General | ISO 17:1 G | 795 | 955 | | 1197 | 960 | | 501 | 1096 | |
| | 19:1 (w 8?) Alcohol | 119 | 214 | * | 251 | 218 | | 0 | 294 | ** |
| | 21:1 w3c | 237 | 226 | | 119 | 108 | | 35 | 294 | |
| Bacteria | 18:0 | 285 | 282 | | 352 | 328 | | 59 | 359 | * |
| Gram + | 15:0 ISO | 172 | 273 | | 291 | 228 | | 43 | 241 | |
| | 15:0 ANTEISO | 114 | 177 | | 157 | 134 | | 0 | 129 | |
| | 16:0 ISO | 146 | 185 | | 200 | 163 | | 0 | 194 | * |
| | 16:1 w9c | 72 | 99 | | 130 | 76 | | 0 | 91 | |
| | 16:0 | 721 | 960 | | 1039 | 852 | | 965 | 993 | |
| | 17:0 ISO | 128 | 150 | | 150 | 139 | | 0 | 166 | * |
| | 17:0 ANTEISO | 185 | 214 | | 187 | 177 | | 0 | 214 | * |
| Gram - | 16:1 w7c | 563 | 766 | | 654 | 561 | | 119 | 661 | |
| | 17:1 w8c | 85 | 86 | | 103 | 72 | | 0 | 84 | |
| | 17:1 Alcohol (w 8?) | 108 | 0 | * | 0 | 19 | | 0 | 54 | |
| | 17:0 CYCLO | 198 | 212 | | 207 | 194 | | 0 | 223 | * |
| | 18:1 w5c | 188 | 203 | | 237 | 196 | | 55 | 292 | * |
| Fungi | 18:2 w6c | 249 | 164 | | 202 | 199 | | 54 | 282 | * |
| | 18:1 w9c | 1163 | 1120 | | 1213 | 1296 | | 1052 | 1477 | |
| AM Fungi | 16:1 w5c | 295 | 408 | | 424 | 336 | * | 71 | 437 | * |
| Proteobacteria | 19:0 cyclo c11-12 | 831 | 798 | | 857 | 838 | | 814 | 1188 | |
| Protazoa | 20:4 w6c | 196 | 55 | | 58 | 24 | | 0 | 42 | |

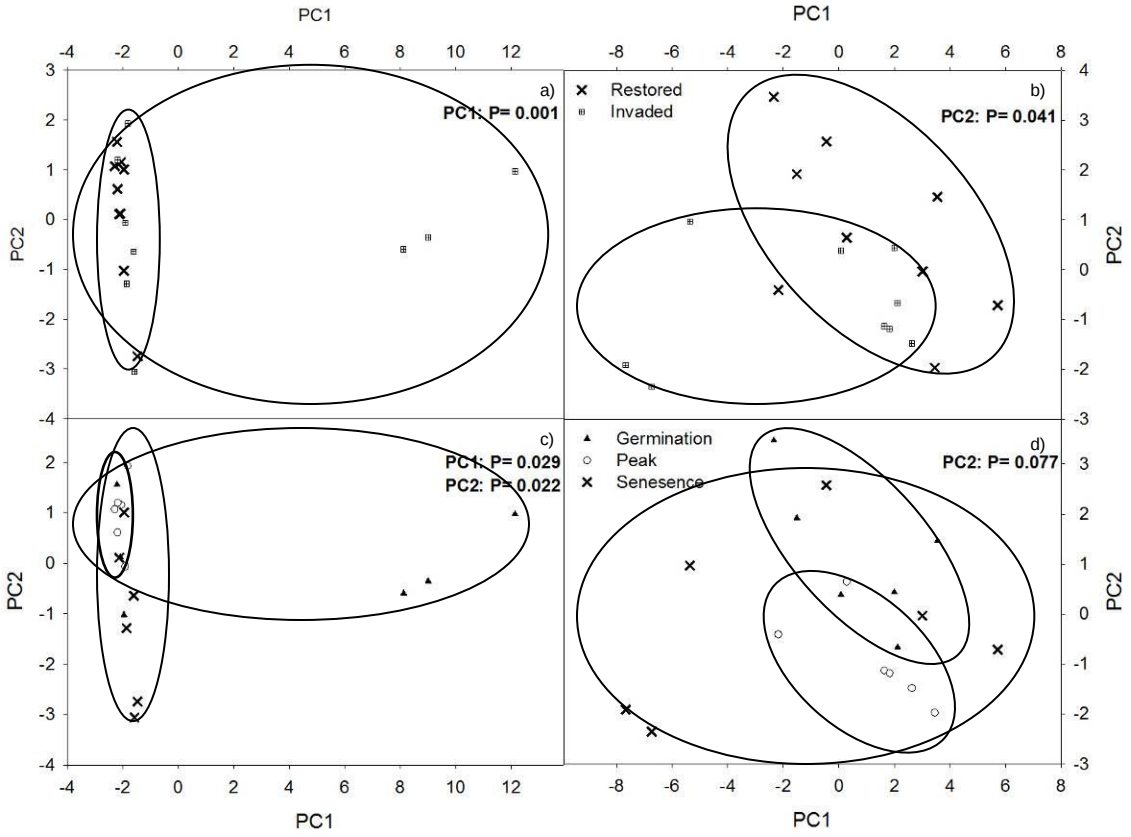


Figure 1.6. PCA results for PLFA microbial community analysis at the inland site (a,c) and coastal site (b,d) during the 2007-08 growing season. Restored data points of graph a) refer to restored-burned treatments of the inland site and those of graph b) refer to restored-weeded treatments of the coastal site. Graphs a and b assess differences between treatment while c and d assess differences between sampling dates. PC1 explains 83% variation and PC2 has a cumulative percent variation of 91% for the inland site, while the coastal site cumulative variance explained by PC1 is 59% and PC2 is 70%. . Elipses indicate statistically different microbial communities determined by ANOVA of PC values with an alpha level $\leq 0.1$.

Table 1.8. Soil microbial PLFA PC percent weights at both locations. Presence or absence of negative signs indicate the direction of the weighting along the corresponding PC. Cum % explained equals the variance within the PLFA data explained by successive PCs.

| | Inland Site | | | Coastal Site | | | |
|---|---|---|---|---|---|---|---|
| | Biomarkers | % wt PC1 | % wt PC2 | Biomarkers | % wt PC1 | % wt PC2 | % wt PC3 |
| **Cum % explained** | | 83 | 90.7 | | 58.9 | 70.3 | 79.3 |
| **Bacteria general** | 18:0 | 4.5 | | 18:0 | 6.2 | 2.9 | |
| | 14:0 | 4.3 | | | | | |
| Gram positive | 16:0 | 4.5 | | 15:0 ISO | | | -8.8 |
| | 17:0 ANTEISO | 4.4 | | 16:0 | 1.7 | -11.9 | 7.3 |
| | 15:0 ANTEISO | 4.4 | | 16:0 ISO | 6.5 | | |
| | 15:0 ISO | 4.4 | | 16:1 w7c | 6.2 | | -4.1 |
| | 16:0 ISO | 4.5 | | 16:1 w9c | | -4.9 | |
| | 17:0 ISO | 4.4 | | 17:0 ANTEISO | 6.4 | | |
| | 24:0 | 4.3 | | 17:0 ISO | 6.4 | | |
| | 22:0 | | 14.6 | 15:0 ANTEISO | | | -5.4 |
| | 16:1 w9c | 4.4 | | | | | |
| Gram negative | 17:0 CYCLO | 4.4 | | 17:0 CYCLO | 6.5 | | |
| | 16:1 w7c | 4.4 | | 18:1 w5c | | 4.2 | |
| | 16:1 2OH | | | 17:1 Alcohol (w 8?) | 0.3 | 13.1 | 9.4 |
| | 18:1 w5c | 4.4 | | | | | |
| Proteobacteria | 19:0 cyclo c11-12 | -4.0 | 6.8 | 19:0 cyclo c11-12 | 3.5 | | 15.4 |
| | 19:0 cyclo c11-12 2OH | -3.2 | 13.1 | | | | |
| Fungi | 18:2 w6c | | | 18:1 w9c | | -6.7 | 14.2 |
| | 18:1 w9c | 4.4 | | 18:2 w6c | | 7.2 | |
| AM fungi | 16:1 w5c | 4.4 | | 16:1 w5c | 6.3 | | -4.2 |
| Protozoa | 20:4 w6c | 4.4 | | 20:4 w6c | -0.1 | 9.8 | -7.4 |
| Microeukaryote | 20:0 | | 16.0 | | | | |
| General | 15:0 3OH | 4.4 | | 20:1 w3c | 1.5 | -8.3 | -12.5 |
| | ISO 17:1 G | 4.4 | | | | | |
| | 19:1 (w 8?) Alcohol | | 11.6 | | | | |

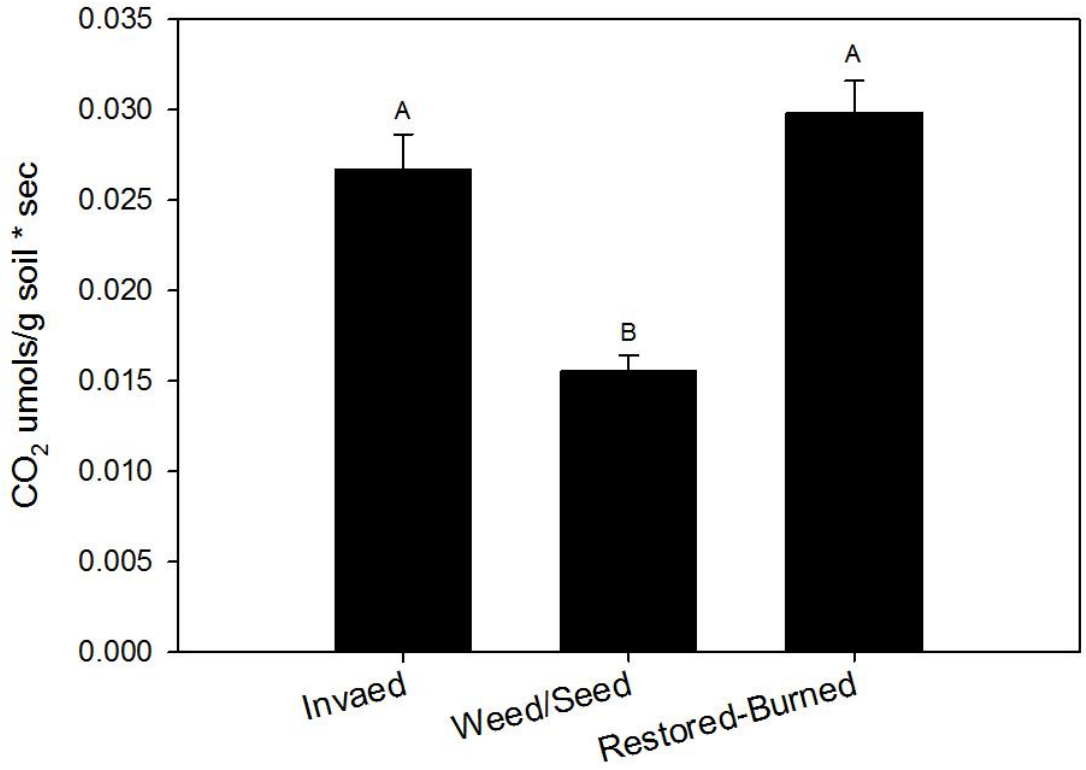


Figure 1.7. Potential soil respiration rates from 10 day laboratory incubations of soil collected at the peak of the growing season at the inland site (a,c) and coastal site (b,d).Bars indicate standard error and letters significant differences ($P \leq 0.1$) determined by ANOVA.

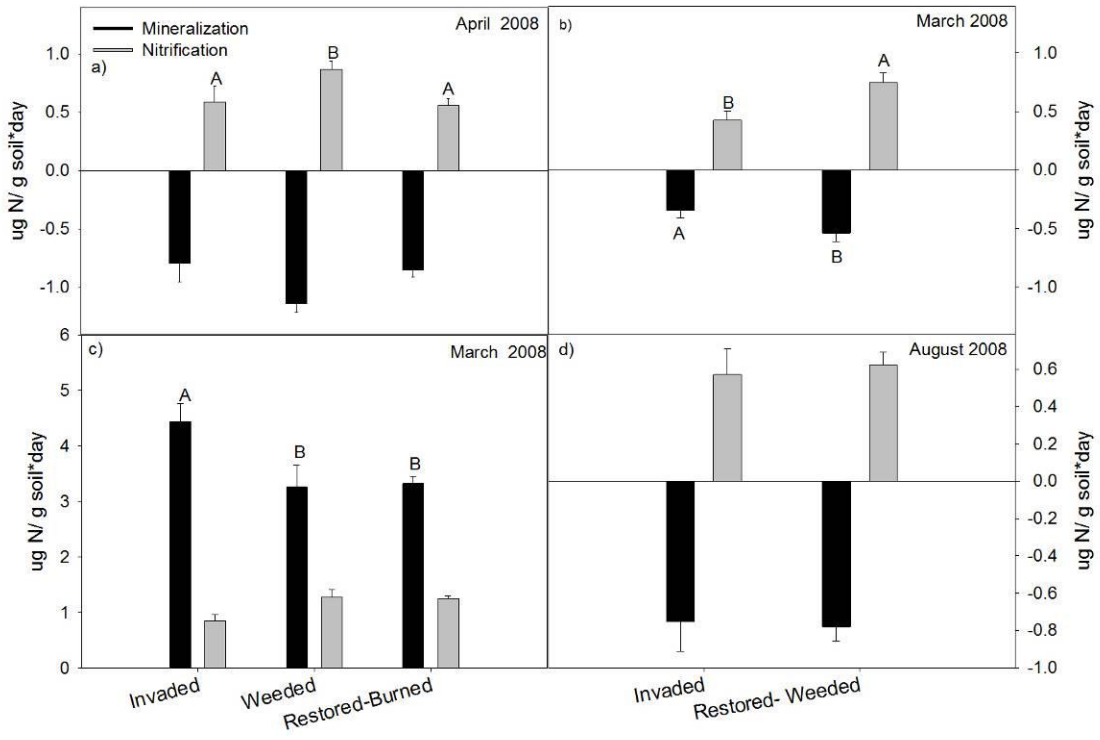


Figure 1.8. Potential nitrogen mineralization and nitrification from 30 day laboratory incubations from the inland site (a,c) and coastal site (b,d) for soils collected in spring (March) and end of summer (August) of 2008. Letters indicate significant differences using Tukey-Kramer HSD test following ANOVA ($P \leq 0.1$). Bars indicate standard error.

**Exotic annuals alter the variation in coastal sage scrub soil chemical and biological characteristics**


## Abstract

Following exotic plant invasion, ecosystem structure and function can be altered above- and below-ground through plant-soil feed backs. Plant inputs to soil provide substrate for soil microbes so altered inputs caused by exotic plants could lead to an altered microbial community. Invasive species have caused chemical and biological feedbacks on soil, but the ability of soils to recover once native plants are restored is less understood. Exotic annual plant invasions into the coastal sage scrub (CSS) have led to the conversion of 80% of original CSS lands to exotic grasslands, but assessment of the effectiveness of restorations have focused on the aboveground plant communities. The ability for CSS ecosystems to resist changes to soil chemical and biological characteristics caused by exotic plant invasion and their resilience following these potential changes is unknown. I examined the resistance and resilience of CSS soil chemical and biological characteristics following exotic annual grasses and forbs. Hypotheses were (**1**) Presence of exotic plant species changes biological and chemical characteristics of CSS soils by altering soil nutrient inputs. (**2**) If exotic plants are controlled and native plants restored, soil characteristics will return to pre-invaded conditions because soil inputs from native CSS plants would be restored. While tissue chemistry of exotic plants differed from natives, the total soil carbon and nitrogen and extractable phosphorus did not differ between invaded, restored and native CSS. Extractable nitrogen pools and nitrogen cycling rates differed between invaded, restored

and native soils, according to the phenological stage of the dominant plant species. Nitrogen mineralization and nitrification rates increased with invasion whereas soil respiration did not differ between invaded, restored and native soils. The largest impact of invasion on soils was an overall reduction of spatial heterogeneity in soil nutrient, nutrient cycling and microbial communities due to introduction of the shallower and more densely spaced rooting structure of exotic annuals. Restoration activities had greater impacts on nitrogen cycling rates than did exotic plant invasion though such impacts did not persist. Coastal sage scrub soil C, N and P and microbial communities (assessed by phospholipid fatty acid (PLFA) profiles) were resistant to the impacts of exotic plant invasion. However, invasion by annual grasses decreased variability of the same resources and microbial PLFAs were altered by invasion, indicating that CSS soil resistance to invasion is scale dependent.

## Introduction

Soil microbial community composition and function are determined by climate (i.e. precipitation and temperature) soil structure (i.e. texture and aggregation), soil chemistry and plant inputs (i.e. litter and exudates) (Buyer et al. 2010; Fierer & Jackson 2006; Hattenschwiler & Vitousek 2000; Potthoff et al. 2006; Yu & Ehrenfeld 2010). Plant inputs to the soil provide substrate for the microbial community such that, in combination with effects of abiotic climate and soil structural factors, plant inputs can influence microbial community composition. Microbes are the key drivers of nutrient cycling so factors that affect microbial community composition can effect soil nutrients (Seybold et al. 1999). Exotic plants alter ecosystem processes such as nutrient cycling by possessing traits that differ from the natives. These traits can include higher quality, quantity and timing of deposition of litter, differing root exudates, different phenology and microbial associations (Christian & Wilson 1999; Ehrenfeld 2003; Klironomos 2002; Yoshida & Allen 2004). Exotics can alter feedbacks to facilitate their persistence through fostering a microbial community or soil nutrient status that either hinders natives, facilitates the exotic or both (Batten et al. 2008; Ehrenfeld 2003; Hawkes et al. 2006; Klironomos 2002; Kourtev et al. 2002; Kulmatiski et al. 2008). Annual exotic plants experience up to four times greater positive feedbacks from plant-soil/microbe interactions than their co-occurring natives when grown in self-cultivated soils (Kulmatiski et al. 2008).

The ability of soil to withstand alterations of microbial community composition, nutrient content and function (nitrogen mineralization, soil respiration) after a disturbance defines the system's capacity for resistance. In the case of exotic plant invasion, soils have two points at which they may be resistant to invasion. First, soil abiotic and biotic factors such as soil moisture, pH and microbial community composition may prevent establishment of exotic plant species. But once an invasion occurs, the second point for resistance is against the impacts of the invading species on soil chemical and biological properties. Understanding what traits of systems make them more or less resistant to invasion would enable managers to prioritize lands for exotic plant management. In systems that lack resistance, the level of resilience of the system after invasive species removal or restoration becomes of interest.

Resilience refers to the response of the system after alteration including rates of recovery, types of thresholds reached in recovery, similarities in the old versus new state of the system and whether the old and new system share levels and forms of stability (Gregory et al. 2009; Pimm 1984; Seybold et al. 1999; Westman 1978). Abiotic factors including soil texture, moisture and chemistry along with biotic factors such as plant and microbial species composition determine soil resistance and resilience (Chapin et al. 1997; Seybold et al. 1999). Soil microorganisms are often considered one of the major components of soil resilience because they are responsible for most nutrient cycling (Seybold et al. 1999). Invasion of exotic plant species has the potential to alter soils as

well as its associated microbial community. Given the importance of both these factors to soil resistance and resilience, exotic plant invasion has the potential to dramatically alter soils both biologically and chemically

Coastal sage scrub (CSS) is currently considered one of the most endangered ecosystems in the United States covering only 20% of its original habitat (Klopatek et al. 1979; Rubinoff 2001; Westman & O'Leary 1986). Coastal sage scrub has experienced threats from urbanization and agriculture since the early 1800's (Allen et al. 2000; Burcham 1957). In addition to these direct anthropogenic threats, invasion of exotic species has resulted in the type conversion of over 18% of the original coastal sage scrub into exotic annual grasslands (Klopatek et al. 1979; Minnich & Dezzani 1998; O'Leary 1995). Following invasion of exotic grasses, coastal sage scrub cover declines leading to the loss of plant and animal diversity commonly associated with this shrubland ecosystem (Alberts et al. 1993; Soulé et al. 1988) . In spite of this loss, the remaining intact areas contain over 200 rare and endangered species (Allen 2003; Bowler 2000; Brussard et al. 1992; Skinner & Pavlik 1994). The vegetation of CSS is neither resistant to exotic plant invasion nor resilient enough to recover following the disturbance of exotic plant invasion without human intervention. The effects of coastal sage scrub loss on plant and animal species has been well documented (Keeley & Swift 1995; Minnich & Dezzani 1998; Weaver 1981), however, the effects on soil biological and chemical characteristics are less understood (Nelson & Allen 1993). It is unknown if ecosystem functions

associated with plant and soil interactions are resistant to alterations caused by exotic plants and if these functions are resilient enough to recover without interventions once exotic plants have been removed and native species restored.

The level of change caused by an exotic species is considered to be related to how much it differs from native species (Ehrenfeld 2003). Exotic annual grasses differ from native shrub species in phenology, rooting structure and depth (Eliason & Allen 1997; Wolkovich et al. 2009; Wood et al. 2006), and tissue nutrient composition (Wolkovich et al. 2010), which gives them the potential to cause significant changes to the shrub ecosystem. Wood and others (2006) found that the invasion of exotic grass species into coastal sage scrub decreases soil moisture depth from 125-175cm to only 50cm. This reduction of available moisture at deeper soil profiles inhibits growth of juvenile shrub species and further facilitates the invasion of grasses (Eliason & Allen 1997).

Plants strongly control decay rates via the litter and root exudates they deposit to the soil (Hobbie 1992). Exotic annual grasses have increased nutrient cycling rates in multiple systems such as grasslands and CSS (Blank 2008; Ehrenfeld 2003; Sirulnik et al. 2007). Given this effect and the trait differences between the invading annual species versus the dominant perennial, woody shrub species, exotic annual invasion into CSS could increase nutrient cycling rates. Such increases in nutrient cycling could lead to further facilitation of exotic, nitrophilous species capable of quickly utilizing free nitrogen to germinate prior to native annuals. Previous studies found soils can be restored with reintroductions of native plant species or soil inoculations after anthropogenic disturbance (Bhojvaid & Timmer 1998; DeGrood et al. 2005; Graham & Haynes 2004;

Izquierdo et al. 2005; Ros et al. 2003; Zhao et al. 2005). However, little work has been done to determine if exotic plant removal and native plant restorations following invasions will promote reestablishment of the original bacterial and fungal communities, and biological and chemical characteristics of invaded soils. My hypotheses were: (**1**) Presence of exotic plant species in the CSS changes the biological and chemical characteristics of the soils by altering soil inputs. (**2**) If exotics are controlled and native CSS species restored, soil biological and chemical characteristics will return to pre-invaded conditions because the soil inputs of the native CSS plant will have been restored.

## Methods

### Study Sites

Research was conducted at two locations, White Point Preserve located in San Pedro, Los Angeles County, California and Trump National Golf Club located in Rancho Palos Verde, Los Angeles County, California. The two sites are 6 km from one another and receive an average of 30cm precipitation annually and experience mean temperatures of 8-26$^{\circ}$C. White Point Preserve, hence forth to be referred to as the grass site due to domination by exotic annual grasses in invaded plots, is a 121-ha reclaimed Department of Defense missile facility in which restoration of the coastal sage scrub began in 2000. Restoration consisted of exotic plant control, seeding of native shrubs and forbs, planting of native shrub seedlings, and irrigation. Soils are classified as a clay loam of Diablo Clay Adobe series (Nelson et al. 1919). Experimental treatments at the grass site are limited to invaded and restored CSS, as native CSS was not available at the site. The

Trump National Golf Club, hereafter to be referred to as the forb site as it is predominantly invaded by exotic forbs, is located on mitigation land adjacent to the golf club. Restoration began in 1999 and consisted of exotic plant removal, seeding of native vegetation, planting of potted plants, fertilization and irrigation. These restoration plots that were established by the land managers will be called the long-term restoration plots. Experimental treatments included invaded, restored and native CSS. Soils are also characterized as clay loam of the Diablo Clay Adobe series (Nelson et al 1919).

To examine the effect invasion had on CSS soil chemical and biological characteristics, nine replicate $1m^2$ plots per treatment were established on a southwest facing slope at each site. Native areas were those with no history of human activity and having exotic plant species cover less than 20 percent. Restored sites included those that experienced exotic plant removal and successful native shrub re-vegetation, while invaded areas contained 50 percent or greater exotic plant species cover.

To address effects of restoration activities, I established two additional sets of nine $1m^2$ plots in the invaded areas at the grass site in which two treatments were added, seeding and weeding + seeding. These will be called the short-term restoration plots. Hand weeding of all exotic species was maintained up to three weeks prior to data collection and seeding occurred following the first rains in the fall of 2007. Due to drought conditions in the 2006-2007 season, much of the seed was lost to grainivory so I seed again in 2008. Seeds of two shrubs, *Artemisia californica* (100 seed/ $m^2$), *Eriogonum fasciculatum* (200 seed/$m^2$) and an annual forb, *Phacelia ramosissima* (100

seed/ $m^2$) where evenly distributed over the plot and raked into the soil. All seed was donated by Palos Verdes Peninsula Land Conservancy and collected on site between 2004-2006.

## Community Composition

To determine the differences in plant species composition between invaded, restored and native communities, species percent cover and richness and percent cover of litter were measured annually at peak growth from 2007-2009. Net annual productivity of annuals was determined by collection of biomass clipped at soil level from $0.25m^2$ plots and scaled up to $1m^2$ using regression models of mass and percent cover. Additional biomass was collected for vegetative plant tissue chemical analysis at that time. Biomass was oven dried at 60°C and weighed then ground and analyzed for total C and N on a soil combustion analyzer system (Thermo-Finnigan model: Flash AlllZ).

## Soils and Microbial Communities

To determine the effects of exotic invasion on soil biological and chemical characteristics, soil core samples of 10 cm depth and 2.5 cm diameter were collected and transported on ice and stored at -20°C for chemical analyses and -80°C for microbial analyses. Soils were passed through a 2mm sieve for analysis of total carbon and nitrogen using the combustion method and phosphorus using the sodium bicarbonate Olsen method at the University of California Division of Agriculture and Natural Resources Analytical Laboratory at UC Davis (www.danranlab.ucdavis.edu). Soil texture was also

analyzed at University of California Analytical Laboratory in soil suspension by hydrometer from three composite soil samples per sampling site. Soil pH was determined with a 2:1 soil:water slurry. Soil cores were also collected once annually at peak plant growth 2007 and 2009, and three times annually (germination, peak and plant senescence) during the 2007-2008 growing season to be analyzed for extractable nitrogen ($NH_4^+$ and $NO_3^-$). Nitrogen was extracted in 1M KCL and shipped on dry ice and analyzed using the flow injection method at the University of California Analytical Laboratory.

Phospholipid fatty acid (PLFA) analysis was used to determine whether microbial community structure was affected by exotic invasion and restoration practices. All living organisms contain PLFAs as a component of their cellular membranes. Once extracted from the organisms, these compounds can be used as biomarkers to identify particular groups of microbes such as gram positive bacteria or arbuscular mycorrhizal fungi (Vestal & White 1989; Zelles 1999). Because the phosphate heads of phospholipid fatty acids separate from the fatty acid tails upon cell death, sampling of PLFA ensures capture of the current microbial community and its response to a recent disturbance such as exotic plant invasion or restoration activities. Samples were collected within 24 hours of rainfall or wetting of soils to a 10 year average rain fall amount. Soil samples were passed through a 2 mm sieve and lyophilized prior to extraction. PLFAs were extracted from 6 g of soil following the modified Bligh–Dyer method (Frostegard et al. 1991). Quantification of fatty acids was done using a gas chromatograph (HP6980; Hewlet Packard, Palo Alto, CA) with flame ionization detector and HP3365 ChemStation

Software. PLFA peaks were converted to PLFA identities and abundances using the Sherlock Microbial Identification System (MIDI Inc., Newark, NJ, USA) followed by a comparison of peak areas to a known internal standard 19:0 of known concentration. Bacterial biomarkers included: 14:iso, 14:0, 15:0 iso, 15:0 antiso, 15:0, 16:0 iso, 16:1 w9c, 16:1 w7c, 16:0, 17:1 alcohol, 17:0 iso, 17:0 antiso, 17:0 cyclo, 18:1 w5c, 18:0, 19:0 cyclo c11-12, 22:0, and 24:0. Fungal biomarkers were: 18:2 w6c, 18 1w9c, and 20: 1w9c, and AM fungi was 16:1 w5c. Nomenclature for PLFAs follow Lechevalier and Lechevalier (1988), Vestal and White (1989), Zelles (1999), Myers et al (2001), and Hebel et al (2009).

## Respiration and Mineralization

Laboratory incubations for nitrogen mineralization were performed over a 30 day period maintaining 25°C and 60% humidity. $NH_4^+$ and $NO_3^-$ were extracted with a 2 M KCL 4:1 solution (Riley & Vitousek 1995) and shipped on dry ice for analysis to University of California Analytical Laboratory. Net mineralization was calculated as the change in $NH_4$-N minus the change in $NO_3$-N over time and net nitrification was calculated as the change of $NO_3$–N over time following Riley and Vitousek (1995). Potential soil respiration rates were determined with laboratory incubations. Soils were maintained at 20% soil moisture and 25°C in sealed mason jars for 10 days. Jar headspace concentrations of $CO_2$ (ppm) were determined using a LiCor 800 infrared gas analyzer (Lincoln, USA) and converted to a rate function of mg $CO_2$-C/ g soil *day (Chatterjee et al. 2008).

## Data Analysis

Data were tested for normality using the Shapiro-Wilk W test and non-normal data were log (x+1) or square root transformed when appropriate. Plant biomass and litter, soil chemistry, soil extractable nitrogen, potential soil respiration and nitrogen mineralization data were analyzed with ANOVA followed by Tukey's HSD test to establish differences between treatments. In cases where the data could not be transformed to normality, Kruskal Wallis was used. Plant species percent cover and richness were analyzed using repeated measures MANOVA. Microbial biomass and F:B were also analyzed using ANOVA to determine coarse microbial community compositional shifts occurring as a result of invasion and restoration activities. Principal Components Analysis was used to create PC's to represent microbial community composition throughout PLFA profiles which were then analyzed with ANOVA to determine if community composition differed between treatments and across sampling dates. For a subset of soil variables a power analysis along with calculations of variance: mean (standard deviation$^2$ : mean), data skewness and Kurtosis were conducted to describe spatial heterogeneity or patchiness of resources and microbial communities across space within each treatment (Klironomos et al. 1999). The above analyses were conducted using JMP9 (SAS Institute 2009) with an alpha level $\leq 0.10$ to determine significance (Klironomos et al. 1999). Power analysis was conducted using Microsoft Office Excel 2003 assuming a power index using $\alpha = 0.05$ and $\beta = 0.20$ and a total treatment effect of 0.30 or treatment difference of 30%.

## Results

### Comparison of Invaded, Native, and Long-term Restoration Plots

*Plant Community Composition*

Plant species composition differed between invaded, 7 to 9 year old restored, and native treatments at both sites during low and average precipitation years (Table 1). Exotic species had significantly higher cover in invaded plots ($P < 0.0001$ for all three sample dates) and natives had higher cover in restored plots (germination $P < 0.0001$, peak $P = 0.001$, senescence $P = 0.112$). These differences were consistent within a growing season and across years. Exotic percent cover was higher in invaded plots sampled in 2007-09 ($P < 0.0001$ for all three years) while native percent cover was higher in restored plots (2007 $P < 0$ .0001, 2008 $P <$ 0.0001, 2009 $P = .056$). Forb site native plant species composition differed between the three treatments during all stages of the growing season (germination $P < 0.0001$, peak $P < 0.0001$, senescence $P = 0.001$). Restored and native plots were similar. Exotics had higher cover in invaded plots during all periods of the growing season (germination $P < 0.0001$, peak $P < 0.0001$, senescence $P < 0.0001$). Again, these patterns were consistent across years 2007-2009 (native percent cover 2007 $P < 0.0001$, 2008 $P = 0$ .078, 2009 $P = 0.002$ and exotic percent cover $P <$ 0.0001 for all sample dates). Plant tissue N of dominant exotic species, *Brassica nigra*, *Avena fatua*, and *Brachypodium distachyon*, was lower and C/N higher than the native shrubs whereas *Centaurea melitensis* had similar chemical composition. *Melilotis indicus* had higher N and lower C/N (Table 2).

Exotic grass biomass was greater in invaded plots at the grass site ($P < 0.0001$, Fig. 1a) and in the restored plots at the forb site ($P < 0.0001$). Exotic forb biomass was greatest in invaded plots and lowest in restored plots ($P = 0.001$, Fig. 1b) at the forb site, but not at the grass site. Litter percent cover was highest in restored plots ( $P < 0.0001$, Fig. 1c) at the grass site and in native plots ($P = 0.006$) at the forb site, while standing litter had higher percent cover only in forb site invaded plots ($P < 0.0001$; Fig.1d).

*Soils and Microbial Community*

Textural analysis of three composite samples from the grass site defined the soils as clay loam, with 33% sand, 33% silt and 34% clay. The forb site was loam with 35% sand, 45% silt and 20% clay in the restored and native areas and clay loam with 29% sand, 38% silt and 33% clay in invaded areas. Invasion of species are capable of changing the soil chemical and biological charecturistics of the systems they invade (Bardgett et al. 1999; Ehrenfeld 2004; Ehrenfeld et al. 2005; Kulmatiski & Beard 2008). Each of the systems studied here experience either a change in chemical mean pools or distribution, microbial community or both. The degree of change was site and season dependent which agrees with other recent work showing abiotic factors such as climate, soil texture and pH may play a greater role in determining soil biological and chemical characteristics (Fierer et al. 2009; Seybold et al. 1999; Ushio et al. 2008)

Soil chemical pools of carbon, nitrogen and phosphorus did not differ between invasion levels. Soil pH was not different between treatments at the grass site, but was higher in the native plots at the forb site (Table 3). Soil $NO_3$-N was twice the

concentration in invaded than in restored plots, but $NH_4$-N was half the concentration in invaded compared to restored plots at the grass site in summer 2006. $NO_3^-$ and $NH_4^+$ did not differ between treatments at the forb site ($NO_3$-N P = 0.038, $NH_4$-N P = 0.063; Table 3, Fig. 2a). Soil $NO_3$–N (P = 0.016) and total extractable nitrogen (P = 0.017) were higher in invaded soils during the germination period of the 2007-2008 growing season at the grass site but did not differ between treatments during the rest of the season ( P = 0.037; Fig. 3a). At the forb site, soil $NO_3$-N was higher in invaded and restored soils and extractable nitrogen lowest in native soils (P = 0.052) during the germination period of the 2007-2008 season and by the peak of the season $NO_3$-N (P = 0.032) and total extractable nitrogen (P = 0.051) were lowest in invaded soils and higher in both restored and native soils for the remainder of the growing season ($NO_3$-NP = 0.005; extractable nitrogen P = 0.010; fig 3b). Total extractable nitrogen was lower in invaded soils at the grass site during the peak of the growing season in both 2008 (P = 0.038) and 2009 (P = 0.010; Fig 2a); however, $NO_3$–N was lower (P = 0.032) in invaded soils at the forb site during the peak of 2008 only. During 2007 and 2009, soil $NO_3$–N concentrations were not different between treatments. Soil $NH_4$–N was higher (P < 0.001) in invaded plots in 2007 and not different between treatments in 2008 and 2009. Total extractable nitrogen was higher at the forb site (Fig 2b) than the grass site on all sample dates (Table 3, Fig 3a and Fig 2a).

Microbial biomass was higher in restored soils at the grass site during senescence (P = 0.076) and higher at the forb site during vegetative peak (P = 0.029), but was lower in the same restored plots at plant senescence when native soils had greater microbial

biomass (Fig. 4a, b). Fungal:bacterial ratio (F:B) was lower in invaded plots during peak plant growth at the grass site ($P = 0.035$), but did not differ at any point in the season at the forb site (Fig.4d). The first three principle components of the PLFA analysis at each site explained 80 percent of the variance in microbial community composition. When PC's were analyzed as representatives of microbial community fingerprints utilizing ANOVA, restored and invaded microbial communities of the grass site differed along PC2 (Fig. 5a) which was composed of bacterial, fungal and general biomarkers (Table 5). The forb site did not experience the same differentiation by treatment (Fig. 5b). When PCs were analyzed by sampling date, microbial community composition at the grass site during plant senescence differed from the two earlier sampling dates and was strongly associated with the fungal biomarker 18:2 w6c (Fig. 5c, Table 5). The microbial community represented by PC1 at the forb site during germination was different from the rest of the season, while PC2 indicated that microbial community composition was different across each season (Fig. 5d). The microbial community during germination was associated with biomarkers from gram negative and positive bacteria and general markers, whereas the other sampling dates had the same markers, but differed in proportions (Table 5). Microbial communities as defined by PC's at the grass site and the forb site share several PLFA's, but had differing compositions (Table 4).

*Respiration and Mineralization*

Nitrogen mineralization rates did not differ significantly between sites that were invaded, restored and native at the grass site during either sample date nor did it differ at

the forb site in March 2008 (Fig. 6a,b,c). Nitrogen mineralization rates of invaded soils were almost twice that of restored soils and about 20 percent more than native soils in August at the forb site ($P = 0.100$; Fig. 6d). Soil nitrification rates were higher at the grass site in March 2008 invaded soil with rates four times greater than in the restored soils ($P = 0.002$; Fig. 6a). August 2008 nitrification rates were not different between treatments. The forb site nitrification rates were higher in invaded soils ($P = 0.097$) in August 2008. Soil respiration rates were similar between sites and did not differ between treatments at either location.

*Heterogeneity of invaded plots*

Reassessment of the soil structure variables of total C and N, P and pH using measures of kurtosis, skewness, variance: mean ratio, and minimum required sample number based on power analysis indicated greater variation of these variables within restored treatments than in the invaded soil at the grass site. The restored treatment also had greater variation in the soil function variables nitrogen mineralization, nitrification and soil respiration (Table 5). Patterns were not as consistent with the same variables from the forb site (Table 6). At this site, invaded plots showed higher spatial variation, as indicated by high kurtosis, skewness, and variance:mean ratios, in all soil function variables and the majority of chemical variables excluding total C and N which were most variable in the native plots.

## Short-term Experimental Restoration

One year after the grass site had been weeded and seeded it was clear that seeding alone did not increase seedling density, however, when seeding occurred after weeding of exotic species, seedling densities increased ($P = 0.001$; Fig. 7). Seedlings germinated in weeded plots but were unable to persist through the summer drought (Dickens personal observation).

Exotic forb and grass biomass was greatest in invaded and seeded plots (forbs: $P = 0.001$, grass: $P < 0.0001$), while native forb biomass was greatest in the weeded + seeded plots ($P = 0.052$) and native grass did not differ between treatments (Fig. 8). Litter had the highest percent cover in the restored plots ($P < 0.0001$; Fig. 9).

Soil $NO_3$–N was lowest in restored plots during the germination period of the 2007-2008 season with invaded soil having the lowest but similar levels to seeded and restored plots at the peak of the season ($P = 0.040$). $NH_4$–N and total extractable nitrogen did not differ between treatments (Fig. 10). Patterns of soil $NO_3$–N concentrations did not hold from year to year in the short-term restoration experiment. $NO_3$–N was highest in the weeded and seeded plots ($P= 0.040$) at the peak of the growing season in 2008 but not in 2009. $NH_4$–N and total extractable nitrogen did not differ between treatments in 2008 or 2009 at the peak of the growing season (Fig.11).

Nitrogen mineralization rates from invaded soils collected in March 2008 were higher than those of soils from seeded only plots ($P= 0.031$). Soils collected in August 2008 from seeded plots had lower nitrogen mineralization rates than all other treatments ($P = 0.053$; Fig. 12). Soil respiration rates were not altered by restoration treatments.

## Discussion

Invasion of exotic annuals into CSS did not alter soil chemical pools of C, N, and P even though the litter quality of natives and exotics differed. Extractable nitrogen availability was reduced by invasion with $NO_3^-$ most impacted. Nitrogen mineralization and nitrification were increased by invasion but respiration was not. Microbial community composition was altered by invasion at the grass site but not the forb site, and sample date was a stronger driver of microbial community composition than invasion at both sites. Microbial biomass and F:B were relatively resistant to invasion with decreases in F:B and microbial biomass only at the grass site during plant senescence and the peak of the growing season. Grass and forb sites were affected differently by invasion and restoration activities caused greater impacts on microbial biomass than invasion at the forb site. More specifically, microbial biomass was increased by invasion and restoration during peak of the season but reduced in theses same treatments at plant senescence in the forb site, but in the grass site microbial biomass was only increased by restoration during plant senescence. In addition, restoration at the forb site led to greater increases in microbial biomass than did invasion. This being said, it appears these CSS soils while not resistant to invasion of exotic annuals, were resistant to the impacts of invasion for most chemical and microbial characteristics. However, further analysis of disparity in variances between data of invaded, restored and native soils indicated a shift in the distribution of resources and microbial activity in response to invasion, with greater

homogeneity of invaded soils. Mean values of chemical pools and overall microbial composition may not have changed, but the heterogeneity of distribution of these variables did. This suggests that CSS soils where not resistant to invasion after all.

Analysis of species composition data between sites showed that active management strategies applied at both the grass site and forb site have successfully increased native shrub cover and reduced exotic annual cover in restored areas. Areas not yet restored at the grass site were dominated by exotic grasses. In native and restored areas, these grasses were limited to interspaces with sparse cover under shrub edges. At the forb site, invaded areas were dominated by exotic forbs with *Brassica nigra*, *Centaurea melitensis* and *Melilotus indicus* as the key invaders. In native and restored treatments, exotic forbs were limited to the interspaces with sparse cover under shrubs if any. However, because exotic plant species occupy the interspaces, active management strategies will need to continue into the future to assist with native shrub recruitment.

The high levels of productivity of exotics found in invaded plots in this study are consistent with other studies of grass invasion into CSS (D'Antonio & Vitousek 1992; Eliason & Allen 1997). The chemical composition of exotic and native plant tissue was also consistent with previous descriptions of CSS vegetation and exotic species (Wolkovich et al. 2010). However, the absence of an impact of these changes in ecosystem structure on soil chemistry and limited impact on nitrogen cycling and microbial community composition was not expected. This suggests that abiotic factors such as soil moisture, soil texture, or other soil physical properties may have promoted resistance by these soils.

Fast growing annuals are often regarded as having high quality litter which may be higher than natives in a shrub dominated community (Cornelissen et al. 2001; Jackson et al. 1988). Many dominant CSS shrubs are aromatic and known to contain high lignin, terpenes and other complex carbon compounds for herbivore deterrence, structural support or other traits (Blank 2008; Gray & Schlesinger 1981; Westman & Oleary 1986; Wolkovich et al. 2010). Furthermore, exotic grasses and forbs may differ in above ground litter quality and in rooting structure and chemistry. For this reason, the impacts of grass versus forb invasion on soils could differ. The difference in litter quality between both natives versus exotics and grasses versus forbs could alter the cycling of nutrients by directly affecting microbial communities and activities. It was expected that invasion would lead to increased nitrogen and carbon cycling rates under higher quality litter eventually causing decreased soil carbon and nitrogen pools, but in this study, invasives had lower quality litter than natives. In fact there were no permanent changes in carbon cycling. The only changes associated with invasion alone were found in grass site soils where nitrification rates increased with exotic grass invasion. This increase in nitrification is likely the result of a flush of carbon resulting from grass root turnover as the exotic grasses senesce. It is also consistent with increasing rates of nitrogen cycling found by Hawkes and others (2005) in invaded grasslands. In the case of grasslands, nitrogen cycling rate increases are due to increases in ammonia-oxidizing bacteria. In this current study, microbial community composition did not show increased microbial biomass but showed shifts in community composition at the grass site primarily in bacterial biomarkers. Without DNA analysis, I cannot be sure if increased ammonia-

oxidizing bacteria increased nitrogen cycling in invaded plots but shifts in microbial community clearly shows a need for future work with DNA to clarify the role of this mechanism.

Alternatively, carbon associated with the exotic grasses and forbs may have been more labile than for woody native plants and provided less complex carbon compounds to microbes in soils with more recalcitrant carbon of the native aromatic shrubs. The dominant grass species *Avena fatua* and *Brachypodium distachyon* were among the exotic species with the highest C:N ratio, much higher than that of the native shrubs but these species contain less complex carbons i.e. no terpenes and less lignin. Once microbes reduce litter quality to a 20:1 C:N, immobilization of nitrogen decreases and net nitrification increases (Paul & Clark 1989).

The most consistent differences in soil chemistry between invaded, restored and native soils where found in concentrations of extractable nitrogen species, specifically $NO_3^-$. These differences, without exception, followed the phenological stages of the dominant plant species in each treatment. $NO_3^-$ was highest in invaded plots just as exotics plant species germinated and nutrient uptake began. Within 1-2 months, $NO_3^-$ concentration dropped below concentrations found in both restored and native soils due to rapid growth and uptake rates until senescence. In shrub dominated plots, native and restored, the plant root uptake began later in the season and progressed at a much slower rate giving restored and native soils higher $NO_3$ concentrations later into the season

(Fig.4). These phenology-linked uptake differences can explain differences in total extractable nitrogen as well. Such seasonal responses of soil nitrogen to vegetation are known to occur in grasslands and managed plant monocultures (Eviner et al. 2006).

The increase in productivity in invaded plots and lack of change in total carbon pools would indicate a change in the rate at which carbon was cycling or increase in aboveground litter storage. Soil respiration results from this study showed no changes as a result of exotic plant invasion. My litter results indicated that while there was an accumulation of litter from year to year, it was a small fraction of the original net primary production, so accumulation alone did not explain the fate of carbon. Therefore there may have been an increase in soil respiration that my measurements were unable to capture or carbon was lost via another unmeasured pathway. The semiarid nature of this system promotes cycling of nutrients in unpredictable pulse events often associated with rains. Further studies that include *in situ*, continuous measurements of soil respiration throughout a growing season would be useful in determining the full effect of invasion on soil respiration. It is also possible that changes occurred within the different fractions of carbon rather than the total pool. Additional studies that determine impacts of invasion on soil carbon fractions would be valuable in assessing long-term effects of exotic plant invasion into shrublands on soil carbon storage.

Changes in microbial community structure were expected as a result of altered aboveground inputs (and also root inputs). The soil microbial community structure was more affected by the sampling date than treatments suggesting that alterations following exotic plant invasion were not strong enough or did not occur long enough to push the

microbial community past its resistance threshold. Microbial biomass was higher in restored plots at the grass site during senescence. The greatest impacts to microbial biomass were found in restored soils of the forb site, which could have been the result of weeding practices that occurred around the peak of the season with removal of high quality litter inputs associated with the invading plant species, i.e. *Melilotus indicus* and introduction of high soil disturbance. Meanwhile, the increased microbial biomass observed at senescence in restored treatments of the grass site was likely a result of a flush of soil litter inputs associated with annual plant species die off. The increase in F:B observed at the grass site in restored soils during peak plant growth was most likely explained by an increase in mycorrhizal associations as shrubs became active for the season and established fungal associations in preparation for the dry, summer months (Egerton-Warburton & Allen 2000).

It is unclear why a suite of invading exotic species with such differing biomass production, litter quality, annual biomass turnover rates and rooting structures would have such negligible effects on the CSS soil system. More likely, shifts in soil chemical and biological characteristics were not detected due to low power of replication in a very spatially heterogeneous or patchy soil resource and biotic environment. Allen and MacMahon (1985) found that soil resources and fungal communities are highly patchy in undisturbed environments of cold shrub-steppe vegetation with fungal communities often strongly associated with shrub organization on the landscape. Furthermore, Klironomos and others (1999) determined that, due to the heterogeneous distribution of resources and microbial communities, 50 samples for microbial communities and 35 replicates would

be required to account for the variability in a chaparral ecosystem. Similar heterogeneity would be expected in other shrublands such as CSS, due to rooting patterns and distribution of rhizosphere and non-rhizosphere soils. Areas under shrubs are more likely to be patchy in resources and microbial activity because of coarse woody roots than soils under fibrous and densely packed annual forb roots and thus more likely to have higher variance within the associated data.

Reassessment of soil total C and N, P, pH and the soil function variables of nitrogen mineralization, nitrification and soil respiration (Table 5) using measures of kurtosis, skewness, variance: mean ratio, and minimum required sample number indicated greater heterogeneity within restored treatments than in the invaded soil at the grass site. At the forb site, invaded plots showed higher spatial variation in all soil function variables and the majority of chemical variables excluding total C and N, which were most variable in the native plots (Table 6). This was likely due to the greater homogeneous nature of fibrous roots produced by grasses invading the grass site versus the annual forbs that dominate invaded plots at the forb site. With reduced homogeneity in the root distribution there are likely to be lower levels of heterogeneity or patchiness in the resources and microbial activities associated with roots.

### Short-term Experimental Restoration

Species like *Artemisia californica* are shown to experience reduced growth and survival in the presence of grasses in the first year, but this effect is lessened in the second year (Eliason & Allen 1997). Annual grasses and juvenile shrubs occupy the same

rooting zone and grasses often out compete native shrub seedlings for water at crucial times during the growing season (Davis & Mooney 1985; Ewing & Menke 1983). Because water tends to be one of the most limiting resources in ecosystems of southern California, plant species that are able to respond quickly following rains may be capable of preempting this valuable resource. Annual grasses can deplete water from the rooting zone and prevent germination of shrub species (Eliason & Allen 1997). Weeding followed by seeding was the only treatment in which seedlings established in this project. These results suggest that grasses in the other invaded plots prevented establishment of shrub seedlings likely either due to water, space or light competition. Others have shown that grass litter may shade out germinating shrub seedlings (Cione et al. 2002; Eliason & Allen 1997; Gillespie & Allen 2004). The invaded plots not treated with weeding had high biomass cover and litter that could have lead to reduced light at the soil surface (Gillespie & Allen 2008) not conducive to shrub seed germination. The majority of shrubs in both restored and native areas were mature with sparse to no new recruitment. In some patches with low grass cover, *Encelia californica Nutt*. seedlings persisted, but natural recruitment of other shrub species was not apparent (S. Dickens, personal observation).

Soil nitrogen was affected by restoration activities. The removal of exotic plants lead to increased $NO_3$ and total extractable nitrogen simply by reducing the levels of plant uptake. The lower rates of nitrogen mineralization found in the seeded treatment were not expected. Perhaps raking, while gentle, may have reduced organic matter and litter contact to the soil leading to reduced surface area exposed to microbial activity.

## Conclusions

The effects of weeding and seeding on extractable nitrogen, nitrogen cycling and seedling establishment occurred after only one year of treatment indicating the ability of disturbance in the form of restoration efforts can alter soil chemistry and function. This suggests that CSS soils are not resistant to such disturbance and that at least alterations in nitrogen cycling can be detected as soon as one year after disturbance. However, considering the results of the longer-term, seven and nine year restorations at the grass and forb sites, these effects did not persist suggesting these soils are resilient and recover given time.

The aboveground community of CSS was not resistant to invasion and recovers only with human-aided restoration indicating that the system lacks both resistance and resilience to exotic plant invasion at the above ground level. Belowground the lines are less clear. At the scale of nutrient mean pool sizes, the CSS soils were resistant to the effects of exotic invasion, but the more mobile nutrients of extractable nitrogen species were not. F:B ratios and microbial biomass were different between treatments, but this was limited to individual sampling dates with the greatest disparities occurring during season peak and senescence. General microbial community composition was only altered at the grass site and sampling date was a larger driver in microbial community composition in both sites than invasion or restoration. This difference, like that of the

extractable nitrogen, diminishes by the start of the new season indicating that for at least these alterations, time is an important factor to consider when assessing CSS soil resistance.

Further studies monitoring soil function measures of nitrogen cycling and soil respiration are necessary to rule out impacts undetected in my study that may exist in pulse events associated with the unpredictable precipitation events of the semiarid environment. Due to the complexity of scales within which soil processes occur, mean pool sizes and functional rates alone may not quantify the whole of possible impacts of exotics and thus do not completely address the issues of resistance and resilience of CSS soils. Because resource cycling is highly linked to microbe and plant activity and microbial activity is strongly linked in space to plant root/rhizosphere, distribution of resources and functional processes will be highly associated with plant rooting structure (Wardle et al. 2004). The rooting structure of native shrubs is patchy in distribution, while that of exotic grasses is fibrous and densely distributed. The invasion of CSS by grasses has led to altered distribution of resources and functional processes indicating that the soils are not resistance to exotic grass impacts at the landscape scale. At the forb site, while the direction of impact is not the same as was in the grass site for all variables, heterogeneity did change following restoration. Furthermore, the native and restored soils of this site appear to have differing heterogeneity of resources and functional processes indicating that CSS soils not only lack resistance to the impacts of exotic forb invasion, but are not completely resilient following these impacts.

Results of this study highlight a common issue in examining impacts of disturbance of soil chemical and biological characteristics in general. Soil resources and microbial activity are strongly driven by microbial association with plants and plant resource use. For this reason, sampling of soils will require a more stratified approach that accounts for known microbe and plant associations that dictate spatial distribution of the resource of interest. Furthermore, these results stress the importance of scale in which exotics may impact the systems they invaded. Single season point sampling of nutrient pools and microbial community may not reveal changes that are occurring at a landscape scale on the level of distribution versus the commonly sampled mean values (Klironomos et al. 1999). In the case of CSS, resistance to exotic invasion appeared to occur when for the nutrient mean pool sizes and microbial composition variables were compared, but heterogeneity decreased following grass invasion, suggesting an important soil characteristic that was not resistant to invasion. Given the changes in extractable nitrogen and resource distribution, it appears that space (rooting and resource distribution) and time (plant phenology) are important factors to incorporate in soil assessments of invaded CSS.

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Table 2.1. Percent cover of the most common species during a dry season (2006-07) and an average precipitation season (2007-08). Means are shown for plant species percent cover. ANOVA were conducted to assess differences in plant composition during the peak for the 2006-08 growing seasons.

| | Grass Site | | | | | | | | | | Forb Site | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Restored | | Invaded | | Weed/Seed | | Seed | | P-value | | Native | | Restored | | Invaded | | P-value | |
| | 2006-07 | 2007-08 | 2006-07 | 2007-08 | 2006-07 | 2007-08 | 2006-07 | 2007-08 | 2006-07 | 2007-08 | 2006-07 | 2007-08 | 2006-07 | 2007-08 | 2006-07 | 2007-08 | 2006-07 | 2007-08 |
| **Native Shrubs** | | | | | | | | | <.0001 | <.0001 | | | | | | | 0.0024 | |
| *Artemisia californica* | 97.2 | 89.8 | 1.4 | 9.6 | 0.1 | 0.1 | 0 | 0 | | | 25.2 | 4.6 | 9.8 | 15.6 | 0.1 | 0.6 | | |
| *Astragalus trichopodus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 | 0 | 0 | 1.6 | | |
| *Encelia californica* | 0 | 0 | 0 | 0 | 0.1 | 0.7 | 0.5 | 1.1 | | | 25.6 | 26.8 | 36.8 | 57.8 | 0.2 | 4.2 | | |
| *Eriogonum cinereum* | 0.7 | 1.4 | 0 | 1.3 | 0 | 0.2 | 0 | 0 | | | 0 | 0 | 1.8 | 1.9 | 0 | 0 | | |
| *Opuntia littoralis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | 5.6 | 6.3 | 0.2 | 0.1 | 0 | 0 | | |
| *Opuntia prolifera* | 0 | 0 | 0 | 0 | 0 | 0 | 0.1 | 0 | | | 0 | 0 | 1.6 | 2.4 | 0 | 0 | | |
| *Rhus integrifolia* | 0 | 0 | 0 | 0 | 0 | 0.0 | 0 | 0 | | | 16.3 | 9.6 | 0 | 0 | 0 | 0 | | |
| *Salvia mellifera* | 0 | 0 | 0 | 0 | 0 | 3.9 | 0 | 0 | | | 0 | 0 | 0 | 0 | 0 | 0 | | |
| **Native Grass** | | | | | | | | | | | | | | | | | 0.368 | |
| *Nassella pulchra* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | 3.0 | 0 | 0 | 0 | 0 | 0 | | |
| **Native Forbs** | | | | | | | | | 0.392 | 0.109 | | | | | | | 0.011 | |
| *Chamaesyce albomarginata* | 0 | 0 | 0 | 0 | 0.3 | 1.1 | 0 | 0 | | | 0 | 0 | 0 | 0 | 0.9 | 0.7 | | |
| *Lupinus succulentus* | 0 | 0 | 0 | 0 | 0 | 9.1 | 0 | 3.2 | | | 0 | 0 | 0 | 0 | 0 | 1.3 | | |
| **Exotic Grass** | | | | | | | | | 0.001 | <.0001 | | | | | | | | 0.039 |
| *Avena spp* | 0 | 0 | 0 | 9.9 | 0.6 | 4.4 | 0 | 19.0 | | | 0 | 0 | 0 | 0 | 0 | 0 | | |
| *Brachypodium distachyon* | 0 | 12.0 | 0.1 | 84.7 | 0.6 | 14.9 | 0.6 | 67.6 | | | 0 | 0 | 0 | 0 | 0 | 0 | | |
| *Bromus diandrus* | 0 | 1.0 | 0.1 | 9.3 | 0.1 | 6.7 | 0.1 | 0 | | | 0 | 0 | 0 | 0 | 0 | 0 | | |
| *Bromus rubens* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | 0 | 1.1 | 0 | 3.9 | 0 | 0 | | |
| **Exotic Forbs** | | | | | | | | | 0.086 | 0.0009 | | | | | | | | 0.003 |
| *Brassica nigra* | 0 | 0 | 0.1 | 23.8 | 0 | 0 | 0.7 | 2.1 | | | 0 | 33 | 0 | 10 | 0 | 62 | | |
| *Centaurea melitensis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | | 0 | 0 | 0 | 0 | 0 | 23.3 | | |
| *Malva parviflora* | 0 | 0 | 0 | 1.1 | 0 | 0.6 | 0 | 0 | | | 0 | 0 | 0 | 0 | 0 | 0 | | |
| *Melilotus indicus* | 0 | 0.6 | 0 | 9.8 | 0 | 15.5 | 0.2 | 22.4 | | | 0 | 1.3 | 0 | 5.1 | 0 | 35.6 | | |
| *Picris echiodies* | 0 | 0 | 0 | 0 | 0 | 1.1 | 0.6 | 2.6 | | | 0 | 0 | 0 | 0 | 0 | 0 | | |

Table 2.2. Nitrogen and carbon composition of leaf tissue from composite samples at both experimental sites. Means are shown for dominant plant species. Due to limited tissue, composite samples were used to characterize plant tissue so replication was insufficient for statistical analysis.

| | N % | C% | C/N |
|---|---|---|---|
| **Natives** | | | |
| Artemisia californica | 2.2 | 45.2 | 20.4 |
| Encelia californica | 2.3 | 40.8 | 17.7 |
| **Exotics** | | | |
| Brassica nigra | 0.9 | 41.2 | 56.5 |
| Avena fatua | 0.7 | 42.6 | 64.5 |
| Brachypodium distans | 1.3 | 42.3 | 31.3 |
| Centaurea melitensis | 1.9 | 40.4 | 21.1 |
| Melilotus indicus | 3.4 | 42.2 | 12.3 |

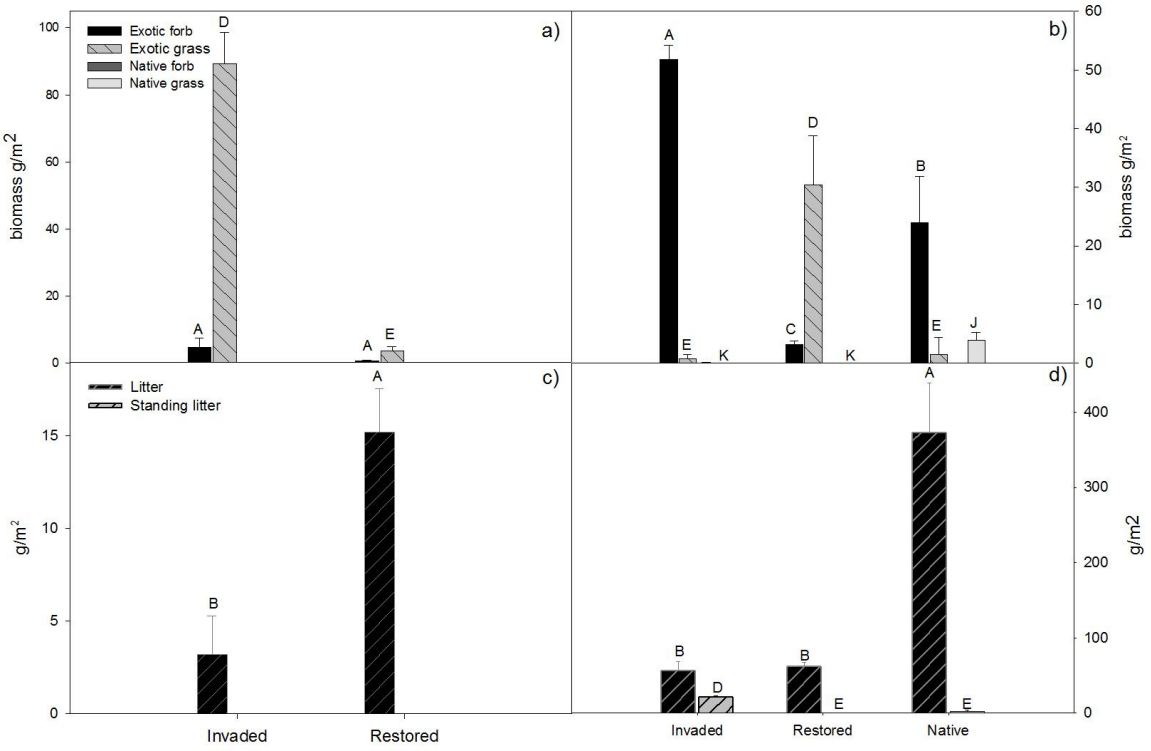


Figure 2.1. Plant biomass clipped at ground level and percent cover of litter collected during plant senescence of the 2007-08 growing season for the grass site (a,c) and forb site (b,d). Bars indicate standard error and letters significant differences ($P \leq 0.05$) determined by ANOVA comparisons within plant functional groups: exotic forbs = A-B, exotic grass = D-E, native forb = G-I, and native grass = J-L.

Table 2.3. Summer 2006 soil chemistry for the grass site (analyzed with Kruskal Wallis statistical analysis due to non-normality of data) and the forb site (analyzed with ANOVA except when Kruskal Wallis was used (*) due to data non-normality).

| | **Grass Site** | | | | | **Forb Site** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Invaded** | | **Restored** | | P-value | **Invaded** | | **Restored** | | **Native** | | P value |
| Total N (%) | 0.2 | (<0.1) | 0.2 | (<0.1) | 0.241 | 0.4 | (<0.1) | 0.3 | (<0.1) | 0.3 | (0.1) | 0.160 |
| Total C (%) | 3.8 | (0.2) | 4.2 | (<0.1) | 0.965 | 1.7 | (0.1) | 1.6 | (0.1) | 1.8 | (0.1) | 0.200 |
| C/N | **19.8** | (0.6) | 18.6 | (0.1) | **0.076** | 4.3 | (0.1) | 5.3 | (0.1) | **6.0** | (<0.1) | **<.0001** |
| NH4 (ug/g) | 10.0 | (0.5) | **24.9** | (0.6) | **0.063** | 2.6 | (0.1) | 2.4 | (0.1) | 2.5 | (0.1) | 0.440 |
| NO3 (ug/g) | **9.3** | (1.9) | 4.6 | (1.4) | **0.038** | 17.8 | (4.6) | 17.2 | (3.5) | 9.9 | (1.6) | 0.220 |
| Olsen-P (ug/g) | 24.6 | (2.5) | 22.5 | (2.7) | 0.453 | 3.0 | (0.1) | 2.8 | (0.1) | 3.1 | (0.2) | 0.310 |
| pH | 7.9 | (0.1) | 7.8 | (0.1) | 0.507 | 7.7 | (<0.1) | 8.0 | (<0.1) | 8.1 | (<0.1) | **<.0001** |

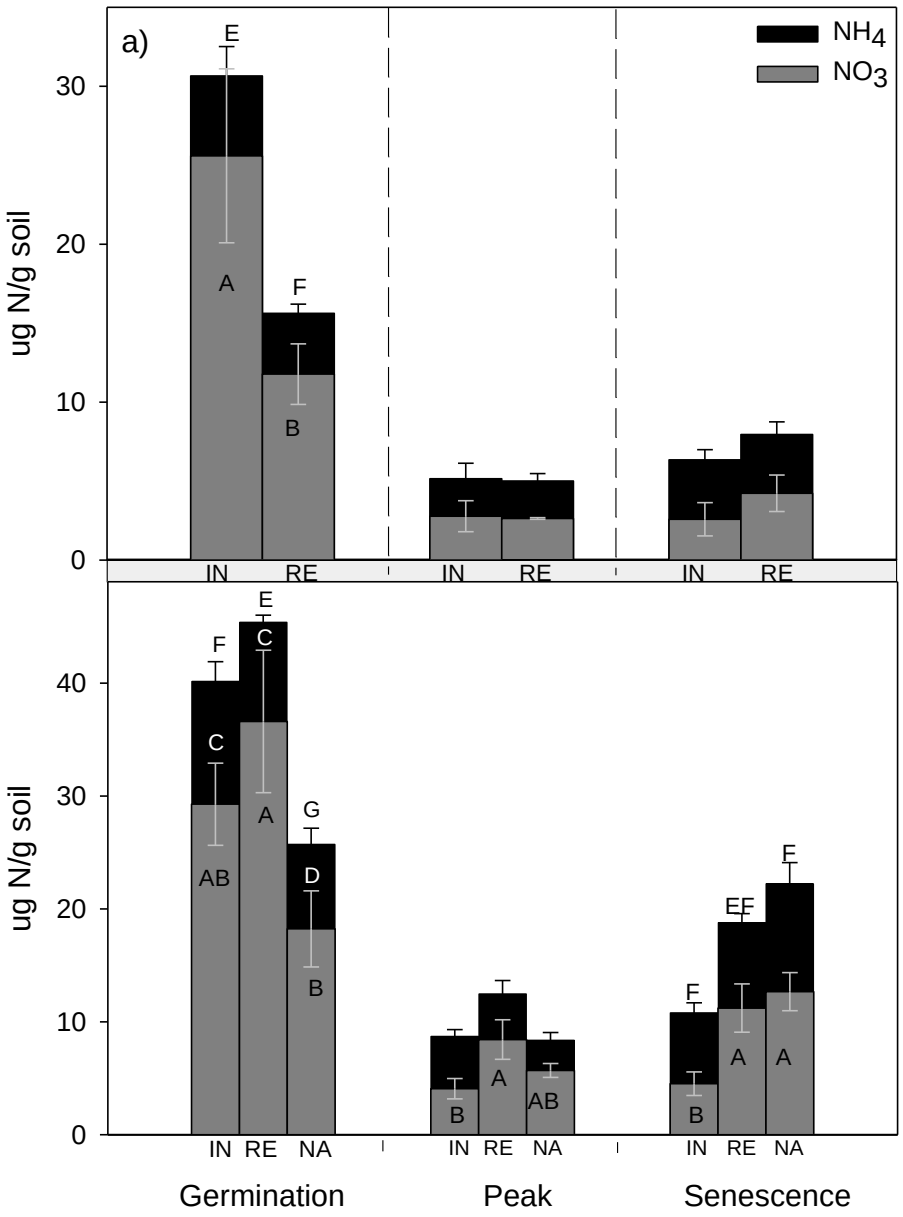


Figure 2.2. Six/seven year restoration soil extractable nitrogen during the 2007-08 growing year at the grass site (a) and the forb site (b). Treatments are as follows: invaded = IN, restored = RE, and native = NA. Letters indicate significant differences using Tukey-Kramer HSD test following ANOVA: $NO_3$ = A-B, $NH_4$ = C-D and total extractable nitrogen = E-G. Bars indicate standard error and letters significant differences ($P \leq 0.1$).

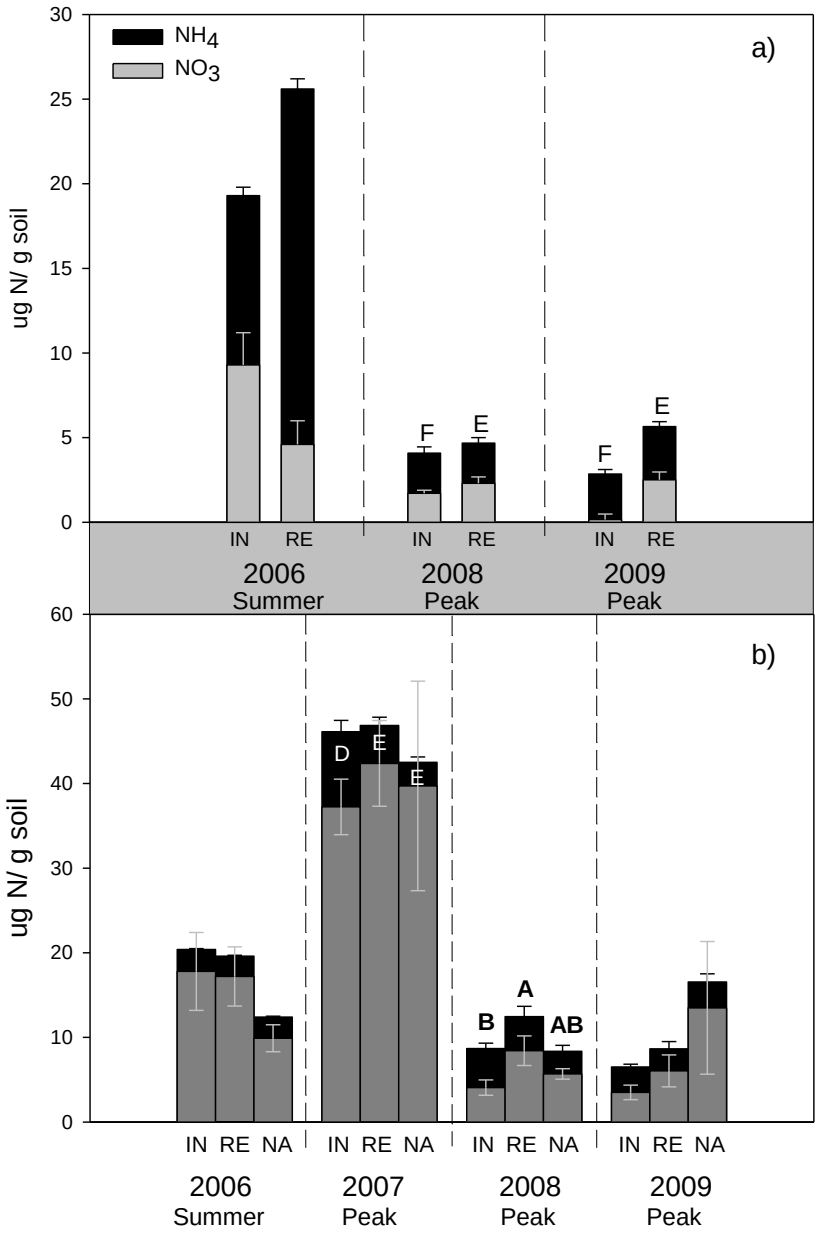


Figure 2.3. Soil extractable nitrogen during the 2007-2008 season at the grass site (a) and forb site (b). Treatments are: IN = invaded and NA = native. Letters indicate significant differences using Tukey-Kramer HSD test following ANOVA: $NO_3$ = A-B, $NH_4$ = C-D and total extractable nitrogen = E-F. Bars indicate standard error and letters significant differences ($P \leq 0.1$).

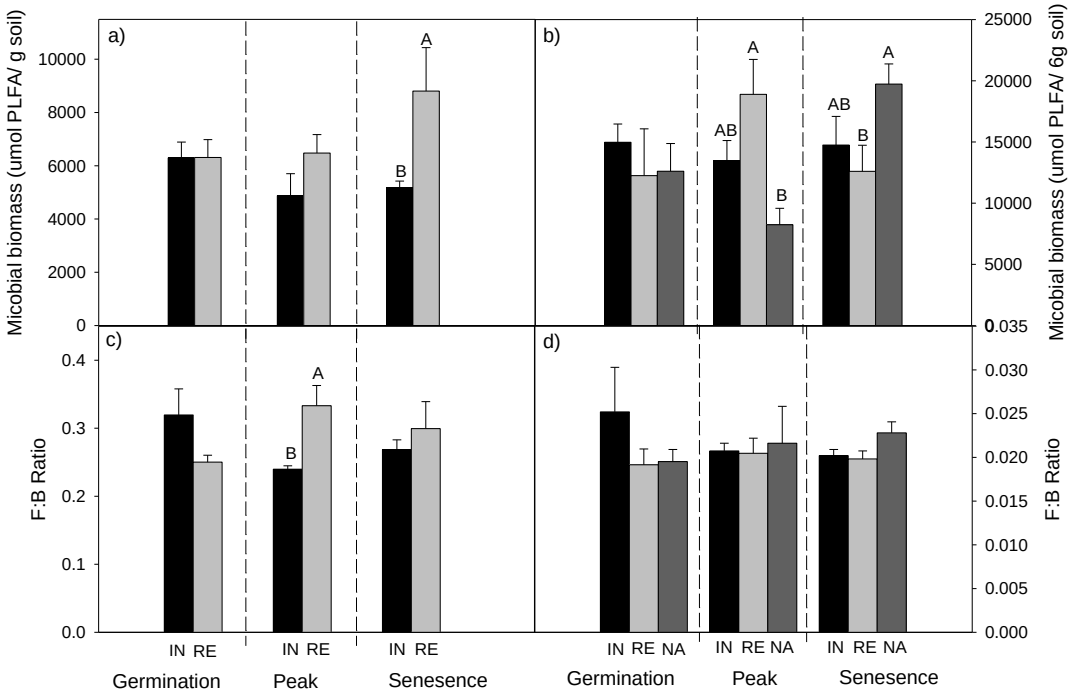


Figure 2.4. Phospholipid fatty acid profiles (µmol PLFA/ g soil) and fungal: bacterial (F:B) ratio representing soil microbial community biomass and composition site (a,c) and the forb site (b,d) for soils collected between fall 2007 and spring 2008. Bars indicate standard error and letters significant differences ($P \leq 0.1$) for within sampling dates and not across dates.

Table 2.4. The common PLFA and corresponding microbial functional groups from the grass site during the 2007-08 growing season. Means are shown for biomarkers making up grater than two percent of total PLFA abundance. Asterisks indicate level of significance * P<0.001. ** P< 0.05 determined with ANOVA.

| Grass site | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | Germination | | Peak | | Senescence | |
| | Biomarker | Invaded | Restored | Invaded | Restored | Invaded | Native |
| General | 20:1 w3c | 0.0 | 0.0 | 0.0 | 0.0 | 74.2 | 0.0 |
| | 19:1 (w 8?) Alcohol | 88.2 | 243.4 | 137.1 | 228.4 | 188.9 | 191.3 ** |
| | 21:1 w3c | 96.3 | 178.9 * | 144.3 | 201.8 * | 71.4 | 157.8 |
| Bacteria | 14:0 | 0.0 | 88.2 | 14.5 | 0.0 | 21.8 | 62.4 |
| | 18:0 | 227.1 | 368.3 | 207.0 | 334.3 ** | 283.4 | 244.4 |
| Gram - | 18:1 w5c | 38.1 | 102.9 | 74.4 | 87.1 | 69.8 | 90.6 |
| | 17:1 w8c | 28.8 | 114.1 | 102.6 | 115.2 | 140.4 | 146.7 |
| | 17:0 CYCLO | 103.3 | 301.0 | 157.5 | 216.7 | 198.2 | 203.6 * |
| | 16:1 w7c | 611.1 | 938.4 | 527.1 | 570.5 | 694.2 | 722.8 ** |
| | ISO 17:1 G | 578.6 | 315.3 | 468.1 | 673.7 | 417.7 | 450.9 |
| Gram + | 16:1 w9c | 33.2 | 140.2 | 74.9 | 48.8 | 122.1 | 123.4 |
| | 17:0 ISO | 26.8 | 101.4 | 82.6 | 100.8 | 121.9 | 90.7 |
| | 15:0 ISO | 201.3 | 334.0 | 176.7 | 171.6 | 232.2 | 250.6 |
| | 15:0 ANTEISO | 176.3 | 330.6 | 141.5 | 151.8 | 210.4 | 238.1 * |
| | 16:0 ISO | 86.5 | 222.0 | 149.6 | 174.6 | 224.5 | 214.1 * |
| | 16:0 | 702.6 | 1148.6 | 621.2 | 831.6 ** | 816.4 | 780.4 * |
| | 17:0 ANTEISO | 84.5 | 235.6 | 117.2 | 178.2 * | 173.6 | 162.8 * |
| Fungi | 18:2 w6c | 286.7 | 569.2 | 174.6 | 287.7 | 316.0 | 226.2 |
| | 18:1 w9c | 850.5 | 1328.3 | 708.1 | 923.2 | 901.5 | 842.7 ** |
| AM Fungi | 16:1 w5c | 352.6 | 551.8 | 304.9 | 312.6 | 323.2 | 352.2 |
| Protozoa | 20:4 w6c | 0.0 | 98.7 | 0.0 | 25.1 | 25.3 | 19.5 |
| Proteobacteria | 19:0 cyclo c11-12 | 595.7 | 924.3 | 493.2 | 759.2 ** | 630.3 | 640.0 ** |

Table 2.5. The common PLFA and corresponding microbial functional groups from the forb site during the 2007-08 growing season. Means are shown for biomarkers making up grater than two percent of total PLFA abundance. Asterisks indicate level of significance * P<0.001. ** P< 0.05 determined with ANOVA.

| Forb site | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Germination | | | Peak | | | Senescence | | |
| | Biomarker | Invaded | Restored | Native | Invaded | Restored | Native | Invaded | Restored | Native |
| General | ISO 17:1 AT 9 | 0 | 0 | 0 | 0 | 1359 | 0 ** | 589 | 1030 | 818 |
| | ISO 17:1 G | 812 | 1452 | 1503 | 1472 | 614 | 1180 | 997 | 333 | 0 |
| | 19:1 (w 8?) Alcohol | 169 | 0 | 126 | 232 | 404 | 133 | 332 | 298 | 416 |
| | 19:2 w6c. | 217 | 0 | 225 | 0 | 100 | 0 | 0 | 0 | 0 |
| | 21:1 w3c | 102 | 0 | 0 | 112 | 253 | 207 | 250 | 159 | 300 ** |
| | 24:1 w3c | 837 | 122 | 396 | 0 | 207 | 0 | 0 | 0 | 0 |
| | C25 N Alcohol | 257 | 215 | 567 | 0 | 0 | 35 | 0 | 0 | 0 |
| | Cholesteryl-palmitat | 975 | 135 | 451 | 0 | 196 | 0 | 138 | 0 | 0 |
| Bacteria | 18:0 | 564 | 504 | 367 | 471 | 583 | 394 | 495 | 456 | 786 * |
| Gram - | 17:1 w8c | 122 | 0 | 132 | 256 | 322 | 50 ** | 248 | 221 | 334 |
| | 16:1 w7c | 1862 | 1731 | 1610 | 1443 | 2165 | 994 ** | 1594 | 1493 | 2409 ** |
| | 17:0 CYCLO | 336 | 549 | 473 | 378 | 547 | 424 ** | 441 | 423 | 619 |
| | 18:1 w5c | 131 | 66 | 254 | 362 | 425 | 253 | 356 | 297 | 487 ** |
| Gram + | 16:0 ISO | 319 | 310 | 288 | 373 | 486 | 123 * | 417 | 380 | 480 |
| | 16:1 w9c | 121 | 55 | 93 | 250 | 397 | 50 * | 299 | 190 | 443 |
| | 16:0 | 1938 | 1826 | 1529 | 1714 | 2332 | 1226 * | 1778 | 1756 | 2760 ** |
| | 15:0 ISO | 502 | 554 | 486 | 560 | 750 | 152 * | 613 | 531 | 868 * |
| | 15:0 ANTEISO | 369 | 477 | 344 | 379 | 465 | 71 ** | 416 | 335 | 594 ** |
| | 17:0 ISO | 84 | 54 | 0 | 238 | 309 | 61 * | 251 | 217 | 355 |
| | 17:0 ANTEISO | 281 | 255 | 244 | 331 | 394 | 109 ** | 354 | 289 | 426 |
| Fungi | 18:2 w6c | 434 | 330 | 398 | 333 | 501 | 56 * | 308 | 351 | 806 ** |
| | 18:1 w9c | 2233 | 1931 | 1682 | 2180 | 3048 | 1374 * | 2299 | 2011 | 3515 ** |
| AM Fungi | 16:1 w5c | 813 | 640 | 552 | 725 | 975 | 359 ** | 881 | 633 | 1104 ** |
| Proteobacteria | 19:0 cyclo c11-12 | 1456 | 1045 | 890 | 1359 | 1473 | 958 | 1354 | 1052 | 1501 |

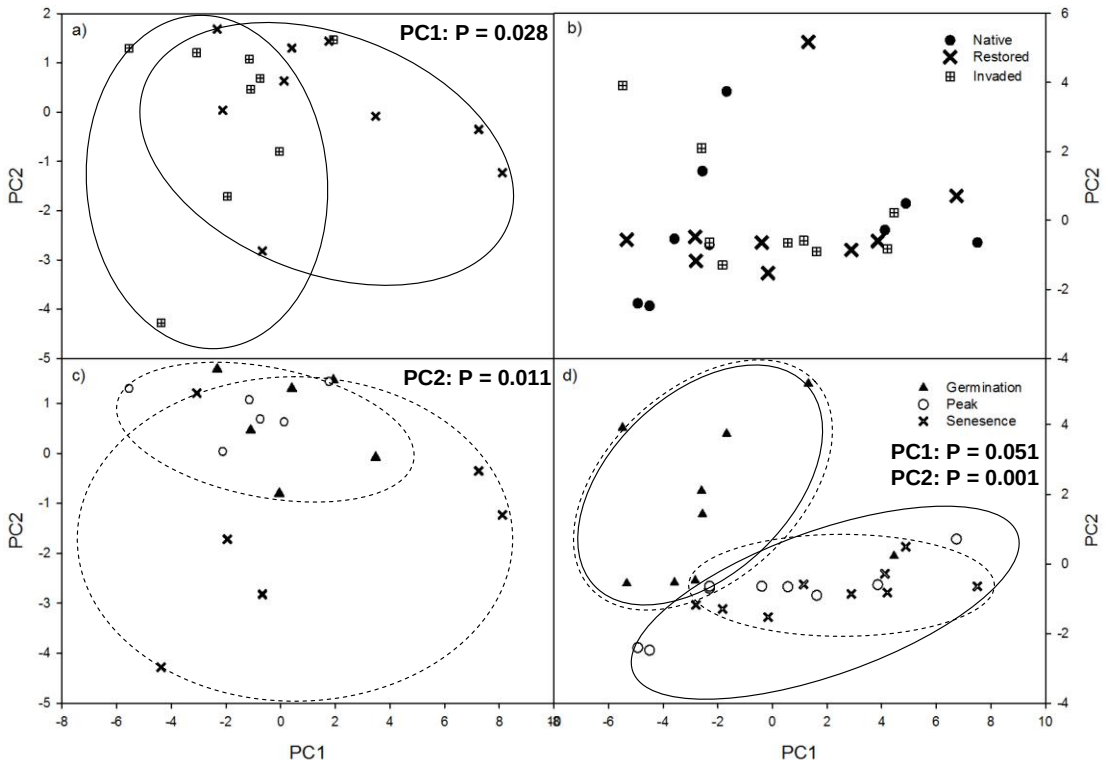


Figure 2.5. PCA results for PLFA microbial community analysis on treatment and sample date at the grass site (a,c) and forb site (b,d) during the 2007-08 growing season. Graphs a and b assess differences between treatment while c and d assess differences between sampling dates. Ellipses indicate statistically different microbial communities determined by ANOVA of PC values with an alpha level $\leq 0.1$. Solid ellipses represent results for PC1 and dashed ellipses represent PC2.

Table 2.6. Soil microbial PLFA weightings for PC's at both locations. Positive and negative signs indicate the direction of the weighting along the corresponding PC. Percent variance equals the variance within the PLFA data explained by successive PCs.

| | | Grass Site | | | | Forb Site | | |
|---|---|---|---|---|---|---|---|---|
| | Biomarker | % wt PC1 | %wt PC2 | % wt PC3 | Biomarker | %wt PC1 | % wt PC2 | %wt PC3 |
| Percent variance | | 59 | 12 | 10 | | 57 | 13 | 9 |
| Bacteria general | 14_0 | | | 6.4 (-) | | | | |
| | 18_0 | | | 8.4 (+) | | | | |
| Gram positive | 15_0 ISO | 5.9 (+) | | 8.0 (-) | 15_0 ANTEISO | 4.4 (+) | 4.5 (+) | 6.4 (-) |
| | 16_0 | 6.2 (+) | | | 15_0 ISO | 5.0 (+) | | 4.3 (-) |
| | 16_1 w9c | | | 8.1 (-) | 16_0 | 4.6 (+) | 4.9 (+) | |
| | 17_0 ISO | | 9.3 (+) | | 16_0 ISO | 4.8 (+) | | 4.9 (-) |
| | | | | | 16_1 w9c | 4.9 (+) | | |
| | | | | | 17_0 ANTEISO | 4.9 (+) | | 4.9 (-) |
| | | | | | 17_0 ISO | 4.7 (+) | 4.7 (-) | |
| Gram negative | ISO 17_1 G | 0.1 (+) | | | 16_1 w7c | 4.6 (+) | 5.9 (+) | 2.0 (-) |
| | 16_1 w7c | 5.9 (+) | | | 17_0 CYCLO | | | 8.9 (-) |
| | 17_0 CYCLO | 6.0 (+) | | | 17_1 w8c | 4.7 (+) | | |
| | 17_1 w8c | 4.5 (+) | 8.2 (+) | | 18_1 w5c | 4.2 (+) | 5.4 (-) | |
| | 18_1 w5c | 3.9 (+) | 9.0 (+) | | | | | |
| Fungi | 18_1 w9c | 6.1 (+) | | | 17_0 | | | |
| | 18_2 w6c | 4.4 (+) | 10.1 (-) | | 18_1 w9c | 5.2 (+) | 2.9 (+) | |
| | | | | | 18_2 w6c | | 6.6 (+) | |
| AM fungi | | | | | 16_1 w5c | 4.9 (+) | 3.0 (+) | |
| Proteobacteria | | | | | 19_0 cyclo c11-12 | 4.3 (+) | | |
| General | 19_1 (w 8?) Alcohol | | | 11.7 (+) | C25 N Alcohol | 1.4 (-) | 10.3 (+) | |
| | 21_1 w3c | 3.3 (+) | 7.0 (+) | 8.8 (+) | Cholesteryl-palmitat | 1.5 (-) | 8.1 (+) | 10.9 (+) |
| | | | | | ISO 17_1 AT 9 | | | 5.7 (+) |
| | | | | | ISO 17_1 G | 3.3 (-) | 3.7 (+) | 6.4 (-) |
| | | | | | 15_1 ISO G | 5.0 (+) | | |
| | | | | | 19_1 (w 8?) Alcohol | 4.2 (+) | | |
| | | | | | 21_1 w3c | | 5.8 (-) | |
| | | | | | 24_1 w3c | 1.4 (-) | 8.1 (+) | 11.6 (+) |

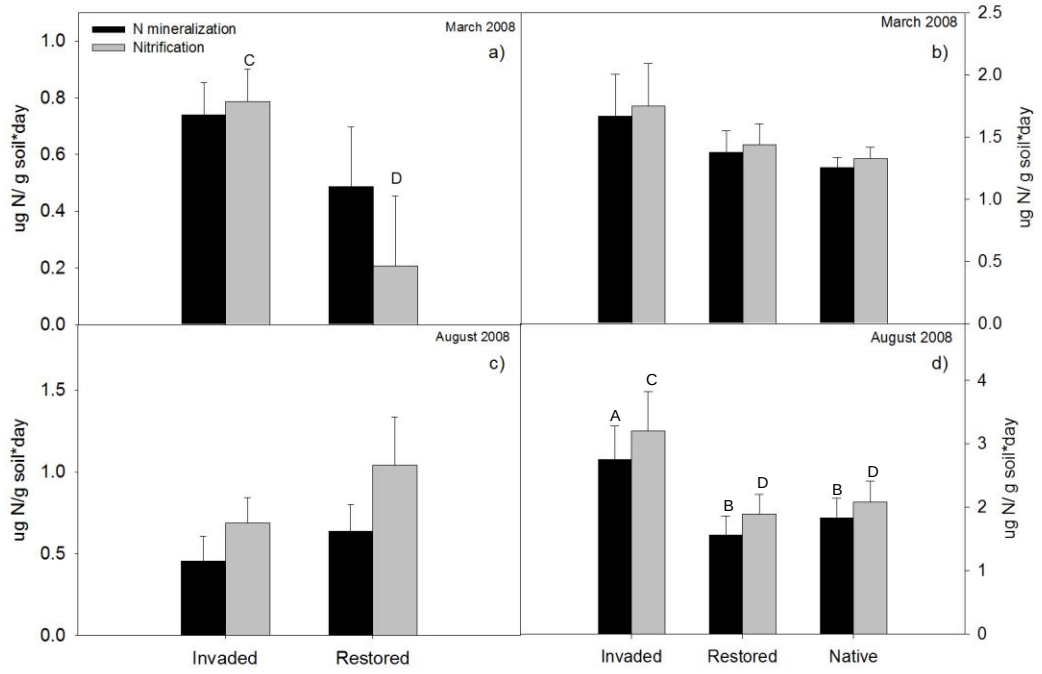


Figure 2.6. Potential nitrogen mineralization and nitrification from 30 day laboratory incubations for the grass site (a,c) and the forb site (b,d) from soils collected in spring (March) and end of summer (August) of 2008. Letters indicate significant differences using Tukey-Kramer HSD test following ANOVA ($P \leq 0.1$): nitrogen mineralization = A-B and nitrification = C-D. Bars indicate standard error.

Table 2.7. Measures of variance/ resource heterogeneity at the grass site. Mean values are shown in previous tables and figures.

| | Invaded | | | | Restored | | | |
|---|---|---|---|---|---|---|---|---|
| | kurtosis | skewness | variance: mean | min sample # | kurtosis | skewness | variance: mean | min sample # |
| **Soil structure** | | | | | | | | |
| Total C (%) | -1.30 | 0.03 | 0.05 | 66.43 | 8.42 | 2.87 | 0.76 | 1136.40 |
| Total N (%) | -0.37 | 0.57 | 0.00 | 0.26 | 8.53 | 2.90 | 0.04 | 3.58 |
| Olsen- P (ppm) | 2.43 | 1.10 | 2.25 | 19300.15 | -1.21 | 0.83 | 3.10 | 24301.17 |
| pH | 0.86 | -0.46 | 0.00 | 8.69 | 0.11 | 0.35 | 0.00 | 11.01 |
| Microbial biomass | 0.41 | -1.29 | 3.66E+04 | 3.61E+12 | 0.90 | -0.34 | 2.51E+04 | 2.98E+12 |
| F:B | 0.85 | 0.97 | 0.01 | 0.70 | -0.07 | 0.04 | 0.01 | 0.88 |
| 16 1w5c (AM fungi) | -0.63 | -0.67 | 9.29E+02 | 2.35E+09 | -1.35 | 0.28 | 1.73E+03 | 5.76E+09 |
| **Soil function** | | | | | | | | |
| CO2 Flux | 0.12 | 0.83 | 0.27 | 144.87 | 1.00 | 0.90 | 0.43 | 342.21 |
| Spring N mineralization (ug N/ g soil*day) | 4.89 | 1.60 | 0.14 | 37.21 | 1.00 | 0.01 | 0.63 | 106.51 |
| Spring Nitrification (ug N/ g soil*day) | 4.09 | 1.11 | 0.13 | 36.35 | 1.57 | 1.54 | 2.03 | 147.08 |
| Summer N mineralization (ug N/ g soil*day) | 3.10 | 2.07 | 0.45 | 70.60 | -1.66 | 1.44 | 0.38 | 83.83 |
| Summer Nitrification (ug N/ g soil*day) | 0.93 | 1.89 | 0.14 | 23.84 | 3.01 | 1.74 | 0.24 | 52.92 |

Table 2.8. Measures of variance/ resource heterogeneity at the forb site. Mean values are shown in previous tables and figures.

| | Invaded | | | | Restored | | | | Native | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | kurtosis | skewness | variance: mean | min sample # | kurtosis | skewness | variance: mean | min sample # | kurtosis | skewness | variance: mean | min sample # |
| **Soil structure** | | | | | | | | | | | | |
| Total C (%) | -1.56 | -0.13 | 0.27 | 491.68 | -0.47 | 0.23 | 0.20 | 352.16 | 6.20 | 2.30 | 1.48 | 3491.02 |
| Total N (%) | -1.66 | 0.32 | 0.03 | 5.14 | 0.95 | 0.92 | 0.02 | 2.23 | 6.75 | 2.54 | 0.08 | 9.38 |
| Olsen- P (ppm) | 0.34 | 0.80 | 10.62 | 65920.90 | -0.55 | 0.35 | 6.50 | 38954.97 | 3.34 | 1.57 | 2.39 | 8507.77 |
| pH | 0.09 | -0.60 | 0.00 | 5.49 | -0.79 | 0.64 | 0.00 | 1.78 | 2.85 | 1.37 | 0.00 | 3.99 |
| Microbial biomass | -0.96 | -0.42 | 576.57 | | -0.84 | 0.33 | 2121.02 | | -1.17 | 0.32 | 2396.83 | |
| F:B | 7.88 | 2.76 | 0.00 | | -0.27 | -0.28 | 0.00 | | 0.90 | 1.01 | 0.00 | |
| **Soil function** | | | | | | | | | | | | |
| CO2 Flux | -1.33 | -0.01 | 0.41 | 342.83 | -2.36 | -0.10 | 0.28 | 207.69 | -1.45 | 0.15 | 0.26 | 164.51 |
| Spring N mineralization (ug N/ g soil*day) | 1.02 | 1.43 | 0.54 | 313.07 | -1.66 | -0.10 | 0.20 | 96.56 | -1.70 | 0.28 | 0.05 | 19.93 |
| Spring Nitrification (ug N/ g soil*day) | -0.08 | 1.15 | 0.54 | 326.96 | -1.70 | -0.14 | 0.18 | 91.79 | -1.51 | 0.25 | 0.05 | 22.34 |
| Summer N mineralization (ug N/ g soil*day) | -0.25 | 1.07 | 1.25 | 1199.47 | -0.47 | 1.04 | 0.72 | 389.90 | -0.27 | 1.16 | 0.59 | 377.56 |
| Summer Nitrification (ug N/ g soil*day) | 0.06 | 1.18 | 1.47 | 1637.43 | -0.37 | 1.05 | 0.60 | 393.85 | -0.28 | -0.12 | 0.56 | 409.34 |

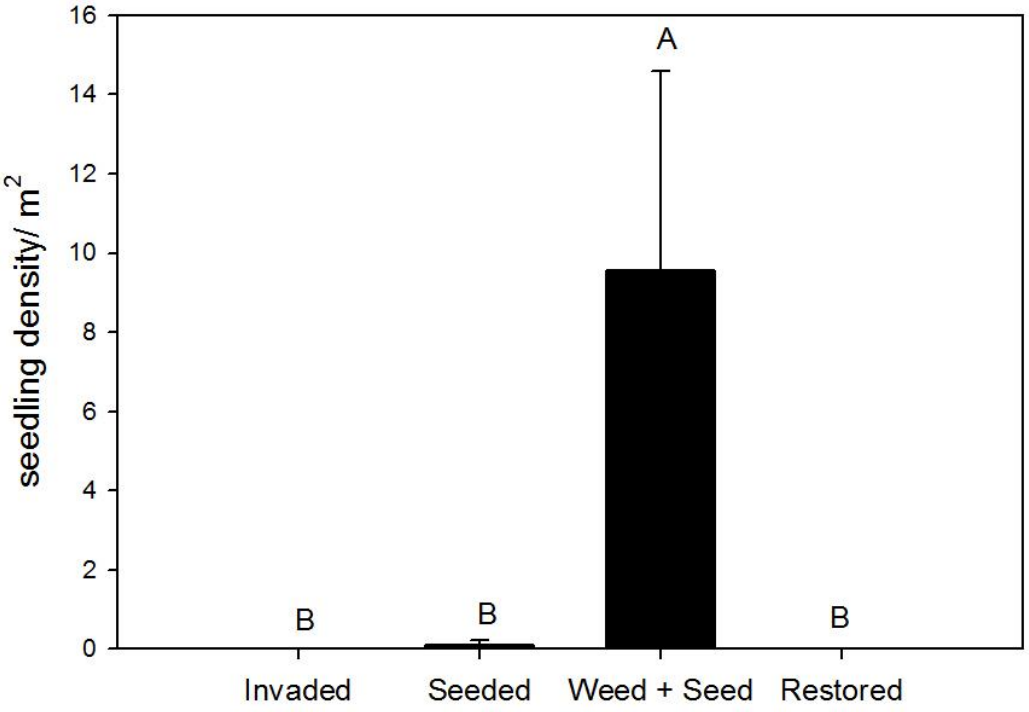


Figure 2.7. Native seedling density per $0.5m^2$ in plots that had been weeded and seeded with native plant species at the grass site. Bars indicate standard error and letters significant differences ($P \leq 0.1$) determined by ANOVA.

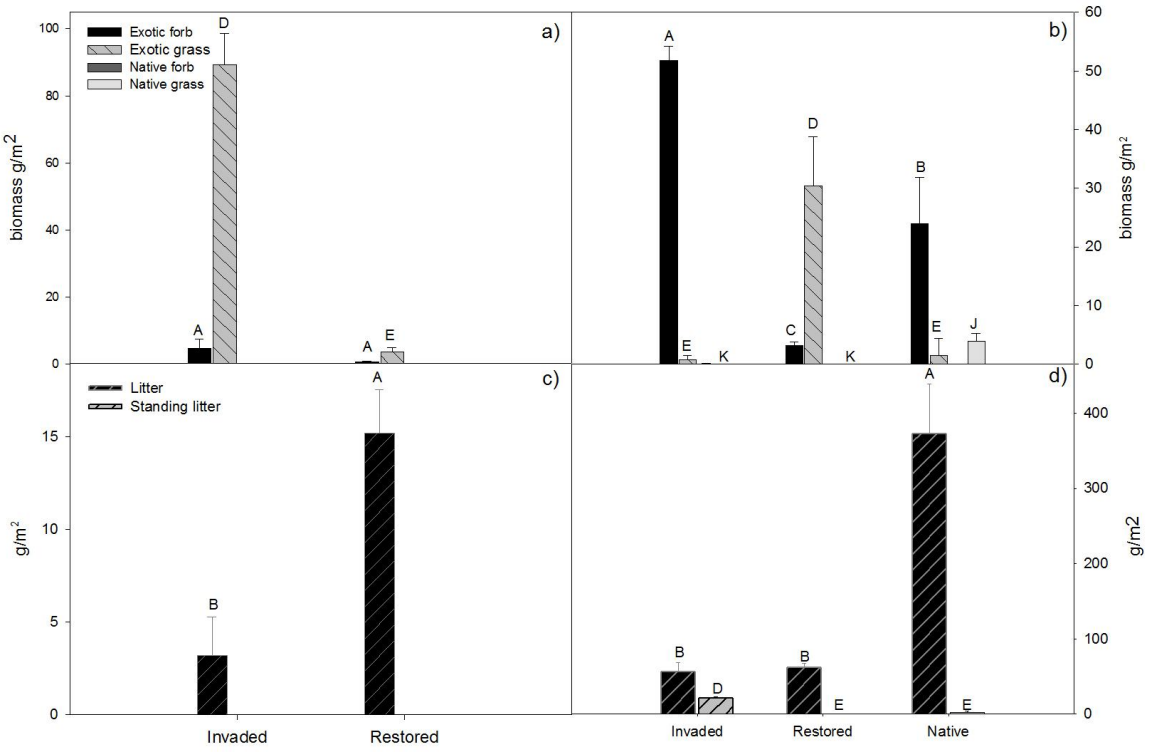


Figure 2.8 Plant biomass clipped at ground level collected during plant senescence of the 2007-08 growing season at the grass site. Bars indicate standard error and letters significant differences ($P \leq 0.05$) determined by ANOVA comparisons within plant functional groups: exotic forbs = A-B, exotic grass = D-E, native forb = G-I, and native grass = J-L.

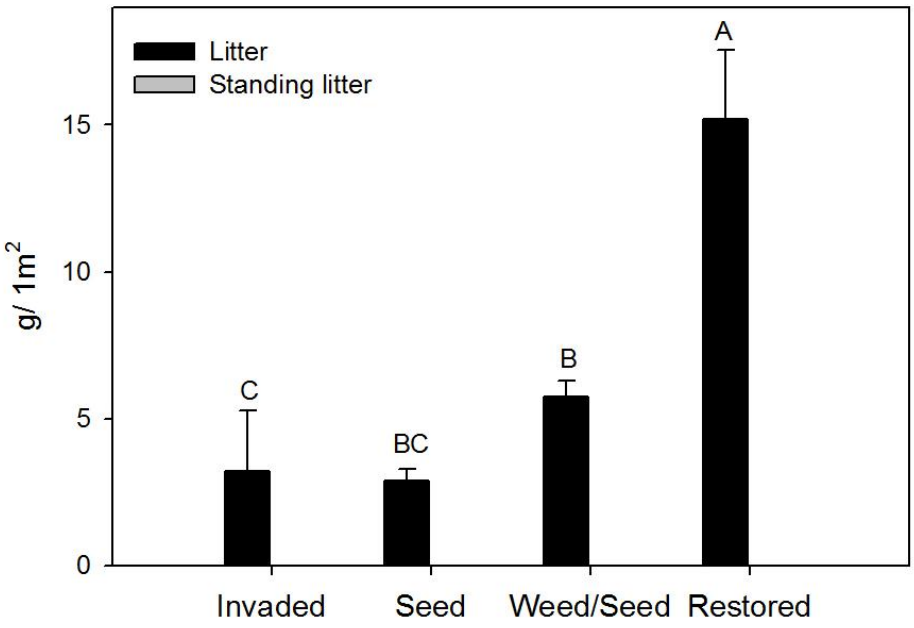


Figure 2.9. Litter mass collected April 2009. Litter is defined as plant biomass from the previous year still remaining on the soil surface or standing. Bars indicate standard error and letters significant differences ($P \leq 0.05$) determined by ANOVA comparisons.

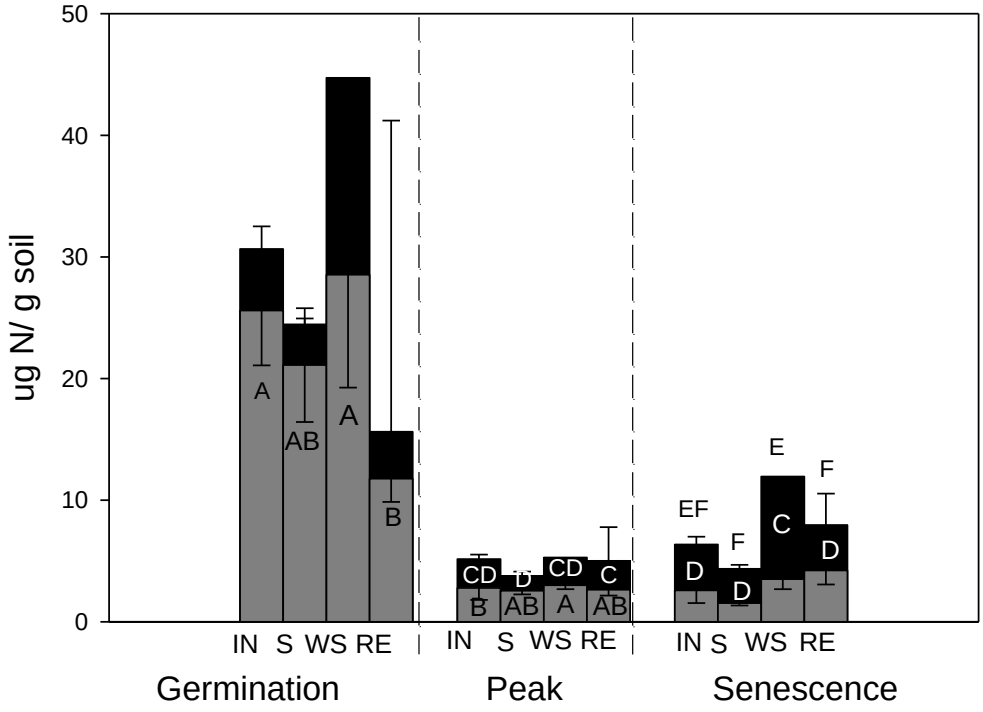


Figure 2.10. Soil extractable nitrogen during the 2007-08 growing season at the grass site one year restoration. Treatments are as follows: invaded = IN, seeded = S, weeded and seeded = WS and restored = RE. Letters indicate significant differences using Tukey-Kramer HSD test following ANOVA: $NO_3$ = A-B, $NH_4$ = C-D and total extractable nitrogen = E-F. Bars indicate standard error and letters significant differences ($P \leq 0.1$).

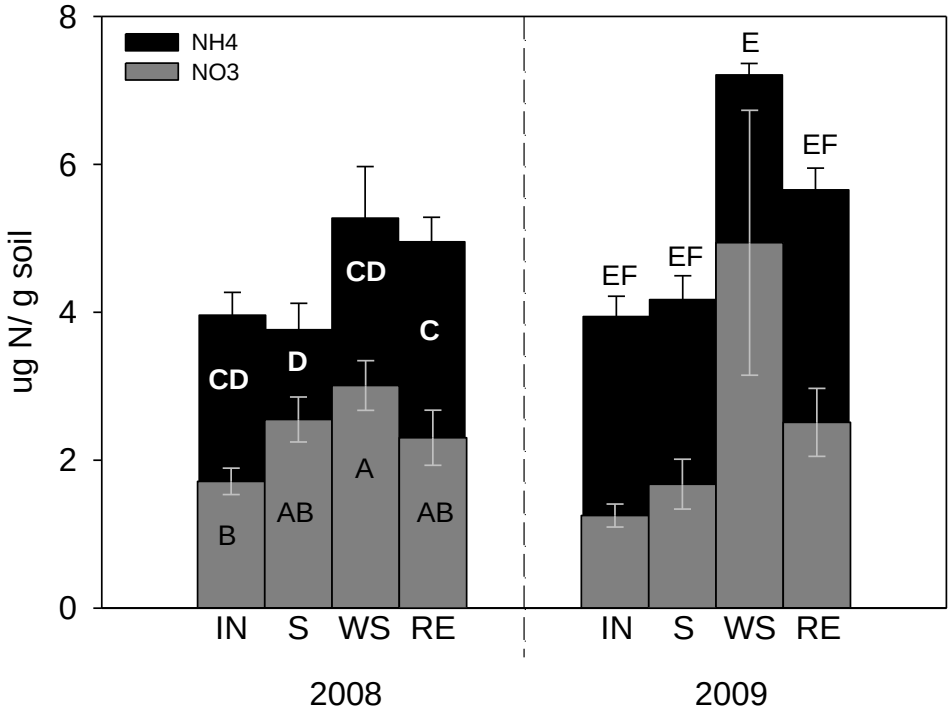


Figure 2.11. The grass site one year restoration soil extractable nitrogen during the years of 2007-09 taken at the peak of the season. Letters indicate significant differences using Tukey-Kramer HSD test following ANOVA: $NO_3$ = A-B, $NH_4$ = C-D and total extractable nitrogen = E-F. Bars indicate standard error and letters significant differences ($P \leq 0.1$).

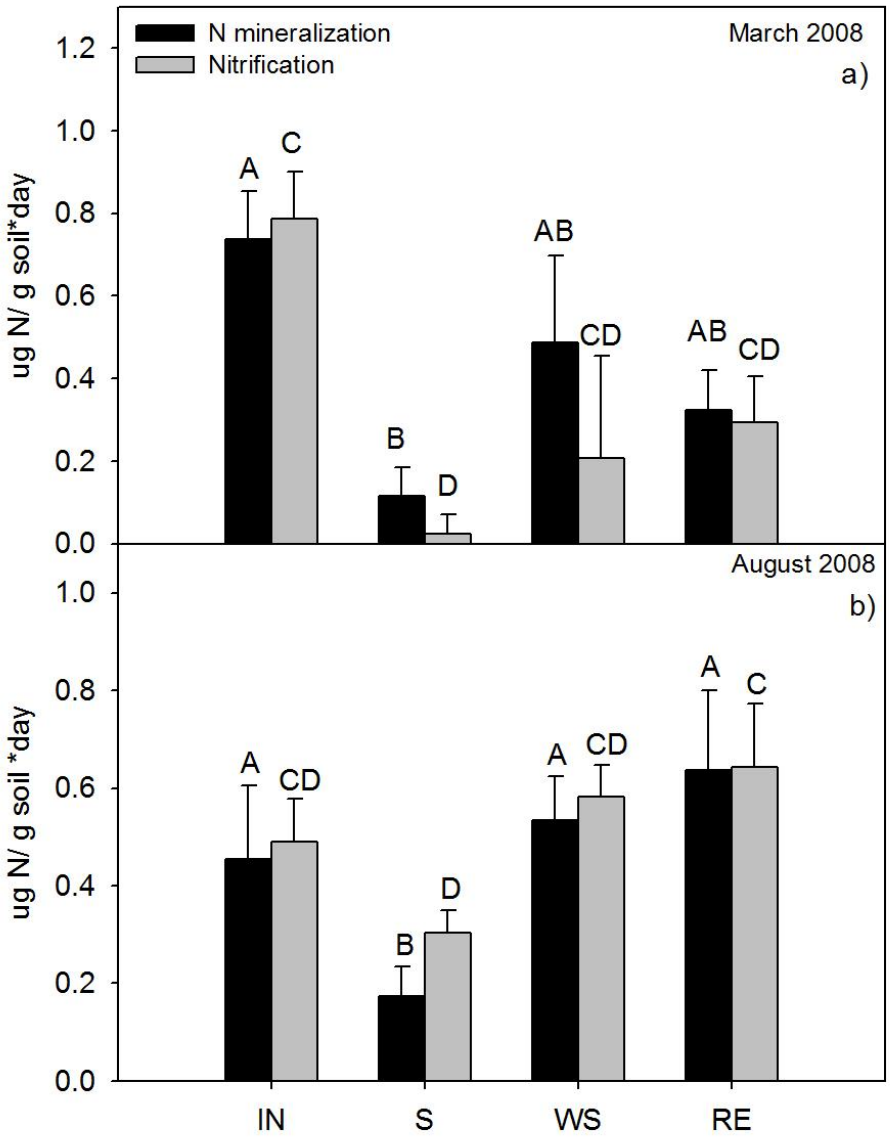


Figure 2.12. Potential nitrogen mineralization and nitrification from 30 day laboratory incubations for the grass site from soils collected in March (a) and (August (b) of 2008. Letters indicate significant differences using Tukey-Kramer HSD test following ANOVA ($P \leq 0.1$): nitrogen mineralization = A-B and nitrification = C-D. Bars indicate standard error.

**Exotic plant invasion alters chaparral ecosystem resistance, resilience and succession**


## Abstract

Invasion by exotic plant species may have feedbacks on the soils, but the extent to which invaded soils are resistant or resilient is not understood. The chaparral vegetation type is resistant to invasion except following disturbances resulting in vegetation removal, such as after fire. The replacement of woody shrub species by herbaceous exotics following disturbance may cause major changes to soil chemical and biological properties. Studies were initiated to assess chaparral system resistance and resilience to exotic plant invasion above and belowground in intact, mature chaparral and post-fire chaparral succession. The hypotheses tested were: (**1**) presence of exotic plant species in the chaparral changes the biological and chemical characteristics of soils by altering soil inputs; (**2**) The presence of exotic plants slows succession of chaparral in above- and belowground system structure and function. **(3)** If exotics are controlled and native chaparral species restored, soil biological and chemical characteristics return to pre-invaded conditions because native soil inputs are restored. Plant species percent cover, soil nutrient pools and cycling rates, and microbial community composition (PLFA) were recorded in native, invaded and recently restored chaparral during the 2006-09 growing seasons. Intact, mature chaparral aboveground plant communities were resistant to invasion. However, where invasion did occur, alterations of the soil chemical and microbial characteristics were found. Post-fire succession was slowed both above- and belowground by the presence of exotic plant species, indicating that post-fire chaparral is

not resistant to invasion or the impacts of invasion. Removal of exotic plants and seeding of natives post-fire facilitated succession rates similar to uninvaded chaparral. As anticipated, exotic plant invasion altered some soil nutrient pools, cycling rates and components of microbial community composition, but these effects were site, time and nutrient/microbe dependant. Overall, the chaparral ecosystem type did not resist the impacts of invasion. Restoration, even in the short two year term used here, led to recovery of extractable nitrogen availability showing chaparral soils, indicating capacity for resilience.

## Introduction

The ability of a system to resist the impacts of exotic plant invasion and its resilience following invasion are dependent on multiple abiotic and biotic factors. An understanding of these factors is increasingly urgent as exotic plant invasion is considered a major threat to biodiversity world wide (Mooney 2000; Pimentel et al. 2005). Several factors determine soil resistance and resilience including climate, soil parent material, vegetation and microorganisms (Chapin et al. 1997; Seybold et al. 1999). Stable systems have greater inertia and thus are more resistant to alteration from outside forces (Westman 1978). Aboveground, this inertia may be determined by traits of the plant community that inhibit exotic plant invasion such as dense canopy cover, or the result of environmental conditions such as annual droughts too severe for invading species. Belowground resistance occurs on at least two scales. The first scale is resistance to invasion through abiotic conditions and microbial activities that inhibit exotic seed germination or seedling survival. The second scale is resistance to the impact of invasion on the soil system such that the soil microbial community and chemical cycling remain unaltered by the presence of exotic plants. If soil resistance to plant invasion is low, the resilience of a system will determine the level and duration of exotic plant impacts. Resilience will be most important if invasive species fluctuate in abundance, or after restoration that begins with invasive removal.

Resistance and resilience can be measured in terms of ecosystem structure and function. Ecosystem structure is composed of abiotic components such as soil type, climate and elevation along with the biotic vegetation, microbial organisms and animals.

The activity of individual organisms and their interactions with abiotic components such as plant-soil feedbacks drive the functions of nutrient mineralization, hydrology and decomposition (Ehrenfeld et al. 2005; Wolfe & Klironomos 2005). De-coupling of such interactions can lead to alterations of the system causing a loss of resistance and impacting the system's capacity for resilience. Invasion of exotic plants have caused alterations not only to the structure of the plant community but have de-coupled long standing feedbacks between native plants and their microbial communities that lead to altered microbial communities and nutrient cycling (Ehrenfeld 2003; Reinhart & Callaway 2006; Reinhart et al. 2003; Wolfe & Klironomos 2005). For example, Kourtev and others (2002) identified alterations to the soil microbial community of forests invaded by *Berberis thunberggi* and *Microstegium vimineum*, along with altered rates of soil enzyme activities and respiratory responses to substrate that correlated closely to microbial community structure changes. In California grasslands, exotic grass invasion altered nitrogen cycling through doubled rates of nitrification as a result of increased ammonia-oxidizing bacteria (Hawkes et al. 2005). Tight coupling of plant inputs to soil and microbial activity has impacted soil nutrient status and led to a situation in which invaders with very different inputs have the potential to greatly alter chemical pools and nutrient fluxes. Aboveground plant community resistance and resilience to exotic plant invasion is well studied in chaparral, grasslands, coastal sage scrub and other ecosystem types (Crawley et al. 1999; Dukes 2001; Fleming et al. 2009; Keeley et al. 2005; Keeley et al. 2003; Symstad 2000). However, the ability of the soils of these ecosystem types to resist and recover from impacts of invasion is less understood.

The chaparral is a major California ecosystem type. With recent increases in exotic plant invasion and fire (Syphard et al. 2007; 2009), the effects invasion have on the chaparral ecosystem will have important roles in slope stability and land and water management. In the chaparral ecosystem of southern California, exotic annual species have limited invasion success into mature systems, but following fire, may dominate a site and alter post-fire soil inputs from that of natives. In addition, exotic plants may mediate the effect of fire on above and belowground systems by altering fire intensity and thus alter conditions for post-fire secondary succession. Following repeated burns of shrublands, exotic annual grasses replaced native shrubs and annuals (D'Antonio & Vitousek 1992; Keeley et al. 2005; Zedler et al. 1983). These species have very different biomass distributions above and belowground, as well as litter inputs and microbial relations than the dominant natives of the chaparral (Kulmatiski et al. 2008; Kummerow 1989; Norton et al. 2008; Williamson et al. 2004). Such differences could alter the ecosystem by changing the plant and microbial community, nutrient cycling rates and nutrient storage potentials.

Williamson and others (2004) found that invasion of grasses into chaparral altered the A and B soil horizons to form a mixed AB soil horizon. Furthermore, lateral and vertical infiltration of water into the soil become more homogeneous under grasses due to the more uniform distribution of grass individuals above ground and their fibrous root systems. Decreased soil heterogeneity was also found by Klironomos and others (1999) where variability in soil measures such as microbial community structure decreased in grass invaded soils. Hydrological alterations have been well studied along with the

rooting structure, depths of penetration and water use of chaparral species in bedrock (Sternberg et al. 1996; Williamson et al. 2004). The impact of exotic plant invasion on other ecosystem characteristics such as soil chemistry and nutrient cycling rates are unclear.

Previous work suggests that the plant community of the chaparral is resistant to invasion. This resistance is often attributed to the closed canopy of mature chaparral and/or allelopathic qualities of individual species with high percent cover (Hanes 1988; Keeley et al. 2005; McPherson & Muller 1969). Even with high resistance, some exotic plant species were able to become established in gaps and along chaparral edges. Following fire, however, canopy cover of native shrubs was reduced or removed creating a window of opportunity for exotic species to become established (Keeley 2000; Keeley et al. 2003). Chaparral species are adapted to an infrequent fire regime of 10-40 years (Müller et al 1968) or 70-100 years (Keeley 2000). Species fall into three categories of fire adaptation: resprouters, facultative seeders and obligate seeders (Hanes 1988; Keeley 2000). Annual species of the chaparral are obligate seeders with long seed dormancy potential. This allows them to persist in the soil under dense shrub overstory until gaps are formed by shrub death or fire. Post-fire chaparral succession progresses with an initial flush of native annual species and sub-shrubs while shrub species slowly resprout from burls and crowns or new individuals germinate (Pickett & White 1985; Keeley 2000). It can take over 25 years for shrubs to reach a closed canopy at which point annual cover declines as a result of decreased light (Hanes 1988; Keeley 2000). Natural post-fire succession in the chaparral has been termed auto-succession because the same species

pre-fire are important components of the post-fire community (Hanes 1988; Pickett 1985; Vogl 1982). Chaparral species have been able to re-establish high canopy cover following infrequent fires, and in most cases even regain invaded lands from exotic species (Franklin et al. 2004; Keeley et al. 2005).

In areas of the chaparral where fires are frequent, exotic grasses and forbs have maintained dominance and shrub recovery has been slowed (Zedler et al. 1983). Additional burns within one year of fire generally cause mortality of resprouting individuals and all seedlings. In areas planted with *Lolium multiflorum* for post-fire slope stabilization, shrub seedlings are unable to establish roots deep enough to ensure survival through summer droughts. This is the result of earlier germination and moisture preemption by the exotic grass, *L. multiflorum* (Kozlowski 1974). The effects of exotic plants on fire frequency, plant and soil microbial communities and soil nutrient status is a topic of growing concern as urban edges increasingly abut against chaparral ecosystems. Further work examining the role of exotics in directing succession post-fire is essential to the proper management these ecosystems.

Further understanding of the potential for chaparral restoration will become increasingly important. The level of perturbation of soil in response to invasion depends on the ability to resist effects of the disturbance. Most soils are not resistant to physical disturbance, but many are resilient and can recover if the disturbance is removed or the appropriate management strategies applied (Lal 1997). Even in extreme cases where microorganisms have been eliminated from soils such as following the eruption of Mt. Saint Helens, mycorrhizae will re-establish gradually due to wind and animal dispersal

(Allen 1991). Soil microbes are the key drivers of nutrient cycling in soil, therefore recovery of soils following stress will require recovery of soil microbes. In the case of exotic plant invasion, microbial communities and nutrient cycling alterations are likely due to altered inputs from the aboveground plant community (Bever et al. 1997; Ehrenfeld 2003; Wardle et al. 2004). For this reason, recovery of soils would require re-establishment of initial conditions. Removal of exotic species would discontinue novel soil inputs and the reintroduction of native plant species would re-establish initial inputs and assist soils in recovery. If soils have been altered by invasion, it is likely they will not be capable of recovering without management of the invading plant species.

In addition to impacts of vegetation type, the soil microbial community and by virtue of its dependence on the microbial community, soil nutrient cycling is determined by abiotic factors including soil pH, phenols within organic matter and soil moisture (Fierer & Jackson 2006; Hattenschwiler & Vitousek 2000; Kuiters 1990; Ushio et al. 2008). The combination of these abiotic factors and vegetation types determines microbial community composition following invasion. For this reason, locations supporting the same vegetation type but possessing different soil textures, pH or other chemical soil characteristics will promote differing microbial communities even with similar vegetation inputs to soil. The chaparral invasion study undertaken here was done at two sites with different soils types, but with the same dominant invasive species. Thus observed alterations of invaded soil within each site must be a result of invasive species impacts.

The objective of this study was to assess the resistance and resilience of the chaparral ecosystem to exotic plant invasion, specifically the impacts of invasion on soil chemical and biological structure and function. Additionally, I observed sites recovering from a wildfire to examine the impact of exotic plants on post-fire succession patterns of chaparral chemical and biological structure and function above and belowground. My hypotheses included: (**1**) Presence of exotic plant species in the chaparral changes the biological and chemical characteristics of the soils by altering soil inputs. (**2**) The presence of exotics slows succession of chaparral for both above- and belowground structure and function. **(3)** If exotics are controlled and native chaparral species restored, soil biological and chemical characteristics would return to pre-invaded conditions because soil inputs of native chaparral plant species would be restored. Ecosystem structure was measured as plant and soil microbial species community composition along with soil chemical pools. Ecosystem function was measured as potential soil respiration and nitrogen mineralization.

## Site description

North Mountain Research Area is located in the San Jacinto Mountains of Riverside County, CA (33$^{o}$43'N, 117$^{o}$10'E and 1150m a.s.l.). The site experiences temperatures that range between 14-35$^{o}$C in the summer months and 3-18$^{o}$C in the winter months with an average of 550mm of precipitation annually (Egerton-Warburton et al. 2003; Sternberg et al. 1996). Soils are sandy, mesic Entic Haploxerolls of the La Posta series and mesozoic granitic in origin (casoilresource.lawr.ucdavis.edu). The dominant shrub species of the site include *Adenostoma fasciculatum, Arctostaphylos glandulosa,*

*Dendromecon rigida* and *Eriogonum fasciculatum*. The site experienced 100 percent burn as a result of the October 26, 2006 Esperanza Fire which consumed 16,800 ha. Prior to the burn, uninvaded areas were dominated by mature, closed canopy chaparral shrub and invaded areas by exotic annual grasses and forbs with intermittent shrubs and sub-shrub species. Following the fire, all shrubs had been burned to ground level with few charred branches remaining. The soils were hydrophobic in nature and winds had begun to transport ash into washes. Henceforth, the North Mountain Research Area will be referred to as the burned site.

Santa Rosa Plateau Ecological Reserve is located in Murrieta, CA ($33^{o}31'$, $117^{o}15'$E and 600m a.s.l.). The site experiences temperatures 1-$37^{o}$C and an average of 480mm precipitation annually. Soils are a fine, silt loam of the smectitic, thermic Natrixeralf San Miguel series (casoilresource.lawr.ucdavis.edu). Native species most common to this site include *Adenostoma fasciculatum*, *Quercus hybrid* (*engelmanii-berberidifolia*) and *Toxicodendron diversilobum.* Vegetation of this site has not experienced fire in 13 years and for this reason, Santa Rosa Plateau Ecological Reserve will be referred to as the unburned site. Both sites have experienced invasion by *Avena fatua*, *A. barbata*, *Bromus diandrus*, *B. rubens* and *Vulpia myuros*, as well as other exotic annual grasses and forbs.

To examine the effect invasion had on chaparral ecosystem structure and function, nine replicate $1m^2$ plots per treatment were established at each site. Native areas were defined as those having exotic plant species cover less than 20 percent, while invaded areas contained 50 percent or greater exotic plant species cover.

To address effects of restoration activities on chaparral ecosystem structure and function, I established 2 additional sets of nine $1m^2$ plots in the invaded areas at the burned site in which two treatments were added, seeding and weeding + seeding. Hand weeding of all exotic species was started at germination after the first rain of the season and after rainfall events that initiated new germination, and was discontinued 3 weeks prior to data collection. Seedlings were pulled with attached roots. Because seedlings were small, soil disturbance was minimal. Seeding occurred following the first rains in the fall of 2007 and again in 2008. Seeds of *Adenostoma fasciculatum* (200 seed/ $m^2$), *Eriogonum fasciculatum* (200 seed/$m^2$) and *Cryptantha intermedia/ muricata* (200 seed/ $m^2$) were evenly distributed over the entire plot and gently raked into the soil. Shrub seeds were treated with 1% liquid smoke (Colgin Companies, Dallas, TX) 24 hours prior to seeding to induce germination. Seeds were collected on site between 2006-07.

**Ecosystem Structure**

To determine the differences in plant species composition between invaded and native communities, plant species percent cover and richness were measured annually at peak growth from 2007-09. Net annual productivity of annuals was determined by collection of biomass clipped at soil level and litter collected at soil level from $0.25m^2$ plots and scaled up to $1m^2$ using regression models of mass and percent cover. Additional biomass was collected for vegetative plant tissue chemical analysis at that time. Biomass

was oven dried at 60°C and weighed. Biomass for tissue analysis was ground and analyzed for total C and N on a Thermo-Finnigan model: Flash AlllZ soil combustion analyzer system.

To determine the effects of exotic invasion on soil biological and chemical characteristics, soil core samples of 10 cm depth and 2.5 cm diameter were collected and transported on ice. Soils analyzed for total carbon (C) and nitrogen (N) by combustion, KCl- extractable $NO_3$, $NH_4$, and bicarbonate-extractable phosphorus (Olsen P) were sieved through a 2mm sieve and sent for analysis at University of California Division of Agriculture and Natural Resources Analytical Laboratory at UC Davis (danranlab.ucdavis.edu) during the summer of 2006. Soil organic matter was determined by combustion and soil pH with 2:1 soil:water slurry. Soil cores were also collected once annually at plant peak growth 2007 and 2009, and three times annually (germination, peak and plant senescence) during the 2007-08 growing season to be analyzed for KCl extractable N ($NH_4^+$ and $NO_3^-$). Soil texture was also analyzed at University of California Division of Agriculture and Natural Resources Analytical Laboratory at UC Davis in soil suspension by hydrometer from three composite soil samples per sampling site.

Phospholipid fatty acid (PLFA) analysis was used to determine whether microbial community structure was affected by exotic invasion. PLFAs are used as biomarkers to identify functional groups of microbes such as gram positive bacteria and arbuscular mycorrhizal fungi. PLFA represent living organisms thus sampling of these compounds ensures capture of the current microbial community response to a disturbance such as exotic plant invasion (White et al. 1979). Samples were collected within 24 hours of

rainfall or wetting of soils to an average rain fall within pre-set steel rings. Soil samples were sieved through a 2 mm sieve and lyophilized prior to extraction. PLFAs were extracted from 6 g of soil following the modified Bligh–Dyer method (Frostegard et al. 1991). Quantification of fatty acids was obtained using a gas chromatograph (HP6980; Hewlet Packard, Palo Alto, CA) with flame ionization detector and HP3365 ChemStation Software. PLFA peaks were converted to PLFA identities and abundances using MIDI Sherlock Microbial Identification System (MIDI Inc., Newark, NJ, USA) followed by a comparison of peak areas to a known internal standard 19:0 (nonadeconoic methyl etser) of known concentration. Bacterial biomarkers included: 14:0, 15:0 iso, 15:0 antiso, 15:0, 16:0, 16:0 iso, 16:0 iso G, 16:1 2OH, 16:1 w9c, 16:1 w7c, 17:1 alcohol, 17:0 iso, 17:0 antiso, 17:0 cyclo, 18:1 w5c, 18:0, 19:0 cyclo c11-12, 22:0, and 24:0, fungi: 17:0, 18:2 w6c, and 18 1w9c,  AM fungi: 16:1 w5c, microeukaryotes: 21:0, Protozoa: 20:4 w6c, Pseudomonas: 18:1 w9t alcohol. Nomenclature for PLFAs  follow Lechevalier and Lechevalier (1988), Vestal and White (1989), Haack et al (1994), Zelles (1999), Myers et al (2001), and Hebel et al (2009).

**Ecosystem Function**

Laboratory incubations for N mineralization were performed over a 30 day period maintaining 25$^{\circ}$C and 60% humidity. $NH_4^+$ and $NO_3^-$ were extracted with a 2 M KCL 4:1 solution (Riley & Vitousek 1995) and shipped on dry ice for analysis at University of California Division of Agriculture and Natural Resources Analytical Laboratory at UC Davis. Net mineralization was calculated as the change in $NH_4^+$ minus the change in

$NO_3^-$ over time and net nitrification was calculated as the change of $NO_3^-$ over time following Riley and Vitousek (1995). Potential soil respiration rates were determined with laboratory incubations. Soils were maintained at 20% soil moisture and 25°C in sealed mason jars for 10 days. Jar headspace concentrations of $CO_2$ (ppm) were determined using a LiCor 800 infrared gas analyzer (Lincoln, USA) and converted to a rate function of µmol $CO_2$-C/ g soil *day (Chatterjee et al. 2008).

## DATA ANALYSIS

Data were tested for normality using the Shapiro-Wilk W test, and non-normal data were log (x+1) or square root transformed when appropriate. Plant biomass and litter, seedling density, soil chemistry, soil extractable N, potential soil respiration and N mineralization data were analyzed with ANOVA followed by Tukey's HSD to establish differences between treatments. In cases where data could not be transformed to normality, the Kruskal Wallis non-parametric test was used. Plant species percent cover and richness and soil chemistry post-fire at the burned site were analyzed using repeated measures MANOVA. Microbial biomass and F:B were also analyzed using ANOVA to determine coarse microbial community compositional shifts, while individual PLFAs were analyzed to determine more detailed shifts occurring as a result of invasion and restoration activities. Principal Components Analysis was used to calculate PCs representing microbial community composition throughout PLFA profiles, which were then analyzed with ANOVA to determine if community composition differed between treatments and across sampling dates. The above analyses were conducted using JMP9 (SAS Institute

2009) with an alpha level of $\leq 0.1$ to determine significance. Variability in soil variables is often high due to heterogeneity of soil organisms and resources, for this reason it is commonly accepted to use an alpha level of $\leq 0.1$ instead of the conventional $\leq 0.05$ for microbial data (Coleman & Crossley 1996; Klironomos et al. 1999).

## Results

### Structural and Functional Responses to Invasion

#### Ecosystem Structure

The 2006 fire resulted in the complete burn of vegetation in all treatments at the burned site. Only one native shrub species, *Eriogonum fasciculatum* was recorded post-fire and this was due to resprouting (Table 1). Within three years, only two shrub species, *Adenostoma fasciculatum* and *Dendromecon rigida*, showed limited recovery while sub-shrub cover was 0.1-14.2 percent. Native forb cover reached levels far greater than pre-fire conditions in native treatments ($P < 0.001$, Tables 1, 2).

The unburned site had higher native shrub and native grass cover ($P = 0.005$, $P = 0.014$) in native plots whereas exotic forbs and grasses had higher cover in invaded plots ($P = 0.004$; $P < 0.001$). Total native forb cover did not differ between treatments at the unburned site, although there were differences in individual species composition (Table 3). Exotic grass biomass was higher in the invaded plots for both sites (burned $P = 0.007$, unburned $P = 0.005$) and exotic forb biomass was significantly higher only at the burned

site in native plots (P = 0.015; Fig. 1). Litter percent cover was greatest in the invaded plots at the burned site (P = 0.004), but lowest in the invaded plots at the unburned site (P = 0.002; Fig. 2).

The invasive grasses *Avena barbata* and *Vulpia myuros* had tissue N concentrations and C/N similar to the native species. The brome grasses (*B. rubens* and *B. tectorum*) had higher N and lower C/N than natives and *Erodium brachycarpum* had lower N with a higher C/N. All exotic species had C concentrations similar to the native grass, *Nassella pulchra*, which were lower than the two native shrubs, *Adenostoma fasciculatum* and *Arctostaphylos glandulosa* (Table 4).

Soil texture at the burned chaparral was 69% sand, 24% silt and 8% clay, whereas soil texture at the unburned site was 44% sand, 44% silt and 12% clay. Total C and N did not differ between treatments pre-fire at the burned site but were higher in the invaded than native plots post-fire. C/N was higher in the invaded plots prior to the fire but not different after the fire. $NH_4$-N, $NO_3$-N, total extractable N and Olsen P did not differ between treatments pre-fire. Soil pH was more basic in invaded plots prior to the fire but became more basic in the native plots following fire (Table 5, Fig. 3). At the unburned site, total C and C/N were higher in the native plots. Total N, $NH_4$-N, $NO_3$-N, total extractable N and Olsen P did not differ between invaded and native treatments at the unburned site (Table 6).

Soil $NO_3$-N was lower at both sites at peak of the 2007-08 season in invaded plots (burned P = 0.091, Fig. 4a; unburned P = 0.012, Fig. 4b) and senescence (burned P = 0.001, Fig. 4a; unburned P = 0.027, Fig. 4b). $NH_4$-N was lower in invaded plots during

the peak of the season only at the burned site (P = 0.063; Fig 4a). Total extractable N was higher in native plots at both sites (burned P = 0.0501, unburned P = 0.007) and remained higher in the native plots into senescence at the burned site only (P = 0.017). When compared across the years 2006-2009, $NO_3$-N was lowest in the invaded plots for years 2008-09 at both sites (burned 2008 P = 0.091, 2009 P = 0.046, Fig 5a; unburned 2008 P = 0.027, 2009 P = 0.001, Fig. 5b). Total extractable N was higher in native plots at the burned site only in 2008 and 2009 (P = 0.050, P = 0.095).

Microbial biomass was lower in the invaded plots at the burned site during senescence (P = 0.023) of the 2007-09 season (Fig. 6a, b). F:B ratios were higher in invaded plots at the burned site during germination (P = 0.050) and during peak (P = 0.0043) and senescence (P = 0.052) at the unburned site (Fig. 6c, d). ANOVA of PC values representing microbial community structure indicate no significant differences between communities at either site; however, the microbial communities of both sites differed between sampling dates throughout the season along PC1 for the burned site (P < 0.001) and along PC2 for the unburned site (P = 0.038; Fig. 7, Table 9). PC1 of both sites was composed of general bacteria, gram positive bacteria, gram negative bacteria, proteobacteria, fungi, AM fungi, protozoa, *Pseudomonas* and several general biomarkers (Table 7 and 8). The unburned site PCs additionally were composed of biomarker 21:0 indicating the importance of this group of microeukaryotes in these communities and not in those of the burned site. Analysis of individual biomarkers representing various soil organism functional groups also show no difference between invaded and native soils at the burned site (Tables 7 and 8) and during germination at the burned site. However,

during the peak of the 2007-08 season 2 gram positive bacteria markers (17:0 anteiso and 17:0 iso) were in greater concentration in the native soils and during senescence, the general bacteria marker 18:0, gram positive bacteria marker 15:0 anteiso, and gram negative bacteria markers 16:1 w7c and 17:0 cyclo were in greater abundance in native soils while the gram negative biomarker 16:1 w9c was in greater concentration in invaded soils of the burned site (Table 7).

**Ecosystem Function**

Potential soil respiration was higher in the invaded plots of the burned site ($P = 0.002$, Fig. 8a) but did not differ between treatments at the unburned site. Nitrogen mineralization and nitrification did not differ between treatments in either the March or August soil collection at the burned site (Fig. 9a,c). The unburned sites had higher rates of N mineralization ($P = 0.070$) and lower net nitrification ($P = 0.078$, Fig. 9b) in the native plots from March soils but was not different between treatments for either N mineralization or nitrification in August (Fig. 9d).

## Short-term Weeding Experimental Restoration Results

**Ecosystem Structure**

Weed/seed treatments increased the cover of *Eriogonum fasciculatum,* but not *Adenostoma fasciculatum* and total shrub cover was significantly higher in the weed/seed treatments across time and treatments (Table 2, $P < 0.001$). Sub-shrub cover was greatest in weed/seed plots ($P = 0.003$) but this was mainly attributed to success of *Lessingia*

*filaginafolia* which appeared to be responding to the weeding treatment as it was not in the seed mix. Native forb cover was greatest in weed/seed plots as well ($P < 0.001$) where addition of *Cryptantha* species and weeding increased the two *Cryptantha* species combined by a factor greater than eight. Species not seeded also showed significant increases in this treatment over all other treatments with lowest native forb cover in invaded and seed treatments. Exotic grass and forb cover was greatest in invaded and seeded treatments ($P < 0.001$) with native sites closely following (Table 2).

Shrub seedling density was two times greater in weed/seed plots than any other treatments ($P = 0.002$, Fig. 10). Exotic forb biomass was highest in the seeded plots and native plots ($P < 0.001$). Exotic grass biomass was highest in the invaded and seeded plots ($P < 0.001$). Native forb biomass was over two times higher in the weed/seed plots compared to all other treatments ($P < 0.001$) and native grass was also highest in the weed/seed plots ($P = 0.005$, Fig. 11a). Litter percent cover was greatest in invaded and seeded plots with lowest cover in the native plots ($P = 0.002$, Fig.11b).

$NO_3$-N was lowest in the invaded plots during senescence of the 2007-08 growing season ($P = 0.003$). $NH_4$-N was lowest in the seeded plots and highest in native plots during the peak of the 2007-08 growing season ($P = 0.032$) and by senescence was lowest in both invaded and the seeded treatments with native and the weeded/seed treatments equal and higher than the other treatments ($P = 0.060$, Fig. 12a). Total extractable N was highest in the native and weed/seed plots for both peak and senescence ($P = 0.070$, $P = 0.012$). In 2009 only, the weeded/seed treatment had the highest levels of $NO_3$-N ($P =$

0.001). $NH_4$-N was lowest in invaded and in seeded plots in both 2008 and 2009 (P = 0.061, P = 0.007; Fig.12b). Total extractable N was higher in native and weed/seed treatments 2008 and 09 (P = 0.070, P = 0.002).

**Ecosystem Function**

Potential soil respiration rates were lowest in the native soils (P = 0.044; Fig. 13). Nitrogen mineralization was not different between any treatments in soils collected in both March and August (Fig. 14a,b). Nitrification rates were most negative in weed/seed plots in March (P = 0.097; Fig. 14a) but did not differ between treatments in August collected soils (Fig. 14b).

## Discussion

Invasive plants may have two major impacts in chaparral, caused by differences in the quality and quantity of carbon inputs to soils and by changing the fire cycle. Exotic annuals that invade chaparral have different ecological traits compared to native shrub species, and have the potential to alter plant-soil feedbacks, which consequently, alter ecosystem structure and function. Secondly, the presence of exotic annuals in fire-prone vegetation provides a fuel that burns at lower surface temperatures and shorter durations than in mature chaparral fires. Although this study was originally intended to focus on invasive plant-soil feedbacks, the accidental wildfire provided the opportunity to study soils and plants following fire. The lower fire temperature of burning grass reduces the

direct impacts of fire on the soil by reducing fire duration and intensity. Therefore, areas that have been invaded will progress through post-fire succession from a different initial condition compared to un-invaded burned mature chaparral.

At the burned site, the fire completely removed aboveground vegetation in both shrub and invasive annual dominated areas. However, the fire impacted the native soils more intensely compared to soils with reduced fuel load of exotic annuals (Christensen 1985; Neary et al. 1999; Rundel 1983). Grasslands fires reach temperatures of 170-245$^{o}$C (Rundel 1983) which can lead to soil temperatures less than 50$^{o}$C at 5cm soil depth (Agee 1973; Miranda et al. 1993; Neary et al. 1999), whereas chaparral fire surface temperatures range from 200-700$^{o}$C with soil temperatures of 200-300$^{o}$C at 3cm depth (Christensen 1985; DeBano 1977; Rundel 1983). The soil pH increase of 1.0 unit in native areas suggest soil temperatures in the areas were greater than 250$^{o}$C based on studies showing temperatures of 250$^{o}$C cause increases in pH and temperatures of 500$^{o}$C will cause an increase of 1.0 pH unit (Badía & Martí 2003a; Rundel 1983). The invaded area did not change in pH indicating that these soils experienced temperatures less than 250$^{o}$C. Soil carbon has been found to increase or decrease following fire, depending on fire intensity (Badía & Martí 2003a; De Koff 2004). Soil temperatures of 250$^{o}$C generally lead to increases in C through the accumulation of incompletely combusted plant carbon in ash, whereas temperatures above 460$^{o}$C cause loss of carbon (Badía & Martí 2003b; Giovannini 1990). In invaded treatments, soil carbon increased by 20 percent, but soil carbon in native soils decreased by 38 percent. These vastly differing effects on soil carbon further indicate fires of greater intensity in native vegetation, showing that

aboveground changes in fuel load caused by invasion have important fire-driven impacts on chaparral soils. These soil differences may lead to contrasting post-fire succession pathways by altering post-fire initial conditions. Although the two sites were on different soil types, the same invasive grass species dominated. Therefore, the shifts in soil chemical pools, nutrient cycling rates and microbial community composition in native vs. invaded plots can be attributed to exotic plant invasion. Invasion into unburned chaparral affected soil chemical and biological characteristics. High soil carbon and C/N ratio in native soils was most likely the result of slower decomposition and long term, recalcitrant carbon molecules, such as phenols and lignin, commonly associated with chaparral shrub leaves (Chou & Muller 1972; Vogl 1982). Litter layers in unburned, native treatments were almost three times greater in cover than invaded areas. These large litter layers are commonly attributed to complex carbon compounds. The low cover of litter in recently burned chaparral is the result of combustion of the litter layer at the burned site followed by limited litter input by shrubs that recover more slowly after fire. The unburned site represents the normal pre-fire cover and depth of slowly decomposing litter under shrubs. In contrast, the invaded sites appear to have attained a 20 percent cover of litter even though the period of time since last fire was different at each site, suggesting some maximum grass litter accumulation following fire. In comparison, unburned native treatments had litter cover three times that of grass plots and six times that of the burned native plots.

Grass invasion introduced litter with less recalcitrant carbon and, in the case of some species, lower C/N ratios (Table 4). These higher quality litters may cycle through the soil system at faster rates than the recalcitrant litter of natives leading to reduction of total soil carbon over time. In grasslands, biomass turns over annually (Jackson et al. 1988; Jones & Woodmansee 1979), consistent with my data showing increased respiration and lower litter accumulation rates of invaded plots dominated by grasses and forbs found in the unburned site and increased respiration in the burned site. Respiration rates were significantly greater in invaded soils at the burned site and trended 18% greater at the unburned site. Although total nitrogen was not affected by invasion, availability of $NO_3$-N was reduced by invasion during periods of active exotic plant growth. Changes in $NO_3$-N, $NH_4$-N and total extractable nitrogen were observed at both sites in most years to be highly related to the dominant plant species phenology. Invaded treatments experienced nitrogen decreases starting soon after germination of the first exotic annuals and continuing until senescence. Meanwhile, native soils experienced nitrogen decreases throughout the growing season and into the summer months until reaching similar pre-season levels as invaded soils. Exotic annuals germinate in late fall following the first rainfalls, whereas native shrubs become active several weeks later (Barbour & Major 1988). These phenological differences create uptake demands that are reflected in soil extractable nitrogen concentrations. My results agree with fluxes in $NO_3^-$ found in grassland nitrogen isotopic partitioning studies by Jackson and others (1989)

where $NO_3^-$ concentrations in soils were strongly related to plant growth and uptake rates. Invasion appears to impact the seasonality of nitrogen cycling, yet does not appear to have long-term impacts on the size of annual extractable nitrogen pools.

Overall, nitrogen mineralization and nitrification were not affected at the burned site, but greater rates of nitrogen mineralization occurred in native soils collected in March at the unburned site. This would be due to the greater soil carbon, soil C/N ratio and trend towards higher soil microbial biomass in the native soils. Increases in substrate for microbes and microbial biomass would promote higher nitrogen mineralization rates and greater nitrate immobilization in native soils. Greater immobilization would explain lower rates of nitrification measured in native soils even in the presence of greater mineralization. Furthermore, the microbial biomass during the peak of the season at the unburned site trended toward higher mass in the native soils, further supporting increased microbial activity and nitrogen immobilization. Retention of nutrients occurs in chaparral because of low quality litter combined with slow decomposition in a seasonally dry environment, and a large amount of living biomass that prevents nutrient losses (Chou & Muller 1972; Norton et al. 2007; Vogl 1982). High levels of litter, slow decomposition as inferred by low levels of respiration, and high rates of nitrogen immobilization by microbes in native shrub soils, are consistent with conservation of nutrients. Invasion of exotics is indeed altering carbon and nitrogen cycling of these chaparral systems, yet the sites vary. Differences between sites could be interpreted as a result of wildfire effects on feedbacks between plants and soils, which could be affected by climate and soil type at the two sites.

Considering the various impacts of invasion on soil carbon and nitrogen in both burned and unburned chaparral along with altered respiration rates in burned soils, I expected greater alterations to microbial communities as a whole in response to invasion with and without fire. Individual PLFAs act as markers for multiple microbial species, so there may be undetected shifts in species with potential impacts on microbial functioning or alternatively soil abiotic factors such as texture influenced microbial community greater than vegetation type in this ecosystem type. Analysis of microbial biomass revealed reduced biomass in invaded treatments at plant senescence but no differences during the rest of the season or at the unburned site. This within-season variation likely reflects a microbial response to the phenology of the dominant plant species within each treatment. Germinating exotic annuals begin actively growing with the first fall/winter rains, whereas native shrubs remain relatively dormant. At the peak of the growing season, both groups of species are active and interacting with their associated microbial communities. By the time annuals have senesced, shrubs are still physiologically active and supporting their associated microbial communities long into the early summer.

F:B ratios are commonly used to indicate shifts in microbial communities in response to disturbance or management (Bailey et al. 2002; Bewley & Parkinson 1985). In all cases where F:B differed between treatments, the ratio was higher in the invaded soils indicating a greater proportion of fungal species in invaded soils. This was an unexpected result as most chaparral shrub species are also highly mycorrhizal, either ectomycorrhizal or arbuscular (Cooper 1922). However, annual grasses are arbuscular mycorrhizal, so this result may be an indication of altered microbial distribution within

the soil in response to different rooting structures of annual grasses which maintain 85% of their fibrous roots within the top 10cm of soil (Jackson et al. 1989). Shrubs on the other hand have a polymorphic rooting morphology in which lateral roots occur in surface soils to capture recent rains and vertical roots that reach depths greater than 10m to obtain stored water (Barbour & Major 1988; Hellmers et al. 1955). Chaparral fine roots have a biomass of 28 $g/m^2$ in the top 20cm of soil (Kummerow et al. 1977) versus the 135-175$g/m^2$ biomass of grass roots in the top 20cm of soil (Wilsey & Polley 2006) and the greatest density of microbes existed within a few centimeters of the root surface (Killham 1991). Ten centimeter deep cores may represent greater proportions of the exotic species-associated microbial community, due to the dense and highly homogeneous root distribution of exotic annuals at this soil depth compared to the more heterogeneous root distribution of native shrubs (Klironomos et al. 1999) My results may reflect sampling a higher proportion of rhizosphere soil in invaded soils than in shrub-dominated plots where samples may include greater bulk soil.

**Short-term Weeding Experimental Restoration**

Post-fire re-establishment of vegetation indicated high grass seed survival in invaded soils and rapid re-establishment within two years of the fire. However, re-establishment of natives was strongly inhibited by exotic annuals. Plots that were weeded and seeded within the invaded area had four times greater native shrub seedling density than any other treatments. Seeding alone did not increase native forb or shrub cover. This suggests that exotic species are inhibiting seedling establishment in invaded areas and

native seedlings are slow to establish in the native area, either due to low seed survival in the more intense fire conditions or the harsh post-fire environment (Keeley et al. 2005). By decreasing fire intensity through altered fuel loads (Christensen 1985; Rundel 1983) exotic grasses may create a positive feedback promoting annual seed survival which, along with early phenology of exotics (Barbour & Major 1988), could lead to exotic annual persistence or expansion into the burned native chaparral.

The removal of exotic annuals promoted extractable nitrogen pools similar to that of the native treatments, further supporting the role of exotic plant uptake and novel phenology as a driver of extractable nitrogen pool changes. Soil nitrification rates in March were lower in the weed/seed treatment while nitrogen mineralization rates were trending higher, suggesting higher substrate availability and leading to higher rates of nitrogen immobilization once exotic plants were removed. The native areas were not similar to the weed/seed plots in nitrogen cycling; however, this most likely is due to higher carbon in the post-fire invaded soils providing greater substrate for microbes.

## Conclusions

Intact chaparral vegetation may be resistant to invasion (Hanes 1988; Keeley et al. 2005), but post-burn chaparral lacks the canopy cover that creates this resistance. Soil biological and chemical characteristics are not resistant to invasion in burned or unburned chaparral. The direction of change and whether change occurred to chemical pools was nutrient, site, and time dependant. Pools of total soil nitrogen and phosphorus were resistant to impacts of invasion in the absence of fire but total soil carbon and the more

mobile and bioavailable nutrients such as, extractable nitrogen species, were not. Following removal of exotics, even limited re-establishment of native plant species allowed extractable nitrogen to recover to levels similar to native soils indicating resilience of this component of the nitrogen cycle. Not all soil functions returned to pre-invasion levels following weeding and seeding suggesting that these functions are not resilient or three years is not long enough to observe impacts of restoration efforts on these rates. Presence of exotics following wildfire slowed recovery of both native vegetation and soil chemical pools. The duration of this study was too short to determine the full resilience of the vegetation and soils following fire. However, the results emphasize the importance of exotic plant species control following fires in chaparral systems experiencing multiple burns (Allen et al. 2000). Recovery of soils depends on the re-establishment of the dense canopy cover of chaparral shrubs, which is inhibited by exotic plant invasion. Functioning of chaparral soils is strongly dependant on preservation and restoration of the plant soil feedbacks long established between native plant species and the soils of this system.

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Table 3.1. Common species percent cover of the chaparral ecosystem at the burned site prior to and post 2006 wildfire. Means are shown for pre- and post-fire plant species percent cover. Repeated measures MANOVA were conducted to assess differences in plant composition between treatments of invaded and native chaparral over three years during the 2006-09 growing seasons.

| | Invaded | | Native | | P-value | | |
|---|---|---|---|---|---|---|---|
| | Pre fire | Post fire | Pre fire | Post fire | Treatment | Time | Treatment x Time |
| Native Shrubs | 3.0 | 0 | 68.50 | 0 | <.001 | <.001 | <.001 |
| *Adenostoma fasciculatum* | 0.4 | 0 | 41.6 | 0 | | | |
| *Arctostaphylos glandulosa* | 0.1 | 0 | 17.3 | 0 | | | |
| *Ceonothus gregii* | 0 | 0 | 3.9 | 0 | | | |
| *Eriogenum fasciculata* | 3.6 | 0.6 | 8.0 | 0 | | | |
| Native Sub-shrubs | 0.1 | 0 | 0.0 | 0 | 0.384 | 0.29 | 0.384 |
| *Eriophyllem confedriflora* | 0.9 | 0 | 0 | 0 | | | |
| Native Forbs | 4.3 | 0 | 0.9 | 0 | 0.118 | 0.023 | 0.118 |
| *Filago californica* | 0.1 | 0 | 0.6 | 0 | | | |
| *Stephanomera virgata* | 0.1 | 0 | 0 | 0 | | | |
| *Trichostema parishii* | 0.7 | 0 | 0 | 0 | | | |
| Exotic Forbs | 3.5 | 0 | 0.0 | 0 | 0.066 | 0.066 | 0.066 |
| *Brassica geniculata* | 0.2 | 0 | 0 | 0 | | | |
| *Centaurea melitensis* | 2.1 | 0 | 0 | 0 | | | |
| *Erodium brachycarpum* | 0.7 | 0 | 0 | 0 | | | |
| *Filago gallica* | 0.1 | 0 | 0 | 0 | | | |
| Exotic Grasses | 18.1 | 0 | 1.4 | 0 | 0.221 | 0.146 | 0.221 |
| *Avena barbata* | 0.7 | 0 | 0 | 0 | | | |
| *Bromus madritensis rubens* | 0.7 | 0 | 0.6 | 0 | | | |
| *Bromus tectorum* | 8.3 | 0 | 0.9 | 0 | | | |
| *Vulpia myuros* | 6.4 | 0 | 0 | 0 | | | |

Table 3.2. Common species percent cover of the chaparral ecosystem at the burned site three years after fire in all treatments. Means are shown for plant species percent cover. Repeated measures MANOVA were conducted to assess differences in plant composition between treatments of invaded and native chaparral over three years during the 2006-09 growing seasons.

| | Invaded | Native | Seed | Weed/Seed | P-value | | |
|---|---|---|---|---|---|---|---|
| | | | | | Treatment | Time | Treatment x Time |
| Native Shrubs | 2.7 | 4.4 | 6.6 | 12.0 | <.001 | <.001 | <.001 |
| *Adenostoma fasciculatam* | 2.2 | 1.5 | 0.6 | 1.6 | | | |
| *Ceonothus gregii* | 0.1 | 0.2 | 0 | 0 | | | |
| *Eriogenum fasciculata* | 0.2 | 0 | 0 | 5.9 | | | |
| *Dendromicon rigida* | 0.2 | 2.7 | 6.1 | 4.4 | | | |
| Native Sub-shrubs | 0.6 | 0.7 | 1.2 | 15.0 | 0.002 | 0.003 | 0.003 |
| *Eriophyllem confedriflora* | 0.1 | 0.1 | 0.4 | 0.2 | | | |
| *Helianthemum scoparium* | 0.2 | 0.6 | 0.0 | 0.1 | | | |
| *Lessingia filafiniflora* | 0.4 | <0.1 | 0.5 | 14.2 | | | |
| Native Forbs | 0.6 | 8.3 | 0.6 | 12.6 | <.001 | <.001 | <.001 |
| *Camissonia hirtella* | 0 | 0 | 0 | 1.0 | | | |
| *Cryptantha intermedia* | 0.1 | 0 | 0 | 0.7 | | | |
| *Cryptantha muricata* | 0.1 | 0.8 | 0.1 | 8.2 | | | |
| *Eriogenum davidsnii* | 0.2 | 3.0 | 0.1 | 0.8 | | | |
| *Muilla maritime* | 0 | 4.4 | 0 | 0.3 | | | |
| *Stephanomera virgata* | 0.1 | 0.1 | 0.1 | 0.5 | | | |
| *Trichostema parishii* | 0.2 | 0 | 0.2 | 0.3 | | | |
| Exotic Forbs | 30.2 | 13.9 | 19.4 | 2.7 | <.001 | <.001 | 0.001 |
| *Brassica geniculata* | 15.2 | 9.1 | 4.9 | 0.2 | | | |
| *Centaurea melitensis* | 0.1 | 0.1 | 0.3 | 0.3 | | | |
| *Erodium cicutarium* | 15.0 | 2.3 | 13.6 | 0.4 | | | |
| *Sisymbrium altissima* | 0.1 | 2.3 | 0.7 | 1.8 | | | |
| Exotic Grasses | 58.1 | 40.9 | 54.0 | 1.1 | <.001 | <.001 | <.001 |
| *Avena barbata* | 0.3 | 0.1 | 0 | 0 | | | |
| *Bromus diandrus* | 0 | 1.6 | 0 | 0.1 | | | |
| *Bromus madritensis rubens* | 5.6 | 11.5 | 0.1 | 4.1 | | | |
| *Bromus tectorum* | 9.4 | 15.5 | 0.5 | 9.9 | | | |
| *Vulpia myuros* | 42.8 | 12.2 | 39.9 | 0.4 | | | |

Table 3.3. Common species of the chaparral ecosystem at the unburned site during an average precipitation season (2007-08). Means are shown for plant species percent cover. Repeated measures MANOVA were conducted to assess differences in plant composition between treatments of invaded and native chaparral over three years during the 2006-09 growing seasons.

| | Invaded | Native | P-values | | |
|---|---|---|---|---|---|
| | 2007-08 | 2007-08 | Treatment | Time | Time x treatment |
| Native Shrubs | 2.9 | 44.7 | <0.001 | 0.008 | 0.005 |
| *Adenostoma fasciculatum* | 0.9 | 0.3 | | | |
| *Quercus hybrid (engelmanii-berberidifolia)* | 1.9 | 72.8 | | | |
| *Rhamnus ilicifolia* | 0 | 0.2 | | | |
| *Toxicodendron diversilobum* | 0 | 9.1 | | | |
| Native Grasses | 5.9 | 0.2 | 0.014 | 0.085 | 0.085 |
| *Nassella pulchra* | 5.9 | 0.2 | | | |
| Native Forbs | 47.1 | 61.2 | 0.398 | <0.001 | 0.062 |
| *Anturium spp.* | 0 | 0.8 | | | |
| *Calandrinia ciliata* | 15.2 | 0 | | | |
| *Castilleja exserta* | 0.6 | 0 | | | |
| *Chlorogalum pomeridanum* | 0.2 | 1.8 | | | |
| *Clarkia purpurea* | 1.3 | 0 | | | |
| *Claytonia perfoliata* | 1.3 | 19.1 | | | |
| *Crassula connata* | 1.1 | 0.8 | | | |
| *Cryptantha intermedia* | 0.8 | 3.7 | | | |
| *Daucus pusillus* | 4.8 | 0 | | | |
| *Dichelostemma capitatum* | 0.7 | 0.8 | | | |
| *Eucrypta chrysanthemifloria* | 1.4 | 6.4 | | | |
| *Linanthus bipinifita* | 2.9 | 0 | | | |
| *Lotus hamatus* | 11.2 | 0 | | | |
| *Marah macrocarpus* | 0 | 6.6 | | | |
| *Plagiobothrys spp.* | 0.7 | 0 | | | |
| *Pterostegia drymarioides* | 0.4 | 7.7 | | | |
| *Sanicula bipinnatifida* | 0.4 | 1.4 | | | |
| *Stylocline gnaphaloides* | 0 | 1.5 | | | |
| *Tauschia arguta* | 0.9 | 0 | | | |
| Exotic Forbs | 37.4 | 8.6 | 0.004 | 0.029 | 0.304 |
| *Anagallis arvensis* | 1.7 | 1.3 | | | |
| *Centuarea melitensis* | 1.0 | 0 | | | |
| *Cerastium glomeratum* | 0.5 | 0 | | | |
| *Erodium brachycarpum* | 11.4 | 0 | | | |
| *Filago gallica* | 9.5 | 0.8 | | | |
| *Hypochaeris glabra* | 10.3 | 4.6 | | | |
| *Lactuca serriola* | 0 | 1.1 | | | |
| *Silene gallica* | 3.4 | 0 | | | |
| Exotic Grasses | 35.7 | 0.3 | <0.001 | 0.001 | 0.002 |
| *Avena fatua* | 5.6 | 0 | | | |
| *Bromus diandrus* | 4.6 | 0 | | | |
| *Bromus hordeaceus* | 13.6 | 0.1 | | | |
| *Bromus madritensis ssp. rubens* | 0.6 | 0.1 | | | |
| *Vulpia myuros* | 11.4 | 0.1 | | | |

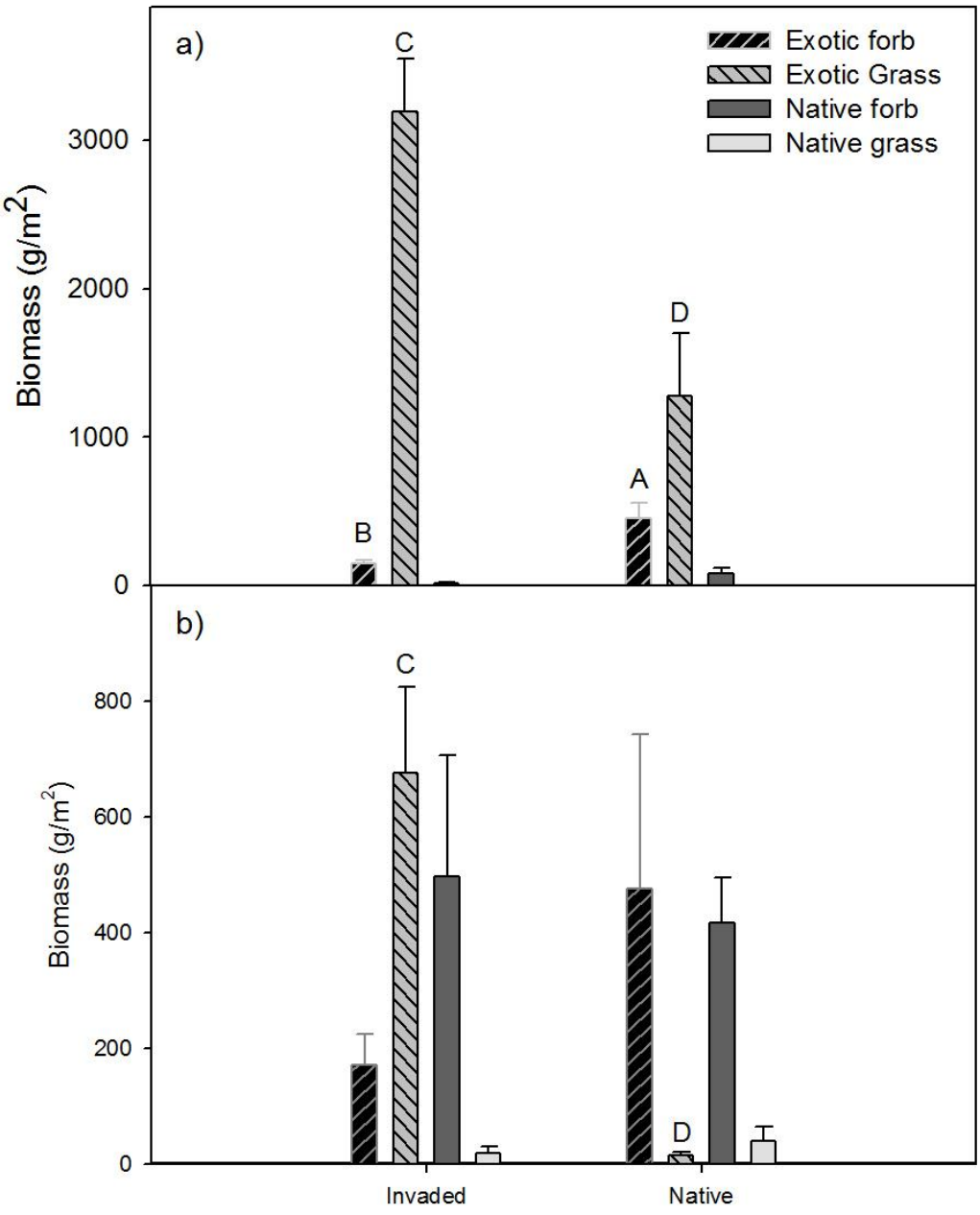


Figure 3.1. Plant biomass clipped at ground level during plant senescence of the 2007-08 growing season for the burned site (a) and the unburned site (b). Bars indicate standard error and letters significant differences ($P \leq 0.1$) determined by ANOVA comparisons within plant functional groups exotic forb, exotic grass, native forb and native grass.

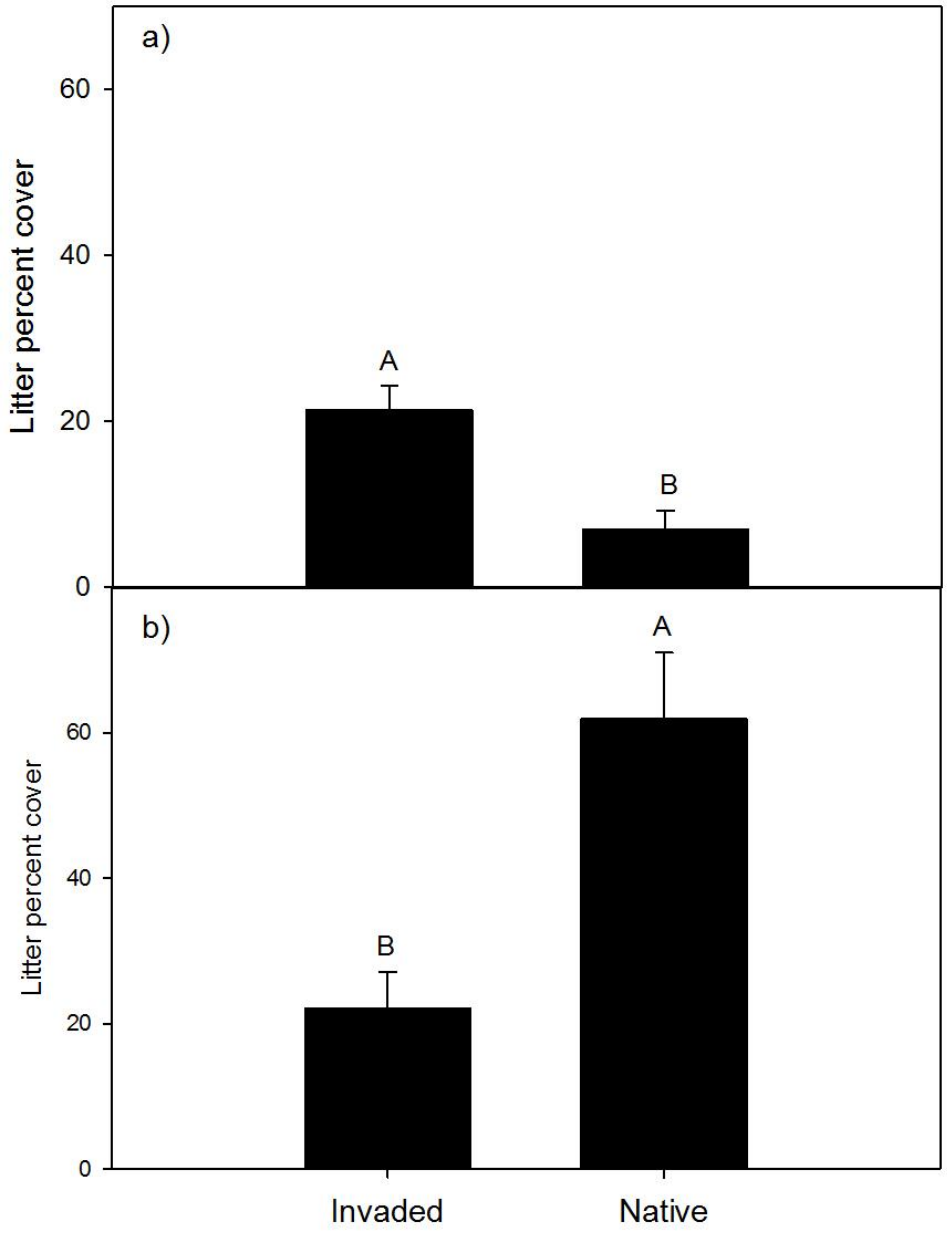


Figure 3.2. Percent litter cover collected at plant senescence in the 2007-08 growing season for the burned (a) and unburned (b) site. Bars indicate standard error and letters significant differences ($P \leq 0.1$) determined by ANOVA.

Table 3.4. Nitrogen and carbon composition of leaf tissue from composite samples at both experimental sites. Means are shown for dominant plant species. Due to limited tissue, composite samples were used to characterize plant tissue so replication was insufficient for statistical analysis.

| | N (%) | C (%) | C/N |
|---|---|---|---|
| **Natives** | | | |
| *Adenostoma fasciculatum* | 0.9 | 49.6 | 55.9 |
| *Arctostaphylos glandulosa* | 0.9 | 50.9 | 55.9 |
| *Nassella pulchra* | 1.0 | 42.7 | 42.1 |
| **Exotics** | | | |
| *Avena barbata* | 0.7 | 41.2 | 62.0 |
| *Bromus madritensis ssp. rubens* | 1.7 | 42.5 | 25.5 |
| *Bromus tectorum* | 1.4 | 43.3 | 30.5 |
| *Erodium brachycarpum* | 0.6 | 42.7 | 67.4 |
| *Vulpia myuros* | 0.9 | 42.6 | 49.7 |

Figure 3.5. Soil chemical data (means and standard errors) for the burned site collected pre-and post-fire. ANOVA was conducted to assess differences in soil chemical characteristics between treatments of invaded and native chaparral during the 2006-07 growing season.

| | Invaded | SE | Native | SE | P-value |
|---|---|---|---|---|---|
| **Pre Fire** | | | | | |
| Total N (%) | 0.3 | <.01 | 0.2 | <.01 | 0.635 |
| Total C (%) | 3.7 | 0.7 | 2.9 | 0.4 | 0.311 |
| Soil organic matter (%) | 2.3 | 0.2 | 1.9 | 0.2 | 0.314 |
| C/N | 14.8 | 0.5 | 12.9 | 0.4 | **0.012** |
| NH4 (ppm) | 76.8 | 17.1 | 56.0 | 9 | 0.572 |
| NO3 (ppm) | 7.4 | 2.1 | 4.6 | 0.9 | 0.235 |
| Total extractable N (ppm) | 84.2 | 55.7 | 60.6 | 28.1 | 0.584 |
| Olsen-P (ppm) | 25.6 | 6.8 | 19.2 | 3.1 | 0.918 |
| pH | 5.9 | 0.1 | 5.5 | 0.1 | **0.008** |
| **Post Fire** | | | | | |
| Total N (%) | 0.2 | 0.1 | 0.1 | 0.1 | **0.046** |
| Total C (%) | 4.6 | 0.8 | 2.1 | 0.3 | **0.012** |
| C/N | 19.0 | 1.0 | 17.6 | 1.9 | 0.233 |
| pH | 5.9 | 0.1 | 6.5 | 0.3 | **0.003** |

Table 3.6. Soil chemical data (means and standard errors) for the unburned site collected summer 2006. ANOVA was conducted to assess differences in soil chemical characteristics between treatments of invaded and native chaparral during the 2006-07 growing season.

| | Invaded | SE | Native | SE | P-value |
|---|---|---|---|---|---|
| Total N (%) | 0.2 | <0.1 | 0.3 | <0.1 | 0.204 |
| Total C (%) | 2.4 | 0.3 | 3.7 | 0.7 | **0.089** |
| Soil organic matter (%) | 5.4 | 0.6 | 6.8 | 0.8 | 0.192 |
| C/N | 13.0 | 1.4 | 15.0 | 1.5 | **0.009** |
| NH4 (ppm) | 10.8 | 1.7 | 8.7 | 0.9 | 0.309 |
| NO3 (ppm) | 9.5 | 1.6 | 7.5 | 1.7 | 0.405 |
| Total extractable N (ppm) | 20.3 | 7.9 | 16.2 | 1.9 | 0.230 |
| Olsen-P (ppm) | 4.1 | 0.9 | 3.7 | 0.5 | 0.730 |

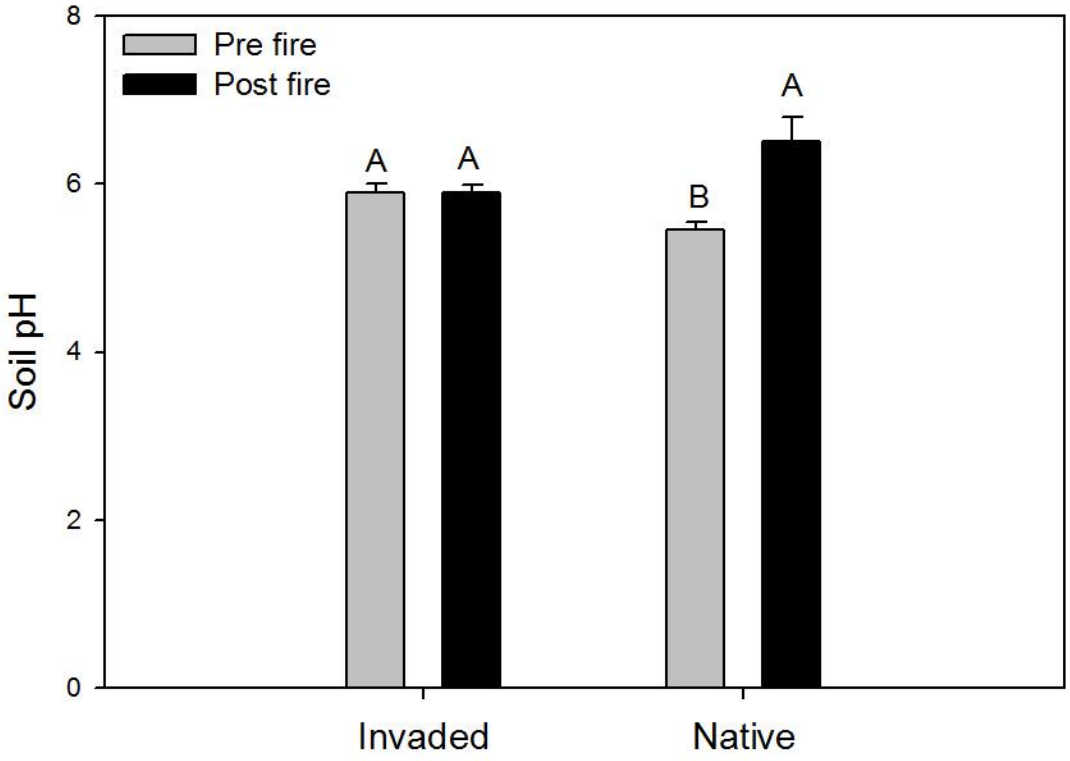


Figure 3.3. pH of soils collected pre- and post-wildfire at the burned site. ANOVA was conducted to assess differences in soil pH between treatments of invaded and native chaparral within each sampling date. Bars indicate standard error and letters significant differences ($P \leq 0.1$).

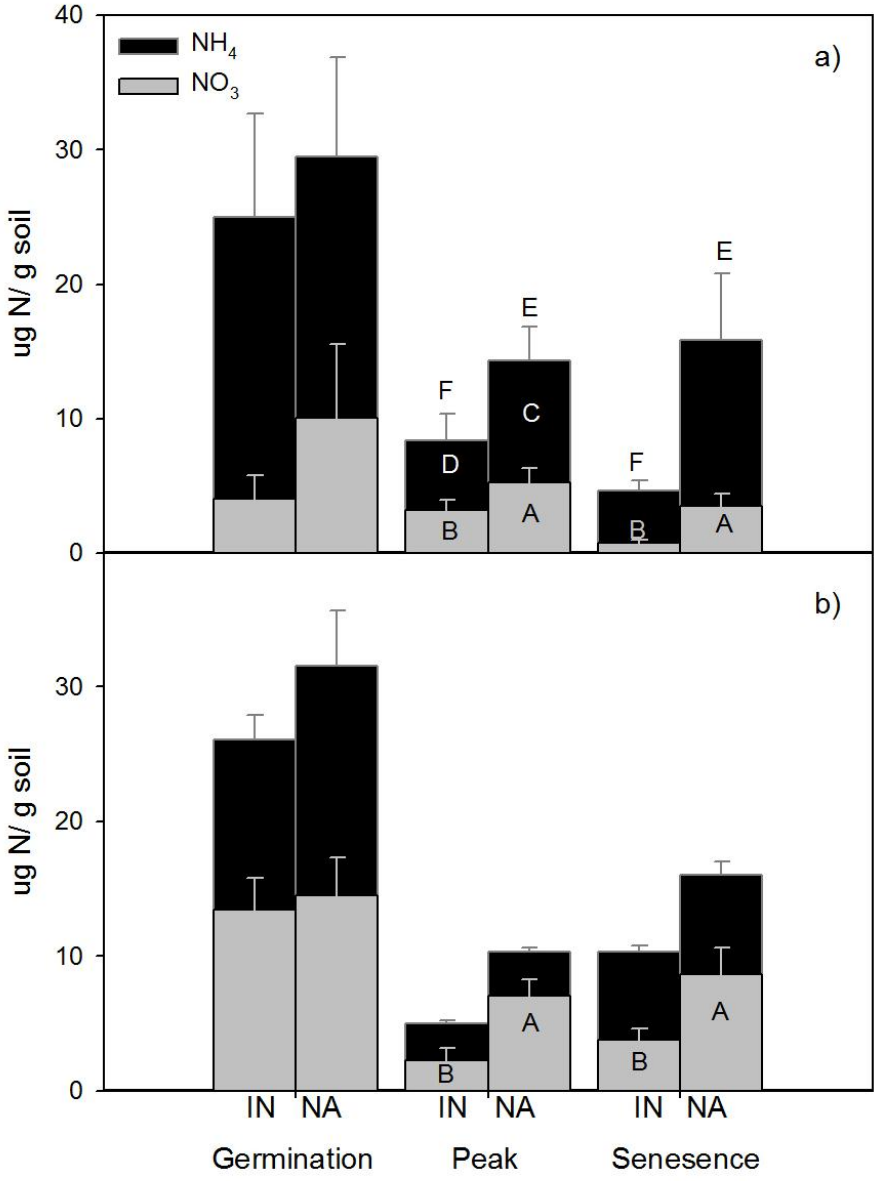


Figure 3.4. Soil extractable nitrogen during the 2007-2008 season at the burned site (a) and unburned site (b). Treatments are: IN = invaded and NA = native. Letters indicate significant differences using Tukey-Kramer HSD test following ANOVA: $NO_3$ = A-B, $NH_4$ = C-D and total extractable nitrogen = E-F. Bars indicate standard error and letters significant differences ($P \leq 0.1$).

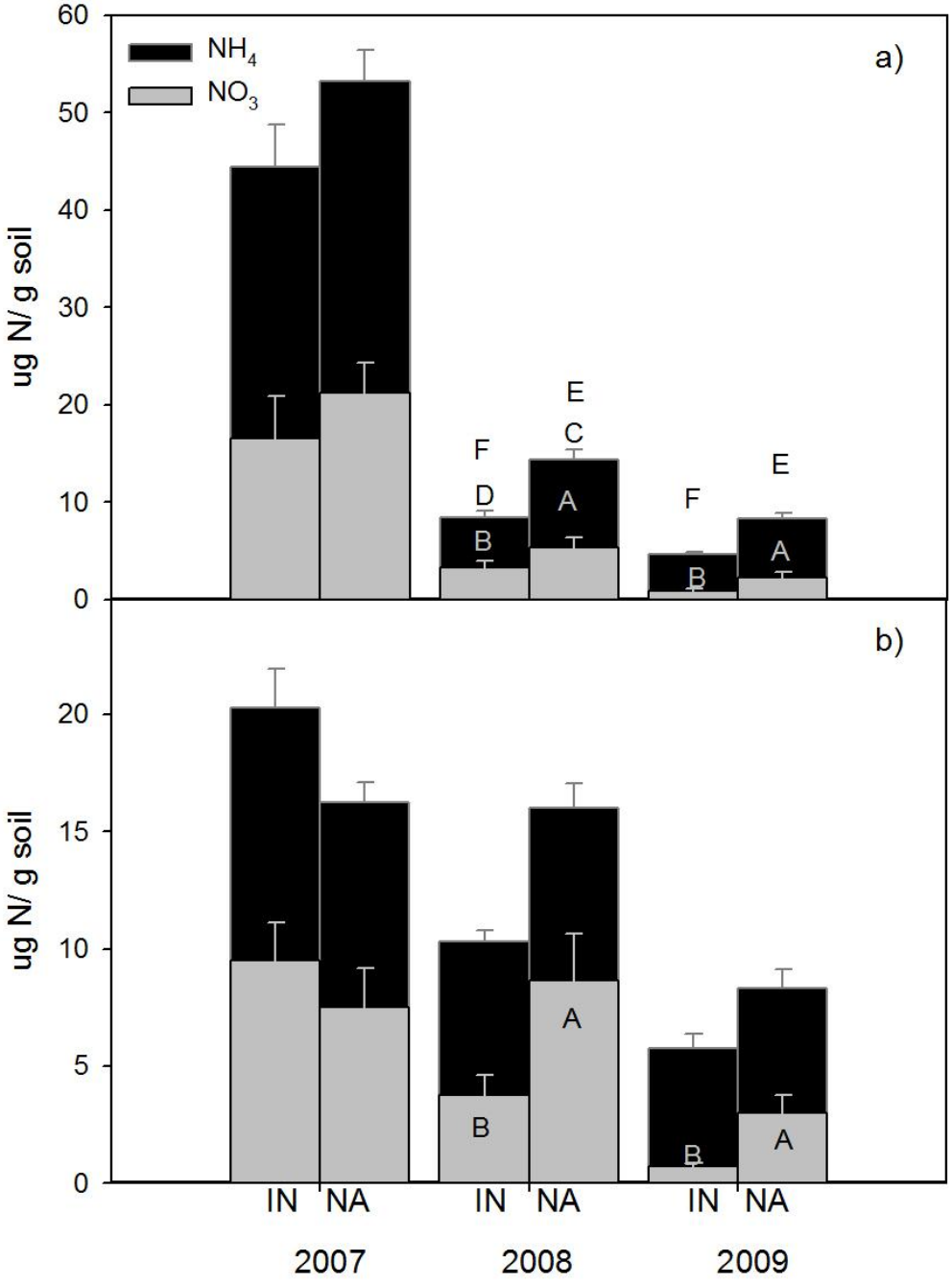


Figure 3.5. Soil extractable nitrogen at the burned site (a) and unburned site (b) during the years of 2007-2009 during at the peak of each season. Treatments are: IN = invaded and NA = native. Letters indicate significant differences using Tukey-Kramer HSD test following ANOVA: $NO_3$ = A-B, $NH_4$ = C-D, and total extractable nitrogen = E-F. Bars indicate standard error and letters significant differences ($P \leq 0.1$).

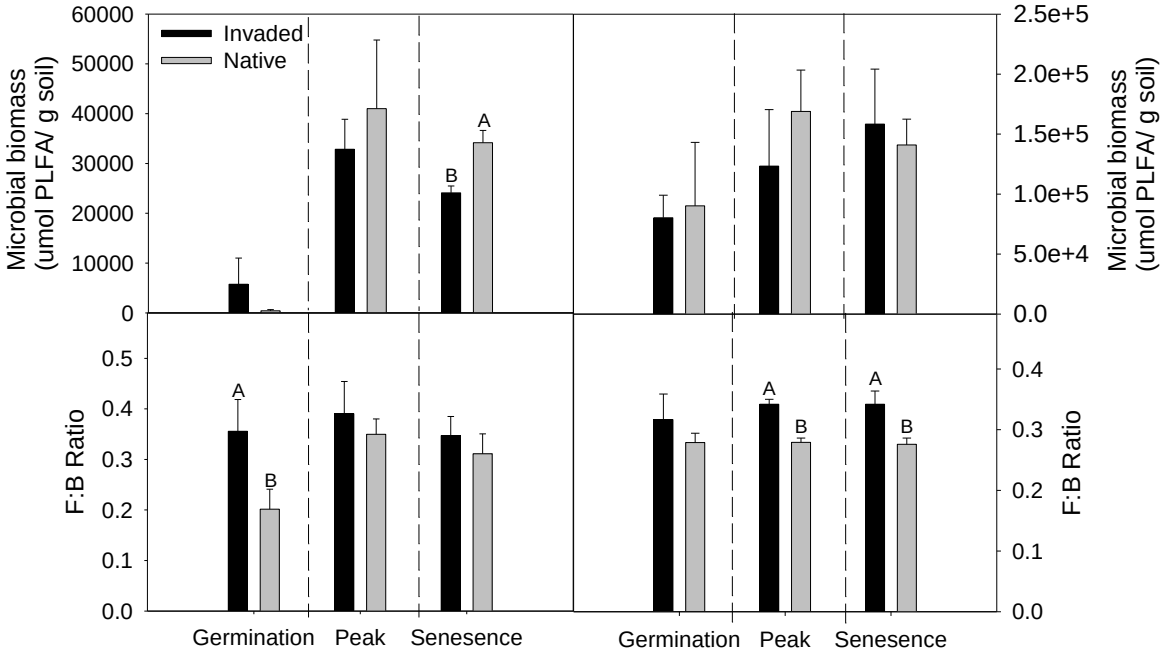


Figure 3.6. Phospholipid fatty acid profiles (μmol PLFA/ g soil) and fungal: bacterial (F:B) ratio representing soil microbial community biomass and composition at the burned site (a,c) and the unburned site (b,d) for soils collected between fall 2007 and spring 2008. Bars indicate standard error and letters significant differences ($P \leq 0.1$) within sampling dates and not across dates.

Table 3.7. The common PLFA and corresponding microbial functional groups from the burned site during the 2007-08 growing season. Means are shown for biomarkers making up grater than two percent of total PLFA abundance. Asterisks indicate level of significance * P<0.001, ** P< 0.05 determined with ANOVA.

| | | Burned site | | | | | |
|---|---|---|---|---|---|---|---|
| | | Germination | | Peak | | Senescence | |
| | Biomarker | Invaded | Native | Invaded | Native | Invaded | Native |
| General | ISO 17:1 G | 86.7 | 18.1 | 258.6 | 336.9 | 280.5 | 300.3 |
| Bacteria | 14:0 | 0.0 | 4.2 | 44.4 | 121.9 | 82.9 | 95.0 |
| | 18:0 | 126.6 | 21.5 | 326.8 | 299.3 | 209.0 | 255.7 ** |
| Gram + | 15:0 ANTEISO | 0.0 | 8.7 | 105.4 | 201.6 | 203.8 | 287.7 ** |
| | 15:0 ISO | 66.1 | 15.0 | 157.3 | 260.7 | 274.4 | 291.0 |
| | 16:0 | 424.0 | 72.4 | 975.0 | 1106.0 | 858.6 | 1016.5 |
| | 16:0 ISO | 63.4 | 9.7 | 106.2 | 270.8 | 196.6 | 264.1 |
| | 16:1 w9c | 0.0 | 0.0 | 0.0 | 50.9 | 81.1 | 0.0 ** |
| | 17:0 ANTEISO | 0.0 | 3.3 | 0.0 | 135.3 ** | 116.6 | 139.3 |
| | 17:0 ISO | 0.0 | 3.0 | 0.0 | 114.0 ** | 96.4 | 110.5 |
| Gram - | 24:0 | 306.2 | 0.0 | 797.4 | 316.3 | 162.7 | 173.0 |
| | 16:1 w7c | 143.8 | 32.9 | 469.0 | 304.7 | 325.4 | 442.0 ** |
| | 17:0 CYCLO | 107.2 | 22.4 | 278.7 | 246.1 | 246.2 | 317.6 ** |
| Fungi | 18:1 w5c | 0.0 | 5.7 | 95.2 | 127.2 | 119.0 | 42.1 |
| | 18:1 w9c | 375.3 | 44.5 | 1099.9 | 914.6 | 858.8 | 835.9 |
| | 18:2 w6c | 0.0 | 0.0 | 262.3 | 348.1 | 200.0 | 299.7 |
| AM Fungi | 16:1 w5c | 0.0 | 7.6 | 107.5 | 143.0 | 133.8 | 149.9 |
| Protozoa | 20:4 w6c | 1138.3 | 0.0 | 11258.2 | 14517.5 | 7159.9 | 11595.5 |

Table 3.8. The common PLFA's and corresponding microbial functional groups from soils of the unburned site collected 2007-08. Means are shown for biomarkers making up grater than two percent of total PLFA abundance. Asterisks indicate level of significance * P<0.001, ** P< 0.05 determined with ANOVA.

| Unburned site | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | Germination | | Peak | | Senescence | |
| | Biomarker | Invaded | Native | Invaded | Native | Invaded | Native |
| General | C25 N Alcohol | 262 | 147 | 147 | 550 | 0 | 368 |
| | ISO 17:1 G | 2446 | 3085 | 3085 | 3761 | 4258 | 4606 |
| | 19:0 CYCLO 11-12 2OH | 421 | 377 | 377 | 818 | 739 | 768 |
| | 19:1 (w 8?) Alcohol | 362 | 491 | 491 | 1199 | 790 | 1079 |
| Bacteria | 18:0 | 1290 | 1372 | 1372 | 2453 | 2316 | 1998 |
| | 14:0 | 437 | 482 | 482 | 744 | 666 | 574 |
| Gram + | 15:0 ANTEISO | 1315 | 1256 | 1256 | 2418 | 2070 | 1867 |
| | 15:0 ISO | 1989 | 2296 | 2296 | 4211 | 3373 | 3343 |
| | 16:0 | 4748 | 5947 | 5947 | 10512 | 9805 | 8361 |
| | 16:0 ISO | 1056 | 1032 | 1032 | 2065 | 1983 | 1725 |
| | 16:1 ISO G | 0 | 261 | 261 | 541 | 358 | 233 |
| | 16:1 w9c | 485 | 429 | 429 | 1127 | 1066 | 1092 |
| | 17:0 ANTEISO | 833 | 725 | 725 | 1379 | 1467 | 1206 |
| | 17:0 ISO | 4748 | 5947 | 5947 | 10512 | 9805 | 8361 |
| | 22:0 | 50 | 177 | 177 | 646 | 731 | 638 |
| | 24:0 | 158 | 191 | 191 | 694 | 744 | 713 |
| Gram - | 16:1 2OH | 340 | 212 | 212 | 581 | 325 | 504 |
| | 16:1 w7c | 2370 | 2783 | 2783 | 5478 | 5190 | 4405 |
| | 17:0 CYCLO | 1412 | 1624 | 1624 | 3171 | 2902 | 2596 |
| | 17:1 w8c | 127 | 215 | 215 | 461 | 327 | 370 |
| | 18:1 w5c | 1121 | 1082 | 1082 | 2351 | 1830 | 2109 |
| Fungi | 18:1 w9c | 5718 | 5459 | 5459 | 9551 | 12143 | 8182 |
| | 18:2 w6c | 1412 | 1600 | 1600 | 3965 | 3439 | 2598 |
| AM Fungi | 16:1 w5c | 1415 | 1399 | 1399 | 3020 | 2777 | 2546 |
| Proteobacteria | 19:0 cyclo c11-12 | 4151 | 4732 | 4732 | 8939 | 7991 | 8369 |
| Microeukaryotes | 20:0 | 0 | 288 | 288 | 733 | 385 | 529 |
| Pseudomonas | 18:1 w9t Alcohol | 239 | 209 | 209 | 366 | 363 | 337 |

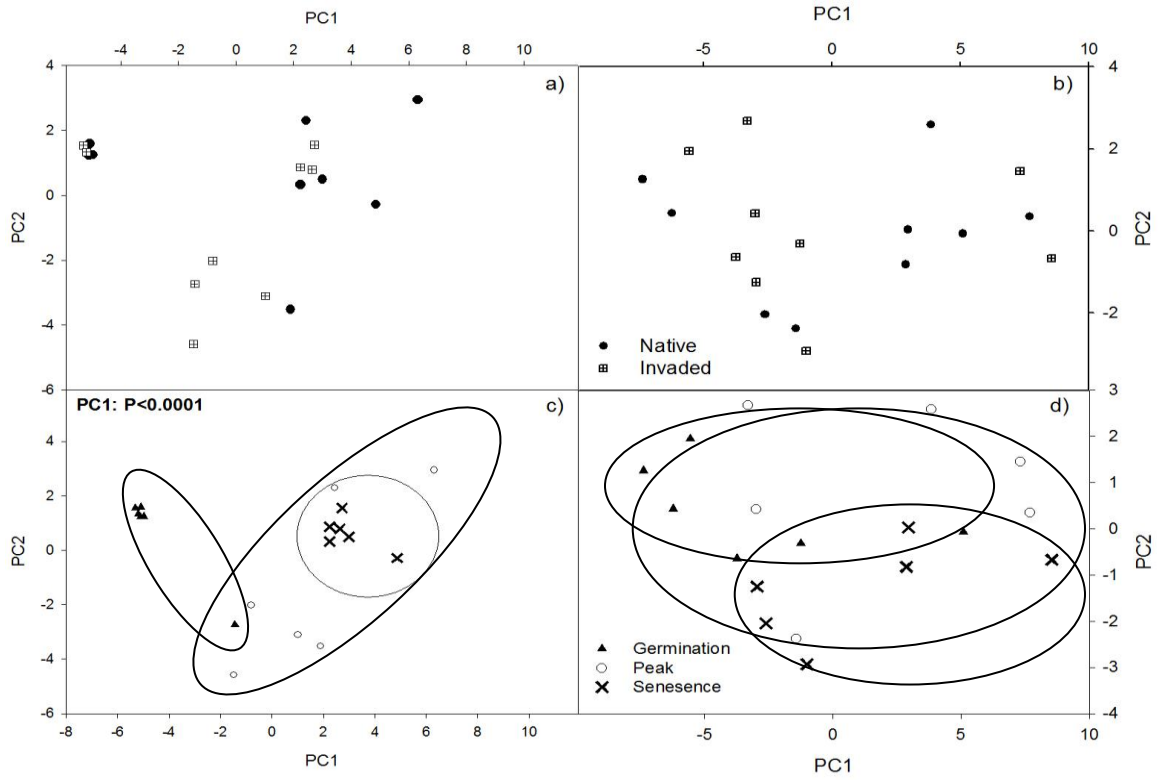


Figure 3.7. PCA results for PLFA microbial community analysis on treatment and sample date at the burned site (a,c) and unburned site (b,d) during the 2007-08 growing season. Graphs a and b assess differences between treatment while c and d assess differences between sampling dates. Elipses indicate statistically different microbial communities determined by ANOVA of PC values with an alpha level ≤ 0.1.

Table 3.9. Soil microbial PLFA percent weightings for PC's at both locations. Presence or absence of a negative sign indicates the direction of the weighting along the corresponding PC.

| | Burned Site | | | | Unburned Site | | |
|---|---|---|---|---|---|---|---|
| | Biomarker | % wt PC1 | % wt PC2 | % wt PC3 | Biomarker | % wt PC1 | % wt PC2 |
| **Bacteria general** | 14:0 | 4.7 | 0.4 | 4.7 | 14:0 | 3.4 | 0.1 |
| | 18:0 | 4.2 | 6.2 | 3.9 | 18:0 | 3.5 | 2.3 |
| Gram positive | 15:0 | 3.1 | 5.1 | 5.0 | 15:0 | 2.6 | 6.9 |
| | 15:0 ANTEISO | 5.2 | 0.6 | 4.1 | 15:0 ANTEISO | 3.5 | 0.5 |
| | 15:0 ISO | 5.4 | 0.3 | 1.3 | 15:0 ISO | 3.5 | 0.4 |
| | 16:0 | 5.0 | 3.1 | 5.5 | 16:0 | 5.5 | 2.1 |
| | 16:0 ISO | 5.4 | 1.5 | 2.4 | 16:0 ISO | 3.5 | 1.7 |
| | 16:1 w9c | 3.3 | 4.9 | 2.0 | 16:0 ISO G | 3.0 | 5.0 |
| | 17:0 ANTEISO | 4.9 | 2.1 | 7.6 | 16:1 w7c | 3.5 | 1.3 |
| | 17:0 ISO | 5.0 | 2.7 | 6.4 | 16:1 w9c | 3.4 | 1.9 |
| | 24:0 | 0.9 | 8.9 | 4.7 | 17:0 ANTEISO | 3.4 | 1.4 |
| | | | | | 17:0 ISO | 3.5 | 2.1 |
| | | | | | 22:0 | 2.9 | 3.9 |
| | | | | | 24:0 | 3.2 | 2.7 |
| Gram negative | 16:1 2OH | 4.7 | 4.6 | 0.2 | 17:0 CYCLO | 3.3 | 2.1 |
| | 16:1 w7c | 4.4 | 4.9 | 5.2 | 17:1 w8c | 3.3 | 3.1 |
| | 17:0 CYCLO | 4.7 | 3.8 | 4.0 | 18:1 w5c | 3.4 | 0.8 |
| | 18:1 w5c | 1.9 | 5.0 | 8.7 | | | |
| Proteobacteria | 19:0 cyclo c11-12 | 3.9 | 4.7 | 0.6 | 19:0 cyclo c11-12 | 3.3 | 2.0 |
| **Fungi** | 18:1 w9c | 4.5 | 5.0 | 4.7 | 17:0 | 2.8 | 6.4 |
| | 18:2 w6c | 4.4 | 0.5 | 4.3 | 18:1 w9c | 3.3 | 1.6 |
| | | | | | 18:2 w6c | 3.3 | 1.2 |
| AM fungi | 16:1 w5c | 4.8 | 1.2 | 2.8 | 16:1 w5c | 3.5 | 1.2 |
| | | | | | 20:0 | 3.2 | 1.6 |
| Microeukaryotes | 21:0 | 4.7 | 4.8 | 0.8 | | | |
| Protozoa | 20:4 w6c | 3.6 | 5.8 | 7.1 | 20:4 w6c | 2.4 | 6.4 |
| Pseudomonas | 18_1 w9t Alcohol | 3.8 | 3.9 | 1.9 | 18:1 w9t Alcohol | 2.8 | 2.8 |
| General | ISO 17:1 G | 3.5 | 4.8 | 5.8 | C25 N Alcohol | 0.6 | 9.3 |
| | 19:1 (w 8?) Alcohol | 4.3 | 4.4 | 1.3 | ISO 17:1 G | 2.0 | 6.4 |
| | 21:1 w3c | 3.0 | 5.7 | 4.1 | 15:0 ISO G | 3.0 | 4.6 |
| | 24:1 w3c | 4.3 | 4.7 | 0.9 | 19:0 CYCLO 11-12 2OH | 2.8 | 3.8 |
| | | | | | 19:1 (w8?) Alcohol | 2.9 | 3.2 |
| | | | | | 21:1 w3c | 2.0 | 6.0 |

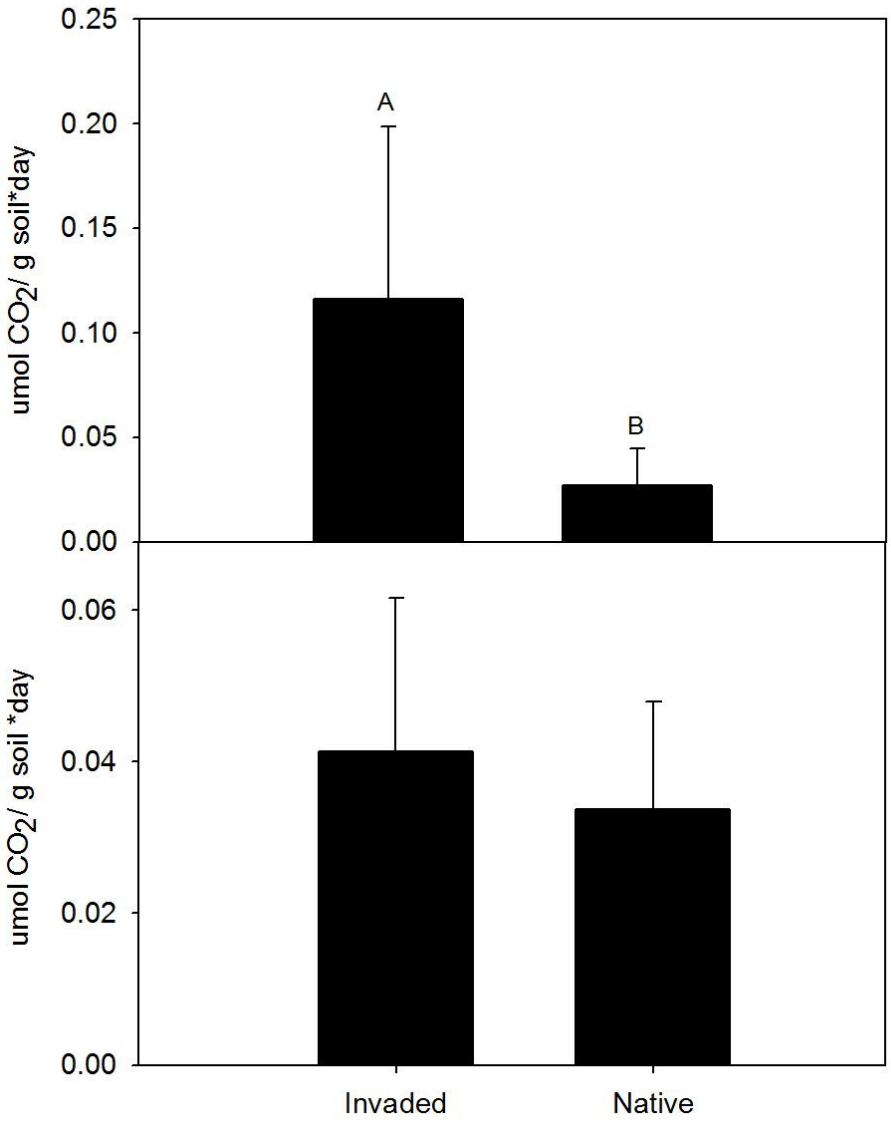


Figure 3.8. Potential soil respiration rates from 10 day laboratory incubations of soil collected at the peak of the growing season for the burned site (a) and unburned site (b). Bars indicate standard error and letters significant differences ($P \leq 0.1$) determined by ANOVA.

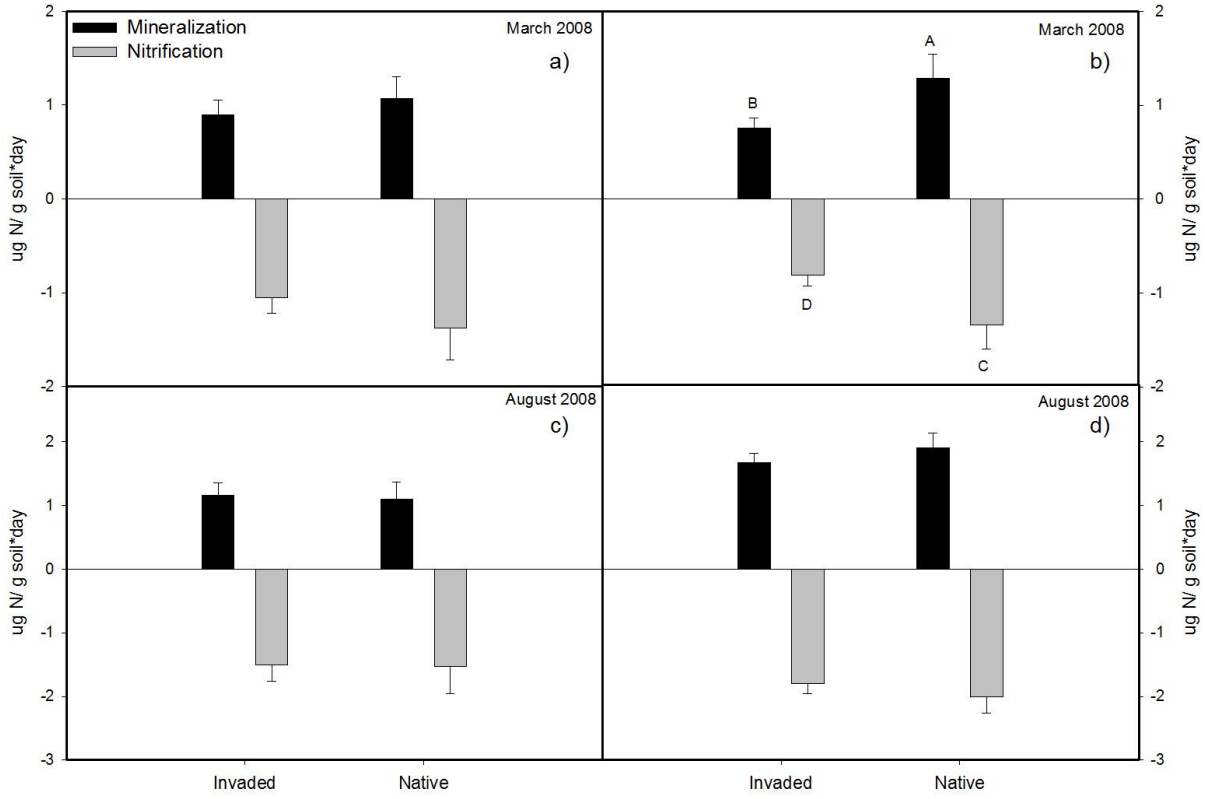


Figure 3.9. Potential nitrogen mineralization and nitrification from 30 day laboratory incubations for the burned site (a,c) and the unburned site (b,d) from soils collected in spring (March) and end of summer (August) of 2008. Letters indicate significant differences using Tukey-Kramer HSD test following ANOVA ($P \leq 0.1$): nitrogen mineralization = A-B and nitrification = C-D. Bars indicate standard error.

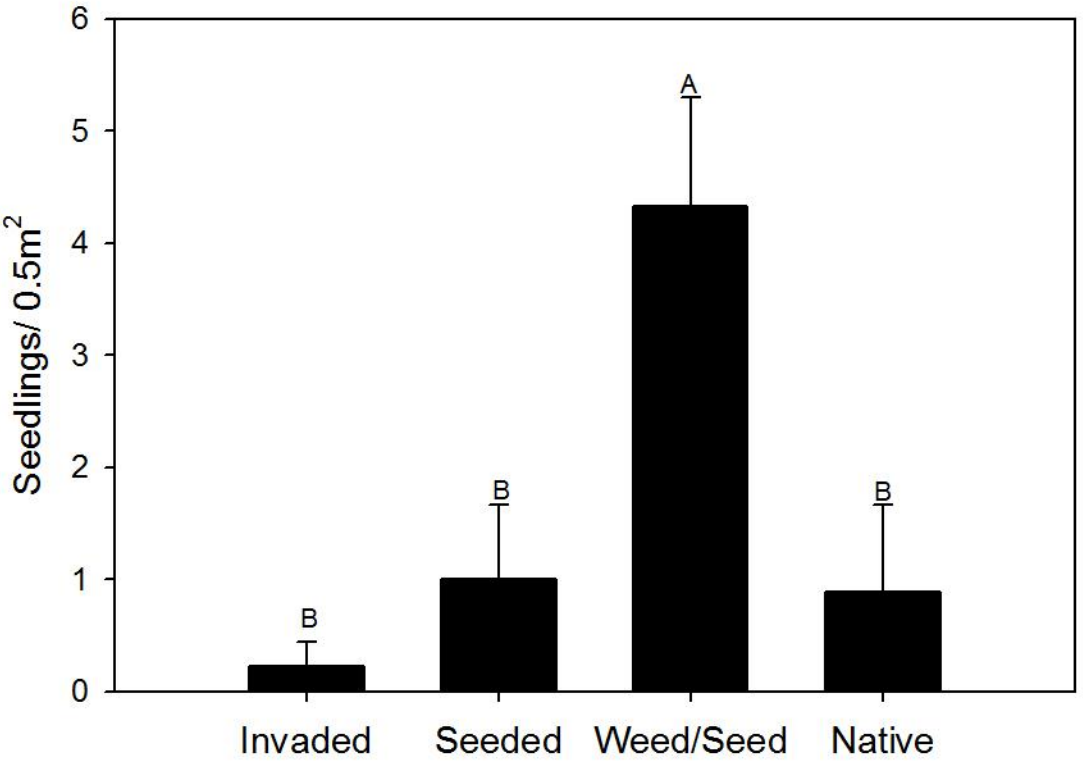


Figure 3.10. Shrub seedling density per $0.5m^2$ in the short-term weeding experiment at the burned site. Bars indicate standard error and letters significant differences ($P \leq 0.1$) determined by ANOVA.

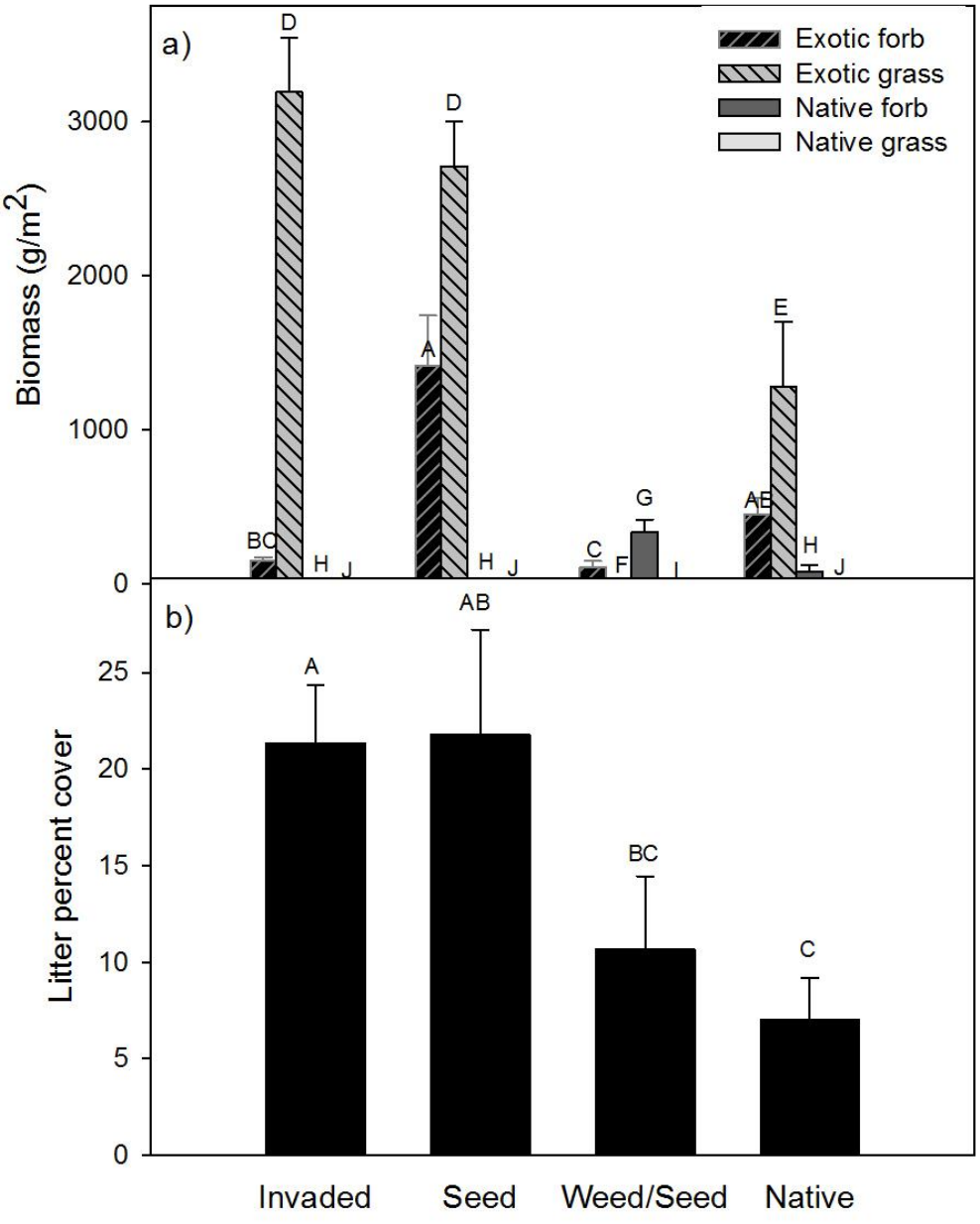


Figure 3.11. Plant biomass clipped at ground level during plant senescence (a) and percent cover of litter at the peak of the 2007-08 growing season at the burned site short-term weeding experimental restoration site. Bars indicate standard error and letters significant differences ($P \leq 0.1$) determined by ANOVA. For biomass data, comparisons are within plant functional groups exotic forb, exotic grass, native forb and native grass.

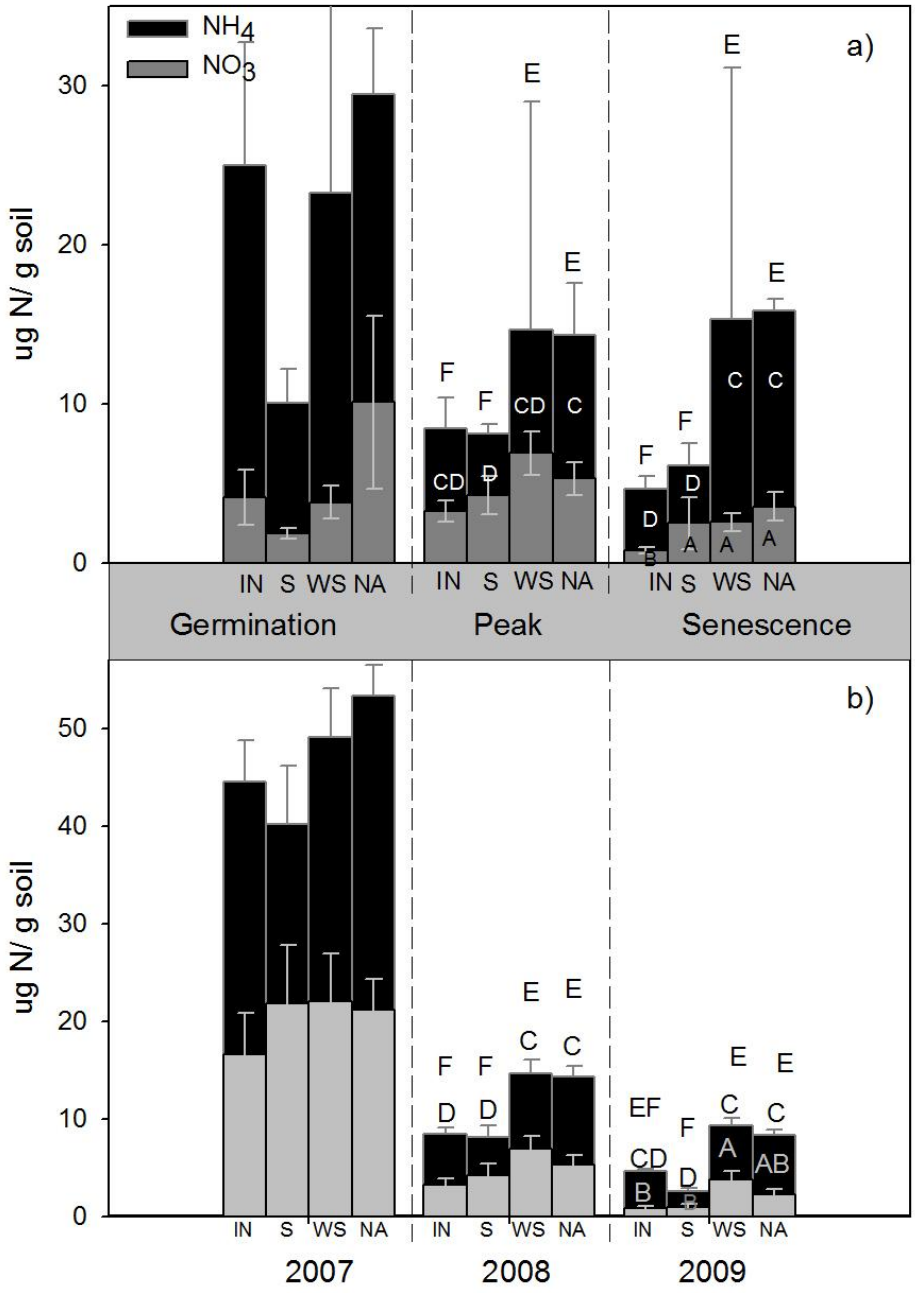


Figure 3.12. Soil extractable nitrogen at the burned site short-term weeding experimental restoration during the 2007-08 season (a) and 2007-09 years at peak of the season. Treatments are as follows: IN = invaded, S = seeded, WS = weeded and seeded, and NA = native. Letters indicate significant differences using Tukey-Kramer HSD test following ANOVA ($P \leq 0.01$): $NO_3$ = A-B, $NH_4$ = C-D and total extractable nitrogen = E-F.

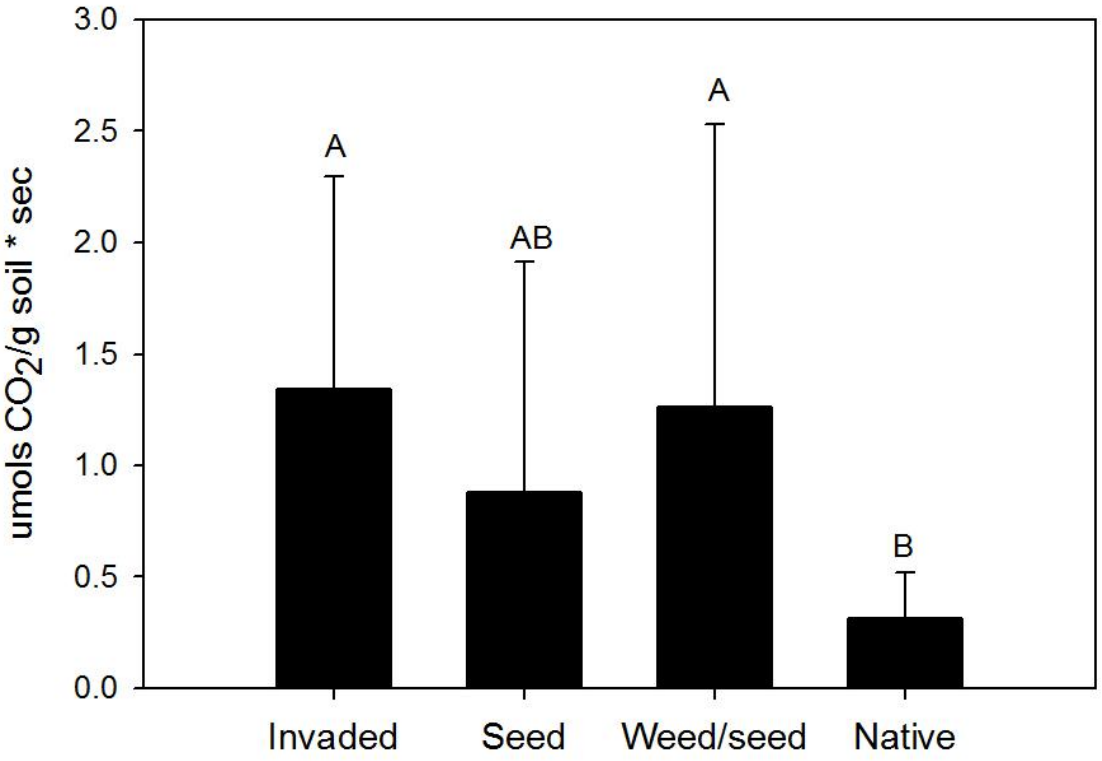


Figure 3.13. Potential soil respiration rates from 10 day laboratory incubations of soil collected at the peak of the growing season from the short-term weeding experimental restoration of the burned site. Bars indicate standard error and letters significant differences ($P \leq 0.1$) determined by ANOVA.

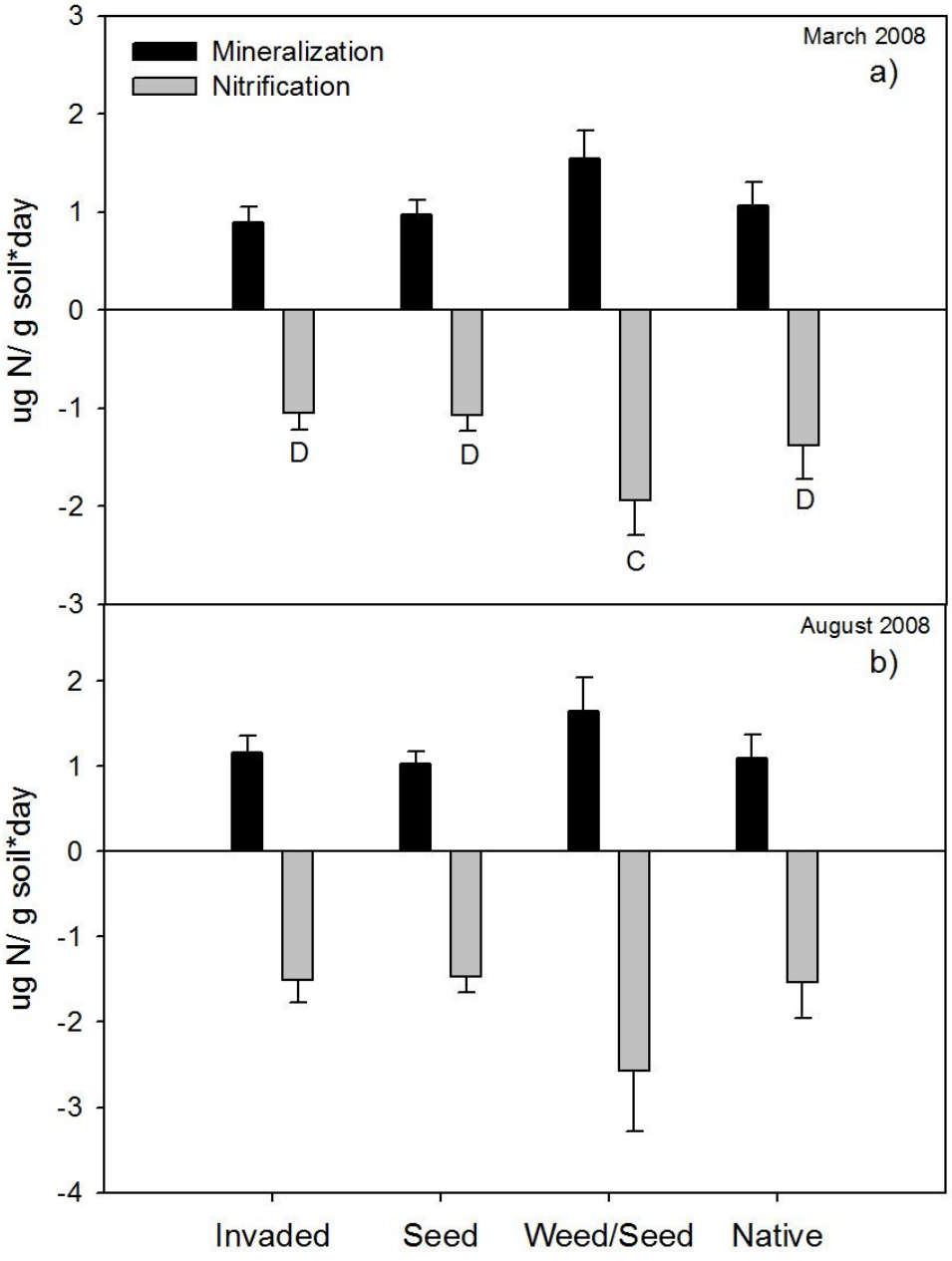


Figure 3.14. Potential nitrogen mineralization and nitrification from 30 day laboratory incubations from the short-term weeding experimental restoration of the burned site (a,c) soils collected in spring (March) and end of summer (August) of 2008. Letters indicate significant differences using Tukey-Kramer HSD test following ANOVA ($P \leq 0.1$): nitrogen mineralization = A-B and nitrification = C-D. Bars indicate standard error. Negative nitrification indicates microbial uptake of $NO_3$-N.

**Environment is a stronger determinant of exotic plant feedbacks to soil than vegetation type in southern California ecosystems**


## Abstract

Impacts of exotic plant invasion on soil chemical and biological characteristics have been studied for a decade ago, but generalizations across ecosystems remain difficult to make. Previous work has been limited to examination of a few species in one system or one species in multiple systems resulting in species- and site-specific conclusions. This project aimed at addressing the impacts of a suite of exotic species invading multiple ecosystem types. In a comparison of three vegetation types, I hypothesized that systems with plant traits most similar to the invading species would be least altered by invasion but that all ecosystems would experience alterations caused by the novel traits of invading plant species. In addition, I hypothesized that soils would be resilient to these impacts and therefore removal of exotics would lead to chemical and biological recovery of soils. I utilized a meta-analytical approach of data from three studies conducted in native and invaded California grasslands and coastal sage scrub and chaparral shrublands, which examined soil chemical pools and cycling rates and microbial community structure. Invasion of exotic annuals altered soil $NO_3$ availability regardless of the native vegetation type. Coastal sage scrub systems experienced the greatest impacts to soil chemistry and grasslands experienced altered microbial community composition. Contrary to expectations, chaparral was least impacted by annual grass invasion even though the replacement of shrubs by annuals constituted a vegetation type conversion from shrubs to grasses representing the greatest shift in plant

traits among the three sites. Changes in chaparral soils as a result of annual invasion are most likely due to differences in the spatial distribution of woody vs. herbaceous roots. While vegetation type affected the soils at each site in this study, abiotic soil and climatic factors had a stronger role in determining soil chemical and biological characteristics than vegetative inputs alone.

## Introduction

Ecosystem processes represent the culmination of vegetative traits in concert with abiotic and biotic factors including climate, soil parent materials and soil microbial community. Low fertility systems are frequently dominated by plant species with traits that facilitate slow decomposition rates leading to nutrient conservation within the system (Berendse 1998; Ehrenfeld et al. 2005; Santiago et al. 2005; Wardle et al. 2004). Many plant species of low fertility environments have evolved to produce tissues that are high in lignin and secondary chemicals and function to conserve the limited nutrients they obtain from herbivory and water loss. These tissues are biochemically expensive so leaf longevity is expanded to balance this cost (Berendse 1998; Peñuelas et al. 2010). Meanwhile, species that are adapted to high fertility soils tend to be fast growing and produce high-quality, short-lived tissue (Wardle et al. 2004). Whether tissue chemistry varies due to soil fertility, physiological characteristics of species, or environmental gradients (Cornwell et al. 2008; Díaz et al. 2004; Santiago 2007), the afterlife effects on the microbial community will be very different because microbial communities respond to shifts in C:N ratios of plant litter inputs to soils (Van der Krift & Berendse 2001; Zak et al. 2003). Traits such as high leaf lignin content play a role in determining microbial substrate quality which in turn determines microbial community structure and function (Ehrenfeld et al. 2005; Kulmatiski et al. 2008; Wardle et al. 2004; Zak et al. 2003).

Exotic plant invasion leads to the introduction of plant traits that may be novel to the ecosystems they invade. Introduction of traits such as higher litter quality and annual versus perennial habit can lead to changes in microbial community structure and function

(Bohlen 2006; Ehrenfeld 2003; Ehrenfeld et al. 2005; Van der Krift & Berendse 2001; Wardle et al. 2004). The magnitude of change is thought to be determined by the degree to which the new traits differ from those of the native vegetation (Ehrenfeld 2003; Wardle et al. 2004) and how those traits impact microbes. Invasive plant species have been shown to alter soil microbial community composition, nutrient cycling and availability, soil hydrology, as well as disturbance regimes such as fire frequency (D'Antonio & Vitousek 1992; Ehrenfeld 2003; Hawkes et al. 2006; Hawkes et al. 2005; Sigüenza et al. 2006b). These alterations may have negative impacts on native plant species and be capable of persisting long after exotics are removed. Soil-related effects are the result of shifted plant-soil interactions that lead to feedbacks on the soil system. Feedbacks occur in plant invasion when the invading plant species alters the plant community leading to shifts in the microbial community that in turn may impact the plant community (Ehrenfeld et al. 2005; Kulmatiski et al. 2008; Wardle et al. 2004; Zak et al. 2003). For example, an invading plant species that increased the population size of microbes associated with nitrogen mineralization could lead to increased rates of nitrogen mineralization and thus increased availability of soil nitrogen. Assuming the invading species is nitrophilous in comparison to natives, this increase in nitrogen availability would facilitate higher productivity in the invasive species. This type of positive feedback could lead to displacement of native plant species as exotic plants increase in dominance (Ehrenfeld et al. 2005). The strong link between plants and their associated soil microbial communities has recently received increased interest (Bohlen 2006; Harrison & Bardgett 2010; Kulmatiski et al. 2008; Sigüenza et al. 2006a; Wardle et al.

2004; Wolfe & Klironomos 2005). Understanding mechanisms by which plant – microbial relationships are maintained is crucial as global change and plant invasion threaten ecosystem processes world wide (Mooney 2000; Pimentel et al. 2005).

Invasion of exotic plants can be met by resistance from the native plant community via competition for resources such as water and light rendering exotics unable to establish. Mature chaparral, for example, produces a dense canopy that reduces soil surface light to levels that shade out exotic plants and provides this system with resistance to plant invasion (Keeley 2006; Keeley et al. 2005). Most ecosystems are not completely resistant to invasion and exotics are able to invade to some level, especially after a disturbance that removes vegetation.

Soil systems, on the other hand, have two points of resistance to invasion. The first is resisting the establishment of exotic plants by having vegetation that excludes invasives, or a microbial community or nutrient and water regime that are unsuitable for the invading species. In addition to this first level of resistance, is a second level that occurs after the invading plant species has established, but has not yet impacted soil chemical and biological characteristics. The extent to which different soils are resistant will depend upon plant traits of native and invading species, and likely other factors such as soil type and environment (Eviner & Hawkes 2008; Seybold et al. 1999; Yelenik & Levine). If a soil is not resistant to changes, then maintaining ecosystem functioning will depend upon resilience (Allen et al. 2001; Allen et al. 1998; Lal 1997). Resilience is defined as the rate of restoration/recovery and measure of permanent change from pre- to post-alteration (Westman 1978). Ecosystems acquire resilience from biotic and abiotic

components that make up the system along with their interactions. In the case of soil function such as carbon cycling, a functionally redundant microbial community may allow for recovery of predisturbance cycling rates while a system without such redundancy may lose necessary species, altering the system and requiring several decades for recovery (Rousk et al. 2009).

Less understood is whether soils are resistant to impacts of exotic plant invasion and resilient enough to recover once exotic plants are removed. Much work on invasion has led to conclusions of species-specific and/or site-specific impacts. To assess the potential for generalizable impacts of invasions, a comparative approach was taken to examine belowground responses of invasion of a suite of invading exotic plants across multiple ecosystems. This study was designed to assess whether invasion of the annual exotic plant functional group into three vegetation types, southern California grasslands, coastal sage scrub and chaparral shrublands, lead to species and site-specific impacts or whether particular impacts of invasion occur similarly across systems. In order to compare across these vegetation types, the same methods were used at each site and data analyzed in the same manor. I hypothesized 1) due to differences in soil inputs from the dominant native species of these three ecosystems, invasion of the same suite of exotic plant species would have impacts that reflect the degree to which exotics alter soil inputs. 2) Soils of each of these systems will be impacted by invasion of exotic plants and the level of resilience of the restored soils where the exotic plant species are removed will depend on natural cycling rates of the system and the degree to which exotics altered the soil chemical and biological characteristics.

## Methods

Data were compiled from three studies conducted concurrently in three ecosystem types of Southern California, grassland and coastal sage scrub and chaparral shrublands (Table 1&2). Data were collected 2006-2008 from $0.5m^2$ plots randomly located in three treatments, native, invaded and restored vegetation. Native areas were those with no history of human disturbance and having exotic plant species cover less than 20 percent. Restored sites included those that experienced manual removal of exotics or prescribed burns and successful native re-vegetation, while invaded areas contained 50 percent or greater exotic plant species cover. In each case soil and microbial response variables were compared between invaded and native vegetation. Only two of the three treatments were available at some sites.

To determine the effects of exotic invasion and restoration on soil biological and chemical characteristics, soil cores (0-10 cm depth and 2.5 cm diameter) were collected during the 2006-2007 growing season and analyzed for total carbon and nitrogen, extractable phosphorus and soil pH. In 2007-2008 additional samples were taken for KCl- extractable $NO_3$, $NH_4$ and soil organic matter and analyzed as reported in chapters 1-3. Nitrogen mineralization and potential soil respiration were determined with laboratory incubations (see chapters 1-3). Phospholipid fatty acid (PLFA) analysis was used to determine whether microbial community structures were affected by exotic invasion following the modified Bligh–Dyer method (Frostegard et al. 1991; White et al. 1979) and quantified according to methods of chapters 1-3. Bacterial biomarkers included: 14:0, 15:0 iso, 15:0 ISO G, 15:0 antiso, 15:0, 15:0 3OH, 16:0, 16:0 iso, 16:1

ISO G, 16:1 2OH, 16:1 w9c, 16:1 w7c, 17:1 alcohol, 17:0 iso, 17:0 antiso, 17:0 cyclo, 17:1 w8c, 18:0, 18:1 w5c, 18:0, 19:0 cyclo c11-12, 19:0 Cyclo 11-12 2OH, 19:1 (w8) alcohol, 20:1 w3c, 21:1 w3c, 22:0, and 24:0, 24:1 w3c, C25 N alcohol, cholesteryl-palmitate, Cis 9,10 epoxy 18-0, ISO 17:1 G; fungi: 17:0, 18:2 w6c, and 18 1w9c, 20:1 w9c, AM fungi: 16:1 w5c, microeukaryotes: 20:0, 21:0; protozoa: 20:4 w6c; *Pseudomonas*: 18:1 w9t alcohol. Nomenclature for PLFAs follows Lechevalier and Lechevalier (1988), Vestal and White (1989), Haack et al (1994), Zelles (1999), Myers et al (2001), and Hebel et al (2009).

## Data Analysis

Principle components analysis (PCA) was conducted on PLFA biomarkers to assess microbial community differentiation by ecosystem type and invasion/restoration treatment for each sample date. Biomarkers that were present in fewer than 25% of the plots within a site were not included in the analysis due to statistical limitations. ANOVA was applied to the first three PCs of each PCA to determine statistical differences between ecosystems and invasion/restoration treatment microbial communities for each of three sampling dates (Sigüenza et al. 2006b). A meta-analysis method was used to determine the effects of invasion and restoration on soil biological and chemical factors. Effect size was calculated as the natural log of the experimental mean divided by the control mean (Cornwell et al. 2008; Hedges et al. 1999; Osenberg et al. 1997; Treseder 2004) where the experimental means were those of invaded and restored treatments and the control mean those of the native treatment. In the case of the southern California

grasslands where no uninvaded native reference sites are available (Biswell 1956; Minnich 2008), restored treatments were used to calculate the control mean and invaded treatments as the experimental mean. Ninety-five percent confidence intervals were calculated for effect size to differentiate between effects across ecosystems and invasion/restoration levels (Cornwell et al. 2008).

## Results

Total carbon was reduced by 33 percent in invaded and 31 percent in restored coastal sage scrub (Fig 1A) and total nitrogen was reduced by 16 percent in restored coastal sage scrub (Fig. 1 A, B). C:N ratios decreased by 23 percent in invaded and 19 percent in restored coastal sage scrub and 5 percent invaded grasslands. Soil phosphorus and pH were lower in invaded and restored treatments of the coastal sage scrub (Fig. 2A, D). Reduction in soil pH is a result of site differences between coastal sage scrub locations as pH did not differ within sites between invasion treatments, but pH of one site was more acidic. Soil pH was also unaffected by invasion in chaparral and grasslands. Invasion of both shrublands led to a 50 percent decrease in $NO_3$ and a 100% percent decrease in invaded grasslands, but a reduction in $NH_4$ only occurred in the invaded chaparral and an increase in $NH_4$ in invaded grasslands (Fig. 2B, C). Restoration and invasion of the coastal sage scrub had no impact on $NH_4$ (Fig. 2C).

Invaded chaparral had two times the potential soil respiration rate of native soils, and restoration of coastal sage scrub increased potential soil respiration by 25 percent (Fig. 3A). Potential total nitrogen mineralization was reduced in coastal sage scrub by

both invasion and restoration and by invasion in grassland (Fig. 3B). Total potential nitrification rates were increased only in restored grasslands (Fig. 3C), but when analyzed by summer versus spring nitrification rates, restored coastal sage scrub nitrification rates were also reduced (Dickens Chapter 1).

Restoration of coastal sage scrub increased PLFA richness by 10 percent (Fig. 4A), while invasion of coastal sage scrub reduced microbial biomass by 27 percent (Fig. 4B). Fungal to bacterial ratios were reduced by 11 percent in restored coastal sage scrub (Fig. 4C) but increased by 30 percent in invaded chaparral (Fig. 4C). Invaded and restored coastal sage scrub had reduced bacteria and fungi (Fig. 5A, B), whereas restored coastal sage scrub had almost twice the protozoa of native soils (Fig. 5E). Invasion of grasslands increased AM fungi by 74 percent and protozoa by 99 percent (Fig. 5C, E), and invasion of grasslands had 30 percent of the proteobacteria found in restored grasslands (Fig. 5D).

The first three PCs explained 80 percent of the variation in microbial communities determined from PLFA analyses of soils collected during plant germination in 2007-2008, but showed no pattern between ecosystem or invasion/restoration treatment (Fig.6A). At the peak and senescence periods of the growing season, microbial communities from the chaparral plots differed from the microbial communities in all other vegetation types. More specifically, at the peak of the season, grassland communities were the same whether invaded or not. Microbial communities in the soils under native and invaded vegetation for the coastal sage scrub ecosystem were more similar to each other than those from restored coastal sage scrub and invaded chaparral

differed from all other shrubland treatments (Fig. 6B). Chaparral microbial communities were associated with gram positive bacteria 24:0, protozoa 20:4 w6c and the general biomarker C25N alcohol along PC2 (Table 3). During plant senescence, the abundance of protozoa, as indicated by biomarker 20:4 w6c, was greater for soils with chaparral vegetation. During this late season sampling date of plant senescence, chaparral soils were additionally associated with general biomarker 24:1 w3c and gram negative 17:1 w8c, while the grassland and coastal sage scrub ecosystems were more associated with the general biomarker 24:1 w3c (Table 3). Invasion and restoration treatments did not alter total microbial community composition at any point in the season.

## Discussion

The hypothesis that plant traits of native and invaded communities would determine the degree of soil chemical and microbial response was not supported by this research. Nitrate concentrations were lower in invaded soils regardless of vegetation type, and season was a stronger determining factor for total microbial community composition than vegetation type. Grasslands which had plant species traits most similar to those of native species, experienced greater shifts in microbial functional groups than the other vegetation types, whereas chaparral, which had plant traits very different from the exotic invaders, was most resistant to change.

In a recent review of soil bacterial community diversity at the continental scale, Fierer and Jackson (2006) determined that while vegetation type is an important factor in determining bacterial diversity, the most important determinants of bacterial diversity are

soil pH and soil moisture deficit. They concluded that microbial community composition is affected by vegetation type, but that other environmental factors (pH soil moisture, organic carbon, C:N and % silt/clay) impact microbes to a greater degree and have a greater influence on microbes than the type of vegetation. Previous research has shown various affects of vegetation, on soil microbes (Ehrenfeld 2003, 2004). For instance, Allen et al. (1998) found that species composition of the arbuscular mycorrhizal community differs under dry tropical forests when compared to adjacent planted grasslands, whereas Johnson and Wedin (1997) observed no differences between dry tropical forests and grasslands. The difference in chaparral microbial community from other ecosystems was observed later in the season at peak and senescent plant growth and might be explained by the earlier period in which the plants are actively growing in the grassland and coastal sage scrub systems. Grassland species will either senescence or go dormant as the spring dry season progresses and coastal sage shrubs are mainly drought deciduous and thus transition into dormancy in late season. With a reduction of growth associated with plant senescence, root exudates would also decline and may lead to a reduction in PLFA richness. Chaparral shrubs would maintain root activity including root exudation late into June supporting the growth of their associated microbial communities until late summer dormancy.

Overall microbial community composition was not driven by vegetation type or invasion/restoration level during the germination periods of 2007-2008. However, during peak and senescence periods, chaparral microbial communities were distinct from other vegetation types. Seasonal variability of microbial community composition was also

found by Bardgett and others (1999) where both microbial biomass and PLFA measures differed across the growing season in response to seasonal patterns of nitrogen mineralization, soil moisture and spring flushes of litter inputs. Their study corroborates the changes in seasonality of microbial communities associated with the three vegetation types of the study reported here. PLFA results were compared at multiple time periods in order to capture feedbacks of vegetation type on microbial community composition that may be associated with key phenological stages of dominant vegetation. Other soil microbial and chemical measures were compared only at the peak of the vegetative growing season because this is when the effect size for these measures was largest. At other times in the season, the effect size of soil chemistry and microbial biomass and F:B were lower or non-existent. Seasonal variability in resources and microbial community is normal in wildland systems and seasonality of microbial community response to invasion is to be expected (Bardgett et al. 1999; Eviner 2004; Eviner et al. 2006).

I had predicted that ecosystems of low fertility and harsh environmental conditions, i.e. drought and cooler temperatures, and nutrient conserving traits would experience greater impacts from exotic annual plant invasion due to the degree to which plant traits of these two vegetation types differ. Exotic annuals invading ecosystems of southern California may exhibit ruderal habits of fast growth rates and high tissue nutrient content which are traits novel to a shrubland vegetation type and to a lesser extent, annual/perennial grassland vegetation type (Berendse 1998; Kulmatiski et al. 2008; Norton et al. 2007). Previous studies indicate invasion of exotic grasses into chaparral shrublands introduce rooting morphology that reduces the thickness of A and B

soil horizons and deep water percolation (Williamson et al. 2004). In addition, the altered quality and quantity of litter introduced to coastal sage scrub by the invasion of exotic grasses leads to increased carbon and nitrogen cycling rates (Wolkovich et al. 2009). As anticipated, invasion of a suite of exotic annuals altered soil chemical and biological characteristics of chaparral, coastal sage scrub and grassland vegetation types of California differently. Soil extractable nitrogen and total carbon and nitrogen in the coastal sage scrub soil were reduced more than in the other two systems, while grassland restoration produced significant alteration of microbial community composition and function. Chaparral systems appeared to be the least impacted by invasion despite the greater disparity in plant traits between chaparral natives and exotic annuals, which indicates that chaparral soils were the most resistant to invasion.

I predicted that chaparral ecosystems would experience the largest impacts to soil biology and chemistry due to the significantly lower quality litter, slower growth rates and heterogeneous distribution of roots associated with species of these lower fertility environments compared to those of annual invaders. My prediction was based upon the concept that vegetation of shrublands with low fertility sites would have slower decomposing litter than exotic annuals which originated from higher fertility environments (Norton et al. 2007) and results of previous studies show shifts in soil nutrients in shrublands in response to annual invasion (Kulmatiski et al. 2008; Williamson et al. 2004). However, the only microbial variation in soil biological properties that was significantly altered following invasion was an increase in F:B ratios which may have been an artifact of increased density of fine roots in soils of invaded

areas compared to native areas. Native shrublands have coarser roots and a greater heterogeneity of root distribution than in systems dominated by annual grasses and forbs (Kummerow 1989; Kummerow et al. 1978). This increase in fine roots would increase opportunity for AM fungi associations and lead to an increased F:B. Increased soil respiration in response to invasion of exotic annuals is a common result of exotic annual invasion (Ehrenfeld 2003) and is usually attributed to the introduction of a higher quality litter. In this study, increased respiration may be attributed to the increase in fine roots within the top 10 cm of soil under exotic annuals. That soil carbon and nitrogen pools did not decrease in response to the higher quality litter inputs of exotics may have several alternative explanations. There may have been residual recalcitrant carbon in chaparral soils with secondary compounds that suppressed decomposition (Handayanto et al. 1997; Swift et al. 1979), or there has been insufficient time since invasion to observe a decrease in soil carbon, or the amount of invasive species biomass produced balances the increased rate of respiration.

Coastal sage scrub soils experienced the greatest soil nutrient losses associated with both invasion and restoration, although invasion and restoration are expected to have opposite effects if the invasive species are the main drivers of soil changes. Carbon and C:N reductions could be the result of reduced soil microbial biomass in the form of lower fungal abundance in both invaded and restored treatments, and additionally from bacterial reduction in invaded coastal sage scrub. Microbial biomass represents a small component of the soil carbon pool at any time so a reduction in microbial biomass could only account for a small percentage of this reduction in soil carbon. More likely, soil carbon

losses were the result of changes in rates or quality of carbon input between invaded and native sites. In the case of the restored site, the management protocol for the past 7 to 9 years has been continual weeding of invasives that represents both carbon removal and soil disturbance from pulling roots.

With fewer bacteria in the soils, nitrogen mineralization rate would be expected to decline as it did in invaded coastal sage scrub. Nitrogen mineralization remained lower in restored coastal sage scrub than in the native treatment indicating that more time is necessary for recovery of nitrogen cycling. Nitrogen cycling rates altered by invasion of northern California grasslands took three to five years to show recovery (Eviner & Hawkes 2008). Grasslands turn over annually supporting rapid nutrient cycling (Eviner et al. 2006; Jackson et al. 1988), whereas CSS systems do not show the same rapid cycling rates and thus may take even longer to recover from altered nitrogen cycling. The reduction of carbon, nitrogen, C:N and nitrogen mineralization in restored coastal sage scrub could also be the result of yearly disturbance in the form of weeding. Regular removal of exotic plant biomass could have caused a slow depletion of soil carbon and nitrogen inputs and eventually the reduction of C:N and nitrogen mineralization. The restoration maintenance practices of these coastal sage scrub sites maintained the initial reduction of carbon and nitrogen but also may have exacerbated the problem. Increases in protozoa in restored coastal sage scrub could be related to higher levels of bacteria in relation to fungi along with higher PLFA or microbial diversity as protozoa are selective bacterial feeders (Bonkowski et al. 2000). In coastal sage scrub dominated by exotics, plant species diversity is reduced and the dominant species would contribute to soil

inputs to a greater degree. With little variation in quality of soil inputs under invasion, F:B may change little. Alternatively, following restoration increased plant diversity may have had minor effects on soils because invasives were still present and left a legacy in soils that promoted both the exotic annual-associated microbial community and the recovering native microbial communities (Buyer et al. 2010; Eviner & Hawkes 2008). Long-term studies following restoration projects are necessary to determine if such results indicate transitional states, slow recovery of soils or if these differences are artifacts of the restoration process.

Restored grasslands had reduced microbial biomass that included reduction of bacteria, fungi and protozoa. F:B ratio was also reduced due to the disproportionate reduction in fungi to bacteria with the majority of decline attributable to AM fungi. This decrease in fungi may be a result of a loss of fungi associated with annual grasses. Annual grasses are associated with AM fungi and endophytes, specifically fine root endophytes (Müller & Krauss 2005; Sigüenza et al. 2006b), as well as non-mycorrhizal fungi species. Nelson and Allen (1993) found that small spore *Glomus* species increase where *Bromus* and *Avena* species invaded coastal sage scrub systems and Hawkes and others (2006) found invasion of exotic grasses in both California and Utah increase *Glomus* species in invaded California grasslands and non-mycorrhizal species in Utah (Hawkes et al. 2006). In addition to increasing *Glomus* species, they determined that invasions of exotic grasses shift the fungi from a specialist to a generalist dominated community. If similar shifts had occurred in the grasslands of this study, restoration may have caused a decline in generalists which reduced fungal biomass until specialist species

recover. Despite the loss of fungal biomarkers, PLFA richness increased, which suggests that the soil microbial community of grasslands has the potential to respond to vegetation changes, although the degree of recovery cannot be assessed in the absence of uninvaded control grasslands. C:N ratios increased under restored vegetation which may be due to the greater accumulation of the native perennial grass, *Nassella pulchra*, with lower quality litter (see chapter 1, Table 3).

Nitrogen mineralization is commonly increased by invasion (Ehrenfeld 2003) but in the grasslands studied here, nitrogen mineralization increased with restoration of natives. The restored grassland soils also had reduced nitrification rates, which is commonly interpreted as an increase in nitrogen immobilization. However, with decreased microbial biomass it is unlikely that microbial immobilization can explain lower nitrate production. More likely, nitrogen losses may have been caused by the high clay content of these soils led to degassing of $N_2O$ under the moist laboratory incubation conditions (60% soil moisture). The same laboratory methods were used for all three vegetation types, but only the grassland soils responded to invasion with lower nitrate production. Alternative explanations for the grassland results are that lower nitrate production is a characteristic of these high clay soils, or it is an artifact of the laboratory method, or the grassland site is different because of the comparison of a restored to an invaded site, rather than a native to an invaded site as in the two shrublands.

$NO_3$ in both grassland and CSS restored ecosystems was greater than in their corresponding invaded soils suggesting the removal of exotics may lead to recovery of native $NO_3$ soil levels. This direct connection suggests that despite the differences in

tissue traits of exotics, the invasion of exotic annuals introduced $NO_3$ utilization rates that altered availability and seasonality of $NO_3$. $NO_3$ is a mobile nutrient making it likely candidate for showing short term change. It appears that the trait of early phenology and fast growth rates (DiVittorio et al. 2007), are mechanisms by which exotic annuals can similarly affect ecosystems with very different vegetation types. $NO_3$ was reduced by invasion and restoration lead to recovery of natural $NO_3$ levels or at least $NO_3$ levels greater than invaded areas.

Generalizations concerning the impacts of exotic plant invasion across ecosystems remain difficult to establish. While the factors that lead to resistance and resilience to the impacts of plant invasion are the same, differences in environmental factors rather than vegetation type may be more important indicators of invasion impacts. Fierer and others (Fierer et al. 2009) found that global distribution of microbial community composition was most affected by soil pH and soil moisture with vegetation being of lesser importance. The results of this study support their findings in that non-vegetative based, site specific characteristics were important drivers in microbial communities and acted as means of resistance and resilience. In addition, within site variation appears to have impacted soil chemical and biological characteristics to a greater degree than exotic plant invasion and site-species specific interactions proved important in determining potential impacts of exotic plant invasion. In all three of the systems here, exotic plant invasion affected both soil chemical and biological characteristics. As expected, the impact was not equal across these systems, but it was unexpected in that the ecosystem with the greatest difference in plant species traits from

the invading suite of species was least impacted. This contradicts the long held ideas about feedbacks associated with invaders and novel traits, but also reiterates the importance of abiotic factors in ecosystem resistance and resilience to plant invasion.

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Table 4.1. Locations and ecosystem types of the six study sites sampled congruently in 2006-08. N = native, I = invaded, and R = restored.

| Ecosystem Type | Location | | Annual Precipitation (cm) | Treatments present |
|---|---|---|---|---|
| High Elevaton Chaparral | North Mountain Experimental Area | San Jacinto Mountains, CA | 35 | N,I |
| Low Elevaton Chaparral | Santa Rosa Plateau Reserve | Murrieta, CA | 48 | N,I |
| Coastal Grassland | White Point Preserve | San Pedro, CA | 30 | I,R |
| Inland Grassland | Santa Rosa Plateau Reserve | Murrieta, CA | 48 | I,R |
| Coastal Sage Scrub | Trump National Golf Club | Ranch Palos Verde, CA | 28 | N,I,R |
| Coastal Sage Scrub | White Point Preserve | San Pedro, CA | 30 | I,R |

Table 4.2. Soil chemical mean values for 2006-07 (C, N, P, pH), and 2007-08 extractable nitrogen, $NO_3$ and $NH_4$. NM = North Mountain Research Area, SRP = Santa Rosa Plateau Ecological Reserve, WP = White Point Preserve and TN = Trump National Golf Club. ANOVA was conducted to assess differences in soil chemical characteristics between treatments within each. Significance is indicated as follows P < * 0.1, ** 0.01, *** 0.05.

| | NM chaparral | | SRP Chaparral | | WP grassland | | SRP Grassland | | WP CSS | | TN CSS Site | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Invaded | Native | Invaded | Native | Invaded | Restored | Invaded | Restored | Invaded | Restored | Invaded | Restored | Native |
| Total N (%) | 0.3 | 0.2 | 0.2 | 0.3 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.2 | 0.4 | 0.3 | 0.3 |
| Total C (%) | 3.7 | 2.9 | 2.4 | 3.7 * | 3.2 | 3.1 | 2.2 | 2.2 | 3.8 | 4.2 | 1.7 | 1.6 | 1.8 |
| C/N | 14.8 *** | 12.9 | 13.0 | 15.0 *** | 14.0 | 15.7 | 13.4 | 13.3 | 19.8 | 18.6 | 4.3 | 5.3 | 6.0 **** |
| NH4 (ug/g) | 76.8 | 56.0 | 10.8 | 8.7 | 7.4 | 8.3 | 6.5 | 9.2 | 10.0 | 24.9 | 2.6 | 2.4 | 2.5 |
| NO3 (ug/g) | 7.4 | 4.6 | 9.5 | 7.5 | 5.8 | 31.9 *** | 3.6 | 1.8 | 9.3 ** | 4.6 | 17.8 | 17.2 | 9.9 |
| Olsen-P (ug/g) | 25.6 | 19.2 | 4.1 | 3.7 | 18.8 | 22.1 | 5.1 * | 4.1 | 24.6 | 22.5 | 3.0 | 2.8 | 3.1 |
| pH | 5.9 | 6.5 *** | 6.9 | 7.7 **** | 8.0 | 8.0 | 5.9 | 5.9 | 7.9 | 7.8 | 7.7 | 8.0 | 8.1 **** |

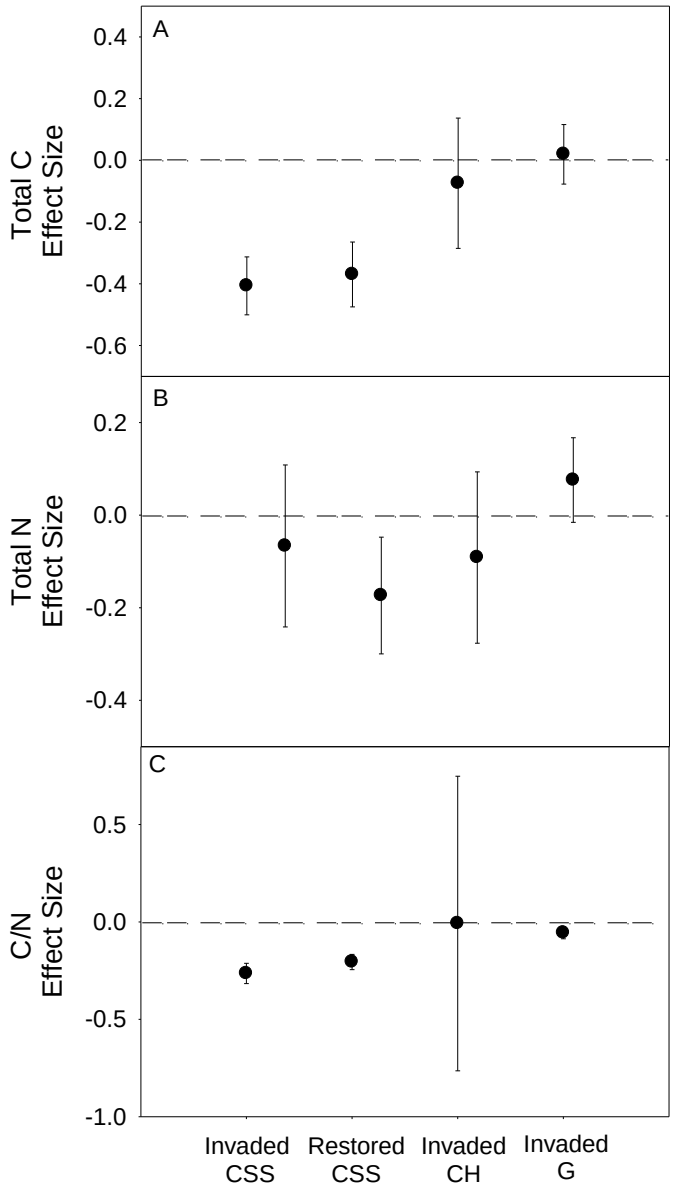


Figure 4.1. Soil nutrient pools effect size from meta-analysis of coastal sage scrub (CSS), chaparral (CH) and grassland (G).The dashed line at zero represents the treatment with the lowest exotic annual cover (for CSS and CH that is the native treatment and for G it is the restored treatment) soil chemical pool and the effect size the degree to which the other treatments diverge from this corresponding baseline. Bars are 95 percent confidence intervals.

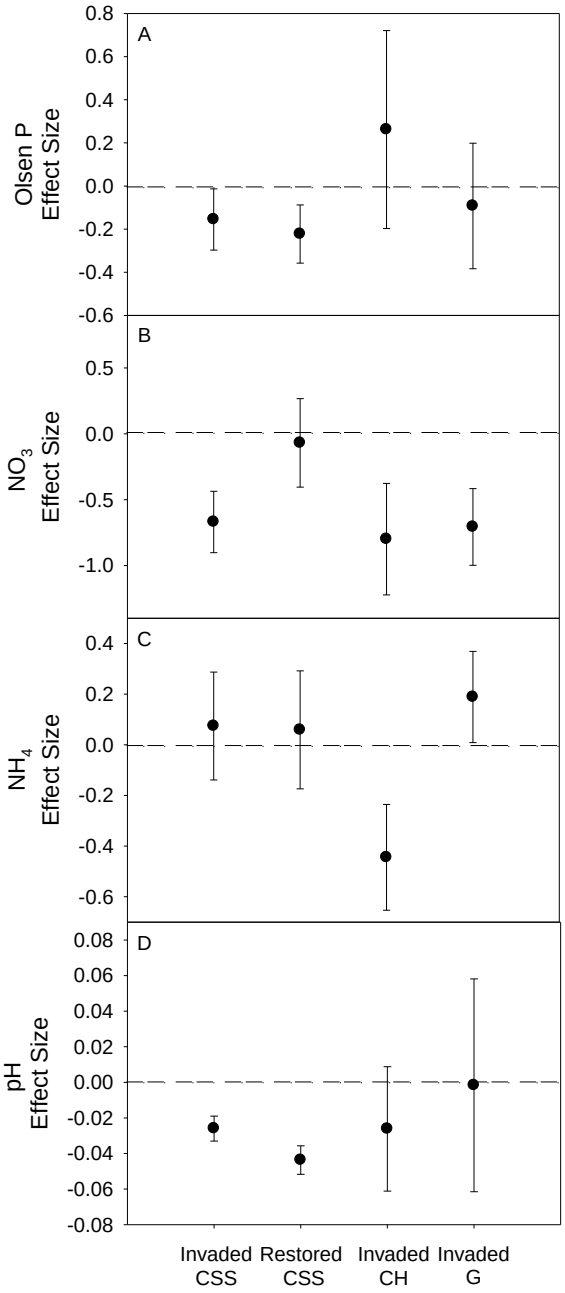


Figure 4.2. Extractable nutrient pool effect size of coastal sage scrub (CSS) and chaparral (CH). (CSS), chaparral (CH) and grassland (G). The dashed line at zero represents the treatment with the lowest exotic annual cover (for CSS and CH that is the native treatment and for G it is the restored treatment) extractable nutrient pool and the effect size the degree to which the other treatments diverge from this corresponding baseline. Bars are 95 percent confidence intervals.

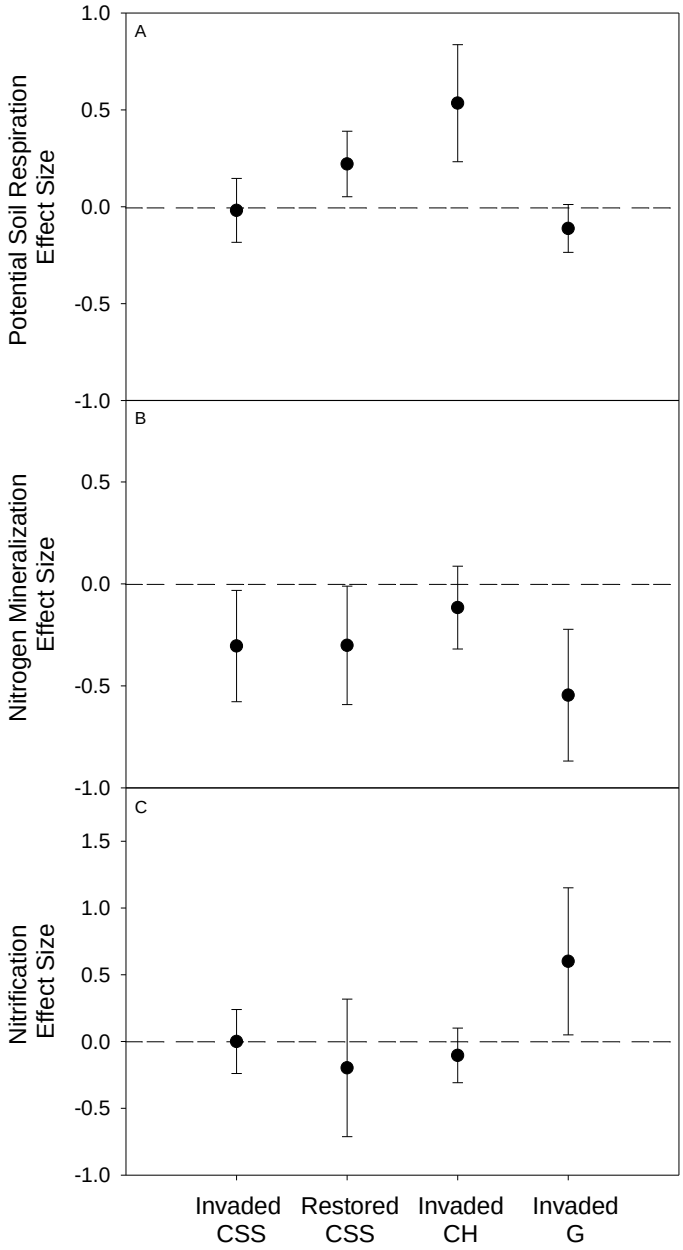


Figure 4.3. Soil function effect size from meta-analysis of coastal sage scrub (CSS), chaparral (CH) and grassland (G).The dashed line at zero represents the treatment with the lowest exotic annual cover (for CSS and CH that is the native treatment and for G it is the restored treatment) soil function and the effect size the degree to which the other treatments diverge from this corresponding baseline. Bars are 95 percent confidence intervals.

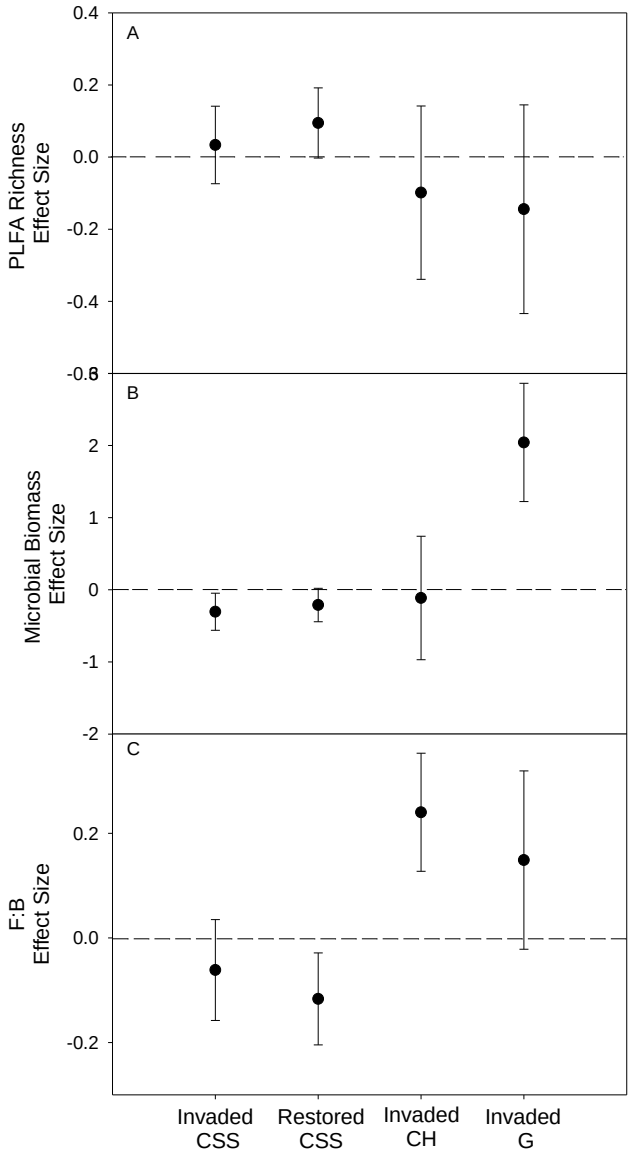


Figure 4.4. Effect size from meta-analysis of microbial community PLFA data of coastal sage scrub (CSS), chaparral (CH) and grassland (G).The dashed line at zero represents the treatment with the lowest exotic annual cover (for CSS and CH that is the native treatment and for G it is the restored treatment) microbial community and the effect size the degree to which the other treatments diverge from this corresponding baseline. Bars are 95 percent confidence intervals.

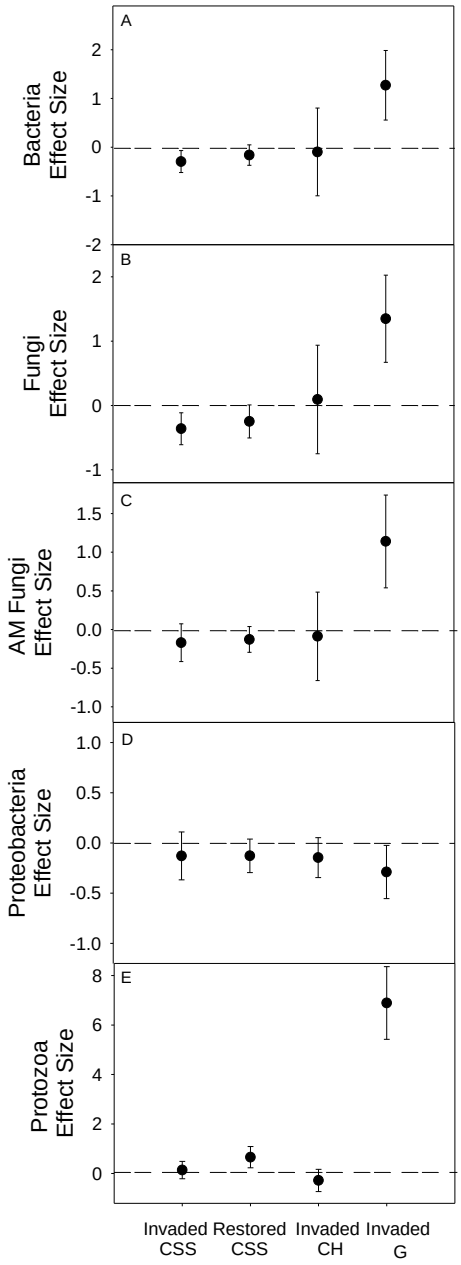


Figure 4.5. Effect size from meta-analysis of microbial PLFA functional groups of coastal sage scrub (CSS), chaparral (CH) and grassland (G).The dashed line at zero represents the treatment with the lowest exotic annual cover (for CSS and CH that is the native treatment and for G it is the restored treatment) microbial PLFA functional groups and the effect size the degree to which the other treatments diverge from this corresponding baseline. Bars are 95 percent confidence intervals.

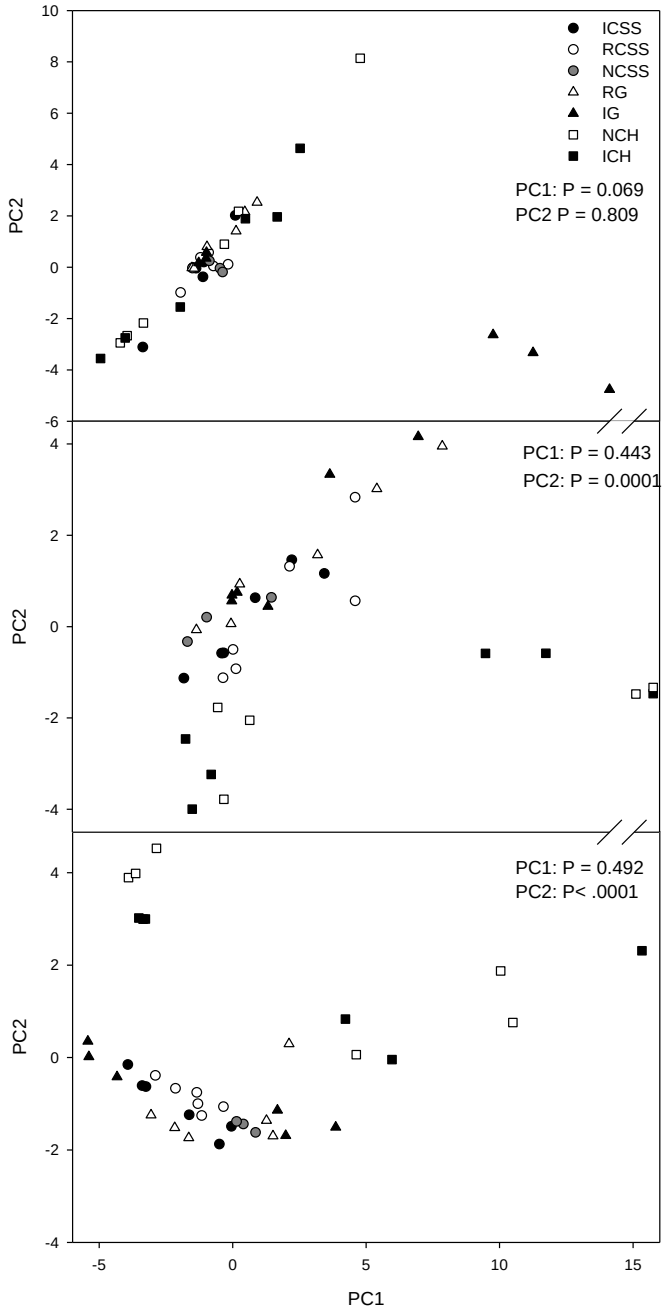


Figure 4.6. Principle components analysis of PLFA composition by ecosystem and exotic plant invasion/restoration treatment of soil from plant (A) germination, (B) peak and (C) senescence periods of 2007-08. Treatments included invaded coastal sage scrub = CSS, restored coastal sage scrub = RCSS, native coastal sage scrub = NCSS, restored grasslands = RG, invaded grasslands = IG, native chaparral = NCH and invaded chaparral = ICH. The axis break along PC1 of graph B occurs between 6 and 12.

Table 4.3. Soil microbial PLFA weightings for PCAs of soils collected in 2007-08. Percentages at column headings indicate the percent variation explained by the corresponding PC. Negative signs indicated a negative direction of weighting along the axis.

| | Germination | | | | | | Peak | | | | | | Senescence | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Biomarker | PC1 53% | | PC2 19% | | PC3 8% | Biomarker | PC1 65% | | PC2 10% | | PC3 7% | Biomarker | PC1 64% | | PC2 10% | | PC3 6% | |
| Bacteria | 14:0 | 4.9 | | | | | | | | | | | 18_0 | | | | | 6.0 | |
| | 18:0 | | | | | 5.6 | | | | | | | | | | | | | |
| Gram positive | 24:0 | | | 3.7 | (-) | | 24:0 | 2.0 | | 6.2 | (-) | 8.0 | 16_0 ISO | | | | | 3.1 | |
| | 15:0 ISO | | | | | | | | | | | | 17_0 ISO | | | | | 4.5 | (-) |
| | 16:1 w9c | 5.0 | | | | | | | | | | | | | | | | | |
| | 17:0 ANTEISO | 5.0 | | | | | | | | | | | | | | | | | |
| | 22:0 | 0.9 | | 5.2 | | | | | | | | | | | | | | | |
| | 16:0 | | | | | 6.3 | | | | | | | | | | | | | |
| Gram negative | 17:1 w8c | 0.6 | | 5.7 | | | 17:1 w8c | 2.0 | | | | 9.2 | (-) | 18_1 w5c | | | | | 4.6 | |
| | 16:1 w7c | | | | | 7.7 | | | | | | | | 17_1 w8c | | | | | 5.3 | (-) |
| Microeukaryote | | | | | | | | | | | | | | 21_0 | 1.3 | (-) | 10.8 | | 4.6 | |
| Proteobacteria | 19 cyclo c11-12 | 0.3 | | 8.0 | | 5.0 | | | | | | | | 19 0 cyclo c11-12 | | | 3.6 | (-) | | |
| Protozoa | 20:4 w6c | | | 4.0 | (-) | | 20:4 w6c | 0.6 | (-) | 7.0 | (-) | 9.1 | | 20_4 w6c | 1.2 | (-) | 11.0 | | 4.7 | |
| Fungi | 18:1 w9c | 4.9 | | | | | | | | | | | | 17_0 | | | | | 3.4 | (-) |
| AM Fungi | 16:1 w5c | 5.0 | | | | | | | | | | | | | | | | | | |
| General | 19:1 (w 8?) Alcohol | 4.9 | | | | | 19:1 (w 8?) Alcohol | 2.8 | | | | 4.4 | (-) | ISO 17_1 G | 0.8 | (-) | | | 7.9 | (-) |
| | 21:1 w3c | 0.5 | | 7.0 | | | 19:2 w6c | 0.3 | | 7.8 | | 9.3 | | 19_0 CYCLO 11-12 2OH | | | | | 4.1 | (-) |
| | ISO 17:1 AT 9 | 1.3 | | 6.9 | | | 20:1 w3c | 0.8 | (-) | | | 4.6 | (-) | 15_1 ISO G | | | | | 4.1 | (-) |
| | ISO 17:1 G | | | 3.8 | (-) | | C25 N Alcohol | 2.7 | | 3.5 | (-) | | | 21_1 w3c | 1.3 | | 7.7 | (-) | 4.9 | |
| | C25 N Alcohol | | | | | 8.4 | ISO 17:1 G | 0.8 | (-) | | | | | 24_1 w3c | 0.9 | (-) | 9.0 | | 7.2 | |
| | Cholesteryl-palmitat | 0.8 | (-) | | | 19.1 | | | | | | | | ISO 17_1 G | 0.2 | (-) | 4.5 | (-) | 10.5 | |
| | 24:1 w3c | 0.8 | (-) | | | 19.1 | | | | | | | | | | | | | | |

## Conclusions

Ecosystem impacts of exotic plant invasion may be attributed to a complex of multiple factors. Invader impacts are determined by their ecological traits as well as the traits of the native vegetation, soil abiotic and biotic factors, climate and plant-soil feedbacks of the native ecosystem (Eviner 2004; Eviner & Hawkes 2008; Wardle et al. 2004). The studies in this dissertation showed that the vegetation type in which exotic annuals invade is important, but that other ecosystem factors associated with soil and climate are stronger drivers of ecosystem resistance and resilience to invasion. In addition, the studies herein challenge a commonly held idea that exotic plant species will have greater impacts on ecosystems if there are greater disparities in traits between native and invading plant species. The chaparral vegetation type differs far more in plant life form, tissue nutrient composition and rooting structure from the invading exotic annuals than did native plant species of the grasslands; yet, chaparral soil was the least impacted by invasion. Coastal sage scrub was intermediate in its response to invasion.

Invaded and restored treatments in grasslands differed in soil microbial community composition, extractable nitrogen concentration, potential nitrogen mineralization and nitrogen immobilization. That soil chemical and biological characteristics changed in response to altered vegetation type shows that grassland soils are not resistant to the impacts of exotic plant invasion, but whether restoration has set these grasslands on a trajectory towards that of native grassland soils cannot be determined because there are no uninvaded native reference grasslands in southern

California (Biswell 1956; Minnich 2008). Restoration by two methods of exotic plant removal, fire and weeding, led to soil characteristics different from invaded treatments suggesting removal of exotics is more important to recovery than the method by which exotics are removed. The short-term weeding experiment showed that removal of exotic annuals led to concentrations of extractable nitrogen, nitrogen cycling rates, and native species establishment more similar to values found in restored plots. Rapid response to restoration activities indicates that grasslands can respond to changes in vegetation and may have the potential for resilience.

Coastal sage scrub soil extractable nitrogen was reduced by invasion, but other chemical pool sizes were unchanged. Microbial biomass and fungal:bacterial ratios (F:B) showed altered levels between invaded and native soils, but this was site and time dependent. Microbial community composition was driven by sampling date (season) more than vegetation type. The greatest impact of invasion into CSS was the introduction of a shallow, dense rooting structure of exotic annuals that reduced heterogeneity of soil nutrients and microbial community composition. Weeding of exotic annuals led to changes in extractable nitrogen, nitrogen cycling and seedling establishment within one year.

In the chaparral, pools of total soil nitrogen and phosphorus were resistant to impacts of invasion in the absence of fire but total soil carbon and extractable nitrogen species were not. Following removal of exotics, even limited re-establishment of native plant species allowed extractable nitrogen to recover to levels similar to native soils indicating resilience of this component of the nitrogen cycle. Exotic annuals also altered

the intensity of chaparral fire which created initial post-fire successional conditions in invaded chaparral that differed (higher concentrations of carbon and nitrogen) from burned chaparral. In addition, presence of exotics post fire slowed recovery of plant species as well as soil characteristics altered by fire.

Meta-analysis of the impacts of exotic plant invasion across the three ecosystem types enabled a comparison of complex responses, and uncovered one pattern that was consistent across all three systems: nitrate concentrations were lower in invaded soils regardless of vegetation type, and restoration via short-term weeding of plots lead to recovery of nitrate concentrations. This indicates that the soils of all three vegetation types were not resistant to impacts of invasion on soil nitrate, but that they are resilient once exotics are removed. Season was a stronger determining factor for total microbial community composition than vegetation type as indicated by the greatest shifts in microbial communities in the grasslands, even though the vegetation of the grasslands differed the least in plant traits from invading species. Seasonal variation of microbial community composition is common in natural soils (Bardgett et al. 1999). However, during peak and senescence periods, chaparral microbial communities were distinct from the microbial communities of other vegetation types. This is likely due to the differences in phenology between these vegetation types such that chaparral would have been in a different growth stage than the other systems at each sampling period.

Both shrubland vegetation types experienced shifts in soil properties likely caused by increased density of fine roots in soils of invaded areas compared to native areas. Native shrublands have more coarse roots and a greater heterogeneity of root distribution

than found in systems dominated by annual grasses and forbs (Kummerow 1989; Kummerow et al. 1978). In the chaparral F:B increased in invaded soils where the denser rooting structure of invasives increased the opportunity for fungal association. Coastal sage scrub soils experienced a loss of heterogeneity of resources and the greatest soil nutrient losses associated with both invasion and restoration of any of the vegetation types. That carbon, nitrogen, C:N and nitrogen mineralization of restored coastal sage scrub was lower than native CSS soils was likely an artifact of the disturbance caused by restoration annually disrupting soil and removing plant biomass (reduced litter inputs). Increased bacteria in restored CSS soils may also be a result of restoration disturbance and likely led to the increase in protozoa in restored coastal sage scrub as protozoa are selective bacterial feeders (Bonkowski et al. 2000). Restored grassland microbial communities were greatly reduced in mass and composition compared to invaded grasslands. A portion of this could be explained by a reduction of fungi and specifically AM fungi due to the loss of annual grass-fungi associations following exotic plant removal. Despite loss of fungal species, PLFA richness increased following restoration, indicating soil microbial community of grasslands had the potential to respond to vegetation changes and may be able to recover after invasion.

Invasion of exotic species is capable of changing the soil chemical and biological characteristics of the systems they invade (Bardgett et al. 1999; Ehrenfeld 2004; Ehrenfeld et al. 2005; Kulmatiski & Beard 2008). Each of the systems studied here experience either a change in soil chemistry, microbial community or both. The degree of change was site and season dependent which agrees with other recent work showing abiotic factors such as climate, soil texture and pH may play a greater role than vegetation in determining soil biological and chemical characteristics (Fierer et al. 2009; Seybold et al. 1999; Ushio et al. 2008). Within-site variation was a stronger driver of soil chemical and biological characteristics than exotic plant invasion, and site species-specific interactions were important in determining impacts of exotic plant invasion for all three vegetation types. It was expected that the impact of invasion would not be equal across these systems and my data supported this prediction. It was unexpected that the ecosystem with the greatest difference in plant species traits from the invading suite of species was least impacted. These results emphasizes that vegetative traits, soil characteristics and climatic factors determine resistance and resilience to invasion (Eviner & Hawkes 2008; Griffiths et al. 2008; Yu & Ehrenfeld 2010) and that the effects of exotic plant invasion on soil properties cannot be predicted by plant traits alone.

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