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Microbial and Environmental Drivers of Soil Respiration Differ Along Montane to Urban Transitions

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ABSTRACT

Microbial and Environmental Drivers of Soil Respiration Differ
Along Montane to Urban Transitions

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In natural ecosystems, like deciduous and coniferous forests, soil CO_2 flux or soil respiration is highly variable and influenced by multiple factors including temperature, precipitation, dissolved soil organic carbon (DOC), dissolved organic matter (DOM), and bacterial and fungal biomass and diversity. However, as the human population continues to grow rapidly, so too do urbanized landscapes with unknown consequences to soil respiration. To determine the extent urbanization influences seasonal shifts in microorganisms and environmental drivers alter soil respiration, we evaluated bacterial and fungal communities, soil physiochemical characteristics, and respiration in forested and urbanizing ecosystems in three watersheds across northern Utah, USA. Based on the next-generation sequencing of the 16s DNA and RNA, we found that montane bacteria were predominantly structured by season while urban bacteria were influenced by degree of urbanization. There was no apparent effect of season on montane fungi, but urban fungal communities followed patterns similar to urban bacterial communities. Bacterial diversity was sensitive to seasonality, especially in montane ecosystems, declining 21-34% from spring to summer and staying relatively low into fall, and fungal diversity was generally depressed in spring. Urban bacterial communities were differentiated by substantially more bacterial taxa with 62 unique OTUs within families structing phylogenetic differences compared with only 18 taxa differentiating montane communities. Similar to bacteria and fungi, DOC and ammonium concentrations fluctuated predominantly by season while these same parameters where highly variable among urban soils among the three watersheds. Structural components of DOM via parallel factor analysis (PARAFAC) of fluorescence excitation-emission matrices show varying patterns between montane and urban systems with humic substance resistance to biodegradability found more dominantly in montane systems. Incorporating all soil chemical parameters, daily temperature and moisture, and fungal and bacterial diversity and richness in mixed linear effects models describing daily CO_2 over all seasons, we found that a single model best described montane soil respiration, while individual watershed models best described urban respiration. Montane respiration was related to the availability of DOC, different DOM components, and rRNA-based bacterial diversity . Alternatively, urban respiration was influenced by either bacterial diversity and richness in our rapidly urbanizing environment, DOM characteristics and soil O_2 in the more agricultural urban soils, or the DOM parameter humification index (HIX) in highly urbanized soils. Our results suggest that urbanization creates distinct bacterial and fungal communities with a single soil biotic or chemical parameter structuring soil respiration, while montane ecosystems select for similar bacterial and fungal communities with respiration sensitive to fluctuations in soil moisture, bacteria and the recalcitrance of carbon (C) resources.

Keywords: soil respiration, soil microbiology, urbanization, DOM, DOC, soil carbon, carbon cycling, biogeochemistry, seasonality

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INTRODUCTION

From inception, terrestrial ecology focuses on interactions among organisms and the natural environment along gradients. The paradigm of gradients is exemplified in soil, vegetation, and natural resources in many classic studies (Hans 1941, Whittaker 1967, Terbraak 1986). As ecology embraces the Anthropocene, the importance of gradients in defining community structure and function has extended into urban landscapes. Human impact on an ecosystem alters its native community and leads to an anthropogenically influenced community structure, as evidenced by aboveground changes in plant and animal diversity (Blair 1996). As ecosystems change along gradients, so too do land use patterns, biogeochemical cycles, and nutrient inputs. A particularly important gradient is the coupling of montane and urban ecosystems, when undisturbed montane regions transition into both rural and urbanized ecosystems with varying levels of land use and disturbance. Mountain ecosystems are ecologically essential regions that cover 25 percent of the planet's land surface while providing ecosystem services and acting as the source of half of our fresh water (Kourous 2003). Mountain regions with undisturbed landscapes can transition into urbanized ecosystems where land use, freshwater resources, and biogeochemical cycles are altered. Montane to urban transitions are often stark, leading to two distinct ecosystems. Each system differs in plant and wildlife species, diversity, land use, and levels of urbanization such as built infrastructure including dams to trap mountain water resources. Urbanization is the most homogenizing human activity (McKinney 2006), and disturbance from urbanization leads to lower biodiversity in urban areas and threatens to reduce the biological uniqueness of local ecosystems (McKinney 2002). The most obvious land use changes occur over soil surfaces through degradation of the local aboveground environment (Foley, DeFries et al. 2005). However, many anthropogenic changes extend

belowground, having dramatic impacts on the form and function of soil microorganisms governing trace gas flux (Bardgett, Freeman et al. 2008, Allison, Wallenstein et al. 2010), nutrient cycling (Schimel, Balser et al. 2007), and carbon (C) composition (Williams, Frost et al. 2016).

Along montane to urban transitions, soil respiration from bacteria and fungi metabolic activity fluctuates and is determined by different environmental drivers, like organic C substrate origin and availability. More than twice the amount of C is stored as organic matter in soil than exists in the atmosphere as carbon dioxide (CO_2) (Tarnocai, Canadell et al. 2009) and soil respiration is the largest source of CO_2 to the atmosphere (Bond-Lamberty and Thomson 2010, Carvalhais, Forkel et al. 2014). Montane forest systems in particular are major contributors to global C cycling and contain most of the terrestrial C sequestered at mid-latitudes in the Northern Hemisphere (Schimel 2002). In montane systems, CO_2 flux is governed by seasonal variations in temperature and moisture (Lloyd and Taylor 1994, Davidson and Janssens 2006), vegetation (Aanderud, Schoolmaster et al. 2011), belowground microbial communities (Creamer, de Menezes et al. 2015), and carbon compounds (Doetterl, Stevens et al. 2015). An attempt to describe the relationship of these factors with soil respiration leads to highly variable models, with unreliability likely due to anthropogenic influences (Heimann and Reichstein 2008). For example, fertilizer is added to urban soils, stimulating C mineralization; while built infrastructures often retard water movement, reduce soil respiration, and potentially create more pulse-driven CO_2 effluxes. Land use changes in urban areas can lead to increased anthropogenic CO_2 emissions: since 1850, more than 35% of anthropogenic CO_2 has come as a result of altered land use (Houghton 1999). Disturbance in urban systems leads to fluctuations in soil organic C and soils with high C content are characterized by high rates of respiration per unit of soil C, and

soil with low C content have lower rates of respiration (Doetterl, Stevens et al. 2015). Rarely do we link changes in CO_2 flux with belowground urban microbial communities, despite their ecological proximity.

Belowground microbial communities are important contributors to aboveground carbon release, and are sensitive to changes above the soil surface. Soil respiration rates are associated with the dominant bacteria and fungi within communities (Pedros-Alio 2012), and abundant species are assumed to regulate C flow through the soil and into the atmosphere. However, low-abundance species in the rare biosphere may break dormancy, bloom, and become metabolically active in response to environmental shifts. For example, in coniferous and deciduous forests, almost 75 percent of bacterial communities consist of rare taxa, suggesting that rare taxa are important for the maintenance of soil bacterial diversity, and the resuscitation of rare taxa contributes significantly to soil processes like CO_2, CH_4, and N_2O cycling (Aanderud, Jones et al. 2015). In addition to bacterial contributions, fungal populations in montane systems comprise between 36 and 76 percent of soil microbial biomass (Joergensen and Wichern 2008) and contribute to C cycling. Roots and their fungal symbionts contribution to C loss may be more influential than temperature influence, and the seasonal influence on fungal activity is a major contributor to the global carbon cycle (Hogberg, Nordgren et al. 2001). The influence of moisture on the rare biosphere becomes more complex in urban soils, where biological, chemical, and physical soil properties and processes are altered, naturally and anthropogenically, leading to changes in below ground communities and influencing the release of organic C to the atmosphere as CO_2.

The sensitivity of microbial communities to changes above ground, both natural and anthropogenic (Brooks, McKnight et al. 2005, Magnani, Mencuccini et al. 2007) leads to more variable oscillations of respiration in urban soils compared to montane soils.

To understand differences in montane and urban environmental contributors to soil respiration and organic matter in conjunction with changes in soil microbial communities and soil chemistry, we evaluated soil microbial community composition, CO_2 respiration, soil dissolved organic carbon (DOC), and soil dissolved organic matter (DOM) components in three watersheds along a montane to urban gradient in northern Utah, USA. We measured soil respiration and soil conditions (i.e. soil oxygen, moisture, temperature) in real-time and measured soil chemistry (i.e. DOC, total nitrogen (TN)) and the quantity and quality of DOM every month for one year. We used 16S and 18S rRNA gene-based community sequencing to characterize bacterial and fungal community composition and activity each month. Our intention was to relate changes in soil respiration with changes in soil biochemistry and microbial communities and to determine drivers of soil respiration between montane and urban systems. We predicted that seasonal effects would play a larger role in montane systems, while soil nutrients, like DOC and TN, and DOM characteristics would drive changes in urban soil respiration and community signatures.

MATERIALS AND METHODS

Study Sites

To evaluate the extent urbanization influenced microorganisms and soil respiration we created study sites spanning three watersheds in northern Utah, USA experiencing different levels of urbanization. All watersheds possessed montane to urban transitions with similar climates and a common water source, mountain winter-derived precipitation. From north-to-south, the watersheds include: the Logan River watershed with montane systems originating high in the Bear River Mountains that slowly transition to agricultural and urban land use areas of Cache Valley (irrigated agriculture to urban transition); Red Butte Creek watershed originating high in the Wasatch Mountains with lower elevation portions incorporating the highly urbanized Salt Lake City; and the Middle Provo River montane systems originating high in the Uinta and Wasatch Mountains with mid-elevation urbanizing center in Heber Valley that is experiencing rapid land use transition from agriculture to exurban, a commuter town with no major commercial or industrial activity. All study sites were associated with long-term climate monitoring stations or the Gradients Along Mountain to Urban Transitions (GAMUT(http://data.iutahepscor.org/mdf/)) monitoring network developed as part of the innovative Urban Transitions and Aridregion Hydro-sustainability, iUTAH (http://iutahepscor.org) grant from the Experimental Program to Stimulate Competitive Research from NSF. Sampling site characteristics are given in Table 1. Montane soils contained 0.40% N (±0.03, mean n=3 and ± SEM) and 4.41% C (±0.30) while urban soils had smaller amounts of N 0.24% (±0.03) and equal amounts of C 4.53 (±0.74) (LECO Saint Joseph MI, USA). pH (Thermo Fisher Scientific Waltham MA, USA) and CEC (RC-16C Conductivity Bridge EC meter Beckman Instruments, Brea CA, USA) of montane and urban soils was 6.42 (±0.06), 7.30

(±0.10), 15.61 (±2.24), and 5.53 (±1.08) respectively. All soils were classified as loams with montane sites being: Logan = Bingham Gravelly Loam; Provo = Kovich loam channeled; Red Butte = Greenson Loam; and urban sites being: Logan = Emigration very cobbly loam; Provo = Skutum loam; Red Butte = Flygare silt loam.

Season Designations

To evaluate the extent season influenced microorganisms, we separated each month into one of four seasons. The GAMUT climate stations offered climatic variables (i.e., soil moisture, snow depth and soil temperature) that allowed months to be assigned into specific seasons so we visualized the changes in soil moisture, soil temperature, and snow depth to determine appropriate seasonal transitions. We grouped the months as follows: December through February as winter months, March and April a spring, May through September as summer, and October and November as fall. For the monthly means and standard error of climatic variables see Table 2, and a more detailed description of climate station equipment, data storage, and data curation see (Jones et al. 2017).

Soil Sampling

We collected samples on a monthly basis to observe annual variation in soil chemical and microbial characteristics. We collected a composited soil sample of 3-5 soil cores taken with a soil probe (7/8”x33”) at 0-10 cm soil depth. Samples were homogenized, stored on ice during transport to the lab, and stored at 4°C until evaluated for soil chemistry. For prokaryotic and eukaryotic DNA or RNA analyses, a subsample was partitioned in the field and the soil was immediately frozen in liquid nitrogen and stored at -80°C. Soil sampling took place beginning in December 2016 through November 2017.

Soil Respiration, Moisture, and Temperature

To evaluate seasonal variation in soil respiration and correlate respiration to soil physiochemical and bacterial and fungal characteristics, we measured soil CO_2 concentrations as an approximation of soil respiration continually in urban and montane soils. Respiration was measured in real-time with Vaisala CO_2 sensors GMP 220 and 221 series probes (Vantaa, Finland). In addition to soil CO_2 concentrations we measured soil oxygen concentrations (Apogee SO 110 oxygen sensors (Logan, UT, USA)), and soil moisture and temperature (Acclima SDI 12 Interface sensors (San Francisco, CA, USA)). After installing our sensors in summer of 2016, our data was collected every minute and logged on a Campbell Scientific CR3000 data logger (Campbell Scientific Logan UT, USA). To remove diel-fluctuations associated with daily temperature and moisture variations, we averaged all variables over a 24-hour period (Riveros-Iregui, Emanuel et al. 2007, Carbone, Winston et al. 2008).
We documented pulses of soil respiration following freeze-thaw cycles (FTCs) and drying rewetting cycles (DRC) by analyzing the fluctuations in volumetric soil moisture measured with ECH_2O-TM sensors (Decagon Devices, Pullman WA, USA) in connection with high concentrations of CO_2. We defined a FTC based on the following criteria involving changes in soil moisture: first, moisture had to decline as free liquid water became ice (i.e., freeze); and second, moisture had to then increase (i.e., thaw) back to similar values prior to the freeze. We defined a DRC as an increase on soil moisture following a precipitation event.

DOC and Inorganic N Concentrations

Each month, we measured soil DOC and inorganic N concentrations to help explain shifts in communities and soil respiration. DOC was analyzed from soil water extractions done via 1:4

weight by volume water extraction using a 10-µm quantitative 454 filter (VWR, Radnor PA, USA), then through a .2-µm nylon filter (Millipore, Billerica MA, USA) using Nalgene filter cups (Aanderud, Jones et al. 2013). TOC/TN was measured on a SHIMADZU TOC analyzer (Shimadzu, Columbia MD, USA). We determined NO_3^{2-} and NH_4^+ concentrations on an OI Analytical Flow Solution IV analyzer (OI Analytical College Station, TX, USA). Soil variables are expressed on a soil dry-weight basis after correction for gravimetric water content (subsample dried at 105 °C for 48 h). We tested for the effect of watershed and season within montane and urban ecosystems on our response variables (i.e., DOC, NH_4^+, and NO_3^- concentrations) using repeated measures (RM) ANOVA in R (v 3.5.0; R Core Development Team 2018).

DOM Chemical Components via Parallel Factor Analysis (PARAFAC) of Fluorescence Excitation-Emission Matrices

Because carbon plays a pivotal role in soil chemistry and contributes to the development of microbial communities, we measured fluorescence excitation-emission matrices (EEMs) using an Aqualog Benchtop Fluorometer (Horiba, Irvine CA, USA) to include in our modeling efforts for soil respiration. Fluorescence characteristics of dissolved organic matter (DOM) can indicate the source as either microbial or terrestrial, by way of fluorescence indices and protein-like and humic-like fluorophores, which are characterized using PARAFAC. EEMs were measured using the soil water extractions as described above. Sample EEMs and their corresponding blank (Milli-Q water) acquisitions were preprocessed to normalize to Raman peak area, correct for dilution, reduce inner filter effects, and to then remove the Raman peak and first- and second-order Rayleigh scatter (Lawaetz and Stedmon 2009, Veverica et al., 2016). The resulting EEM

dataset (n = 149) was analyzed by employing ten simultaneous Parallel Factor Analyses using PLS_Toolbox (Eigenvector Research Inc., Wenatchee, WA). Differences in DOM components among watersheds and season in montane and urban soils were analyzed with RM-ANOVA in R.

Bacterial and Fungal Communities in Montane and Urban Ecosystems

Using a target-metagenomic approach, we characterized the bacterial and fungal composition of montane and urban communities using 16S rDNA- and 16S rRNA-based for bacteria and 18S rDNA for fungi. Our intention was to use the 16S rDNA to reflect the total bacterial community or all taxa present in soils and refer to these communities as our total community. We focused on bacterial 16S rDNA and fungal 18S communities for much of our analyses since our intention was to evaluate a general representation of bacteria across multiple seasons (Campbell and Kirchman 2013, Hugoni, Taib et al. 2013). 16S rRNA-based communities represent the active community based on the relatively short half-life of ribosomal RNA, and its necessary presence for protein synthesis (Flardh, Cohen et al. 1992, Steglich, Lindell et al. 2010, Muscarella, Jones et al. 2016). We only used metrics from the 16S RNA-based communities, alpha diversity and OTU (operational taxonomic units) richness, as inputs in our soil respiration modeling efforts since an accurate assessment of the active community may better correlate with daily soil respiration.

We evaluated the bacterial and fungal community compositions present in soils from genomic DNA extractions from 0.25 g soil and a Qiagen PowerSoil DNA Isolation kit (Qiagen, Valencia, CA, USA). Further, to estimate active bacterial species, we used RNA transcripts as an analog for organisms present, extracted from 2 g soil and a Qiagen RNA Isolation kit with the

DNA Elution. We used RNA as an indicator of the active community (Buckley and Schmidt 2003, Jones and Lennon 2010). We extracted DNA and RNA using the Qiagen PowerSoil DNA Isolation kit for samples where only DNA was extracted and the Qiagen RNA Isolation kit with the DNA Elution kit (Qiagen, Valencia, CA, USA) for samples we obtained RNA and DNA from. We used SuperScript III Reverse Transcriptase and ExoSAP-IT PCR Product Cleanup Reagent (ThermFisher, Waltham, MA, USA) to prepare the rRNA for sequencing. We PCR-amplified the V4 region of the bacterial 16S rRNA gene with primer set 515F and 806R (Caporaso, Lauber et al. 2011). We also PCR-amplified the V9 region of the eukaryotic 18S rRNA gene with primer set 1391f and EukBr (Amaral-Zettler, McCliment et al. 2009). After purifying and normalizing samples (SequalPrep Normalization Plate Kit, Invitrogen, Carlsbad, CA, USA), we pooled samples and performed further purification using a BluePippin system (Sage Science, Beverly, MA, USA) to select DNA fragments between 225-425 bp (bacteria) and 225-500bp (eukaryotes), then analyzed using an Agilent 2100 Bioanalyzer (Agilent, Santa Clara, CA, USA). Our samples were submitted to the Brigham Young University DNA Sequencing Center (http://dnac.byu.edu/) for 2x250 bp paired-end sequencing on an Illumina HiSeq 2500 System. To cluster OTUs and analyze sequences, we used a modified Mothur pipeline and a 97% OTU similarity cutoff (Schloss, Westcott et al. 2009). All further statistical analysis was done in R (v 3.5.0; R Core Development Team 2013) after using the 'decontam' package to remove contaminant OTUs (Davis et al. 2017).

Bacterial and Fungal Community Shifts Along Montane and Urban Gradients

To assess the differences in montane and urban ecosystems, watershed, and season, we first visualized differences in community composition using Principal Coordinates Analysis

(PCoA) based on a Bray-Curtis distance matrix with the 'vegan' package (Jari Oksanen 2018) in R. We visualized the outcome using the principal coordinated analysis (PCoA) using the 'phyloseq' package for reproducible interactive analysis and graphics of microbiome census data. (McMurdie and Holmes 2013). We then used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) to assess the effects of ecosystem, watershed, and season on the temporal dynamics of the bacterial and fungal communities. PERMANOVA was implemented with the function *adonis* in the 'vegan' package of R. Second, we quantified alpha diversity as the inverse Shannon index and richness as the total number of OTUs in bacterial and fungal rDNA-based and rRNA-based bacterial communities as varaibles to help interpret soil repiration and bacterial and fungal shifts due to watershed differences and season. Also, to determine variations in microbial communities across watersheds and seasons, we ran an analysis of composition of microbiomes (*ANCOM*) at the family level, using a one-way ANOVA test with Bonferroni-corrected alpha of 0.1 as the rejection threshold (Mandal, Van Treuren et al. 2015) and visualized the families in heat maps with hierarchal clustering using the *heatmap* function in the 'gplot' package in R (Warnes et al., 2016). Last, to relate fungal and bacterial community differences among watersheds and season within montane and urban soils, we performed redundancy analyses incorporating all soil edaphic characteristics and chemistry with the function *envfit* in the 'vegan' package of the R.

Environmental Drivers on Soil Respiration

To identify factors influencing seasonal fluctuations in soil respiration, we created mixed linear effects models for each watershed using soil edaphic characteristics, soil chemistry including DOC and all DOC components, and microbial diversity and richness. Each model used

a forward selection procedure to find significant variables ($P < 0.3$) and selected the resulting variables final models by testing the inclusion and exclusion of significant variables to generate the lowest the Aikaike information criterion (AIC). We used the Ljun-Box test to check for autocorrelation between model parameters. Models were generated using the *lme* function in the 'lme4' package in R.

RESULTS

Bacterial and Fungal Communities in Montane and Urban Ecosystems

Montane bacteria were predominantly structured by season while urban bacteria were influenced by watershed (Fig. 1). Bacterial communities in montane and urban ecosystems were distinct regardless of watershed, season, or depth and separated along axis 1, which explained 23% of the variation among communities. Seasonal variation in montane communities separated into two clusters, winter and spring, and fall and summer. Among urban communities, Red Butte and Logan watershed separated the farthest from each other with Provo in the middle along axis two, which explained 13% of the variation. The PERMANOVA complimented the ordination findings. Montane compared to Urban ecosystems accounted for much of the model (F statistic = 25, $R^2 = 0.21$, $P < 0.001$). Also, interactions occurred between the montane and urban systems and watershed (F statistic = 7.7, $R^2 = 0.13$, $P < 0.001$) and season (F statistic = 1.6, $R^2 = 0.04$, $P = 0.02$).

Fungal communities followed a similar pattern as bacteria across urban ecosystems but seasonal effects were not apparent in montane ecosystems (Fig. 2). Fungi in the Red Butte watershed were distinct from the other two watersheds and separated along axis 1, which explained 15% of the variation in communities. Based on the ordination and PERMANOVA results, montane and urban differences accounted for most of the variation among communities (F statistic = 12, $R^2 = 0.13$, $P < 0.001$) and the interaction between the montane and urban systems and watershed (F statistic = 5.1, $R^2 = 0.11$, $P < 0.001$) described the variation among urban communities.

Bacterial and Fungal Community Diversity and Richness

Bacterial diversity declined at least 21-34% during the summer and fall in a given watershed, and was consistently lower in the Red Butte, montane watershed (Fig. 3). Alpha diversity (inverse Shannon index) dramatically declined from spring to summer and stayed relatively low into fall, especially in montane ecosystems (RM-ANOVA, montane vs. urban season, F statistic = 4.7, P= 0.006, df = 3). Red butte bacteria in montane soils experienced the most dramatic decline in diversity of any montane soils (RM-ANOVA, montane vs. urban watershed, F statistic = 6.5, P= 0.004, df = 2). OTU richness was depressed by 35% in Red Butte soils relative to the two other watersheds regardless of being from montane or urban systems or different seasons (RM-ANOVA, watershed, F statistic = 13, P< 0.001, df = 2; Fig. 4). In RNA-based or the active bacterial community differed among watersheds. Diversity was 32% higher in the Logan than the Red Butte watershed (F statistic = 18, P< 0.001, df = 2; Fig. 5) and richness was 61% higher in in the Logan than the Red Butte watershed (F statistic = 20, P< 0.001, df = 2; Fig. 6).

Fungal diversity was similar between montane and urban ecosystems but was influenced by season and watershed. Alpha diversity was generally depressed in spring (RM-ANOVA, season, F statistic = 6.0, P= 0.002, df = 3; Fig. 7) and lowest in the Logan watershed, especially in spring and summer (RM-ANOVA, watershed, F statistic = 13, P< 0.001, df = 2). Richness of fungi followed a similar trend where the number of OTUs declined 23% in spring (RM-ANOVA, season, F statistic = 3.1, P= 0.04, df = 3; Fig. 8) and was 13% lower in Logan and Provo urban soils than montane soils from these systems (RM-ANOVA, montane vs. urban watershed F statistic = 3.7, P< 0.001, df = 2).

Family-Specific Responses Along Montane to Urban Gradients

Based on ANCOM results, urban bacterial communities have higher variation between watersheds as determined by the abundant taxa found in each location. Urban communities were discovered to have 62 differentially abundant taxa between watershed locations, more than three times than were found in montane systems where there were only 18 as determined by ANCOM. Heatmaps showing the significant assigned taxa from montane and urban systems show strong watershed groupings occur in urban systems, but less so in montane systems (Fig. 9 and 10). Proteobacteria and actinobacteria dominate the total phylum in both urban and montane systems with almost 50 percent composition composed of alpha and gamma proteobacteria in each system.

Soil fungi had drastically fewer taxa structuring phylogenetic differences than bacterial taxa. Between watersheds, there were only three differentially abundant taxa found in montane communities and eight found in urban communities (data not shown). When compared together across season, we found that in montane systems Ascomycota species dominate the community composition, making up 60 percent of the total phylum and in urban systems there was more phylum diversity with four different phylum making up the eight total phylum found to be dominant in urban systems (data not shown).

Montane and Urban Soil DOC and Inorganic N

DOC and inorganic N in montane soils were primarily structured by season and in urban soils by watershed. Montane DOC availability increased dramatically, at least 3-fold, between spring and summer and remained elevated into the fall (RM-ANOVA, season: $F = 3.2$, $P = 0.04$, $df = 3$; Table 3). In urban soils, DOC followed the same trend but was more variable only

leading to an elevated level of DOC in Provo relative to the two other watersheds (RM-ANOVA, watershed, F = 6.0, *P*= 0.02, df =1). Soil ammonium concentrations were: elevated in winter and spring across montane (RM-ANOVA, season, F = 8.2 *P*< 0.001, df = 3) and urban (RM-ANOVA, season, F = 14 *P*< 0.001, df = 3) soils, but Provo soils exhibited lower concentrations in montane and higher concentrations in urban soils. Ammonium declined in Provo montane soils and in urban soils (RM-ANOVA, watershed, montane, F = 5.5 *P*= 0.03, df = 2, urban, F = 5.8, *P*= 0.02, df = 2).

DOM Chemical Components via PARAFAC

The model found to best fit the DOM dataset along montane to urban transitions was comprised of five components, representing different organic carbon characteristics that indicate structure and source, and accounted for a total of 55% of total dataset coverage (Table 4). Examination of the residual fluorescence in each EEM found that most residual fluorescence was due to first-order Rayleigh scatter artefacts, and interfered with the estimation of Component 5. Split-half validation (n = 4 splits) was performed with 87% agreement between splits and the overall model. Deviations from 100% agreement were found again to be revictual rather than indicative of actual fluorescence. PARAFAC scores of all components are presented in Table 5. As with DOC, components of DOM varied seasonally in montane and by watershed in urban soils. For example, all DOM components except fluorescence index (FI)—indicating the source of DOM whether terrestrial, microbial, or autochthonous—which varied by location (RM-ANOVA, watershed, F = 4.0 *P*= 0.03, df = 2) varied seasonally (RM-ANOVA, season, ranges: *F* statistic = 11 – 3.6, *P*= 0.03 – > 0.001, df = 3). Season did influence the freshness index (BIX), a characteristic indicating whether the DOM is recently produced or more decomposed, and FI in

urban ecosystems (RM-ANOVA, season, *F* statistic = 3.3 and 10, *P*= 0.03 and > 0.001, df = 3 respectively) but the majority of differences in DOM components: comp3, abs 254, and FI were inherent in montane systems (RM-ANOVA, season, ranges: *F* statistic = 5.9 – 42, *P*= 0.04 - > 0.001, df = 2). EEM characteristic abs254 is representative of humic material.

Physiochemical Drivers of Bacterial and Fungal Communities

In montane soils, bacterial communities were influenced by different components of DOM determined by PARAFAC modeling. RDA analysis identified that BIX (R^2 = 0.229, *P*= 0.021) and daily soil moisture (R^2 = 0.423, *P*< 0.001) structured winter and spring communities but presence of humic compounds (R^2 = 0.223, *P*= 0.032), daily soil temperature (R^2 = 0.515, *P*< 0.001), and percent component one contribution to total DOM (R^2 = 0.257, *P*= 0.014) influenced communities in summer and fall (Fig. 11). Urban bacterial communities and montane fungal communities were not directly structured by soil chemistry. Fungi dominant in in Red Butte were most strongly influenced by percent composition of DOM component 5 (R^2 = 0.21, *P*= 0.041) and were inversely related to HIX (R^2 = 0.20, *P*= 0.048, Fig. 12).

Soil Respiration, Moisture, and Temperature

In situ data collection showed soil respiration was generally highest in summer and dipped in spring and fall; and while the magnitude of fluctuations in CO_2 concentrations were higher in summer than in winter, there were generally more fluctuations in winter than in summer (Fig. 13). These pulses of respiration occurred in soils associated with drying-rewetting cycles in summer and fall and freezing-thawing cycles in winter and spring. Seasonal moisture dynamics in montane systems follow respiration patterns with higher magnitude fluctuations in

summer compared to winter, while urban systems experienced almost all moisture fluctuations in winter (Fig. 14). Winter temperatures were steady in montane winter systems because of snowpack insulation, while urban systems lack a consistent snowpack and undergo fluctuations in winter soil temperature (Fig. 15). Soil oxygen fluctuations were more prevalent in montane systems, and typically saw lowest levels in spring and summer (Fig. 16) Urban system soil oxygen remained steady across seasons with the expectation of Logan where summer soil drying took place much later compared to Provo or Red Butte. The maximum and minimum soil CO_2 concentrations, moisture, and temperature; and number of pulses across watersheds and seasons are presented in Table 6.

Soil Respiration Linear Mixed-Effects Models

One model explained the variation of soil respiration across all montane soils, while individual models for each watershed best explained respiration from urban soils. The mixed linear effects model that best described daily montane soil respiration incorporated data from all watersheds (AIC = 415) and (*F* statistic = 10, R^2 = 71, *P*value = 0.001, df = 10, 17). Specifically, in montane soils, daily soil respiration was influenced positively by DOC, (t value = 3.0, *P*= 0.008), RNA bacterial diversity (t value = 2.2, P=.04) and percent composition of DOM components three and four (t value = 5.1, *P*< 0.001, and t value = 3.3, *P*= 0.004) and negatively by DNA bacterial richness (t value = -2.9, *P*= 0.009). Alternatively, in urban soils, the fit of daily soil respiration models was vastly improved when models were created by watershed (AIC Logan = 164, Provo = 76, and Red Butte = 150) over combining all watersheds together (AIC = 400). In the Logan urban soils, daily respiration was positively related to total the percent composition of component one (t value = 2.6, *P*= 0.03) and negatively related to daily O2

concentrations (t value = -11, $P< 0.001$) creating a model explaining 94% of the variation in respiration (F statistic = 70.9, $R^2 = 0.94$, Pvalue < 0.001, df = 2, 7). Respiration in Provo urban soils was negatively related to bacterial richness in rDNA-based communities (t value = -8.2, $P= 0.01$) and positively related to rRNA-based bacterial diversity (t value = 8.8, $P= 0.01$; F statistic = 40, $R^2 = 96$, Pvalue = 0.02, df = 4, 2). Soil respiration in the Red Butte urban system was driven by HIX (t value = 3.8, $P= 0.01$; F statistic = 6.6, $R^2 = 71$, Pvalue = 0.03, df = 4, 5). All model parameters are shown in Table 7.

DISCUSSION

Montane ecosystems are major contributors to global C cycling and observing the biogeochemical processes occurring in these systems is crucial for predicting future climate scenarios. Further, montane systems also fall along a continuum where rural, exurban, and urban ecosystems benefit from montane services. Anthropogenic influences often interrupt natural cycles with urbanization only intensifying the inexactness in predicting soil respiration and ecosystem services. Our investigation of microbial differences among montane and urban ecosystems confirm the complexity surrounding anthropogenic effects on microorganisms and the services they provide. Montane microbial communities supported higher levels of species diversity than their urban counterparts, were sensitive to seasonality, and their respiration was related to the availability of different DOM components. Respiration by the less complex urban microbial communities, which varied substantially across the three watershed systems, was influenced by a unique set of factors related to bacterial species metrics, DOM characteristics, and/or physical soil conditions.

Microbial Community Structure in Montane Ecosystems

Soil microbial communities were similar among watersheds with only bacterial communities demonstrating a distinct seasonal trend with community differences occurring between two seasonal groups-winter-spring and summer-fall. During summer and into fall, soils experienced drying-rewetting events that potentially influenced bacterial composition and led to the lower diversity we observed in summer and fall bacterial samples. In general, under moist soil conditions, microbial populations in warm compared to cool temperature soils have higher abundance but lower diversity (Sheik, Beasley et al. 2011), and the community structure in

summer-fall is often related to the presence of aromatic carbon compounds associated with vegetation growth. Although fall conditions brought milder temperature and lower moisture regimes, community structure from summer conditions likely carried over into fall, causing bacterial community structure to go virtually unchanged. Conversely, bacterial diversity was highest in winter and spring and community structure was driven by the presence of moisture and more recently derived (freshness index BIX) labile carbon substrates. In winter, snowpack insulation prevents freeze-thaw cycles, maintaining moisture availability and creating favorable conditions for microbial activity (Schimel, Bilbrough et al. 2004, Aanderud, Jones et al. 2013). Legacy effects of winter extended into spring as snowmelt provided a flush of moisture and still relatively cool temperatures. Our findings corroborate that seasonal fluctuations in community structure are dictated primarily by changes in moisture, temperature, and carbon availability (Allison, Wallenstein et al. 2010). Similarly, the community variation from fall to winter may be driven by a flush of humic material becoming mobilized at the onset of winter precipitation.

Fungal communities are more resilient than bacteria to the effects of temperature, moisture variability, (Evans and Wallenstein 2012), and changes in soil chemistry (Schimel, Balser et al. 2007). Our data supports this overarching consensus. We found no substantial variation in fungal communities among the four seasons.

Comparing the composition of the microbiome (ANCOM) among watersheds, we found significant differences in bacterial taxa grouped by our seasonal pairing as evident in the overall community composition. The dominant phyla was the Proteobacteria, which composed 47% of communities' relative abundance containing seven families: Alphaproteobacteria *beijerinckiaceae*, *azospirillaceae*, *xanthobacteraceae*, and *hyphomicrobiaceae*; Gammaproteobacteria *methylophilaceae*, and *nitrosomonadaceae*. Acetobacteraceae is N_2 fixing

bacteria that is associated with promoting plant growth (Saravanan, Madhaiyan et al. 2008) and were present in highest abundance during winter; *beijerinckiaceae* and *methylophilaceae* are methane consuming bacteria (Lueders, Wagner et al. 2004, Lau, Ahmad et al. 2007) that were found most abundantly in winter; *nitrosomonadaceae* are ammonia oxidizing bacteria that were found most abundantly in fall (Fernandez, Sheaffer et al. 2016).

Differences in fungal communities were almost non-distinguishable with only three different phylum-family varying between watersheds. The *physalacriaceae* (Basidiomycota) are a plant pathogen colonizing woody species and were dominant in Red Butte, *trichomeriaceae* (Ascomycota) dominating Provo fungal compositions, and *aspergillaceae* (Ascomycota) most abundant in Logan.

Urbanization and land use Influence on Microbial Community Structure

Location and subsequent level of urbanization defined microbial communities in urban systems, where we found each watershed was home to unique bacterial and fungal communities. Because of the high variability between watershed location (i.e., % built infrastructure, % vegetation, % impervious surfaces), urban bacterial community structure was not driven by seasonal fluctuations of any particular environmental variable, and urban fungal community structure was negatively associated with only changes in DOM components, specifically, tryptophan like compounds (Stedmon and Markager 2005). Tryptophan components are amino acids, either free or bound in proteins indicating intact proteins or less degraded peptide material that can be autochthonous or, terrestrially or microbially derived (Fellman, Hood et al. 2010). The presence of more protein like compounds is expected in urban environments (Williams, Frost et al. 2016). Organic inputs in urban systems may be quite diverse between watersheds. For

example, in Provo systems, DOM components one, two, and three, representing humic like terrestrially derived compounds and fulvic like terrestrial and autochthonous compounds (Stedmon and Markager 2005, Fellman, D'Amore et al. 2008) were higher in the urban location across all seasons compared to its montane counterpart. But these same three DOM components were relatively lower in urban compared to montane sites in Red Butte and Logan. DOM components in urban systems varied across watersheds with no distinct patterns with one exception. In all urban sites, the concentration of recently derived organic C as indicated by the freshness index (BIX) was relatively high and consistent across seasons. In addition to the variability in soil chemistry and microbial communities in urban systems, each urban site was unique in its level of urbanization and land use. For example, in the Provo urban location, residential development is happening in the areas directly surrounding our sampling location that historically was encompassed by agricultural fields growing alfalfa and wheat. In the Provo urban site, we found a higher presence of component one, a humic like component often present at relatively high-levels in agricultural catchments (Stedmon and Markager 2005). The site differences are certainly influencing the soil chemistry, microbial communities, and subsequent soil respiration.

Land use and level of urbanization was the driving influence of microbial communities in urban systems and as a result, we found much higher diversity between locations when comparing the composition of the microbiome (ANCOM). Unlike montane systems where we found only 16 significantly abundant OTU's among watersheds, urban systems had almost three and a half times more unique taxa (62 OTU's) driving community structures that were distinct among each watersheds. Phylum level diversity was composed of 49 percent Proteobacteria (50 percent alphaproteobacterial and 50 percent gammaproteobacterial), 32 percent Actinobacteria,

and the remainder composed of four other Phylum. The high presence of Proteobacteria is likely influenced by the high variability of DOM chemistry characteristics since Proteobacteria are found in both high and low organic C environments (Fierer, Bradford et al. 2007). Several species exhibited characteristics expected in urban soil bacteria. For example, *burkholderiaceae* metabolize aromatic carbons (Perez-Pantoja, Donoso et al. 2012), *gaillaceae* are found in areas with anthropogenic influences and tolerate low C:N conditions (Hermans, Buckley et al. 2017), *nitrosomonadaceae* are ammonia oxidizers (Fernandez, Sheaffer et al. 2016), and *pseudonocardiaceae* are chemoorganotrophs that metabolize hemicellulose (Meier-Kolthoff, Lu et al. 2013).

DOM Characteristics in Montane and Urban Ecosystems

DOM components 1 and 5, a humic-like and tryptophan-like fluorophore, were higher in urban systems than montane (Hosen, McDonough et al. 2014). DOC component one was higher in seven out of twelve instances (seasonal average in each watershed) and component 5 was higher in ten out of twelve instance. Component 1 is a low molecular weight fluorophore derived from terrestrial substance in warm temperatures and has low biodegradability. Component 2 is a quinone like, higher weight fluorophore biologically produced and dominant in hydrophobic, acidic fraction of DOM (Ohno and Bro 2006).

Soil Respiration in Montane Ecosystems

Our linear mixed effects modeling results indicated that montane respiration was positively related to total DOM, DOM components and rRNA-based bacterial diversity. Specifically, DOM components three and four—high-molecular weight humic-like substances

associated with freshly produced DOM (Fellman, Hood et al. 2010) were found in higher concentrations in our systems and undisturbed montane systems in general (Hosen, McDonough et al. 2014). We found a negative correlations with total bacterial community (DNA-based). This contrast in influence of the diversity of the active component of the community (rRNA-based) to the total bacterial community (DNA-based) suggests that the taxa active at one point is more important than the overall backdrop of community composition. Despite the complex structure of DOM and inconsistent moisture availability in summer conditions, soil respiration was higher in summer than winter and immense pulses of CO_2 coincided with fluctuations in moisture (Davidson, Verchot et al. 2000). Conventionally, temperature is the ultimate predictor of soil C dynamics in soil (Bennett and Lenski 1993, Lloyd and Taylor 1994) and subsequent soil respiration (Raich and Potter 1995, Rustad, Campbell et al. 2001, Knorr, Prentice et al. 2005, Davidson and Janssens 2006), but moisture is at least a co-factor and climate predictions show that moisture will likely play a more significant role, at least equal to that of temperature (Carvalhais, Forkel et al. 2014). Drier summers combined with more severe rainfall events may cause soil respiration to become even more sporadic. Temperature and moisture were not significant predictors of seasonal fluctuations in the soil respiration. We believe an artifact of our microbial sampling that reduced respiration into a daily mean once a month. If we had just used our sensor data, soil moisture, temperature, and O_2 concentration, we should have captured the diel fluctuations and seasonal trends in temperature and moisture that most definitely drive respiration.

We only tangentially captured the effects of snow on microbial communities and soil respiration. As climate changes alter winter to include warmer temperatures and more precipitation occurring as rain, there is an immense potential to stimulate soil respiration and

create more freeze-thaw events and more pulse-driven systems. Snowpack is expected to decline as temperatures rise (Bavay, Lehning et al. 2009, Ishida, Ercan et al. 2018) and soils that have historically been insulated by snowpack will be susceptible to freeze-thaw cycles, a harsh process that the microbial communities won't be adapted to (Fierer and Schimel 2003). As a result, microbial communities in montane systems will respond more sensitively to climate changes and the consequence in C cycling will be more significant in montane winter systems where a possible positive C feedback could take place (Friedlingstein, Cox et al. 2006).

Soil Respiration in Urban Ecosystems

Soil respiration in urban systems was variable between watersheds, with unique influences contributing to respiration patterns. Modeling results denote respiration in Provo was positively related to rRNA-based bacterial diversity, the active bacterial community, and negatively associated with rDNA bacterial richness, similar to what we found in the overall montane model. Logan and Red Butte systems were influenced by DOM component one and soil O_2, and the level of humification of organic matter (HIX) respectively. Logan watershed had the most significant decline in soil O_2 due to its location in an intermittent wetland and while we expected to see lower soil respiration, our results showed the contrary. The combination of anaerobic respiration and the presence of humic organic C indicated the likelihood of microbial organisms that may utilize humic substances as an electron acceptor during anaerobic respiration (Lovley, Coates et al. 1996). As stated above, Logan respiration increased by eight-times the magnitude of winter respiration from May through July likely due to anaerobic respiration. Red Butte was the only watershed where winter respiration was greater than summer respiration, and the only location where soils underwent multiple freeze-thaw events, reaching peak

concentrations of almost 7000 and 5000 ppm coinciding with spikes in soil temperature and freeze thaw cycles. Provo saw the fewest fluctuations, with summer respiration concentrations almost equal to that of winter. The lack of pattern in urban soil respiration was likely a result of the land use and level of urbanization in each watershed altering soil carbon dynamics. Making predictions for soil respiration in areas undergoing land use change is difficult and in doing so must consider the C substrate availability and chemistry (Houghton and Goodale 2004), and the soil conditions altering metabolic processes.

CONCLUSION

Given the significance of montane system contributions to global C cycling, the complexity of anthropogenic influences on C cycling in urbanizing ecosystems, and the rate of urbanization occurring in previously undisturbed systems, predicting urban and montane C cycling under future climate scenarios is vastly important. To do this it is essential to better understand three ecosystem processes. Mainly, how changes in climate influence soil C substrates and subsequent soil respiration in montane ecosystems, how C substrate characteristics and respiration dynamics change when exposed to the effects of urbanization, and finally, at what point human proximity to undisturbed montane ecosystems, where the majority of C cycling takes place, begins to influence global C cycling on a considerable scale. Our results corroborate the influence of seasonal dynamics on soil respiration and the complexity introduced by human effects on microbial community structure and the consequent effect on respiration in these systems.

FIGURES

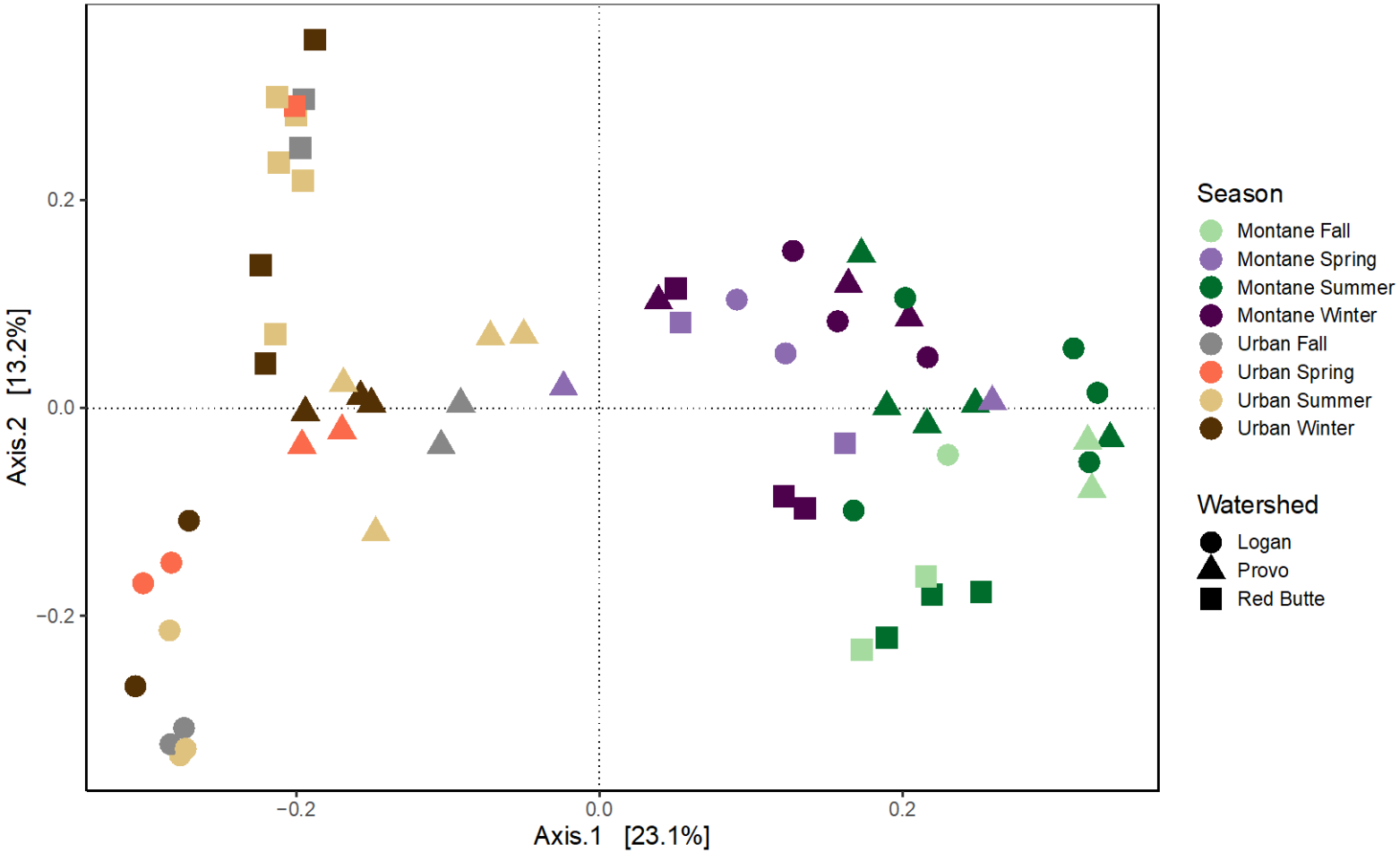

Figure 1 Bacterial communities primarily separated along montane and urban transitions with watershed location only creating unique communities in urban environments. Multivariate ordination plots were generated using principal component analysis (PCoA) on sample x OTU, Bray-Curtis matrices of 16s rDNA community (97% similarity cut off).

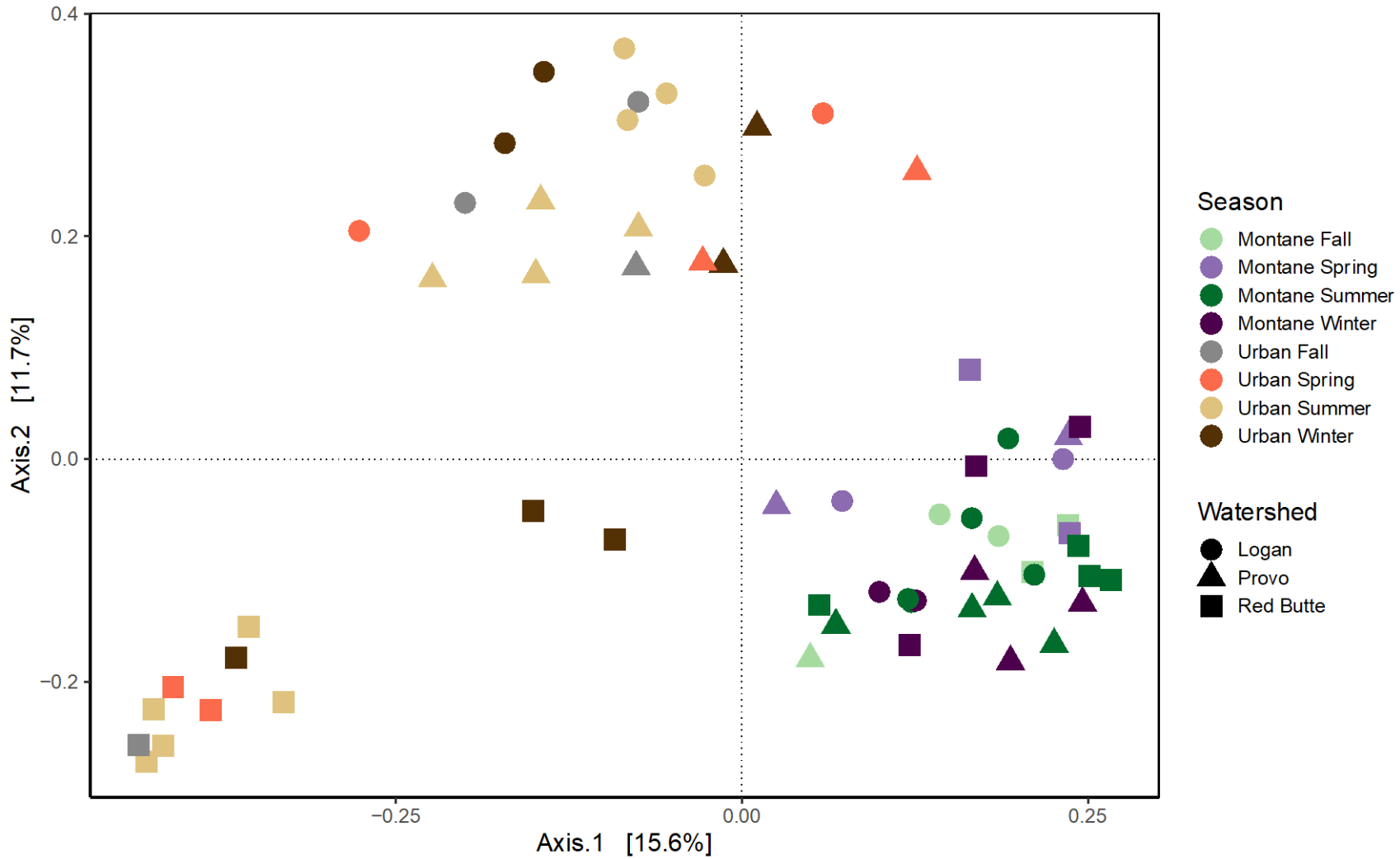

Figure 2 Fungal communities separated along a montane to urban gradient with watershed influencing composition in only urban systems. Multivariate ordination was generated using PCoA on a sample OTU on 18s rDNA community libraries (97% similarity cut off).

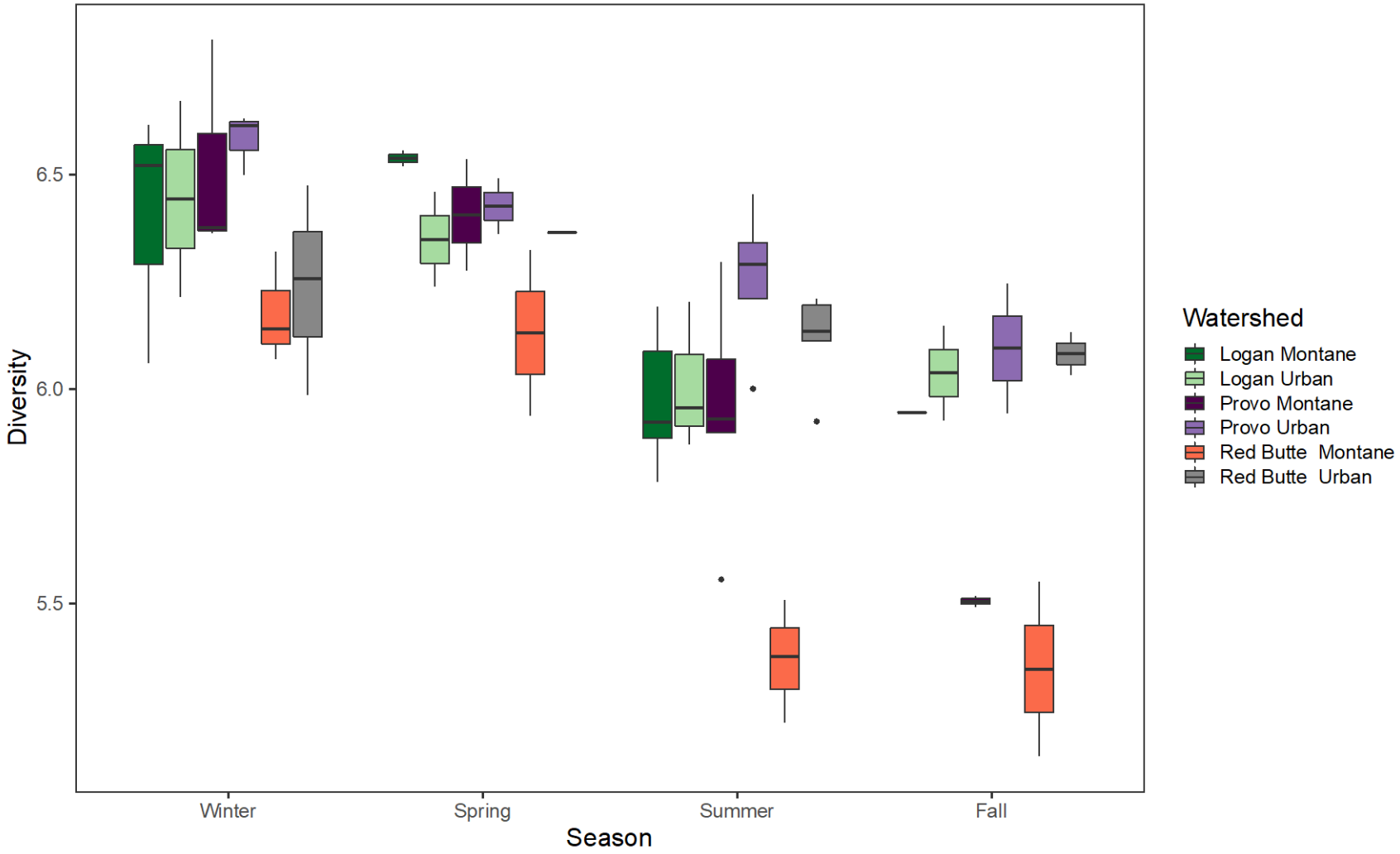

Figure 3 DNA diversity declined with seasonal progression from winter into summer, and increased toward winter levels in fall. Values were generated using OTU abundance with the Shannon diversity index.

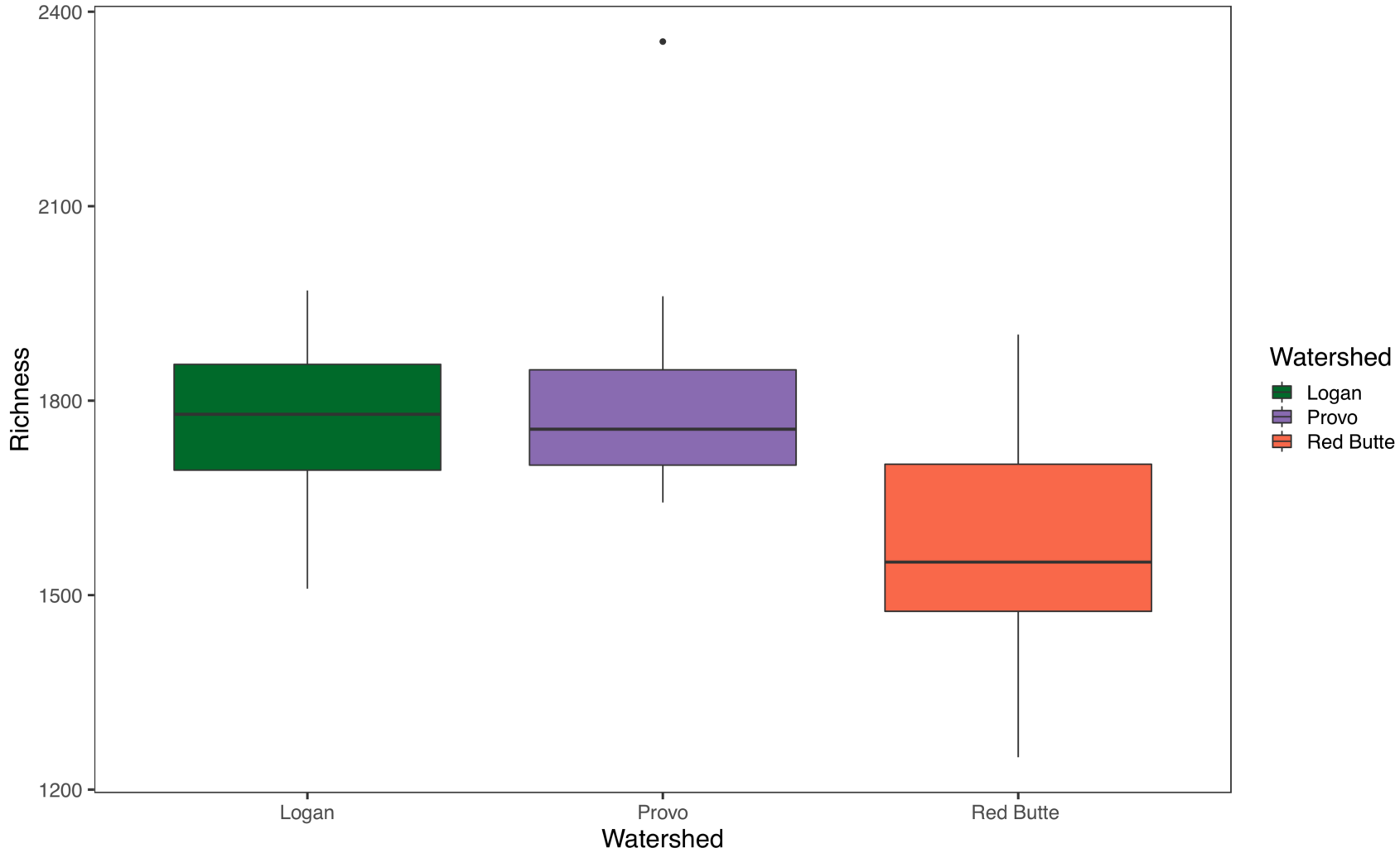

Figure 4 DNA richness was similar in Logan and Provo watersheds and was suppressed in the Red Butte watershed. Values were generated using OTU abundance with the Shannon diversity index.

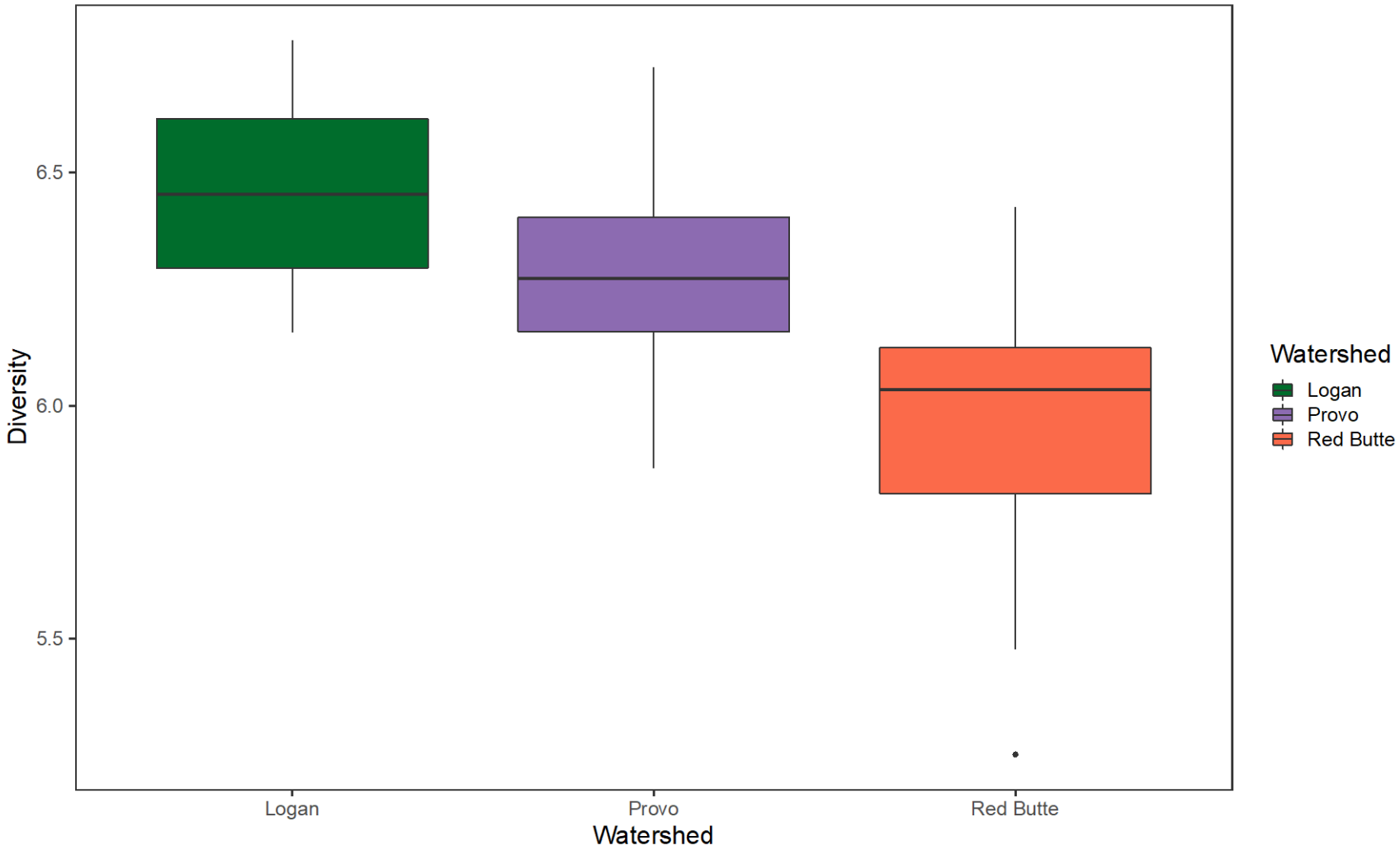

Figure 5 RNA diversity declines steadily between Logan, Provo, and Red Butte watershed. Values were generated using OTU abundance with the Shannon diversity index.

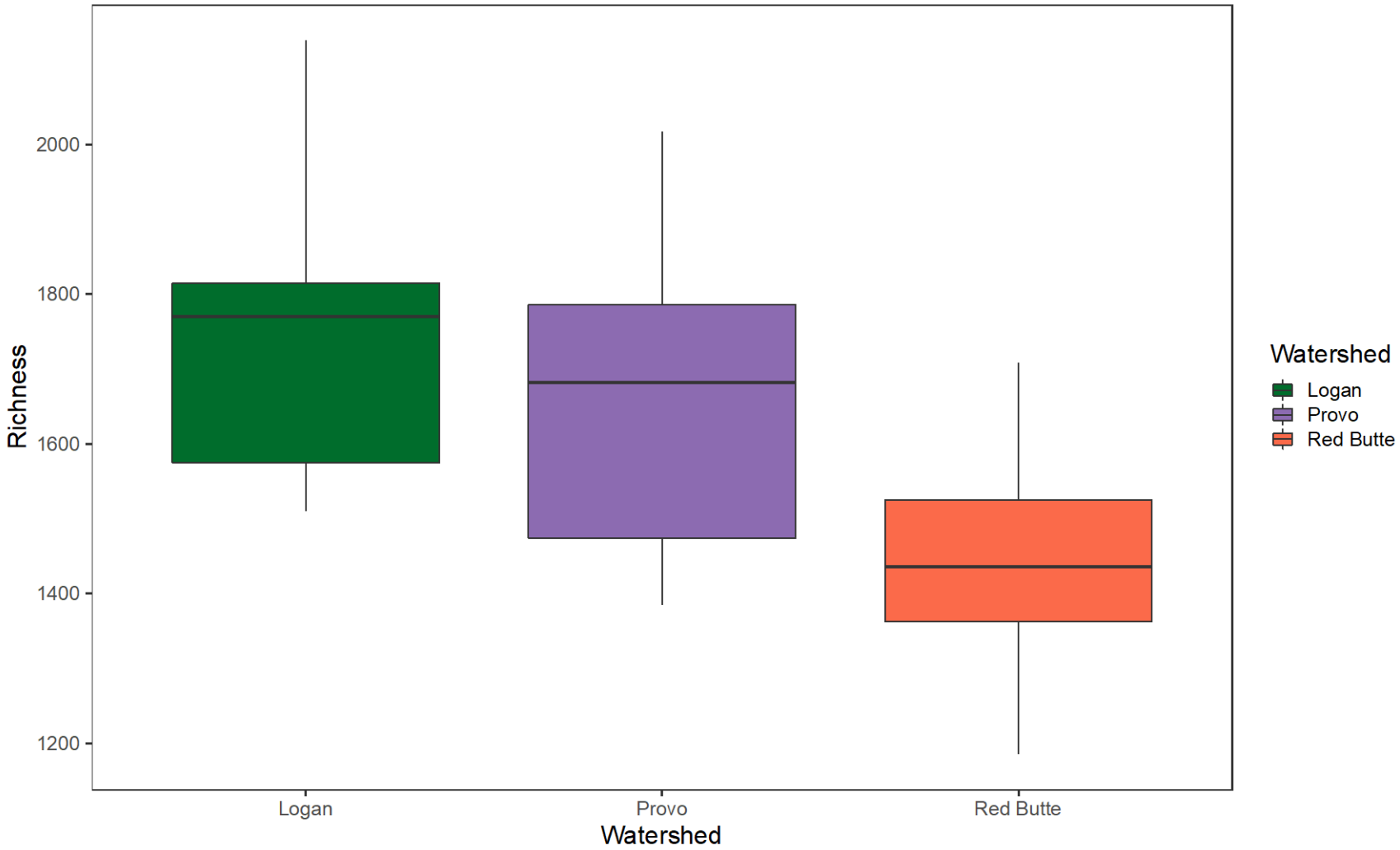

Figure 6 RNA richness remained similar between Logan and Provo watersheds and was lower in Red Butte watershed. Values were generated using OTU abundance with the Shannon diversity index.

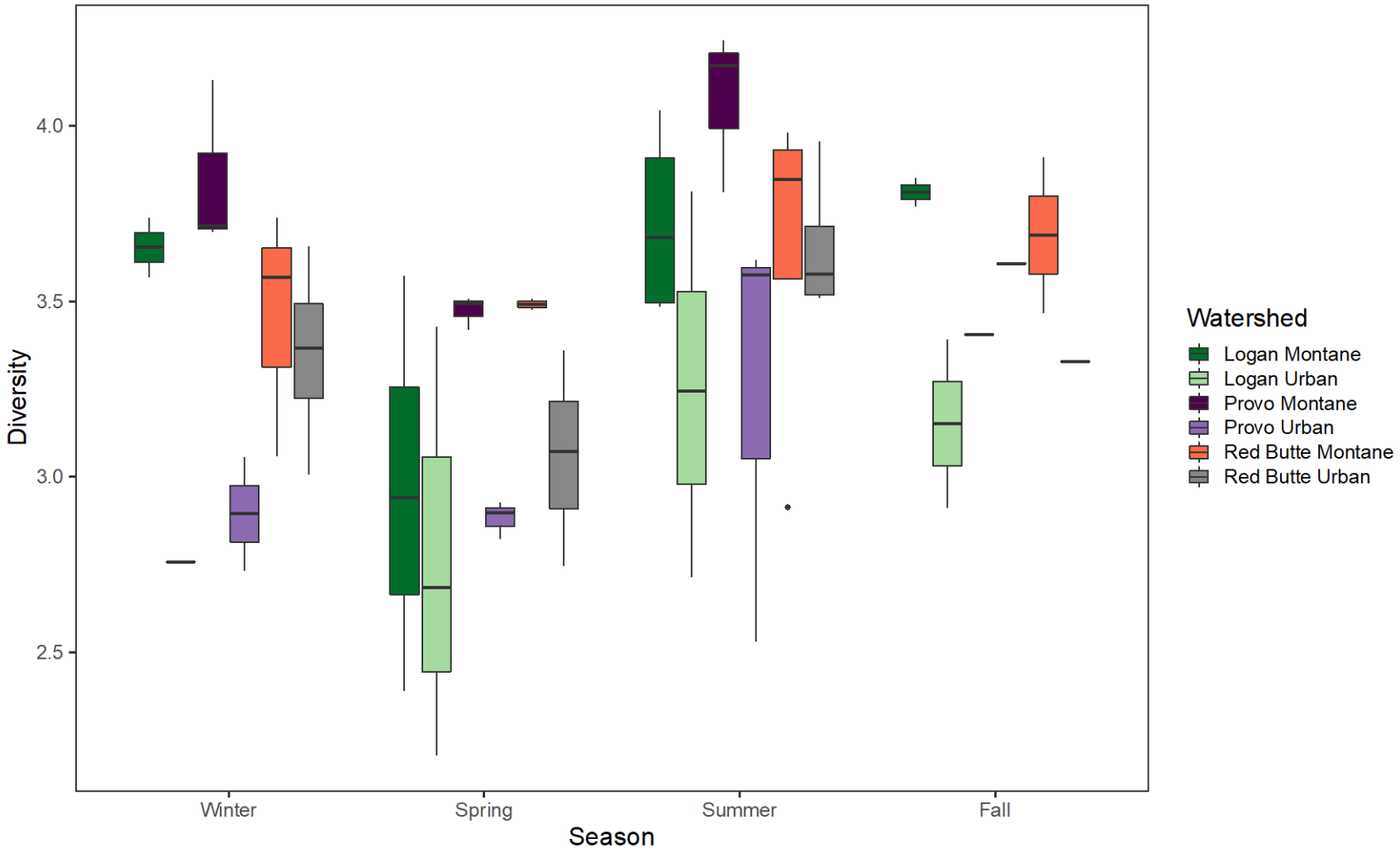

Figure 7 Fungal population diversity declined with seasonal progression from winter into spring, and increased toward winter levels summer and fall. Values were generated using OTU abundance with the Shannon diversity index.

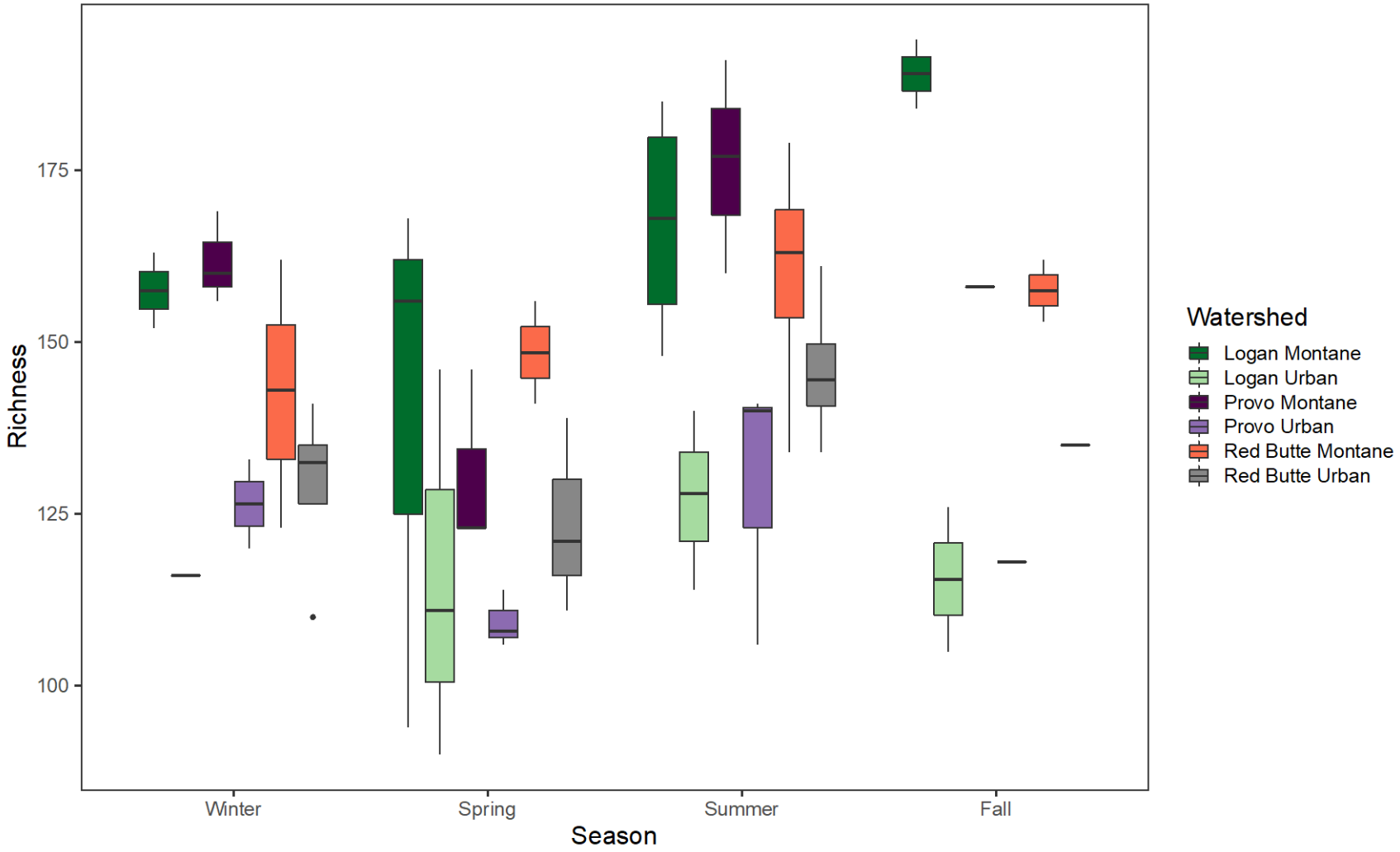

Figure 8 Fungal population richness declined in Provo montane and Red Butte urban systems from winter into spring, all other locations saw similar richness across seasons. Values were generated using OTU abundance with the Shannon diversity index.

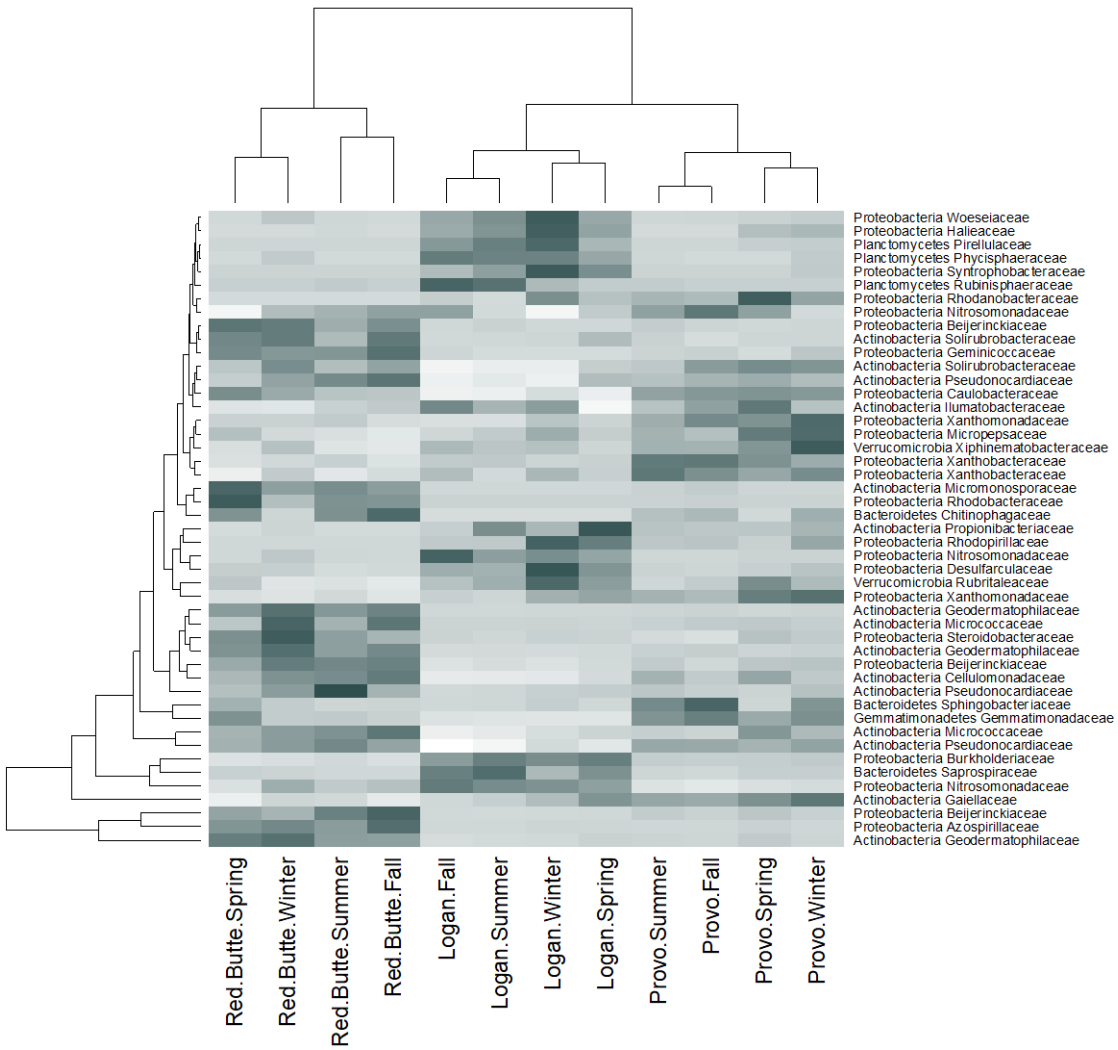

Figure 9 Heat map of bacterial families listed with phylum level taxa from all soils in urban systems based on ANCOM (analysis of composition of microbiomes). Families represent the top significant assigned taxa found between watersheds from one way ANOVA test with Bonferroni corrections (alpha = 0.1 as the rejection threshold).

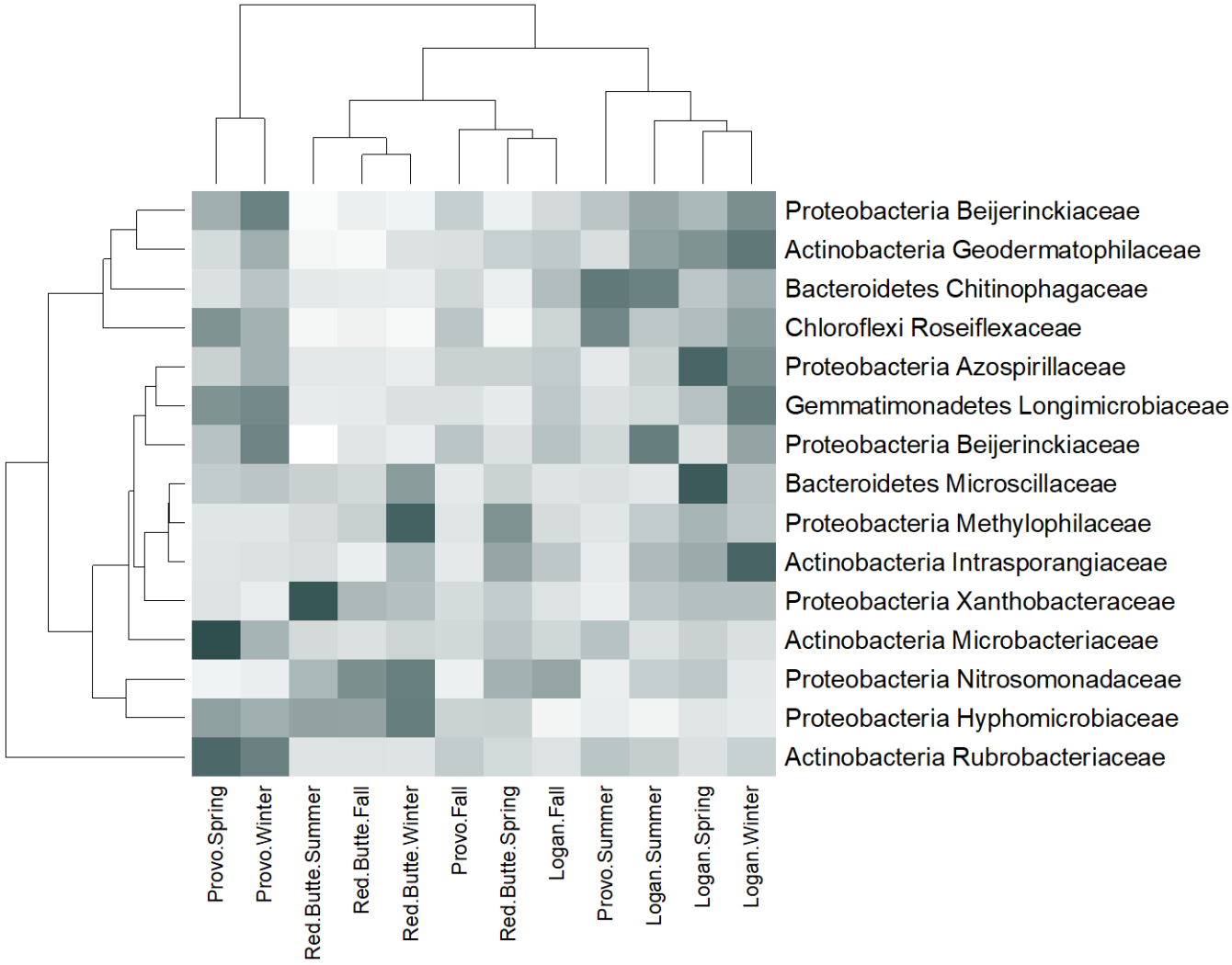

Figure 10 Heat map of bacterial families listed with phylum level taxa from all soils in montane systems based on ANCOM (analysis of composition of microbiomes). Families represent the top significant assigned taxa between watersheds found from one way ANOVA test with Bonferroni corrections (alpha = 0.1 as the rejection threshold).

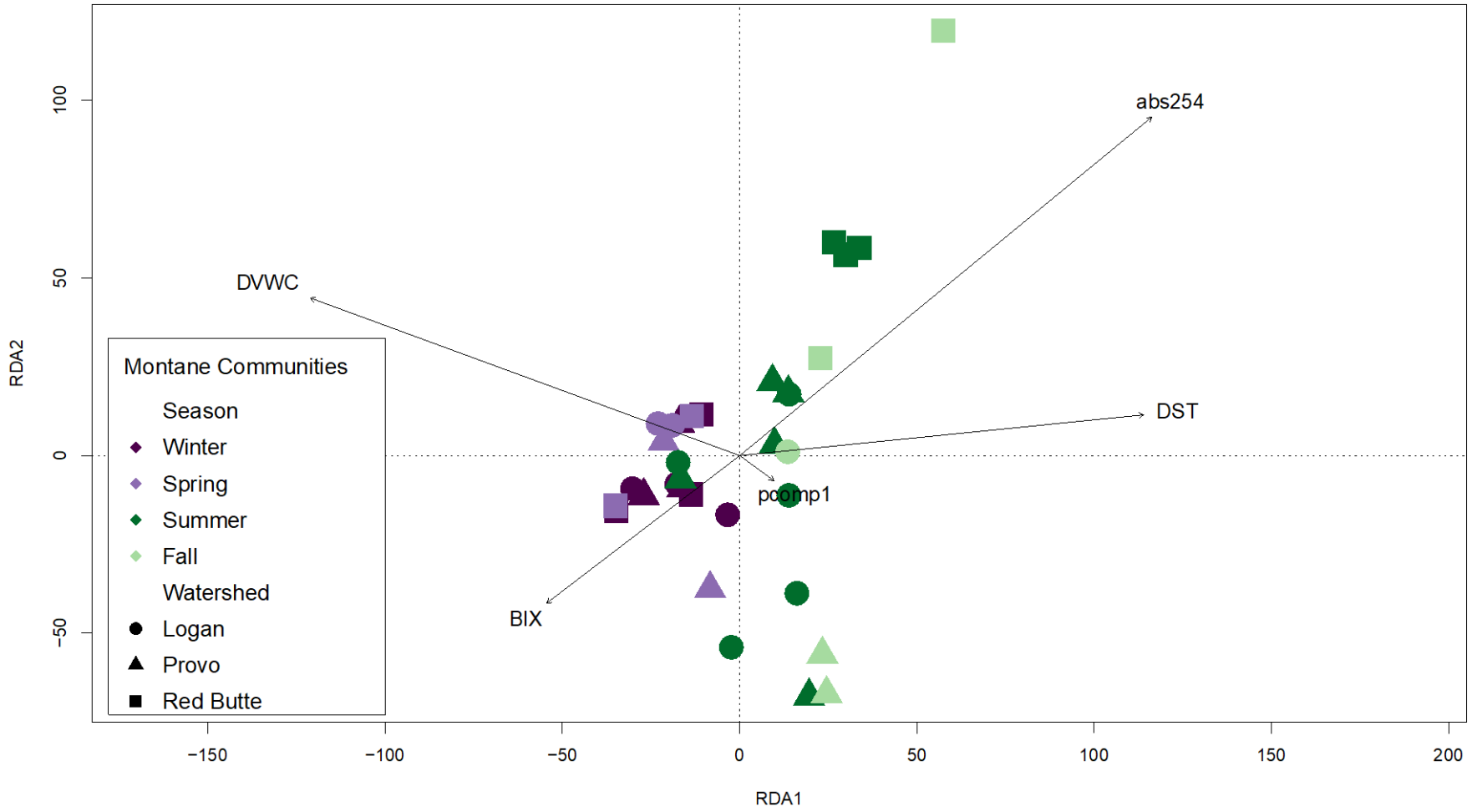

Figure 11 RDA analysis illustrating the relationship between microbial community composition and environmental variables in montane samples. Multivariate ordination plots were generated using principal component analysis (PCoA) on sample x OTU, Bray Curtis matrices of 16s rDNA community (97% similarity cut off).

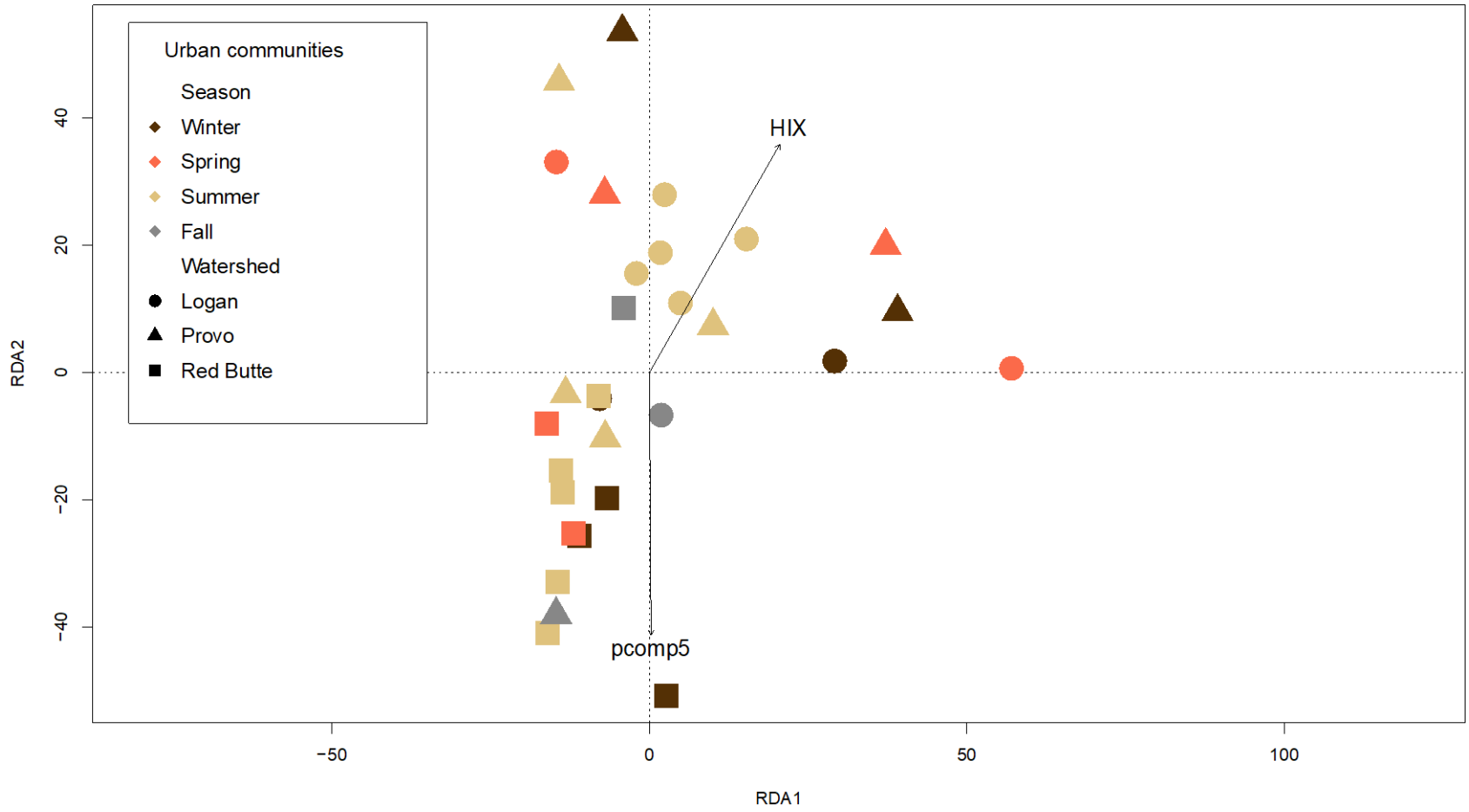

Figure 12 RDA analysis illustrating the relationship between microbial community composition and environmental variables in urban samples. Multivariate ordination plots were generated using principal component analysis (PCoA) on sample x OTU, Bray-Curtis matrices of 16s rDNA community (97% similarity cut off).

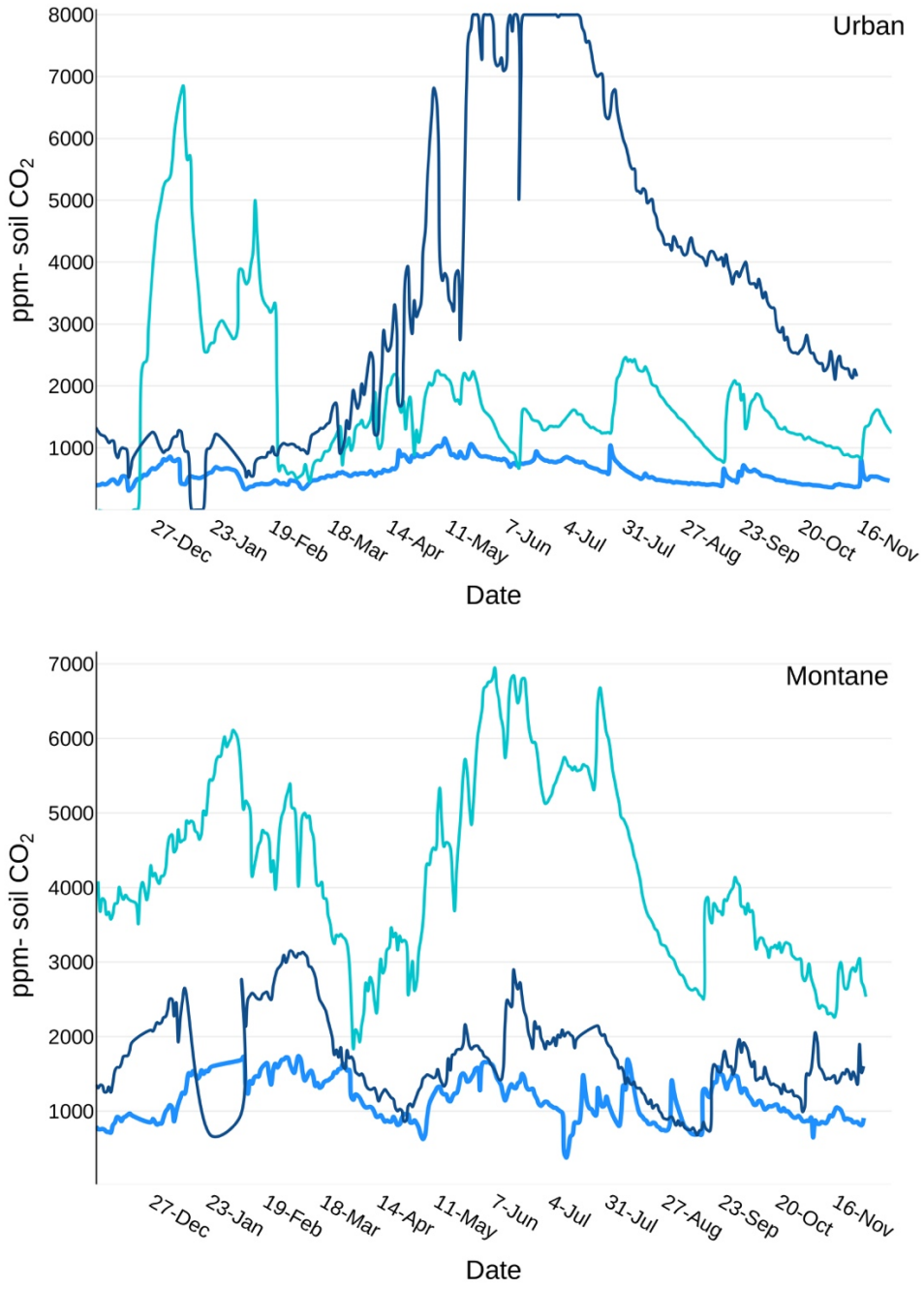

Figure 13 Soil CO_2 concentrations measured in situ during the sampling period from December 2016 through November 2017. Values plotted were averaged over a 24-hour period to remove diel fluctuations.

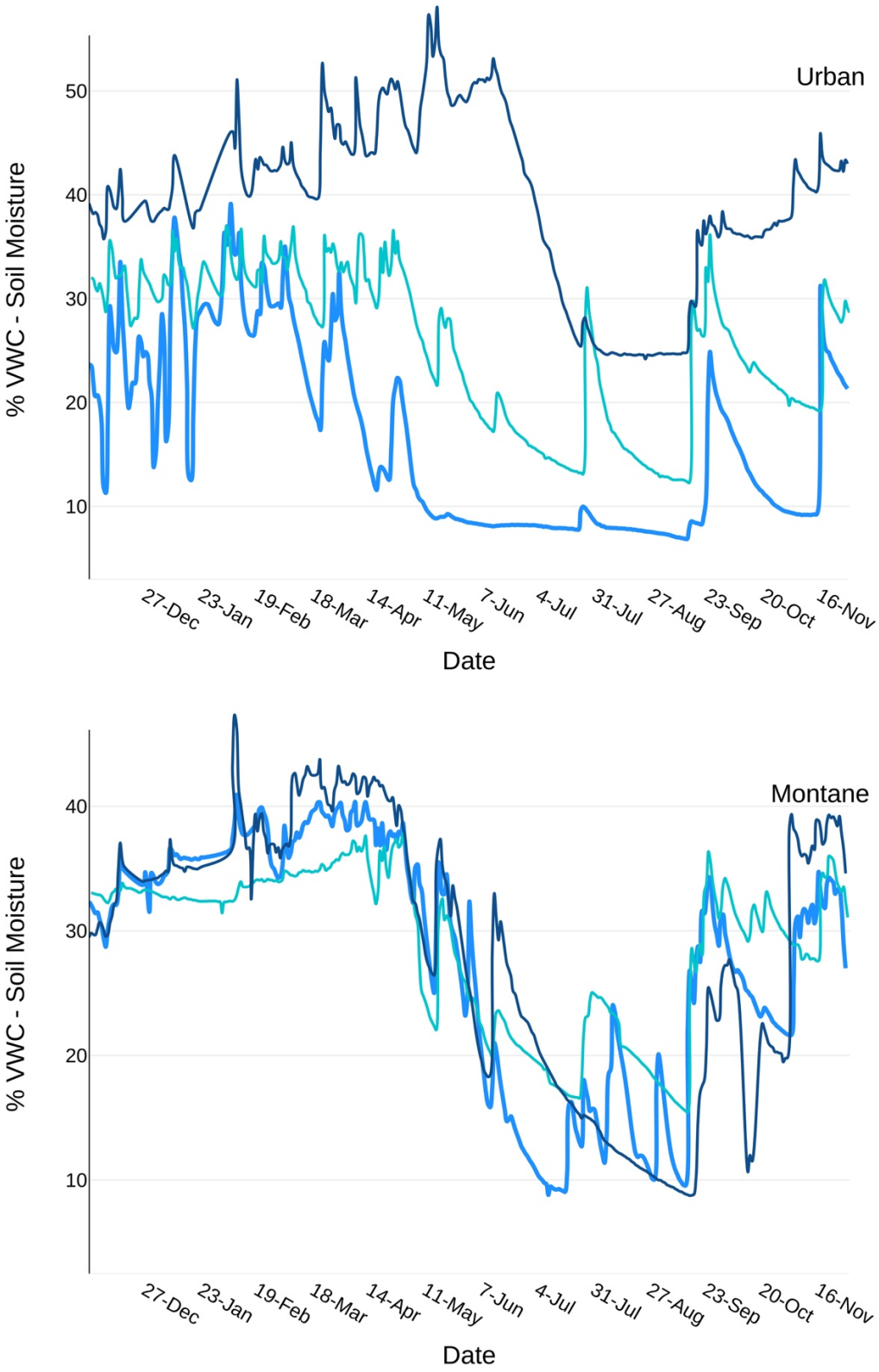

Figure 14 Soil moisture concentrations measured in situ during the sampling period from December 2016 through November 2017. Values plotted were averaged over a 24-hour period.

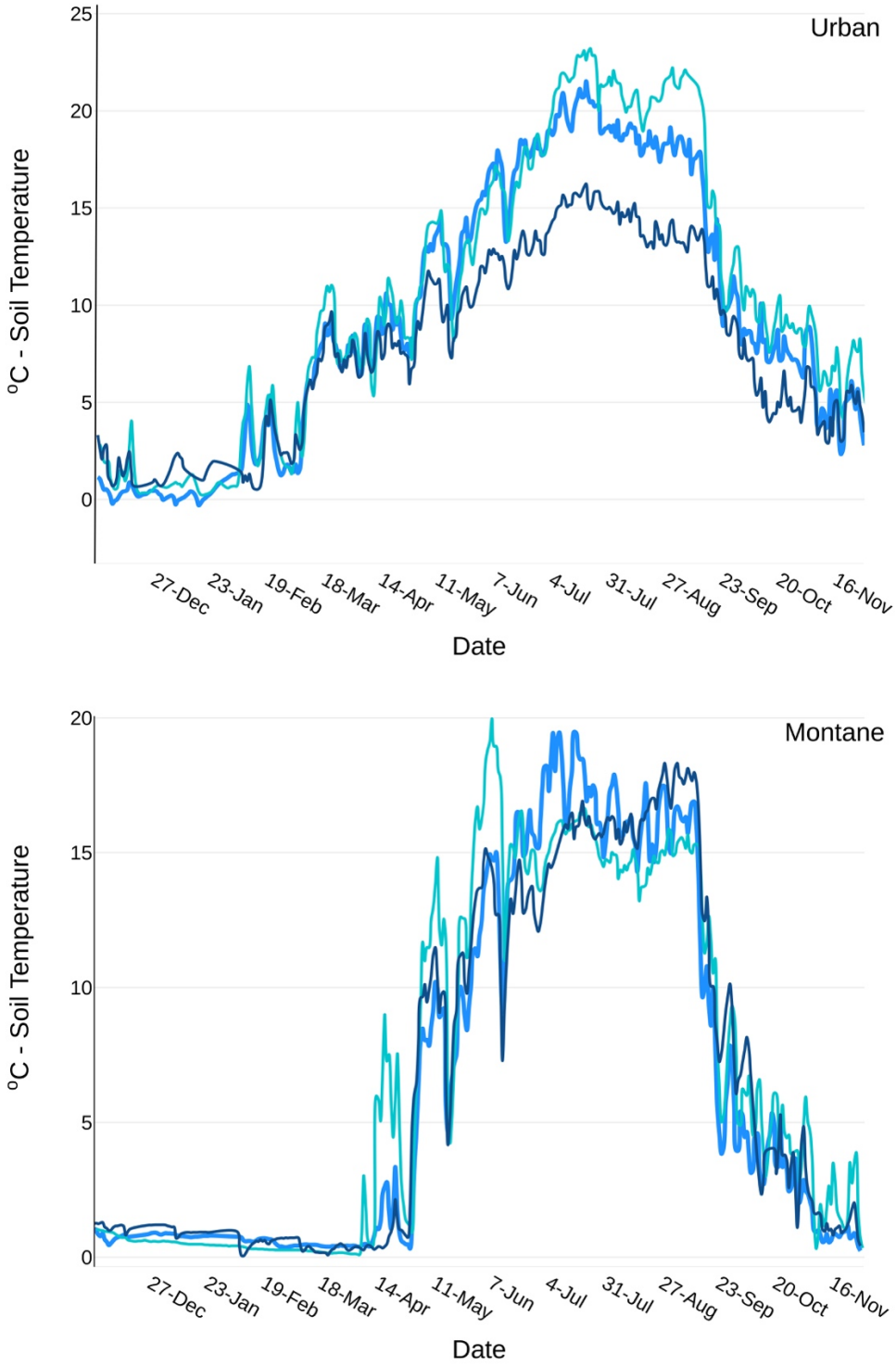

Figure 15 Soil temperature concentrations measured in situ during the sampling period from December 2016 through November 2017. Values plotted were averaged over a 24-hour period.

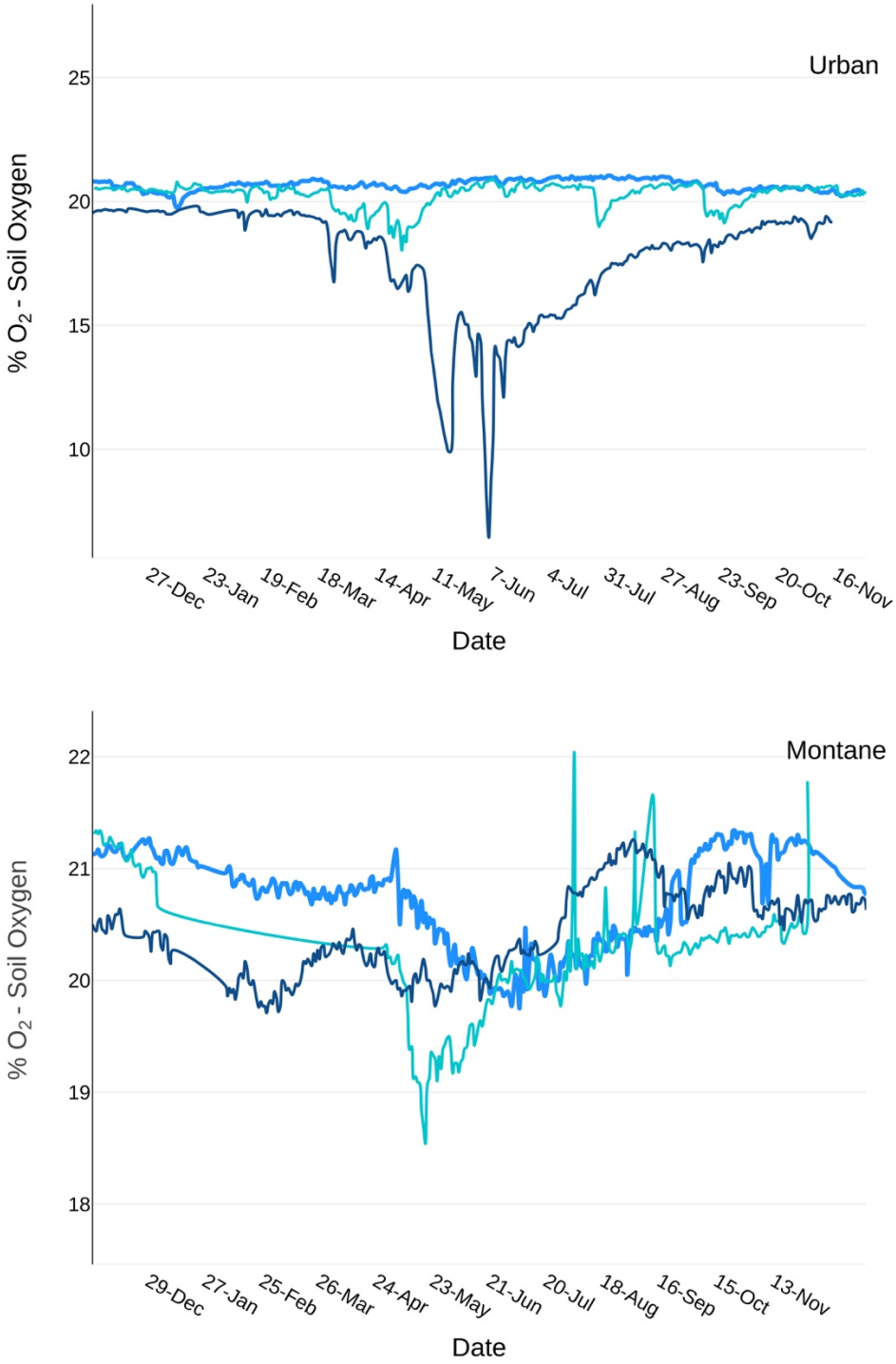

Figure 16 Soil O_2 concentrations measured in situ during the sampling period from December 2016 through November 2017. Values plotted were averaged over a 24-hour period.

TABLES

Table 1 Sampling site description. Sample area represents exclusively the area where samples were collected. Surrounding area represents surrounding vegetation/infrastructure.

	Sampling site characteristics							
		Urban				Montane		
Variable	**Area**	**Provo**	**Red Butte**	**Logan**		**Provo**	**Red Butte**	**Logan**
Number of species	Sample	1	1	2		5	3	4
% Vegetation cover	Sample	65	65	85		90	95	85
% Built infrastructure	Surrounding	30	70	35		0	0	0
% Impervious surfaces	Surrounding	35	80	50		0	0	0
Irrigation	All	Y-(surrounding area only)	Y	N		N	N	N
Latitude		40.484717	40.7608	41.705643		40.57.928	40.810122	41.949815
Longitude		-111.462558	-111.830474	-111.854268		-111.043503	-111.76695	-111.581352
Elevation		1659.0	1487.1192	1364.89		2388.41	2178.1008	2109.52

Table 2 Climate data from three watersheds along montane to urban transitions for the annual sampling period. Values shown are monthly averages ± SEM.

Climate data													
Watershed	**Parameter**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**
Urban													
Provo	Air temperature	-4.05 ± 0.90	-6.68± 1.16	0.96± 1.05	5.35± 0.97	6.57± 0.64	11.5± 0.56	17.1± 0.46	20.6± 0.35	18.5± 0.24	13.0± 0.87	5.63± 0.45	4.45± 0.80
	Barometric Pressure	83.5± 0.12	83.4± 0.17	83.2± 0.10	83.5± 0.10	83.3± 0.07	83.3± 0.09	83.4± 0.07	83.8± 0.03	83.7± 0.04	83.6± 0.08	83.7± 0.10	83.6± 0.09
	Snow depth	1.15±0.39	22.1± 1.59	9.35± 1.99	1.77± 0.79	0.00± 0.00	0.00± 0.00	0.00± 0.00	0.00± 0.00	0.00± 0.00	0.00± 0.00	0.00± 0.00	0.00± 0.00
	Relative Humidity	78.9±1.50	84.2±0.84	74.5±1.51	63.7±2.11	59.0±2.33	58.4±1.28	54.3±1.50	61.6±1.17	60.8±0.89	67.7±1.65	60.1±1.51	66.8±2.26
Red Butte	Air temperature	-1.62±0.81	-2.88±0.83	4.20±1.02	9.38±0.95	9.00±0.81	14.67±0.83	21.9±0.67	26.6±0.37	24.5±0.36	17.5±1.30	9.4±0.51	7.52±0.79
	Barometric Pressure	85.2±0.12	85.1±0.17	84.9±0.11	85.2±0.10	85.0±0.08	84.9±0.09	85.0±0.07	85.3±0.03	85.3±0.04	85.2±0.07	85.4±0.10	85.2±0.09
	Snow depth	5.08±0.82	9.43±1.37	2.45±0.67	0.37±0.20	0.10±0.10	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00
	Relative Humidity	69.5±2.29	79.8±1.56	63.1±2.36	48.2±3.11	51.0±3.24	44.3±2.15	34.2±2.01	33.9±1.94	33.1±1.42	47.3±3.54	46.1±1.67	55.2±2.07
Logan	Air temperature	-3.68±0.83	-8.03±1.21	0.34±0.89	-10.1±0.78	7.17±0.58	12.7±0.71	18.3±0.53	22.6±0.26	20.3±0.30	13.9±0.95	6.2±0.37	4.20±0.66
	Barometric Pressure	86.6±0.13	86.5±0.18	86.2±0.12	86.5±0.10	86.3±0.08	86.3±0.09	86.3±0.07	86.6±0.04	86.6±0.04	86.5±0.07	86.8±0.11	86.6±0.10
	Snow depth	4.13±1.20	32.3±2.08	9.27±2.36	1.52±0.53	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00

	Relative Humidity	80.8±2.19	89.0±1.41	82.0±1.61	66.1±1.96	64.5±2.25	60.1±1.40	55.0±1.27	55.0±0.94	38.0±1.11	67.9±1.88	63.7±1.29	75.6±1.88
Montane													
Provo	Air temperature	-7.47±0.89	-7.18±0.87	-3.61±1.24	0.61±0.78	1.18±0.66	7.20±0.72	14.01±0.56	18.1±0.30	16.2±0.32	9.76±1.22	—	—
	Barometric Pressure	76.0±0.08	75.7±0.11	76.0±0.10	76.4±0.10	76.1±0.07	76.3±0.08	76.6±0.07	77.0±0.03	76.9±0.04	76.6±0.09	—	—
	Snow depth	34.5±3.68	106±3.11	118±2.12	104±4.40	47.2±3.55	2.55±1.14	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	—	—
	Relative Humidity	73.3±1.88	76.8±1.63	70.4±2.22	61.9±2.25	58.9±2.78	53.9±2.14	44.5±2.00	47.5±2.20	46.3±2.23	58.3±3.28	—	—
Red Butte	Air temperature	-5.00±0.82	-5.33±0.82	-0.24±0.90	3.21±0.76	3.41±0.74	9.44±0.86	15.4±0.59	18.5±0.23	17.3±0.29	11.5±1.12	4.53±0.55	3.48±0.85
	Barometric Pressure	79.8±0.11	79.6±0.15	79.5±60.10	79.9±0.10	79.7±0.07	79.8±0.08	80.0±0.07	80.4±0.03	80.3±0.04	80.1±0.08	80.2±0.10	80.0±0.08
	Snow depth	50.0±2.49	98.7±4.47	96.6±3.41	62.3±5.79	3.51±0.89	0.07±0.07	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.02±0.02	1.81±0.76
	Relative Humidity	75.3±1.88	78.6±1.28	72.0±1.96	64.7±2.64	62.5±3.08	56.0±2.41	53.1±2.23	63.3±1.90	55.7±1.61	65.4±3.34	58.0±2.48	64.7±3.18
Logan	Air temperature	-7.69±0.92	-8.12±0.88	-2.53±0.90	1.28±0.66	1.05±0.53	7.34±0.72	12.9±0.57	17.9±0.25	16.1±0.30	10.0±1.12	2.83±0.48	0.35±0.78
	Barometric Pressure	78.8±0.11	78.7±0.15	78.6±0.10	79.0±0.10	78.8±0.07	78.9±0.09	79.2±0.07	79.6±0.03	79.5±0.04	79.2±0.09	79.3±0.10	79.0±0.08
	Snow depth	55.5±3.76	101±28.46	27.5±2.00	111±4.56	47.6±3.52	1.17±0.68	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	0.00±0.00	11.6±1.38
	Relative Humidity	76.0±1.65	82.3±1.13	76.3±2.42	69.5±2.38	68.7±2.25	61.5±1.83	58.1±1.85	53.1±1.49	48.9±2.01	62.8±3.41	57.5±2.59	75.1±2.42

Table 3 Soil chemistry data from three watersheds along montane to urban transitions through seasons. Values are means ±SEM (n=8) by season.

Soil Chemistry								
	Urban				Montane			
Variable	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Provo								
TN (mg TN kg soil^{-1})	0.83 ±0.34	3.36 ±1.45	11.4 ±4.55	8.22 ±4.75	0.29 ±0.14	0.64 ±0.04	1.19 ±0.34	1.24 ±0.45
Nitrate (mg N-NO_3^{2-} kg dry soil^{-1})	61.6 ±41.7	48.3 ±7.73	44.1 ±14.1	20.6 ±11.8	104 ±91.8	4.25 ±3.52	1.51 ±0.66	2.46 ±1.41
Ammonium (mg N-NH_4^+ kg dry soil^{-1})	20.9 ±10.7	6.75 ±1.73	2.93 ±1.13	6.13 ±5.40	20.4 ±6.18	8.60 ±2.94	1.02 ±0.28	1.22 ±0.08
DOC (mg DOC kg soil^{-1})	7.03 ±2.00	7.53 ±1.75	39.8 ±23.1	29.7 ±9.13	5.13 ±0.67	6.63 ±1.90	21.1 ±5.82	13.6 ±6.15
Red Butte								
TN (mg TN kg soil^{-1})	50.0 ±23.0	40.0 ±7.00	192 ±40.0	152 ±32.0	33.0 ±21.0	85.0 ±2.0	175 ±31.0	165 ±34.0
Nitrate (mg N-NO_3^{2-} kg dry soil^{-1})	42.8 ±26.2	0.90 ±0.70	3.43 ±0.98	0.83 ±0.09	27.7 ±12.2	16.7 ±7.77	11.1 ±4.00	4.11 ±4.09
Ammonium (mg N-NH_4^+ kg dry soil^{-1})	25.5 ±7.96	1.73 ±1.38	3.39 ±1.90	0.18 ±0.12	22.2 ±5.71	24.0 ±20.7	3.57 ±1.23	0.23 ±0.23
DOC (mg DOC kg soil^{-1})	3.33 ±1.13	3.82 ±0.63	14.4 ±2.41	22.4 ±14.4	15.3 ±12.4	7.10 ±0.38	11.8 ±1.19	71.8 ±42.9
Logan								
TN (mg TN kg soil^{-1})	48.0 ±30.0	91.0 ±29.0	222 ±34.0	243 ±40.0	94.0 ±66.0	59.0 ±25.0	154 ±44.0	105 ±4.00
Nitrate (mg N-NO_3^{2-} kg dry soil^{-1})	23.4 ±9.76	65.6 ±45.8	15.5 ±4.52	10.8 ±3.66	4.46 ±2.94	0.87 ±0.84	3.27 ±1.32	0.64 ±0.55
Ammonium (mg N-NH_4^+ kg dry soil^{-1})	105 ±27.6	35.0 ±12.1	5.63 ±1.33	16.4 ±9.18	4.60 ±2.62	2.85 ±2.85	1.25 ±0.43	1.06 ±0.77
DOC (mg DOC kg soil^{-1})	5.56 ±2.14	3.79 ±3.43	16.5 ±1.56	16.3 ±3.85	3.54 ±0.59	9.34 ±4.62	13.5 ±2.81	49.5 ±10.9

Table 4 Description of PARAFAC components comprising the best fit model accounting for 55% of total dataset coverage.

Component	Excitation maxima (nm)	Emission maxima (nm)	Comps. Identified from previous studies	Description
1	< 250 (315)	435	Ishii and Boyer (2012) Comp. 1	UVC Humic-like fluorophore
2	275 (385)	480	Ishii and Boyer (2012) Comp. 2	UVC +UVA Humic-like fluorophore
3	245 (450)	530	Ishii and Boyer (2012) Comp. 2	UVC+UVA Humic-like fluorophore
4	325	465	Fellman, D'Amore et al. (2008) Comp. 2; Ohno and Bro (2006) Comp. 1	Humic-like fluorophore
5	285	345	(Fellman, D'Amore et al. 2008) Comp. 8; Stedmon, Thomas et al. (2007) Comp. 7	Tryptophan-like fluorophore

Secondary maxima are shown in parentheses

Table 5 PARAFAC scores of each component comprising the best fit model accounting for 55% of total dataset coverage. Values are averaged across seasons.

EEMs Data								
	Urban				Montane			
Variable	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Provo								
Abs254	0.14±0.02	0.17±0.01	0.20±0.01	0.16±0.00	0.12±0.02	0.17±0.01	0.19±0.01	0.17±0.00
BIX	0.52±0.01	0.54±0.01	0.57±0.02	0.53±0.01	0.50±0.01	0.53±0.01	0.42±0.02	0.50±0.01
HIX	8.68±0.75	14.4±2.20	8.36±0.93	9.48±0.14	7.07±1.74	11.3±2.23	8.20±1.38	10.6±0.90
FI	1.36±0.01	1.41±0.00	1.41±0.01	1.42±0.00	1.33±0.00	1.38±0.02	1.57±0.10	1.33±0.01
Max Emission	3.40E+4±185	1.96E+4±214	2.57E+4±130	1.22E+4±230	1.97E+4±342	1.30E+4±904	1.40E+4±2.56E+3	1.34E+4±5.38E+2
Raman Area	7.68E+3±567	6.04E+3±40.3	6.10E+3±1.36E+3	5.67E+3±43.3	6.90E+3±541	6.04E+3±40.3	4.27E+3±5.38E+2	4.27E+3±452
Component 1	45.6±9.20	40.8±2.88	169±76.3	104±27.3	16.1±2.12	26.3±1.71	39.9±4.48	44.8±1.87
Component 2	23.2±4.27	27.0±1.56	63.4±20.06	38.6±9.00	10.3±1.39	17.3±1.25	24.2±3.01	29.3±1.15
Component 3	22.2±3.29	25.1±1.15	46.3±10.11	29.2±6.41	12.0±1.89	17.8±1.49	24.2±3.47	31.6±0.86
Component 4	3.36±0.36	6.67±0.48	6.63±1.51	6.88±1.51	2.54±0.17	3.46±0.27	25.4±9.34	6.87±0.43
Component 5	7.95±2.22	5.72±1.22	26.6±11.12	11.8±2.79	4.88±1.26	4.66±0.83	10.4±2.42	6.20±0.30
Red Butte								
Abs254	0.09±0.02	0.14±0.01	0.21±0.01	0.23±0.02	0.10±0.02	0.19±0.00	0.21±0.01	0.18±0.00
BIX	0.58±0.02	0.57±0.02	0.59±0.01	0.59±0.00	0.48±0.02	0.46±0.00	0.44±0.01	0.47±0.00
HIX	5.88±1.30	8.22±1.26	6.02±0.73	6.39±0.09	6.97±1.30	12.2±0.01	12.4±1.19	14.2±0.48
FI	1.50±0.01	1.49±0.01	1.57±0.02	1.52±0.01	1.25±0.01	1.28±0.00	1.25±0.01	1.31±0.01
Max Emission	1.67E+4±3.62E+3	6.45E+4±8.36E+3	1.44E+4±2.59E+3	7.83E+3±4.74E+2	4.27E+4±1.18E+4	1.56E+4±8.07E+2	1.84E+4±4.90E+3	1.71E+4±3.22E+3

Raman Area	7.65E+3±5.56E+2	8.81E+3±1.02E+3	4.82E+3±5.46E+2	2.79E+3±7.36E+1		9.50E+3±7.55E+2	6.04E+3±4.03E+1	4.85E+3±5.84E+2	4.19E+3±5.69E+2
Component 1	20.21±2.43	15.95±1.04	55.14±5.79	38.27±0.69		27.9±3.25	33.6±0.45	49.9±2.59	43.8±6.59
Component 2	11.58±1.18	10.12±0.51	32.41±3.46	21.26±0.72		19.5±2.59	25.8±0.36	35.4±1.86	31.1±4.73
Component 3	9.22±1.06	7.82±0.46	21.6±2.55	14.8±0.19		26.8±3.87	32.6±0.45	47.3±3.15	37.6±6.26
Component 4	1.82±0.14	1.85±0.01	9.67±1.82	4.46±0.01		4.86±0.94	6.77±0.13	10.3±0.64	7.01±1.00
Component 5	6.78±2.20	4.15±0.89	15.9±3.16	9.87±0.27		7.09±0.72	4.75±0.10	6.92±1.03	4.27±0.55
Logan									
Abs254	0.08±0.02	0.16±0.00	0.18±0.01	0.18±0.00		0.10±0.03	0.18±0.00	0.17±0.02	0.18±0.01
BIX	0.56±0.00	0.53±0.02	0.64±0.01	0.64±0.00		0.46±0.01	0.44±0.00	0.44±0.01	0.46±0.00
HIX	6.30±1.26	4.73±0.71	8.64±0.99	11.5±0.39		7.61±1.08	14.5±0.86	15.5±1.40	15.5±1.62
FI	1.42±0.01	1.34±0.02	1.53±0.02	1.54±0.01		1.28±0.01	1.32±0.00	1.36±0.03	1.34±0.00
Max Emission	2.93E+4±9.56E+3	4.78E+4±1.24E+4	2.66E+4±1.29E+4	7.56E+3±4.63E+2		4.46E+4±1.33E+4	2.86E+4±4.38E+3	1.03E+4±1.95E+3	8.95E+3±1.04E+2
Raman Area	7.65E+3±5.56E+2	6.04E+3±4.03E+1	4.82E+3±5.46E+2	2.79E+3±7.36E+1		7.65E+3±5.56E+2	6.04E+3±4.03E+1	3.86E+3±5.23E+2	2.79E+3±7.36E+1
Component 1	22.2±1.64	62.5±11.40	66.8±6.37	60.1±7.20		23.5±1.32	41.5±0.53	79.5±10.89	57.4±5.61
Component 2	12.9±0.99	45.0±7.32	35.6±2.47	32.7±3.48		16.5±0.68	31.1±0.31	50.6±6.22	40.1±4.03
Component 3	11.8±0.72	53.0±10.99	23.7±2.09	20.5±1.78		21.0±0.75	35.8±0.37	55.6±6.68	42.2±4.18
Component 4	2.22±0.30	9.93±2.25	5.84±0.58	4.62±0.57		3.66±0.13	7.54±0.09	19.1±5.09	8.41±0.74
Component 5	6.58±1.32	23.2±0.62	12.9±2.58	7.02±0.55		5.69±0.83	4.91±0.57	7.68±1.46	5.44±0.21

Table 6 Seasonal soil respiration means with max and min reading reported with soil temperature and moisture conditions as well as freeze thaw and drying rewetting instances for three montane to urban transitions.

Soil respiration dynamics										
		Urban					Montane			
Variable		**Winter**	**Spring**	**Summer**	**Fall**		**Winter**	**Spring**	**Summer**	**Fall**
Provo										
Soil CO_2 ppm	Mean	531	609	695	456		1220	1250	1140	990
	high	609	959	1150	814		1730	1740	1690	1460
	low	309	336	383	361		711	813	377	648
Soil temperature C	Mean	1.00	7.11	16.6	6.56		0.73	0.71	13.5	2.53
	high	5.36	10.6	21.5	10.4		1.08	3.35	19.5	5.60
	low	-0.30	1.37	8.93	2.34		0.40	0.32	3.84	0.24
Soil moisture %VWC	Mean	26.5	22.2	9.16	14.8		35.3	38.3	19.7	27.7
	high	39.1	35.0	24.9	31.2		40.9	40.1	36.9	34.7
	low	11.3	11.6	6.86	9.17		28.7	34.3	8.80	21.6
Freeze thaw cycles		5	0	0	0		0	0	0	0
Drying and Rewetting		5	2	1	1		0	1	5	1
Red Butte										
Soil CO_2 ppm	Mean	2780	1220	1630	1220		4610	3444	4810	2890
	high	6850	2190	2460	1810		6110	5393	6950	4030
	low	578	449	666	817		3510	1833	2500	2260
Soil temperature C	Mean	1.62	7.81	17.6	8.21		0.53	1.64	13.8	3.70
	high	6.85	11.4	23.2	12.2		1.05	9.00	20.0	7.55
	low	0.22	1.32	8.15	4.17		0.27	0.09	4.23	0.32
Soil moisture %GWC	Mean	32.0	32.6	19.9	23.8		33.0	35.4	23.0	31.2
	high	37.0	36.9	36.2	31.8		34.2	37.8	36.4	36.0
	low	37.2	27.3	12.3	19.2		31.4	32.2	15.4	27.6
Freeze thaw cycles		0	0	0	0		0	0	0	0
Drying and Rewetting		0	4	4	1		0	2	3	3
Logan										
Soil CO_2 ppm	Mean	971	1930	5890	2650		2120	1890	1590	1490
	high	1330	4190	8000	3730		3090	3150	2900	2060
	low	310	905	2850	2110		664	863	678	991

Soil temperature C	Mean	1.80	6.73	12.7	5.15		0.88	0.53	13.5	3.04
	high	5.13	9.67	16.2	8.80		1.29	2.14	18.3	8.16
	low	0.53	1.85	7.28	2.90		0.05	0.08	4.17	0.42
Soil moisture %GWC	Mean	40.3	45.4	36.9	39.1		32.3	41.0	20.0	29.9
	high	51.1	52.7	58.1	45.9		47.3	43.8	37.6	39.4
	low	35.7	39.6	24.2	35.8		29.5	35.9	8.74	10.6
Freeze thaw cycles		0	0	0	0		0	0	0	0
Drying and Rewetting		0	0	3	2		0	0	3	2

Table 7 Linear mixed effects model results indicating environmental drivers of soil respiration

Model Selection					
Location	Model	R^2	*P*	*F*	*df*
Montane	$y = 2.22_{(DOC)}-42.1_{(TN)}-4.34_{(DNA\ richness)}-1020_{(DNA\ diversity)}+3850_{(RNA\ diversity)}+38800_{(percent\ component\ 3)}+22700_{(percent\ component\ 4)}+5720$	0.714	<0.000	9.57	7, 17
Logan Urban	$y = 8990_{(comp1)}-1440_{(O2)}+25800$	0.934	<0.000	70.87	2, 7
Provo Urban	$y = -2.74_{(Ammonium)}-1.48_{(Nitrate)}-2.07_{(DNA\ richness)}+826_{(RNA\ diversity)}-752.3$	0.962	0.025	39.98	4, 2
Red Butte Urban	$y = 398_{(HIX)}+0.42_{(RNA\ richness)}-21700_{(percent\ component\ 1)}+12600_{(percent\ component\ 3)}+5340$	0.715	0.030	6.643	4, 5

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