THESIS

BREAKING UP IS NATURAL:

PLANT LITTER DEGRADATION IN THE SAN LUIS VALLEY

Submitted by

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ABSTRACT

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Nutrient cycling of carbon (C) and nitrogen (N) is critical for maintaining ecosystem processes. In many ecosystems where water availability is not limiting, microbial degradation of plant litter is the dominant process driving nutrient turnover. However, in water-limited regions such as semi-arid systems, photodegradation is likely to become more important to the degradation of vegetation. We attempted to quantify photodegradation across different land uses within the semi-arid San Luis Valley of Colorado. In a 20-week field study, we measured plant litter mass and chemical composition over time under varying degrees of exposure to solar radiation. The study was conducted on managed and unmanaged agroecosystems at three locations, using the dominant vegetation type at each site. At each site litter bags were placed at three positions: above the surface (no contact with soil), on the soil surface (in contact with soil), and below the surface (buried in soil). This arrangement allowed us to assess the key degradation processes associated within each land use. Results showed that, regardless of litter chemistry or land use, litter samples exposed to solar radiation (above the soil) exhibited the greatest nitrogen and lignin mineralization. Unexpectedly, litter total, mass loss due to photodegradation was observed to be greater than that due to microbial degradation at only at one of the sites. Nutrient fluxes due to plant litter degradation associated with photodegradation varied from microbial degradation and can substantially alter ecosystem structure and function. Understanding these degradation processes is crucial for managing agricultural activities and maintaining overall soil health in semi-arid systems.

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CHAPTER 1: INTRODUCTION

1.1. INTRODUCTION

Globally, drylands (semi-arid and arid ecosystems) cover over 40% of terrestrial land surface (Berenstecher 2021) and are important in the global biogeochemical cycling of nutrients, including carbon (C) and nitrogen (N). From an ecological perspective, semi-arid ecosystems are some of the most sensitive to global change drivers (Loarie et al., 2009). Due to the growing extent (Dai 2013) of these drylands throughout the world, and the dependence of a significant part of the human population on them for food, fiber and ecosystem services, it is crucial to understand how they function so that we may assess how they are influenced by global environmental change.

Although there have been numerous successful efforts to understand the key mechanisms that regulate soil biogeochemical cycling (Schimel 1994), there is not sufficient information about semi-arid regions. In semi-arid systems, the processes and rates at which litter degradation of organic materials occurs may not be well understood (Throop & Archer 2009 (Figure 1.1A). This uncertainty is due, in part, to the way models have failed to identify and incorporate non-biological processes of litter degradation across time and space in terrestrial ecosystems. In most cases, litter degradation rates in ecosystems are modeled primarily in terms of litter chemistry and climatic variables—e.g., temperature and precipitation--as these variables are important for determining rates of microbial litter degradation in water limited ecosystems (Esch 2019). Additionally, accounting for land use is important because in semi-arid systems, water availability and soil management practices are known to exert strong controls over degradation processes (Noy-Meir 1973, Nielsen 2015). Stemming from research on the degradation of materials via solar radiation—such as dissolved organic matter (DOM) in water, plastics, paints, wood, paper, and pesticides—the addition of solar radiation degradation as a key pathway in terrestrial ecosystems has gained

increasing interest among scholars over the last two decades. The literature suggests that photodegradation processes may explain the higher rate of litter degradation in semi-arid systems when compared to predictions from ecosystem models (Adair et al. 2017, Parton et al. 2007, Throop & Archer 2007, Brandt 2010, Austin & Vivanco 2006, Gallo 2009, Lin & King 2014, Baker & Allison 2015, Gliksman 2017, Day et al. 2007, Barnes 2012, 2015, 2023).

The interaction of solar radiation with plant litter chemistry has been estimated to increase litter degradation rates by up to 60% as compared to microbial degradation (Austin & Vivanco 2006; Barnes 2012, King et al. 2012, Throop & Archer, 2009, Esch et al. 2019). This process involves the mechanisms of solar-induced breakdown of photoreactive compounds, and photooxidation of chemical bonds, primarily in lignin (Moorhead & Reynolds, 1989) and N (Brandt 2010), increasing the emissions of CO_2 and NOx into the atmosphere. These mechanisms can increase C and N losses from soils due to direct photomineralization or enhance carbon input for more efficient microbial litter degradation via Photofacilitation (Kirschbaum et al. 2011). For example, enhancing lignin degradation could provide greater access to cellulose and hemicellulose by microbes (Austin 2016), increasing overall rates of litter degradation (Austin et al. 2016, Foereid 2010, Esch et al. 2019, Neale 2021).

This study examines the processes of photo- and microbial litter degradation in Colorado's San Luis Valley (SLV). The SLV's high elevation and persistent solar radiation, make it an optimal location to study photodegradation above ground as well as in soils. The study integrates field and laboratory-based methods to examine two litter degradation processes– photodegradation and microbial degradation. These two processes will be compared to determine which is dominant in driving litter degradation and potentially regulating nutrient flux pathways as a function of land uses that are common in the SLV. These land uses are further distinguished by natural water

availability and management strategies —most importantly, irrigation but also cultivation and grazing, which provide different controls on organic matter inputs and soil conditions.

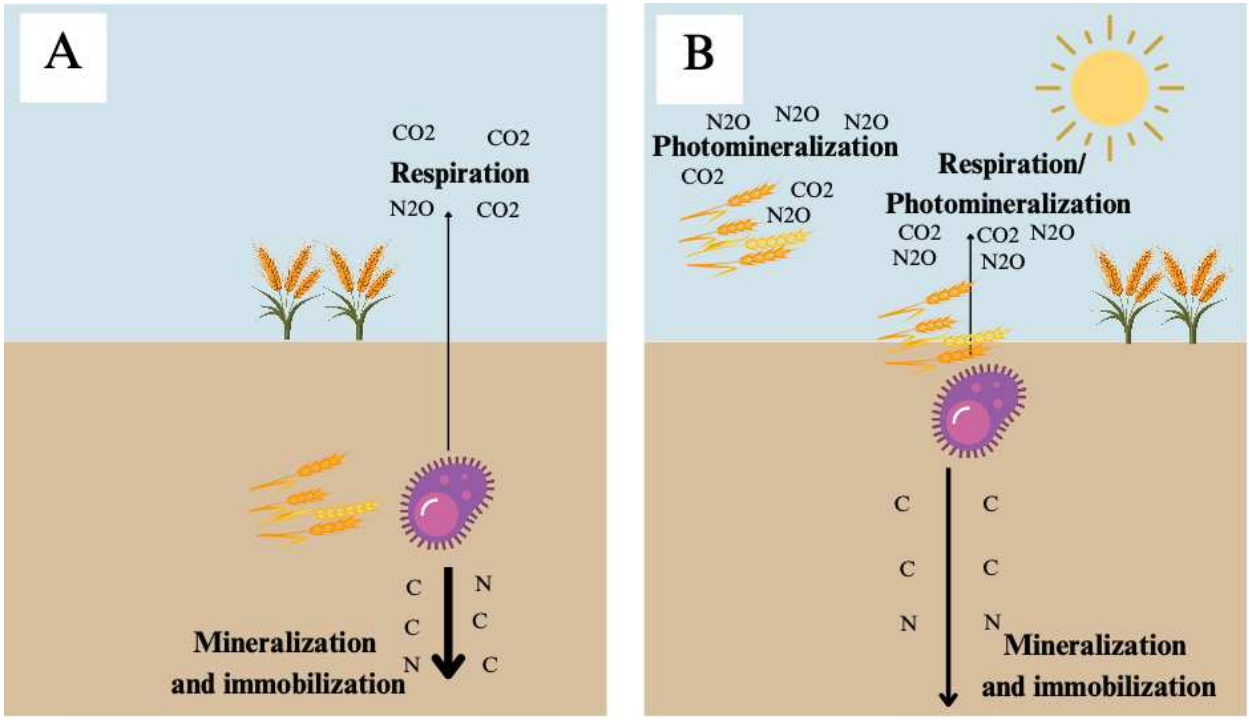

Figure 1.1 Litter degradation processes explored in this study: A) Microbial degradation utilizes microbes to "extract" C and N from litter material in the soil, decreasing C and N. B) Photodegradation includes photomineralization, where C and N are lost to the atmosphere with no return of nutrients to the soil, or limited return when litter samples exposed to both solar radiation and the soil surface respiration.

1.2. LITERATURE REVIEW

Arid and semi-arid regions are a major area for food production, with 45 % of the world's cultivated land located within these dryland regions (Burrell 2020). Climate models suggest that semi-arid and arid systems will experience more frequent, severe, and widespread drought (IPCC,

2022), which could threaten agricultural production. It is therefore critical to understand nutrient turnover via litter degradation in these regions.

In regions where drought is frequent, litter photodegradation processes, in addition to microbial degradation, are critical (Austin & Vivanco 2006). Microbial and photodegradation processes regulate biogeochemical cycles, but the degree to which they do so may be a function of land use and management strategies —defined primarily by water inputs— in addition to litter chemistry (e.g., C:N ratio), and litter placement in relation to the surface (Berg & McClaugherty 2008,Thenevot et al. 2010). By breaking down nutrients in the litter, microbial degradation contributes to physical and chemical properties of soil. Nutrient fluxes in the soil associated with photodegradation can alter ecosystem functions and processes (Brandt 2010, Brandt 2007). Therefore, understanding the relative influence of these degradation processes is significant for agricultural activities and overall soil health.

The availability of water—whether from natural sources or applied irrigation—is a key determinant of microbial degradation of litter (Austin 2011). Water is the limiting factor in nutrient cycling, ecosystem function, and primary productivity (Schwinning 2004). Water content of soils varies regionally with changes in climatic conditions and may control litter N availability, litter C degradation and storage, and plant production (Lauenroth & Bradford 2006).

Soil properties and subsequent ecosystem services are a function of climate, microbiology, and vegetative inputs. These inputs reflect Hans Jenny's state factor approach (Jenny 1941), which relies on five key conditioning variables or state factors—climate, organism, relief, parent material, and time—to characterize soil. Although these conditioning variables are considered independent, the biological, physical, and chemical components within soils are highly interconnected, and the feedback among them can create complex soil patterns. Changes in these soil forming factors can

result in large-scale shifts in litter inputs, chemistry and degradation within nutrient cycling and overall ecosystems.

1.2.1 THE SAN LUIS VALLEY

This study was conducted in the Northern Basin of southern Colorado's SLV between June and November 2023 (Figure 2.1). The SLV is the largest high-elevation valley in the world, spanning approximately 125 miles long by 75 miles wide at an elevation of about 7,600 feet above sea level. This expansive area, comparable in size to New Jersey, is surrounded by the granitic Sangre de Cristo Mountain range to the east and the basaltic San Juan Mountain range to the west.

The SLV's unique geological, hydrological, and ecological characteristics create a diverse habitat for a wide array of plant and animal life. Its climate is semi-arid, characterized by cold winters, moderate summers, and abundant sunshine. The surrounding mountain ranges, with elevations up to 14,000 feet, create a rain shadow effect, resulting in low precipitation in the valley basin, but snowfall at the peaks. Climate data from 1971-2000 shows that the valley receives less than 228 mm of annual precipitation, with most areas receiving only 177 mm. In contrast, the surrounding mountains receive 762-1219 mm annually, serving as the primary water source for the region. The average annual temperature is about 5°C, with extremes ranging from -45°C to 32°C.

Agriculture is central to the SLV's economy, especially the growing of potatoes, alfalfa, barley, and cattle grazing. However, the short growing season of 90-120 days limits crop variety. Additionally, human activities, particularly irrigated agriculture, have significantly altered the SLV's hydrology. Organic materials stored in soil can play an important role in infiltration and storage of water. Thus, understanding litter degradation processes in this semi-arid region is crucial for the SLV's economic system, and both human and nonhuman ecologies (Ahlström 2015, Brandt

2007, Esch er. al. 2019), microbial activity, and nutrient dynamics (Allison 2013). The SLV provides both challenges and opportunities for sustainable agriculture, hydrology, and environmental understanding that make it an enticing area for interdisciplinary research on variations in litter degradation processes. Additionally, this study of litter degradation processes, influenced by changing environmental factors, offers insights into soil health, nutrient turnover, and ecosystem resilience more generally. Such insights can contribute significantly to updating and integrating frameworks for controlling crop residue degradation in agroecosystems.

1.3. GOALS, QUESTIONS, OBJECTIVES, HYPOTHESIS.

The research presented in the following chapters highlights the influence of photodegradation, relative to microbial litter degradation, on plant litter degradation across land uses in the SLV.

Research questions:

1) What is the impact of litter chemistry on the amount of litter degradation?
2) Do soil properties regulate the difference between microbial degradation and photodegradation?
3) Do photodegradation processes enhance or diminish the effects of biological degradation of organic materials?

Objectives:

1) Characterize the physical, chemical and biological properties of soils within the study area as a function of land use.
2) Determine the litter chemistries at the study sites, the amount of mass loss, and the regulation of mass loss by initial litter chemistries as a function of land use and position.

3) Assess relationships between soil properties (the physical, chemical and biological) and microbial litter degradation by land use.

Specific hypotheses for the study are:

1) Soil properties as a function of land use regulate the diversity and composition of microbial communities, and thus the microbial degradation.
2) Lignin will be the most photoreactive chemical fraction in litter, therefore the greater concentration of lignin in a litter sample exposed to solar radiation the greater mass loss—a positive correlation.
3) Litter mass losses via solar radiation will be greater than those due to microbial degradation.

1.4. OUTLINE OF THESIS

This chapter introduced the project, including a review of prior related research, statement of research questions and hypotheses that together provide the necessary background for the remaining chapters. Chapter 2 details the methods and experimental design used in the study, which includes both an analysis of litter degradation processes and land use features—such as soil properties and microbial communities. Chapter 3 presents the results of the analysis, covering the soils, their microbiomes, and then litter degradation. Chapter 4 discusses these results in terms of the study's hypotheses Chapter 5 revisits the research questions raised in Chapter 1. This conclusion relates the study's results to the challenges of agricultural production, grazing and other activities that continue to be important to the socio-economy of the SLV in a changing climate.

CHAPTER 2: EXPERIMENTAL DESIGN AND METHODS

2.1. SOILS AND LAND USE IN THE SAN LUIS VALLEY

The soils of the San Luis Valley (SLV) are characteristic of high-elevation, water-limited ecosystems, exhibiting properties that reflect the valley's unique climatic and geological conditions. These soils are typically sandy to loamy, with varying amounts of clay, affecting their water-holding capacity and permeability, making them prone to both rapid drainage and erosion. Due to the arid climate and limited vegetation, the organic matter (OM) content is relatively low, impacting the soil's fertility and its ability to retain moisture and nutrients. These soils are often alkaline, with pH levels and saline conditions influencing the availability of certain nutrients to plants.

Hydrologically, the soil has limited water holding capacity (WHC), a significant factor in an environment where precipitation is scarce, and evapotranspiration (ET) rates are high. They are hydrologically complex, presenting challenges in maintaining adequate moisture levels for crops. The low natural precipitation necessitates irrigation for agriculture in the SLV, but the efficiency of irrigation can be hampered by the soil's permeability and the risk of leaching nutrients away from the root zone.

The high elevation (7,600 feet) of the SLV contributes to significant temperature variations, affecting soil processes such as microbial activity and nutrient cycling, and results in a short growing season that limits the types of crops that can be grown and affects the timing and methods

of soil management practices. Ecologically and agriculturally, the combination of low organic matter, sandy texture, and limited vegetation cover makes the soils susceptible to erosion—via aeolian processes, particularly under intensive agricultural management practices and native lands. Additionally, the sandy texture limits their WHC and can increase their salinity and alkalinity. Conservation practices such as the use of cover crops and reduced tillage are often employed to mitigate erosion and improve soil quality, maintaining soil structure, reducing runoff, and increasing organic matter content.

Non-irrigated sites in the SLV reflect natural changes in climate over time, with diverse vegetation types that include grasses, hardwood shrubs, and succulents. These native sites, their soils, microbiomes, and vegetation reflect the variability within this physiographic region within the SLV. They are utilized for this research as benchmarks for evaluating changes due to land use type. Salt-tolerant halophytes are prevalent in the east, while the western portion of the valley is generally less affected by salt. Cultivation and irrigated management strategies are typically necessary for agriculture in the SLV, as the soils and aquifer provide opportunities for both surface and sub-surface water applications. Soils in the irrigated pastures of the SLV, in combination with water sources such as creeks, rivers, and proximity to the water table, support saline-tolerant native plants (greasewood, grasses, etc.) and other grass species (Baltic rush, alkali sacaton, etc.). This study evaluates non-irrigated soils as a benchmark and compares them to irrigated soils to understand the effects of land management strategies on soil properties of differing land uses (native, cultivated, and pastures).

2.2. STATE FACTOR APPROACH

Jenny's state factor approach provides the framework for the experimental design. This approach, which conceptualizes soil ecosystems as a function of state factors—climate, organisms, parent material, relief, time, and humans—has been instrumental in understanding soil formation processes. These variables are largely independent of each other at the spatial and temporal scales typically considered in studies of soil development in terrestrial ecosystems. However, the biological, physical, and chemical components within ecosystems are highly interrelated, and the feedback among these components can create complex soil patterns. Attempts to integrate soils into global and regional simulation models emphasize the temporal and spatial complexities associated with these systems (Schimel 1994). What differentiates soils within ecosystems is the extent to which soil-forming processes are regulated by the driving variables of climate, organisms, parent material, relief, and time (Jenny, 1941).

The state factor model has been effectively used to assess key processes that influence soil organic carbon (SOC) litter degradation in extreme environments. By isolating and manipulating individual state factors while keeping others constant, researchers can identify and develop natural experiments that contribute to comparative ecosystem research. For example, chrono sequences have been used to explore how ecosystems evolve over time, including how forest soils develop following human-caused disturbances and within urban ecosystems (Yesilonis 2016, Setälä 2016).

2.3. EXPERIMENTAL DESIGN

The field sites in this research were selected utilizing local state factors—e.g., climate, organisms, parent material, relief, time, and humans—in the northern basin of the SLV, the region north of the Rio Grande River and south of Saguache (Figure 2.1). The main variable across all sites included in the study is land use (identified, in part, by associated land management strategies)

which affects vegetation and microbial communities. Management differences—e.g., irrigation—contributes to variation in microbial communities via diversification of speciation and selection (Vellend 2010), as well as litter types, and soil properties. Differences in all other state factors are minimized (Table 2.1).

The process of site selection required field visits, careful analysis of property ownership maps, and discussions with property owners. Six sites (Figure 2.1, Figure 2.2) were selected for the study to reflect dominant land use type and ensure adequate variation in litter type and soils within the SLV. Three land use types for the region were identified: native rangeland, cultivated, and pastures that included an irrigated and non-irrigated treatment (Figure 2.2). The sites were chosen to be west and east of the valley's center because it positions them in proximity to differing parent material—reflective of soils across the valley. Within the six sites, both soil and plant material were collected for analysis. This collection process included soil cores of surface soil horizons (~8 cm), and plant material. Coring soil provided an opportunity to analyze and assess the impact of varying land uses on soil to a depth of 100 cm. Litter samples derived from collected plant materials were used to assess litter degradation. Litter samples were placed in mesh screen fiberglass bags (Figure 2.3A) and placed in positions to control the process of litter degradation. A three-tier system was implemented to vary exposure to solar radiation. One litter sample was above the soil surface (abiotic position), one was on the land in contact with the soil surface (surface position), and one was buried in the surface soil horizon (biotic position) to about 10 cm (Figure 2.3B). This approach incorporated methods and procedures commonly used in litter degradation studies, including Austin & Vivanco (2006), Brandt (2010), Day et al. (2007), and Throop & Archer (2009). While these studies emphasized distinct aspects of litter degradation as appropriate to the authors' specific investigative foci, the design of this study integrated the

aspects—i.e., site selection, litter composition, bag design and placement, collection schedule, and analyses—that were best suited to this project.

Table 2.1. Soil forming state factors of studied sites. The climate (MAP/MAT 7 cm /5°C), relief (<2%), parent material (alluvium mostly), and time were kept constant. The land use and its management, as well as plant litter quality/type were the variables in question across the sites.

Site	Age	Land Use	Management	Dominant Plant Species
West Native	Holocene	Native	Non-Irrigated	Rabbitbrush (*Chrysothaminis nauseosus*)
West Cultivated	> 60 years	Cultivated	Irrigated	Wheat (*Triticum*)
East Native	Holocene	Native	Non-Irrigated	Greasewood (*Sarcobatus vermiculatus*
East Cultivated	> 100 years	Native	Irrigated	Barley (*Hordeum vulgare*)
Pasture Native	Holocene	Pasture	Non-Irrigated	Alkali Sacaton (*Sporobolus airoides*)
Pasture Irrigated	> 100 years	Pasture	Irrigated	Baltic Rush (*Juncus Balticus*)

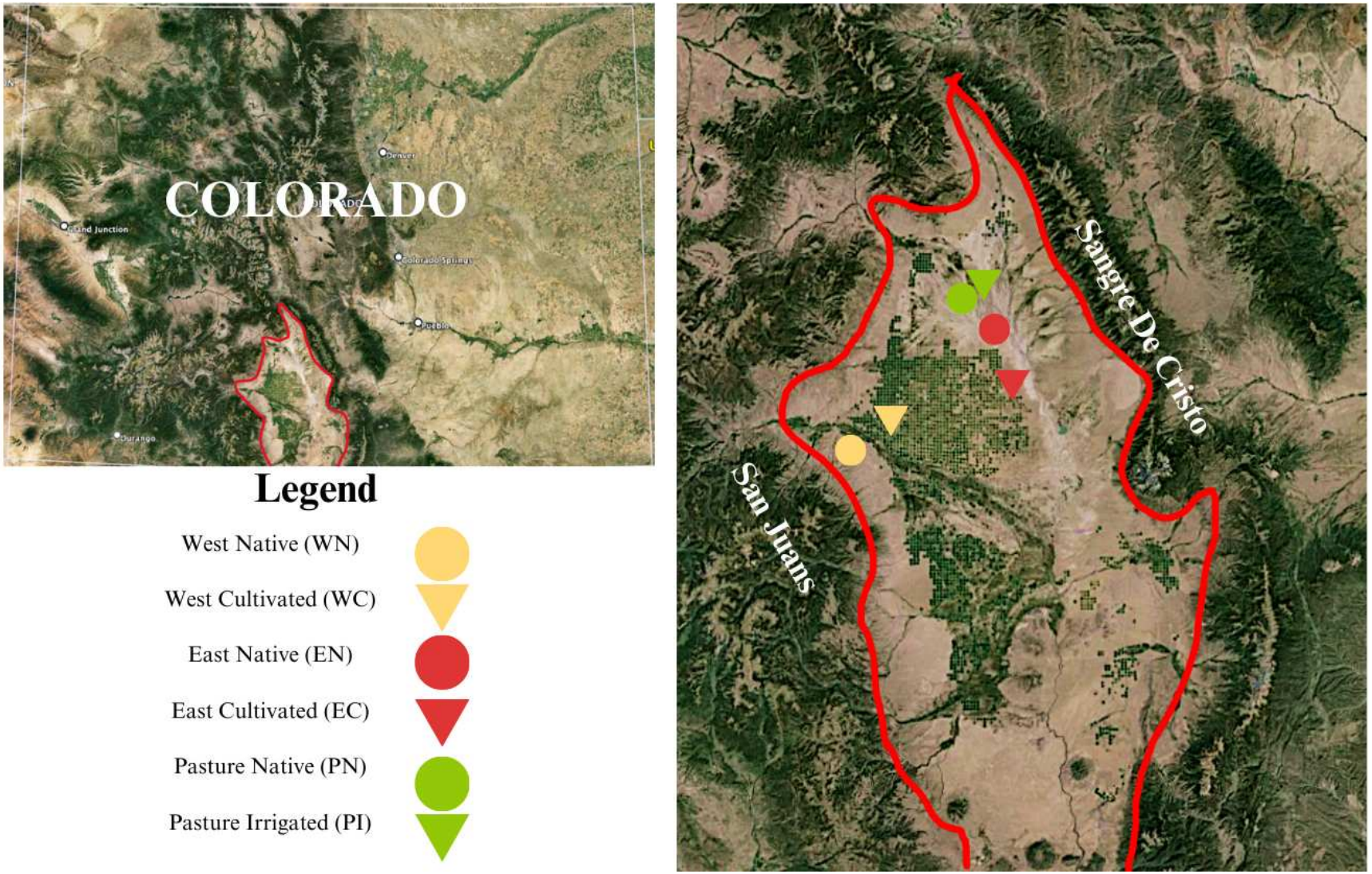

Figure 2.1. Site map of San Luis Valley (SLV) with points on regional map for sites and land use type. Colors per each site represent, location (color) and management (fill), where non-irrigated managements are : native; and irrigated : cultivated and irrigated;

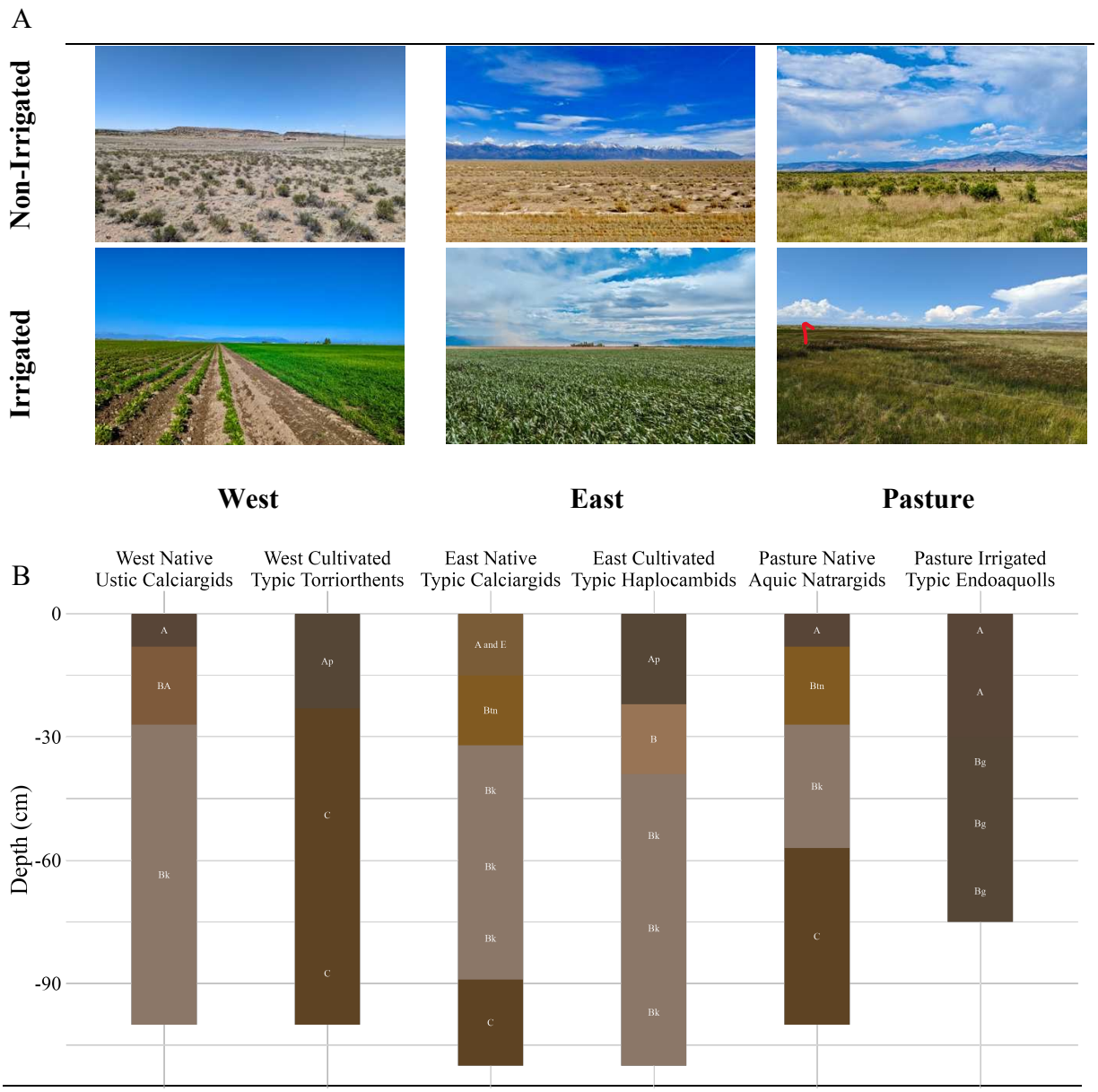

Figure 2.2. A) The criteria used to select the sites based on the location (West, East, Pasture) and management (irrigated and non-management), composing three land uses (Native, Cultivated, Pasture). B) Soil profiles for each site, to provide a visual of what a soil profile looks like as well as a visual of differences among each land use discussed in chapter 3.

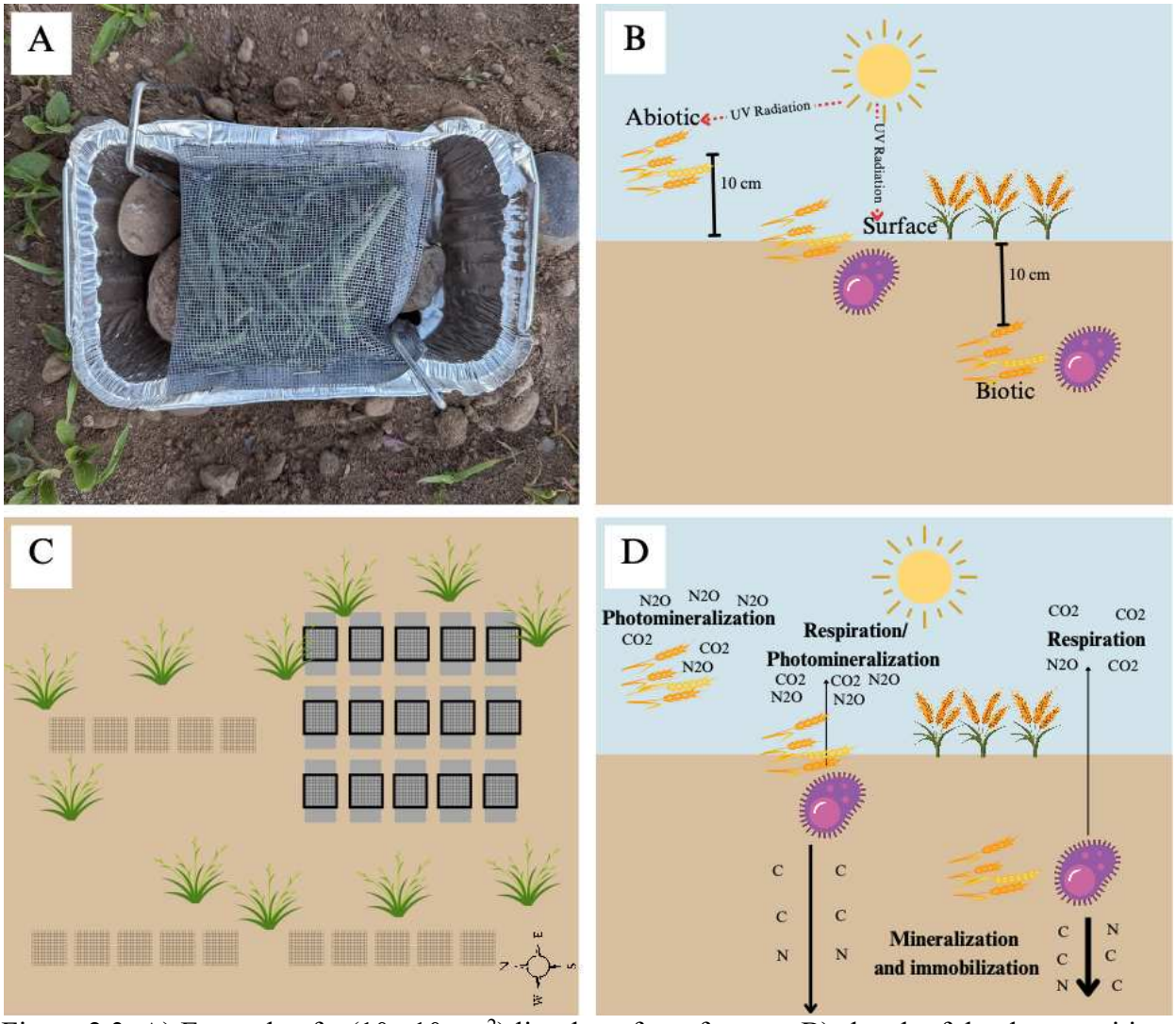

Figure 2.3. A) Example of a (10 x10 cm^2) litterbag, for reference. B) sketch of the three positions of litter placement at each site. C) layout at each site, buried litter bags were placed in front (east) of the surface litterbags. D) The three positions/processes of litter degradation and their potential effects (bold) on nutrient (C and N) turnover. Photomineralization: C and N mineralized by solar radiation, resulting in mineralized CO_2 and N_2O respectively. Microbial immobilization and mineralization: pathways of C and N in the soil. Microbial respiration from the microbial consumption of OM and emissions of CO_2. The pathway of surface litter can result in respiration, photomineralization, or mineralization and immobilization of C and N.

2.4. METHODS

2.4.1 FIELD METHODS

Soil profile samples were collected with an auger in August 2023 between 0-175 cm depths. Surface samples were collected at 8 cm to characterize the niches for microbial communities

(Berenstecher et al. 2021). Pedons were described using USDA genetic horizons and air-dried until further analysis. Additionally, eighteen surface soil samples—3 replicates at each field site—were collected in November 2023.

The dominant litter type was identified at each site and sampled above the roots. Samples were then placed in a cool storage for seven days to obtain three days of consistent weight before constructing litter bags (Throop & Archer 2007). The litter bags were constructed following the methods from Brandt (2010), using 1mm fiberglass mesh (10 x 10 cm) filled with 3 g of litter (Figure 2.3 A).

Three replicate litter bags were placed at every position (abiotic, surface, and biotic) (Lin 2018) at each site in June 2023. Litter bags (Figure 2.3A) were buried (biotic), held to the surface with two garden staples (surface), or stapled on tinfoil containers weighed down with rocks to be above the surface (abiotic) (Figure 2.3 B, Figure 2.3 C). Nine litter bags (three replicates for each position) were collected from each site over 20 weeks. Collections were completed every four weeks to maintain consistency over this short period (Li 2017), given that most mass loss occurs over the first three months (Throop 2018). Collected litter bags were placed in paper bags for transport to the lab. In the lab, litter was removed from the bags, placed in an oven to dry at 55°C, and weighed to a consistent weight (36-48 hours). The litter was then kept in paper bags in a cool, dry, dark space until chemical analysis in March 2024.

2.4.2 LAB AND ANALYTICAL METHODS

Soil Analyses

Soil samples were air-dried, sieved (< 2mm) and prepared for physical and chemical analyses (Table 2.2). Soil particle size distribution was determined by a 24-hour hydrometer method (Gavlak et al. 2005). Soil electrical conductivity (SEC) was determined by the soil paste extraction method (U.S. Salinity laboratory staff, 1954). pH was determined using the 1:1 saturated

paste method. The soil Calcium Carbonate Equivalent (CCE) was measured using a gravimetric method (Leopert & Suarez 1996).

Total nitrogen (N) and total carbon (C) in the soils were measured using an elemental analyzer. Inorganic carbon was determined by the pressure transducer method (Sherrod 2002). Inorganic nitrogen (NH^+_4 and NO^-_3) was determined using the KCl extraction method (Keeney & Nelson 1982). Potential Mineralizable Nitrogen (PMN) was determined via a 28-day anaerobic PMN test, where NH^+_4 and NO^-_3 from soil samples were measured via KCl extraction and summed every seven days (Keeney & Nelson 1982, Mulvaney 1996).

Table 2.2. Soil Physical, chemical, and biological properties assessed per each soil surface horizon. Asterisk (*) denotes analysis on soil profile horizons as well.

Physical	**Chemical**	**Biological**
Particle Size Analysis (%Sand, %Silt, and %Clay*)	pH*	Total Organic C
	Electrical conductivity (SEC)	Total N
Structure*		
	Calcium carbonate equivalent (CCE)*	16S rRNA microbiome
Color*		
		Potential Mineralizable N (PMN)
	Inorganic C	
	Inorganic N (NO^-_3 and NH^+_4)	

Soil samples from the surface horizons collected in November for microbial analysis and were processed by the CU Boulder Fierer Lab. Typically, there are approximately 100–9000 individual prokaryotic taxa (bacteria and archaea; operationally referred to as amplicon sequence variants (ASVs)) per cubic centimeter of soil (Schloss 2021). Using the 16S rRNA analysis method, RNA sequences in soil can be translated to ASVs, which serve as microbial approximations of species (Callahan 2016). Due to the novel nature of ASVs, taxonomic assignments beyond the phylum level are limited (Overmann et al., 2017).

The method for extracting ASVs and quantifying taxonomy at each site involved five steps, following soil sampling and filtering (Figure 2.4): (1) DNA was extracted from each sample using the DNeasy PowerSoil Pro kit from Qiagen, including one extraction blank processed alongside the samples. (2) PCR was performed in duplicate using Platinum II Hot Start Master Mix from ThermoFisher, with no template controls processed alongside the samples. For 16S, the 515F/806R primers (V4 amplification) with barcodes on 515F, as described by the Earth Microbiome Project, were used. This involved 35 cycles of PCR. After confirming amplification via gel electrophoresis, the amplicons were cleaned and normalized using the SequalPrep Normalization Kit from ThermoFisher. (3) Sequencing was performed on a MiSeq instrument using a v2 300-cycle kit (2x150) with a 15% phiX spike. (4) Data was demultiplexed using the idemp program, and quality filtering and processing were done using the DADA2 pipeline. (5) Taxonomy was assigned using the Silva database v138.1 and was subdivided down to the species level where available.

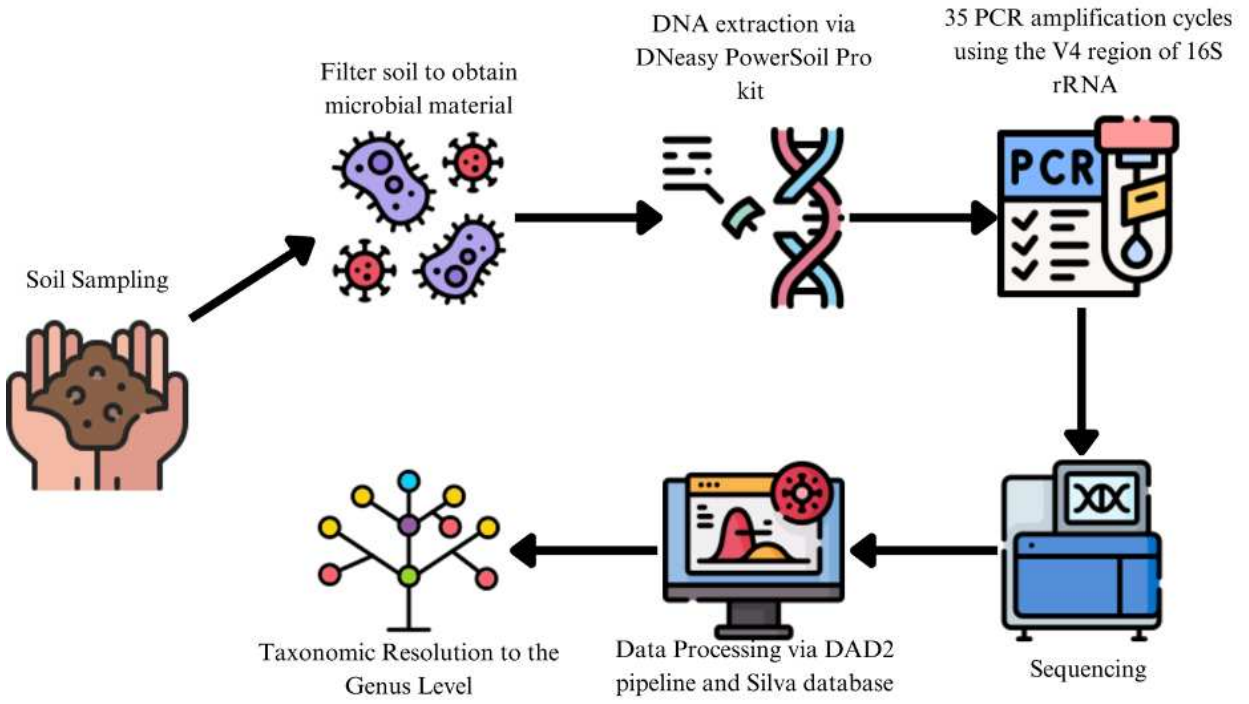

Figure 2.4. Workflow for microbial analysis via 16S rRNA sequencing to obtain amplicon sequence variants (ASVs), taxonomic ꞉ IDs꞉ for each taxon within each microbiome. The process involved the following. 1. Soil was collected in the field and transported. 2. Filter soil for contaminants, 3. DNA extraction from each sample, 4. 35 cycles of PCR, performed in duplicate, with no template controls. After, the ASVs were cleaned and normalized, 5. Sequencing was then completed on a MiSeq instrument, 6. Data was demultiplexed, filtered, and processed with the DADA2 pipeline. 7. Taxonomy was assigned using the Silva database v138.1.

Plant Litter

Subsamples of litter material were dried and ground for chemical analysis. Litter was mechanically ground in and passed through a 1 mm mesh. Total carbon (C) and nitrogen (N) in the litter were measured with an elemental analyzer (Brandt 2010, Austin & Vivanco 2006).

The carbon fractions of plant cell walls (lignin and cellulose) were determined using an acid detergent fiber (ADF) and acid detergent lignin (ADL) analysis (Van Soest et al., 1967, 1980) (Figure 2.5). This standard procedure among plant chemical analysis studies included a multi-step process where 0.45 - 0.50 g of ground litter was placed in F57 Filter Bags for sequential digestion of ADF and ADL via an ANKOM fiber analyzer (ANKOM Technology, Macedon, NY). Neutral Detergent Fiber (NDF) was also measured but not recorded for all samples due to limited litter

remaining in several samples. ADF measured cellulose and lignin concentrations, ADL only measures lignin concentration, and NDF captures cellulose, lignin, and hemicellulose concentrations.

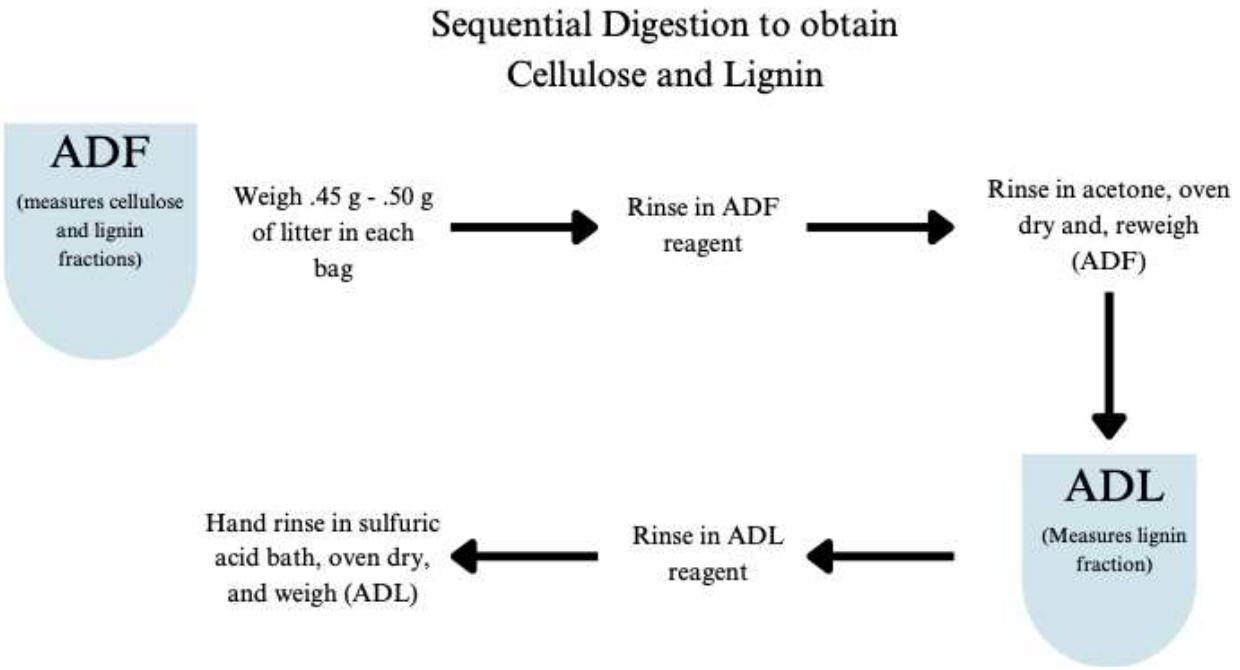

Figure 2.5: Sequential digestion method (Van Soest 1967, 1980) to determine ADF and ADL (cellulose and lignin concentrations) in each litter sample. Litter is placed in the Ankom 57 acid resistant bags, rinsed in an acid-based detergent, dried and reweighed for cellulose and lignin concentrations. ADL utilizes the same litter and Ankom 57 bag after the ADF processing. It is further rinsed in an acid-based reagent, hand rinsed in sulfuric acid, dried, weighed, and ashed to determine the lignin concentration, ADF-ADL = cellulose concentration (%). Hemicellulose concentration is not included in this analysis due to low quantities of mass in the litter samples.

2.5. STATISTICAL ANALYSIS

2.5.1 SOILS

Pearson correlations were calculated with other soil properties, litter chemistry, rates of decay, and microbial community diversities. Within microbiome data, the soil variables were incorporated into the microbial analysis. Calculations were analyzed in R (v. 4.3.1) (R Core Team 2017).

2.5.2 MICROBIAL CHARACTERIZATION

The microbial data was analyzed in R (v. 4.3.1) (R Core Team 2017) using the phyloseq, vegan, and envifit packages. Initially, the data was filtered to remove zero-count amplicon sequencing variants (ASVs), as well as chloroplast and mitochondrial sequences (which are not bacterial). Any ASV with an abundance of less than 2% was excluded in the data set. Rarefaction was then performed using an internal function of phyloseq, standardizing to the lowest count among all samples. Statistical analysis included alpha diversity, beta diversity, and taxonomic analysis.

Alpha diversity, which measures the richness (or number of different taxa in a sample) and diversity (the number and abundance of species and relationships among them) of taxa within each sample, was assessed using the richness function in the phyloseq package and the Shannon, Simpson, and Chao1 alpha indices. Analysis of variance (ANOVA) and Tukey's Honest Significant Difference (HSD) tests were employed to compare diversities across sites and into variables of soil, litter, and sites. Further, the alpha diversities (Shannon and Simpson indexes, which also measure the distributional evenness of taxa) were used in correlational analysis with site variables.

Beta diversity analysis evaluated differences in taxa composition between sites. Permutational multivariate analysis of variance (PERMANOVA), via the Adonis function, was performed using the bray-Curtis distance to determine the effect of soil and litter variables on beta diversity distances. Additionally, non-metric multidimensional scaling (NMDS) was used to visualize patterns from PERMANOVA between sites using ASVs in the microbiome data.

Compositional analysis at the phylum level provided an overview of soil microbial communities. ANOVA and Tukey HSD were used to assess where and what differences existed between Sites on the phylum level.

2.5.3 PLANT LITTER

Pearson correlations were calculated for litter mass loss, litter chemistries, soil properties, and microbial alpha diversities for all sites. The data collected and analyzed included: initial litter chemistry (cellulose, lignin, N, and C) concentrations (%), mass loss, and the percent of initial litter chemical component remaining. For mass loss, the percent remaining was used:

$$\frac{Mass_t}{Mass_i} \times 100$$

where M_t is the mass at any given time point and M_i is the mass at initial time point per each litter sample. Additionally, the chemical concentrations, obtained from ADL and ADF laboratory analysis were used in conjunction with the mass at time (t) to obtain the mass of the chemical component over time, useful in assessing nutrient release (mineralization/losses and immobilization/enrichments):

$$\frac{(Mass_t)(C_t)}{(Mass_i)(C_i)} \times 100$$

where the C_t and C_i are the concentrations of chemical fractions (%) at time t and the initial concentration. All calculations were analyzed in R (v. 4.3.1, R Core Team 2017) via ggplot functions.

CHAPTER 3: RESULTS

This study compared irrigated and non-irrigated treatments across three dominant land uses of the region (native rangeland, cultivated farmland, and managed pastures) at three geographical locations in the SLV (Fig 2.1). The results below provide a basis for the discussion in Chapter 4 and conclusions that follow in Chapter 5.

3.1 SOILS

Determination of soil properties between paired sites provides an understanding of the variability among soils based on land use. Across all sites, the soil textural composition was predominantly sand (>75%) with modest increases in clay content of the surface A horizons at the WN and PN sites (12-17%) (Table 3.1). Additionally, nearly all soil horizons for the eastern profiles were sandier than the western profiles. Land use did not create differences in the soil texture through the profiles. The variations in soil pH values within all six soil profiles (7.2-9.0) are relatively similar, however, pH varied with location. The EN, EC and pasture sites were generally higher than WN and WC sites, (Table 3.1).

Soil on the western side of the valley (WN and WC) were weakly developed in their morphology, with few variations in the surface A horizons. Additionally, the Soil Electrical Conductivity (SEC) (.2-.4 dS/M), pH (7-8.5), and CCE (4-6%) were similar within each profile and with depth—except for an increase to 15% CCE in the WN Bk horizon. The most variation in surface soil horizons between the WN and WC sites was observed in NH^{+}_{4} content (Table 3.1) measurements; three times the amount of NH^{+}_{4} was measured at WN (38 mg/kg-soil v 13 mg/kg-soil) compared to WC. The PMN—which showed some mineralization potential (Figure 3.1, Table

A3.1), and measurements for other surface chemical and physical properties for both western sites were similar (Table 3.1).

Table 3.1. Soil profiles. Selected chemical and physical properties of horizons. TOC, TN, NO^{-}_{3}, and NH^{+}_{4} only analyzed on surface horizons. Replicated samples for pH, Soil Electrical Conductivity (SEC), and CCE (n=3). Particle Size Distribution (PSD).

Site	Depth (cm)	Horizon	pH	SEC (dS/M)	CCE (%)	Sand (%)	Silt (%)	Clay (%)	PSD	TOC (%)	TN %	NH^{+}_{4} %	C:N
West Native	0-8	A	7.03	0.28	4	70	17.5	12.5	sl	1.09	.11	37.5	9.0
	8-27	BA	7.98	0.2	5	65	15	20	scl	—	—	—	—
	27-100	Bk	8.54	0.24	15	62.5	17.5	20	scl	—	—	—	—
West Cult.	0-23	Ap	8.08	0.35	5	72.5	17.5	10	sl	0.81	.09	13	9.0
	23-75	C	8.08	0.36	5	75	10	15	sl	—	—	—	—
	75 +	C	8.08	0.01	1	77.5	7.5	15	sl	—	—	—	—
East Native	0-15	A	8.98	3.1	6	90	5	5	s	0.05	.03	23	1.67
	15-32	Bt	9.5	3.3	7	77.5	7.5	15	sl	—	—	—	—
	32-54	Btk	9.8	1.51	15	62.5	7.5	30	scl	—	—	—	—
	54-69	Bk	9.72	2.45	8	72.5	10	17.5	sl	—	—	—	—
	69-89	Bk	9.68	2.7	7	77.5	5	17.5	sl	—	—	—	—
	89-105	C	9.64	1.75	8	85	2.5	12.5	ls	—	—	—	—
East Cult.	0-22	Ap	8.87	0.32	7	80	10	10	sl	0.83	.12	7.5	6.92
	22-39	B	8.78	0.73	7	77.5	10	12.5	sl	—	—	—	—
	39-69	Bk	9.22	0.28	6	87.5	2.5	10	ls	—	—	—	—
	69-84	Bk	9.19	0.39	5	90	5	5	s	—	—	—	—
	84-110	Bk	9.11	0.52	5	92.5	2.5	5	s	—	—	—	—
Pasture Native	0-8	A	8.06	7.49	6	70.0	12.5	17.5	sl	5.36	.48	10.5	11.2
	8-27	Bt	8.45	7.32	6	72.5	10	17.5	sl	—	—	—	—
	27-57	Bk	8.83	5.9	5	72.5	10	17.5	sl	—	—	—	—
	57-100	C	8.95	3.03	5	72.5	12.5	15	sl	—	—	—	—
Pasture Irrigated	0-8	A	8.04	4.18	5	77.5	12.5	10	sl	14.6	1.15	28	12.9
	8-30	A	8.24	4.04	6	75	12.5	12.5	sl	—	—	—	—
	30-42	Bg	8.25	3.23	9	72.5	15	12.5	sl	—	—	—	—
	42-60	Bg	8.32	2.52	5	77.5	10	12.5	sl	—	—	—	—
	60-75	Bg	8.22	2.12	5	75	5	20	scl	—	—	—	—

Similar to the western soil profiles, eastern (EN and EC) soils demonstrated little variation in their soil properties in terms of CCE (5-7%) and pH (8-9.5), but SEC varied (3-5 dS/M at EN versus .2-.3 dS/M at EC) (Table 3.1). The EN surface horizon soils were typical of native, non-irrigated soils in the SLV: lower soil OC (.05% vs .83%) and soil N (.03% vs .12%), and greater NH^{+}_{4} (23% vs 7.5%) than EC (Table 3.1). Irrigation and biomass input likely accounts for the stronger development of an Ap horizon at EC. Additionally, the PMN study indicates only N immobilization was detected for the EN soil samples, while the EC soil samples indicated a N mineralization peak (max 2.5 mg/kg) similar to that of the western sites (Figure 3.1, Table A3.1).

The pasture site's soil profiles had higher clay content throughout (Table 3.1). At both pasture sites their SECs were considered saline (>4 dS/m) in the surface horizon soil with PN being more saline than (7-8 dS/M vs 4- dS/M) and with depth, the SEC values decreased (Table 3.1). There were continued variations in the surface horizon chemistries, where PI had greater soil OC (14.6% vs 5.36%), soil N (1.15% vs .48%), and NH^{+}_{4} (28 mg/kg-soil vs 10.5 mg/kg-soil) than PN. Although both soil surface horizons saw greater PMN values than the other sites, the mineralization was greater in the PI than in the PN soil sample and reached peak mineralization (15 mg/kg) (Figure 3.1, Table A3.1).

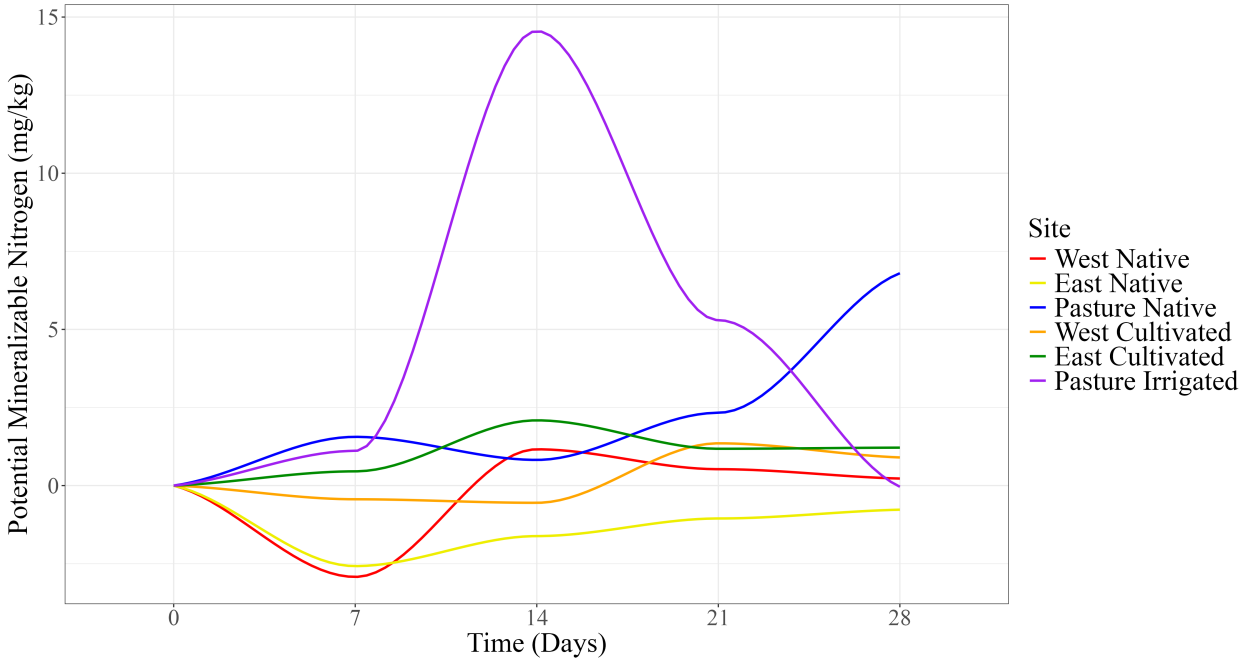

Figure 3.1, Table A3.1. Potential Mineralizable Nitrogen (PMN) over 28 days (4 weeks). For each sampling date (7, 14, 21, and 28 days) the amount of NO^-_3 and NH^+_4 in the anaerobically incubated soil was analyzed via KCl extraction, and the sum of the two inorganic N values (NO^-_3 and NH^+_4) was the PMN at that time. Values below 0 are indicative of immobilization, as seen in EN and the first 14 days of WN.

3.2 CHARACTERIZING THE MICROBIAL COMMUNITIES

Before statistical filtering and normalization of the processed microbial data from the six soils, there were 116, 284 counts of sequences across all ASVs (amplicon sequence variants), an ID for microbial taxa. The microbial communities at the native and pasture sites had the highest total counts of ASVs (6-10k). There were 42 identified phyla—including an "NA" group. Within these phyla, the dominant 10 phyla across all sites in the research accounted for 95% of the phyla within each site (Table A3.2), including phyla that are commonly included as dominant in ecological research globally (Delgado- Baquerizo et al. 2018).

3.2.1 ALPHA DIVERSITY

There are three measures of alpha diversity in microbial studies. First, species counts are measured according to the Chao1 index, which identifies the richness of all species observed for

each ASV. The Shannon and Simpson indexes are alternative ways to measure species in a community by considering the richness and variety of species in the community. The Shannon index identifies all species and includes the low ASV counts, while the Simpson index is a better indicator of dominant ASVs across sampled microbiomes.

The results of the microbial analysis according to sites and location—west, east, and pastures—indicated that the EN and pasture microbial communities held the greatest richness, evenness, and diversity across all sites (Figure 3.2). The Shannon index was highest at the EN site, indicative of a rich and evenly distributed microbial community. Then, contrary to initial expectations that non-irrigated—native—microbial communities would exhibit the greatest diversity and be similar due to similar land use, the microbial community at the WN site had the lowest richness, evenness, and diversity—suggesting that it was less diverse in terms of featuring fewer taxa. As a result, the native sites demonstrated a high significant difference between them ($p < .05$, Table A3.3). Then, although the cultivated land uses varied by location, they displayed no significant differences between them. Alternatively, the EN and EC microbial communities demonstrated significant differences ($P < .05$) across all measures of alpha diversity, while WN and WC did not (Table A3.3). Additionally, the EN and WC microbial communities were significantly different, and the WN microbial community differed significantly from both pasture microbial communities according to the Simpson index ($p < .05$) (Table A3.3). The pastures shared higher richness and diversity values than cultivated sites, as well as no significant differences between them.

Across all sites, the observed soil SEC could possibly account for alpha diversities patterns among the sites (Table A3.4). This finding suggests that salinity and microbial diversity are positively associated ($R^2 = .75$, Table A3.5).

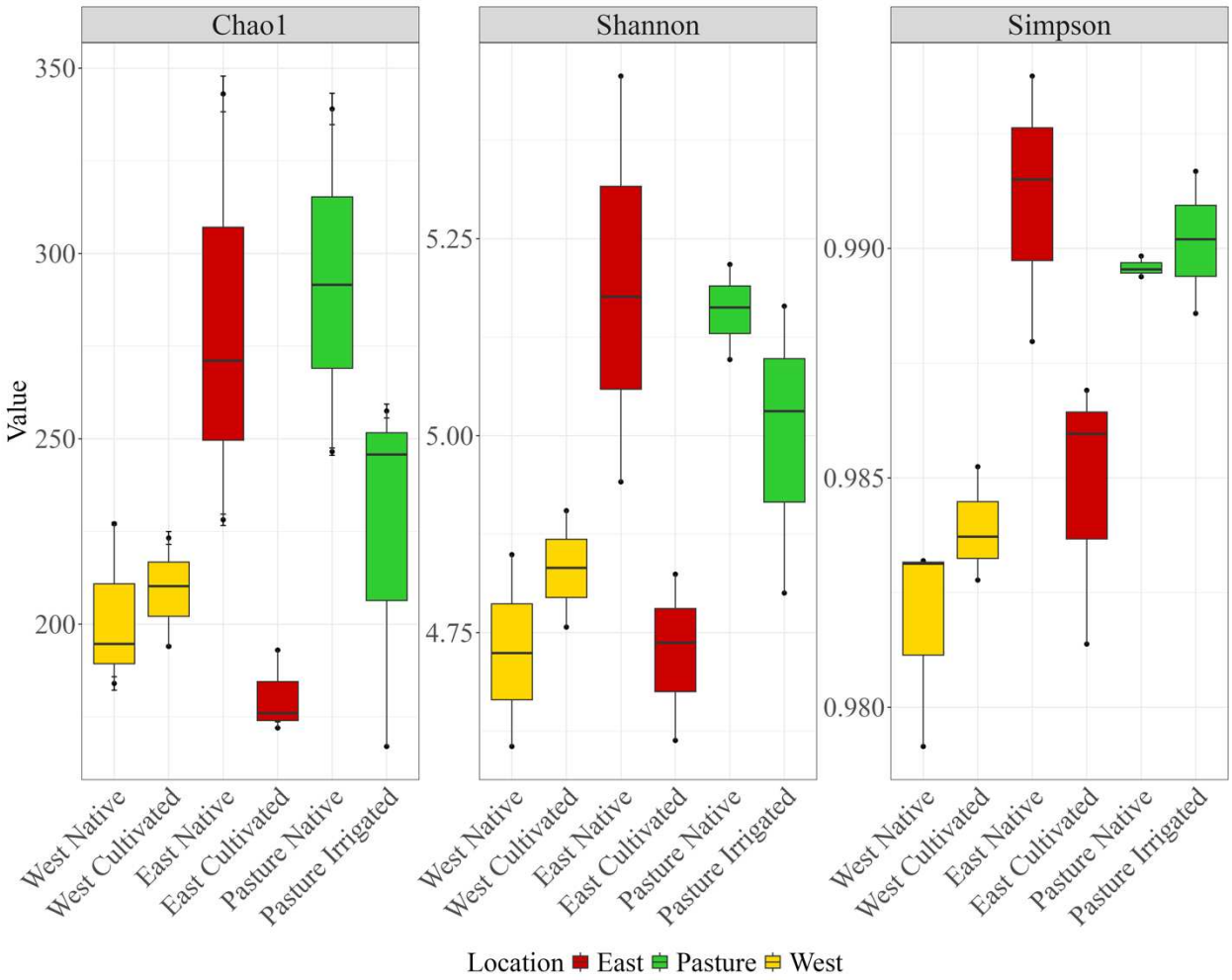

Figure 3.2. Alpha diversity indices accessing sites in the study independently. Significant differences in Table B

3.2.2 BETA DIVERSITY

The microbial communities across sites were assessed with an NMDS based on Bray–Curtis distance dissimilarities to demonstrate beta diversity in the SLV. Beta diversity measures the similarities in community compositions based on the distances between the microbiomes. Results indicate that compositions of site microbial communities—independently—could explain 71% of the variation observed (Figure 3.3) and land use could explain 38% of the variation (Table A3.6). For example, the Bray–Curtis distances from PI to PN and WN to EN were farther from each other than the distance of EC to WC (Figure 3.3). This result implies there are differences in

microbial communities between the two pastures and the two native sites, while the cultivated sites had similar communities. Distances between location (e.g. east, west, and pasture) explained 20% of the variation in communities, making it a poor variable for explaining variation in community composition. In this study, the sites and their specific properties best explain the variation observed, followed by land use types.

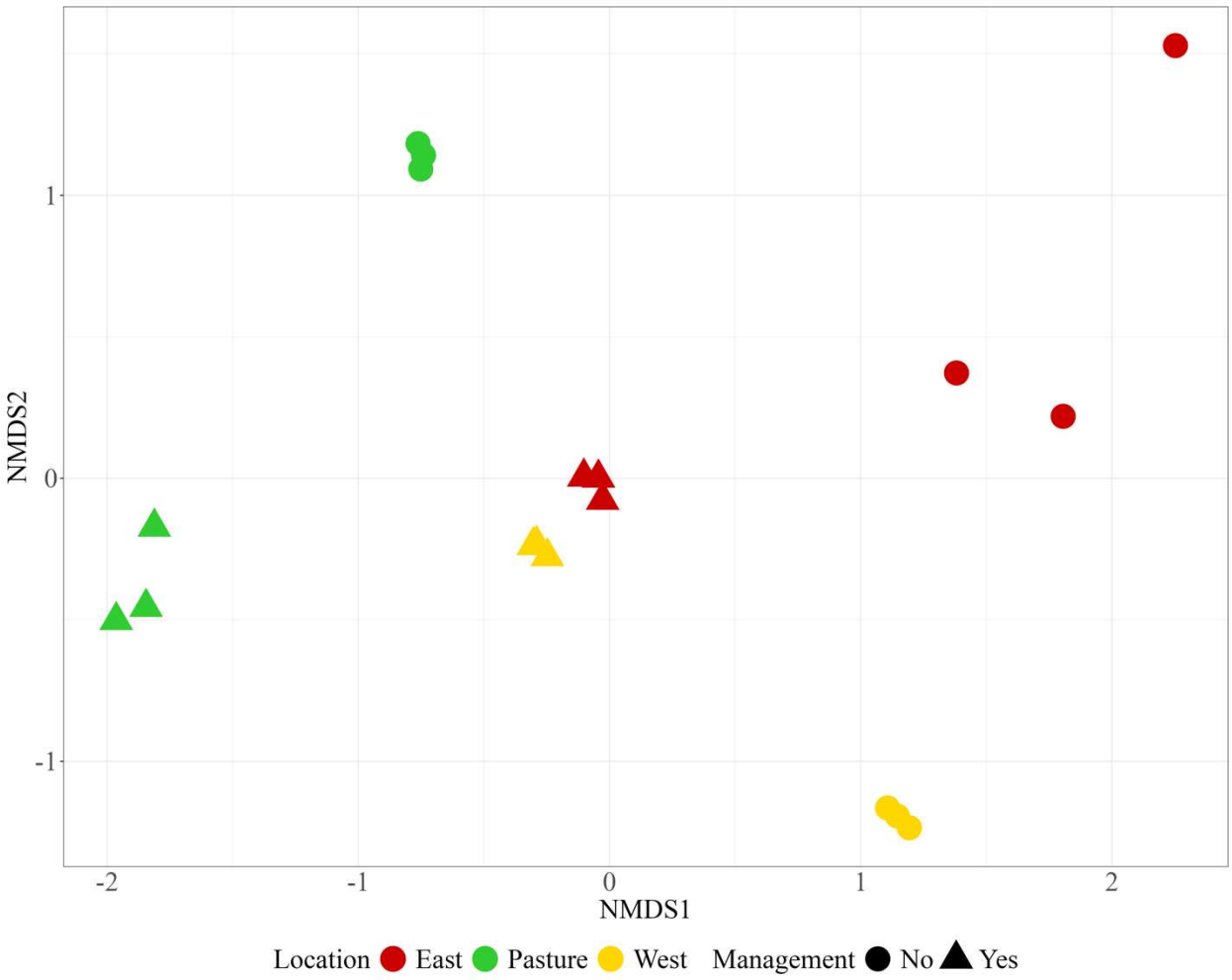

Figure 3.3. NMDS ordination using the bray-Curtis distance of β-diversity for dissimilarities in Bacteria between sites. The assessment of sites internal diversities can explain 71% of the variation in distances. Then, land-use, explaining 38% of the variation in distance.

3.3 PLANT LITTER

The study investigated litter degradation across diverse land uses (pasture, cultivated, native) in the SLV. Each site had unique plant species and litter chemistry (Table 3.2), which divides the litter samples by their C:N values as above or below the stoichiometrically favorable 20:1. The composition of the litter shifted during degradation, with some components decreasing while others increased compared to the overall mass loss. Microbial degraded litter samples were used as a basis for comparing litter samples exposed to solar radiation (those placed on the surface/abiotic positions).

Table 3.2 Initial Chemistry of selected litter samples across the six sites.

Site	Species	C %	Lignin %	Cellulose %	N %	C:N	Cellulose:N
West Native	Rabbit brush	50.34	18.72	18.95	2.39	21.03	7.93
West Cultivate	Barley	41.02	14.65	16.07	4.12	9.96	3.90
East Native	Grease wood	42.81	11.31	11.92	2.40	17.83	4.97
East Cultivated	Wheat	37.52	13.55	21.44	2.95	12.70	7.27
Pasture Native	Alkali sacaton	40.99	12.65	28.59	1.27	32.15	22.51
Pasture Irrigated	Baltic Rush	41.40	6.09	29.35	1.95	21.19	15.05

3.3.1 PLANT LITTER CHEMISTRY

C in litter accounts for cellulose, lignin, hemicellulose, and other C-based compounds in the plant cell. The initial total C concentration in litter samples did not differ much across samples. Total C concentration was largest at WN (50%), lowest at EC (37%), and similar for litter samples from the remaining sites (41-42%). In litter samples placed in the biotic position, total C concentration decreased except for samples from the pasture sites (Figure 3.4). With regard to litter

samples placed in the abiotic and surface litter positions, the total C concentration usually increased except for litter samples from WN and cultivated sites.

Lignin is a recalcitrant C fraction in plant cells walls. Initial lignin concentrations were greatest for litter samples from WN (18%), and lowest for litter samples from PI (6%), and between 11-14% for the other four litter samples. Lignin concentration was enriched in all litter samples (figure 3.4), with the most enrichment observed in the litter samples from the cultivated sites, and the least enrichment observed in litter samples from the pasture sites. These results show that the changes in lignin concentration do not reflect initial lignin concentrations.

Cellulose, a greater C fraction compared to lignin was initially greatest in litter samples from the pasture sites (29%), lowest in the litter samples from EN (11%), and ranged elsewhere from 16% (litter samples from WC) to 21% in litter samples from EC). Cellulose enriched in concentration (Figure 3.4) in all litter samples, except for those placed in the biotic position at the cultivated and PI sites.

Initial N concentration in the litter samples was overall low (< 2%) for samples from the pasture sites, >2.4% for samples from the cultivated sites, and 2.4% for samples from the native sites. N concentration in the litter samples at all sites decreased in for surface and abiotic positions. Changes in N concentrations (Figure 3.4) for samples placed in biotic positions depended on C:N. N concentration increased for litter samples with higher C:N--specifically pastures--and decreased in samples with lower C:N. The most variation in N concentration between positions was observed between the pasture sites.

Together, the effect of position on litter C:N distinguished microbial and photodegradation processes (Figure 3.5). Litter C:N in litter samples in the biotic position decreased, whereas it

increased in litter samples in the surface and biotic positions, showing similar processes like photodegradation (Figure 3.5).

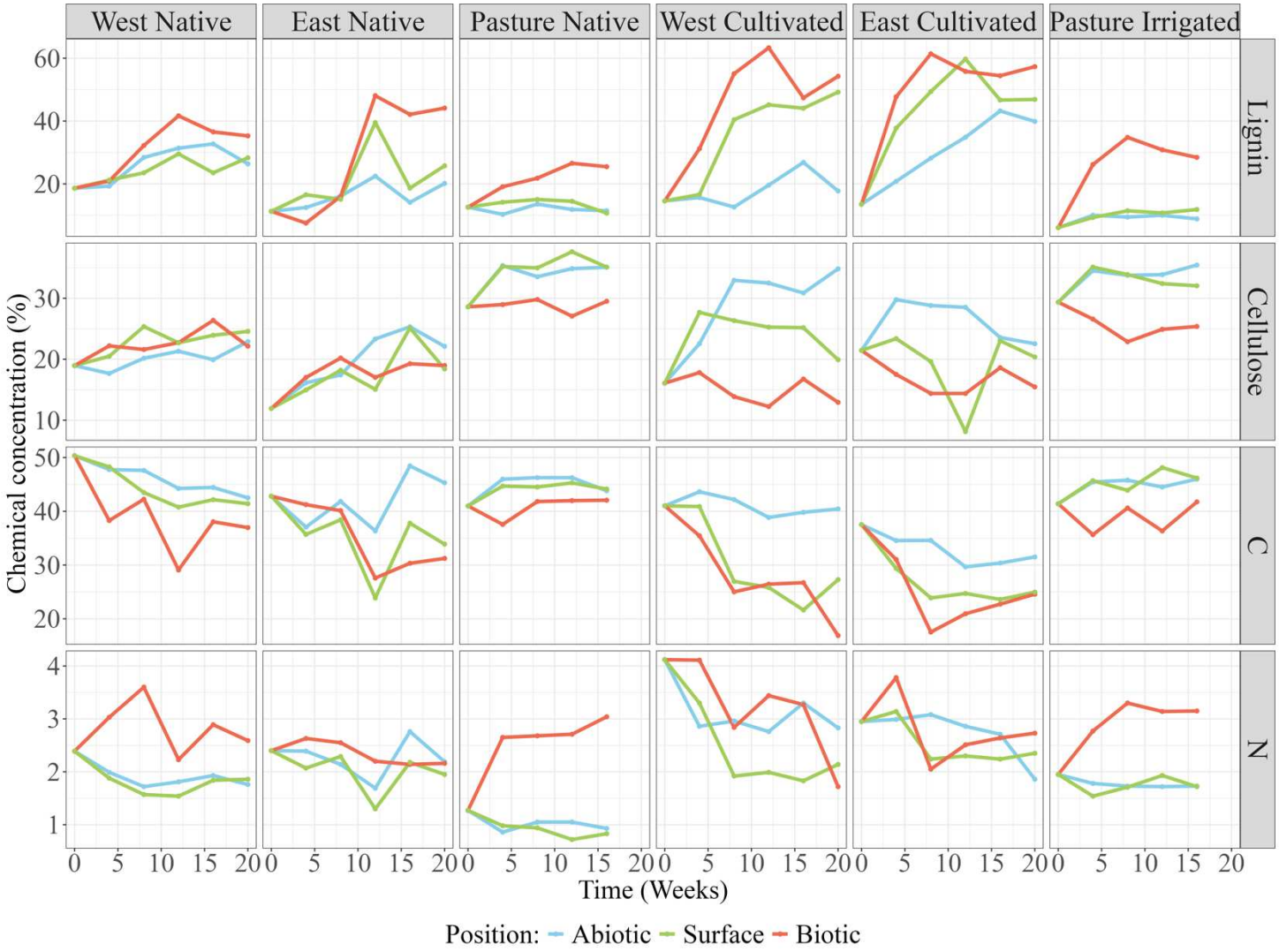

Figure 3.4 Grid style figure with the concentration (%) of each chemical fraction (Lignin, Cellulose, C, and N) over time, for each site, and position (Color).

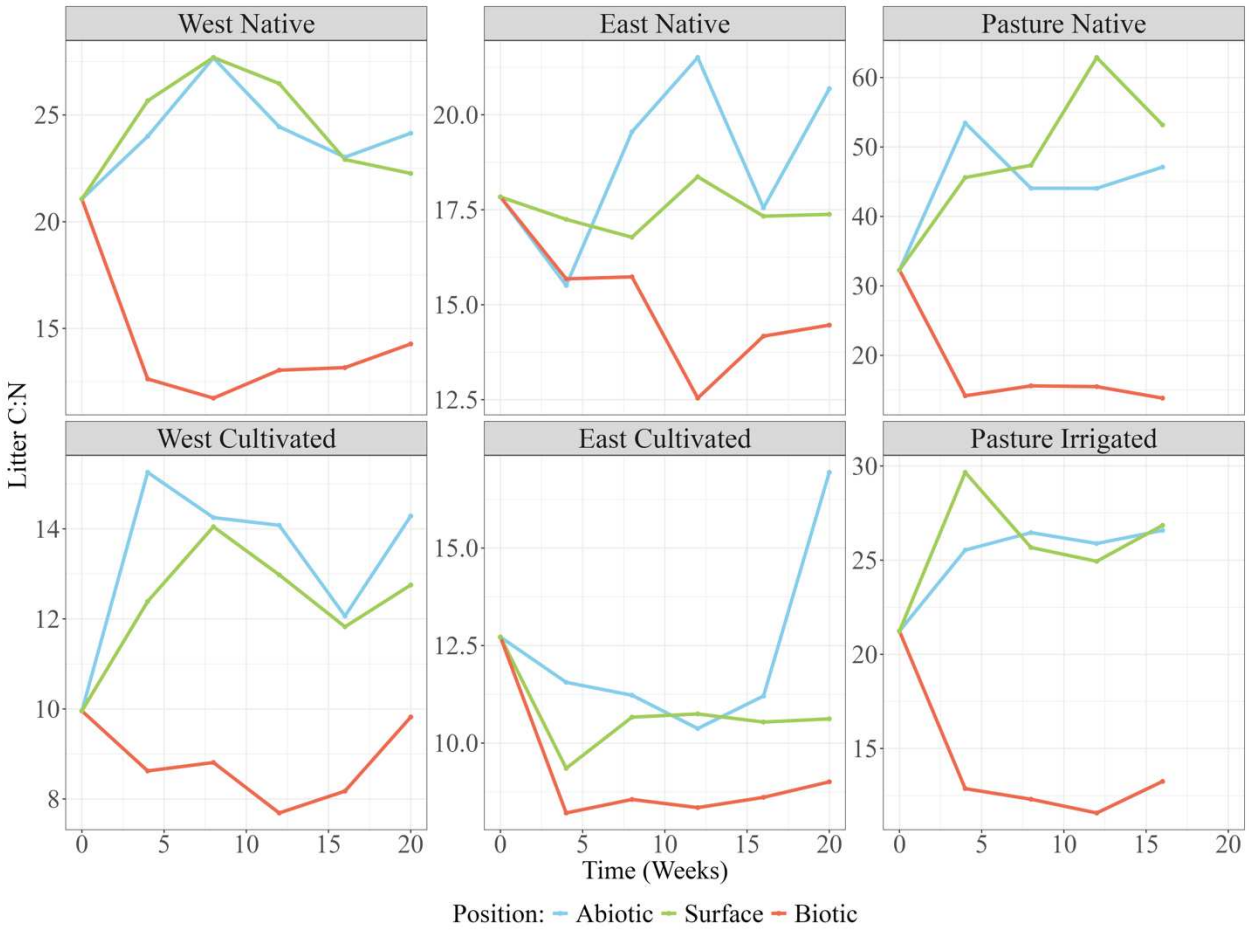

Figure 3.5. Litter C:N ratio over time, from the initial C:N of each litter and the changes in response to changes in concentration from each position until. Contributions to the changes in the ratio are dependent on the litter chemistry and position.

3.3.2 PLANT LITTER MASS LOSS

The mass loss (Figure 3.6) varied among litter samples depending on their positions, land use and initial litter chemistries. The greatest variation in mass loss associated between positions was observed in the litter samples collected from the pastures and EN, while the least variation was observed in the litter samples collected at the cultivated and WN sites. That is, there was greater mass loss in litter samples in the biotic position than litter samples in the surface and abiotic positions at the pastures (~45% vs ~25%). Alternatively, there was greater mass loss from litter samples at the surface and abiotic positions than litter sample in the biotitic position at EN (72%-90%). There was virtually no observed difference in mass loss between litter samples collected at

the two cultivated and WN sites, and the effects of position were minimal (75%-80% for EC, 78-83% for WC, and 42-49% for WN).

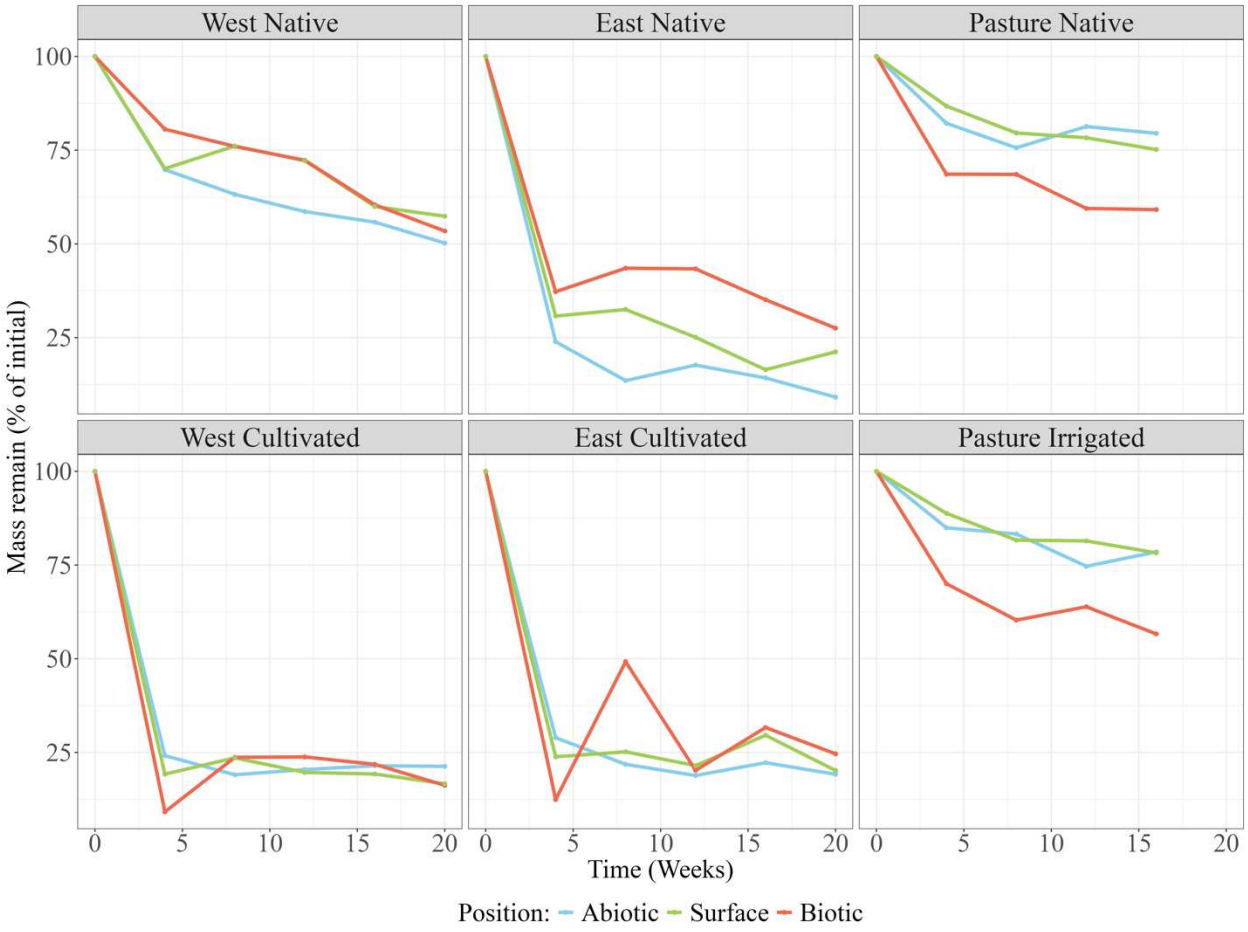

Figure 3.6. Mass remaining (% of initial mass) across all positions, sites, and replicates (n = 3) at each collection point

The initial litter chemistries may explain mass loss patterns observed for each position (Table 3.3). Initial C:N and N concentration in the litter samples were strongly correlated with mass loss (R^2 =.85), increasing mass losses for litter samples in the biotic position with a lower C:N (higher quality litter sample). The initial N and cellulose concentrations better explained mass loss patterns in litter samples exposed to solar radiation (R^2 =.75 and R^2 =.85), those litter samples in the surface and abiotic positions.

Table 3.3: Pearson's correlation of litter initial chemical concentrations and the percent mass remaining of the litter, the N concentration, lignin concentration, C concentration and Cellulose concentration. Bold values indicate significant differences ($p < 0.05$).

	Position	Initial [N]	Initial [Lignin]	Initial [C]	Initial [Cellulose]	Initial C:N	Initial Cell.:N
% Litter mass remaining	Abiotic	-0.75	-0.29	0.21	**0.88**	0.81	**0.88**
	Surface	-0.75	-0.27	0.24	**0.88**	0.79	**0.85**
	Biotic	**-0.85**	-0.08	0.52	0.65	**0.85**	0.73
% N mass remaining	Abiotic	-0.74	-0.4	0.2	**0.87**	0.75	**0.83**
	Surface	-0.74	-0.4	0.25	**0.84**	0.86	0.74
	Biotic	**-0.87**	-0.2	0.16	0.8	**0.95**	**0.96**
% Lignin mass remaining	Abiotic	-0.4	-0.15	0.2	0.77	0.37	0.5
	Surface	-0.1	-0.5	-0.2	0.73	0.03	0.3
	Biotic	-0.5	-0.8	-0.08	0.6	0.26	0.4
% total C mass remaining	Abiotic	-0.76	-0.4	0.1	**0.88**	0.8	**0.9**
	Surface	-0.8	-0.4	0.1	**0.88**	**0.8**	**0.89**
	Biotic	**-0.87**	-0.3	0.3	0.78	**0.9**	**0.87**
% Cellulose mass remaining	Abiotic	-0.7	-0.4	0.13	**0.84**	0.8	**0.89**
	Surface	-0.8	-0.2	0.35	**0.79**	**0.87**	**0.85**
	Biotic	-0.65	0.2	**0.83**	-0.1	0.67	0.32

3.3.3 PLANT LITTER CHEMICAL FLUXES

Mass loss was influenced by initial litter chemistry and land use (Table 3.3). This mass loss resulted from the mineralization and release of chemical fractions in the litter, leading to nutrient fluxes. The final nutrient release in a litter sample depended on the initial litter chemistry, and position for each land use. Consequently, mass loss of chemical fractions was closely tied to overall litter mass loss.

N mass losses contributed least to overall mass losses, due to their minimal initial concentrations in the litter samples. Regardless, N is an important nutrient in ecosystem processes, but usually limited in mineralization (mass losses) in microbial degradation processes and when litter samples are high in their C:N. In this study (Figure 3.7A), litter samples placed in the biotic position were limited in N mass loss (mineralization) at PN instead, immobilization (enrichment

of N mass) of N was observed (150%). When exposed to solar radiation, the litter samples in the abiotic and surface position at PN had N mass loss (50%).

With the other higher C:N litter samples (PI and WN), there were minimal N mass losses in the litter samples placed in the biotic position (12% at PI and 45% at WN). Litter samples in the abiotic and surface positions at these sites increased N mass losses (25% at PI and 50% at WN).

For the lower C:N litter samples placed in the biotic position at the cultivated and EN sites, N mass loss was greater than at the other sites (75% at EC and EN and 92% at WC). N mass losses for litter samples exposed to solar radiation, in the abiotic and surface positions, at the cultivated sites were about the same as those recorded for litter samples placed in the biotic position. In contrast, N mass loss increased to about 92% for litter samples exposed to solar radiation at EN. Patterns in the observed N mass losses of litter samples in the abiotic and surface positions can be attributed to the initial cellulose concentration (Table 3.3, R^2= .87), while the N mass loss in the litter samples placed in the biotic position can be attributed to the initial N concentration and C:N (Table 3.3, R^2= -.87).

Relative to the litter samples buried in the soil, those exposed to solar radiation clearly increased lignin mass losses, except at PI (Figure 3.7B). The litter samples in the abiotic and surface positions showed losses of lignin mass in all sites, with no clear pattern, ranging from 12-83% in lignin mass losses. Additionally, in the biotic position, only the WC litter sample saw lignin mass losses (39%), while all others saw lignin mass enrichment (1-165%).

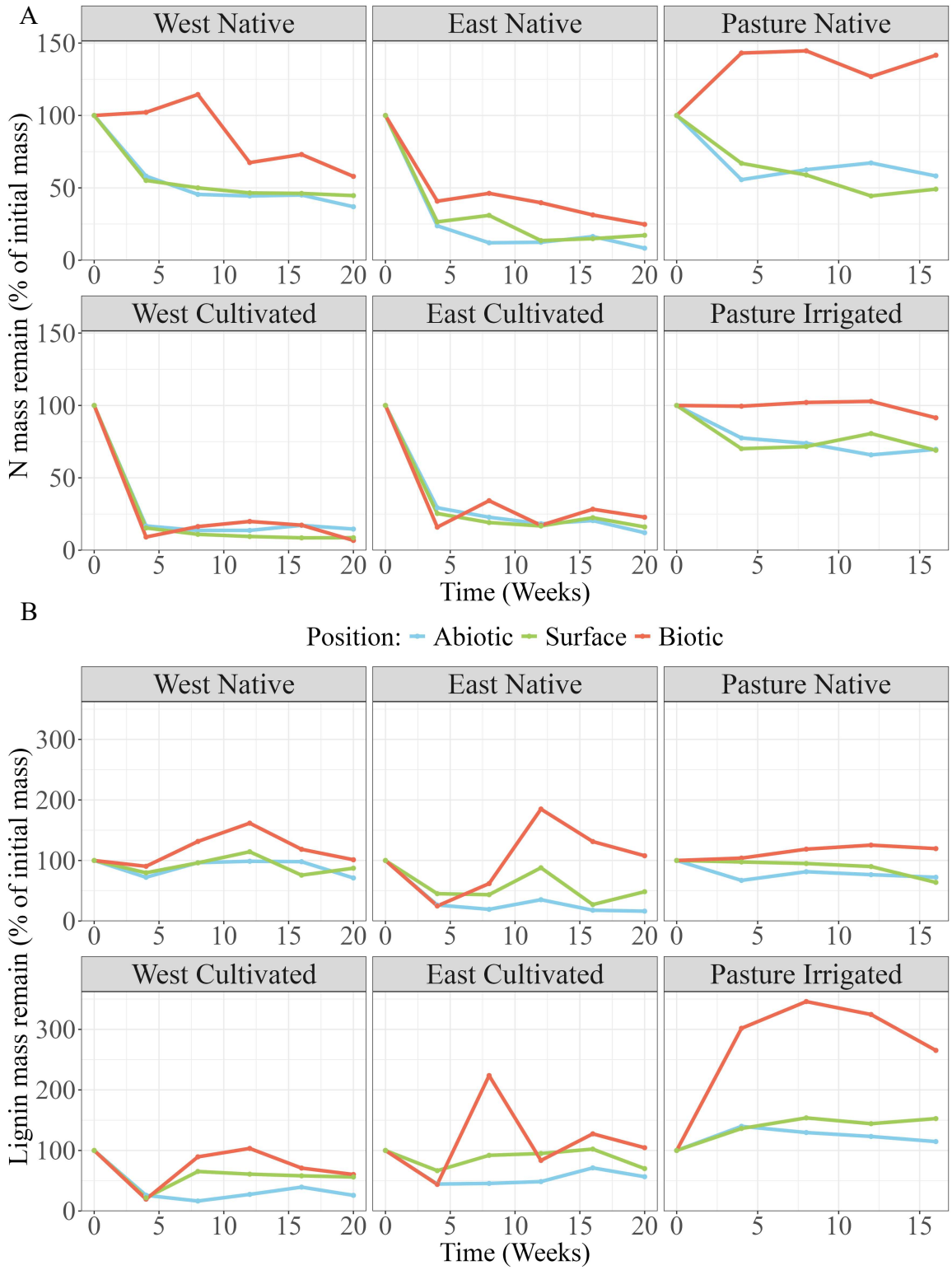

Figure 3.7 A) Litter N mass remain (% remain from initial) over time. Values over 100% indicate immobilization, below 100% indicates mineralization in litter N. B) Litter lignin mass remain (% remain from initial) over time. Values over 100% indicate enrichment, below 100% indicate losses in litter lignin.

Cellulose mass losses trended with total mass losses because cellulose is a dominant chemical component in litter samples assessed in this study (Table 3.2). Litter samples from the cultivated sites experienced the greatest cellulose mass losses across all positions in the study (Figure 3.8A). More variation in cellulose mass loss was observed in litter samples from WC than EC; there was noticeably less mass loss from samples in the abiotic and surface positions than from those in the biotic position (53% vs 86%) at WC in comparison to EC (79-82%).

Litter samples at EN showed greater cellulose mass losses than WN overall (Figure 3.8A). Observed mass loss in litter samples in the surface and abiotic positions was greater than those in the biotic position at EN (83% vs 56%. In contrast, in WN, there was almost equal cellulose mass losses in the litter samples across positions (37% for those in the abiotic and surface positions versus 39% for the sample in the biotic position).

Cellulose mass loss in litter samples from the pasture sites (Figure 3.8A) were the most similar, with the greatest difference in cellulose mass loss across positions (2-5% for samples in the abiotic and surface positions vs 38-51% for samples in the biotic position).

Overall, the final percent cellulose mass loss in the litter samples in the biotic position is best explained by the initial C concentration ($R^2 = .83$), whereas cellulose mass losses associated with the abiotic and surface positions are strongly correlated with Cellulose concentration ($R^2 = .8$) (Table 3.3).

The litter samples' total C mass losses reflected the mass loss of C fractions (lignin, cellulose, and hemicellulose) and non-structural C components in the plant cell. Lower C:N litter samples—at the EN and cultivated sites experience the greatest C mass losses across all positions (Figure 3.8B), but the cultivated litter samples were very similar across all positions, with minimally more C mass loss at EC in the litter samples exposed to solar radiation (83%-86% for

EC, 79%-93% for WC). In contrast, C mass loss at the EN site was more variable between positions, with greater losses associated with the surface and abiotic positions than the biotic position (83-90% vs 79%). Higher C:N litter samples were lowest in C and total mass losses. The C mass losses were greater and less variable (52-60%) at WN than at the pasture sites. Then C mass losses for samples in the biotic position at the pasture sites was greater than that observed in samples in the abiotic and surface positions (39-42% vs 12-15%). C mass losses were correlated to the initial N concentration and C:N for samples in the biotic positions (Table 3.3, $R^2 = .9$ and $R^2 = .87$), while C mass losses are correlated with cellulose concentration and cellulose:N (Table 3.3, $R^2 = .88$ and $R^2 = .9$) (Table 3.3) for samples in the abiotic and surface positions.

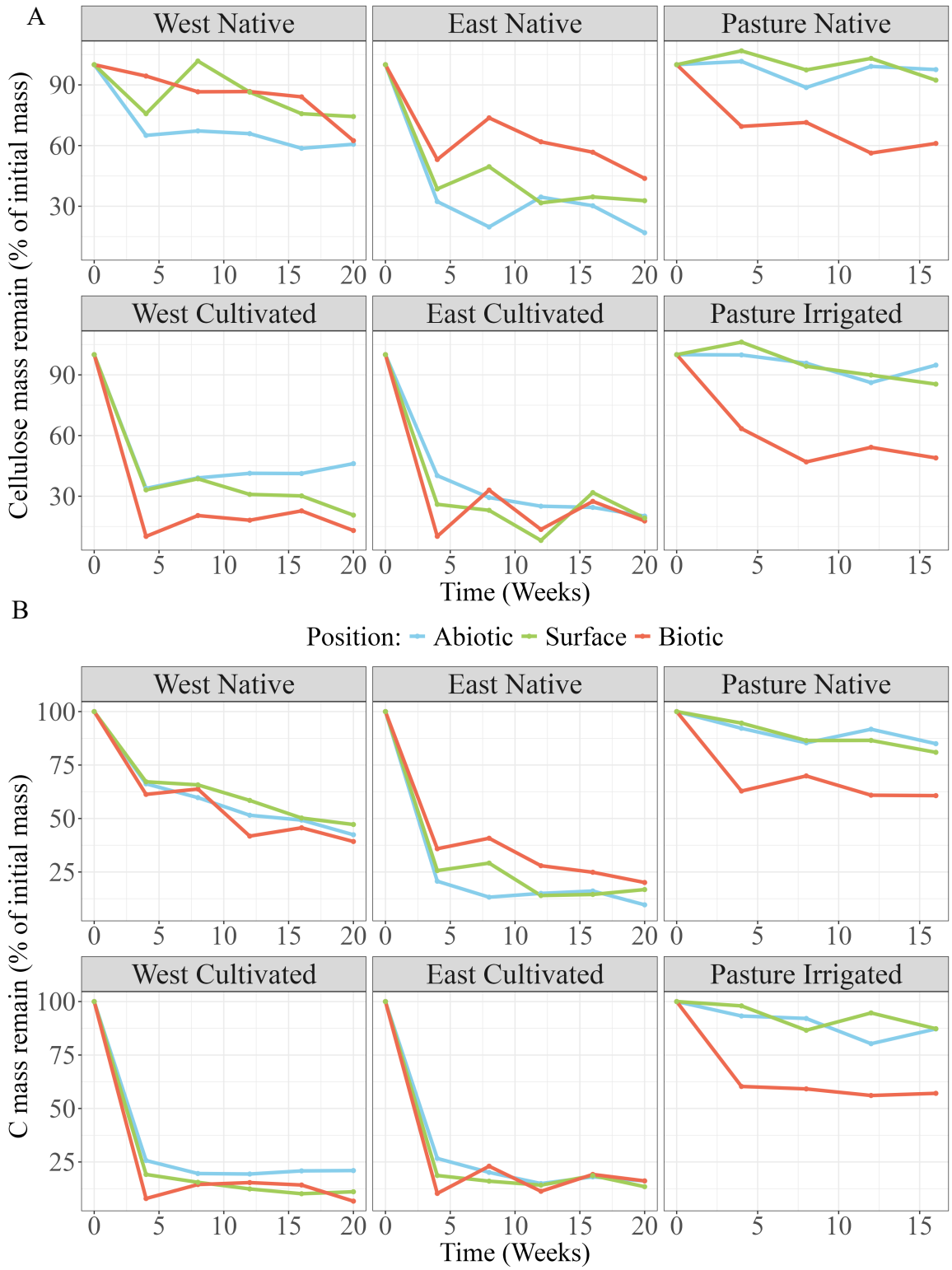

Figure 3.8. A) Litter cellulose mass remains (% remain from initial) over time. Values over 100% indicate enrichments, below 100% indicate losses in litter cellulose. B) Litter total C mass remain (% remain from initial) over time. Values over 100% indicate immobilization, below 100% indicates mineralization in litter total C.

CHAPTER 4: DISCUSSION

Our findings reveal that the importance of litter chemistry varied depending on the dominant degradation process – photodegradation or microbial degradation. The impact of the soil environment on regulating litter degradation was less pronounced than expected because observed soil properties were relatively similar between paired sites. By examining litter samples placed in biotic, surface, and abiotic positions, we were able to differentiate and evaluate the distinct processes of microbial degradation and photodegradation. Specifically, this discussion focuses on photodegradation in nutrient cycling, exploring how litter chemistry, land use and management strategies influence litter degradation processes. Furthermore, we analyze how soil samples and their associated microbial communities vary based on land use and management strategies in selected locations, providing a basis for comparing the degradation processes observed. Specifically, this study compared irrigated and non-irrigated management practices across three typical uses of land in the SLV—native rangeland, cultivated farmland, and pastures, one of which benefited from natural irrigation due to mountain runoff.

The research design provided a "spectrum" of potential litter degradation processes related to the usual placement of plant residues in field conditions, depending on management strategies—e.g. irrigation as well as tilling, mowing, and harvesting. The litter samples placed in the abiotic position ensured that only the effects of photodegradation would be measured, while those placed in the biotic position ensured only microbial degradation. Litter samples placed on the surface could have been subject to both processes. These three positions controlled which chemical components were affected by the dominant litter degradation processes (Austin & Vivanco 2006); litter chemistry (specifically the litter quality C:N ratio and N) regulated the amount of nutrients

released (Brandt 2010); features of land use at the study sites, such as water availability altered the expected effects of photodegradation in the region, except at EN. The observed litter mass losses and the litter C:N trends over time suggest that litter samples placed on the surface tended to be influenced more by solar radiation than by the soil environment, suggesting that the litter degradation was photochemically driven there, like litter samples placed above the surface

Microbial litter degradation depends on land use and management strategies and is most significant in ecosystems where water is available and plant residues are incorporated into the soil– e.g., via cultivation (Lee 2014, Hartmann & Six 2022). Resulting microbial communities, in combination with litter chemistries—specifically the C:N ratio (Brandt 2010, Swift et al. 1979) and lignin content (Austin & Ballare 2010, Thevenot et al. 2010, Austin et al. 2016, Chapin et al., 2002)—regulate microbial degradation. Microbial degradation of litter involves two general processes: immobilization and mineralization of N and C, which are essential for nutrient cycling in all ecosystems. Immobilization is the process whereby microbial communities immobilize inorganic N (e.g. NO^{-}_{3} and NH^{+}_{4}) from the soil to support their own metabolic needs (e.g. metabolizing C). Microbial mineralization converts organic N (from litter) into bioavailable inorganic forms (NO^{-}_{3} and NH^{+}_{4}) and increases the mineralization of C fraction into respired CO2.

Although photodegradation occurs in all ecosystems, semi-arid systems often lack the conditions (e.g., irrigation, sufficient litter input, favorable soil pH, and SEC) necessary to support robust microbial degradation. Therefore, studies of photodegradation of litter emphasize solar-induced litter degradation as a more prominent pathway to litter mass loss and chemical mineralization in semi-arid and arid regions, like the SLV (Throop & Archer 2007, Brandt 2010, Austin & Vivanco 2006, Gallo 2009, Baker & Allison 2015, Day et al. 2007, Barnes 2015, 2023).

Soil development is weakly expressed in semi-arid climates, like the SLV's, due to lack of water, which restricts chemical, as opposed to physical, weathering (Verheye 2009). The climate is characterized by low precipitation (less than 300 mm of rain annually) and high evapotranspiration, contributing to increased salinity (measured as SEC in this thesis) and more challenging environments for vegetation. The Physiochemical properties of soil horizons at depth are broadly similar across land uses and locations (see Table 3.1). Observed soil pH, CCE and textures at depth for all but the PI site are reflective of a semi-arid soil order—an aridisol. The soil profile for the PI site, associated with more abundant water and biomass, was previously identified as a mollisol order (see Figure 2.2). Additionally, the western sites were similar in properties and exhibited less soil development than the eastern sites which were more alkaline and slightly more variable between them. Pasture sites were different from the other four sites in their morphology at depth. These soil horizons at depth are consistent with expectations for the region, but are irrelevant to short term nutrient cycling, which was the focus of this study.

Soils in the SLV are unique due to the availability of groundwater and runoff from snowmelt in the nearby mountains, which generally supports some vegetation and enables a range of land uses, including cultivation and pasture development. Concentrations of soil nutrients, root development and organic matter, can emerge where vegetation is present. These "fertility islands" feature long-rooted halophytes capable of drawing water and cations to the surface. Given water availability and limited disturbances, concentrations of nutrients in the soil surface horizons can increase due to more abundant aboveground biomass—as observed at the pasture sites.

Comparing paired land uses at each location, results provide some evidence of directional change due to effects of irrigation-based management at the surface horizon. This change is more pronounced at the eastern sites (EN and EC), than at the western sites (WN, WC). Soil disturbance

and irrigation together explain observed Ap horizons in both cultivated soils; in the absence of cultivation, the native soils lacked a developed A horizon. The location of the undisturbed pasture sites (PN, PI) in the sump location—a topographic low in the SLV (Mayo et al. 2007, Emery et al. 1969)—where water is relatively plentiful despite the absence of irrigation, accounts for observed A horizons there.

4.1 ROLE OF SOILS AND MICROBIAL COMMUNITIES IN LITTER DEGRADATION

It was expected that the composition and/or diversity of microbial communities would be related to soil properties, given land use and management, and therefore also to the microbial degradation observed in this study. Instead, soil properties, microbial communities, and microbial potential mineralization of N did not indicate expected relationships—likely due to of sampling. Collecting soil and plant material at the same is critical for ensuring the accuracy of observed degradation processes associated with the interactions between plant litter and the soil microbiome (Jayaramaiah et al. 2025). In this study, soil cores, soil samples, and litter samples were collected at different times. making it difficult to generalize about the relationships among soil, microbial processes, and litter degradation. Despite this timing limitation, our results concerning soil and microbial properties still provide insight into the effects of land use, management strategies, and geographical location within the SLV.

Land use alters the soil physiochemical environment, depending on management strategy and location. Regardless of management strategies (specifically, non-irrigated control, versus irrigated experimental in each location), soil surface horizons in the study primarily reflect land use (native, cultivated, and pasture) and location (east, west, and pasture). Site-specific variables–i.e., irrigation and the resulting biomass–likely contributed to observed soil chemistries at the

surface horizons for EC, WC, and PI sites compared to their control sites (Austin et al., 2006; Vitousek, 2009).

Generally, microbial communities are conditioned by site variables, including soil properties, land use and management strategies. Soil properties, such as pH and texture are commonly considered significant regulators of soil microbial communities (Fierer & Jackson 2006). Therefore, in the SLV, microbial communities would be expected to vary with management or pH, but this study revealed that they were more closely explained by land use and SEC at each site, or location. This finding is consistent with Maestre (2015) and Zhang (2019), who both found that aridity and saline soils determine the alpha diversity of the soil community. Land use disturbances can both decrease the diversity of microbial communities, and speciate the necessary microbial taxa (Lacerda-Jùnior et al. 2019, Philippot et al. 2021). Cultivation drives similarities among soil properties as well as microbial communities, regardless of location. For example, tillage destroys microbial niches (Kladivko 2001), and harvesting removes OM in the soil system (West & Whitman 2022), reducing both alpha and beta diversities (Gossner 2016) via selection and speciation of microbes in response to the conditions in the soil necessary for producing crops in semi-arid conditions (Chapparro 2013). While the land management practices at cultivated sites can help to manage salinity (Tarolli et al. 2024), observed lower SEC and microbial diversity there as well as at the WN site was likely also due to the proximity of these sites to mountain runoff. In contrast, reduced access to water at the EN site and water source of the pastures may explain the observed relatively higher SEC.

Environmental disturbances affect the composition of microbial communities by influencing microbial speciation (arising of new species) and therefore also speciation (selection of species for reproduction) (Maurice et al. 2024). Both microbial speciation and selection were

less prevalent at the EN and pasture sites due, in part, to the lack of manual disturbance (e.g. plowing) associated with these cultivated sites. As was the case for the less disturbed EN site, the resulting higher alpha diversity associated with higher speciation yielded greater resilience of the microbial communities (Hobbs 2009). Despite their similar alpha diversities, the microbial communities at the PN and PI sites differed both from one another, and from the other four sites, as reflected in their Bray-Curtis distances (see Figure 3.3).Because climate change is expected to threaten water availability throughout the SLV, the diversity of microbial communities may be key to their resilience (Lozsupone & Knight 2007, Griffiths & Philippot 2013), it is beneficial to have more taxa, or redundancy, in the community (Canfora 2014, Rath 2015). This finding characterizes the microbial response to land use and location in the SLV, but does not provide information about microbial functions.

Irrigation can promote functions of the microbial communities, as well as biomass and increased organic matter inputs for growing them (Fontaine et al. 2003). Microbial diversities do not equate to function; rather, PMN is a measure of the function of a microbial community's potential capability of mineralizing N within the soil. The PMN analysis indicates that microbial metabolic function is not determined by the richness and diversity of the microbial communities found at the study sites (Fierer 2017). Rather, these functions are regulated by soil OC and N, which are a consequence of location and land use—specifically, those that influence litter placement and below-ground biomass water accessibility. PMN analysis of SLV soil surface horizons (represented in Figure 3.1) overall indicates a strong relationship between maximum PMN and soil OC and N (see Table 3.1). Yet the relationship between the microbial alpha diversity (refer to Figure 3.2) and max soil PMN indicates that a microbial community does not determine its function. This result confirms that the potential of the microbial community to metabolize N is

related to land use and resulting substrate (soil OC and N), not the richness and/or diversity of the relevant microbial community. Although both the pasture and EN sites feature diverse microbial communities, the substrate (very low OC and N) at EN appears to inhibit microbial function there.

4.2 ROLE OF CHEMICAL COMPONENTS IN LITTER DEGRADATION

Studies of photodegradation of litter emphasize solar-induced degradation as a more prominent pathway to litter mass loss and chemical mineralization in semi-arid and arid regions, which lack conditions (e.g., irrigation, sufficient litter input, favorable soil pH, and SEC) necessary to support robust microbial degradation (Throop & Archer 2007, Brandt 2010, Austin & Vivanco 2006, Gallo 2009, Baker & Allison 2015, Day et al. 2007, Barnes 2015, 2023). Plant litter with high lignin content is particularly photoreactive to solar radiation, breaking down much faster when exposed to sunlight than it would if subject only to microbial processes (Day et al. 2007, Henry et al. 2008). In contrast to the litter samples in the biotic position, which lost mass due to their litter C:N as expected, litter samples in the surface and abiotic positions did not. The results in the previous chapter do not support the hypothesis that litter lignin content will be the most photoreactive compound in litter samples, driving greater mass losses and lignin mineralization.

Instead, the N concentration in all litter samples regulated mass losses, consistent with Brandt (2010). Mass losses trended with N concentrations in the samples, as an increased initial N concentration led to an increased total mass loss, but the observed decreases in N concentrations did not account for observed mass losses, as the total N in litter samples was less than 5%. Furthermore, the initial cellulose concentrations in litter samples appear to hinder photodegradation. Given observed mass losses based on initial N concentrations in these litter samples, lower total mass losses were observed when litter cellulose was greater. For example, the

initial N concentrations at the native sites were the same, but litter samples collected at WN contained higher cellulose concentrations, and less mass loss was observed than in samples collected at EN. Also, the lignin and cellulose concentrations increased in photodegraded litter samples over time. These increases are arguably due to decreases in the concentrations of other chemical components: N and some C fractions, as mass of litter samples decrease (Day et al. 2007, Day 2015). This observation suggests that mass loss may have been attributed to a non-measured litter component—e.g., hemicellulose (Brandt et al. 2010, Day et al. 2007)—and will require further exploration.

Notably, C:N ratios changed in all litter samples due to the degradation process. Specifically, changes in the C:N for litter samples in the abiotic and surface positions similarly showed higher C and lower N concentrations, yielding higher C:N compared to litter samples in the biotic position. This result indicates that plant litter exposed to solar radiation (at or above the soil surface) becomes less favorable for microbial degradation after 20 weeks; moreover, this process of litter degradation is distinct from microbial degradation, which decreases the C:N ratio in affected litter samples to stoichiometrically favorable levels (<20:1). This difference between positions was most apparent in higher C:N litter samples—i.e., pasture and WN sites. With the limitation in C:N of litter samples, all litter samples in the study resulted in lignified samples.

4.3 PATTERNS OF PHOTO- AND MICROBIAL LITTER DEGRADATION

The results presented do not support the hypothesis that litter samples exposed to solar radiation will experience greater mass loss than those affected only by microbial degradation, except at one site: EN. Unlike previous studies of photodegradation, litter samples exposed to direct sunlight in this study did not always accelerate or increase mass loss (Brandt 2010, Day et

al. 2007, Henry et al. 2008). This unexpected finding can be explained by differences in litter chemistry due to litter degradation processes, land use and management strategies, and this study's short length. These findings suggest three relationships between the effects of photo- and microbial degradation: (1) observed mass loss was greater for litter subject to microbial degradation as opposed to photodegradation processes (pastures); (2) observed mass loss was greater for photodegraded versus microbial degraded litter (EN); and (3) observed mass loss was about the same for litter, regardless of the degradation process (cultivated and WN sites).

Similar to Brandt (2007), King (2010), and Austin (2021), this study suggest that litter chemistries based on position regulate changes to both C and N concentrations, which in combination with total litter mass over time, contribute to nutrient fluxes as a function of litter sample position at a given site. The main compounds of litter chemistry are C fractions and N. The N concentration in the litter samples used in this study was relatively low (<5%), so its contribution to total mass loss appears weak relative to total C concentrations (including lignin and cellulose, (37-50%) Table 3.2).

Land use contributed to litter degradation indirectly, because land use in combination with management strategies—especially the availability of water—generates distinct soil properties that should regulate litter degradation. Water regulates the microbial functions in the soil and the mass loss associated with microbial degradation. Generally, the study results indicate that application of water and proximity to water at a site will decrease the effect of photodegradation relative to microbial degradation. In this study, the total mass loss of litter samples placed on the surface was similar to that observed for litter samples in the abiotic position, and distinct from mass losses observed in litter samples placed in the biotic position. This result suggests that,

contrary to expectations, microbial degradation does not enhance photodegradation of litter samples on the soil's surface.

4.3.1 PASTURE SITES

The litter samples showed the clearest contrast to the hypothesis in mass loss. Cellulose, a non-photomineralized component, was the dominant fraction in these samples, with low initial N (<2%). This condition likely limited mass loss from solar radiation, as cellulose is less susceptible to photodegradation. When exposed to solar radiation, mass loss was primarily attributed to lignin and N mineralization, despite their low initial fractions. However, in the absence of solar radiation, mass loss was primarily attributed to cellulose degradation. This finding explains the greatest variation in mass loss between degradation processes for pasture litter. While the C:N ratio suggests potential inhibition of microbial degradation, photodegradation did not significantly enhance litter degradation. This finding may be due to an active microbial community with available N resources, supported by high PMN mineralization and no immobilization across both sites. The soil's OC and N content, likely influenced by land use management, may promote microbial degradation, albeit at a slower rate. The litter chemistry inhibited the effects of photodegradation, while at this land use and management appears to have benefited microbial degradation.

4.3.2 EAST NATIVE (EN) SITE

The analysis of litter samples at EN supports the hypothesis that exposure to solar radiation makes photodegradation more influential than microbial degradation**.** When exposed to solar radiation, litter samples at this site lost more mass than litter samples in the biotic position—attributed to increased mass loss of both C fractions and N. This result further supports the

argument that litter samples with greater initial N concentrations (King et al.2010) and lower cellulose concentrations are more susceptible to the effects of solar radiation.

Yet litter samples from EN also experienced a surprising degree of microbial degradation. Low measured PMN (immobilization) supports the expectation that microbial degradation would be limited due to lack of water due to location far away for water sources, higher SEC, and lower OM content in the soil. However, the placement of non-senesced litter samples in sandy soil at EN may have created a situation in which there was an increased OM content in addition to the rich microbiome in a sandy soil, creating the observed higher than expected microbial degradation. Still, this microbial degradation was arguably regulated by the lower litter C:N, though lignin mass losses were limited, evidenced by the observed enrichment of lignin mass. Despite the relatively high level of microbial degradation, observed mass losses at EN supports the hypothesis. Due to litter chemistry and land use and management, photodegradation had a greater effect on nutrient turnover.

4.3.3 CULTIVATED AND WEST NATIVE (WN) SITES

The variation in litter mass losses between the positions at each of the cultivated and WN sites demonstrated minimal variation per each site. Litter samples at the cultivated sites consistently exhibited greater mass loss than litter samples at WN, regardless of position, where litter chemistry can account for the differences in mass losses among the sites. These sites had some of the highest initial N concentrations in the study, potentially supporting both microbial and photodegradation processes. Additionally, these sites had similar OM content in the soil and low SEC values, potentially supporting the observed microbial degradation, which was supported by the PMN. It is likely that these sites may have sufficient microbial activity, OM content, and water availability for litter degradation, thus reducing the relative importance of photodegradation

(Austin et. al 2021). It is not clear why and how mass losses did not differ much; however, though there were minor variations between the processes of litter degradation. Lignin and N contributed to increased mass losses, while cellulose—a major driver in total mass losses—differed very little, which may be due to the relatively high initial litter N concentration. Additionally, decreased total C concentration due to solar radiation exposure were observed in samples from the cultivated an WN sites, along with increases in lignin and cellulose fractions—suggesting that another C fraction (e.g. hemicellulose) contributed to the decreases in concentration of C.

4.4 SUMMARY

Photodegradation's role in nutrient cycling was particularly notable at the EN site, where limited water availability inhibited the development of the soil and limited the mineralization via microbial degradation. Alternatively, in the pastures, irrigation appeared to promote C mineralization associated with microbial degradation, albeit at a slower rate. These findings underscore the complex relationships among microbial processes, management practices associated with land use, and photodegradation in regulating nutrient turnover in semi-arid systems.

CHAPTER 5: CONCLUSION

The analyses in the preceding chapters address the role of litter chemistry, land use, and management strategies that contribute to litter degradation processes, emphasizing the impact of photodegradation across different litter types compared to microbial degradation under various land uses in the SLV. These findings contribute to understanding how soils and their microbial communities influence litter degradation processes. While limited sample sizes for some variables (soil biochemical and litter chemical) prevented assessment of statistical significance, they are sufficient to provide empirical support for theoretical relationships and open avenues for future research.

This research project focused on photodegradation, one of several litter degradation processes contributing to nutrient turnover. A key feature of this study is its assessment of litter degradation across selected land uses in a semi-arid system, encompassing a range of litter chemistries and soil ecosystems rarely explored in previous photodegradation studies. To address gaps in understanding nutrient turnover in semi-arid regions and across varying land uses, this study proposed research questions and objectives aimed at critically examining current knowledge of nutrient cycling.

It was hypothesized that solar radiation would increase litter mass loss, that the lignin content in litter samples would preferentially photomineralize to amplify photodegradation effects, and that similar land uses, and management strategies would result in comparable soil properties and explain patterns of litter degradation. To test these hypotheses, this study utilized field research, laboratory methods, and quantitative analysis. The findings revealed that land use and management strategies influence soil and microbial characteristics, as well as the relative importance of litter

photodegradation. With the study completed and results analyzed, the three proposed research questions can now be addressed in this conclusion.

5.1 RESEARCH QUESTIONS

Question 1:

The impact of initial litter chemistries on degradation processes was influenced by both the litter's position and the land use. Litter samples in the biotic position were regulated by their C:N ratio, which affected total mass losses and changes in C and N concentration. High C:N ratios limited microbial degradation and restricted carbon and nitrogen mass losses (mineralization), leading to reduced total mass losses due to decreased losses in C and N components compared to low C:N litter samples.

In contrast, litter samples exposed to solar radiation altered litter degradation dynamics. In these cases, degradation patterns were instead driven by initial litter N concentration, with cellulose concentrations acting as a limiting factor in total mass loss. This exposure to solar radiation led to increased N and lignin mass losses regardless of initial chemistries, but decreased cellulose mass losses in pasture litter samples—with the highest cellulose concentrations and lowest N concentrations, ultimately reducing overall mass loss when compared to the litter samples in the biotic position. For these same pasture litter samples, photodegradation had less impact on mass losses because the litter samples were predominantly cellulose, which limited C and N mineralization's compared to other litter samples exposed to solar radiation. Conversely, litter with lower concentration of cellulose and greater concentration of N experienced greater mass losses due to solar radiation and therefore increased C and N mineralization's relative to the pasture sites.

Question 2:

The study found that soil properties, influenced by land use and management strategies , did not directly regulate microbial litter degradation but appeared to have an indirect effect. Results suggest that nutrient turnover across land uses depends on soil properties, litter chemistry, and the position of litter samples relative to the soil. Increased water availability, particularly at the pasture and cultivated sites, enhanced microbial degradation compared to photodegradation, likely due to water's role in supporting microbial activity.

Litter chemistry significantly influenced microbial degradation. Although litter degradation was slower in pastures, due to the higher C:N in litter samples, it benefited from C mass losses facilitated by an active microbial community, specifically mass losses in the cellulose fraction. Photodegradation also contributed to equivalent mass losses at the cultivated and WN sites, but the combination of irrigation or location, and low SEC likely further supported microbial activity, highlighting the critical role of water availability.

In litter samples from EN, litter degradation appeared constrained by low water availability, low OM availability, potentially higher SEC, and reduced microbial activity, favoring photochemical over microbial processes.

Overall, soil properties influenced microbial degradation indirectly, with their effects primarily mediated by litter chemistry.

Question 3:

Solar radiation influenced litter degradation depending on land use, management strategies, and litter chemistry. Semi-arid regions have significant potential for photodegradation, often exceeding microbial degradation. However, this effect depends on land use constraints—irrigation and an active microbial community—which can enhance microbial degradation, thereby reducing

the relative contribution of photodegradation to mass loss (Brandt 2010, Araujo et al. 2022). Additionally, litter chemistry plays a critical role, with lower cellulose concentration and higher N concentration increasing the relevance and efficiency of photodegradation. Overall N and C (from the lignin fraction) increased mineralization under solar radiation, while C mineralization overall was greater in litter samples in the biotic position. This study has identified clear responses of variety of litter chemistries to litter degradation processes, showing that there are pathways of C and N turnover not accounted for solely by microbial processes.

5.2 IMPLICATIONS

The primary implication of the photodegradation process, irrespective of land use, is the release of nitrogen and carbon—primarily from lignin—into the atmosphere due to solar radiation. Although these chemical components represent smaller fractions compared to cellulose, they are essential nutrients within ecosystems. Recognizing the pathways of their release is crucial, because increased mass loss of these chemical components can reduce their return to the soil and instead contribute to atmospheric emissions, potentially exacerbating greenhouse gas (GHG) levels.

Microbial processes are a critical pathway for litter degradation across both high and low C:N litter samples. However, in land uses with limiting factors such as potentially higher SEC water availability, the influence of photodegradation becomes more pronounced, particularly when litter chemistry is favorable. Given the projected increases in drought frequency, water limitations, and expansion of semi-arid regions, the findings of this study are increasingly relevant. Saline soils and reduced water availability constrain microbial degradation and nutrient turnover, thus amplifying the effects of photodegradation. Water limitations and variations in biomass inputs can

alter microbial community functions, particularly in semi-arid ecosystems (King et al. 2012; Stevenson et al 2015).

In agroecosystems, regardless of any particular management, surface residues and standing dead litter are periodically exposed to solar radiation (Novelli et al., 2017; Varela et al., 2014). This exposure can result in nutrient losses, but when litter is incorporated into the soil, it may be better primed for microbial degradation—due to a decreased lignin mass, but they are limited via the increased C:N in litter samples (Austin et al., 2016). Alternatively, the use of cover cropping can mitigate these losses by providing soil coverage, which reduces the exposure of litter residues to solar radiation and minimizes the extent of photodegradation.

5.3 FUTURE RESEARCH

This study raised as many questions as it answered, opening numerous avenues for further explorations. Several modifications could enhance or expand upon this work. While evidence supported photodegradation, its effects might have been more pronounced with a different litterbag material. The 1 mm^2 mesh used in this study blocks up to 50% of solar radiation penetration (Archer & Throop, 2009; Brandt, 2010), potentially underestimating photodegradation effects. Further research should employ litter bags with a larger mesh or alternative material to permit greater exposure to solar radiation

Second, understanding how photodegraded litter influences microbial degradation under actual land use conditions is crucial. This study used non-senesced (green) litter, which is richer in C and N content than aged litter and more sensitive to processes affecting C and N (Cornelissen, 1996). Future research should incorporate litter that more closely resembles naturally senesced material and design studies to reflect real-world land management strategies. Additionally,

replicating natural field placements—such as standing residues after harvest or surface litter photomineralizing before incorporation into the soil through tilling, mowing, or trampling—would provide more accurate insights into nutrient cycling.

Future research must extend study durations. While prior studies spanned 1 to 5 years, the limited timeframe of this study constrained longer term processes. High-elevation semi-arid landscapes like the SLV are defined by diurnal temperature fluctuations and pulsed wet-dry rainfall cycles, factors not deeply examined here. A longer-term investigation into litter photodegradation across seasons could reveal the influence of seasonality on degradation processes. Moreover, microbial communities are not active year-round (Austin, 2022), and an extended study could capture periods of low microbial activity, providing a more comprehensive understanding of microbial degradation dynamics.

5.4 CONCLUSION

Although the SLV is a semi-arid region, where photodegradation has been proposed as the dominant mechanism of nutrient losses and higher decay rates, results in this study demonstrate that land use management has caused this region to deviate from that of other semi-arid regions in several ways. Due to local land use and management strategies, microbial degradation resulted in greater or equivalent mass loss than photodegradation across irrigated land uses. Additionally, lignin concentration did not regulate litter mass losses in litter samples exposed to solar radiation as expected, rather solar radiation did increase the mass losses of lignin relative to all litter samples in the biotic position. Also, litter N regulated mass losses in the litter samples exposed to solar radiation and resulted in increased N mass losses relative to litter samples in the biotic position.

The amount and rates of nutrient turnover in plant litter degradation are crucial for soil health, such as for WHC, a measure of the soil's ability to hold water. Not only is this soil property improved via soil texture, specifically with clay and loamy soils, but also with the addition of OM in the soils. This OM can increase the retention of water—similar to the properties of clay in soils. The quicker mass loss of litter samples in the biotic positions at the cultivated and EN sites limited OM accumulation and therefore decreased the WHC, specifically at EN, which is characterized by the sandiest soils. Alternatively, at the pasture and WN sites, mass loss was slower, potentially increasing and accounting for the higher-than-expected OM in the soil, which promoted higher WHC at these sites.

With exposure to solar radiation, litter samples at the cultivated and native sites, experienced equivalent or greater C and N mineralization's which can decrease nutrient turnover to the soil, future vegetation, and OM inputs. Instead, these chemical components are photomineralized, increasing the emissions of CO_2 and NOx into the atmosphere. In contrast, pasture also experienced increased N and decreased C mineralization's, which slowed down litter degradation, and may potentially help with OM in the soil, if the litter were reincorporated into the soil. Semi-arid regions, like the SLV, are predicted to grow and face challenges associated with that growth as well as climate change and other higher-level transitions. It is imperative to understand the limitations and challenges to these stresses, analyze options to address them. Results from this study and future ones like it are integral to this planning. Landowner and public policy specialists as well as researchers will benefit from the findings of this and suggested research in many ways. Considering how much of the planet is arid/semi-arid and how many societies are impacted by the health and sustainability of these regions, this research is more

broadly relevant to humanity, providing a bridge from science-based knowledge to practical applications by landowners.

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APPENDIX

Table A3.1. PMN over time. PMN is measured first by summing the NH^{+}_{4} and NO^{-}_{3} at each time point, then by subtracting from the initial sum. If less than the initial sum, then potential immobilization and greater than the initial sum then potential mineralization.

Site	**Time**	NH^{+}_{4}	NO^{-}_{3}	**PMN?**
East Native	**0**	23	0.00	0
	1	4.96	0.00	Immobilize
	2	0.36	0.00	Immobilize
	3	0.88	0.00	Immobilize
	4	1.39	0.00	**Immobilize**
East Cultivated	**0**	7.5	0.00	0
	1	3.86	6.83	Mineralize
	2	4.13	32.62	Mineralize
	3	1.66	30.60	Mineralize
	4	7.55	33.96	**Mineralize**
West Native	**0**	37.5	0.00	0
	1	4.42	12.62	Immobilize
	2	5.59	48.18	Mineralize
	3	4.34	44.18	Mineralize
	4	1.22	42.59	**Mineralize**
West Cultivated	**0**	13	0.00	0
	1	0.43	9.50	Immobilize
	2	5.28	0.00	Immobilize
	3	3.57	37.84	**Mineralize**
	4	2.43	35.79	Mineralize

Pasture Native	**0**	10.5	0.00	0
	1	0.94	20.49	Mineralize
	2	22.00	0.00	Mineralize
	3	59.45	0.00	Mineralize
	4	53.63	147.24	**Mineralize**
Pasture Irrigated	**0**	28	0.00	0
	1	35.78	0.00	Mineralize
	2	26.71	205.02	Mineralize
	3	3.99	135.23	Mineralize
	4	0.78	26.16	**Mineralize**

Table A3.2. Abundance of the top 10 phyla from the study, along with the 'Other' phyla that make up the remaining 5-15% of the community at each site.

Phylum	East Cultivated	East Native	Pasture Native	Pasture Irrigated	West Cultivated	West Native
Acidobacteriota	22.51	18.04	13.70	15.61	20.99	21.15
Actinobacteriota	9.28	25.02	19.73	11.88	13.98	21.01
Bacteroidota	3.39	2.95	3.57	1.85	2.43	2.69
Chloroflexi	12.62	17.48	14.43	26.48	10.56	8.91
Crenarchaeota	22.90	8.20	14.49	6.40	18.57	22.06
Firmicutes	1.47	1.51	3.42	5.80	1.80	1.18
Gemmatimonadota	1.22	1.43	1.91	1.64	1.40	1.91
Planctomycetota	8.20	4.95	9.54	5.45	8.06	2.77
Proteobacteria	10.92	7.86	11.35	10.95	13.64	3.79
Verrucomicrobiota	3.66	2.03	2.89	7.46	3.65	7.58
Other	3.85	10.54	4.97	6.47	4.93	6.93

Table A3.3. Represents the p values from ANOVA analysis of microbial alpha diversities between sites. If $p < .05$, the value is bolded.

Comparison	Shannon	Simpson	Chao1
East Native-East Cultivated	**0.0237**	**0.0292**	0.0633
Pasture Native-East Cultivated	**0.0371**	0.1224	**0.0340**
Pasture Irrigated-East Cultivated	0.2924	0.0716	0.7376
West Cultivated-East Cultivated	0.9473	0.9958	0.9328
West Native-East Cultivated	1.0000	0.5558	0.9795
Pasture Native-East Native	0.9998	0.9478	0.9988
Pasture Irrigated-East Native	0.6298	0.9934	0.4799

West Cultivated-East Native	0.1008	**0.0128**	0.2678
West Native-East Native	**0.0241**	**0.0018**	0.1910
Pasture Irrigated-Pasture Native	0.7767	0.9993	0.3014
West Cultivated-Pasture Native	0.1535	0.0552	0.1544
West Native-Pasture Native	**0.0378**	**0.0072**	0.1070
West Cultivated-Pasture Irrigated	0.7471	**0.0317**	0.9969
West Native-Pasture Irrigated	0.2969	**0.0042**	0.9798
West Native-West Cultivated	0.9500	0.8225	0.9999

Table A3.4 ANOVA and Tukey HSD from alpha diversity of the microbiome being explained by the Soil Electrical Conductivity (SEC). The qualitative values represent SEC (low < 3 dS/m and high >3 dS/m).

SEC	Shannon	Simpson	Chao1
Low-High	**0.0001**	**0.0000**	**0.0028**

Table A3.5 Pearson's Correlation of Soil properties and alpha indices, bolded indicates significance (p< .05)

	Shannon	Simpson
Soil N	0.27	0.49
SOC	0.27	0.48
CCE	0.79	0.63
EC	**0.83***	0.76
Sand	0.38	0.55
Silt	-0.6	-0.75

Table A3.6: Data from PERMANOVA/ADONIS tests for categorical and numeric variables' effects on β-diversity patterns based on the bray-curtis distance matrix, across all sites.

Variable	R2	F	P-Value
Site	**0.713**	5.976	<.001
Land use type	**0.372**	4.447	<.001
Location	0.273	2.827	<.001
Management	0.171	3.331	<.001

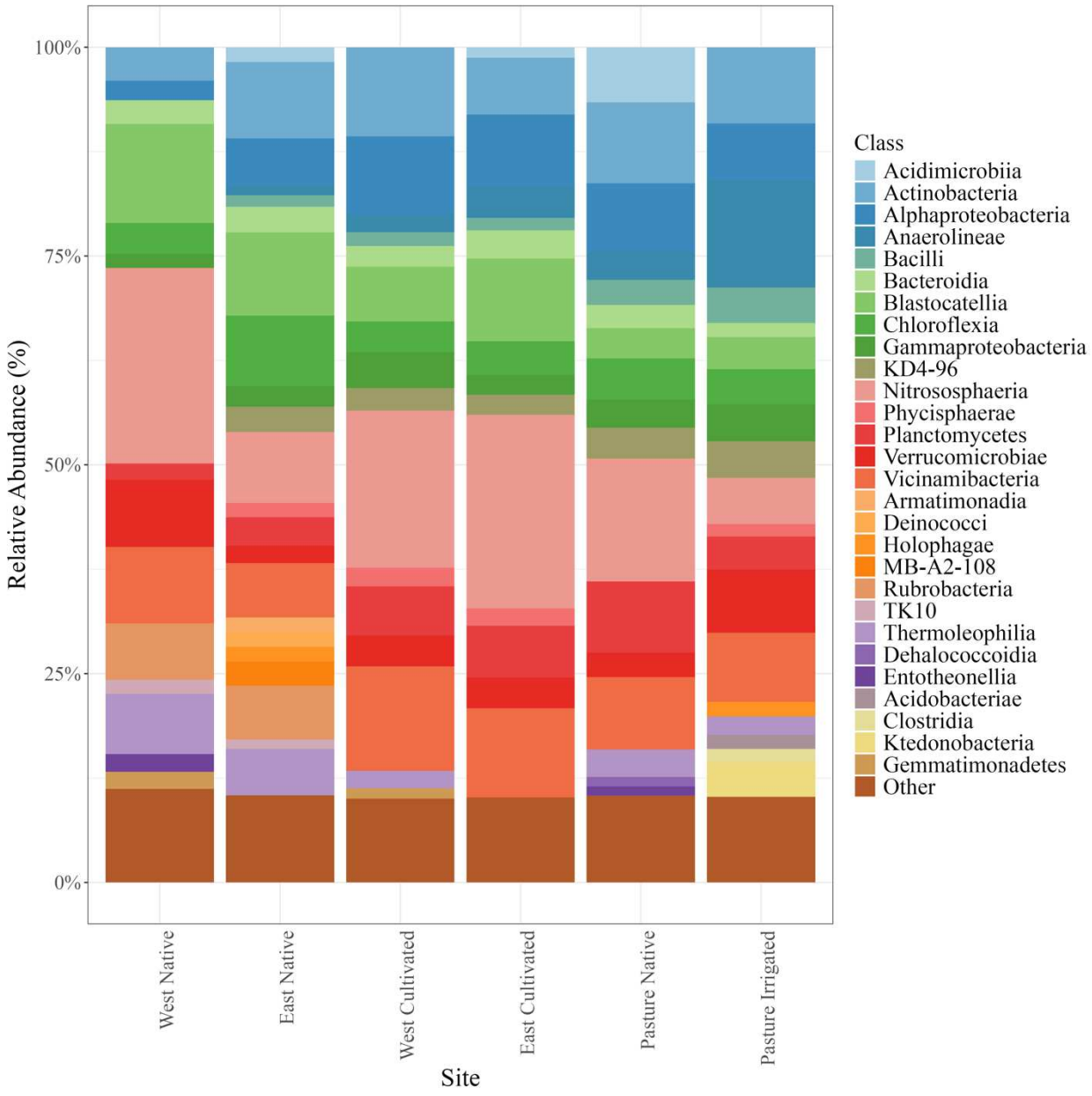

Figure A3.1 Relative Abundance of top 90% classes within each site. The microbiome was defined as ASVs with prevalence >4 in a sample/site (n=3).

Total elemental per site, measured in ppm (mg/kg-soil) by ICP-OES.

Site	Ca (ppm)	Fe (ppm)	Mg (ppm)	K (ppm)	Al (ppm)	Na (ppm)	P (ppm)	Mn (ppm)	S (ppm)
West Native	3934.3	11191.8	2692.1	2687.3	7587.8	104.8	427.7	714.4	188.7
West Cult.	4322.2	13830.9	2057.3	1747.0	5132.0	157.0	566.8	583.3	144.5
East Native	32798.7	6663.2	4230.1	2635.4	2313.2	660.4	575.3	440.8	109.3
East Cult.	5491.2	8188.0	2166.4	1753.5	2889.8	178.6	488.8	363.6	146.8
Pasture Native	15937.0	13272.7	4538.3	3686.9	5465.0	3165.1	652.5	351.6	2589.6
Pasture Irrigated	7830.7	10334.3	2862.5	3024.6	6374.3	672.7	564.7	203.9	2593.6