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Gasch, Caley, K, Recovery of soil properties, sagebrush steppe community structure, and environmental heterogeneity following drastic disturbance and reclamation, PhD, Department of Ecosystem Science and Management, Program in Ecology, December, 2013.

The objective of this research was to investigate vegetation and soil property structure in sagebrush steppe ecosystems as they recover from drastic disturbance, particularly in assessing the variability of properties across space. On reclaimed pipelines, I collected vegetation data and analyzed soil for organic carbon, total nitrogen, microbial community structure, moisture, salinity, and alkalinity. Using a Bayesian hierarchical mixed model, I quantified soil properties with posterior predictive distributions to compare reclaimed areas with the reference areas. The variance of most soil properties was affected by disturbance, and not always accompanied by a shift in the mean. Distributions for soil properties in reclaimed areas became more similar to those of undisturbed reference areas as recovery time increased. I then explored the differences in sampling designs, analysis, and inference gained from spatial and non-spatial soil data. I also conducted side-by-side analyses of each data type for a reclaimed area and an undisturbed area. The analysis of random data revealed differences in soil property averages between treatments. These differences were also apparent in the geostatistical analysis, which also provided information about the spatial structure in soil properties at the scale of individual plant effects (10 cm – 10 m). The third project expanded the assessment in both space and time, by including reclaimed pipelines that spanned 55 years, and by sampling at a scale up to 100 meters. I used Bayesian geostatistical models to quantify the correlation structure and to create surface predictions for measured properties. The reclaimed areas maintained uniform grass cover with

low diversity and shrub establishment, while the responses of soil properties to disturbance and reclamation were variable. All three modeling approaches indicated that soil properties closely associated with vegetation experienced reduced variability and homogenization across space following disturbance. Soil abiotic properties appeared to be affected by the physical effects of disturbance, but were not associated with homogenization. Development of belowground heterogeneity was possibly delayed by the slow recovery of the plant community, particularly the shrub component. This research illustrates some long lasting ecological consequences of disturbance in sagebrush steppe and emphasizes the need for establishing shrubs in reclaimed sagebrush steppe.

RECOVERY OF SOIL PROPERTIES, SAGEBRUSH STEPPE COMMUNITY STRUCTURE, AND ENVIRONMENTAL HETEROGENEITY FOLLOWING DRASTIC DISTURBANCE AND RECLAMATION

by

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CHAPTER 1

Background and Introduction

Sagebrush steppe rangelands have historically occupied an estimated 44.8 Mha of land in western North America (West, 1983), and approximately 11 Mha of land area in Wyoming is currently classified as sagebrush steppe or sagebrush shrubland (United States Geological Survey, 2010; West, 1983). Thus, 24.3% of land area classified as sagebrush steppe is within the state of Wyoming. The sagebrush steppe provides habitat for wildlife species including nearly 450 mammals, birds, amphibians, and reptiles (Wyoming Interagency Vegetation Committee, 2002), and likely many other species (including invertebrates). Many of "Wyoming's Species of Greatest Conservation Need" depend on sagebrush dominated habitats for all or a portion of their life, including the Greater sage-grouse (*Centrocercus urophasianus*) and many other bird, rodent, small mammal, and bat species (Wyoming Game and Fish Department, 2005). Sagebrush steppe rangelands in Wyoming are also used for domestic livestock grazing, cultural and recreational use, and mineral and energy extraction (Wyoming Bureau of Land Management, 2012). In addition to these ecosystem services, sagebrush steppe rangelands support biodiversity, biomass production, biogeochemical cycling, water capture, retention, and purification, and food and fiber production (Brown and MacLeod, 2011; Sustainable Rangelands Roundtable, 2008,). Also of interest is the ability of sagebrush steppe rangelands to capture atmospheric carbon and store it as recalcitrant organic matter and inorganic calcium carbonate in soils (Lal, 2004; Schlesinger, 2000; Schuman et al., 2002). Clearly, sagebrush steppe ecosystems impart great value to humans and the environment because of the vast area they occupy and the goods and services they provide.

Sagebrush steppe is characterized as semiarid plant community dominated by big sagebrush (*Artemisia tridentata* Nutt.) species and associated perennial grasses (West, 1983). In addition to the fairly distinct plant community composition, the sagebrush component imparts distinct spatial patterns on the distribution of other plant species and these patterns in the vegetation are associated with the spatial distribution of soil physical, chemical, and biological characteristics and ecosystem processes. This phenomenon is well studied in arid and semiarid shrublands, and researchers have bestowed shrubs with creating and maintaining hotspots of nutrients, water, and biotic activity, coined "islands of fertility" (Crawford and Gosz, 1982; Noy-Meir, 1985; Schlesinger, 1996; Schlesinger and Pilmanis, 1998; Yu and Steinberger, 2012). In general, sagebrush steppe ecosystems have very patchy structure in vegetation and soil properties (West, 1983), low rates of organic matter turnover ("tight" nutrient cycles), and high dependence on biologically available water and labile substrate (Burke, 1989; Burke et al., 1989; Mummey et al., 1997).

Environmental heterogeneity, in general, imparts essential, yet complex consequences on an ecosystem and its biota. Heterogeneity influences where organisms are, how they interact with one another, and their fate (reproductive and survival success, predation risk, growth, and resource acquisition), and these characteristics occur at variable temporal and spatial scales (Weins, 2000). As such, the patchiness and distinct spatial variability of the sagebrush steppe imparts effects that extend beyond soils and neighboring vegetation. Specifically in the sagebrush steppe, wildlife species depend on vegetation species and functional group diversity and variability in vegetation vertical and horizontal structure. Greater sage-grouse require sagebrush stands with varying shrub height and canopy cover for nesting (Hagen et al., 2007; Kirol et al., 2012), but also need a diverse understory of forbs and grasses to accommodate

seasonal shifts in diet (Connelly et al., 2000; Crawford et al., 2004). Other sagebrush obligates have different requirements, for instance, Sage sparrows, Brewer's sparrows, and sage thrashers nest in the sagebrush canopy, but have different preferences for sagebrush stand density, continuity, and understory composition (summarized by McAdooo et al., 2004). Small mammals, ungulates, and reptiles have yet different habitat preferences, which may relate to variable sagebrush age and size structure, shrub density, and shrub patchiness—all dependent at scales specific to the wildlife species of interest (summarized by McAdoo et al., 2004). Clearly, heterogeneity within the sagebrush steppe, from microhabitat to landscape scales, is important for supporting a diverse collection of wildlife species, as well as supporting individual species that have seasonal dependence on a variety of unique habitat characteristics. Successful management of sagebrush steppe, especially in a restoration context, should recognize the importance of establishing and maintaining heterogeneity within the sagebrush steppe ecosystem.

Among the most devastating effects to sagebrush steppe ecosystems, are drastic disturbances associated with energy extraction, processing, and transportation. These disturbances remove vegetation and remove, mix, and store the top 15 cm of soil. Following disturbance, restoration efforts of semiarid ecosystems face many challenges (reviewed by Allen, 1995), and aboveground and belowground effects are long lasting. Specifically, disturbed and reclaimed areas have lower vegetation diversity (Bowen et al., 2005), soil organic matter (Ganjegunte et al., 2009; Wick et al., 2009,), microbial biomass (Anderson et al., 2008; Dangi et al., 2012; Mummey et al., 2002), and altered soil structure (Wick et al., 2009). Furthermore, previously collected datasets indicate a reduction in soil property variability following disturbance, as indicated by the coefficient of variation (Table 1.1).

Table 1.1: Coefficients of variation for soil properties at two depths in reclaimed mine soils and undisturbed reference soils. (Stahl and Huzurbazar, unpublished data).

Soil Property	Reclaimed		Undisturbed	
	0-5 cm	5-15 cm	0-5 cm	5-15 cm
pH	3	2	6	4
Electrical Conductivity	24	26	41	36
Bulk Density	6	9	25	10
Organic Carbon Content	59	76	97	79
Total Carbon Content	35	64	43	79
Total Nitrogen Content	7	35	37	54
Microbial Biomass Content	31	42	58	56
AM Fungi Biomass Content	38	58	64	116
Collembola sp. Numbers	150	91	157	57
Nematode Numbers	70	63	71	74

Based on our knowledge of the structural characteristics of the sagebrush steppe (both above- and belowground), the effects of drastic disturbance on vegetation and soil properties, and observations in the field and from previously collected data, I suspect that disturbance impacts the degree of environmental heterogeneity within sagebrush steppe. Specifically, I hypothesize that disturbance alters the vegetation and soil characteristics, primarily by reducing plant species diversity, soil microbial abundance, and soil organic carbon and nitrogen content. Additionally, I expect that the vegetation community following reclamation maintains low diversity and uniform coverage, and associated soil properties will also display homogenization compared to the pre-disturbance state. I predict that the degree of vegetation and soil variability will increase over time as the shrub component recovers, and that vegetation and soil properties will demonstrate coupled spatial patterns as recovery time increases.

The overall objective of this research was to investigate aboveground and belowground ecosystem structure (abundance, variability, and spatial distribution of properties) of sagebrush steppe as it recovers from drastic disturbance. I developed three separate, but related research projects to meet this objective, with sub-objectives as follows:

1. Examine soil properties on disturbances of different ages, in terms of Bayesian posterior predictive distributions, to better understand how disturbance and recovery influence the nature of the property, and to better assess similarity of a reclaimed area to undisturbed reference sites.
2. Illustrate differences in statistical applications and inference between spatially explicit and randomized soil data, while simultaneously investigating the impacts of recent reclamation on soil properties at a spatial scale less than ten meters.
3. Assess the effects of disturbance, reclamation, and recovery time on vegetation and soil property spatial distribution at a 100 m scale using Bayesian geostatistical modeling.

The following three chapters are designed as individual manuscripts prepared for submission to peer review journals (Chapter 1: Applied Soil Ecology; Chapter 2: Ecological and Environmental Statistics; Chapter 3: Soil Biology and Biochemistry). I expect this research to contribute to the knowledge bases of soil ecology, restoration ecology, and ecological and applied statistics.

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CHAPTER 2

Measuring soil disturbance effects and assessing soil restoration success by examining distributions of soil properties

Abstract

Successful restoration of an ecosystem following disturbance is typically assessed according to similarity between the restored site and a relatively undisturbed reference area. While most comparisons use the average parameter to represent measured properties, the variance in the properites may assist in a more robust assessment of site recovery. Our purpose was to compare soil properties in different ages of reclaimed soils to reference areas in a manner incorporating the range of values existing within the reference area and each treatment. We examined soil properties on a chronosequence of reclaimed natural gas pipelines spanning recovery ages of <1 year to 54 years. For two consecutive years, we measured soil moisture, organic carbon, nitrogen, electrical conductivity, pH, and microbial abundance. We analyzed our data with a Bayesian hierarchical linear mixed model, which produced posterior predictive distributions and assisted in treatment comparisons. This type of model also allowed us to quantify the probability that a soil property in a reclaimed treatment was similar to that of the undisturbed reference soil. We observed the variance of most soil properties was particularly sensitive to disturbance and reclamation—especially within the first few years of recovery. Response of the variance to disturbance, reclamation, and recovery was not necessarily accompanied by a shift in the mean value of the property. Patterns for all soil properties changed over time, with soil properties generally becoming more similar to those of the undisturbed reference sites (in terms of their mean and variance) as recovery time increased. We suspect these trends in altered variability

coincide with the degree of spatial heterogeneity in soil properties existing following disturbance and reclamation, which is coupled to patterns of vegetation recovery.

2.1. Introduction

Disturbances that remove vegetation and temporarily remove and mix topsoil (hereafter "disturbance") have lasting effects on above- and belowground ecosystem properties. Such disturbances are associated with extraction and transportation of fossil fuels, minerals, and other resources, and are widespread in the semiarid sagebrush steppe of intermountain North America. Restoration of semiarid ecosystems faces many challenges (reviewed by Allen, 1995), and successful restoration of sagebrush steppe is influenced by soil and micro-topographical characteristics (Chambers, 2000) and climate and precipitation patterns (Bates et al., 2006). As expected, disturbance in semiarid steppe results in reduction of plant species diversity and native plant species abundance, and revegetation efforts face multiple challenges (Allen, 1995; Bowen, 2005; Wick, 2011). These aboveground effects are coupled with reduced soil organic carbon and nitrogen pool sizes (Anderson et al., 2008; Ganjegunte et al., 2009; Mummey et al., 2002; Wick et al., 2009a), and reduced mineralization rates (Ingram et al., 2005). Soil microbial communities also experience declines following disturbance (Dangi et al., 2012; Mummey et al., 2002; Stahl et al., 1988). These previously collected data suggest vegetation and soil properties are regularly affected by disturbance (consistently negatively), and these effects may last in excess of 15-20 years (Mummey et al., 2002; Wick et al., 2009a).

The goal of restorationists is to "assist the recovery of ecosystems that have been degraded, damaged, or destroyed" to a stable, self-supporting state (Society for Ecological Restoration International Science and Policy Working Group, 2004). We use a historical or

adjacent undisturbed reference site as an example of the specific site conditions that a recovered system should approximate (Aronson et al., 1995; White and Walker, 1996). Ecological condition of the restored and reference sites may be assessed through measurements of ecosystem structure and function, specifically: organism identity, abundance, and distribution; carbon and nutrient pools and transformation rates; soil chemical condition; water cycling; and site resistance to further degradation (Aronson et al., 1993; reviewed in detail by Whisenant, 1999).

The average value of a property is the commonly used parameter for making comparisons across treatments. Like an average parameter, the degree of variability of a property (the "spread" of its values) holds ecological relevance and has been recognized as a parameter of specific interest (Benedetti-Cecchi, 2003; Micheli et al., 1999; Palmer et al., 1997). As such, the variability of ecosystem properties should be a consideration in the selection and use of reference sites in restoration settings (White and Walker, 1996). Understanding the patterns of variability that existing in the undisturbed state can inform an acceptable range of values for indicating a property's recovery. Furthermore, a change in a property's variance in response to perturbation aids in our understanding of the ecological consequences of disturbance, stability, and recovery (Collins, 1992; reviewed by Fraterrigo and Rusak, 2008).

When incorporating an explicit assessment of variability in an analysis, commonly used mean comparison methods (t-test, analysis of variance) fall out of favor because of the homoscedasticity assumption in which variances must be equal across groups. Fraterrigo and Rusak (2008) present a selection of analytical approaches to detecting changes in variability across disturbance treatments—many of which require equal means across treatments or specific characteristics in the distribution of the data. However, it is desirable to have an approach

allowing us to directly examine the characteristics of a property across experimental treatments, regardless of equal means or heteroscedasticity.

Bayesian models require that groups be independent, while other restrictive assumptions of the frequentist statistical approaches are alleviated. In a Bayesian model, each treatment group is allowed to have its own mean and variance, which are conditional on the observations, so that the data model assumes a distribution accordingly. Through simulation, we construct posterior distributions for parameters of interest (*i.e.* mean, variance, shape, scale, degrees of freedom, regression coefficients, error terms, etc.) and we can directly compare them across treatment groups. Furthermore, we can generate posterior predictive distributions to examine the property of interest directly, as it reflects the model parameters and the data. Posterior predictive distributions provide an intuitive way to explore differences in treatment groups through simultaneous examination of the mean and variance of a property.

Figure 2.1 illustrates this approach, where the distributions represent the posterior predictive density of a given property (*P*) observed and modeled for two treatment groups. In scenario A, the treatments have equal means and equal variances; in scenario B, the treatments have equal means, but different variances; and so on. We can compare distributions to understand how the property differs across treatment groups, by either visually examining the relative location and shapes of the plots, or by quantifying overlap of treatments. The latter corresponds directly to the probability the property will assume similar values across the overlapping treatments. For instance, groups in Figure 2.1 scenario A have high probability of similarity, while groups in scenario D have low probability of similarity. Furthermore, we can compute 95% credible intervals, which indicate the range of values for which 95% of the probability lies—and these can also be compared for proximity and overlap. From this type of

analysis, we do not obtain a p-value, but when two treatments are different, we can infer how the nature of the data influences the difference (i.e. is it due to a difference in means, variances, or both?). Examination of posterior predictive distributions provides a visual and intuitive method for treatment comparison. This approach is discussed in general in Gelman and others (2004) and Christensen and others (2011) and demonstrated for a soil science application in Wick and others (2009b) and Huzurbazar and others (2013).

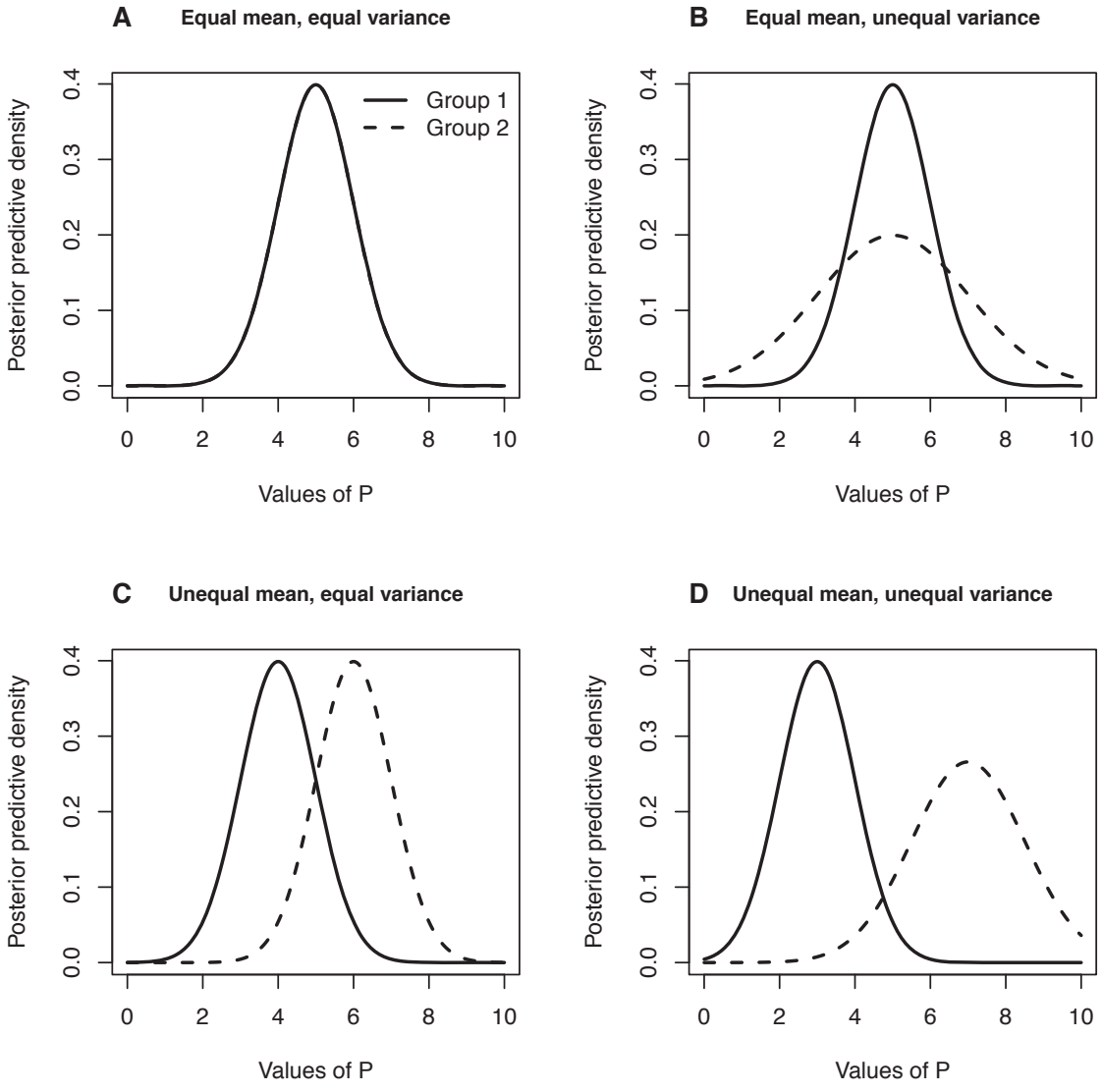

Figure 2.1: A conceptual diagram that illustrates group comparisons for any soil property (*P*) using posterior predictive distributions that have different means and variances. The area of distribution overlap corresponds to the probability that *P* will be similar for both groups.

Group comparisons based on examining distributions can refine our assessment of ecosystem recovery relative to reference sites; we believe distribution comparisons are superior to currently used comparison approaches. Our purpose is twofold: (1) to examine soil properties on disturbed soils of different ages, in terms of both their mean and variance, to better understand how disturbance and recovery influences the nature of the properties; and (2) to directly compare properties of restored soils to reference soils in a manner that indicates the probability of similarity and illuminates the factors influencing remaining differences.

2.2. Materials and Methods

2.2.1. Study site description and sampling design

The field sampling location was located near Wamsutter, Wyoming (41° 41’ 17.11” N, 107° 58’ 24.41” W, elevation = 2052 m). This site lies within Wyoming’s Red Desert Basin and receives an estimated average 180 mm (historic high: 346 mm, historic low: 96 mm) of precipitation per year (Western Regional Climate Center, 2010). The Red Desert is dominated by vegetation associated with Big Sagebrush (*Artemisia tridentata* Nutt.) and Greasewood (*Sarcobatus vermiculatus* (Hook.) Torrey). All research plots were established in Sagebrush steppe vegetation communities. Soils are classified as frigid typic haplocalcids: well draining, non-saline to slightly saline, calcareous soils originating from weathered sandstone (Natural Resources Conservation Service, 2012).

All research plots were established on a reclaimed pipeline corridor, wherein pipelines were installed directly adjacent to one another, allowing for climate, topography, and parent material to be consistent across study plots. The different installation dates allow for establishment of a chronosequence, or space-for-time substitution. This approach has effectively

been used to examine the effect of time on soil development or soil and vegetation recovery following disturbance (Fraterrigo et al., 2005; Insam and Domsch, 1988; Jastrow, 1996; Johnson et al., 1991; Li et al., 2010; Miller and Jastrow, 1990). Exact reclamation practices and seeding mixes were variable between pipeline disturbances, but all installations entailed removal and windrowing of topsoil (top 15 cm), soil storage (3-6 months), subsoil compaction and trenching, topsoil respreading, and seeding.

Two undisturbed reference sites and five reclaimed pipelines were sampled, with pipeline treatments including the following recovery times (in years): <1, 4, 28, 35, and 54 (in 2010). On each pipeline and on each reference area (one on either side of the pipeline corridor), three 40 meter transects were randomly established toward the center of the pipeline scar (and oriented parallel to the pipeline), which served as the basis for all sampling. The entire sampling area, including all treatments, fell within approximately one hectare. Vegetation and soil sampling was conducted during springs of 2010 and 2011 during periods of active vegetation growth and prior to vegetation senescence.

2.2.2. Vegetation and soil sampling and analysis

Vegetative cover and ground surface characteristics were assessed via the basal cover method, with species and ground surface observations noted every 0.5 meters along the 40 m transect (Bonham, 1989). The endpoint of each transect served as a location for a one-square meter quadrat, wherein all herbaceous biomass was clipped at the soil surface, dried at 65 °C for 24 hours, and weighed.

Four randomly located points along each transect served as locations for soil sampling for assessment of key soil characteristics (moisture, pH, electrical conductivity, carbon and nitrogen analysis, and microbial community structure). The top five centimeters of soil were collected

with a trowel. All soils were frozen in the field with dry ice, and then transported to a freezer (-20 °C) until analysis. Three additional points were randomly located within each treatment wherein the top five centimeters were sampled with a hammer-driven corer. These samples were analyzed for particle size, bulk density, and root biomass.

Soils collected for particle size, bulk density, and root biomass were dried at 105 °C until constant mass, and bulk density was calculated based on the known core volume (101.29 cm) (Blake and Hartge, 1986). Samples were then sieved to 2 mm to remove coarse fragments and large litter and debris. Roots were air-elutriated from soils using a seed and chaff separator, dried, and weighed. Forty grams of soil were then assessed for particle size using the hydrometer method (Gee and Bauder, 1986).

Soil samples were weighed, lyophilized, and re-weighed to obtain gravimetric moisture content of field-moist soil. Dry soil was sieved to 2 mm to remove coarse fragments and debris. Ten grams of dry soil were combined with 10 mL of deionized water, and the pH of the slurry was assessed using a SympHony pH meter (VWR, Randor, PA) (Thomas, 1996). The supernatant of the slurry was analyzed for electrical conductivity using a SympHony conductivity meter (VWR, Randor, PA) (Rhoades, 1982). Remaining soil was pulverized and approximately 20 mg were assessed for elemental carbon and nitrogen content by combustion with a Costech 4010 (Valencia, CA). Inorganic carbon (calcium carbonate) was assessed on 0.5 gram samples using the modified pressure-calcimeter method (Sherrod et al., 2002). Soil organic carbon was estimated as the total carbon less the inorganic carbon.

Phospholipid fatty acid (PLFA) analysis was modified from Frostegård et al. (1993). Five grams of lyophilized soil was sonicated and shaken with 20 ml of a 1:2:0.8 mixture of chloroform, methanol, and phosphate buffer (0.05 M, pH 7.4). Phospholipids were isolated with

a silica chromatography column, methylated in alkaline 0.2 M methanolic potassium hydroxide, and purified in an amino-propyl chromatography column. Extracts were suspended in 200 µl solution of 1:1 solution of methyl *t*-butyl ether and hexane containing 25 µg ml^{-1} of an internal standard (20:0 ethyl ester). Fatty acid methyl esters were analyzed on an Agilent 6890 Gas Chromatograph (Palo Alto, CA) using Sherlock software (MIDI, Inc., Newark, NJ). Microbial fatty acids by functional group included bacteria (i14:0, i15:0, a15:0, i16:0, 16:1ω9c, i17:0, a17:0, cy17:0, 18:1ω9c, cy19:0), saprotrophic fungi (18:2ω6c) and protozoans (20:3ω6c, 20:4ω6c) as in Vestal and White (1989), Frostegård and Bååth (1996), and Zelles (1999) and arbuscular mycorrhizal fungi (16:1ω9c) as in Olsson (1999). Sample summary statistics were computed for each microbial group. Total microbial abundance was estimated as the sum of all signatures and included as a soil property for statistical modeling.

2.2.3. Statistical modeling and analysis

Each reclaimed pipeline was subject to different reclamation histories and microsite conditions and was considered an independent treatment, rather than as a point in a time series. We were also only interested in comparing our key soil properties across treatments; thus, general soil properties (bulk density, particle size, texture) and vegetation properties were not statistically analyzed. Sample descriptive statistics were compiled to help describe the field site, rather than explore impacts of disturbance and reclamation on those properties.

We employed a Bayesian hierarchical linear mixed model to obtain posterior densities of model parameters and posterior predictive densities of the soil properties of interest. Gili et al. (2013) present frequentist applications of hierarchical linear mixed models for nested soil sampling designs. That model forms the basis of the likelihood for the Bayesian model, and allows us to incorporate the nested nature of our data (observations within treatments within

years), to explicitly obtain estimates of mean and variance parameters, partition sources of variation, and still examine trends in reclamation treatments in terms of the soil properties of interest.

2.2.3.1 Data model (to obtain likelihood):

$$P_{ijk} \mid \mu_{jk}, \beta_j, \tau_{jk}, \alpha_{j(k)} \sim independent\ Normal\ (\mu_{jk}, \tau_{jk}) \quad \textbf{(2.1)}$$

$$\mu_{jk} = \beta_j = \alpha_{j(k)} \quad \textbf{(2.2)}$$

In equation 2.1, the notation '~' denotes 'is distributed as' with *P* denoting any soil property on which data is collected at $i = 1 \ldots 12$ locations (observations) in $j = 1 \ldots 7$ treatments over $k = 1, 2$ years. Given the parameters to the right of the '|', the properties P_{ijk} are (conditionally) independent, and each P_{ijk} has a normal distribution with mean μ_{jk} and precision, τ_{jk}, which is the inverse of the variance ($\tau = (1/\sigma^2)$). The mean model (equation 2.2) allows for each treatment to have a mean value (β_j), while the nested effect ($\alpha_{j(k)}$) accounts for variability due to treatment within year. Each P_{ijk} contributes a normal distribution to the overall data model, which, as a function of all the parameters (collectively called θ), gives the likelihood function, $L(\theta \mid P_{111,\ldots} P_{12,7,2})$, namely, a function of θ the given all the data.

2.2.3.2 Prior models: The final prior model is a product of the probability distributions arising from the following distributional assumptions,

$$\beta_j \mid \mu_\beta, \tau_\beta \sim\ independent\ Normal\ (\mu_\beta, \tau_\beta) \quad \textbf{(2.3)}$$

$$\alpha_{j(k)} \mid \tau_\alpha \sim\ independent\ Normal\ (0, \tau_\alpha) \quad \textbf{(2.4)}$$

$$\mu_\beta \sim Normal\ (0, 0.001) \quad \textbf{(2.5)}$$

$$\tau_{jk}, \tau_\beta, \tau_\alpha \sim Gamma\ (0.001, 0.001) \quad \textbf{(2.6)}$$

The mean model parameters (β_j and $\alpha_{j(k)}$) are modeled hierarchically to allow dependence of samples within a treatment. All terminal nodes ($\mu_\beta, \tau_{jk}, \tau_\beta, \tau_\alpha$) are assigned conjugate, non-informative priors. See Gelman et al. (2004) for prior assignment for a similar hierarchical linear model.

2.2.3.3 Posterior probability distribution: The prior probability distribution for all the parameters is updated given the data via the following equation,

(2.7)

$$\Pr\left(\theta \middle| P_{1,1,1}, \ldots P_{12,7,2}\right) = \frac{\mathrm{L}(\theta \,|P_{1,1,1}, \ldots P_{12,7,2}) \cdot \Pr(\theta)}{\int \mathrm{L}(\theta \,|P_{1,1,1}, \ldots P_{12,7,2}) \cdot \Pr(\theta)}$$

The posterior probability (Pr) distribution of the model parameters (θ), conditional on the data ($P_{1,1,1}, \ldots P_{12,7,2}$), is the integral of the likelihood function times the prior distribution (equations 2.3 – 2.6). As described below, this integration is performed via numerical methods. Also, if one is only interested in the parameters such as the means and variances, one would stop with this step, obtain posterior distributions and draw conclusions. To obtain distributions of observables, one can go a step further and obtain a predictive distribution.

2.2.3.4 Posterior predictive probability distribution of observables:

$$\Pr(\widetilde{P_{jki}} \,|P_{1,1,1}, \ldots P_{12,7,2}) = \int_\theta \Pr(\widetilde{P_{jki}} \,|\theta) \cdot \Pr\left(\theta \middle| P_{1,1,1}, \ldots P_{12,7,2}\right) d\theta \qquad \textbf{(2.8)}$$

The posterior predictive probability distribution of a soil property ($\widetilde{P_{jki}}$), is conditional on all the data ($P_{ijk}, i = 1,..01, j = 1,..7, k = 1,0$), but averaged over the posterior distribution of the parameters via the integration. Rather than analytically performing the integrations in equations 2.7 and 2.8, the posterior densities are obtained through Markov chain Monte Carlo (MCMC) sampling (see Carlin et al, 2006; Gilks et al., 1996). The MCMC algorithm produces a set of

samples drawn from the posterior (2.7) or posterior predictive distributions (2.8), which are then compiled into kernel density estimates of the posterior and posterior predictive distributions.

In some cases, posterior distributions included zero and negative values. Because our soil property measurements exist as continuous values on the positive real line, we constrained the sampling to positive values by applying a log-normal data model. For modeling organic carbon, electrical conductivity, and total microbial abundance, we simply obtained the natural log of the observed values and applied the same data model and prior model to the log-transformed values. Posterior predictive samples were then exponentiated to obtain the posterior densities on the original scale.

To ensure the prior model was non-informative, we examined posterior distributions generated with different prior distributions and hyperparameter values. In all cases, the observations overwhelmed the choice of prior model, which did not alter the posterior distributions. All models were simulated by three chains for 150,000 iterations, with the first 500 iterations eliminated for burn-in period, and thinning by five to eliminate chain autocorrelation. The software generated initial values for all models. A total of 90,000 iterations were included for posterior inference. Deviance and chain behavior were assessed through examination of trace plots, which displayed chain convergence and mixing for the selected set of iterations (see Carlin et al., 2006 for a discussion of MCMC computation and diagnostics). We assessed model fit by generating replicated values from posterior predictive distributions and compared them to the observed values (included in supplemental Figure S2.1). We were satisfied to find that the majority of predicted values and their 95% credible intervals (the range of values that encompass 95% probability around the estimate) overlapped with the observed values, especially considering the small sample size.

To meet our second objective: the comparison of reclaimed soil properties to reference area soil properties; we computed the 95% credible interval for each reference area. By combining both reference area intervals and obtaining the outer bounds of the combined intervals, we defined a range of values having high probability of occurring in the undisturbed reference soils. This range incorporates variability across both reference areas, and serves as a basis for comparing reference and treatment distributions. We then computed the probability that a sample drawn from the posterior predictive distribution of a treatment fell within the reference interval. This probability represents the overlap of reference and treatment posterior predictive distributions, and indicates similarity between the two. We repeated this process with the 50% credible intervals. By constricting the reference range to include values closest to the center of reference soil distributions, we can gain a better understanding of which treatment distributions are most different. However, the probabilities may be slightly more difficult to interpret. In short, a probability of approximately 0.50 would indicate a fairly similar distribution to the reference, while a probability substantially lower would indicate a vastly different distribution. Additionally, a high probability would indicate most of the distribution falls within the center of the reference distribution. It is important to note that a low probability of falling within the 50% credible interval could be due to differences in either the mean or the variance of a distribution, whereas a high probability likely indicates only a difference (reduction) in the variance of a distribution.

All analyses were conducted using the open-source Markov chain Monte Carlo Gibbs sampling software JAGS for Mac OS X (mcmc-jags.sourceforge.net), in R for Mac OS X version 2.13 (www.r-project.org) using the rjags package (Plummer, 2012). All MCMC output

was managed with the coda package (Plummer et al., 2012). Example model code is included as supplementary material (Figure S2.2).

2.3. Results

Vegetation summary statistics are illustrated in Figure 2.2 with values in a supplementary table (Table S2.1), and general soil properties are listed in Table 2.1. In general, vegetation composition following reclamation was dominated by annual weedy species, but as recovery time increased, grasses dominated, and species richness increased, reflecting the recovery of the shrub and forb components. The most notable difference in soil physical properties was the increase in gravel in all reclaimed treatments. This can be attributed to mixing the soil profile, and incorporation of gravel found below 5 cm into topsoil, associated with the pipeline installation process.

Figure 2.3 includes the posterior predictive distributions for each soil property, in each treatment, and each year. Corresponding mean and standard deviation values of the posterior distributions are included in a supplementary table (Table S2.2). In 2010, soil moisture (Figure 2.3A) was consistently higher and more variable in the <1 year, 4 year, and 28 year old treatments than the undisturbed references, while the two oldest treatments had similar distributions to the undisturbed references. In 2011, soil moisture values were higher than in 2010. All reclaimed soils, except the 35 year old treatment, had more soil moisture than the reference soils, and again, the three youngest treatments had larger variance than the undisturbed reference values.

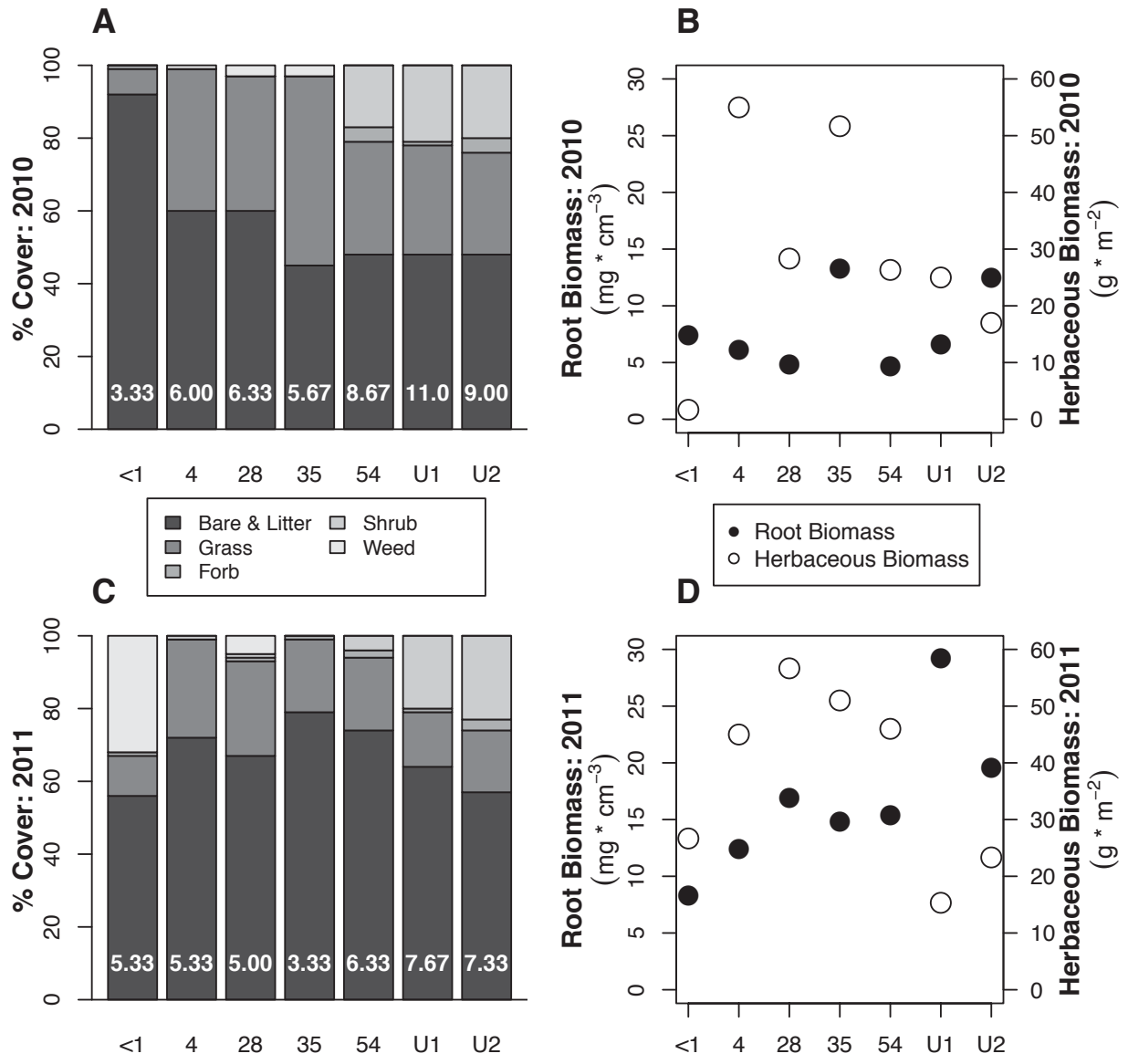

Figure 2.2: Vegetation properties for each treatment. Mean percent cover by plant functional group or bare ground and litter for 2010 (A) and 2011 (C) (n=3). Numerical values on bars represent mean species richness within a treatment. Mean root biomass (filled dots) and herbaceous biomass (hollow dots) for 2010 (B) and 2011 (D) (n=3). Values of sample means and standard error of the mean are included as a supplementary table (Table S1). Treatments are designated by recovery time (in years) or as undisturbed references (U1 and U2).

Table 2.1: General soil properties for each treatment with years combined. Treatments are designated by recovery time (in years) or as undisturbed references (U1 and U2). Values are sample mean, with standard error of the mean in parenthesis (n=6).

	Bulk Density ($g * cm^{-3}$)	**Gravel** (% by wt)	**Sand** (%)	**Silt** (%)	**Clay** (%)	**Textual Class**[§]
< 1 yr	1.68 *(0.09)*	1.64 *(0.39)*	69.71 *(2.46)*	13.25 *(1.03)*	17.04 *(1.56)*	SL
4 yrs	1.48 *(0.05)*	1.44 *(0.42)*	46.85 *(3.44)*	14.31 *(0.81)*	38.84 *(3.66)*	SC
28 yrs	1.50 *(0.06)*	5.05 *(1.08)*	69.72 *(2.92)*	13.25 *(0.91)*	17.03 *(2.11)*	SL
35 yrs	1.50 *(0.08)*	2.49 *(1.00)*	69.58 *(1.96)*	9.78 *(1.04)*	20.64 *(1.05)*	SCL
54 yrs	1.61 *(0.09)*	1.69 *(0.44)*	66.47 *(2.79)*	11.39 *(1.44)*	22.14 *(1.50)*	SCL
U1	1.42 *(0.06)*	0.65 *(0.22)*	51.81 *(3.89)*	12.67 *(0.95)*	35.52 *(4.02)*	SCL
U2	1.65 *(0.04)*	0.61 *(0.19)*	72.20 *(0.71)*	9.48 *(0.64)*	18.32 *(0.43)*	SL

[§] Textural Class codes: SL = Sandy Loam; SC = Sandy Clay; SCL = Sandy Clay Loam

The mean values of total soil nitrogen (Figure 2.3B) did not vary across treatments, or differ from the undisturbed reference soil values in either year. However, in all treatments the distributions were narrower, compared to the undisturbed reference soils, indicating a reduction in the variability of observed total nitrogen values following disturbance and reclamation. Soil organic carbon (Figure 2.3C) displayed a similar trend in 2011, with mean values similar to the undisturbed references across treatments, but with smaller variance. This effect was not observed in 2010; in fact, all treatments and reference soils had similar mean and variance values in 2010.

It is also notable that the oldest reclaimed soil (54 years old) had slightly less organic carbon in 2011 compared to all other soils.

The posterior predictive distributions of soil electrical conductivity (Figure 2.3D) and soil pH (Figure 2.3E) were generally shifted to the right in reclaimed soils compared to undisturbed references, indicating higher values following disturbance and reclamation. The effect of disturbance and recovery on the electrical conductivity variance was neither consistent across years nor predictable according to recovery time. Conversely, soil pH was consistently more variable in the reclaimed soils compared to the reference soils.

Total microbial abundance (Figure 2.3F) showed a distinct trend in 2010, with the three older treatments assuming distributions similar to the undisturbed references, but with the two youngest treatments displaying narrower distributions. Further, the <1 year old soil had lower microbial abundance, and the 54 year old soil had higher microbial abundance, compared to all other treatments and references. The pattern was not the same in 2011, when all soils had lower microbial abundance, and lower variance, especially in the three youngest treatments. Composition of major microbial groups, in terms of relative abundance, was not different across treatments or years (in supplemental Figure S2.3). Absolute abundance of each microbial group reflected the same trends observed in the total abundance values (Figure 2.3F).

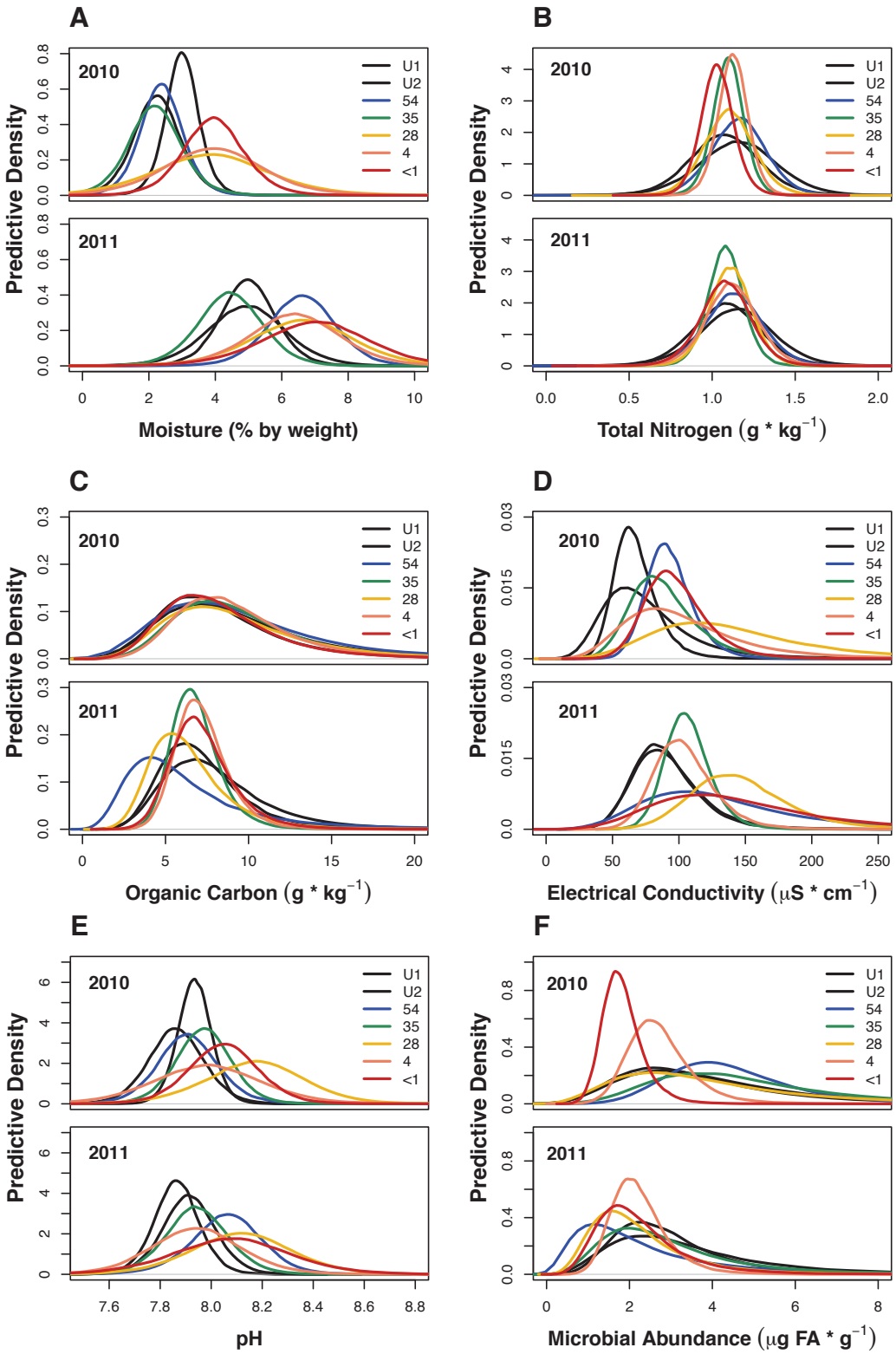

Figure 2.3: Posterior predictive distributions for soil moisture (A), total soil nitrogen (B), soil organic carbon (C), soil solution electrical conductivity (D), soil solution pH (E), and soil microbial abundance (F) measured in all treatments in 2010 and 2011. Treatments are designated by recovery time (in years) or as undisturbed references (U1 and U2).

The posterior predictive distributions illustrate the soil properties in terms of their mean and variance, but we also wanted to examine the variance parameter more directly. As mentioned, the mean model is parameterized in terms of the precision (τ), the inverse of the variance. For each treatment in each year, we computed the standard deviation as the inverse of the precision's square root. These values are plotted in Figure 2.4. For soil moisture (Figure 2.4A) and pH (Figure 2.4E), the standard deviation is typically higher in reclaimed soils than in the undisturbed reference soils. The opposite is true for soil total nitrogen (Figure 2.4B), organic carbon in 2011 (Figure 2.4C), and microbial abundance (Figure 2.4F). Soil electrical conductivity (Figure 2.4D) standard deviation was variable across treatments and years. However, it should be noted that the 95% credible intervals around the standard deviation estimates for all soil properties regularly overlap with one another and those of the undisturbed reference soils.

To assess the degree of similarity between a reclaimed soil property and the undisturbed reference values, we computed the probability of observing a value within the "reference range" of values (based on a combination of their 95% credible intervals). The resulting probabilities are listed in Table 2.2. Note that these probabilities do not indicate the direction of a shift, or a change in shape, of the distribution relative to the references (information gained from the Figure 2.3), but rather an indication of distribution overlap. Clearly, most of the soil properties in most of the different aged reclamation sites have a high probability of falling within the reference range. The lowest probabilities occur for soil moisture in the three youngest treatments, electrical conductivity in the 28 and 54 year old treatments in 2011, and soil pH in the three youngest treatments.

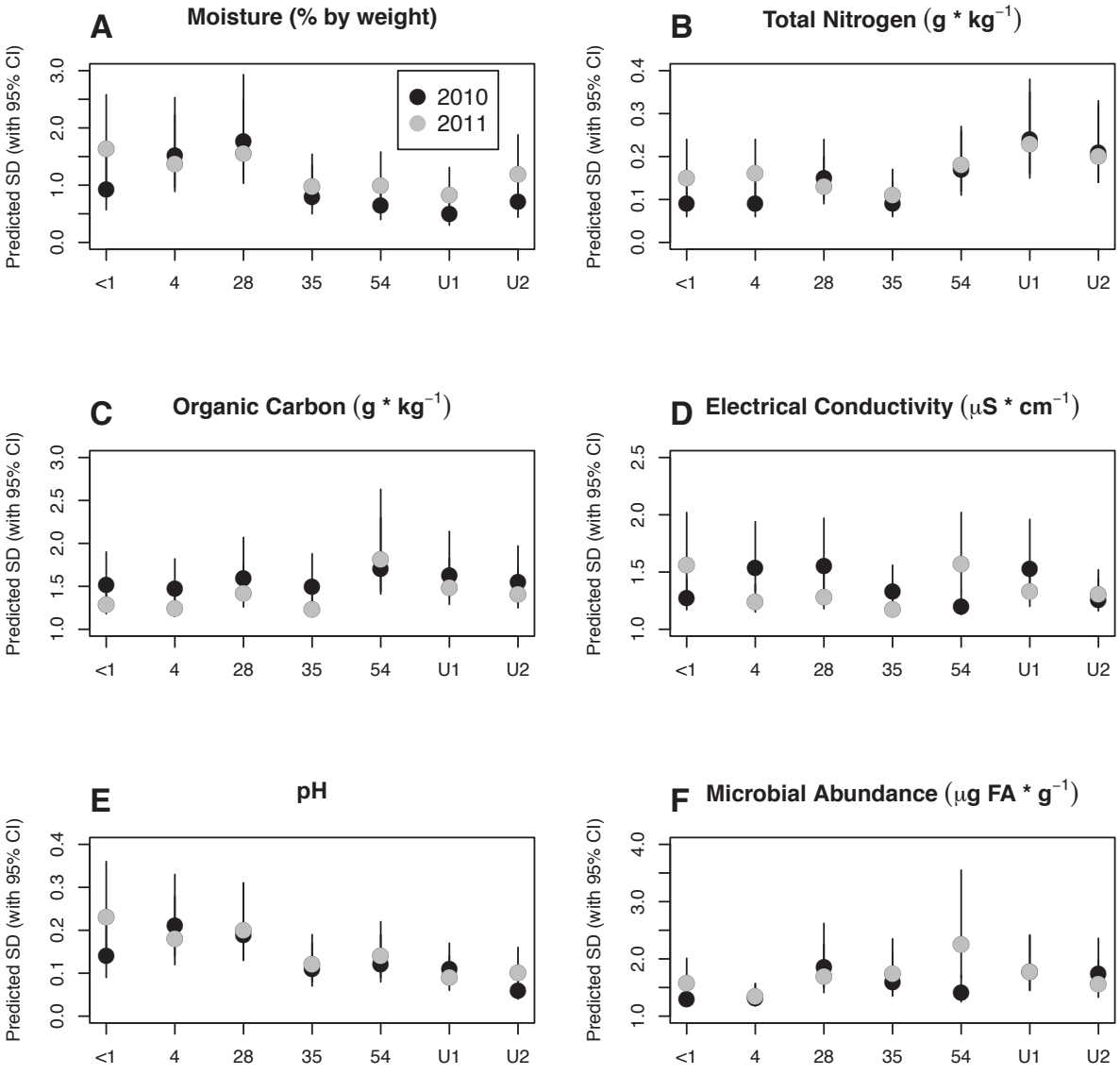

Figure 2.4: Dots represent the standard deviations with whiskers representing the 95% credible intervals for each soil property in each treatment in 2010 (black) and 2011 (gray). Treatments are designated by recovery time (in years) or as undisturbed references (U1 and U2).

A similar analysis was conducted using the 50% credible intervals for the reference values. As mentioned, these probabilities represent the similarity of treatment distributions to the "core" of the reference distributions. Resulting probabilities are listed in Table 2.3. High probabilities are observed in total nitrogen for all treatments in both years and soil organic

carbon for the <1, 4, and 35 year old treatments in 2011. These probabilities reflect the narrow distributions stacked on the reference distributions in Figure 2.3. As with the 95% credible intervals, lowest probabilities occur for soil moisture and pH in the youngest three years. Electrical conductivity in the 28 year old treatment in both years, and in the <1 and 54 year old treatments in 2011 are also low. Also, especially low was the microbial abundance in the <1 year old treatment in 2010.

Table 2.2: Probability that samples from the posterior predictive distributions for each treatment fall within the reference range of values, obtained from the 95% credible intervals of the undisturbed reference distributions. Treatments are designated by recovery time (in years) or as undisturbed references (U1 and U2).

	Moisture (% by wt)	**Total Nitrogen** ($g * kg^{-1}$)	**Organic Carbon** ($g * kg^{-1}$)	**Electrical Conductivity** ($\mu S * cm^{-1}$)	**pH**	**Microbial Abundance** ($\mu g\ FA^{\S} * g^{-1}$)
	----------***2010***----------					
< 1 yr	0.56	1.00	0.97	0.99	0.61	0.98
4 yrs	0.52	1.00	0.98	0.90	0.63	1.00
28 yrs	0.51	1.00	0.96	0.74	0.33	0.94
35 yrs	0.94	1.00	0.98	0.99	0.86	0.97
54 yrs	0.98	0.99	0.93	1.00	0.91	0.99
U1	0.97	0.96	0.95	0.95	0.95	0.95
U2	0.96	0.97	0.97	1.00	0.98	0.96
	----------***2011***----------					
< 1 yr	0.60	0.99	0.99	0.63	0.53	0.95
4 yrs	0.77	0.99	1.00	0.97	0.78	0.99
28 yrs	0.70	1.00	0.94	0.67	0.50	0.92
35 yrs	0.97	1.00	1.00	0.99	0.91	0.95
54 yrs	0.80	0.98	0.77	0.70	0.68	0.79
U1	0.99	0.95	0.95	0.95	0.97	0.95
U2	0.95	0.96	0.97	0.96	0.95	0.98

[§] FA = fatty acid derived from membrane phospholipids

Table 2.3: Probability that samples from the posterior predictive distributions for each treatment fall within the reference range of values, obtained from the 50% credible intervals of the undisturbed reference distributions. Treatments are designated by recovery time (in years) or as undisturbed references (U1 and U2).

	Moisture (% by wt)	**Total Nitrogen** ($g * kg^{-1}$)	**Organic Carbon** ($g * kg^{-1}$)	**Electrical Conductivity** ($\mu S * cm^{-1}$)	**pH**	**Microbial Abundance** ($\mu g\ FA^{\S} * g^{-1}$)
	----------***2010***----------					
< 1 yr	0.24	0.82	0.61	0.43	0.27	0.16
4 yrs	0.26	0.95	0.64	0.38	0.31	0.69
28 yrs	0.26	0.78	0.55	0.18	0.13	0.50
35 yrs	0.61	0.93	0.62	0.56	0.49	0.56
54 yrs	0.75	0.73	0.49	0.52	0.57	0.68
U1	0.74	0.57	0.54	0.50	0.61	0.54
U2	0.67	0.62	0.58	0.76	0.74	0.55
	----------***2011***----------					
< 1 yr	0.17	0.73	0.74	0.21	0.20	0.47
4 yrs	0.26	0.74	0.82	0.52	0.36	0.58
28 yrs	0.22	0.81	0.53	0.12	0.18	0.41
35 yrs	0.53	0.86	0.80	0.52	0.48	0.51
54 yrs	0.18	0.68	0.34	0.25	0.23	0.32
U1	0.66	0.56	0.56	0.51	0.63	0.52
U2	0.50	0.60	0.60	0.53	0.58	0.61

[§] FA = fatty acid derived from membrane phospholipids

2.4. Discussion and Conclusions

Our purposes were to examine the effects of disturbance and reclamation on soil properties in terms of their distributions, and to compare their recovery to undisturbed reference soils in a manner that might best help us identify why differences exist. The posterior predictive distributions, obtained with a Bayesian hierarchical linear model, allowed us to accomplish both of these goals. All soil properties we measured were altered by disturbance and reclamation, either in the central tendency of their values, in the spread of their values, or both. Each property differs in the presumed causes and implications of these changes.

We observed an increase in both the mean and variance in soil moisture values in the three youngest treatments in both years compared to the reference soils, which lead to a low probability of observing values similar to the reference soils. The disturbance process alters the physical structure of the soil; wherein, reclaimed soils experience compaction and reductions in aggregate size, porosity, and infiltration (Schroeder et al., 2010; Shukla et al., 2004; Wick et al., 2009b). The observed mean bulk density values were similar across all soils. However, we noticed that undisturbed soils and soils in the older treatments were physically crusted in areas, while recently reclaimed soils were loose and friable. The increased variability in the youngest soils may be a reflection of the soil structural influences on water infiltration and retention. Furthermore, variability in herbaceous cover may have contributed to the widening of the distribution. The young areas were dominated by bare ground, with some weedy and grassy vegetation (Figure 2.2), which perhaps led to small patches of soil drying through transpiration, while bare soil retained soil moisture. Disturbance appears to increase water infiltration and retention by the soil, aided by physical changes; conversely, soil moisture release may be regulated by vegetation. These effects appear to ameliorate as the soil recovery time increases, as indicated by the values observed in the older treatments. Soil moisture values were higher in 2011, than in 2010. The site received approximately 22 cm of precipitation in the year prior to sampling in 2010 and approximately 27 cm in the year prior to sampling 2011 (Western Regional Climate Center, 2013). The increase in soil moisture in the young reclaimed plots and the overall increase in 2011 potentially contributed to some of the patterns in the other soil properties that we observed. Soil carbon, nitrogen, and microbial abundance dynamics are all highly dependent on available water, and are likely influenced by the observed increase.

For example, soil organic carbon values were almost identical across treatments in 2010, but diverged in 2011. Perhaps low moisture availability in 2010 had a stabilizing effect on total soil organic carbon, and more soil moisture in 2011 allowed more carbon processing (Linn and Doran, 1984). The near doubling of soil moisture in 2011 compared to 2010 may have contributed to the differences in the variance observed in soil organic carbon across the two years. Reclaimed soils exhibited minimal changes in the central tendency of nitrogen and carbon values, but did indicate narrower ranges of values (aside from the uniformity in soil carbon in 2010). The sagebrush steppe is characteristically patchy and heterogeneous (West, 1983), with soil organic matter concentrated beneath shrubs (Burke et al., 1989; Davies et al., 2007; Halvorson et al., 1994; Mummey et al., 2002; Smith et al., 1994). The soil mixing, associated with the disturbance, along with the absence of the shrub component in the reclaimed soils is likely contributing to the reduced variance observed in those soils. However, it was surprising we did not observe a reduction in the mean values of the nitrogen and carbon, which is often reported following similar disturbances (Anderson et al., 2008; Ganjegunte et al., 2009; Ingram et al., 2005; Mummey et al., 2002; Wick et al., 2009b) due to dilution and mineralization. We did not analyze mineral pools of nitrogen, or the different forms of organic carbon, and it is possible that sub-pools are dynamic in response to disturbance and reclamation. Particularly, disturbance can cause heightened nitrogen mineralization rates (Ingram et al., 2005), converting organic forms to inorganic (NH_4^+ and NO_3^-). An investigation into the nitrogen dynamics in semiarid reclaimed soils is in progress, and initial reports support these hypotheses (Mason et al. 2011). We observed high probabilities that reclaimed soil carbon and nitrogen values fall within the central 50^{th} percentile of the reference soil values.

Soil calcium carbonate does not typically accumulate in the top 5 cm of the soil, where we sampled, but the disturbance process allows for deeper soil, containing carbonates and other salts, to be mixed with the surface soils (Ganjegunte et al., 2009). The increase in carbonates in the surface is accompanied by elevated soil electrical conductivity and pH. For both soil properties, all reclaimed soils had higher values, even after 54 years. Neither the soil electrical conductivity, nor the pH that result from the disturbance are restrictive of plant or microbial growth in these soils, but it is notable nonetheless. Furthermore, these differences were reflected in the low probability of observing values in the reclaimed soils to be similar to the reference values, based either on the 95% or the 50% credible interval.

The soil microbial abundance was reduced immediately following disturbance and reclamation, as indicated by the low abundance in the youngest site in 2010. The following year, the same treatment exhibited a higher probability of similarity to the reference soils, likely due to a widening of its distribution. The reduction in microbial abundance in response to disturbance and reclamation has been previously documented (Anderson et al., 2008; Dangi et al., 2012; Ingram et al., 2005; Mummey et al., 2002; Stahl et al., 1988), but has also been observed to require a longer time period (*i.e.* 20 years) to reach undisturbed levels (Frost et al., 2001; Mummey et al., 2002). In our dataset, microbial abundance values were similar to the undisturbed reference values within the first few years. This may be partially due to the high variability observed in the reference soils, which was not as high in the reclaimed soils. In this case, the reference range is so wide, it is inclusive of most of the values observed in reclaimed soils. We attribute the reduction in the variability in the youngest treatments to the “islands of fertility” effect discussed with regard to carbon and nitrogen; microbial abundance and activity exhibit the same spatial dependency on sagebrush shrubs (Bolton et al., 1993; Burke et al., 1989;

Halvorson et al., 1994; Mummey et al., 2002; Smith et al., 1994). We expect that the reestablishment, development, and diversification of the plant community will heavily influence the abundance and variability of the microbial community. The microbial community composition was fairly stable across treatments, with the exception of a high relative abundance of fungi in the youngest site in 2011 (Figure S2.3). As mentioned, soil moisture was higher in 2011, perhaps allowing for a more responsive microbial community. The damaged vegetation is typically mixed into the soil during disturbance, and would provide woody substrate for the fungi as moisture and temperature conditions became favorable in the spring of 2011. In any case, the microbial abundance is low in these sagebrush steppe soils, which is limited by water and substrate availability in this semiarid ecosystem (Burke, 1989; Mummey et al., 1997).

The use of posterior predictive distributions served as an intuitive tool for examining both the mean and the variance of the soil properties. It allowed us to identify that all soil properties that we examined were affected by disturbance and reclamation, but in different ways. Soil moisture, electrical conductivity, and soil pH experienced increases in their values and in their variability. These effects were likely driven by the physical mixing of the soil, and the mixing of eluted salts and carbonates from deeper in the profile. However, the more biologically tied properties (nitrogen, organic carbon, and microbial abundance) experienced some reduction in values, and consistent reduction in their variance. Investigation into the spatial patterns of these properties in these treatments will help elucidate the role of vegetation in influencing their variability. In most cases, the oldest treatments displayed ranges of values similar to the undisturbed reference soils, indicating recovery.

An important point of inference from this study is the recovery of these soil properties to undisturbed reference levels. The approach of using the 95% and 50% credible intervals for

assessing reclaimed soil property similarity to reference values was useful, but has its pitfalls. When the soil property was extremely variable in the reference soils, as with microbial abundance, the reclaimed soils had high probability of assuming “acceptable” values, even if their distributions were visibly different. The use of the 50% credible interval assisted in identifying drastically different distributions, but it could also be quite inclusive and more difficult to interpret. A more refined comparison that incorporates the locations and shapes of the distributions would be useful here. The combination of the visual assessment of the posterior predictive distributions along with the probabilities allowed us to identify that disturbance and reclamation has lasting effects on soil properties. These changes may not have been detected if only the average parameter was examined.

Overall, the use of distributions for examining effects of disturbance and restoration did provide more information than a statistical comparison of averages. By allowing the data to maintain their spread in values, we were able to examine the effect of disturbance on soil property distributions, and make inference on what changes in data distributions mean for the ecology and structure of the system. Specifically, we learned that while soil moisture was elevated in reclaimed treatments, it was also patchier; or that variability of biologically important properties (nitrogen, organic carbon, and microbial abundance) was consistently reduced by disturbance. The effect of disturbance on distributions can help us formulate future investigations, which, in this case, indicate the potential importance of vegetation structure, and perhaps a spatial approach to measuring soil properties.

We observed that drastic soil disturbance alters soil properties. While not surprising, we were able to illustrate that in addition to shifts in the central tendency of the values, the range of values are also altered by disturbance and reclamation. Whether the variability increases or

decreases in response to disturbance depends on the nature of the property, and how physical, chemical, or biological recovery of the site influences its values. We observed that some soil properties recover to values similar to the reference soils rather quickly, but developing the variability of values similar to the reference soils requires more time. For nearly all of the properties, only the oldest treatments assumed a range of values comparable to the reference soils. We presume that most of the observed changes in soil properties in response to disturbance and reclamation are highly dependent on the reestablishment and development of the plant community. This emphasizes the importance of successful revegetation practices. As restorationists, we should continue to develop approaches for quantifying reference sites, assessing restoration success, and facilitating rehabilitation of ecosystem properties according to multiple metrics.

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CHAPTER 3

Spatial and non-spatial soil data: applications and inference from a reclamation scenario

Abstract

Soils are heterogeneous systems, and many soil studies employ randomized sampling designs and statistical methods for comparisons or describing differences across treatments and relationships between variables. These methods aim to minimize the variability across space that is inherent in many soil properties. While geostatistical methods have been recognized in soil science, they are underutilized and can provide information about the influence of space on patterns and processes. Here, we discuss differences between non-spatial and spatial soil data, and illustrate their respective applications using two datasets. We sampled soil in recently reclaimed areas and adjacent undisturbed areas using both a randomized design, and a spatially explicit design. We employed traditional statistical analyses for each dataset, and discussed the inference gained from each approach. We found that soil properties are affected by disturbance and reclamation, and that soil mixing results in homogenization of soil properties across space, particularly for soil properties that are associated with the vegetation in an undisturbed state. The spatial component in this study provided useful information about the effects of disturbance on soil properties—information that was not obtainable with randomized sampling and analysis.

3.1. Introduction

The physical, chemical, and biological properties of a soil are of interest to a wide range of scientists and research problems. Soil properties are inherently variable across space (Leo, 1963; Mulla and McBratney, 2000) and analysis of soil can be time-intensive and costly, so sampling designs aim to minimize the number of samples needed to represent a study area.

However, maintaining accuracy in representing the sampled area is essential, especially because sampling error is oftentimes greater than analytical errors (Reed and Rigney, 1947). Thus, proper sampling design is imperative for accurate and meaningful inference (Cline, 1944).

When quantifying soil properties, two approaches can be employed (discussed by Brus and deGruijter, 1997 and Parkin and Robinson, 1994); one in which soil samples are taken randomly within a study area (perhaps in blocks, treatments, sites, etc.), and one in which the specific location of each soil sample is retained and included in the analysis. In the former approach, all samples are given equal weight in the analysis, and considered to be independent and identically distributed. These data are typically explored and examined through "classical" approaches: through their central tendency (mean, median, or mode), through comparison (t-test or ANOVA models), or through relationships (correlation and regression models). The resulting inference is based on study areas (blocks, treatments, sites, etc.), which have one mean, one variance, and an indication of their similarity or difference to the other units.

Conversely, spatial data and geostatistical analyses can provide information on how values vary across the sampled space (distribution and pattern), but also how data values and their variance are correlated across space (autocorrelation). Furthermore, geostatistical parameters obtained from spatial data can allow for making predictions at unknown locations, with the production of interpolation surfaces (maps) for qualitative interpretation (Mulla and McBratney, 2000; Trangmar et al., 1985). In this case, inference is based on examining variability and how it influences the measured soil property across space. This information can be used to inform future sampling designs, since it provides information on the distance at which two points become uncorrelated, or independent (Trangmar et al., 1985). Or, the variation can be directly examined to provide information about the nature of a property, and the factors or

processes controlling it (Webster, 2000). Comparison across study areas is not the primary focus; rather, the analysis provides information about the unique site-specific characteristics of soil properties as a function of space.

Table 3.1: Summary of spatial and non-spatial sampling design, analysis, and inference

		Non-spatial	**Spatial**
Sampling Design	*Location of samples*	Random (stochasticity introduced through sampling scheme)	Transect or grid with known distance between points (exact or relative location known)
	Number of samples	Samples need to maximize power and sufficiently represent the study area	Samples need to sufficiently cover the study area
	Replication	Experimental unit (i.e. treatment)	Point pairs with a given separation distance
Analysis	*Assumptions*	Normality, equal variances, independent and identically distributed	Stationarity (optional), correlation solely a function of lag distance
	Exploration and Description	Frequencies, ordination	Covariates, mean trends, directionality
	Parameters of interest	Mean, variance, coefficients	Range, sill, nugget
	Significance tests	p-value	--
Inference	*On parameters*	Treatment similarity or difference	Distance of independence, factors influencing patterns and autocorrelation
	Prediction	Predict relationships between variables (regression)	Prediction of variables at unknown locations

The research question and required inference should drive the analysis, and therefore the sampling design. Both approaches have been used and promoted for soil science research. Table 3.1 summarizes some of the major differences between these two approaches. Simply, non-spatial data allows for treatment comparisons through description and hypothesis testing, whereas spatial data provides information on soil patchiness, heterogeneity, and insight into the processes (vegetation, topography, land management) influencing those patterns.

Soil scientists more commonly use the non-spatial approach, rather than geospatial analyses. Yet, the benefits of incorporating a spatial component in soil analysis have received attention in soil science. Webster and Cuanalo (1975) recognized the usefulness of incorporating spatial scale in soil properties for soil surveys. Texts (Webster and Oliver, 2001) and book chapters (Mulla and McBratney, 2000; Trangmar et al., 1985) have provided both theory and application of geostatistics specific to soil science. Soil ecologists have also recognized the value of geostatistics (Ettema and Wardle, 2002; Frey, 2007); specifically, for describing the spatial pattern of soil microbes and nutrients (Ettema et al., 1998; Feng et al., 2004; Franklin et al., 2002; Katsalirou et al., 2010). Additionally, soil spatial heterogeneity can contribute to maintenance of soil biotic diversity (Ettema et al., 2000; Mummey and Rillig, 2008), and the distribution of soil microbial biomass, nutrients, and carbon and nitrogen processing align with vegetation patterns (Jackson and Caldwell, 1993; Mummey et al., 1997; Schlesinger et al., 1996; Smith et al., 1994), particularly in shrub-dominated systems. Many of these studies focus on parameter estimation, relating to distance from environmental features, patch size, and degrees of heterogeneity. However, kriging and visualization of interpolated surfaces can assist in understanding how soil spatial patterns develop under different land uses (Fraterrigo et al., 2005;

Mummey et al., 2010; Robertson et al., 1993) or following restoration (Mummey et al., 2002), or cultivation (Robertson and Freckman, 1995).

Yet, geospatial analyses are under-represented, and perhaps under-utilized in soil science especially in light of their potential contribution to refining soil process models (greenhouse gas fluxes, carbon sequestration, biomass distribution), maintenance of biodiversity, inputs for precision agricultural applications, and assessing ecosystem response to disturbance and environmental change. We suspect that many soil scientists remain unaware of the potential and power of spatial soil data in research, and that two analytical "camps" remain in the discipline with little crossover. With analogous data obtained from two sampling designs, our purpose was to demonstrate the inference gained from non-spatial and spatially explicit soil datasets. Using a reclamation scenario as a study system, we illustrate the usefulness of each approach individually, as well as together.

The sagebrush steppe, like other shrub ecosystems, is known to exhibit patchiness and heterogeneity in both aboveground and belowground properties (Burke et al., 1989; Davies et al., 2007; Halvorsen et al., 1994; Jackson and Caldwell, 1993; Smith et al., 1994; West, 1983). Rangelands occupied by sagebrush steppe are subject to a variety of surface disturbances that alter vegetation and move and mix soil. These drastic disturbances have noticeable and meaningful effects on soil physical, chemical, and biological properties (Anderson et al., 2008; Ingram et al., 2005; Stahl et al., 1988; Wick et al., 2009). In addition to changes in the magnitude of observed properties, we expect to see homogenization in soil properties as a result of soil mixing and re-spreading. Effects of similar disturbances and plowing on the spatial patterns of soil properties have been reported, and support this expectation (Fraterrigo et al., 2005; Robertson et al., 1993; Robertson and Freckman, 1995), although they are usually measured at

the field- scale. Here, we aim to elucidate the effects of recent disturbance and reclamation on a few key soil properties (soil moisture, organic carbon, total nitrogen, microbial community structure, pH, and electrical conductivity).

3.2. Materials and Methods

3.2.1 Study site description and sampling design

Soils were collected from two locations in south central Wyoming, near Wamsutter (41° 41’ 17.11” N, 107° 58’ 24.41” W, elevation = 2052 m). Wamsutter lies within Wyoming’s Red Desert Basin and receives an estimated average 180 mm (historic high: 346 mm, historic low: 96 mm) of precipitation per year (Western Regional Climate Center, 2010). Both sample sites were established in Sagebrush (*Artemisia tridentata*) steppe vegetation communities. Soils are classified as typic haplocalcids; they are well draining, non-saline to slightly saline, calcareous fine sands originating from weathered sandstone (Munn and Arneson, 1998).

Both sampling locations included two treatments: (1) a reclaimed natural gas pipeline scar, installed within one year; and (2) an adjacent undisturbed reference site. Figure 3.1 illustrates the soil sampling designs employed. At one location (non-spatial), four soil sample points were randomly located along three 50 m transects (n = 12 per treatment) (Figure 3.1C). At the other location (spatial), soils were sampled using an equilateral triangular grid, where 66 points were sampled at a scale of 0-100 cm (Figure 3.1B), and 33 additional points were sampled at a scale of 100-1000 cm (Figure 3.1A). All soils were sampled using a 2.5 cm diameter step-probe to 5 cm depth. Soils were placed on dry ice during transportation and stored at -20 °C until analysis.

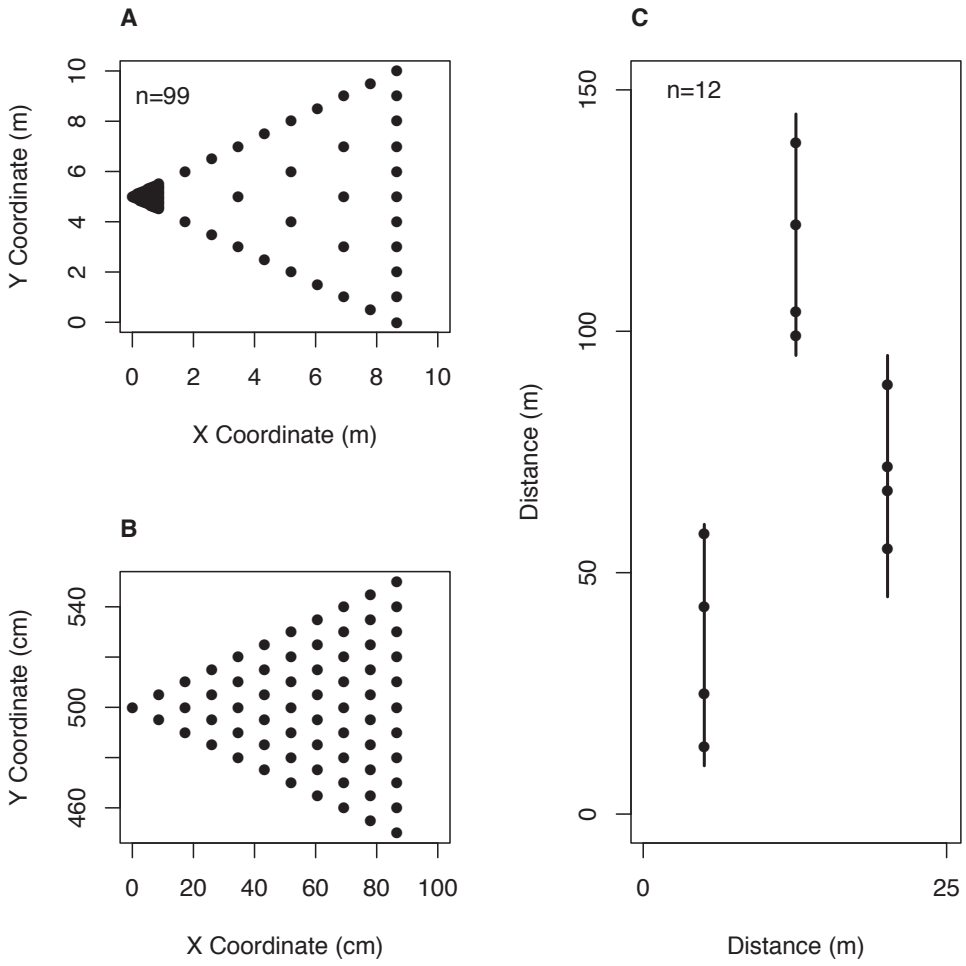

Figure 3.1: Sampling design for the spatial (A and B) and non-spatial (C) datasets. The spatial design included samples collected on a grid <1 m (B) nested within a 10 m grid (A). Samples in the non-spatial design (C) were randomly located along three randomly stratified (but parallel) 50 m transects. Each design was established in a reclaimed soil and an adjacent undisturbed soil

3.2.2 Soil analyses

Fresh soil samples were analyzed for gravimetric water content, lyophilized, sieved to 2 mm, and subject to phospholipid fatty acid (PLFA) analysis, as modified from Frostegård et al. (1993). Briefly, five grams of lyophilized soil was sonicated and shaken with 20 ml of a 1:2:0.8 mixture of chloroform, methanol, and phosphate buffer (0.05 M, pH 7.4). Phospholipids were isolated with a silica chromatography column, methylated in alkaline 0.2 M methanolic

potassium hydroxide, and purified in an amino chromatography column. Extracts were suspended in 200 µl solution of 1:1 solution of methyl *t*-butyl ether and hexane. Fatty acid methyl esters were analyzed on an Agilent 6890 Gas Chromatograph (Palo Alto, CA) using Sherlock software (MIDI, Inc., Newark, NJ). Microbial fatty acids by functional group included bacteria (i14:0, i15:0, a15:0, i16:0, 16:1ω9c, i17:0, a17:0, cy17:0, 18:1ω9c, cy19:0), saprotrophic fungi (18:2ω6c) and protozoans (20:3ω6c, 20:4ω6c) as in Vestal and White (1989), Frostegård and Bååth (1996), and Zelles (1999) and arbuscular mycorrhizal (AM) fungi (16:1ω9c) as in Olsson (1999). The total abundance was calculated as the sum of all signatures. The PLFA data was analyzed in terms of absolute values (pmol fatty acid * g^{-1} soil for the spatial dataset, and µg fatty acid * g^{-1} soil for the non-spatial dataset) and as relative abundance (percent of total), which provides an indication of community structure.

Ten grams of each dried soil sample was used to measure electrical conductivity (Rhoades, 1982) and pH (Thomas, 1996) of a 1:1 soil : deionized water slurry using a SympHony multi-purpose meter (VWR, Randor, PA). Remaining soil was finely ground and 20 mg were analyzed for elemental carbon and nitrogen on a Costech 4010 (Valencia, CA). Inorganic carbon ($CaCO_3$) was determined on 0.5 g sample using the modified pressure calcimeter method (Sherrod et al., 2002) and organic carbon was calculated as total carbon less inorganic carbon.

3.2.3 Statistical treatment of data

Some site specific differences exist between the two sample locations (baseline soil chemistry, vegetation composition differences), so our purpose was not to compare data values directly across datasets, but rather to focus on the sampling design differences and the type of information each design provides. For the non-spatial data, descriptive statistics were computed

for each variable in each treatment, and treatment means were compared with a Student's t-test. Boxplots were constructed for each soil property for a visual comparison of differences across treatments. Reporting mean values, standard error, and testing for significance are the standard statistical methods for non-spatial soil data (discussed by Webster 2001).

The geostatistical analyses were aimed to meet two goals: (1) to obtain semi-variogram model parameter estimates and (2) to obtain prediction surfaces (through kriging) for each soil property in each treatment. The empirical semi-variogram is created by plotting, against the lag distances (x-axis), the calculated semi-variances for point pairs within given lags (y-axis). As the lag distance increases, the semi-variance values typically increase, but then plateau, at which point spatial independence occurs between data points. The semi-variance value corresponding to the plateau is denoted as "σ^2," the sill, and the lag distance corresponding to the plateau is denoted "ϕ," the range. A measure of variability at a lag distance of zero is designated as "τ^2," the nugget. The shape of the empirical semi-variogram, and the associated parameters, suggest candidate semi-variance models.

It is common to obtain a mean trend for the modeled property, and then combine it with the spatial correlation model to obtain the prediction surfaces. The mean trend is a regression that can include the plot coordinates or covariates; which assists in explaining the dependent variable through its correlation to other independent variables. For example, soil carbon and nitrogen occur together in soil organic matter, as such, they vary together and serve as good predictors for one another. The purpose of the mean trend is to describe the baseline trend in the data, such that the semi-variance models only the residuals. This approach is standard for geostatistical analyses and the reader is referred to Cressie (1991), Diggle and Ribeiro (2007) and Gelfand et al. (2010) for a thorough discussion of geostatistics.

For the spatial dataset, all soil properties, $P_j(s_i)$, were modeled according to equation 3.1, where $s_i = (x_i, y_i)$ for $i = 1…99$ sampled locations and $j = 1,2$ treatments.

$$P_j(s_i) = \mu_j(s_i) \; = \; \varepsilon_j(s_i) \tag{3.1}$$

Here, $\mu_j(s_i)$ represents the large scale variation, or mean trend, while $\varepsilon_j(s_i)$ is the residual variation. Each soil property in each treatment was examined for correlations with the coordinates and covariates; covariates with a correlation greater than 0.5 were included in a linear regression model. Significant covariates were then retained to obtain a linear mean trend, $\mu_j(s_i)$, for each soil property (equation 3.2); for k significant covariates:

$$\mu_j(s_i) = \beta_0 = \beta_1 Z_{1j}(s_i) = \cdots = \beta_k Z_{kj}(s_i) \tag{3.2}$$

The residuals were then specified according to equation 3.3; independently distributed as (~) normal, with mean zero and a constant (stationary) covariance structure defined by Σ_j.

$$\varepsilon_j(s_i) \sim independent\ Normal\ (0, \Sigma_j) \tag{3.3}$$

An empirical semi-variogram was constructed from the residuals for each soil property. For variables with high data values (electrical conductivity and microbial group abundances), the semi-variograms were constructed on the log-scale. Equation 3.4 describes the general spatial covariance structure of the residuals, illustrated by the semi-variogram.

$$\Sigma_j = \; \sigma_j^2 \, H(\phi_j) = \; \tau_j^2 \tag{3.4}$$

Here, H is an $n \; x \; n$ correlation matrix for point pairs separated by distance h and of a form consistent with a semi-variance model with partial sill (σ^2_j), range (ϕ_j) and nugget (τ^2_j). The nugget variance includes both microscale variability of a property and measurement error.

We used restricted maximum likelihood estimation (REML) to fit exponential and Matèrn semi-variance models to each soil variable in each treatment, incorporating both the mean trend model and the log-transformation (if applicable). The REML estimation has been

used in geostatistical applications, and is accepted as a less biased estimator of variance in datasets with small sample sizes (Zimmerman and Zimmerman 1991). The REML method provided estimates of all model parameters ($\boldsymbol{\beta}$, σ^2_j, ϕ_j, τ^2_j). In all cases, the Matèrn semi-variance parameter estimates were consistent with those of the exponential model estimates, so the more parsimonious exponential model was retained (standard form in equation 3.5).

$$\gamma(|h|) = \sigma^2 \left(1 = \exp\left(=\frac{|h|}{\phi}\right)\right) = \tau^2 \qquad \textbf{(3.5)}$$

By combining the mean trend and the spatial covariance models (according to equation 3.1) through kriging, we obtained a predicted surface for each soil property (P_j) in each treatment The prediction surfaces (presented as a shaded map or contour map) allow for a visual, qualitative assessment of differences in magnitude of a measured property between treatments, and it reflects the differences in patterns of variability across space (determined by the covariance structure). For the variables that required a log-transformation, the predicted values were exponentiated to produce a prediction surface on the original scale.

All analyses were conducted in R for Mac OS X (www.r-project.org). Summary statistics for non-spatial data were obtained with the "Pastecs" package (Grosjean 2013). We used the spatial statistics package, "geoR," for all geostatistics (Diggle and Ribeiro 2007; Ribeiro and Diggle 2001). Example code for non-spatial and spatial analyses is included as supplementary material (Figure S3.1).

3.3. Results

Summary statistics for soil properties collected from transects is presented in Table 3.2, and the corresponding boxplots (Figure 3.2) illustrate quartiles of soil properties, with treatments side-by-side. Soil moisture at the time of sampling was higher in the reclaimed soil (Figure

3.2A). Soil total nitrogen and organic carbon were not different between treatments; however, the variability in values for both properties was larger in the undisturbed treatment (Figure 3.2B and C). Soil solution electrical conductivity (Figure 3.2D) and pH (Figure 3.2E) were higher in the reclaimed treatment, and for both properties, variability of data values was also higher in the reclaimed treatment.

Microbial abundance was examined in two ways: absolute abundance and relative abundance. Total microbial abundance was reduced over 50% in the reclaimed treatment (Table 3.2, Figure 3.2F), compared to the undisturbed treatment. The same reduction was also reflected in the absolute values of bacteria (Figure 3.2G), AM fungi (Figure 3.2I), and fungi (Figure 3.2K). The spread of data values was also lower for all microbial groups in the reclaimed soils. The relative abundance provides an indication of shifts in community composition. While none of the microbial groups experienced drastic shifts in relative abundance (Table 3.2), the bacteria appeared to slightly increase (about 6 %) in proportion to the total microbial abundance (Figure 3.2H), while both the AM fungi (Figure 3.2J) and fungi (Figure 3.2L) appeared to slightly decrease in proportion (1 % and 5% respectively).

The empirical semi-variograms with fitted semi-variance models are depicted in Figure 3.3, and Table 3.3 includes the estimated mean trend models and the geostatistical model parameters for each soil property in each treatment. The x-coordinate covaried with soil moisture in the undisturbed plot, and both coordinates covaried with moisture in the reclaimed plot. Soil total nitrogen and organic carbon covaried in both plots, while electrical conductivity and pH did not have covariates. Bacterial abundance (absolute) and fungi abundance covaried in both plots, while AM fungi varied with bacteria in the undisturbed plot and fungi in the disturbed plot.

Table 3.2: Descriptive statistics (mean with standard error of the mean in parenthesis) and Student's t-tests (n=12) for soil properties from non-spatial data in undisturbed and reclaimed areas.

	Undisturbed	Reclaimed	t	df	p-value
Moisture *(% by weight)*	2.21 (0.21)	3.93 (0.28)	-4.87	14.98	<0.001
Total Nitrogen *(g N * kg^{-1} soil)*	1.04 (0.06)	1.01 (0.03)	0.55	15.11	0.59
Organic Carbon *(g C * kg^{-1} soil)*	8.55 (1.24)	8.52 (0.95)	0.02	20.59	0.98
Electrical Conductivity *(µS * cm^{-1})*	64.84 (4.24)	96.43 (6.21)	-4.20	19.43	<0.001
pH *-log [H^+]*	7.94 (0.02)	8.05 (0.04)	-2.85	15.51	0.01
Total Microbial Abundance *(µg $FA^{§}$ * g^{-1} soil)*	3.83 (0.59)	1.78 (0.12)	3.38	11.86	0.006
Bacteria *(µg FA * g^{-1} soil)*	2.64 (0.38)	1.37 (0.08)	3.30	11.98	0.006
Bacteria *(% of total)*	71 (2.94)	77 (1.06)	-2.09	13.79	0.06
AM[¶] Fungi *(µg FA * g^{-1} soil)*	0.37 (0.06)	0.16 (0.01)	3.65	12.49	0.003
AM Fungi *(% of total)*	10 (0.52)	9 (0.27)	1.78	16.59	0.09
Fungi *(µg FA * g^{-1} soil)*	0.81 (0.19)	0.25 (0.03)	2.95	11.52	0.01
Fungi *(% of total)*	19 (2.51)	14 (0.96)	2.04	14.13	0.06

[§]FA = fatty acid derived from membrane lipids. [¶]AM = Arbuscular mycorrhizal

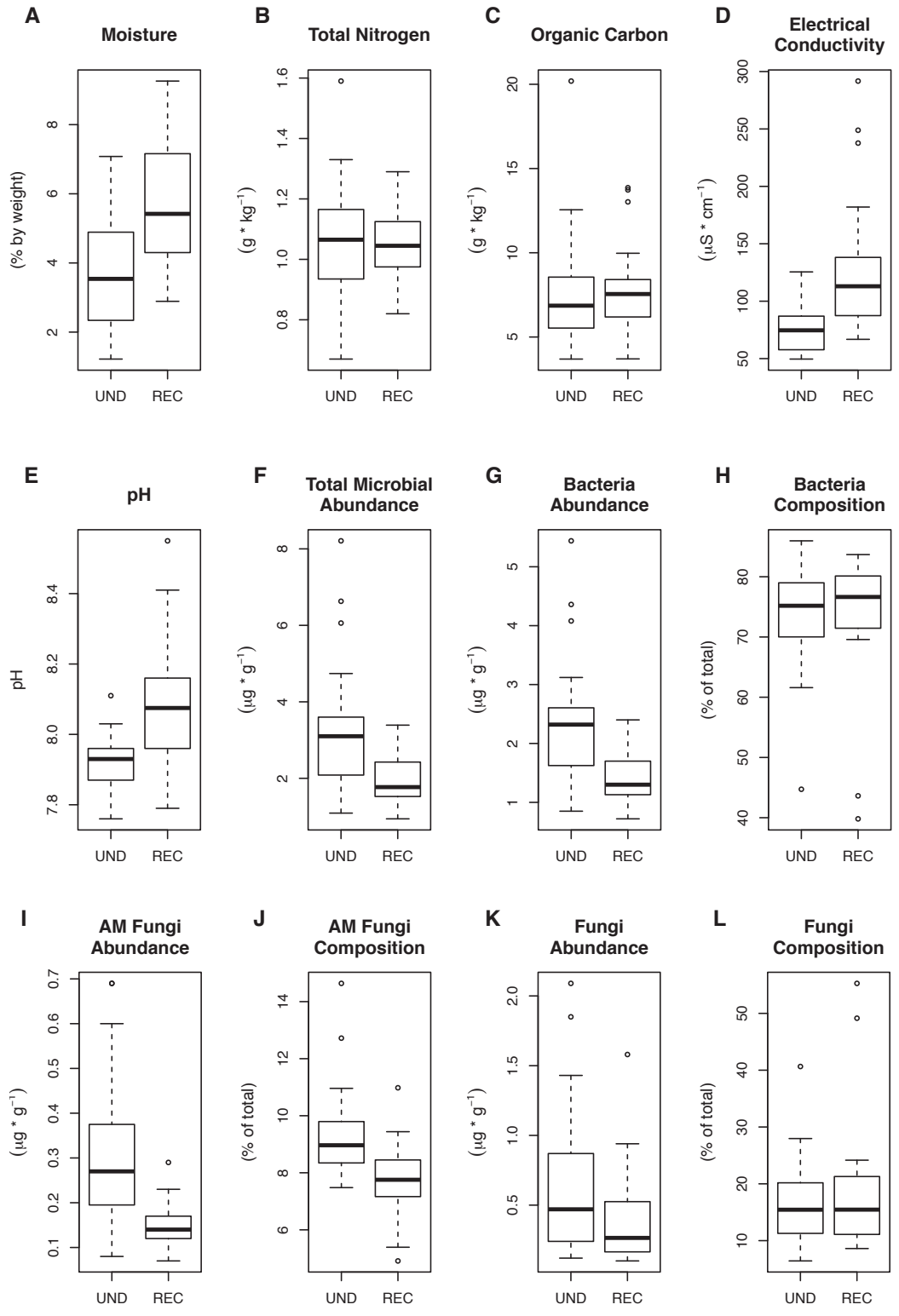

Figure 3.2: Boxplots with whiskers (variation outside of first and third quartiles) for each soil property from non-spatial data in undisturbed (UND) and reclaimed (REC) treatments

All semi-variograms were fitted with an exponential semi-variance model, except the fungi abundance in the undisturbed plot, wherein a pure nugget model was the most appropriate model. For all soil properties except electrical conductivity and pH, the partial sill parameter was lower in the undisturbed plot (Table 3.3), and the nugget effect was consistently lower in the reclaimed plot.

The sum of the partial sill and the nugget indicate the full sill, or value at which the semi-variance plateaus. The proportion of the full sill that each parameter contributes can provide additional information on the sources of variance for each soil property. If the proportion of nugget variance is high relative to the full sill, most of the variance is due to micro-scale variability or measurement error (assumed to be consistent across all samples). If the partial sill contributes a large proportion to the full sill, the variance is due to variability across space. These trends are illustrated in the variography in Figure 3.3. In the undisturbed plots, the fungi abundance had 100% contribution from the nugget effect, while total nitrogen and organic carbon had high (> 80%) contributions from the nugget effect. Soil pH, bacterial, and AM fungi abundance had near equal contributions from the nugget and partial sill, while soil moisture and electrical conductivity had high (> 80%) contributions from the partial sill. In the reclaimed plots, the nugget effect generally decreased, with the partial sill contributing more to the full sill. Only total nitrogen, organic carbon, and fungi abundance had nugget effects greater than 20% of the full sill. Thus, following disturbance and reclamation, variability in soil properties across space became a stronger influence on the total variance observed in the data values.

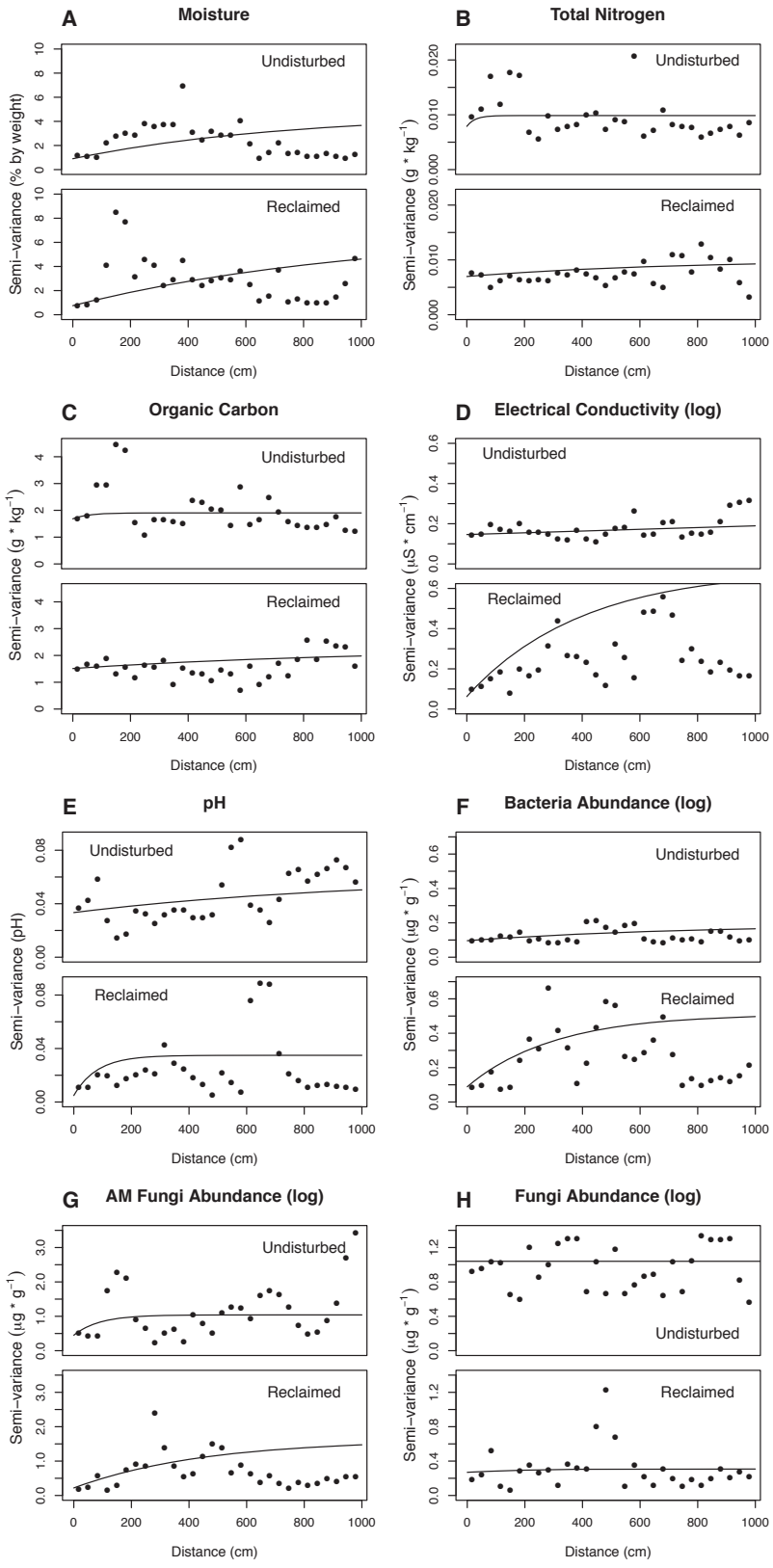

Figure 3.3: Empirical semi-variograms plotted with their fitted semi-variance models for each soil property in undisturbed and reclaimed plots, created from spatial data

Table 3.3: Fitted parameters for mean trend and semi-variance models for each soil property in undisturbed and reclaimed plots. Units for the partial sill and nugget are equivalent to the unit of measure (i.e. % by wt for moisture), while the range is expressed in distance (cm).

	Mean trend	σ^2 (partial sill)	ϕ (range)	τ^2 (nugget)
Undisturbed				
Moisture	= - 0.005 * *X* + 7.56	3.75	750	0.9
Total Nitrogen	= 0.06 * *Organic C* + 0.35	0.002	28	0.008
Organic Carbon	= 12.31 * *Total N* – 2.69	0.22	55	1.68
Electrical Conductivity	-	2.95	>1000	0.15
pH	-	0.03	1000	0.03
Bacteria	= 0.03 * *Fungi* + 5.13	0.09	750	0.1
AM[¶] *Fungi*	= 0.004 * *Bacteria* + 1.06	0.59	88	0.45
Fungi	= 0.006 * *Bacteria* + 0.07	0.00	0	1.04
Reclaimed				
Moisture	= 0.003 * *X* – 0.003 * *Y* + 6.05	6.11	1000	0.75
Total Nitrogen	= 0.04 * *Organic C* + 0.5	0.003	700	0.007
Organic Carbon	= 0.18 * *Total N* + 6.78	0.74	1000	1.51
Electrical Conductivity	-	0.63	400	0.06
pH	-	0.03	81	0.005
Bacteria	= 0.008 * *Fungi* + 6.04	0.42	300	0.09
AM[¶] *Fungi*	= 0.01 * *Fungi* + 3.4	1.41	200	0.21
Fungi	= 0.002 * *Bacteria* + 2.41	0.04	175	0.27

[§]FA = fatty acid derived from membrane lipids. [¶]AM = Arbuscular mycorrhizal

The range parameter, or lag distance corresponding to the partial sill and the distance at which samples become independent, was reduced in the reclaimed plot for electrical conductivity, pH, and bacterial abundance. Conversely, the range parameter increased in the reclaimed plot for all other soil properties. An increase in the range parameter indicates more autocorrelation (less independence) at a given distance. So, for most soil properties, their values became more correlated and less heterogeneous across space following disturbance and reclamation.

The effect of differing degrees of heterogeneity across space (measured by the range parameter) is illustrated in the prediction surfaces obtained by kriging (Figure 3.4). For electrical conductivity (Figure 3.4D), pH (Figure 3.4E), and bacteria abundance (Figure 3.4F), we see more “patchiness” and smaller “patches” in the reclaimed plots. These patches indicate larger changes in values over space (small range = small patches). For the remaining soil properties, the undisturbed plots were more heterogeneous while the reclaimed plots had smoother transitions from low to high values.

In addition to variability across space, the differences in the values of a soil property between plots are also visible. For example, total nitrogen (Figure 3.4B) and organic carbon (Figure 3.4C) had similar values in both plots, whereas electrical conductivity (Figure 3.4D) and the microbial groups (Figure 3.4 F – H) had lower (darker) values in the undisturbed plot compared to the reclaimed plot. These surfaces are helpful for interpreting the quantitative models discussed above.

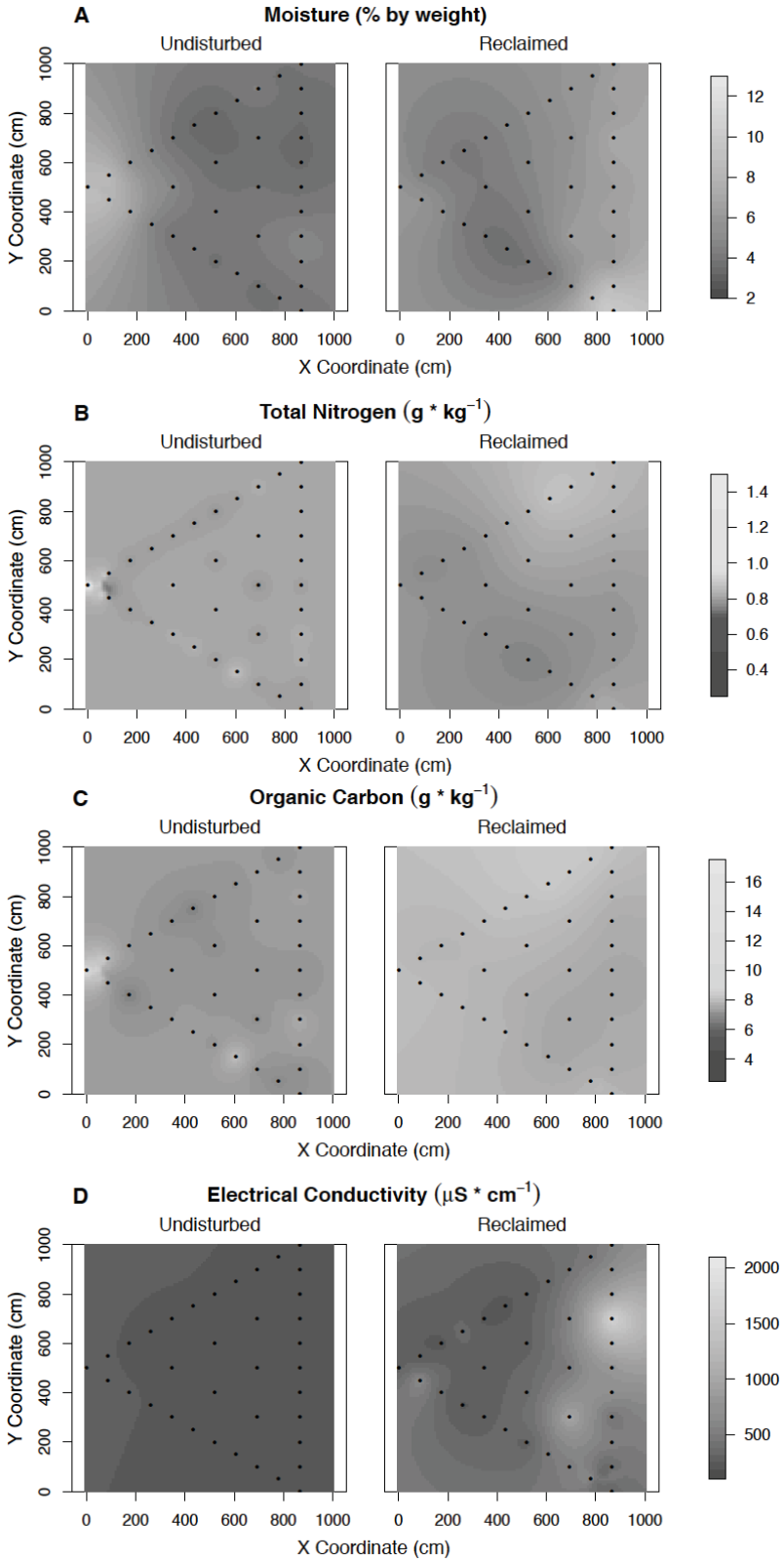

Figure 3.4: Kriged prediction surfaces created from semi-variance models, for each soil property in undisturbed and reclaimed plots. Sample locations are indicated by dots. FA = fatty acid derived from membrane lipids, AM = arbuscular mycorrhizal

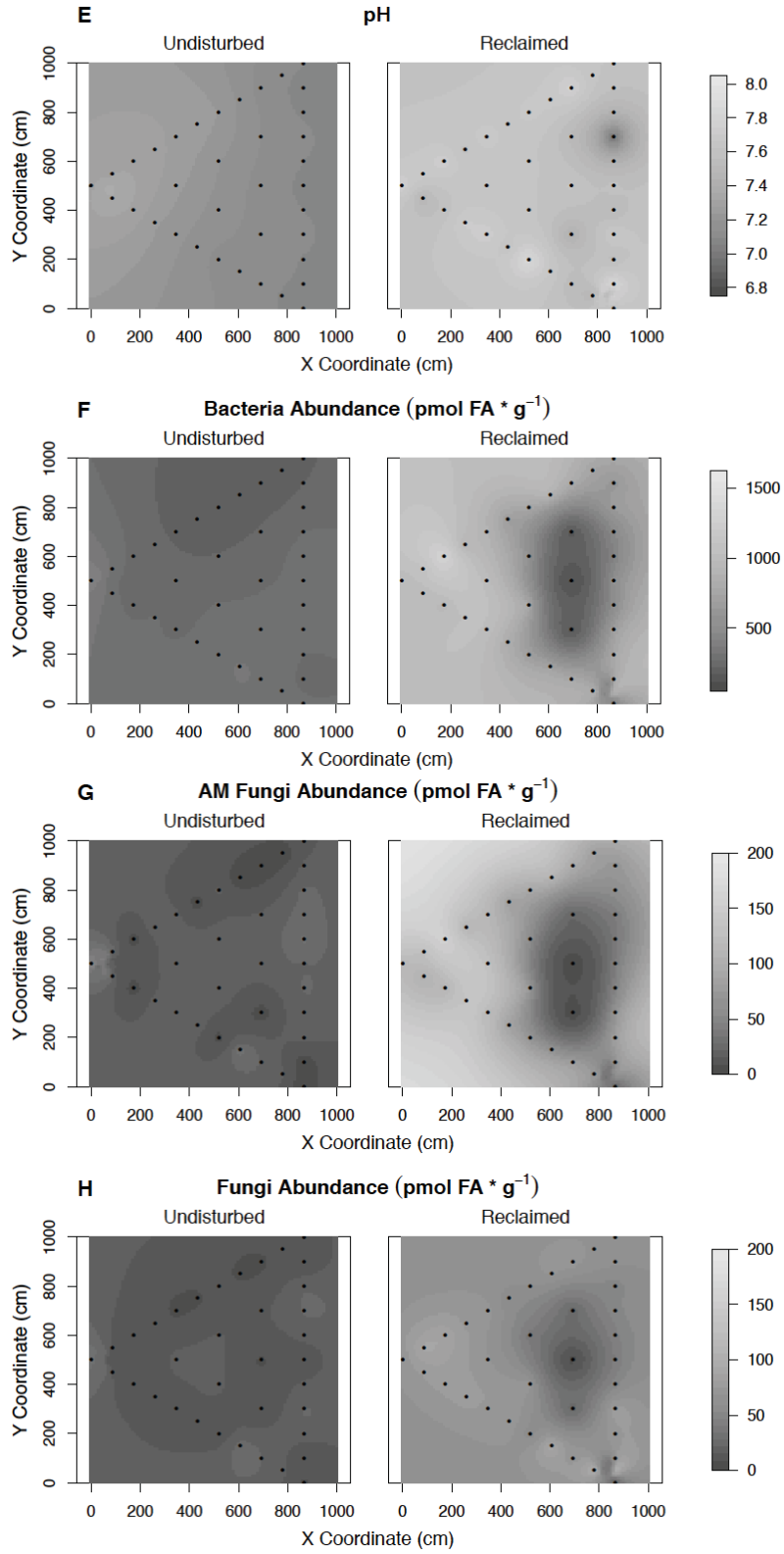

Figure 3.4 continued

3.4. Discussion and Conclusions

Our purpose was two-fold: to demonstrate the different sampling designs, analyses, and inference gained from non-spatial and spatially explicit datasets; and to employ both approaches to investigate the influence of recent soil disturbance and reclamation on soil properties. Both types of data illuminate differences in soil properties following reclamation, but they differ in the type of information and the details that they provide.

The non-spatial dataset indicated an increase in soil moisture in the reclaimed soil. The disturbance and reclamation process disrupts soil surface crusting, profile structure, and aggregation (Schroeder et al., 2010; Shukla et al., 2004; Wick et al., 2009). These effects result in a "fluffier" soil in the reclaimed areas, which is likely associated with differences in water infiltration and retention. The mean values of total soil nitrogen and organic carbon appeared stable across treatments. This is contrary to previous reports, wherein soil nitrogen and carbon experience dilution and mineralization during disturbance (Anderson et al., 2008; Ganjegunte et al., 2009; Wick et al., 2009). Both electrical conductivity and pH displayed an increase in the reclaimed soils. Calcium carbonate and other salts accumulate below the soil surface, and when the soil profile is mixed, these materials can appear in the reclaimed topsoil (Ganjegunte et al., 2009). While the soil pH was significantly higher in the reclaimed treatment (Table 3.2), a difference of 0.11 pH units (0.77 Molar H^+) is not likely to be biologically meaningful. The average microbial abundance, of all microbial groups, was reduced following disturbance and reclamation. This effect has been previously reported in reclaimed soils (Dangi et al., 2012, Ingram et al., 2005; Mummey et al., 2002). The slight shift in community composition may reflect the ability of bacteria to respond to labile substrates made available through disturbance

of soil and vegetation, while both types of fungi suffered physical disruption during soil handling (Allison et al., 2005; Frey et al., 1999; Stahl et al., 1999).

Interpreting parameters of the geostatistical models is, perhaps, not as intuitive as examining mean values and significance tests. The mean trend models indicate which variables are related, while the semi-variance models allow us to differentiate sources of variability, especially with regard to space. Moisture covaried with the spatial location of the plot. Electrical conductivity and pH were uncorrelated with other variables, while nitrogen and carbon were covariates with one another and microbial groups were covariates with one another. These relationships are reasonable and reflect the nature of these properties to vary together regardless of disturbance. For example, organic carbon and nitrogen reside in soil organic matter together, and the fate of organic matter in general will determine the response of its components. Biomass of microbial groups may vary together in response to availability of common substrates or favorable growth conditions.

The semi-variograms illustrate three related sources of variability: the inherent variability of a property at one location (nugget effect), variability across space at the plot level (partial sill), and the effective distance of encountering different, independent values (range). In this dataset, disturbance and reclamation reduced the nugget effect, or the inherent variability in a property, increased the range, or distance of autocorrelation, for all but three properties, and increased the partial sill, or variability across the plot, for all but two properties. As a result, soil electrical conductivity and pH (and arguably bacteria abundance) became more heterogeneous across the plot, while all other soil properties experienced homogenization. Soil moisture, nitrogen, carbon, and microbial abundance are all properties that are strongly associated with vegetation distribution, especially in sagebrush steppe (Burke et al., 1989; Halvorsen et al., 1994; Mummey

et al., 1997; Mummey et al., 2002; Smith et al., 1994), which is a patchy, heterogeneous system. The effects of vegetation removal and soil mixing were expected to have a homogenizing effect on soil properties; which has been observed in response to wildland disturbance and field cultivation (Fraterrigo et al., 2005; Robertson et al., 1993; Robertson and Freckman, 1995). Soil electrical conductivity, pH, and bacterial abundance following reclamation may reflect areas of high salt or substrate concentration, which disappear over time and as the vegetation recovers.

The increase in variability observed in electrical conductivity and pH in the reclaimed spatial plots was also observed in the non-spatial dataset, with the increase in spread of data values in the reclaimed plots. Furthermore, differences in magnitude between treatments we observed in the non-spatial dataset are consistent with the prediction surfaces for the spatial plots, excepting microbial abundance. In the non-spatial dataset, the mean microbial abundance was lower in reclaimed soils, while the opposite is true in the spatial plots. This difference could be due to site-specific differences between the sampling locations (substrate availability, soil moisture, pre-disturbance conditions, etc.). In any case, from both datasets and analyses, we can make conclusions about changes in the magnitude of the measured properties in response to disturbance and reclamation.

The non-spatial dataset provided an indication the variability within the observed values was also affected, through the range of values observed within a treatment. The spatial dataset allowed a detailed analysis of how soil disturbance influenced sample variability, and what role space played in influencing the observed variability. Further, the prediction surfaces provided a visual representation of changes in spatial patterns, which aid us in understanding the effects of disturbance on soil properties. With this information, we may relate the belowground patterns to revegetation success, implications for biogeochemical processes, and belowground succession.

There are few reports on the spatial soil patterns at the scale (< 10 m) that we chose to examine. In a study examining the spatial structure of soil microbial groups, carbon, and nitrogen in undisturbed and reclaimed soils (Mummey et al., 2002), spatial structure was revealed at scales less than 50 cm for microbial properties. Furthermore, many of the microbial measures adhered to pure nugget semi-variance models in the undisturbed soil, but demonstrated spatial structure in the reclaimed plots. Ettema and Wardle (2002) summarize a number of studies examining spatial patterns of soil ecological properties, and microbial biomass has been observed to adhere to spatial structure (indicated by the range parameter) at scales varying from < 1 m to 250 m. Vegetation, substrate, topography, and land use all play a role in influencing the belowground structure, and autocorrelation may be nested at multiple scales. We presume that the spatial structure we observed is closely tied with the vegetation, and the shrub component in particular. Without spatial vegetation data, we cannot confirm such a link.

The research question should drive what inference is desired from the analysis, and therefore the sampling design and statistical applications. Here, we've demonstrated two approaches to studying soil properties in two land-management treatments. While both procedures are used in soil science, the non-spatial classical approach is far more popular, and the two applications rarely co-mingle. Yet, soil is a heterogeneous system, and will remain so. Clearly the usefulness of spatial analysis of soil properties can contribute much to our understanding of soil properties, processes, and responses to environmental change.

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CHAPTER 4

Development of aboveground and belowground spatial structure in sagebrush steppe following disturbance, reclamation, and recovery

Abstract

Sagebrush (*Artemisia tridentata* Nutt.) steppe is an inherently heterogeneous system in both vegetation structure and the spatial distribution of soil properties. Sagebrush steppe lands are experiencing a multitude of disturbances that involve vegetation removal and soil mixing. We hypothesize that these disturbance activities result in homogenization of above and belowground properties, and that spatial structure would recover with time. We established a spatially explicit sampling design on a chronosequence of reclaimed buried pipelines. Plot ages ranged from 1 year to 55 years, and were compared to two undisturbed plots. We used Bayesian geostatistical models to investigate spatial trends and correlation structures of vegetation and soil properties (< 90 m). Disturbance results in uniform cover of weedy plant species, then replaced by uniform cover of grasses, which persist. Shrub and forb cover were low after 55 years of recovery. Soil properties experienced changes in response to disturbance, and their recovery was not tightly associated with vegetation community development. Soil microbial abundance patterns were most associated with vegetation patterns, but recovery of soil moisture, nitrogen, salinity, and alkalinity appear to be driven by other environmental factors. Overall, surface predictions demonstrated that disturbance does result in homogenization, but does not strongly affect the correlation structure of vegetation and soil properties. Additionally, recovery of semiarid sagebrush steppe above- and belowground structure may require in excess of 55 years.

4.1. Introduction

Sagebrush steppe is characterized as semiarid rangeland dominated by big sagebrush (*Artemisia tridentata* Nutt.) species and associated perennial grasses (West, 1983). In addition to the fairly distinct plant community composition, the sagebrush component imparts distinct spatial patterns on the distribution of other plant species. These patterns in the vegetation are associated with the spatial distribution of soil physical, chemical, and biological characteristics and ecosystem processes. This phenomenon is well studied in arid and semiarid shrublands, and researchers have bestowed shrubs with creating and maintaining hotspots of nutrients, water, and biotic activity, coined "islands of fertility" (Crawford and Gosz, 1982; Noy-Meir, 1985; Schlesinger, 1996; Schlesinger and Pilmanis, 1998; Yu and Steinberger, 2012). Specifically, sagebrush steppe ecosystems exhibit strong associations between the shrub component and soil property structure and function. Sagebrush islands have higher amounts of organic carbon and total and inorganic nitrogen (Burke et al., 1989; Halvorson et al., 1994; Smith et al., 1994; Mummey et al., 2002a; Davies et al., 2007), carbon and nitrogen processing (Burke, 1989; Mummey et al., 1997; Smith et al., 1994), microbial and decomposer biomass (Bolton et al., 1993; Burke et al., 1989; Halvorson et al., 1994; Mummey et al., 2002a; Smith et al., 1994), and soil moisture (Burke, 1989; Davies et al., 2007; Mummey et al., 1997). The shrub component also imparts strong influences on the distribution of other plant species (Davies et al., 2007; Ewers and Pendall, 2008). Depending on shrub size, these effects can occur within one meter from the center of the shrub, exhibit a high degree of spatially autocorrelation, and are extremely variable in shape and magnitude (Halvorson et al., 1994; Halvorson et al., 1995; Jackson and Caldwell, 1993; Mummey et al., 2002a). In general, sagebrush steppe ecosystems have very patchy structure in vegetation and soil properties (West, 1983), low rates of organic matter

turnover (“tight” nutrient cycles) (Burke, 1989; Burke et al., 1989), and high dependence on biologically available water and labile substrate (Burke, 1989; Burke et al., 1989; Mummey et al., 1997).

While sagebrush steppe ecosystems face many threats (Davies et al., 2011), drastic disturbance associated with various forms of natural resource development are among the most widespread. Furthermore, restoration of semiarid ecosystems faces many challenges (reviewed by Allen, 1995), and successful restoration of sagebrush steppe is influenced by many soil and micro-topographical characteristics (Chambers, 2000), disturbance regimes (Davies et al., 2011), and climate and precipitation patterns (Bates et al., 2006). Specifically, drastic disturbance has been shown to result in reduction in plant species diversity, and reduction of native plant species abundance (Bowen et al., 2005), reduction in soil organic carbon and nitrogen (Anderson et al., 2008; Ganjegunte et al., 2009; Mason et al., 2011; Mummey et al., 2002b; Wick et al., 2009), with effects lasting beyond 16-20 years following reclamation. In addition to effects on carbon and nitrogen pools, carbon and nitrogen mineralization rates are reduced following disturbance, as is their variability (Ingram et al., 2005; Mason et al., 2011). Drastically disturbed sagebrush steppe soils also experience a reduction in abundance and efficacy of arbuscular mycorrhizal fungi (Stahl et al., 1988), which recovered after nearly 20 years following reclamation (Frost et al., 2001). Microbial biomass carbon is also reduced following disturbance (Anderson et al., 2008; Ingram et al., 2005; Mummey et al., 2002b), along with an initial reduction in total microbial abundance, abundance of major microbial groups, and microbial diversity and richness as indicated by microbial cell membrane phospholipids (Dangi, 2012; Mummey et al., 2002b). In Wyoming’s Powder River Basin microbial abundance recovered to undisturbed levels between five and ten years following reclamation (Dangi, 2012), but remained low after 20 years

following reclamation in Wyoming's Shirley Basin (Mummey et al., 2002a). Effects of disturbance on biota of sagebrush steppe extend to arthropods as well—arthropod assemblages demonstrated initial reduction following disturbance, but most arthropod groups recovering to undisturbed levels within 16 years following reclamation (Regula, 2007). Physical effects of disturbance on soil properties include mixing and alteration of soil profiles (Stahl et al., 1988), increases in soil bulk density, variable changes in water infiltration rates (Shrestha, 2005), and reduction in soil aggregates following disturbance, with recovery of micro- and macro-aggregate structure within 16 years following reclamation (Wick et al., 2009).

Clearly, drastic disturbance in sagebrush steppe affects many ecosystem properties, with long lasting impacts. However, regulatory frameworks exist to ensure successful reclamation of disturbed lands and restoration of ecosystem structure. Most reclamation criteria in Wyoming focus on a site's erosion potential, establishment of vegetative cover, and absence of noxious or invasive weedy species; soil chemical and biological properties are rarely directly assessed. Regardless, successful restoration has been achieved in disturbed sagebrush steppe ecosystems throughout Wyoming.

While spatial heterogeneity poses challenges for obtaining representative samples in soil ecology, it is important for understanding ecosystem structure and function (Ettema and Wardle, 2002), and it is likely important in a land management and disturbance-restoration context. Analytical approaches for quantifying and visualizing spatial characteristics in the environment include examination of variance, as well as characterization of spatial trends. Spatial patterns of vegetation and soil characteristics at many spatial and temporal scales have been examined in systems subject to agricultural use (Ettema et al., 2000; Fraterrigo et al., 2005; Fromm et al., 1993; Li et al., 2010; Robertson et al., 1993; Robertson and Freckman, 1995) and wildland

disturbance (Ettema et al., 1998; Gilliam and Dick, 2010; Mummey et al., 2002a; Mummey et al., 2010; Zhou et al., 2008). While specific effects of disturbance depend on the nature of the disturbance and the system examined, in general, changes in spatial patterns of vegetation and soil properties are apparent and long lasting. According to studies that have examined soil spatial patterns following disturbance, vegetation removal and soil mixing results in homogenization of vegetation and soil properties across space.

Observations suggest vegetation removal and soil mixing *definitely* alters vegetation and soil characteristics and *may* reduce the degree of variability (ecosystem heterogeneity) in vegetation and soil properties. Given the sagebrush component plays a strong role in shaping the sagebrush steppe ecosystem (both structurally and functionally), and that reestablishing the sagebrush component on reclaimed sagebrush steppe has proven difficult, we hypothesize that reclaimed lands lacking the shrub component maintain a low level of spatial structure in vegetation and soil properties, and that the spatial structure increases over time and as the shrub component is restored. The purpose of this study was to assess the effects of disturbance, reclamation, and recovery time on vegetation and soil property spatial structure. We used a spatially explicit sampling design and Bayesian geostatistical models to quantify and compare the spatial characteristics of soil and vegetation properties in a reclamation chronosequence.

4.2. Materials and Methods

4.2.1 Field Site Description

The field sampling location is in south central Wyoming, near Wamsutter (41° 41’ 17.11” N, 107° 58’ 24.41” W, elevation = 2052 m). Wamsutter lies within Wyoming’s Red Desert Basin and receives an estimated average 180 mm (historic high: 346 mm, historic low: 96 mm) of

precipitation per year (Western Regional Climate Center, 2013). Soils are classified as a frigid typic haplocalcid: a well draining, non-saline to slightly saline, calcareous soil originating from weathered sandstone (Natural Resources Conservation Service, 2012).

All research plots were established on a reclaimed pipeline corridor, wherein pipelines were installed directly adjacent to one another, allowing for climate, topography, and parent material to be consistent across study plots. The different installation dates allow for establishment of a chronosequence, or space-for-time substitution. This approach has effectively been used to examine the effect of time on soil development or soil and vegetation recovery following disturbance (Insam and Domsch, 1988; Jastrow, 1996, Johnson et al., 1991; Miller and Jastrow, 1990). Exact reclamation practices and seeding mixes were variable between pipeline disturbances, but all installations entailed removal and windrowing of topsoil (top 15 cm), subsoil compaction and trenching, topsoil respreading, and seeding.

Two undisturbed (UD) reference sites and four reclaimed pipelines were sampled, with pipeline treatments including the following recovery times (in years): 1, 5, 36, and 55. On each pipeline and on each reference area (one on either side of the pipeline corridor), a 10 m by 90 m sampling grid (minimum lag = 1 m, 108 points) was established based on the cyclic sampling design (Clinger and Van Ness, 1976) installed in two dimensions. Lag distances were chosen according to the vegetation analysis requirements (section 4.2.2). The entire sampling area, including all treatments, fell within approximately one hectare. Both vegetation and soil sampling was conducted during the spring of 2011 during periods of active vegetation growth and prior to vegetation senescence.

4.2.2 Vegetation Sampling and Analysis

A 1 m^2 quadrat frame was centered around each sample point (marked with flagging) and photographed from 2 m directly above the sample point with an Olympus E620 SLR digital camera. The photo (in .JPG format) was quantified for vegetation and ground surface cover using "SamplePoint" (www.samplepoint.org), a software program developed for assessing cover from imagery (Booth et al., 2006). One hundred sample points were equally stratified across the quadrat area and each point was classified as bare ground, litter, grass, forb, shrub, or weed. Cover data is automatically summarized by the software and recorded in a spreadsheet as a percentage of cover for each cover classification. For each sample quadrat, we calculated the total vegetation cover as the sum of grass, forb, shrub, and weed cover.

4.2.3 Soil Sampling and Analysis

At each sample point, the top five centimeters of soil were sampled with a trowel. All soils were frozen in the field with dry ice, and then transported to a freezer (-20 °C) until analysis. Soil samples were weighed, lyophilized, and re-weighed to obtain gravimetric moisture content of field-moist soil. Dry soil was sieved to 2 mm to remove coarse fragments and debris. Ten grams of dry soil were combined with 10 mL of deionized water, and the pH of the slurry was measured for pH and electrical conductivity using a combination SympHony pH and conductivity meter (VWR, Randor, PA) (Rhoades, 1982; Thomas, 1996). Remaining soil was pulverized and approximately 20 mg were assessed for elemental carbon and nitrogen content with a Costech 4010 (Valencia, CA). Inorganic carbon (calcium carbonate) was assessed on 0.5 gram samples using the modified pressure-calcimeter method (Sherrod et al., 2002). Soil organic carbon was estimated as the total carbon less the inorganic carbon.

Phospholipid fatty acid (PLFA) analysis was modified from Frostegård et al. (1993). Five grams of lyophilized soil was sonicated and shaken with 20 ml of a 1:2:0.8 mixture of

chloroform, methanol, and phosphate buffer (0.05 M, pH 7.4). Phospholipids were isolated with a silica chromatography column, methylated in alkaline 0.2 M methanolic potassium hydroxide, and purified in an amino-propyl chromatography column. Extracts were suspended in 200 µl solution of 1:1 solution of methyl *t*-butyl ether and hexane containing 25 µg ml^{-1} of an internal standard (19:0 fatty acid methyl ester). Fatty acid methyl esters were identified and quantified on an Agilent 6890 Gas Chromatograph (Palo Alto, CA) using Sherlock software (MIDI, Inc., Newark, NJ). Microbial fatty acids by functional group included bacteria (i14:0, i15:0, a15:0, i16:0, 16:1ω9c, i17:0, a17:0, cy17:0, 18:1ω9c, cy19:0), saprotrophic fungi (18:2ω6c) and protozoans (20:3ω6c, 20:4ω6c) as in Vestal and White (1989), Frostegård and Bååth (1996), and Zelles (1999) and arbuscular mycorrhizal (AM) fungi (16:1ω9c) as in Olsson (1999). Total microbial abundance was estimated from the sum of all microbial signatures.

Twelve sampling locations, stratified across the sampling grid, were sampled for soil particle size analysis. These soils were air dried, sieved to 2mm, and assessed for particle size using the hydrometer method (Gee and Bauder, 1986). Three samples were also randomly taken from the sample area for bulk density estimates using a hammer-driven corer. These samples were oven dried at 105 °C until constant mass, and bulk density was calculated based on the known core volume (101.29 cm) (Blake and Hartge, 1986). Soil particle size and bulk density data were not included in the geostatistical analyses; their purpose was to aid in describing the soil conditions at the sample location (Table 4.1).

Table 4.1: Mean values (with standard error of the mean) for soil physical properties of different pipeline recovery ages and undisturbed (UD) reference areas.

	Bulk Density ($g * cm^{-3}$)	**Sand** (%)	**Silt** (%)	**Clay** (%)	**Textual Class**
1 yr	1.68 (0.09)	59 (1.0)	9 (0.8)	32 (0.8)	Sandy Loam
5 yrs	1.48 (0.05)	55 (2.4)	12 (0.6)	33 (1.9)	Sandy Loam
36 yrs	1.50 (0.08)	50 (1.4)	11 (0.6)	39 (1.2)	Loam
55 yrs	1.61 (0.09)	44 (1.7)	12 (0.3)	44 (1.7)	Loam
UD1	1.42 (0.06)	59 (3.4)	6 (0.8)	35 (2.7)	Sandy Loam
UD2	1.65 (0.04)	62 (2.3)	6 (0.9)	32 (2.2)	Sandy Loam

4.2.4 Statistical Analysis

Geostatistical analyses provide both estimates of model parameters as well as predictions at locations not sampled. Model parameters explain the correlation structure across space, while predictions assist in understanding property behavior across space. Cressie (1991) and Gelfand et al. (2010) provide thorough background for geostatistics and their application. The geostatistical model for a measured property, P_j, in each treatment (j = 1…6) at a given location s_i (with coordinates (x_i, y_i) for i = 1…108), was defined by a mean model $\mu_j(s_i)$ plus residual variation ($\varepsilon_j(s_i)$), (equation 4.1).

$$P_j(s_i) = \mu_j(s_i) = \varepsilon_j(s_i) \quad \textbf{(4.1)}$$

In our case, the mean model (equation 4.2) consisted of one coefficient, β, or the intercept.

$$\mu_j(s_i) = \beta \quad \textbf{(4.2)}$$

The residuals were then specified according to equation 4.3; independently distributed as (~) normal, with mean zero and a constant (stationary) covariance structure defined by Σ_j.

$$\varepsilon_j(s_i) \sim independent\ Normal\ (0, \Sigma_j) \quad \textbf{(4.3)}$$

An empirical semi-variogram was constructed from the residuals for each soil property. Equation 4.4 describes the general spatial covariance structure of the residuals, illustrated by the semi-variogram.

$$\Sigma_j = \sigma_j^2 H(\phi_j) = \tau_j^2 \quad \textbf{(4.4)}$$

Here, H is an $n\ x\ n$ correlation matrix for point pairs separated by distance h and of a form consistent with a semi-variance model with partial sill (σ^2_j), range (ϕ_j) and nugget (τ^2_j). The partial sill is related to the variance in values across the sampled space, while the range corresponds to the distance of sample separation where samples become independent. The nugget variance (variance at h = 0) includes both microscale variability of a property and measurement error. The shape of the empirical semi-variogram reflects the correlation structure defined by these parameters, and is mathematically described by a valid semi-variance model.

From each treatment, we removed 18 points, stratified across the sample space. From the remaining data points, we applied a Bayesian model to estimate model parameters and make predictions at the withheld locations. Diggle and Ribeiro (2007) provide a detailed discussion of Bayesian geostatistical modeling. One benefit of the Bayesian approach is the ability to simultaneously make estimations, predictions, and quantify probability around those values. For each property, in each treatment, we obtained model parameters defined under Matérn semi-variance functions with the "smoothness" parameter, κ, set to 0.5, 1, and 2. In all cases, the value of κ was inconsequential to the parameter estimates, based on overlap of 95 % credible intervals around the estimates. The most parsimonious model (κ = 0.5) was retained, and is also referred to as the "exponential" semi-variance (γ) model (general form is in equation 4.4).

$$\gamma(|h|) = \sigma^2 \left(1 = \exp\left(=\frac{|h|}{\phi}\right)\right) = \tau^2 \quad \textbf{(4.4)}$$

Non-informative prior models were defined according to equations 4.5 – 4.7; discussed in detail by Diggle and Ribeiro (2007). Alteration of the prior models did not result in differences in model parameter estimates, based on overlap of 95% credible intervals.

$$\phi_j \sim Uniform\ (0, 100) \quad \textbf{(4.5)}$$

$$\tau_j^2 \Big/ \sigma_j^2 \sim Uniform\ (0, 100) \quad \textbf{(4.6)}$$

$$\Pr(\beta, \sigma_j^2) \propto 1 \Big/ \sigma_j^2 \quad \textbf{(4.7)}$$

Note that for computational ease, the nugget variance (τ^2_j) is defined in relative terms. Model parameters (collectively θ), were estimated with Bayesian inference according to equation 4.8. In short, prior probability distributions were updated with the data.

(4.8)

$$\Pr\left(\theta \middle| P_{1,1}, \dots P_{6,108}\right) = \frac{\mathrm{L}(\theta\ |P_{1,1}\ , \dots P_{6,108}) \cdot \Pr(\theta)}{\int \mathrm{L}(\theta\ |P_{1,1}\ , \dots P_{6,108}) \cdot \Pr(\theta)}$$

The posterior probability (Pr) distribution of the model parameters (θ), conditional on the data ($P_{1,1}$,… $P_{6,108}$), is the integral of the likelihood function (L) times the prior distribution (equations 4.5-4.7). The unsampled locations were predicted as in equation 4.9, conditional on the data and averaged over the posterior distribution of the parameters via integration.

$$\Pr(\widetilde{P_{\iota j}} | P_{1,1}\ , \dots P_{6,108}) = \int_\theta \Pr(\widetilde{P_{\iota j}} | \theta) \cdot \Pr\left(\theta \middle| P_{1,1}, \dots\ P_{6,108}\right) d\theta \quad \textbf{(4.9)}$$

Rather than performing the integrations analytically, they were evaluated through Monte Carlo simulation. From the posterior and predictive distributions, 3000 samples were drawn to estimate the probability distributions for model parameters and predicted locations. From these samples, we also obtained 95% credible intervals around parameter estimates (credible intervals for all parameters are included as supplementary material). Because we are interested in comparing

each of the recovery ages with the undisturbed reference areas, we distinguished differences in parameter values based on whether or not the credible interval of a reclaimed treatment overlapped with that of the undisturbed reference areas.

The 18 predicted values were correlated with the withheld observed values for an indication of model fit (included in supplementary material). Surface predictions were also created, by applying equation 9 to a prediction grid that spanned the entire sampled space (10 m x 90 m with 1 m grid size). From these predictions, we then created "maps" to visualize the measured property across space.

All analyses were conducted in R for Mac OS X (www.r-project.org), using the spatial statistics package, "geoR," for all geostatistics (Diggle and Ribeiro, 2007; Ribeiro and Diggle, 2001), and the "coda" package (Plummer et al., 2012) for computing 95% credible intervals from samples. Example code for analyses is included as supplementary material.

4.3. Results

4.3.1 Vegetation characteristics

The mean model parameter (Table 4.2) indicated some differences in vegetation cover between recovery ages and undisturbed references, while the spatial correlation parameters in reclaimed treatments were similar to undisturbed areas. The intercept is an indication of the magnitude of values across the plot. In Table 4.3, it is clear that the vegetation composition, according to vegetation group, was different as recovery time changes. The 5 and 36 year old plots had higher grass cover than the undisturbed plots, but all reclaimed plots had lower forb and shrub cover than the undisturbed plots. Additionally, weeds were absent in the undisturbed plots, but present in all reclaimed plots. Early in recovery, weedy species dominated the 1 year

old plot, while after 5 and 36 years, grasses dominated, but then waned in the 55 year old plot. Shrub cover does not appear to recover to undisturbed levels even after 55 years. These vegetation group characteristics resulted in a lower total cover in the 1 and 36 year old plots (Table 4.2).

Spatial correlation parameters were consistently similar across all recovery ages for all the vegetation cover characteristics. The relative nugget was variable across recovery ages, as was the partial sill. The full sill (sum of the nugget effect and the partial sill) reflects the degree of variability across the sampled space, and is perhaps easier to interpret than the partial sill or relative nugget effect. The semi-variance models in Figure 4.1 provide a visual comparison of the full sill across the recovery ages. A full sill associated with a higher semi-variance value indicates more variability of the measured property across the sampled space; more curvature in the semi-variance model is the result of a higher partial sill value. A very low full sill value is most likely a result of low abundance of the measured property.

Litter cover (Figure 4.1A) in the 1 year old plot was higher than all other plots, indicating more variable litter coverage across the surface of the plot. Bare ground (Figure 4.1B) was more variable in the undisturbed plots and the 1 year old plot. Grass cover (Figure 4.1D) was most variable in the 5 year old plot, and secondly in the 55 year old plot, while it was lowest in the undisturbed plots. Forb cover (Figure 4.1E) was most variable in the 55 year old and one undisturbed plot. Shrub cover (Figure 4.1F) was by far more variable in the undisturbed plots compared to all reclaimed plots; however, the 55 year old plot was intermediate. Weed cover (Figure 4.1G) was most variable in the 1 year old plot, with the 5 year old plot intermediate. Again, characteristics of the different vegetation cover characteristics were somewhat

represented by the total vegetation cover (Figure 4.1C), indicating highest variability in total cover in the undisturbed plots.

Table 4.2: Fitted mean trend intercept and semi-variance model parameters for cover characteristics. Asterisks indicate parameter difference from one (*) or both (**) undisturbed (UD) parameters, based on overlap of 95% credible intervals.

	β (intercept)	σ^2 (partial sill)	ϕ (range)	τ^2/σ^2 (relative nugget)
Litter				
1 yr	32.26	198.54	18.66	3.06
5 yrs	41.46	81.76	11.45	1.23
36 yrs	34.50	8.03	22.19	42.16
55 yrs	22.56	10.62	20.07	38.52
UD1	32.01	78.11	28.53	2.88
UD2	22.96	55.07	8.39	7.41
Bare Ground				
1 yr	47.85	133.93	15.66	10.85
5 yrs	37.27	138.68	14.69	1.22
36 yrs	47.91	41.47	34.41	8.45
55 yrs	55.04	6.28	20.37	52.98
UD1	40.51	113.27	36.34	6.05
UD2	40.72	111.94	29.91	6.83
Total Vegetation Cover				
1 yr	6.33**	5.46	27.99	16.92
5 yrs	18.40	26.48	26.73	7.07
36 yrs	11.55**	1.91	17.54	47.08
55 yrs	21.24	21.48	32.89	18.12
UD1	27.68	9.17	23.56	49.97
UD2	22.22	12.49	28.38	43.22

Table 4.3: Fitted mean trend intercept and semi-variance model parameters for vegetation groups. Asterisks indicate parameter difference from one (*) or both (**) undisturbed (UD) parameters, based on overlap of 95% credible intervals.

	β (intercept)	σ^2 (partial sill)	ϕ (range)	τ^2/σ^2 (relative nugget)
Grasses				
1 yr	6.10	6.10	27.16	15.12
5 yrs	18.36**	25.67	26.77	7.68
36 yrs	10.6**	1.74	15.45	45.88
55 yrs	8.98	33.84	16.96	1.71
UD1	4.51	4.33	25.88	4.93
UD2	5.33	3.54	26.77	19.44
Forbs				
1 yr	0.09*	0.006	20.86	55.08
5 yrs	0.01*	0.00	18.87	55.09
36 yrs	0.05*	0.001	17.93	55.83
55 yrs	2.85	2.96	25.07	11.64
UD1	0.76	0.23	36.12	18.66
UD2	3.06	1.97	24.59	18.26
Shrubs				
1 yr	0.12**	0.29**	4.32	10.17
5 yrs	0.04**	0.002**	20.39	48.93
36 yrs	0.88**	0.46	23.49	45.33
55 yrs	9.45*	22.18	19.39	27.7
UD1	22.37	17.87	28.77	34.78
UD2	13.89	16.05	29.59	38.33
Weeds				
1 yr	10.8**	10.88	12.09	33.70
5 yrs	2.94**	19.53	29.86	2.11
36 yrs	0.03**	0.002	17.77	52.25
55 yrs	0.009**	0.00	19.61	54.75
UD1	NA	NA	NA	NA
UD2	NA	NA	NA	NA

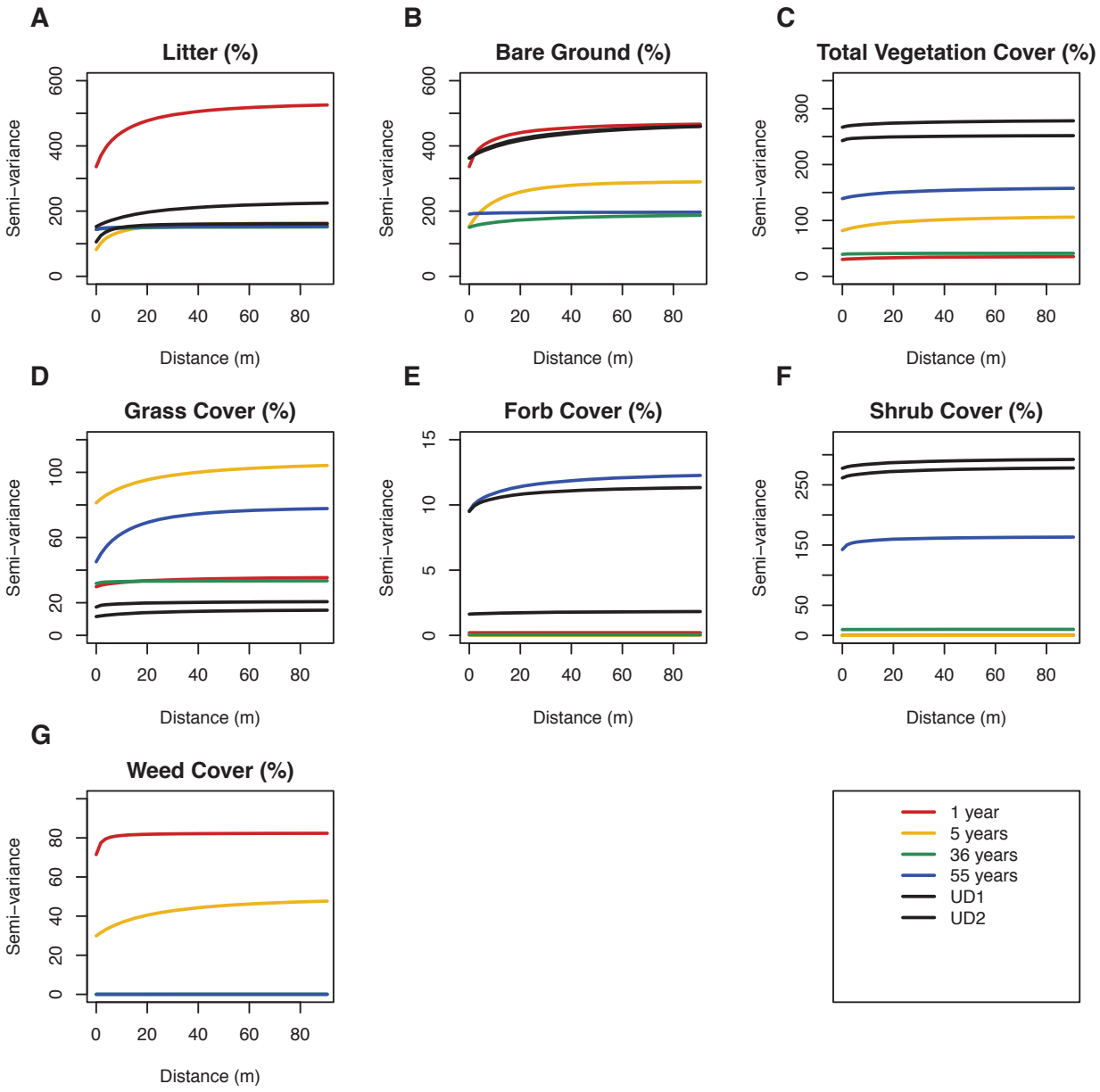

Figure 4.1: Fitted semi-variance models for cover characteristics and vegetation groups for different recovery ages and the two undisturbed (UD) treatments.

While the range parameter was fairly similar across all surface cover and vegetation characteristics and across all recovery ages, small differences are apparent in the semi-variance models (Figure 4.1). In general, the range was lower than 40 m (Tables 4.2 and 4.3). The range parameter indicates the distance at which samples acquire independence, and can also be

interpreted as “patch size.” A large range indicates correlation in samples across larger areas, while a small range indicates abrupt changes in variance across space.

Range effects, along with the magnitude, and variability patterns are most apparent when viewing the prediction surfaces (Figures 4.2 and 4.3). Litter (Figure 4.2A) and bare ground (Figure 4.2B) cover were both variable across the surface of plots and their shading is consistent with the intercepts discussed above. Variability of the litter cover in the 1 year old plot (Figure 4.2A) reflected the high full sill in that plot, as with bare ground cover for the 5 year old and undisturbed plots. Total vegetation cover surfaces (Figure 4.2C), coupled with the different vegetation group cover surfaces (Figure 4.3), illustrate the vegetation groups driving total vegetation patterns. Undisturbed plots are associated with high shrub cover, while the 5 year old plot reflects its high grass cover. The 1 and 36 year old plots were generally low and homogeneous in all vegetation groups.

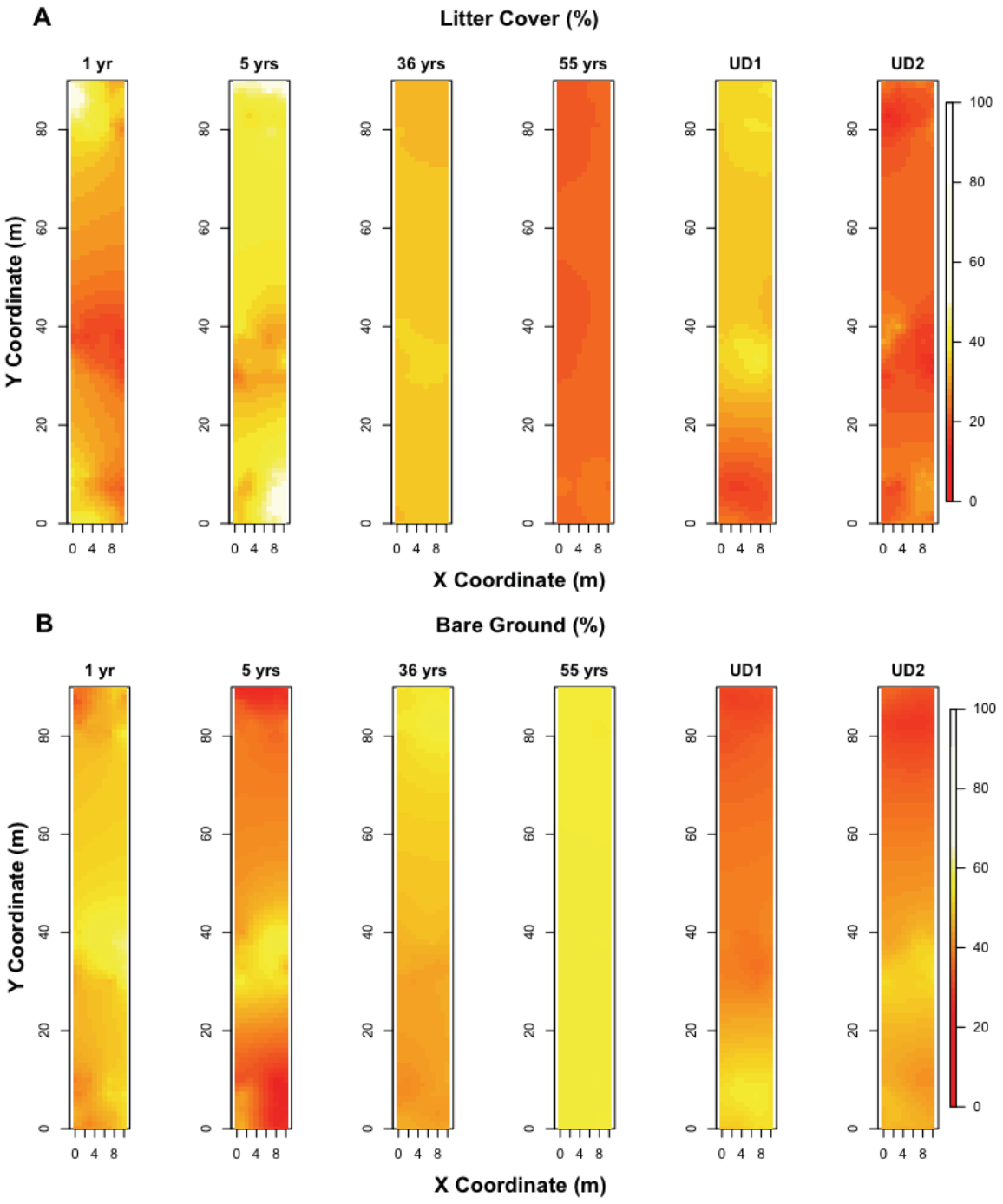

Figure 4.2: Predicted surfaces (maps) for litter, bare ground, and total vegetation cover for different pipeline disturbance recovery ages and the two undisturbed (UD) treatments (10 m x 90 m plots). Red colors indicate low values of the measured property, while white values indicate high values.

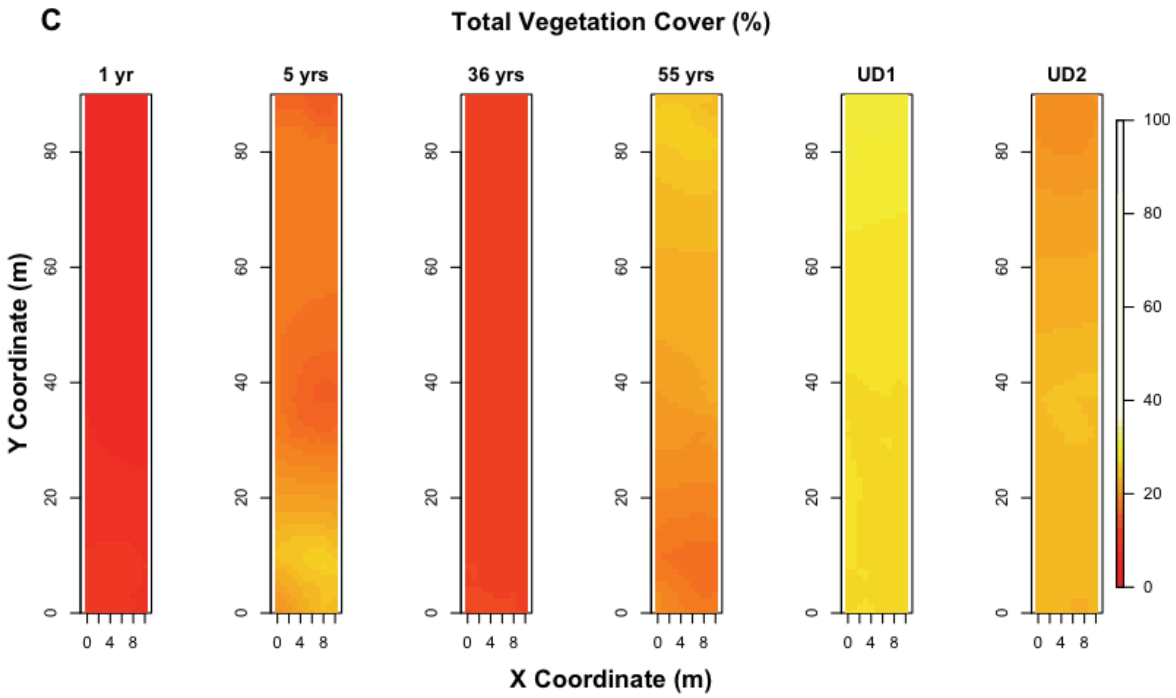

Figure 4.2 continued

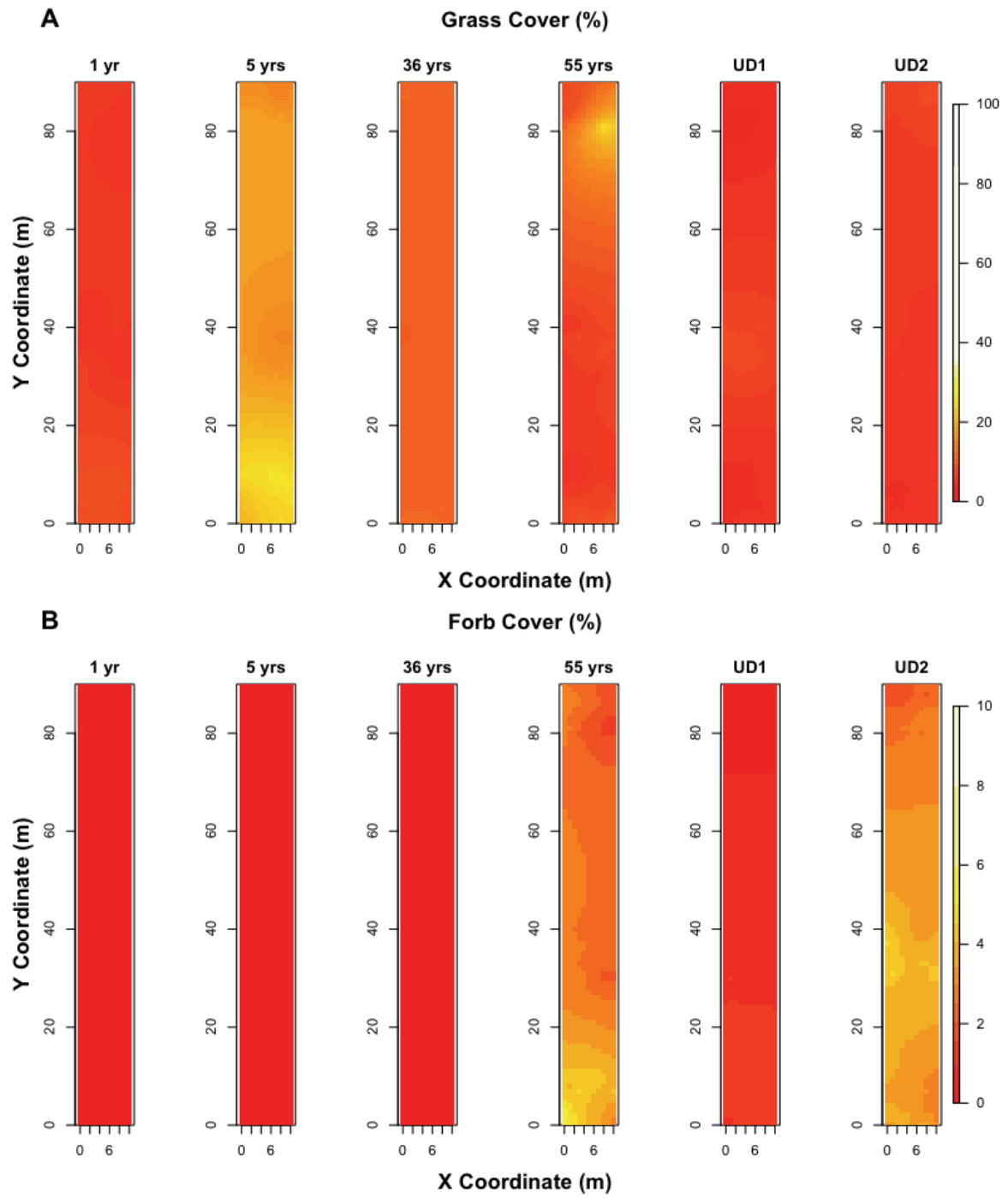

Figure 4.3: Predicted surfaces (maps) for vegetation groups for different pipeline disturbance recovery ages and the two undisturbed (UD) treatments (10 m x 90 m plots). Red colors indicate low values of the measured property, while white values indicate high values.

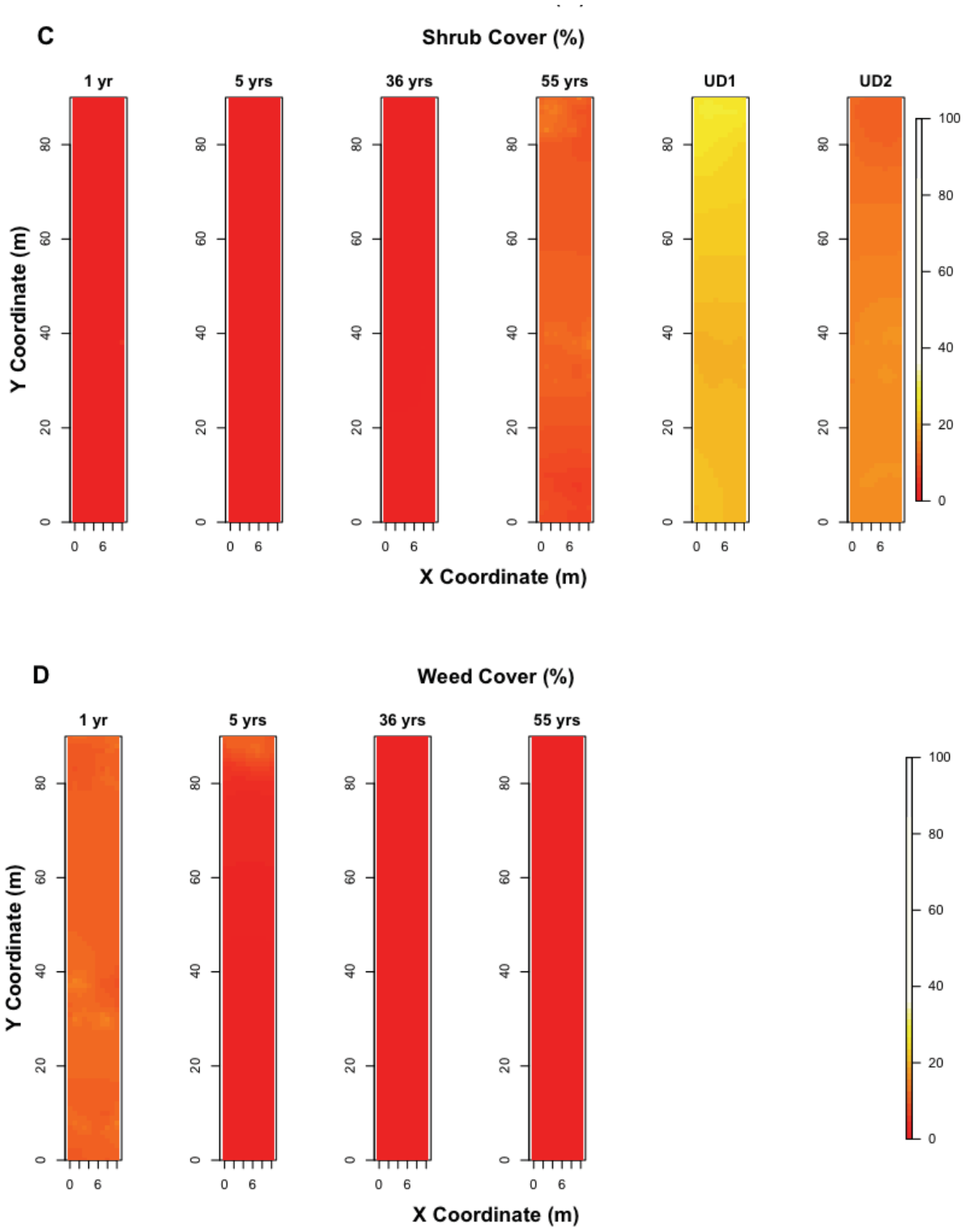

Figure 4.3 continued

4.3.2 Soil properties

Soil moisture was higher in the 1 and 55 year old plots than the undisturbed plots (Table 4.4). Total nitrogen was similar across all plots, while organic carbon was lower than one undisturbed plot in the 1 and 55 year old plots. Only the 1 year old plot had lower total microbial abundance, which corresponded to a reduction in all microbial groups in that plot (Table 4.5). Electrical conductivity was higher than the undisturbed plots in the 1 and 36 year old plots; all reclaimed plots had higher pH than the undisturbed plots.

Semi-variance models for soil properties and microbial groups, illustrated in Figure 4.4, show soil moisture (Figure 4.4A) had highest full sill in the 1 and 55 year old plots. For both total nitrogen and organic carbon (Figure 4.4B and C), undisturbed plots had the highest semi-variance. Electrical conductivity (Figure 4.4E) in the 1 year old plot was highly variable, as indicated by the sill, while all plots had similar semi-variance models for soil pH. The bacteria semi-variance models (Figure 4.4G) are nearly identical to the total microbial abundance models (Figure 4.4D), which is a reflection of the dominance of the microbial community by bacteria (approximately 70-80%). Both bacteria and fungi (Figure 4.4J) were most variable in the 36 year old plot, as indicated by their high full sill values. Actinomycetes, AM fungi, and protozoans were all most variable in undisturbed plots, and least variable in the 1 year old plot. Semi-variogram models for AM fungi and protozoans were also very similar to one another.

Table 4.4: Fitted mean trend intercept and semi-variance model parameters for soil properties. Asterisks indicate parameter difference from one (*) or both (**) undisturbed (UD) parameters, based on overlap of 95% credible intervals.

	β (intercept)	σ^2 (partial sill)	ϕ (range)	τ^2/σ^2 (relative nugget)
Moisture				
1 yr	4.13**	0.04	17.08	52.58
5 yrs	1.98	0.04	19.28	45.30

36 yrs	1.91	0.07	35.83	22.96
55 yrs	2.49*	0.13	21.37	35.48
UD1	1.58	0.09	24.53	13.72
UD2	2.16	0.08	24.81	31.68
Total Nitrogen				
1 yr	1.79	0.20	40.77	18.11
5 yrs	1.82	0.06	28.11	42.79
36 yrs	1.85	0.18	38.83	20.77
55 yrs	1.79	0.21	39.47	17.86
UD1	2.00	0.21	39.66	19.49
UD2	1.71	0.12	33.87	32.61
Organic Carbon				
1 yr	6.09*	6.85	4.94	8.03
5 yrs	9.34	2.19	37.16	2.96
36 yrs	7.96	6.38	32.39	3.49
55 yrs	7.55*	0.64	17.08	51.02
UD1	12.03	33.06	4.33	2.15
UD2	6.97	1.64	33.01	34.07
Total Microbial Abundance				
1 yr	4.07*	0.87	18.23	13.23
5 yrs	5.90	2.41	31.20	1.28
36 yrs	5.68	2.69	30.12	4.60
55 yrs	6.12	0.22	18.31	50.59
UD1	7.23	0.33	18.10	45.83
UD2	5.38	1.35	25.23	7.01
Electrical Conductivity				
1 yr	411.79*	2013.83	21.33	46.70
5 yrs	325.34	4160.55	43.90	2.17
36 yrs	410.57*	2495.44	14.65	28.65
55 yrs	290.66	301.65	20.22	50.11
UD1	237.83	7665.08	5.35	3.25
UD2	284.27	2010.89	15.81	39.32
pH				
1 yr	7.48*	0.001	17.84	55.5
5 yrs	7.53*	0.01	34.96	8.89
36 yrs	7.70**	0.004	14.99	42.92
55 yrs	7.56*	0.002	22.63	46.59
UD1	7.18	0.003	22.09	39.58
UD2	7.50	0.004	19.25	52.45

Table 4.5: Fitted mean trend intercept and semi-variance model parameters for microbial groups. Asterisks indicate parameter difference from one (*) or both (**) undisturbed (UD) parameters, based on overlap of 95% credible intervals.

	β (intercept)	σ^2 (partial sill)	ϕ (range)	τ^2/σ^2 (relative nugget)
Bacteria				
1 yr	3.12*	0.55	17.62	11.96
5 yrs	4.50	1.37*	31.52	1.33
36 yrs	4.38	1.58	28.87	3.66
55 yrs	4.76	0.11	17.97	50.95
UD1	5.48	0.15	18.61	47.35
UD2	4.13	0.86	24.4	5.45
Actinomycetes				
1 yr	0.44*	0.01	17.68	1.55
5 yrs	0.62	0.01	24.18	1.11
36 yrs	0.55*	0.01	23.37	1.30
55 yrs	0.63	0.01	25.19	10.68
UD1	0.77	0.004	18.56	32.66
UD2	0.61	0.004	24.85	23.74
AM Fungi				
1 yr	0.20*	0.002	17.76	20.14
5 yrs	0.32	0.009	36.45	1.43*
36 yrs	0.32	0.007	32.15	11.09
55 yrs	0.36	0.001	17.24	52.31
UD1	0.43	0.002	17.11	48.53
UD2	0.30	0.009	21.89	3.33
Fungi				
1 yr	0.31*	0.004	19.03	46.61
5 yrs	0.41	0.04	33.63	1.46
36 yrs	0.46	0.02	27.55	33.07
55 yrs	0.35	0.002	19.32	53.37
UD1	0.51	0.01	21.30	38.40
UD2	0.32	0.007	23.63	26.87
Protozoa				
1 yr	0.20*	0.002	17.76	20.14
5 yrs	0.32	0.009	36.45	1.43
36 yrs	0.32	0.007	32.15	11.09
55 yrs	0.36	0.001	17.24	52.31
UD1	0.43	0.002	17.11	48.53
UD2	0.30	0.009	21.89	3.33

Semi-variance models with a large partial sill but a small range value result in distinct patterns in the surface predictions. For example, organic carbon in the 1 year old and UD1 plots and electrical conductivity in the UD1 plot have high variation over small areas, illustrated in Figure 4.5C and 4.5E by the speckled appearance. Conversely, the lower partial sill of other variables, in other treatments, results in a more smooth, more correlated surface across space.

The high soil moisture values in the 1 and 55 year old plots are represented in the surface predictions (Figure 4.5A). Total nitrogen varied little across the different recovery ages, and a trend in the y-direction is apparent from the surface predictions. Organic carbon (Figure 4.4C) did not display the same pattern, but the higher values in the UD1 plot are apparent. The organic carbon surfaces are similar to the microbial abundance surfaces, and all microbial group surfaces (Figure 4.6) also have the same patterns. Lastly, the electrical conductivity and soil pH values appear higher than the undisturbed plots, although only the 5 year old and UD1 plots have much heterogeneity.

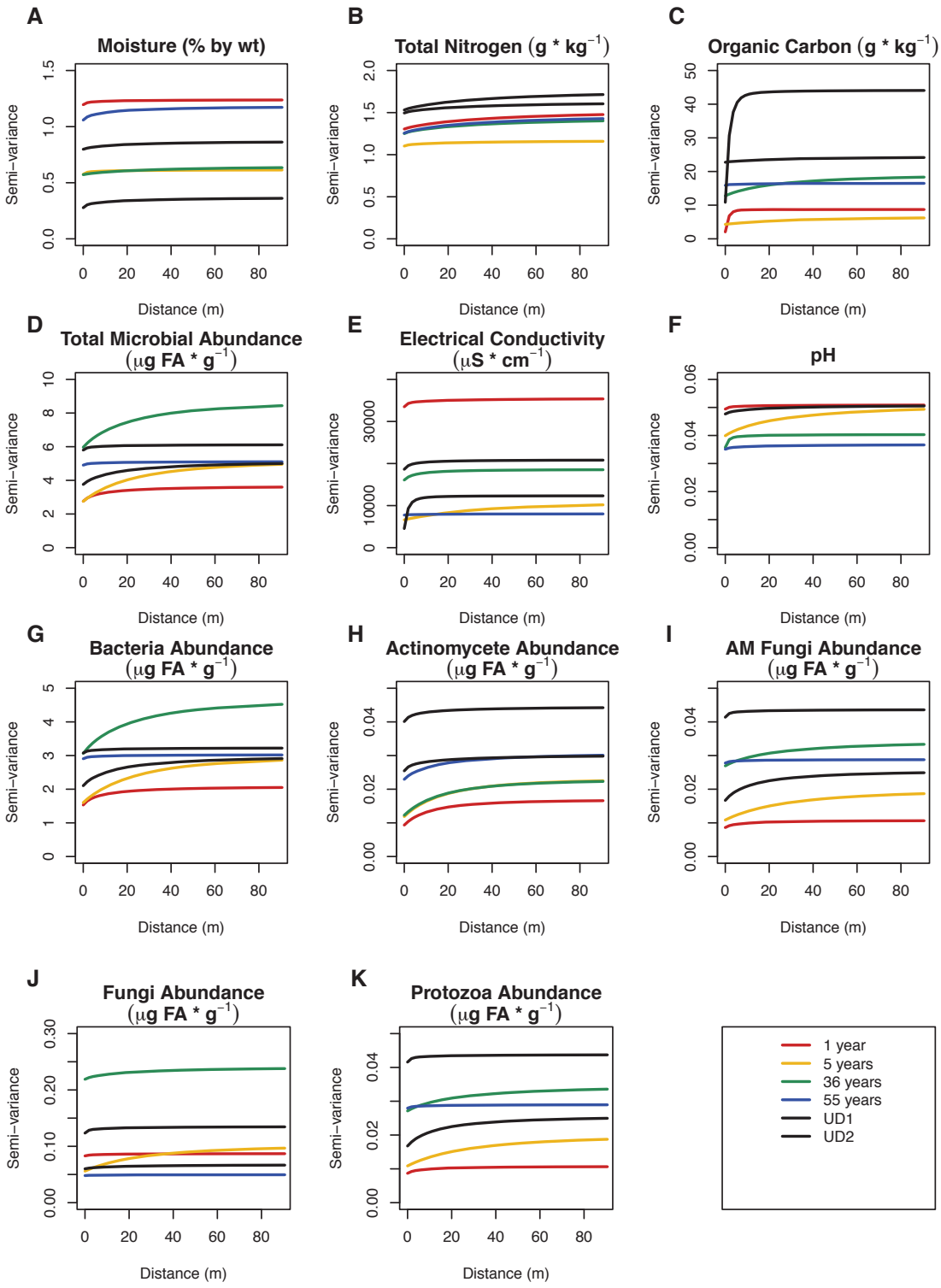

Figure 4.4: Fitted semi-variance models for soil properties and microbial groups for different recovery ages and the two undisturbed (UD) treatments.

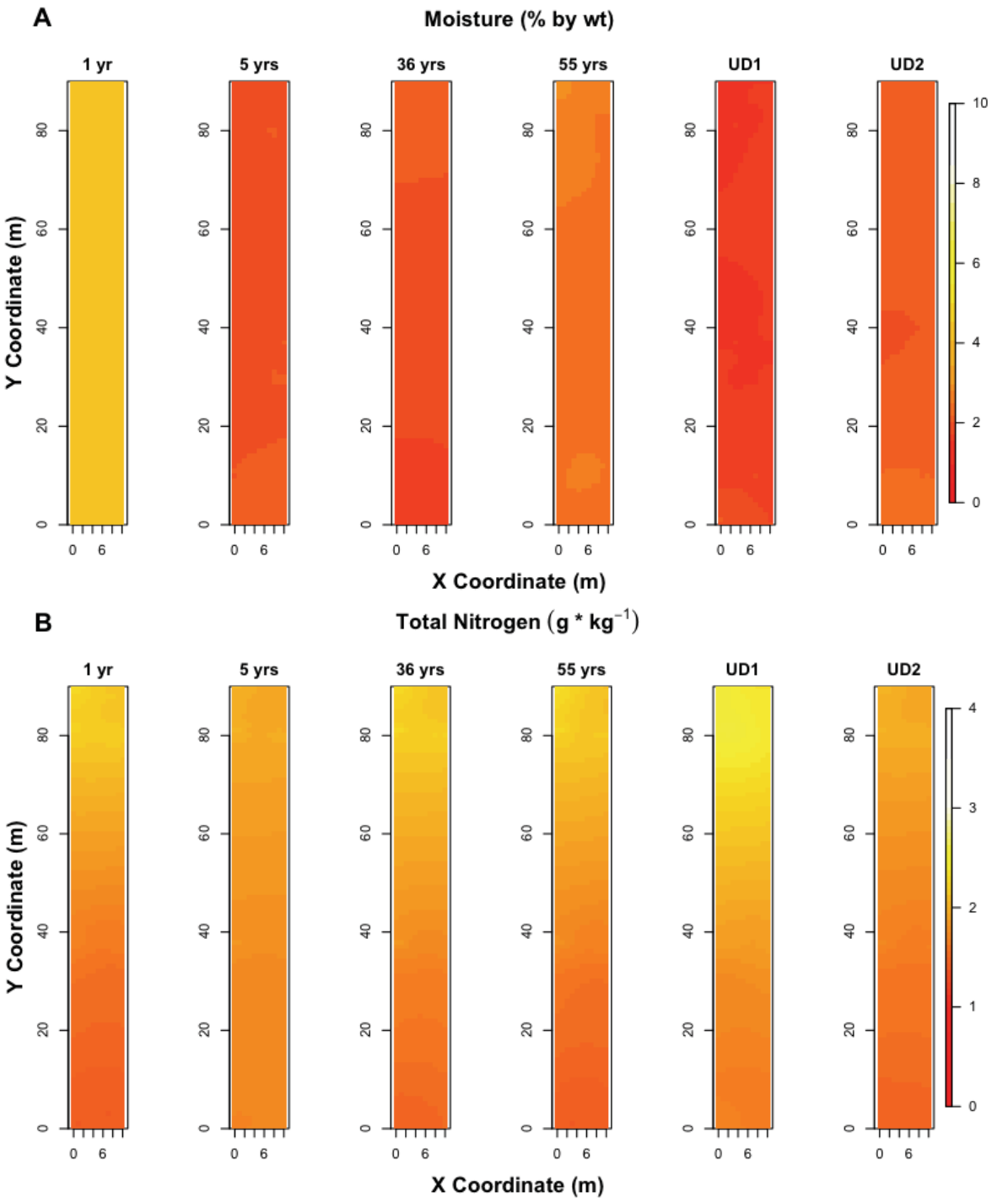

Figure 4.5: Predicted surfaces (maps) for soil properties for different pipeline disturbance recovery ages and the two undisturbed (UD) treatments (10 m x 90 m plots). Red colors indicate low values of the measured property, while white values indicate high values.

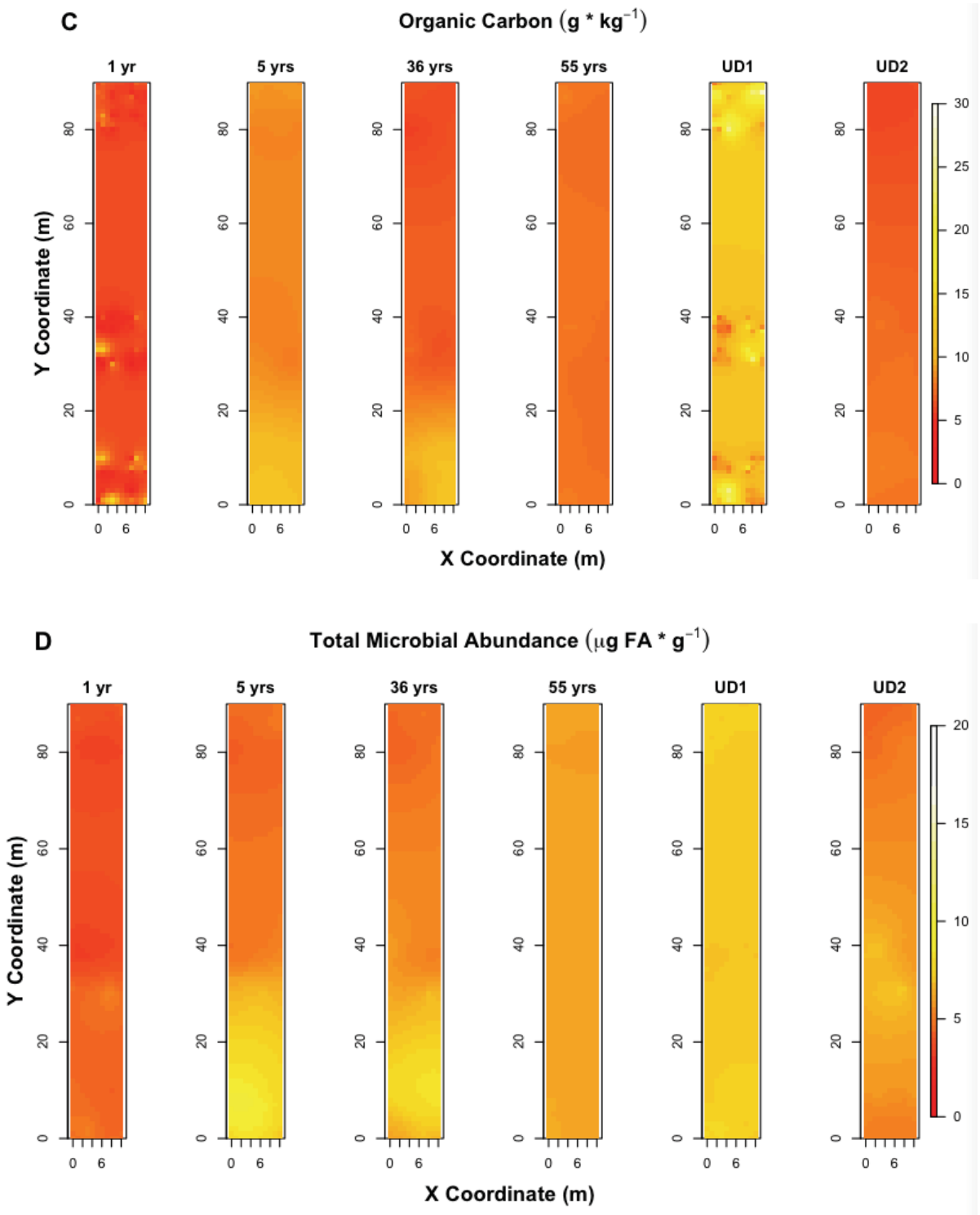

Figure 4.5 continued

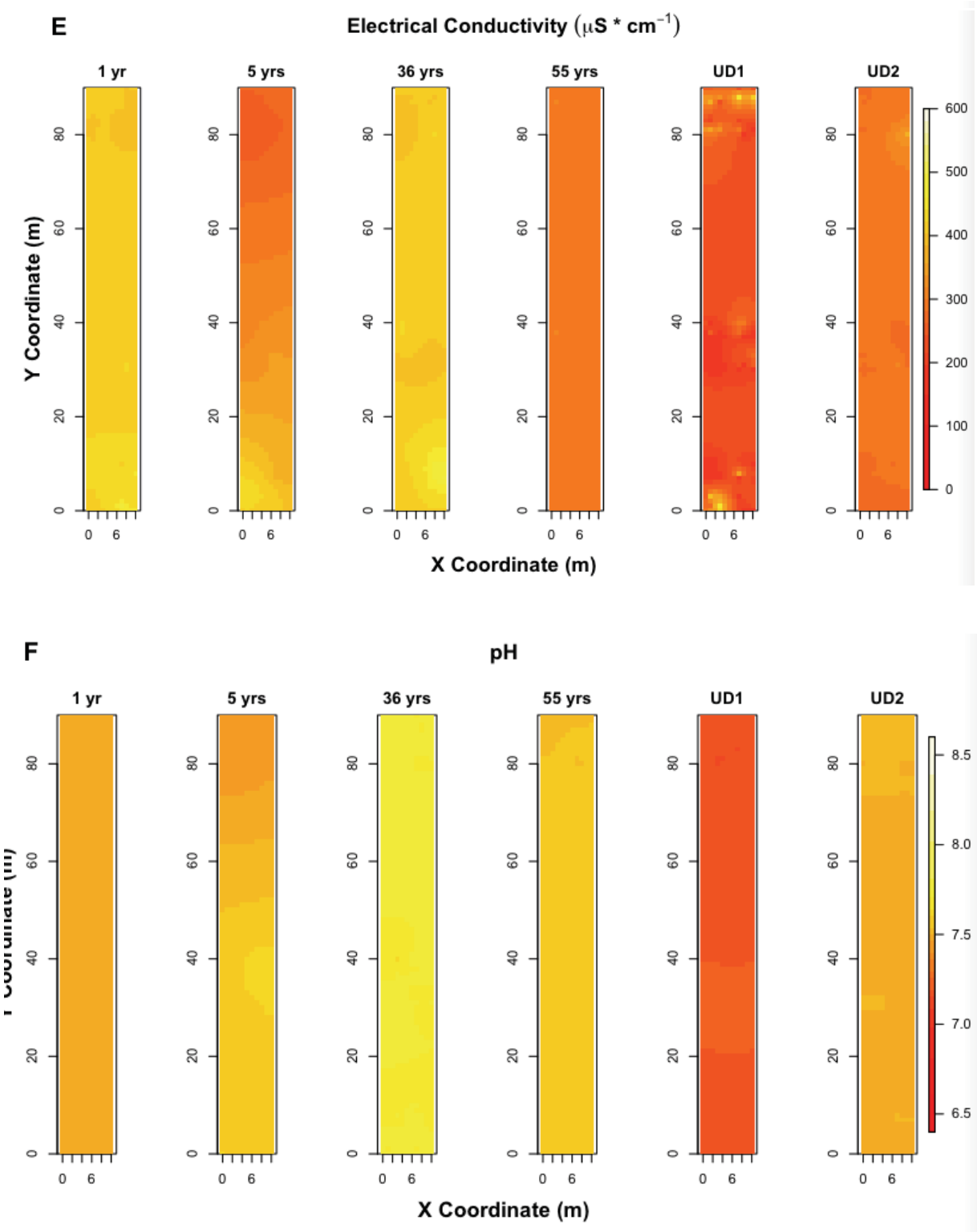

Figure 4.5 continued

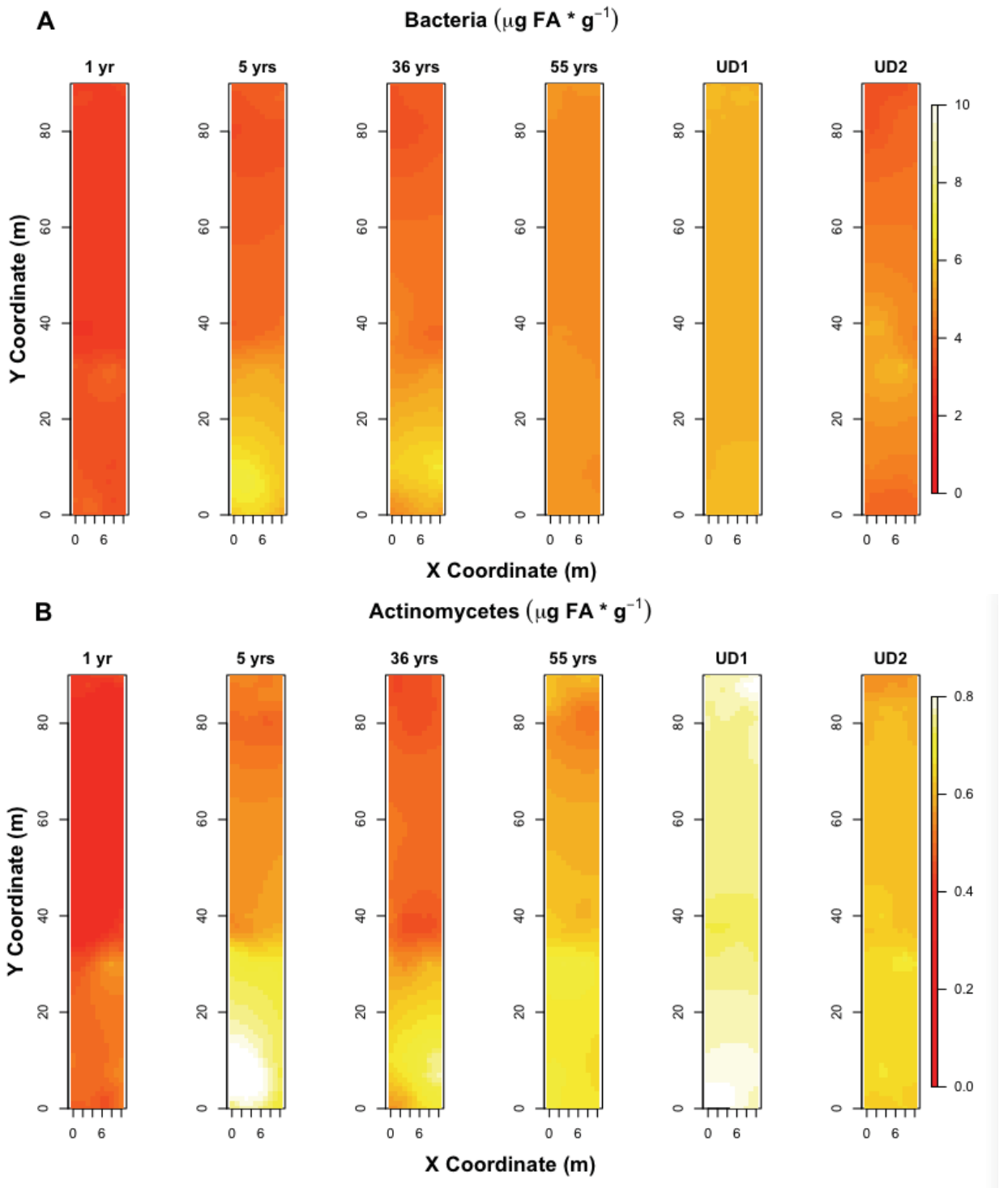

Figure 4.6: Predicted surfaces (maps) for soil microbial groups for different pipeline disturbance recovery ages and the two undisturbed (UD) treatments (10 m x 90 m plots). Red colors indicate low values of the measured property, while white values indicate high values.

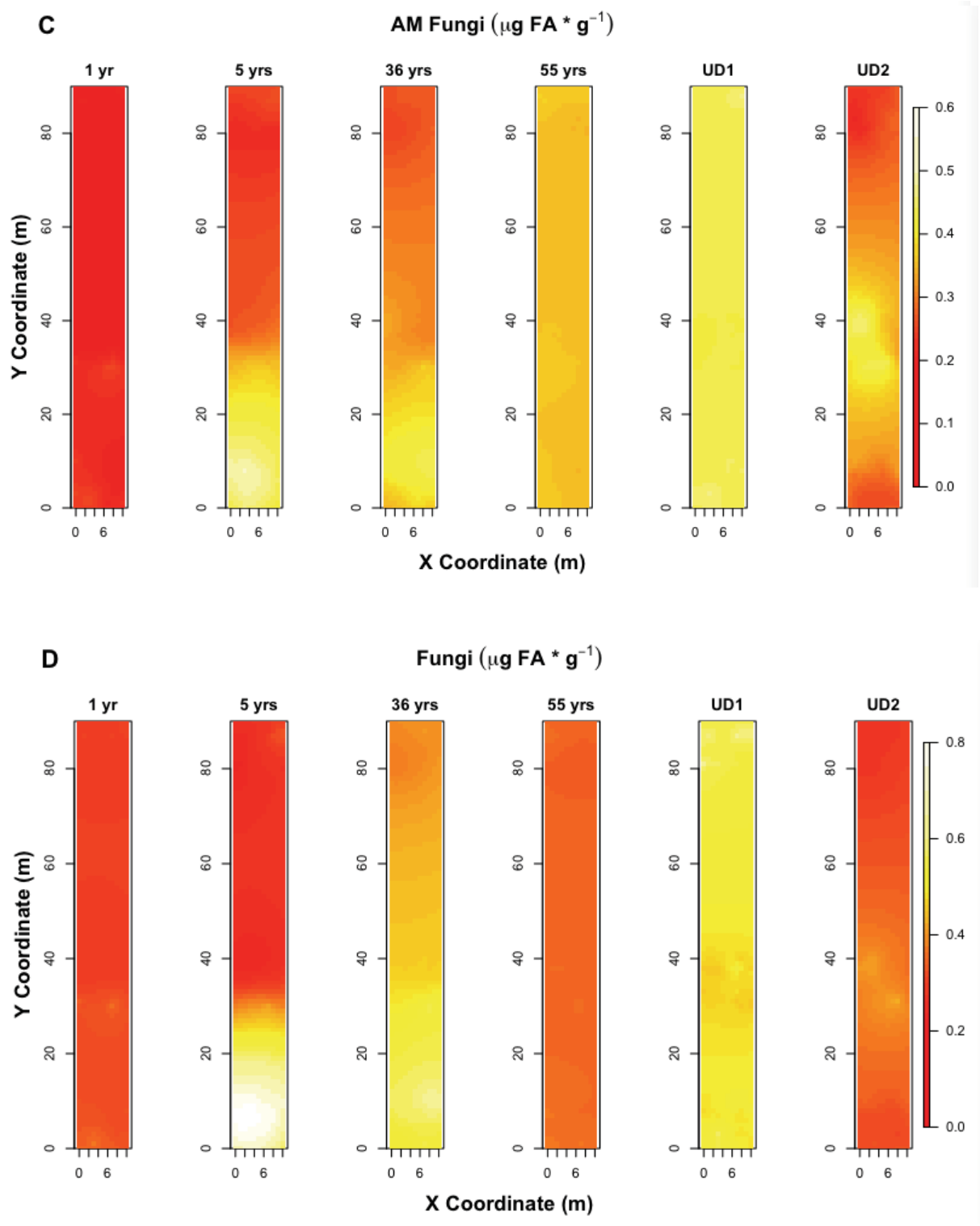

Figure 4.6 continued

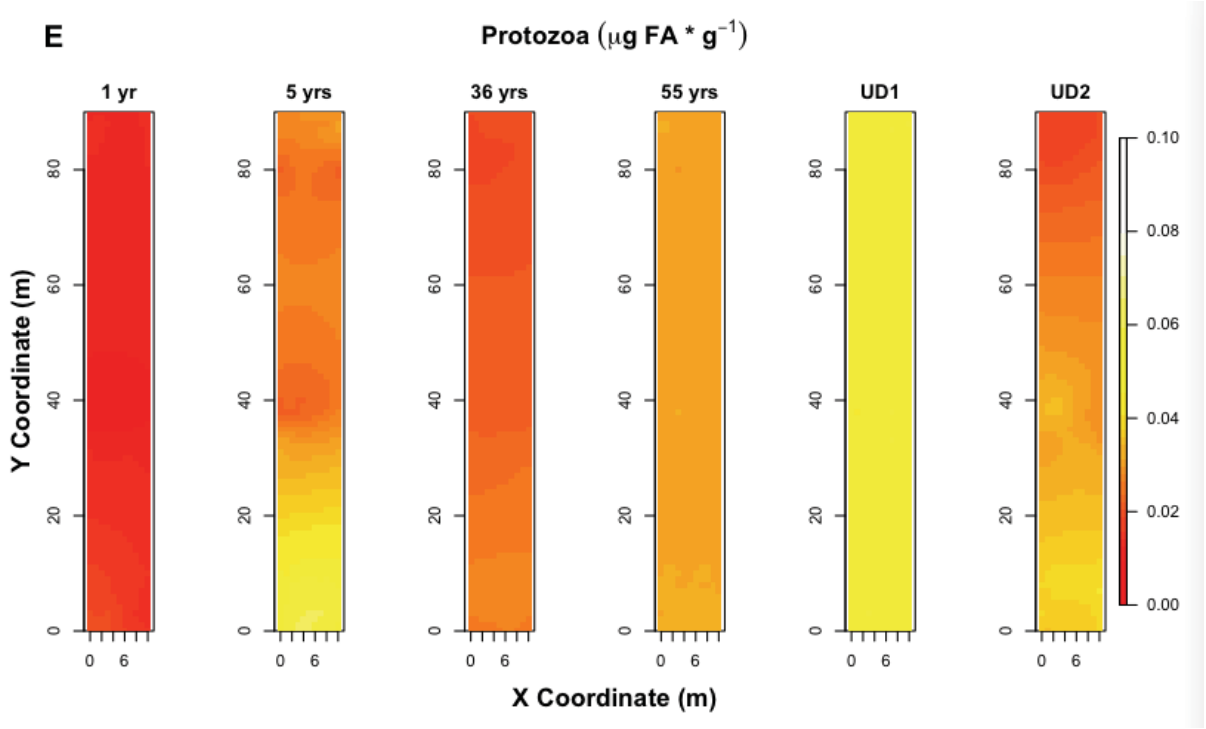

Figure 4.6 continued

4.4. Discussion and Conclusions

We hypothesized that drastic disturbance associated with buried pipeline installations would result in homogenization of vegetation and soil properties. Heterogeneity can be measured in multiple ways, and we implemented a spatial sampling design across a chronosequence, analyzed with geostatistics. These methods allowed us to identify and compare the magnitude and variability of data values within the sampled area, and to visualize patterns, patch size, and smoothness of values across space.

In terms of spatial distribution, the vegetation characteristics did not display strong spatial heterogeneity. Patchiness distinct to the sagebrush steppe (West 1983) was not detected through our analyses at the scale sampled. Most reports of sagebrush steppe spatial patterns indicate spatial correlation at scales less than 1 meter (Halvorson et al., 1994; Halvorson et al.,

1995; Jackson and Caldwell, 1993; Mummey et al., 2002a), so spatial dependency may not be a strong effect at the scale sampled. However, the composition of vegetation in each of the recovery ages aligns with our understanding of secondary succession and development of heterogeneous plant communities. Directly following disturbance and reclamation, weedy plant species colonized and dominated, but within a few years, grasses colonized with high, uniform cover. As recovery time increased, forbs and shrubs colonized, and grasses experienced a decline. However, even after 55 years of recovery, grass cover was slightly higher, and shrub cover was lower than the undisturbed reference areas. The combination of shrubs, grasses, and forbs in the undisturbed plots creates the distinct heterogeneity of the sagebrush steppe; analysis of each vegetation component alone makes it more difficult to detect the patchiness and spatial patterns observed in the field. Analysis of vegetation as point patterns or individual plant and species mapping, rather than 1 m^2 plot composite data, may provide a better illustration of vegetation heterogeneity, species diversity, and community recovery. However, the 36 and 55 year old plots displayed vegetation characteristics more similar to the undisturbed plots than the 1 and 5 year old site—indicating some degree of recovery with time.

The “young” plots had fairly continuous cover of either weeds or grasses, and the shrub component influencing the distribution of soil properties was absent. Because of these aboveground patterns, we expected to observe patchiness of soil properties (especially carbon, nitrogen, and microbial biomass) in the undisturbed plots, while those patterns would be lacking in the young reclaimed plots. Specifically, we expected for the range parameter, or distance between uncorrelated samples, to increase in response to reclamation. This response of the correlation structure has been observed in other studies of land use disturbances (Gilliam and Dick, 2010; Li et al., 2010; Mummey et al., 2010). We did not observe changes in the range

parameter, but the soil property values were often more uniform in the 1 year old plot, than any other plot. While the correlation structure was not strongly affected by the disturbance and recovery age (according to 95% credible interval overlap), the observed data values demonstrated less heterogeneity across the sampled space in the reclaimed plots.

The magnitude of soil values, as indicated by the intercept values in the models, responded to disturbance and reclamation as we expected. Soil moisture increases in freshly disturbed soils as a result of soil structural changes, which influence water infiltration and retention (Schroeder et al., 2010; Shukla et al., 2004). Soil organic carbon and microbial abundance displayed a decrease, as previously documented in reclaimed semiarid soils (Anderson et al., 2008; Ganjegunte et al., 2009; Mummey et al., 2002a; Wick et al., 2009), due to mineralization and dilution with soil mixing. Microbial abundance may also experience dilution, but also physical disruption and reduction in labile substrates. Microbial abundance has also been documented to decrease in response to disturbance of semiarid soils (Dangi et al., 2012; Ingram et al., 2005; Stahl et al., 1988), but has been reported to require up to 20 years to reach undisturbed levels (Frost et al., 2001; Mummey et al., 2002a). Total nitrogen was invariant to disturbance and reclamation; rather, the predicted surfaces illustrated an obvious and universal trend along the plot y-coordinate. Mineral and organic nitrogen pools were not measured, and nitrogen, like carbon, likely experienced some mineralization that was undetectable with our analyses. Soil chemical properties, electrical conductivity and pH, were both elevated in reclaimed soils. During disturbance, shallow soil is mixed with lower horizon material, often high in calcium carbonates and mineral salts. These materials appear in the re-spread soil, with the observed effect on salinity and alkalinity.

Soil properties were not strongly correlated with any of the surface and vegetation cover characteristics in reclaimed and undisturbed plots (analysis not presented). The predicted surfaces of the soil properties slightly matched the vegetation surfaces of the undisturbed plots—especially the UD2 plot, with a "hotspot" of vegetation and soil microbes near the middle of the plot. Also, the "southern" end of the 5 year old plot, with high grass cover, was associated with high microbial abundance. However, most of the reclaimed prediction surfaces show little similarity between the soil and vegetation patterns. It appears the soil properties that we measured are less dependent on the vegetation structure at the sampled scale, and perhaps more dependent on microtopography (total nitrogen), soil physical alteration (soil moisture), or soil chemical alteration (electrical conductivity and pH).

Clearly, the spatial patterns and distribution of vegetation and soil properties are affected by drastic soil disturbance and recovery age. These differences appear in the surface trends, but not strongly in the correlation structure. A recent discussion by Lark (2012) recognizes some challenges in soil spatial modeling; specifically, that these geostatistical models assume stationarity—the idea that the correlation structure is consistent across the sampled space. Furthermore, semi-variance models rely on lag distance (h) as a sole argument. Both of these assumptions may require some relaxation and modification in a soil spatial model, in order to incorporate the complexity of the soil environment and its many related properties. As a simple example, the correlation structure associated with organic carbon may differ between bare interspaces and underneath shrub canopies. Refining these geostatstical approaches to incorporate the processes that we already understand about the soil environment may facilitate a clearer picture of patterns of variance in soil properties across space and in relation to other

environmental properties. These modifications are certainly worth exploring for complex systems, such as the plant and soil environments.

Overall, we can confirm that aboveground and belowground spatial structure in sagebrush steppe changes in response to drastic disturbance. Yet, we observed that over time, the plant community develops heterogeneity in vegetation group composition, although not to the extent observed in the undisturbed areas, due to the slow recovery of shrubs and forbs. Soil properties displayed homogenization immediately following disturbance, but many properties did not develop spatial structure in association with the vegetation changes. Soil microbial abundance displayed the strongest spatial relationships to the vegetation patterns, while the spatial patterns of other soil properties were likely influenced by other environmental factors. This study illustrates that disturbance in these semiarid sagebrush steppe plots may require in excess of 55 years for above- and belowground structure to recover to undisturbed levels. Furthermore, the reestablishment of shrubs, particularly sagebrush, appears to be an essential step toward restoring aboveground and belowground ecosystem structure.

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CHAPTER 5

Summary and Conclusions

The objective of this project was to investigate aboveground and belowground ecosystem structure of sagebrush steppe immediately following disturbance and as it recovers. I predicted that vegetation and soil properties would experience reduction in variability and heterogeneity in response to disturbance. In these studies, disturbance definitely had an impact of the vegetation and soil properties measured. Specifically, uniform cover of weedy forbs dominated vegetation communities immediately after disturbance. The weedy species were replaced with uniform cover of grasses, which persisted even in the oldest disturbance (55 years). The shrub component was present, but low in abundance in all reclaimed areas compared to reference areas.

Soil properties were also impacted by disturbance, with reductions in microbial abundance and organic carbon. The total nitrogen pool was stable, although it may have experienced shifts in mineral and organic pool sizes. In general, soil moisture, salinity, and alkalinity increased in reclaimed soils. Soil properties that are closely associated with the vegetation (carbon, nitrogen, microbial biomass) displayed a reduction in variability in general, and in their spatial dependence at a scale less than ten meters. At the larger scale sampled (up to 100 meters), microbial abundance appeared to be most tightly associated with vegetation patterns. Conversely, the spatial effects of organic carbon and total nitrogen were less affected by disturbance and reclamation at that scale. The variability and spatial patterns of moisture, salinity, and alkalinity were not distinctly responsive to disturbance and recovery time at either spatial scale. I presume that these properties are influenced by the effects of soil mixing, and not as dependent on vegetation for their distribution across space.

Overall, the sagebrush steppe plant community and the soil properties that are tightly associated with it experience changes in abundance, variability, and spatial distribution following drastic disturbance and reclamation. At the field sites sampled, these ecosystem structure characteristics, and the accompanying environmental heterogeneity, were not restored after 55 years. While this project examined ecosystem structure, these patterns likely hold functional significance, resulting in net differences in ecosystem function. Reclaimed areas are also potentially altered in their carbon and nitrogen acquisition, cycling, and loss, biomass production, and maintenance of biodiversity—all functions valued in sagebrush steppe. These areas of sagebrush steppe that functioned as wildlife habitat prior to disturbance are not meeting wildlife needs after a half-century of recovery because they lack the structural development required by sagebrush obligate species. These results emphasize the ecological consequences of drastic disturbance on the sagebrush steppe as a valuable resource. In practice, every effort should be taken to limit the footprint and spatial extent of drastic disturbance. Reclamation efforts should strive to encourage shrub re-establishment to initiate restoration of the heterogeneous environment inherent to the sagebrush steppe.

Figure S2.1: Observed values plotted against replicated values obtained from the posterior predictive distributions, with the 1:1 line included for reference. Whiskers represent the 95 % credible interval around the prediction. Correlation coefficients (ρ) are also included

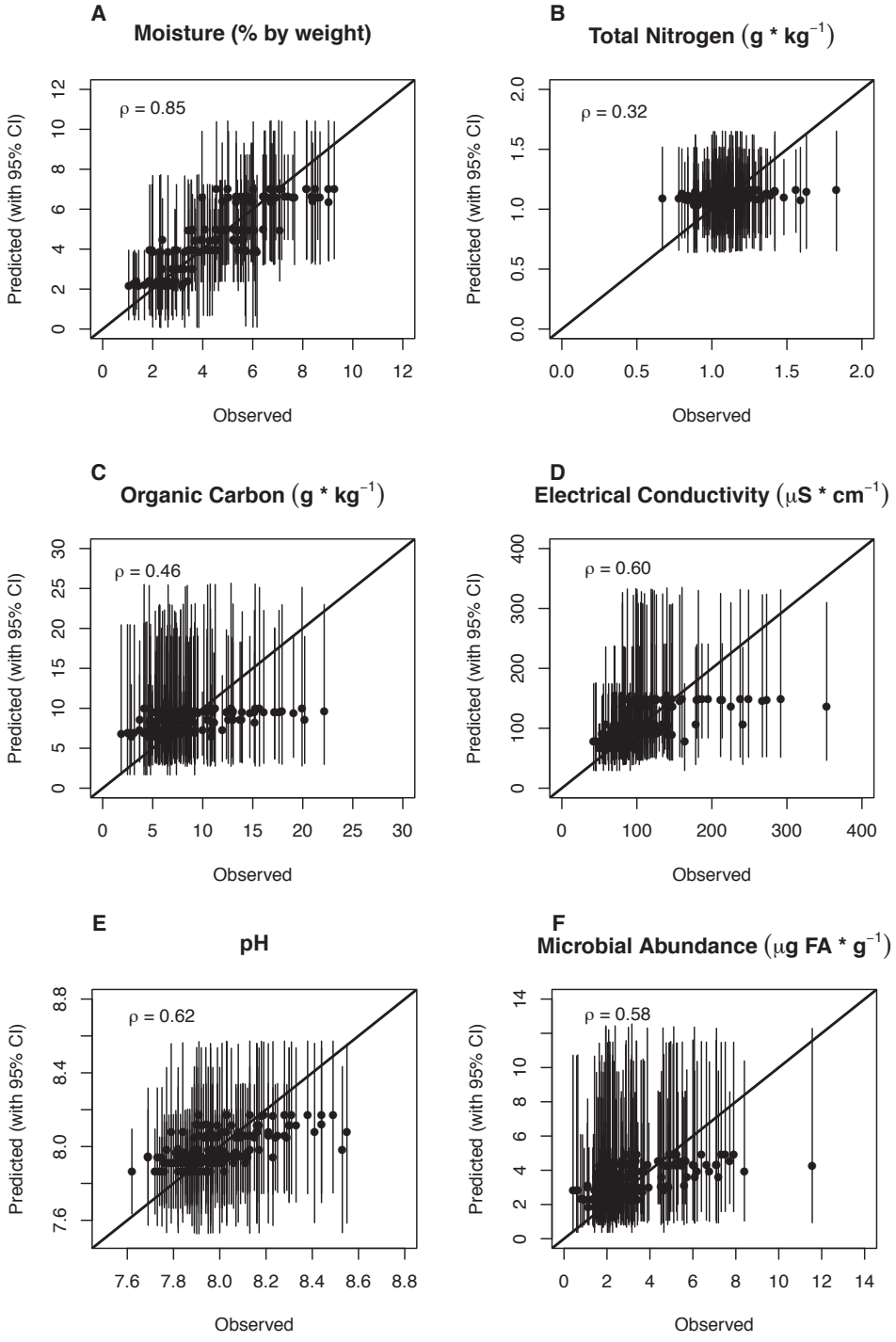


Figure S2.2: Example code for hierarchical linear mixed model

```
## Hierarchical mixed effects model for chronosequence data:
## 2 years (k), 7 treatments (j), 12 observations (i)

model{
     for(k in 1:2){
          for(j in 1:7){
               for(i in 1:12){
               P[i,j,k] ~ dnorm(mu[j,k], tau[j,k])
               Prep[i,j,k] ~ dnorm(mu[j,k], tau[j,k])
               }
          mu[j,k] <- beta[j] + alpha[j,k]
          tau[j,k] ~ dgamma(0.001, 0.001)
          alpha[j,k] ~ dnorm(0, tau.alpha)
          Ppred[j,k] ~ dnorm(mu[j,k], tau[j,k])
          }
     }
     for(j in 1:7){
     beta[j] ~ dnorm(mu.beta, tau.beta)
     }
tau.alpha ~ dgamma(0.001, 0.001)
mu.beta ~ dnorm(0, 0.001)
tau.beta ~ dgamma(0.001, 0.001)
}
```

Table S2.1: Sample mean and standard error of the mean for cover, biomass, and richness (n=3).

	Bare & Litter (%)	**Grasses** (%)	**Forbs** (%)	**Shrubs** (%)	**Weeds** (%)	**Roots** (mg * cm^{-3})	**Biomass** (g * m^{-2})	**Richness** (# of sp.)
				2010				
< 1 yr	48.33	30.67	0.67	20.67	0	6.59	25.00	11.00
	(3.18)	*(3.84)*	*(0.33)*	*(0.88)*	*(0)*	*(1.04)*	*(5.51)*	*(0.58)*
4 yrs	60.33	39.33	0	0	0.33	6.13	55.00	6.00
	(4.18)	*(4.33)*	*(0)*	*(0)*	*(0.33)*	*(1.53)*	*(6.93)*	*(0.58)*
28 yrs	48.00	31.00	3.67	17.33	0	4.67	26.33	8.67
	(6.24)	*(8.08)*	*(0.67)*	*(5.78)*	*(0)*	*(0.85)*	*(5.78)*	*(0.67)*
35 yrs	44.67	51.67	0	0.33	3.00	13.26	51.67	5.67
	(3.76)	*(5.36)*	*(0)*	*(0.33)*	*(3.00)*	*(2.27)*	*(10.41)*	*(1.45)*
54 yrs	60.00	36.67	0	0	3.00	4.81	28.33	6.33
	(1.53)	*(2.91)*	*(0)*	*(0)*	*(1.15)*	*(0.88)*	*(5.24)*	*(0.88)*
U1	91.67	6.67	1.00	0	0.33	7.41	1.67	3.33
	(2.73)	*(2.85)*	*(1.00)*	*(0)*	*(0.33)*	*(0.93)*	*(0.33)*	*(0.67)*
U2	48.00	28.00	4.00	19.67	0	12.52	17.00	9.00
	(4.62)	*(4.93)*	*(0.58)*	*(4.06)*	*(0)*	*(1.09)*	*(6.03)*	*(0.58)*
				2011				
< 1 yr	64.33	15.00	1.33	19.33	0	29.19	15.33	7.67
	(1.20)	*(1.00)*	*(0.33)*	*(1.45)*	*(0)*	*(7.74)*	*(3.48)*	*(0.33)*
4 yrs	72.67	26.67	0	0.67	0	12.38	45.00	5.33
	(2.96)	*(3.18)*	*(0)*	*(0.67)*	*(0)*	*(3.71)*	*(1.00)*	*(0.88)*
28 yrs	74.00	19.67	2.33	4.00	0	15.37	46.00	6.33
	(3.21)	*(4.48)*	*(0.33)*	*(2.31)*	*(0)*	*(9.48)*	*(5.20)*	*(0.67)*
35 yrs	78.67	20.33	0.67	0.33	0	14.81	51.00	3.33
	(1.67)	*(1.45)*	*(0.67)*	*(0.33)*	*(0)*	*(1.58)*	*(3.46)*	*(0.88)*
54 yrs	67.33	26.00	0.33	1.33	5.00	16.88	56.67	5.00
	(4.18)	*(3.46)*	*(0.33)*	*(0.33)*	*(2.52)*	*(8.90)*	*(5.36)*	*(0.58)*
U1	56.33	11.33	0.67	0	31.67	8.29	26.67	5.33
	(4.98)	*(0.88)*	*(0.67)*	*(0)*	*(6.06)*	*(1.45)*	*(10.73)*	*(0.88)*
U2	57.33	17.33	2.67	22.67	0	19.58	23.33	7.33
	(4.18)	*(4.91)*	*(1.20)*	*(3.18)*	*(0)*	*(1.61)*	*(7.84)*	*(0.88)*

Table S2.2: Mean with standard deviation in parenthesis for posterior predictive distributions.

	Moisture (% by wt)	**Total Nitrogen** ($g * kg^{-1}$)	**Organic Carbon** ($g * kg^{-1}$)	**Electrical Conductivity** ($\mu S * cm^{-1}$)	**pH**	**Microbial Abundance** ($\mu g\ FA * g^{-1}$)
	2010					
< 1 yr	3.95 *(1.02)*	1.03 *(0.10)*	8.52 *(4.04)*	98.70 *(25.2)*	8.05 *(0.14)*	1.84 *(0.52)*
4 yrs	3.94 *(1.65)*	1.03 *(0.10)*	9.37 *(4.01)*	106.4 *(53.4)*	7.89 *(0.23)*	2.74 *(0.83)*
28 yrs	3.87 *(1.91)*	1.13 *(0.10)*	9.55 *(5.28)*	146.5 *(73.1)*	8.17 *(0.21)*	4.30 *(3.45)*
35 yrs	2.18 *(0.87)*	1.10 *(0.16)*	9.53 *(4.36)*	89.75 *(28.2)*	7.97 *(0.11)*	4.91 *(2.70)*
54 yrs	2.37 *(0.69)*	1.16 *(0.17)*	9.95 *(6.30)*	93.50 *(18.7)*	7.91 *(0.13)*	4.53 *(1.77)*
U1	3.00 *(0.55)*	1.16 *(0.25)*	9.60 *(5.52)*	77.75 *(42.3)*	7.86 *(0.11)*	4.29 *(3.09)*
U2	2.26 *(0.79)*	1.09 *(0.22)*	8.51 *(4.38)*	67.59 *(17.2)*	7.93 *(0.07)*	3.92 *(2.66)*
	2011					
< 1 yr	7.00 *(1.74)*	1.08 *(0.16)*	7.28 *(2.04)*	149.1 *(75.8)*	8.08 *(0.24)*	2.29 *(1.22)*
4 yrs	6.37 *(1.48)*	1.12 *(0.16)*	7.22 *(1.69)*	104.8 *(24.3)*	7.94 *(0.19)*	2.26 *(0.73)*
28 yrs	6.61 *(1.68)*	1.11 *(0.14)*	6.48 *(2.70)*	147.9 *(40.0)*	8.12 *(0.21)*	2.33 *(1.58)*
35 yrs	4.45 *(1.05)*	1.08 *(0.11)*	6.84 *(1.55)*	107.0 *(18.0)*	7.94 *(0.13)*	3.07 *(2.16)*
54 yrs	6.61 *(1.07)*	1.13 *(0.19)*	6.86 *(7.09)*	136.4 *(69.5)*	8.06 *(0.15)*	2.85 *(5.01)*
U1	4.98 *(0.89)*	1.15 *(0.24)*	8.20 *(3.66)*	92.56 *(28.8)*	7.86 *(0.09)*	3.63 *(3.85)*
U2	4.94 *(1.27)*	1.09 *(0.22)*	7.28 *(2.87)*	90.88 *(27.0)*	7.91 *(0.11)*	3.00 *(1.56)*

Figure S2.3: Microbial community composition assessed by phospholipid fatty acid analysis. Bars represent the sample mean relative abundance of each microbial group in each treatment, calculated as a percentage of the total microbial abundance.

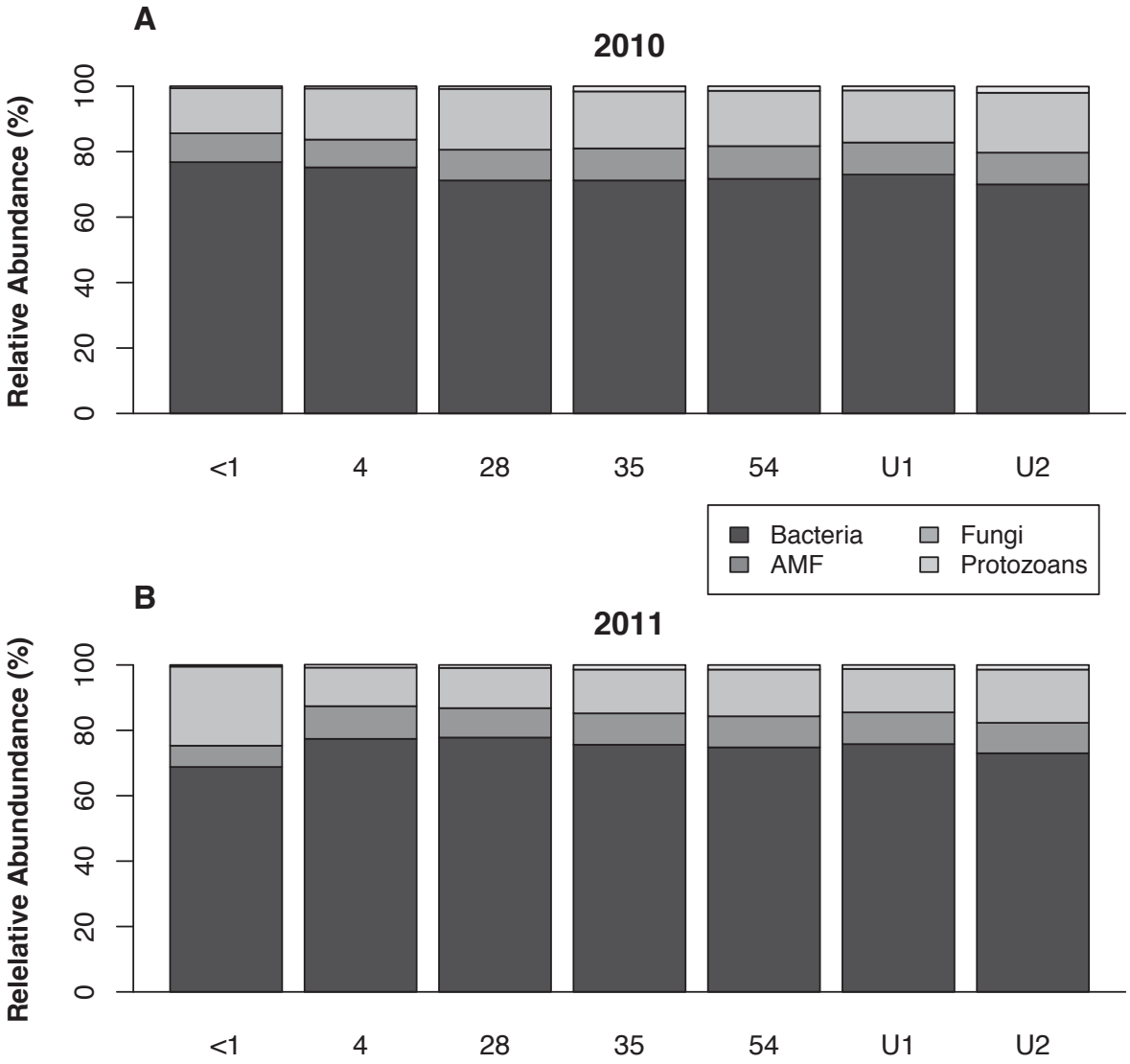


Figure S3.1: Example code for hierarchical linear mixed model

```
#################################################################
## Analysis of non-spatial data
# Complete dataset: data
# Undisturbed dataset: und
# Reclaimed dataset: rec
# Variable in example: Moisture
# Descriptive statistics
library(pastecs)
stat.desc(und)
stat.desc(rec)
# Boxplots
boxplot(Moisture~Treatment, data=data, main="moisture",
          names=c("undisturbed", "reclaimed"))
# Student's t-tests
t.test(und$Moisture, rec$Moisture)
#################################################################
## Analysis of spatial data
# Undisturbed dataset: und
# Reclaimed dataset: rec
# Variable in example: Moisture
# Correlations
cor(und, use="complete.obs")
cor(rec, use="complete.obs")
# Linear models for mean trend
model.moisture <- lm(Moisture~ 1 + X, data=und)
summary(model.moisture)
# Plotting empirical semi-variograms of residuals
library(geoR)
und.gd <- as.geodata(und, coords.col=3:4, data.col=c(5:12),
          na.action="ifany")
rec.gd <- as.geodata(und, coords.col=3:4, data.col=c(5:12),
          na.action="ifany")
moist.und.variog.resid <- variog(und.gd, coords=und.gd$coords,
          data=und.gd$data[,1],
          max.dist=1000, option="bin", uvec=30,
          trend= ~ 1 + und.gd$coords[,1])
plot(moist.und.variog.resid, main="Undisturbed Moisture
     Residuals")
# Fitting semi-variance models
# List initial values of semi-variance model parameters
cov.pars <- expand.grid(sigmasq=c(0,2,4,6,8,10),
phi=c(0,200,400,600,800,1000))
nugget <- c(0,2,4,6,8,10)
kappa <- c(0.2,0.4,0.6,0.8,1,1.2,1.4,1.6,1.8,2.0)
# Use REML to fit an exponential semi-variance model to the
# residuals
```

```
moist.und.likfit.exp <- likfit(und.gd, coords=und.gd$coords,
          data=und.gd$data[,1],
          trend= ~ 1 + und$coords[,1],
          ini.cov.pars=cov.pars, nugget=nugget,
          cov.model="exponential",
          lik.method="REML")
# Obtain parameter estimates
moist.und.likfit.exp
summary(moist.und.likfit.exp)
# Use REML to fit a Matern semi-variance model to the residuals
moist.und.likfit.mat <- likfit(und.gd, coords=und.gd$coords,
          data=und.gd$data[,1],
          trend= ~ 1 + und$coords[,1],
          ini.cov.pars=cov.pars,
          nugget=nugget, kappa=kappa,
          cov.model="matern",
          lik.method="REML")
# Obtain parameter estimates
moist.und.likfit.mat
summary(moist.und.likfit.mat)
# Plot the empirical semi-variogram and the two semi-variance
# models
plot(moist.und.variog.resid, main="Moisture undisturbed")
lines(moist.und.likfit.exp)
lines(moist.und.likfit.mat, lty=2)
# Make and plot prediction surfaces
# Set prediction grid to the plot area
pred.grid <- expand.grid(x=seq(0,1000,10), y=seq(0,1000,10))
          dim(pred.grid)
# Kriging using the fitted exponential semi-variance model
moist.und.krige <- krige.conv(und.gd, coords=und.gd$coords,
          data=und.gd$data[,1],
          locations=pred.grid,
          krige=krige.control(type.krige="ok",
          obj.model=moist.und.likfit.exp))
# Plot the surface, add sample point locations
image(moist.und.krige, col=gray.colors(30), ylim=c(0, 1300),
     xlim=c(0,1000), zlim=c(2,13))
points(u.points$X, u.points$Y, pch=16, cex=0.5)
title(main="Undisturbed Moisture")
# Repeat for moisture in reclaimed plot
# For data on log scale, use lambda=0 command in variog() and
# likfit()functions
#################################################################
```

Figure S4.1: Example code for geostatistical analysis of cover characteristics and soil properties.

```
library(geoR)
library(coda)

## Create geodata object
data.gd <- as.geodata(data, coords.col=3:4, data.col=5)

## Create empirical semi-variogram and plot
variog <- variog(data.gd, coords=data.gd$coords,
          data=data.gd$data,
          max.dist=100, option="bin", bin.cloud=TRUE, uvec=40)
plot(variog)

## Bayesian kriging, with prediction at 18 locations
pred.loc <- matrix(c(7,8,10,0,1,3,0,1,3,7,8,10,7,8,10,0,1,3,
          0,1,3,7,8,10,30,31,33,37,38,40,80,81,83,87,88,90),
          ncol=2)
krige <- krige.bayes(data.gd, coords=data.gd$coords,
data=data.gd$data,
               locations=pred.loc,
               model=model.control(
                    trend.d= "cte",
                    trend.l= "cte",
                    cov.model="exponential"),
               prior=prior.control(
                    beta.prior="flat",
sigmasq.prior="reciprocal",
                    phi.discrete=seq(0,100,1),
phi.prior="reciprocal",
                    tausq.rel.discrete=seq(0,100,1),
                    tausq.rel.prior="uniform"),
               output=output.control(n.post=3000, moments=TRUE))

## Print summaries of posterior estimates of model parameters
krige$posterior$beta$summary
krige$posterior$sigmasq$summary
krige$posterior$phi$summary
krige$posterior$tausq.rel$summary

## Convert all posterior samples to an mcmc object, and compute
## 95% credible intervals
krige.samples <- as.mcmc(krige$posterior$sample)
HPDinterval(krige.samples)

## Add the estimated semi-variance model to the plot
lines.variomodel(krige, sum=mean)
```

```
## Obtain mean values at predicted locations for checking model
## fit
pred <- krige$predictive$mean.simulations

## Compute Pearson correlation coefficient for observed vs
## predicted values and plot, with 1:1 line for reference
cor(obs, pred, use="complete.obs")
plot(obs, pred, pch=16, xlab="Observed", ylab="Predicted")
abline(0,1)

## Repeat with different semi-variance models, priors,
## parameters, etc. as needed, to attain best model

## Bayesian kriging with prediction across entire sampling grid
## space to create predicted surfaces
## WARNING: surface prediction is time consuming
pred.grid <- expand.grid(x=seq(0,10,1), y=seq(0,90,1))
krige.pred <- krige.bayes(data.gd, coords=data.gd$coords,
data=data.gd$data,
               locations=pred.grid,
               model=model.control(
                    trend.d= "cte",
                    trend.l= "cte",
                    cov.model="exponential"),
               prior=prior.control(
                    beta.prior="flat",
sigmasq.prior="reciprocal",
                    phi.discrete=seq(0,100,1),
phi.prior="reciprocal",
                    tausq.rel.discrete=seq(0,100,1),
                    tausq.rel.prior="uniform"),
               output=output.control(n.post=100, moments=TRUE))
image(krige.pred, xlim=c(0,10), ylim=c(0,90))

## Repeat for all variables in all treatments
```

Figure S4.2: Plots of observed versus predicted values for vegetation and cover characteristics, with a 1:1 line included for reference.

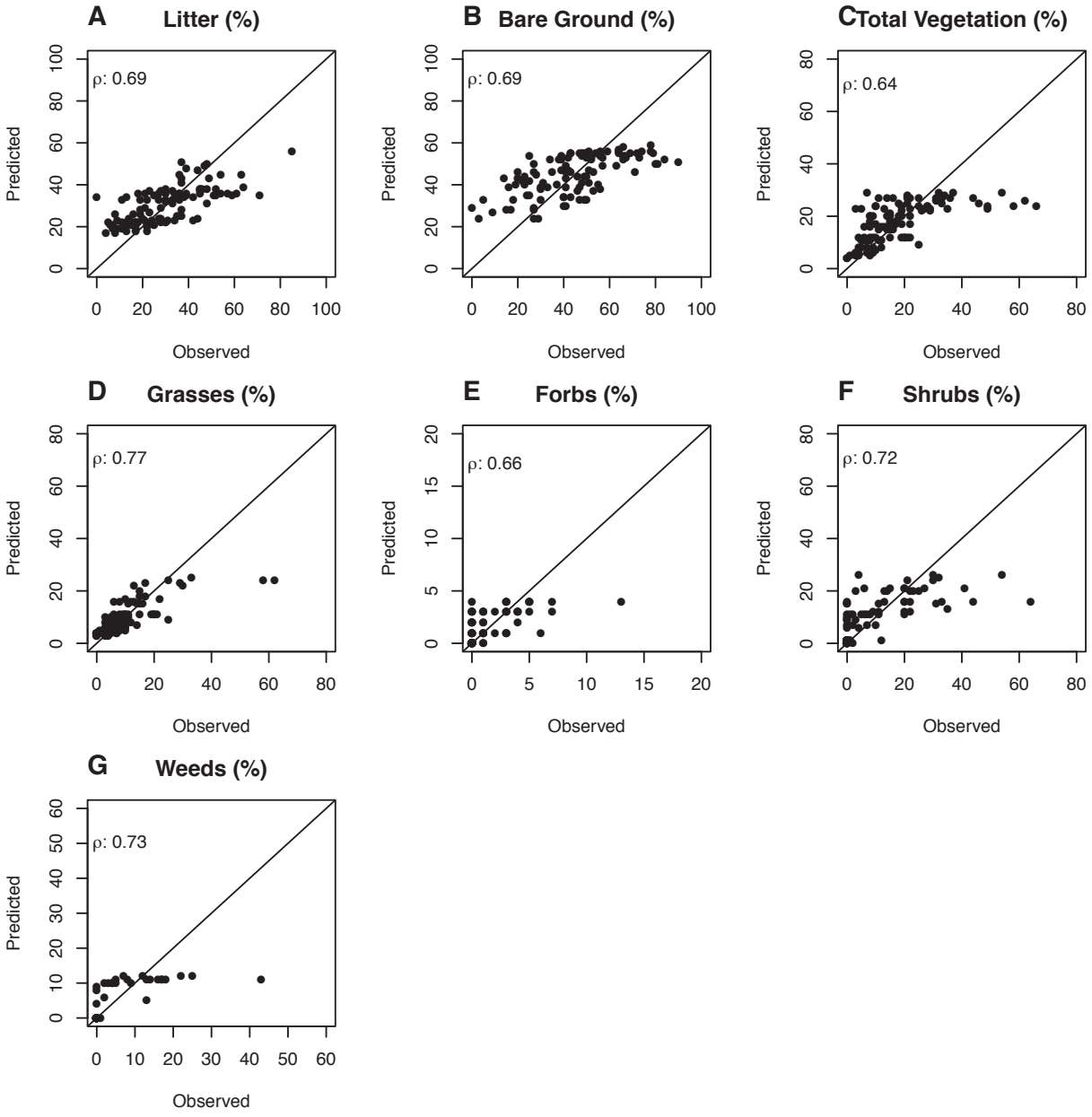
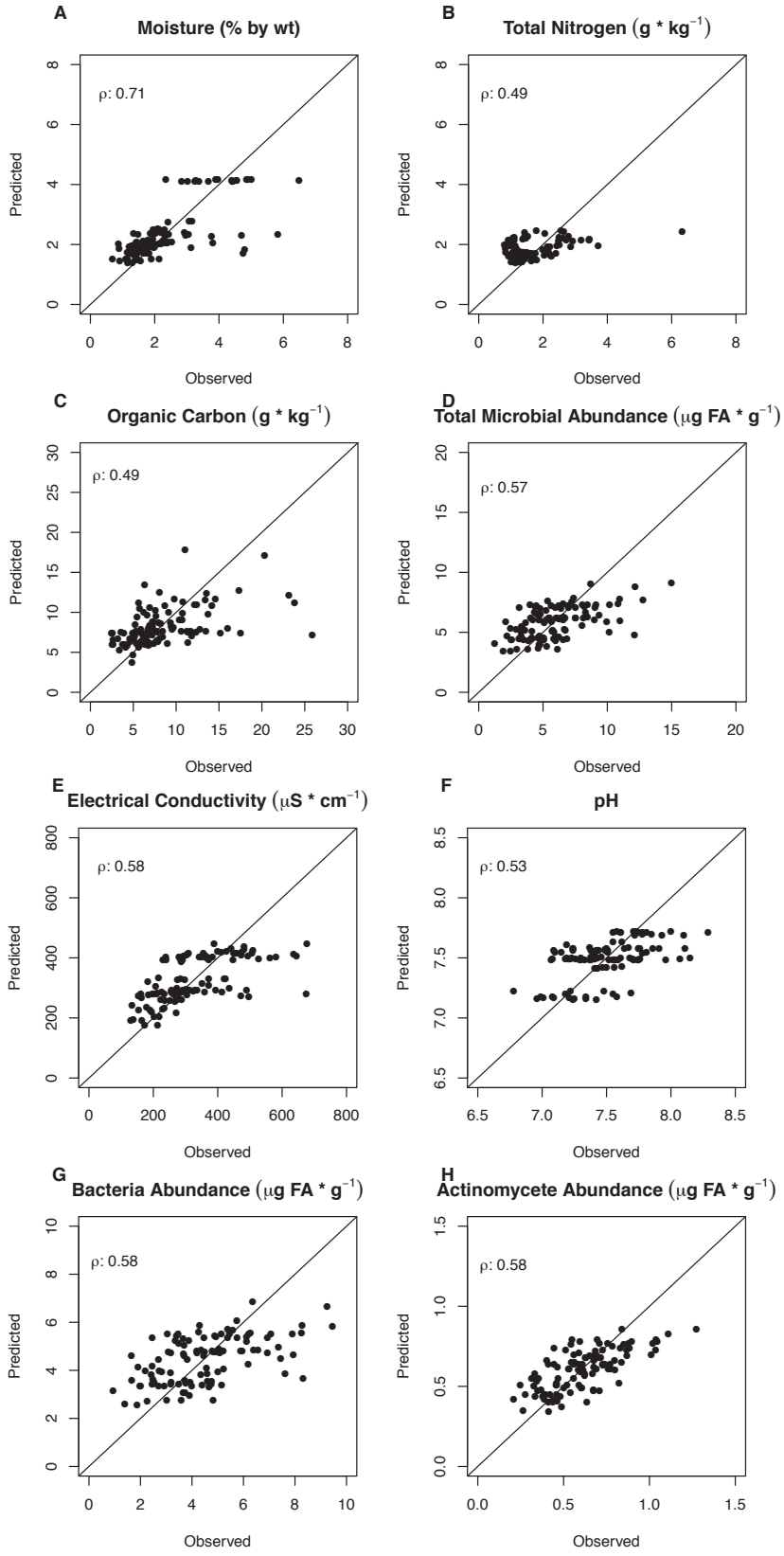


Figure S4.3: Plots of observed versus predicted values for soil properties, with a 1:1 line included for reference (AM = arbuscular mycorrhizal).



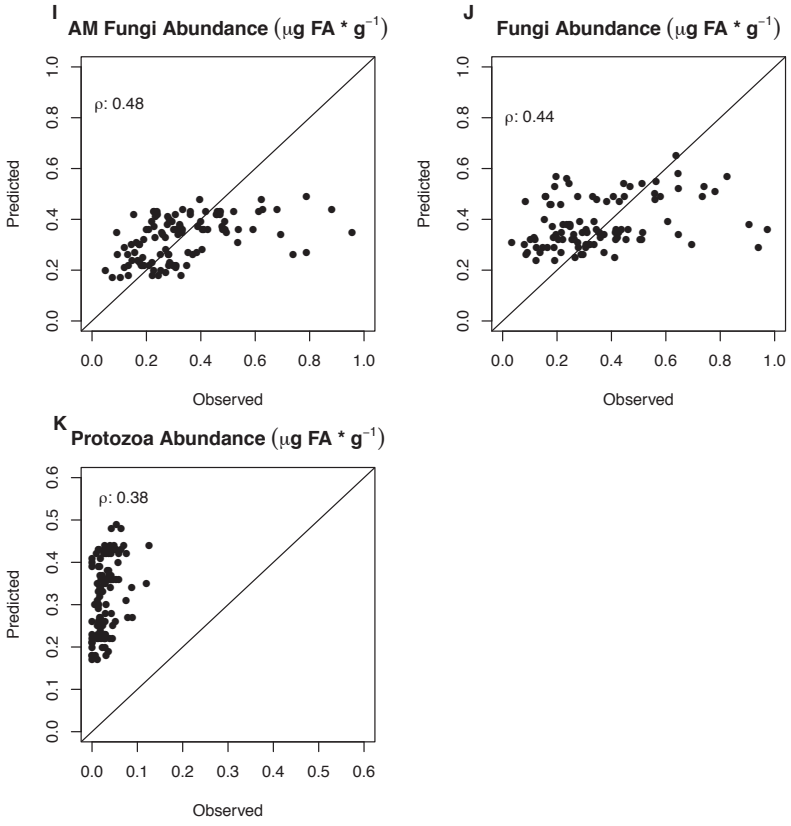

I
AM Fungi Abundance (μg FA * g⁻¹)
ρ: 0.48
Predicted
Observed
J
Fungi Abundance (μg FA * g⁻¹)
ρ: 0.44
Predicted
Observed
K
Protozoa Abundance (μg FA * g⁻¹)
ρ: 0.38
Predicted
Observed

Table S4.1: 95% credible intervals for fitted model parameters for cover characteristics

	β (intercept)	σ^2 (partial sill)	ϕ (range)	τ^2/σ^2 (relative nugget)
Litter				
1 yr	[16, 48]	[17, 390]	[1, 60]	[0, 8]
5 yrs	[33, 50]	[14, 148]	[1, 30]	[0, 3]
35 yrs	[31, 38]	[1, 28]	[1, 78]	[2, 94]
55 yrs	[19, 26]	[1, 39]	[1, 80]	[1, 92]
UD1	[20, 43]	[17, 170]	[3, 77]	[1, 7]
UD2	[16, 48]	[17, 390]	[1, 60]	[0, 8]
Bare Ground				
1 yr	[36, 59]	[3, 350]	[1, 54]	[0, 62]
5 yrs	[25, 49]	[59, 200]	[2, 34]	[1, 2]
35 yrs	[40, 57]	[1, 130]	[1, 85]	[0, 28]
55 yrs	[51, 58]	[1, 20]	[1, 78]	[7, 98]
UD1	[26, 56]	[4, 322]	[2, 86]	[1, 16]
UD2	[27, 54]	[5, 331]	[2, 81]	[1, 21]
Total Vegetation Cover				
1 yr	[4, 9]	[0, 16]	[1, 81]	[0, 67]
5 yrs	[12, 25]	[1, 75]	[2, 74]	[1, 21]
35 yrs	[10, 13]	[0, 7]	[1, 75]	[3, 96]
55 yrs	[15, 27]	[1, 66]	[1, 85]	[1, 70]
UD1	[23, 32]	[2, 28]	[1, 84]	[7, 99]
UD2	[17, 27]	[2, 40]	[1, 85]	[2, 94]

Table S4.2: 95% credible intervals for fitted model parameters for cover characteristics

	β (intercept)	σ^2 (partial sill)	ϕ (range)	τ^2/σ^2 (relative nugget)
Grasses				
1 yr	[3, 9]	[0, 21]	[1, 78]	[1, 65]
5 yrs	[12, 25]	[1, 75]	[1, 75]	[1, 26]
35 yrs	[9, 12]	[0, 7]	[1, 70]	[1, 95]
55 yrs	[3, 16]	[11, 56]	[2, 43]	[1, 4]
UD1	[2, 7]	[0, 12]	[1, 75]	[1, 13]
UD2	[3, 8]	[0, 14]	[1, 83]	[0, 73]
Forbs				
1 yr	[0, 0.2]	[0, 0.02]	[1, 80]	[12, 100]
5 yrs	[0, 0.03]	[0, 0]	[1, 80]	[11, 100]
35 yrs	[0, 0.09]	[0, 0.004]	[1, 76]	[9, 99]
55 yrs	[1, 5]	[0, 9]	[1, 77]	[0, 51]
UD1	[0, 1]	[0,1]	[1, 88]	[1, 66]
UD2	[1, 5]	[0, 7]	[1, 79]	[0, 74]
Shrubs				
1 yr	[0, 0.3]	[0, 0.5]	[1, 19]	[0, 74]
5 yrs	[0, 0.01]	[0, 0.01]	[1, 80]	[3, 95]
35 yrs	[0, 2]	[0, 2]	[1, 83]	[2, 94]
55 yrs	[5, 14]	[1, 87]	[1, 69]	[0, 89]
UD1	[16, 28]	[2, 59]	[1, 83]	[1, 90]
UD2	[8, 20]	[2, 54]	[1, 82]	[2, 93]
Weeds				
1 yr	[8, 13]	[1, 43]	[1, 59]	[0, 93]
5 yrs	[0, 9]	[4, 35]	[2, 75]	[1, 5]
35 yrs	[0, 0.08]	[0, 0]	[1, 77]	[5, 99]
55 yrs	[0, 0.03]	[0, 0]	[1, 77]	[12, 100]
UD1	NA	NA	NA	NA
UD2	NA	NA	NA	NA

Table S4.3: 95% credible intervals for fitted model parameters for cover characteristics

	β (intercept)	σ^2 (partial sill)	ϕ (range)	τ^2/σ^2 (relative nugget)
Moisture				
1 yr	[3.85, 4.41]	[0, 0.13]	[1, 74]	[6, 98]
5 yrs	[1.74, 2.20]	[0, 0.16]	[1, 77]	[0, 94]
35 yrs	[1.58, 2.32]	[0, 0.22]	[1, 87]	[1, 80]
55 yrs	[2.07, 2.90]	[0, 0.53]	[1, 78]	[0, 91]
UD1	[1.27, 1.98]	[0, 0.30]	[1, 77]	[0, 66]
UD2	[1.79, 2.55]	[0, 0.25]	[1, 75]	[1, 89]
Total Nitrogen				
1 yr	[1.18, 2.55]	[0.01, 0.62]	[1, 90]	[1, 67]
5 yrs	[1.50, 2.18]	[0.00, 0.21]	[1, 85]	[2, 94]
35 yrs	[1.25, 2.49]	[0.01, 0.57]	[1, 89]	[0, 74]
55 yrs	[1.08, 2.51]	[0.01, 0.63]	[1, 89]	[0, 71]
UD1	[1.30, 2.69]	[0.01, 0.65]	[1, 89]	[1, 73]
UD2	[1.21, 2.24]	[0.02, 0.41]	[1, 88]	[0, 88]
Organic Carbon				
1 yr	[5.13, 7.18]	[0.07, 11.76]	[1, 27]	[0, 66]
5 yrs	[7.36, 11.32]	[0.28, 4.62]	[5, 86]	[1, 7]
35 yrs	[4.55, 11.68]	[0.74, 13.69]	[3, 82]	[1, 9]
55 yrs	[6.43, 8.55]	[0.11, 2.15]	[1, 74]	[2, 95]
UD1	[9.23, 14.71]	[0.46, 58.76]	[1, 16]	[0, 8]
UD2	[4.94, 8.82]	[0.18, 5.46]	[1, 87]	[1, 89]
Total Microbial Abundance				
1 yr	[3.02, 5.00]	[0.02, 2.53]	[1, 65]	[0, 71]
5 yrs	[4.02, 7.87]	[1.02, 3.65]	[5, 71]	[1, 2]
35 yrs	[3.59, 7.79]	[0.10, 6.11]	[2, 80]	[1, 13]
55 yrs	[5.51, 6.72]	[0.04, 0.75]	[1, 77]	[4, 97]
UD1	[6.57, 7.96]	[0.04, 1.22]	[1, 77]	[0, 94]
UD2	[3.90, 6.70]	[0.04, 3.54]	[1, 72]	[0, 23]
Electrical Conductivity				
1 yr	[360.42, 463.33]	[252.33, 7185.33]	[1, 80]	[2, 96]
5 yrs	[232.14, 416.19]	[1064.38, 7613.01]	[7, 91]	[1, 5]
35 yrs	[361.45, 461.19]	[123.77, 9750.24]	[1, 63]	[1, 89]
55 yrs	[266.41, 315.74]	[53.38, 994.69]	[1, 79]	[5, 97]
UD1	[193.88, 283.51]	[105.79, 15305.61]	[1, 22]	[0, 12]
UD2	[243.11, 327.65]	[142.06, 10009.37]	[1, 67]	[0, 93]
pH				
1 yr	[7.42, 7.53]	[0.0003, 0.004]	[1, 75]	[12, 100]
5 yrs	[7.38, 7.67]	[0.0004, 0.03]	[2, 84]	[1, 30]

35 yrs	[7.65, 7.76]	[0.0002, 0.02]	[1, 70]	[0, 95]
55 yrs	[7.51, 7.62]	[0.0002, 0.006]	[1, 83]	[1, 94]
UD1	[7.10, 7.26]	[0.0003, 0.01]	[1, 76]	[1, 92]
UD2	[7.40, 7.58]	[0.0008, 0.011]	[1, 76]	[9, 100]

Table S4.4: 95% credible intervals for fitted model parameters for cover characteristics

	β (intercept)	σ^2 (partial sill)	ϕ (range)	τ^2/σ^2 (relative nugget)
Bacteria				
1 yr	[2.34, 3.94]	[0.02, 1.46]	[1, 63]	[0, 64]
5 yrs	[2.94, 6.00]	[0.53, 2.06]	[5, 75]	[1, 3]
35 yrs	[2.64, 6.02]	[0.10, 3.31]	[3, 77]	[1, 10]
55 yrs	[4.32, 5.23]	[0.02, 0.39]	[1, 75]	[7, 99]
UD1	[4.97, 5.98]	[0.02, 0.51]	[1, 75]	[1, 95]
UD2	[2.88, 5.25]	[0.03, 2.05]	[1, 71]	[1, 19]
Actinomycetes				
1 yr	[0.34, 0.53]	[0.003, 0.01]	[2, 48]	[1, 3]
5 yrs	[0.48, 0.73]	[0.006, 0.02]	[4, 58]	[1,2]
35 yrs	[0.43, 0.66]	[0.004, 0.02]	[4, 54]	[1, 2]
55 yrs	[0.52, 0.75]	[0.0002, 0.02]	[1, 77]	[1, 56]
UD1	[0.69, 0.84]	[0.0003, 0.02]	[1, 73]	[0, 90]
UD2	[0.53, 0.69]	[0.0002, 0.02]	[1, 79]	[0, 84]
AM[§] Fungi				
1 yr	[0.16, 0.25]	[0, 0.007]	[1, 68]	[0, 79]
5 yrs	[0.19, 0.44]	[0.003, 0.01]	[6, 83]	[1, 3]
35 yrs	[0.20, 0.42]	[0.0003, 0.02]	[1, 83]	[1, 48]
55 yrs	[0.32, 0.40]	[0.0002, 0.004]	[1, 74]	[3, 96]
UD1	[0.38, 0.49]	[0.0003, 0.008]	[1, 76]	[4, 99]
UD2	[0.18, 0.40]	[0.001, 0.02]	[1, 64]	[1, 9]
Fungi				
1 yr	[0.23, 0.39]	[0.0006, 0.02]	[1, 75]	[1, 95]
5 yrs	[0.13, 0.69]	[0.01, 0.07]	[5, 77]	[1, 3]
35 yrs	[0.24, 0.65]	[0.002, 0.08]	[1, 83]	[1, 89]
55 yrs	[0.29, 0.40]	[0, 0.005]	[1, 80]	[9, 99]
UD1	[0.40, 0.63]	[0.001, 0.04]	[1, 77]	[0, 93]
UD2	[0.21, 0.43]	[0.0005, 0.02]	[1, 73]	[1, 85]
Protozoa				
1 yr	[0.15, 0.25]	[0, 0.007]	[1, 67]	[0, 82]
5 yrs	[0.19, 0.45]	[0.003, 0.01]	[5, 80]	[1, 3]
35 yrs	[0.20, 0.44]	[0.0002, 0.02]	[1, 84]	[1, 47]
55 yrs	[0.31, 0.41]	[0.0002, 0.004]	[1, 76]	[8, 100]
UD1	[0.37, 0.48]	[0.0003, 0.008]	[1, 73]	[1, 96]
UD2	[0.17, 0.40]	[0, 0.02]	[1, 65]	[1, 9]

[§]AM = arbuscular mycorrhizal