Vegetation and elevation influence the timing and magnitude of soil CO_2 efflux in a humid, topographically complex watershed

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Abstract:

In topographically complex watersheds, landscape position and vegetation heterogeneity can alter the soil water regime through both lateral and vertical redistribution, respectively. These alterations of soil moisture may have significant impacts on the spatial heterogeneity of biogeochemical cycles throughout the watershed. To evaluate how landscape position and vegetation heterogeneity affect soil CO_2 efflux (F_{SOIL}) we conducted observations across the Weimer Run watershed (373 ha), located near Davis, West Virginia, for three growing seasons with varying precipitation. An apparent soil temperature threshold of 11 °C at 12 cm depth on F_{SOIL} was observed in our data—where F_{SOIL} rates greatly increase in variance above this threshold. We therefore focus our analyses of F_{SOIL} when soil temperature values were above this threshold. Vegetation had the greatest effect on F_{SOIL} rates, with plots beneath shrubs at all elevations, for all years, showing the greatest mean rates of F_{SOIL} (6.07 µmol CO_2 m^{-2} s^{-1}) compared to plots beneath closed-forest canopy (4.69 µmol CO_2 m^{-2} s^{-1}) and plots located in open, forest gaps (4.09 µmol CO_2 m^{-2} s^{-1}) plots. During periods of high soil moisture, we find that CO_2 efflux rates are constrained and that maximum efflux rates occur during periods of average to below average soil water availability. While vegetation was the variable most related to F_{SOIL}, there is also strong inter-annual variability in fluxes determined by the interaction of annual precipitation and topography. These findings add to the current theoretical constructs related to

the interactions of moisture and vegetation on biogeochemical cycles within topographically complex watersheds.

1 Introduction

Soil respiration (R_{SOIL}) is a major component of the terrestrial carbon cycle (Raich and Potter, 1995; Schimel, 1995), and is 30-60% greater than net primary productivity globally (Raich and Potter, 1995). Estimates of annual soil carbon emissions range from 68 – 100 Pg of carbon per year (Schlesinger, 1977; Raich and Schlesinger, 1992; Bond-Lamberty and Thomson, 2010). Temperate systems contribute approximately 20% of the annual global R_{SOIL} (Bond-Lamberty and Thomson, 2010), but have been shown to be recent carbon sinks, averaging 0.72 Pg of C uptake per year from 1990 – 2007 (Pan et al., 2011). R_{SOIL} can be estimated in the field by measuring soil CO_2 efflux (F_{SOIL}) — the direct rate of CO_2 crossing the soil surface over a period of time (Raich and Schlesinger, 1992). F_{SOIL} can vary spatially and temporally within and across systems as a result of the varied and complex interactions of controlling mechanisms (Drewitt et al., 2002, Trumbore, 2006; Vargas et al., 2010). The edaphic controls on F_{SOIL} at the landscape scale include soil temperature, soil moisture, root biomass, microbial biomass, soil chemistry, and soil physics (Fang et al., 1998; Davidson et al., 1998; Kang et al., 2000; Xu and Qi, 2001; Epron et al., 2004). These factors do not simply elicit additive or monotonic responses, but rather create complex responses of F_{SOIL} across spatial and temporal scales (Dilustro et al., 2005; Pacific et al., 2009).

Soil temperature is quite commonly a primary driver of F_{SOIL} (e.g. Fang and Moncrieff, 2001), and in complex terrain, temperature regimes can be mediated by elevation, slope, and aspect (Wu et al., 2013). The effects of elevation and topography on soil temperature can in turn affect carbon cycling (Schindlbacher et al., 2010) either directly or through indirect processes (Murphy et al,. 1998). Soil water content (SWC) however often serves as an important secondary control on F_{SOIL}. At high SWC values, CO_2 transport through the soil pore space is limited (Davidson and Trumbore, 1995; Jassal et al., 2005). Production of soil CO_2 can also become limited at high SWC values due to anoxia and decreased microbial aerobic respiration (Oberbauer et al., 1992).

At low SWC values, F_{SOIL} is decreased as well due to microbial desiccation and concomitantly reduced microbial activity (Van Gestel et al., 1993), resulting in decreased CO_2 production (Scanlon and Moore, 2000).

In topographically complex landscapes, precipitation gradients that exist as a function of elevation affect decomposition rates, CO_2 production, and movement of CO_2 through the soil (Schuur, 2001). The complex landscape structure and heterogeneity of mountain catchments also directly affect local soil moisture regimes through the lateral redistribution of soil water, adding to the spatial heterogeneity of these biogeochemical and physical processes. F_{SOIL} therefore varies across landscape positions as a function of this soil water redistribution (Riveros-Iregui and McGlynn, 2009). In subalpine forested systems for example, soil water content has been shown to be a strong driver of the spatial (Scott-Denton et al., 2003) and temporal (Pacific et al., 2008) variability of F_{SOIL}.

In addition to meteorological variables, vegetation (itself controlled by the spatial heterogeneity of micrometeorology), can influence carbon cycling within a watershed. Vegetation affects carbon cycling directly through photosynthesis (Raich and Schlesinger, 1992; Ekblad and Högberg, 2001; Högberg et al., 2001), above- and below-ground tissue allocation (Chen et al., 2013), and litter production (Prevost-Boure et al., 2010). Vegetation therefore controls the quantity and quality of soil organic matter (SOM) within systems, which in part will determine decomposition rates and soil CO_2 production (e.g. Berg, 2000). However, the role of belowground plant and microbial processes in the dynamics of SOM has become increasingly more apparent—showing that root and rhizosphere contributions to SOM are substantive (e.g. Schmidt et al., 2011). Vegetation also exerts controls on production of CO_2 through root respiration in the soil and through complex mycorrhizal associations that can mediate the response of soil CO_2 production to rain pulse events (Vargas et al., 2010). Finally, vegetation also elicits feedbacks on the abiotic aspects of a system, including the soil moisture and soil temperature regimes, further impacting biogeochemical cycling (Wullschleger et al., 2002; Metcalfe et al., 2011; Vesterdal et al., 2012).

Inter-annual variation in R_{SOIL} within systems can be high and exceed the inter-annual variation of net ecosystem exchange (NEE) of carbon (Savage and Davidson, 2001); this inter-annual variation can be driven in large part by the dynamics of precipitation (Raich et al., 2002). Current climate models project potentially dramatic changes in precipitation in the coming years (Kirtman et al., 2013), and presently the controls on inter-annual variation of R_{SOIL} in response to changing precipitation regimes are poorly understood at spatial scales ranging from landscapes to regions. The interactions among topography, vegetation cover, and climate are therefore an important and complicated area of study.

Inter-annual climate variability in mountainous, subalpine catchments, however, has been shown to alter the spatio-temporal heterogeneity of carbon dynamics within those systems (Riveros-Iregui et al., 2011; Riveros_Iregui et al., 2012). In a subalpine watershed in Montana, Riveros-Iregui et al. (2012) found that areas with low upslope accumulated area (generally uplands and drier areas) showed F_{SOIL} increases during wet years, while poor-drainage areas (riparian areas) showed F_{SOIL} decreases during wet years. This resulting bidirectional response is a function of the landscape heterogeneity of the system, soil biophysics, and inter-annual climate variability (Riveros-Iregui et al., 2012).

Given the possible interactions among precipitation, topography, and vegetation, we examined how F_{SOIL} varies as a function of landscape position and vegetation cover in response to inter-annual variation in precipitation within a complex, humid watershed. To do this we used a plot-based approach with repeated measures sampling to account for spatial and temporal variation of the biophysical controls on F_{SOIL} within our study watershed. The empirical nature of this study design, coupled with the use of portable infra-red gas analyzers (IRGAs) to measure soil CO_2 efflux, is a robust and proven way of quantifying the seasonal dynamics of F_{SOIL} and allows for greater consideration of the spatial variability of F_{SOIL} (Riveros-Iregui et al. 2008; Riveros-Iregui and McGlynn, 2009) at the watershed scale. We attempted to answer the following questions:

1. How does F_{SOIL} respond to inter-annual variation of precipitation in a humid, complex watershed?

2. How do landscape position and vegetation heterogeneity affect F_{SOIL}, and how do they interact with inter-annual variation in precipitation?

2 Methods

2.1 Site description

The Weimer Run watershed (374 ha) is located in the Allegheny Mountain range in north-eastern West Virginia within the Little Canaan Wildlife Management Area near Davis, WV (39.1175, -79.4430) and is a sub-watershed of the Blackwater River, a tributary of the Cheat River. The watershed has an elevation range of 940 m (confluence of Weimer Run and the Blackwater River) to 1175 m (Bearden Knob) (Fig. 1). For the climate period 1980-2010, mean annual precipitation (MAP) for the watershed was 1450 mm yr^{-1} (PRISM Climate Group). The mean daily maximum July temperature is 18.8° C, and the mean daily maximum January temperature is -3.9° C (NCDC, Station ID DAVIS 3 SE, Davis, WV). Precipitation varied during the study period, producing a relatively dry year in 2010 (1042 mm), a wet year in 2011 (1739 mm) and a mesic year in 2012 (1244 mm) (precipitation data from BDKW2 station, MesoWest, University of Utah) (Fig. 5A).

The Weimer Run watershed is adjacent to the Canaan Valley in West Virginia—which exists in a transitional zone between the Appalachian Valley and Ridge and the Appalachian Folded Plateau (Matchen, 1998). The surrounding ridge tops and the study site are underlain by Pennsylvanian sandstone from the Pottsville formation (Allard and Leonard, 1952). The over-story vegetation within the watershed is a mixed northern hardwood-coniferous forest, consisting of yellow birch (*Betula alleghaniensis*), red maple (*Acer rubrum*), red spruce (*Picea rubens*), and black cherry (*Prunus serotina*) (Allard and Leonard, 1952; Fortney, 1975). The under-story is comprised of *Rhododendron maximum*, *Kalmia latifolia*, *Osmundastrum cinnamomeum*, and *Osmunda claytoniana* (Fortney, 1975).

2.2 Vegetation and elevation classes

Three elevation classes were established along the north-eastern aspect of the watershed to form an elevation gradient: LOW (975 m), MID (1050 m), and HIGH (1100 m). Site elevations were determined using a digital elevation map (DEM) derived from 1/9 arc second elevation data from the Shuttle Radar Topography Mission (SRTM) (USGS 2006) processed with ArcGIS® software (ESRI; Redlands, CA). In order to address the effects of vegetation cover on F_{SOIL}, three vegetation cover classes were established: CANOPY – closed canopy, forest interior with no shrub layer; SHRUB – closed canopy, forest interior, with dense shrub layer; OPEN – forest gap with no canopy closure, within the forest interior. Differences among vegetation classes were confirmed using plant area index (PAI) which was measured for each plot in June 2010 with a LAI-2000 Plant Canopy Analyzer (LI-COR Lincoln, Nebraska). PAI was strongly statistically significantly different among vegetation cover types (F = 13.39; p-value = 0.0003). SHRUB plots were the greatest (3.46 m^{-3} m^3) followed by CANOPY plots (2.14 m^{-3} m^3) and then OPEN plots (1.75 m^{-3} m^3) (Appendix A).

At each elevation level in the watershed, three 2 x 2 m plots of each vegetation class were established—for a total of 27 plots across the entire watershed (Fig. 1). One of the SHRUB replicate plots at the LOW elevation had to be removed from analysis due to inundation during the summer of 2011. Data from the remaining 26 plots were analyzed.

2.3 Environmental variables

2.3.1 Soil CO_2 efflux

An EGM-4 Portable Infrared Gas Analyzer (IRGA) with an attached SRC-1 Soil Chamber (PP Systems, Amesbury, MA) was used to measure soil CO_2 efflux rates. The EGM-4 has a measurement range of 0 - 2,000 ppm (μmol mol^{-1}) with an accuracy of better than 1% and linearity better than 1% throughout the range. The SRC-1 has a measurement range of 0 – 9.99 g CO_2 m^{-2} hr^{-1}. Plots were sampled approximately weekly (every 5 – 10 days) from the middle of May until the end of September, from 2010 to 2012. For March until mid-May, and during

October and November, plots were measured approximately every two weeks (12-21 days) during times when they were snow-free. F_{SOIL} was measured 1 – 3 times at different locations within the plot at each measurement interval and averaged for a plot level estimation of F_{SOIL}. Plots were sampled between 900 and 1600 EST, and the sequence of plot measurements was varied to avoid a time-of-day bias in the results and account for diurnal variation in soil CO_2 flux over time. Our sampling followed a rotating scheduling where for one sampling period we would start at say the HIGH elevation, then proceed to work down the mountain (MID, then LOW), and the next week we would start at the MID and then work down to the LOW, then finish with the HIGH and the next would then start at the LOW, then HIGH, then MID, and so on. This method was followed through the experiment.

2.3.2 Volumetric water content

Volumetric water content (Θ_{field}) was measured using a Campbell HydroSense CD 620 (Campbell Scientific) set to water content measure mode with 12 cm probes (Campbell Scientific; +/- 3.0 % $m^{-3}m^{3}$, with electrical conductivity <2 dS m^{-1}; sampling volume using 12 cm rods = ~650 cm^3). A minimum of three measurements was taken in each plot per sampling event and averaged to make a plot level estimation of Θ_{field}.

Measurements taken by the Campbell HydroSense CD 620 have a known bias in soils where bulk density is outside of the 1 – 1.7 g cm^3 range, where organic matter is >10%, and where clay content is >40%. (Campbell Scientific). In order to calibrate field measurements, a calibration procedure from Kelleners et al. (2009) was followed where *P*, the period, which is the square wave output from the probe in milliseconds, is converted to K_a, the relative soil permittivity (unitless). *P* is related to Θ_{field} as shown in Equation (1):

$$P = \left(-0.3385 * \theta_{field}^2\right) + \left(0.7971 * \theta_{field}\right) + 0.7702 \qquad (1)$$

Equation (2) converts P to K_a.

$$\sqrt{K_a} = \frac{(P - P_{air})}{(P_{water} - P_{air}) * ((\sqrt{K_{water}} - 1) + 1)} \quad (2)$$

where P_{air} is the period in air, and P_{water} is the period in deionized water. P_{air} was calculated empirically at 0.79 ms. P_{water} was calculated at 1.37 ms following the procedure outlined in Kelleners et al. (2009) by placing the probes of the Campbell Hydrosense CD 620 in deionized water in an 18.92 L acid-washed container, with total vessel conductivity measured at 0.47 µmhos.

Soil samples were taken in conjunction with HydroSense measurements in 2012 (depth= 12 cm, volume= 56.414 cm^3, n=37), and actual VWC (Θ_{lab}) was calculated using Equation (3) from Rose (2004), where w is the gravimetric water content of the soil sample (g^{-3} g^3), ρ_b is the soil bulk density (g cm^{-3}), and ρ (g cm^{-3}) is the density of water:

$$\theta_{lab} = \frac{w\rho_b}{\rho} \quad (3)$$

In order to calibrate field measurements of VWC (Θ_{field}), $\sqrt{K_a}$ values were then regressed against Θ_{lab} to create an equation (4) relating $\sqrt{K_a}$ to Θ (R^2 = 0.74) such that field measurements of VWC (Θ_{field}) could be converted to Θ in order to account for discrepancies in organic matter, soil bulk density, and clay content:

$$\theta = 7.0341 * (\sqrt{K_a}) + 0.0806 \quad (4)$$

Θ was then converted to water-filled pore space (WFPS; m^{-3} m^3) using the soil porosity (Φ; m^{-3} m^3):

$$WFPS = \theta * \Phi \quad (5)$$

WFPS provides a more mechanistic variable that takes into account the bulk density and porosity of the soil, which influence the transport and storage capacity of the soil with regard to soil CO_2.

2.3.3 Soil temperature

During each field sampling session, soil temperature (T_{SOIL}; C°) was measured at 12 cm using a 12 cm REOTEMP Soil Thermometer (REOTEMP San Diego, CA) at a minimum of two locations within the plot. These measurements were averaged to create a plot mean temperature for each sampling event.

2.3.4 Soils

Soil pH was determined using a 1:1 measure of soil (from 0 – 5 cm depth) with deionized water and measured with a Fieldscout Soilstik pH Meter (Spectrum Technologies, Inc. Plainfield, IL) with an accuracy of ±0.01 pH, ±1°C.

Soil samples were taken from 0 – 5, 0 – 12, and 0 – 20 cm profiles within the soil. Soil bulk density (ρ_s), total bulk density (ρ_t), soil particle density, and soil porosity (Φ) were also calculated for each sample (Grossman and Reinsch, 2002; Flint and Flint 2002). Soil bulk density (ρ_s) is defined as the bulk density of the soil fraction, where the soil fraction consists of soil that has been sieved to less than 2 mm and all gravel and root material have been removed. Total bulk density (ρ_t) is defined as the absolute density of the sampled soil, including soil, roots, and gravel and is simply the sample dry mass over the sample volume. Total soil carbon and nitrogen were assessed using a NA 2500 Elemental Analyzer (CE instruments; Wigan, United Kingdom). Soil organic matter (SOM) content was estimated using loss-on-ignition at 500°C (Davies, 1974).

2.3.5 Data analysis

We chose to parse our data at 11°C rather than strictly by growing/dormant seasons in order to develop a more functional understanding of the controls on F_{SOIL}. The 11°C threshold was chosen for multiple reasons. 1) mean measured soil temperature at 12 cm across our watershed during our three years of observations exceeded 11°C for the period May 6 to October 13. This period coincides with the growing season, and allows for slight variance with a buffer on either end. 2) Piecewise regression (using the segmented package in R) identifies an estimated break-point of 11.58°C ±0.47 standard error when the ln(F_{SOIL}) is regressed against soil temperature. Based on our observations, we opted for the more conservative threshold of 11°C. 3) Below 11°C, the F_{SOIL} values are tightly coupled to temperature, while above 11°C there is increasing variance in F_{SOIL} that we feel warrants exploration. All analyses and means presented are for measurement periods where soil temperatures are above 11°C, unless otherwise noted.

We employed a mixed-model analysis of variance (ANOVA) with repeated measures to identify main and interactive effects of elevation and vegetation on soil CO_2 efflux, soil temperature, and water-filled pore space using the proc mixed procedure in SAS 9.3 (SAS Institute, North Carolina USA). All means presented are least-squares means calculated using a Tukey-Kramer adjustment.

To decouple the effects of soil temperature and soil moisture on F_{SOIL}, linear regressions of soil temperature against the natural-log of F_{SOIL} were done by year (2010, 2011, 2012), by vegetation cover type (OPEN, CANOPY, SHRUB), by elevation (LOW, MID, HIGH), by year and vegetation (OPEN 2010, CANOPY 2010, etc.), and by year and elevation (LOW 2010, MID 2010, etc.). The residuals from each model were then regressed against WFPS by each combination. All linear regressions use the lm function in R 3.0.1 (R Core Team 2013).

Differences in soil organic matter (SOM) were examined with a Kruskal-Wallis rank sum test using the kruskal.test() in R 3.0.1 (R Core Team, 2013). A two-way mixed-model ANOVA using the proc mixed procedure in SAS 9.3 was used to examine main and interactive effects of elevation, vegetation, and soil depth on soil bulk density and total bulk density. Soil bulk density, soil organic matter, total soil carbon, total soil nitrogen, and plant area index were individually regressed against the mean plot-level soil CO_2 efflux for each corresponding plot (e.g. High-Canopy 1, High-Open 2, etc.). Means were calculated from all flux data above 11°C for all three years (2010-2012).

3 Results

Exponential regression of F_{SOIL} measurements against soil temperature at 12 cm (T_{SOIL}) (Fig. 2A) shows a positive relationship ($R^2 = 0.316$; $y = 0.829 + e^{(0.1149x)}$) with increases in temperature resulting in increased efflux rates. The amount of variance explained by T_{SOIL} lessens above 11° C ($R^2 = 0.104$), with F_{SOIL} measurements below 11° C showing a much tighter relationship with temperature ($R^2 = 0.434$). To explore this variance, all data above 11° C were isolated and examined in order to parse out controls above this apparent temperature threshold for this system.

The natural log of flux measurements above 11° C for all years were regressed against T_{SOIL} (Fig. 2B) showing a significant positive relationship with soil temperature ($R^2 = 0.119$; $y = 0.096x – 0.010$). From this linear model, the residuals were then regressed against WFPS. The residuals from the ln(F_{SOIL}) values above 11°C show a significant negative relationships with WFPS (Fig. 2C) but this explains only marginally more of the variance ($R^2 = 0.019$).

3.1 Soil CO_2 efflux (F_{SOIL})

Repeated measures ANOVA analyses show no significant differences in F_{SOIL} among years when data are pooled. Significant differences among years do occur when data are parsed by elevation ($F_{4, 633} = 3.17$; $p = 0.013$) and by vegetation ($F_{4, 633} = 2.96$; $p = 0.019$).

Across all data above 11° C, there was a significant effect of elevation ($F_{2, 633}$ = 3.44; p = 0.032), with plots at HIGH elevation sites showing the highest F_{SOIL} rates and HIGH sites statistically differing from LOW sites, with MID elevation sites not differing from either (Fig. 3A). 2010 was the only year to show a statistically significant difference in F_{SOIL} among elevation classes within a year, with LOW elevation sites exhibiting significantly lower F_{SOIL} rates ($F_{2, 633}$ = 3.17, p = 0.013).

Differences among vegetation classes were stark ($F_{2, 633}$ = 37.58; p = <.0001). SHRUB classes across all elevation classes and all years had higher rates of F_{SOIL} (6.07 ±0.42 µmol CO_2 m^{-2} s^{-1}) than CANOPY (4.69 ±0.42 µmol CO_2 m^{-2} s^{-1}) or OPEN (4.09 ±0.42 µmol CO_2 m^{-2} s^{-1}) plots. This SHRUB effect was most notable during 2010, the driest year during the study, when SHRUB plots showed the highest rates of F_{SOIL} recorded during the study (7.48 ±0.674). Statistical differences among vegetation classes among years were complex. SHRUB 2010 and OPEN 2011 were uniquely different among all combinations (Fig. 3B).

3.2 Water-filled pore space (WFPS)

WFPS tracked well with precipitation across years, with 2010 having the lowest values of WFPS and 2011 having the highest rates of WFPS. WFPS in 2011 was significantly greater than either 2010 or 2012 ($F_{2, 633}$ = 17.27; p = <.0001) (Table 2). During 2010, when precipitation was lower than average, an apparent elevation effect on WFPS is observed, with HIGH elevation plots exhibiting significantly lower WFPS measurements than either LOW elevation or MID elevation plots (Fig. 3E). During 2011 and 2012, under extreme and moderate moisture regimes, this elevation effect is not evident. During 2010, vegetation treatment types are not significantly different, but in 2011, when there is more moisture in the system, statistical differences among vegetation classes are apparent, as SHRUB and CANOPY plots exhibit higher WFPS values than OPEN plots (Fig. 3F).

3.3 Soil temperature (T_{SOIL})

Data for all years showed a significant effect of elevation on T_{SOIL} across elevation classes for all data above 11°C ($F_{2, 633}$ = 170.76; p = <.0001). LOW elevation sites were warmer (15.99 ±0.35 °C), than MID sites (14.71 ±0.35 °C) and HIGH (14.94 ±0.35 °C) elevation sites. There was no statistical difference in soil temperature by elevation within years (Fig. 3C).

Vegetation (Fig. 3D) had a statistically significant effect on T_{SOIL} (F = 52.79; p = <.0001). SHRUB plots were the coolest (14.93 ±0.35 °C), OPEN plots the warmest (15.62 ±0.35 °C), and CANOPY plots were in between (15.10 ±0.35 °C). No within year comparisons were statistically significant. There were also no differences in temperature among years, when data were pooled and compared by year alone.

3.4 Soil physical and chemical characteristics

Soils within the Weimer Run watershed are heavily acidic, with pH ranging from 3.87 – 4.32 across the sampling area (Appendix A). Soil bulk density (ρ_s) from 0 – 12 cm ranges from 0.49 – 1.11 g cm^{-3} (Fig. 4A and 4B), with lower values occurring beneath the shrub understory at lower elevations and higher values found in open, forest gap areas. There is an effect of elevation ($F_{2, 56}$ = 5.77; p = 0.005) and vegetation ($F_{2, 56}$ = 10.55; p = 0.0001) on ρ_s for all soil profiles (0 – 5, 0 – 12, and 0 – 20 cm). Elevation effects on ρ_s by soil depth are mixed, with statistical differences at 5 cm depth ($F_{2, 12}$ = 4.11; p = 0.044) and at 20 cm depth ($F_{2, 18}$ = 4.15; p = 0.003). By elevation classes across all vegetation types, ρ_s from 0 – 12 cm is lowest at LOW elevations (0.0.65 ±0.08 g cm^{-3}), highest at MID elevations (0.95 ±0.08 g cm^{-3}), and in between at HIGH elevations (0.73 ±0.08 g cm^{-3}). Vegetation shows significant differences at 12 cm ($F_{2, 18}$ = 3.60; p = 0.048) and 20 cm ($F_{2, 18}$ = 5.15; p = 0.002). By vegetation classes across all elevations, ρ_s from 0 – 12 cm is lowest in SHRUB plot (0.58 ±0.08 g cm^{-3}), highest in OPEN plots (0.92 ±0.08 g cm^{-3}), and in between at CANOPY plots (0.83 ±0.08 g cm^{-3}). No interactive effects of elevation and vegetation were evident (Appendix B).

Soil porosity from 0 – 12 cm ranges from 0.58 - 0.82 m^{-3} m^3 and is correlated with vegetation cover—with higher values beneath the SHRUB plots (0.77 ±0.03 m^3 m^{-3}), medial values in CANOPY plots (0.68 ±0.03 m^3 m^{-3}), and lower values in OPEN plots (0.65 ±0.03 m^3 m^{-3}). (Appendix E). SHRUB plots also show the highest concentrations of total soil carbon (9.35 %) significantly greater than other vegetation types (F = 9.79; p = 0.0002). Vegetation also influences total soil nitrogen, with SHRUB plots exhibiting higher proportions of total soil N than other plots (Appendix E) (F = 6.36; p = 0.0029). Total soil carbon also differed by elevation, with LOW and HIGH classes showing greater proportions of total soil carbon in samples than MID elevation sites (Appendix D) (F = 6.28; p = 0.0031). MID level plots also showed lower proportions of total soil nitrogen than other elevation levels (Appendix D) (F = 6.45; p = 0.0027).

Kruskal-Wallis tests show that soil organic matter (SOM) for all soil depths (0 - 5, 0 - 12, and 0 - 20 cm) varied significantly by vegetation (χ^2 = 8.21; p = 0.016) and by soil depth (χ^2 = 36.18; p = <.0001), but not by elevation (χ^2 = 1.82; p = 0.401). Differences in SOM by vegetation treatment through the soil column were significant for the 0 – 5 and the 0 – 20 cm soil profiles (Appendix D). The highest rates of SOM were found at the HIGH elevation plots (40.14%) compared to the MID (21.73%) and LOW elevation plots (33.03%) (Fig. 4C). SHRUB plots (33.54%) and CANOPY plots (33.14%) had similar SOM values. OPEN plots were lower (27.76%) (Fig. 4D).

Regressions of mean plot-level soil CO_2 efflux against soil bulk density, soil organic matter, total soil carbon, total soil nitrogen, and plant area index yielded a statistically significant relationship only between soil bulk density (R^2 = 0.302; p = 0.003; Fig. 5).

4. Discussion

The threshold approach employed in this paper allows for a quantification of the controls on soil CO_2 efflux during periods when fluxes are not temperature limited. This threshold was chosen empirically after analyzing the data. While the exact threshold of 11°C may not be applicable to all watersheds, if similar or related methods for threshold determination (e.g. piece-wise regression, or Bayesian change-point analysis) are used, this approach offers potential for comparisons and insights into controls on fluxes. If varying thresholds are found, it would be of research interest to examine the variance.

4.1 Vegetation effects

Significantly greater CO_2 fluxes from plots with shrub cover is apparent in our data, despite consistently lower soil temperatures in these plots. We propose that increases in soil CO_2 efflux from beneath shrubs is related to the observed differences in soils beneath plots with shrub cover compared to our other vegetation plots in this watershed. Soil bulk density, soil porosity, soil carbon, and other soil properties have been shown to drive the spatial variability of carbon fluxes (Jassal et al., 2004; Fiener et al., 2012; Luan et al., 2011).

Here we see shrubs decrease soil bulk density (Fig. 4B; Appendix E) and increase soil porosity (soil porosity (Φ) for SHRUB plots averaged 0.77 m^3m^{-3} from 0 – 12 cm depth, compared to 0.65 m^3m^{-3} for OPEN plots and 0.68 m^3m^{-3} for CANOPY plots; Appendix E), allowing for greater diffusivity within the soil matrix, and increased transportation potential of soil CO_2 through the soil. While soils under SHRUB plots have higher concentrations of SOM and soil C, soil bulk density is lower, which results in overall lower values of SOM and comparable values of soil C by volume. The increased soil porosity in soils beneath shrub cover is likely resulting in increased oxidation of labile soil C. It should be considered that SHRUB plots, to 20 cm soil depth, had the highest mean values of SOM (18.13%), higher soil C (9.35 %), higher soil N (0.47%), higher C:N ratios (19.36), and lower ρ_s (0.39 g cm^{-3}) compared to CANOPY (SOM = 12.48%; soil C = 6.35%; soil N = 0.37%; soil C:N = 16.30) and OPEN plots (SOM = 12.48%; soil C = 5.14%; soil N = 0.31; soil C:N = 15.76) (Appendix D). The high C:N ratios for SHRUB plots indicate possibly lower amounts of available, labile carbon and possibly lower rates of decomposition than other areas of the watershed. This is corroborated by early results from a two-year litterbag experiment conducted in this watershed (Atkins et al., in prep). This indicates that root respiration contributions from shrubs may be substantive and may also be influenced by varying soil moisture and precipitation regimes. The effect of the soil microbial community on the temperature sensitivity of soil respiration can also be enhanced in soils with high soil C:N ratios (Karhu et al., 2014).

4.2 Interactions of vegetation and inter-annual climate variability

While, SHRUB plots exhibit greater rates of soil CO_2 fluxes than other classes in this watershed during the course of this study, the magnitude of these fluxes is also influenced by the inter-annual variability in precipitation. Across the three study years,, there is evidence of an intrinsic link between the movement of carbon and water in this watershed in response to landscape heterogeneities (i.e. vegetation and elevation) and inter-annual climate dynamics. During 2010, our comparatively dry year, we see increased rates of F_{SOIL} across the watershed, but more pronounced increases in fluxes from SHRUB plots. Conversely, during 2011, the relatively wet year, vegetation-level differences in F_{SOIL} are statistically unapparent. When changing precipitation regimes are considered, along with future projections of warming and carbon dynamics, the importance of this coupling among water, carbon, and vegetation within humid watersheds cannot be understated. Changes in the distribution, variability, and amount of rainfall, as a result of climate change, are expected to have a major effect on carbon cycling (Borken et al., 2002). The magnitude of this effect, however, remains uncertain (Wu et al., 2011; Ahlström et al., 2012; Reichstein et al., 2013).

4.3 Interactions of inter-annual climate variability and topography

During 2010 (driest year), we see a strong effect of elevation on water-filled pore space (WFPS). During 2011 and 2012, however, there is no apparent effect of elevation on WFPS. When precipitation decreases across the watershed, as is the case during 2010, a different soil moisture regime manifests at higher elevations, with lower values of WFPS that contribute, in the case of this watershed, to increased rates of F_{SOIL}. During periods of increased precipitation, the watershed exhibits a more uniform soil moisture regime. The difference in the magnitude of carbon fluxes across elevation levels decreases during years with higher precipitation. During periods of higher precipitation and increased soil moisture, air space within the soil remains filled and transportation of CO_2 through the soil is limited, resulting in decreased rates of F_{SOIL}.

Production of CO_2 in the soil is also decreased due to the increased incidence of anoxic conditions as a function of increased WFPS. Our LOW elevation plots were statistically similar in wetness to the MID plots, both of which were wetter than the HIGH plots during the study. The LOW elevation plots were also the warmest for each year of the study, yet exhibited the lowest rates of F_{SOIL} for the entire study period. One consideration not explicitly detailed in our study is the effect of topographic aspect on soil water redistribution as plots in our study all had an east-northeasterly aspect. Landscape positions with varying aspect can have differing soil water contents while having similar soil temperature regimes (Kang et al., 2003) that still result in varied soil carbon fluxes. Another contributor to the magnitude of carbon fluxes can be the amount of upslope accumulated area or the connectivity of varying landscape positions to flow paths within watersheds (McGlynn and Seibert, 2003; Pacific et al., 2012). During our wet year, however, we see a diminished effect of these topographic heterogeneities.

Enhanced fluxes during years of decreased precipitation suggest that soil respiration in humid mountain watersheds is strongly controlled by soil water, and to a lesser extent, soil temperature. During average and above-average precipitation years, soil respiration values are lower due to limited CO_2 production and/or diffusion through the soil. During years where precipitation is below average, soil respiration values increase. However, what is not considered here are the cumulative effects of inter-annual variability in precipitation. Would consecutive dry or consecutive wet years result in increases or decreases following the second year?

4.4 Implications of vegetation dynamics

The most dominant shrub species in this watershed is *Rhododendron maximum*, an ericaceous understory shrub that has been shown to increase SOM and soil N in forests where it is present (Boettcher and Kalisz, 1990; Wurzberger and Hendrick, 2007). *R. maximum* occurs most commonly in forest coves and on north-facing slopes with mesic to moist soil water regimes (Lipscomb and Abrams, 1990). Ericaceous litter also contributes to declines in soil fertility, lower N mineralization rates, and lower decomposition rates due to higher concentrations of foliar polyphenols (Hättenschwiler and Vitousek, 2000; DeLuca et al., 2002; Côté, 2000; Wurzberger and Hendrick, 2007). Ericaceous plants have ericoid mycorrhizae that provide a competitive advantage to breaking down organic N over ectomycorrhizae associated with many deciduous and coniferous species (Bending and Read, 1997) which leads to the inhibition of over-story species regeneration (Nilsen et al., 2001).

The areal extent of *R. maximum* has increased in some areas of southern and central Appalachia (Phillips and Murdy, 1985; Rollins et al., 2010; Brantley et al., 2013; Elliott et al., 2014). Shrub cover in the region is expected to continue to increase given fire suppression, lack of grazing, and forest canopy die-off from infestations (Nowacki and Abrams, 2008; Ford et al., 2011). If precipitation increases in this area in accordance with climate projections, the accompanying increase in soil moisture availability may further the expansion of *R. maxiumum*. The loss of previously dominant foundational species in these systems (e.g. *Picea rubens* in West Virginia due to logging and fire in the late 1800s and early 1900s; *Tsuga canadensis* die-off from hemlock woolly adelgid across the Appalachians and eastern US) may result in possible, multiple stable-states (Ellison et al., 2005).

Increase in shrub cover has the potential to further impact ecosystem fluxes and biogeochemical cycling and may contribute strongly to future forest community dynamics. However, conversely, if the variance of inter-annual precipitation continues to increase, drought years may serve as a possible control on shrub expansion.

4.5 Implications of dynamic precipitation

Data from the National Climate Data Center's (NCDC) station in Canaan Valley, WV (Station ID 461393) show that precipitation in this region of WV is increasing, notably so since 1993 (Fig. 6B). This increase in precipitation appears to be driven by a notable increase in the number of extreme precipitation days (EPDs), defined here as days where precipitation exceeds 25.4 mm (Fig. 6C). While precipitation is generally increasing in the Weimer Run watershed, and similar areas across West Virginia, the year-to-year variance is increasing as well. A Breusch-Pagan test, which tests for the presence of heteroscedasticity in linear regression models, shows that NCDC precipitation data from Canaan Valley since 1970 exhibit a statistically significant increase in inter-annual variance (BP = 8.58; $p = 0.003$). Meaning, the low precipitation years are trending much lower than the mean, while the high precipitation years are trending much higher than the mean, with fewer overall "average" precipitation years. This increased variance appears to again be driven by the increased variance in EPDs from year-to-year (Fig. 6B and 6C) and has been attributed to changes in the North Atlantic Subtropical High and anthropogenic climate change (Li et al., 2011). As soils are subject to year-to-year wet/dry cycles, cumulative effects on carbon cycling and carbon fluxes are likely. It is beyond the scope of this study to answer the question posed above; however, with the observed dynamics in precipitation for the region, this may be an important line of future research. These relative extremes in rainfall amounts that occurred during this study resulted in significant differences in soil moisture regimes (measured as WFPS) across the entire watershed and among both our elevation and vegetation cover classes (Section 3.2; Tables 1 and 2). During 2011, there were 34 EPDs, whereas in 2010 there were only 11 and in 2012 only 9. Precipitation also affected the variance of WFPS within the watersheds by year, as measured by the coefficient of variation (CV) with 2011 showing decreased variance of WFPS (CV = 27.85) compared to either 2010 (CV = 41.11) or 2012 (CV = 29.48). Increased precipitation and increased numbers of EPDs changes the soil moisture regime within the watershed that in turn affects CO_2 fluxes.

4.6 Theoretical contributions

Our findings indicate that for this relatively humid watershed, increased precipitation may result in decreased soil water heterogeneity and decreased fluxes of carbon from the soil surface, while decreased precipitation may result in increased soil water heterogeneity and increased carbon fluxes—especially from areas of higher elevation and/or with greater shrub coverage. This study adds to a growing body of literature that deals theoretically with the effects of topography and vegetation on water and carbon cycling, and more specifically on carbon cycling across watersheds with varying degrees of moisture availability.

Similar studies in drier watersheds have found that increases in soil water availability largely result in increases in soil carbon fluxes. Pacific et al. (2008) showed that for the Stringer Creek watershed, a sub-alpine, montane watershed in Montana, the spatial variability of soil CO_2 efflux was controlled by the input of soil water driven by seasonal snowmelt. Fluxes at riparian areas lower in the watershed were suppressed at high levels of soil water early in the growing season, but as soil water decreased, fluxes increased. Pacific et al. (2009) further compared a wet and a dry year in the same watershed, finding that cumulative fluxes were 33% higher in riparian areas during the dry year, but 8% lower at landscape positions higher in the watershed. Decreased moisture inputs for Stringer Creek resulted in significant responses in fluxes across landscape positions, but the riparian areas respond similarly to the entirety of the Weimer Run watershed in our study, with dry years resulting in increases in carbon fluxes. It has been shown in previous studies (Clark and Gilmour, 1983; Davidson et al., 2000; Sjogersten et al., 2006; Pacific et al., 2008) that a production optimality of surface CO_2 efflux exists in response to soil water content such that peak rates of surface CO_2 efflux coincide with medial values of soil water content, with soil water varying both temporally and spatially (with eleveation). Our study adds the dimension of vegetation to this model, demonstrating that vegetation heterogeneity can have significant effects on surface CO_2 efflux within humid watersheds, particularly during periods of below-average soil water availability.

There are other possible avenues of carbon loss not considered here that may be affected by inter-annual climatic variability. It is possible that dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) fluxes from the watershed are increased during wet years due to increased flow in the system. Fluxes from these pools may be significant, but are difficult to measure and often carry a high-degree of uncertainty. DIC and DOC fluxes are highly variable spatially, coinciding with preferential flow paths within watersheds as a function of run-off (McGlynn and McDonnell, 2003; Kindler et al., 2011). Manipulative experiments have shown that simulated drought decreases DOC leaching across an elevation gradient by as much as 80 – 100% (Hagedorn and Joos, 2014), indicating that these fluxes are also responsive to inter-annual climate variability.

5 Conclusions

We completed a three-year plot-based study focusing on evaluating the effects of vegetation cover and elevation on soil carbon cycling in response to inter-annual variability in precipitation. By looking at data above 11° C for soil temperature measured at 12 cm depth, we were able to focus on the effects of soil moisture on carbon cycling without having to control for temperature limitation. We found that during a relatively dry year (2010; 1042mm) the magnitude of soil carbon flux was enhanced across the watershed, but the increase was differential due to statistically greater fluxes from plots with high shrub coverage. Greater fluxes of carbon from plots with high shrub cover were due in part to decreased soil bulk density, high quantities of soil organic matter, and possible increased root respiration present beneath shrubs as compared to either closed-canopy or open-area plots. For 2011 and 2012, relatively wetter years, fluxes were decreased, and the effects of vegetation cover on the magnitude and variability of fluxes were statistically insignificant. Elevation had an effect on carbon cycling in the system by exacerbating vegetation effects during dry periods through increased effects on soil water distribution in the system. While soil water was correlated with elevation for all of our data, the effect was more pronounced during our driest year (2010) where areas higher in the watershed were much drier than lower positions. With the expected increase in precipitation as forecast by climate models and the empirical basis of increased inter-annual variance in precipitation, these findings offer important insights on the relations among landscape, vegetation, soil, and the associated biogeochemical effects for complex, humid watersheds. Given the increased likelihood of greater inter-annual variance in precipitation in the future, the coupling between carbon movement and vegetation cover is potentially quite crucial and under-considered. Further, the role of ericaceous shrubs and their future in this system are quite complex and may have profound influence on biogeochemical cycles.

Data

All data and scripts used for this paper are available on Figshare and GitHub:

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https://github.com/atkinsjeff/atkins_et_al_2014_vegetation_heterogeneity.git

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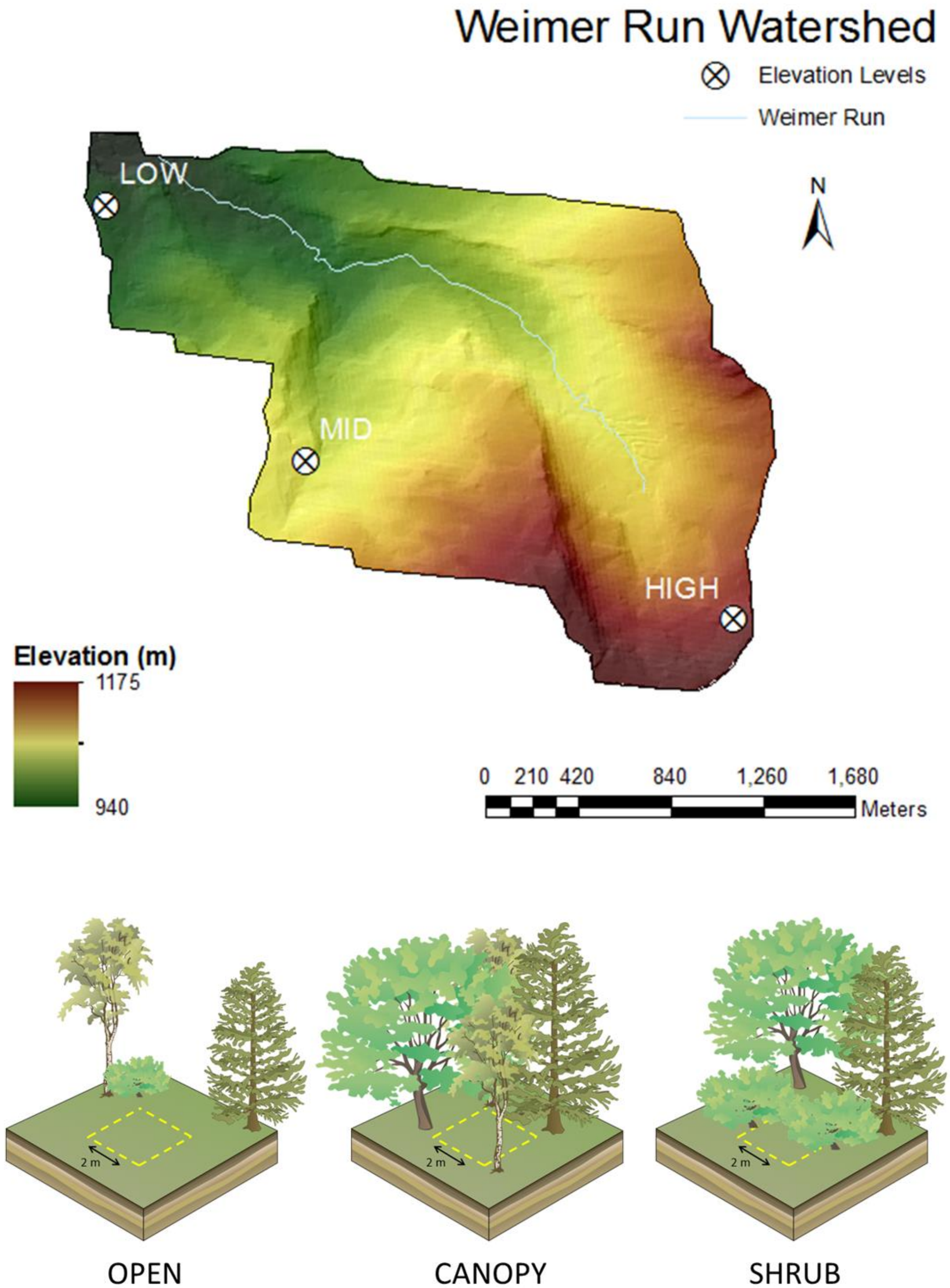

Figure 1. (Above) Weimer Run watershed (374 ha) with elevation levels indicated on map. (Below) Conceptual diagram showing vegetation classes. Images courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

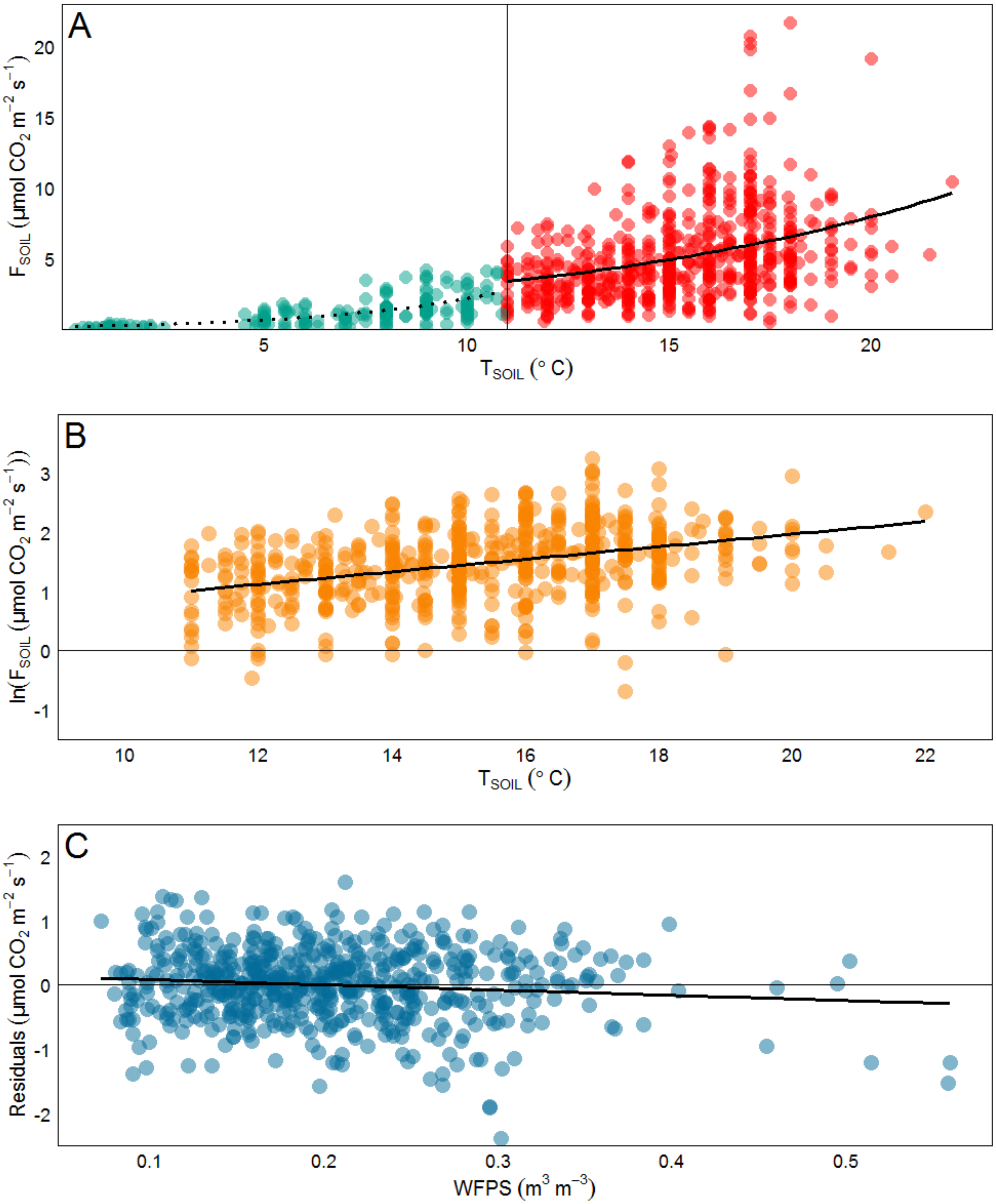

Figure 2. (A) Soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) against soil temperature (°C) at 12 cm with data split at 11° C. For all data, exponential regression shows an $R^2 = 0.3163$. For flux rate values below 11° C, $R^2 = 0.434$, for flux rate values above 11° C, $R^2 = 0.104$. (B) Natural log of soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) against soil temperature (°C) at 12 cm for all data above 11° C.

For flux rate values below 11° C, linear regression gives an $R^2 = 0.1188$, p=<<0.0001. (C) Residuals of the natural log of soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}) against water-filled pore space (0 – 12 cm) for all data above 11° C. $R^2 = 0.0208$, p = <<0.0001.

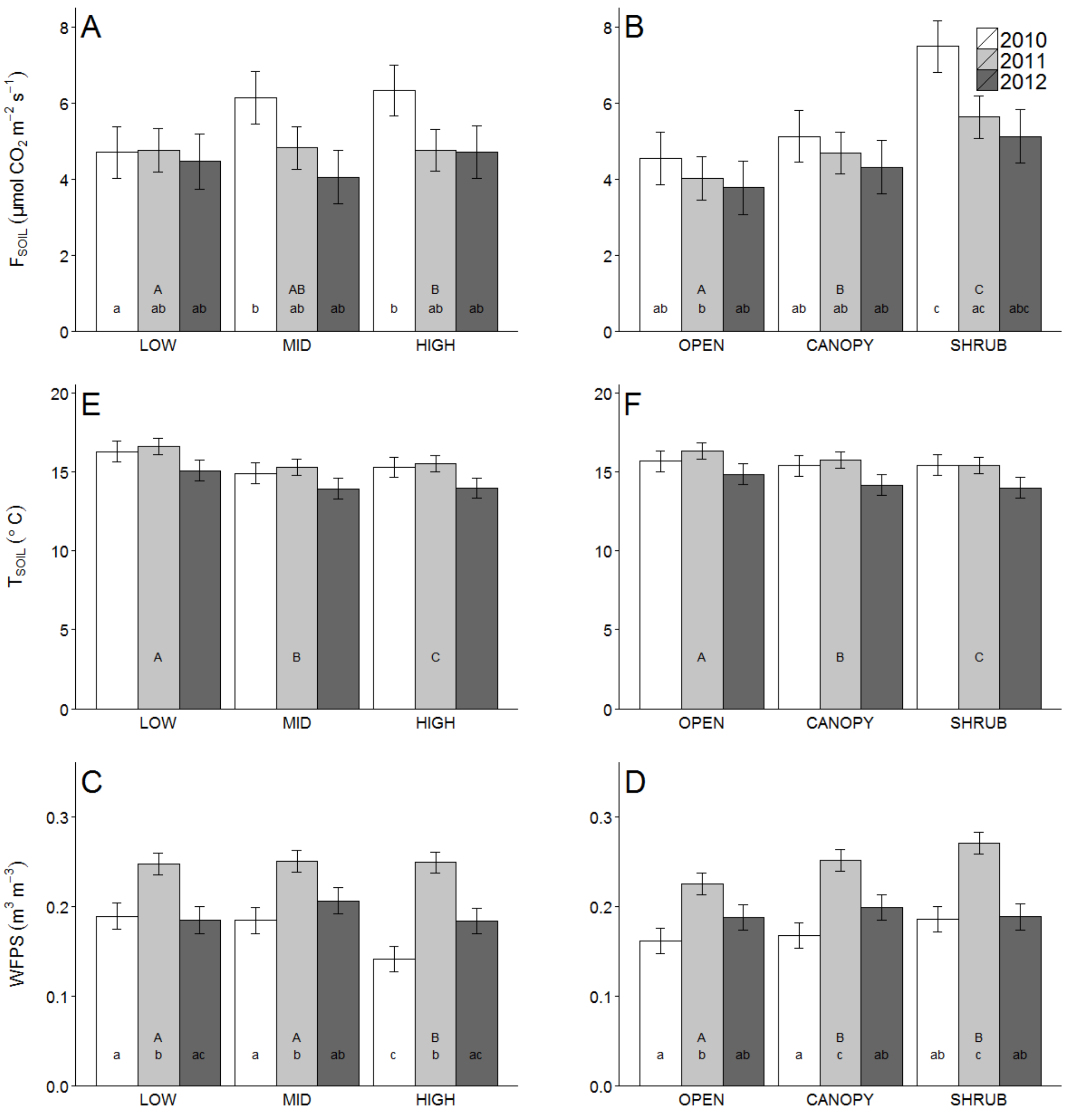

Figure 3. (A, C, E) Least-squares means of soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}); WFPS (m^3 m^{-3}); and soil temperature at 12 cm (C°) by elevation. (B, D, E) Least-squares means of soil CO_2 efflux (μmol CO_2 m^{-2} s^{-1}); WFPS (m^3m^{-3}); and soil temperature at 12 cm (C°) by vegetation. Capital letters indicate difference between elevation classes and lower case letters indicate differences between treatment * year interactions. Bars indicate standard error. Colors indicate sampling year.

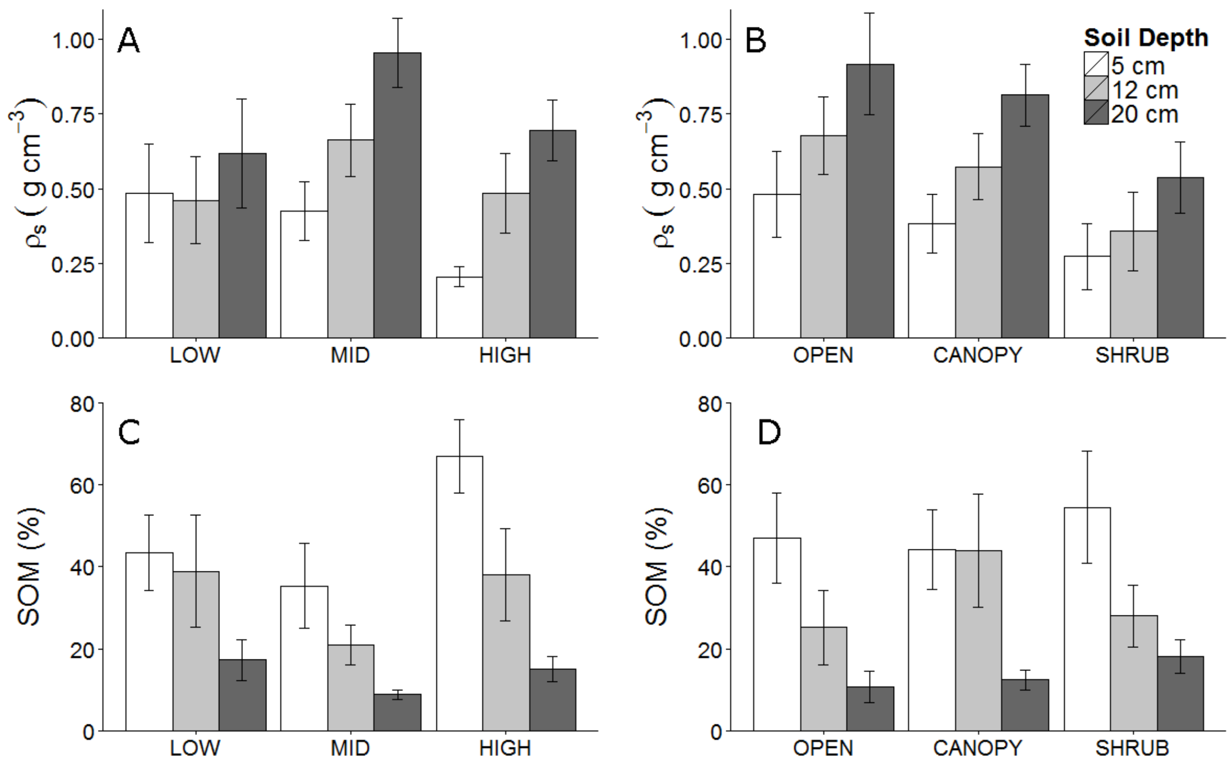

Figure 4. (A, C) Means of soil bulk density (g cm^{-3}) and soil organic matter (%) by elevation treatment. (B, D) Means of soil bulk density (g cm^{-3}) and soil organic matter (%) by vegetation treatment. Bars indicate standard error. Colors indicate soil depth profiles.

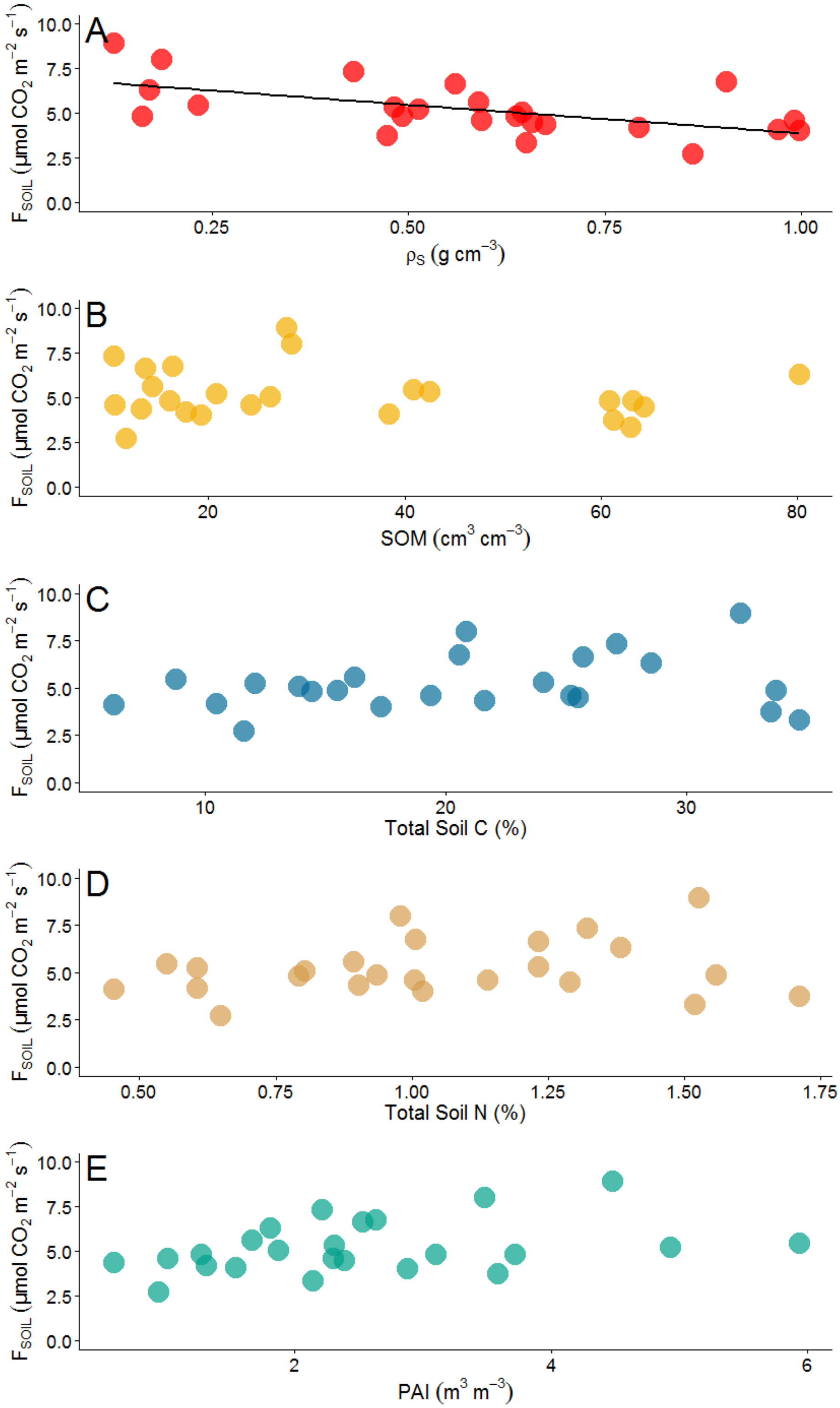

Figure 5. (A) Soil bulk density (g cm^{-3}), (B) soil organic matter (%), (C) total soil carbon (%), (D) total soil nitrogen (%), and (E) plant area index (m^{-3} m^{3}) against mean plot-level soil CO_2 efflux by plot for all measurements across all three years where soil temperature (°C) was above 11 °C.

Only soil bulk density (A) shows a significant relationship ($R^2 = 0.302$; $p = 0.003$) with mean plot-level soil CO_2 efflux.

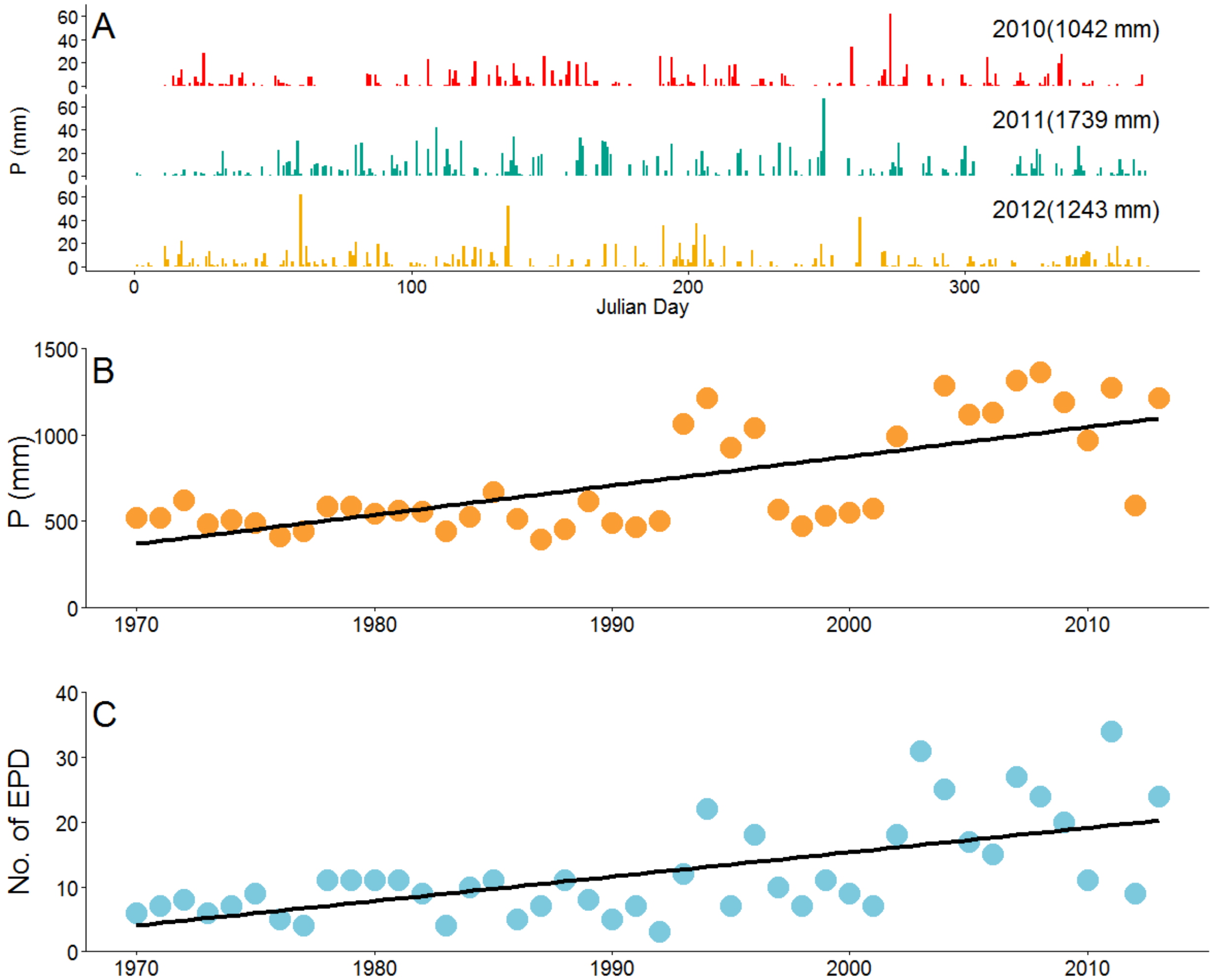

Figure 6. (A) Hyetographs for 2010, 2011, and 2012 from the Bearden Knob weather station located within the Weimer Run watershed (BDKW2 MesoWest; University of Utah). Precipitation totals by year are indicated within each graph and are in mm yr^{-1}. (B) Precipitation for the years 1970 – 2013 (mm yr^{-1}) from NCDC station Canaan Valley, WV (461393). Linear regression shows that mean annual precipitation is increasing by 17.88 mm yr^{-1} ($r = 0.697$; $F_{1,42} = 39.74$; $r^2 = 0.474$; $p = <.0001$). The year to year variance in precipitation is also increasing (BP = 8.58; $p = 0.003$). (C) Number of extreme precipitation days (EPD) per year (defined as days where total precipitation exceeded 25.4 mm per day). The number of EPDs are increasing by 0.38

days per year (r = 0.637; $F_{1,42}$ = 28.69; r^2 = 0.392; p = <.0001). The variance is also increasing (BP = 11.12; p = <.0001).

Table 1. Least-squares means of dynamic environmental variables. Error terms indicate standard error.

YEAR	TREATMENT	F_{SOIL} (μmol CO_2 m^{-2} s^{-1})	WFPS (m^3 m^{-3})	SOIL TEMPERATURE (°C)
2010	LOW	4.69 ±0.687	0.189 ±0.014	16.29 ±0.656
2010	MID	6.13 ±0.691	0.184 ±0.014	14.90 ±0.656
2010	HIGH	6.32 ±0.668	0.141 ±0.014	15.30 ±0.654
2011	LOW	4.75 ±0.571	0.247 ±0.012	16.61 ±0.520
2011	MID	4.82 ±0.561	0.250 ±0.012	15.31 ±0.519
2011	HIGH	4.76 ±0.551	0.249 ±0.012	15.54 ±0.518
2012	LOW	4.45 ±0.722	0.184 ±0.014	15.08 ±0.659
2012	MID	4.04 ±0.702	0.206 ±0.014	13.93 ±0.658
2012	HIGH	4.71 ±0.681	0.183 ±0.014	13.98 ±0.656
2010	OPEN	4.54 ±0.685	0.164 ±0.014	15.67 ±0.656
2010	SHRUB	7.48 ±0.674	0.187 ±0.014	15.42 ±0.655
2010	CANOPY	5.11 ±0.674	0.167 ±0.014	15.39 ±0.655
2011	OPEN	4.02 ±0.562	0.225 ±0.012	16.31 ±0.519
2011	SHRUB	5.63 ±0.559	0.270 ±0.012	15.38 ±0.518
2011	CANOPY	4.68 ±0.557	0.251 ±0.012	15.76 ±0.518
2012	OPEN	3.77 ±0.698	0.188 ±0.014	14.86 ±0.656
2012	SHRUB	5.12 ±0.705	0.188 ±0.014	13.98 ±0.658
2012	CANOPY	4.31 ±0.697	0.198 ±0.014	14.15 ±0.657
	LOW	4.61 ±0.431	0.207 ±0.010	15.99 ±0.356
	MID	4.99 ±0.427	0.214 ±0.009	14.71 ±0.356
	HIGH	5.25 ±0.418	0.191 ±0.009	14.94 ±0.355
	OPEN	4.09 ±0.425	0.191 ±0.009	15.61 ±0.355
	SHRUB	6.07 ±0.424	0.214 ±0.009	14.93 ±0.355
	CANOPY	4.69 ±0.423	0.206 ±0.009	15.10 ±0.355
2010		5.71 ±0.634	0.172 ±0.013	15.50 ±0.652
2011		4.78 ±0.525	0.248 ±0.011	15.82 ±0.516
2012		4.36 ±0.647	0.192 ±0.013	14.36 ±0.653

Table 2. Statistical table from repeated measures mixed-model ANOVA. For all comparisons by ELEVATION, VEGETATION and YEAR, *n* = 633; *df* = 2, 633. For ELEVATION BY YEAR and VEGETATION BY YEAR comparisons, *n* = 633; *df* = 4, 633.

ELEVATION	F	*p*
F_{soil}	3.44	0.0326
WFPS (0 - 12 cm)	11.13	<.0001
Soil Temp (12 cm)	170.76	<.0001
VEGETATION		
F_{soil}	37.58	<.0001
WFPS (0 - 12 cm)	11.20	<.0001
Soil Temp (12 cm)	52.79	<.0001
ELEVATION BY VEGETATION		
F_{soil}	2.47	0.0436
WFPS (0 - 12 cm)	24.48	<.0001
Soil Temp (12 cm)	9.55	<.0001
YEAR		
F_{soil}	1.40	0.2464
WFPS (0 - 12 cm)	17.27	<.0001
Soil Temp (12 cm)	1.66	0.1918
ELEVATION BY YEAR		
F_{soil}	3.17	0.0134
WFPS (0 - 12 cm)	6.05	<.0001
Soil Temp (12 cm)	1.02	0.3945
VEGETATION BY YEAR		
F_{soil}	2.96	0.0192
WFPS (0 - 12 cm)	4.08	0.0034
Soil Temp (12 cm)	5.46	0.0003

Appendix A. Least-squares means of vegetation variables and soil chemical and physical properties. Error terms indicate standard error.

ELEVATION	VEGETATION	PAI (m^3 m^{-3})	MI (lux)	SOIL pH
LOW	OPEN	1.06 ±0.42	46856.33 ±2697.8	3.99 ±0.14
LOW	SHRUB	2.01 ±0.42	72819.75 ±3672.5	4.26 ±0.14
LOW	CANOPY	1.82 ±0.42	29966.01 ±1589.6	3.99 ±0.14
MID	OPEN	1.49 ±0.42	42500.11 ±3796.2	4.32 ±0.14
MID	SHRUB	3.68 ±0.42	19923.95 ±1194.9	4.11 ±0.14
MID	CANOPY	1.54 ±0.42	25855.61 ±1465.3	4.13 ±0.14
HIGH	OPEN	2.70 ±0.42	26230.93 ±1556.2	4.11 ±0.14
HIGH	SHRUB	4.71 ±0.42	12060.48 ±931.0	3.87 ±0.14
HIGH	CANOPY	3.05 ±0.51	20273.25 ±1174.5	4.17 ±0.14
LOW		1.63 ±0.24	49879.7 ±1932.9	4.08 ±0.08
MID		2.23 ±0.24	29138.82 ±1486.5	4.18 ±0.08
HIGH		3.49 ±0.26	19521.56 ±801.0	4.05 ±0.08
	OPEN	1.75 ±0.24	47346.97 ±2179.5	4.14 ±0.08
	SHRUB	3.46 ±0.24	26375.92 ±1389.7	4.08 ±0.08
	CANOPY	2.14 ±0.26	25361.26 ±852.7	4.10 ±0.08

Appendix B. Mixed-model ANOVA results for the main and interactive effects of elevation, vegetation, and soil depth on soil bulk density (ρ_s) and total bulk density (ρ_t).

		SOIL BULK DENSITY (ρ_s)		TOTAL BULK DENSITY (ρ_t)	
TREATMENT	DEPTH (cm)	*F*	*p*-value	*F*	*p*-value
Elevation		5.77	0.0053	4.79	0.0120
Vegetation		10.55	0.0001	9.93	0.0002
Soil Depth		15.70	<.0001	17.80	<.0001
Elevation*Vegetation		0.40	0.8089	0.29	0.8851
Elevation*Depth		1.70	0.1619	1.57	0.1951
Vegetation*Depth		0.31	0.8719	0.18	0.9501
Elevation	5	4.11	0.0436	4.67	0.0316
Vegetation	5	2.72	0.1059	3.10	0.0822
Elevation*Vegetation	5	1.28	0.3300	1.27	0.3342
Elevation	12	1.63	0.2228	1.17	0.3333
Vegetation	12	3.60	0.0483	3.47	0.0533
Elevation*Vegetation	12	0.73	0.5856	0.66	0.6286
Elevation	20	4.15	0.0330	3.35	0.0582
Vegetation	20	5.15	0.0170	4.19	0.0321
Elevation*Vegetation	20	0.30	0.8733	0.16	0.9551

Appendix C. Kruskal-Wallis rank sum test results for the effects of elevation, vegetation, and soil depth on soil organic matter (SOM %).

		SOM (%)		SOIL C (%)		SOIL N (%)		SOIL C:N	
TREATMENT	DEPTH (cm)	χ^2	*p* -value	χ^2	*p* -value	χ^2	*p* -value	χ^2	*p* -value
Elevation		1.82	0.401	4.59	0.101	5.08	0.078	1.4	0.496
Vegetation		8.21	0.016	10.64	0.004	6.83	0.032	30.08	<.0001
Depth		36.18	<.0001	98.61	<.0001	111.28	<.0001	13.52	0.004
Elevation	5	0.39	0.822	10.63	0.004	11.05	0.004	6.47	0.039
Vegetation	5	8.99	0.011	5.60	0.061	4.19	0.123	12.09	0.002
Elevation	12	2.03	0.361	4.72	0.094	6.35	0.042	0.47	0.812
Vegetation	12	2.55	0.278	3.05	0.216	2.72	0.257	4.21	0.122
Elevation	20	5.72	0.057	9.29	0.009	11.68	0.002	0.64	0.724
Vegetation	20	6.14	0.046	15.28	<.0001	11.30	0.004	23.66	<.0001

Appendix D. Total soil carbon (%), total soil nitrogen (%), total soil C:N ratio and soil organic matter (SOM) (%) by all combinations of elevation, vegetation, depth levels and classes.

ELEV	VEG	DEPTH	SOIL C (%)	SOIL N (%)	SOIL C:N	SOM (%)
LOW	OPEN	5	14.11 ±1.14	0.87 ±0.069	16.12 ±0.33	42.06 ±7.88
LOW	OPEN	12	13.89 ±2.47	0.67 ±0.065	18.69 ±1.84	25.79 ±8.92
LOW	OPEN	20	7.43 ±0.87	0.42 ±0.042	15.42 ±0.45	15.26 ±4.71
LOW	SHRUB	5	29.62 ±1.37	1.53 ±0.063	19.02 ±0.22	53.44 ±8.21
LOW	SHRUB	12	26.13 ±1.20	1.23 ±0.060	21.42 ±0.78	18.20 ±2.38
LOW	SHRUB	20	10.92 ±0.55	0.54 ±0.027	20.19 ±0.18	22.46 ±3.31
LOW	CANOPY	5	19.41 ±1.07	0.96 ±0.041	20.19 ±0.51	34.83 ±2.46
LOW	CANOPY	12	20.47 ±2.39	1.05 ±0.112	18.64 ±0.30	68.45 ±3.42
LOW	CANOPY	20	5.96 ±0.49	0.36 ±0.023	14.85 ±0.42	14.32 ±2.90
MID	OPEN	5	11.11 ±0.85	0.66 ±0.044	15.57 ±0.35	33.13 ±6.91
MID	OPEN	12	14.47 ±0.63	0.81 ±0.034	17.89 ±0.30	17.41 ±2.61
MID	OPEN	20	3.71 ±0.06	0.23 ±0.002	15.99 ±0.12	7.06 ±0.44
MID	SHRUB	5	15.62 ±1.51	0.75 ±0.060	19.97 ±0.42	29.17 ±7.44
MID	SHRUB	12	18.79 ±1.06	0.90 ±0.041	20.00 ±0.40	21.86 ±2.03
MID	SHRUB	20	4.42 ±0.13	0.25 ±0.005	17.37 ±0.20	10.26 ±0.94
MID	CANOPY	5	17.32 ±2.60	0.92 ±0.125	17.90 ±0.50	43.67 ±9.03
MID	CANOPY	12	19.47 ±1.05	1.02 ±0.041	18.51 ±0.43	23.57 ±5.61
MID	CANOPY	20	6.59 ±0.35	0.37 ±0.019	17.81 ±0.16	9.43 ±0.56
HIGH	OPEN	5	27.22 ±2.86	1.30 ±0.120	19.14 ±1.21	65.76 ±4.91
HIGH	OPEN	12	23.51 ±2.44	1.18 ±0.093	18.75 ±0.79	32.76 ±8.74
HIGH	OPEN	20	4.63 ±0.26	0.28 ±0.006	15.80 ±0.54	9.95 ±1.01
HIGH	SHRUB	5	48.12 ±1.17	2.12 ±0.007	22.65 ±0.48	80.80 ±3.38
HIGH	SHRUB	12	28.13 ±3.15	1.34 ±0.117	19.88 ±0.65	44.01 ±5.95
HIGH	SHRUB	20	11.76 ±0.39	0.60 ±0.019	19.55 ±0.13	21.67 ±2.28
HIGH	CANOPY	5	24.27 ±3.25	1.22 ±0.166	20.16 ±0.45	54.29 ±7.70
HIGH	CANOPY	12	29.59 ±3.40	1.47 ±0.128	19.22 ±1.01	37.40 ±16.8
HIGH	CANOPY	20	6.52 ±0.19	0.39 ±0.009	16.42 ±0.12	13.69 ±0.38
LOW		5	21.61 ±0.55	1.15 ±0.026	18.38 ±0.14	43.44 ±9.26
LOW		12	20.21 ±0.81	0.99 ±0.035	19.45 ±0.30	38.94 ±13.5
LOW		20	8.13 ±0.22	0.44 ±0.010	16.87 ±0.15	17.35 ±5.01
MID		5	14.17 ±0.49	0.76 ±0.022	17.57 ±0.16	35.33 ±10.2
MID		12	17.70 ±0.32	0.91 ±0.013	18.84 ±0.13	20.95 ±4.88
MID		20	4.80 ±0.07	0.88 ±0.003	16.99 ±0.06	8.91 ±1.10
HIGH		5	31.46 ±1.25	1.48 ±0.053	20.36 ±0.34	66.95 ±8.95
HIGH		12	26.90 ±0.93	1.32 ±0.035	19.29 ±0.24	38.14 ±11.2
HIGH		20	7.90 ±0.15	0.44 ±0.006	17.40 ±0.11	15.10 ±3.09
	OPEN	5	16.30 ±0.58	0.89 ±0.026	16.68 ±0.20	46.98 ±10.91
	OPEN	12	16.99 ±0.54	0.89 ±0.022	18.33 ±0.24	25.26 ±9.05
	OPEN	20	5.144 ±0.16	0.31 ±0.007	15.76 ±0.11	10.76 ±3.9
	SHRUB	5	27.84 ±0.90	1.35 ±0.039	20.06 ±0.14	54.47 ±13.6
	SHRUB	12	23.02 ±0.62	1.10 ±0.024	20.28 ±0.18	28.03 ±7.57
	SHRUB	20	9.134 ±0.17	0.47 ±0.008	19.06 ±0.07	18.13 ±4.12
	CANOPY	5	20.05 ±0.74	1.02 ±0.035	19.36 ±0.17	44.27 ±9.64
	CANOPY	12	21.92 ±0.63	1.12 ±0.027	18.70 ±0.17	43.86 ±13.7
	CANOPY	20	6.353 ±0.11	0.37 ±0.005	16.30 ±0.10	12.48 ±2.42
LOW			17.01 ±0.19	0.88 ±0.009	18.10 ±0.05	33.03 ±22.0
MID			14.09 ±0.13	0.74 ±0.006	18.06 ±0.03	21.73 ±17.1
HIGH			19.52 ±0.24	0.97 ±0.010	18.55 ±0.05	40.14 ±27.2
	OPEN		13.36 ±0.15	0.73 ±0.007	16.94 ±0.05	27.76 ±22.6
	SHRUB		20.16 ±0.19	0.99 ±0.009	19.68 ±0.03	33.54 ±24.3
	CANOPY		16.33 ±0.18	0.84 ±0.008	18.03 ±0.04	33.14 ±23.9
		5	21.14 ±0.26	1.07 ±0.011	18.55 ±0.06	48.58 ±23.4
		12	20.73 ±0.20	1.04 ±0.008	19.11 ±0.06	32.21 ±21.2
		20	6.93 ±0.05	0.38 ±0.002	17.09 ±0.03	13.79 ±7.80

Appendix E. Least-squares means of soil porosity (Φ) and soil bulk density (ρ) for the 0 – 12 cm soil depth used in calculating WFPS.

ELEVATION	VEGETATION	Φ (m^3 m^{-3})	ρ (g cm^{-3})
LOW	OPEN	0.68 ±0.05	0.83 ±0.14
LOW	SHRUB	0.81 ±0.05	0.49 ±0.14
LOW	CANOPY	0.75 ±0.05	0.64 ±0.14
MID	OPEN	0.58 ±0.05	1.11 ±0.14
MID	SHRUB	0.72 ±0.05	0.72 ±0.14
MID	CANOPY	0.61 ±0.05	1.01 ±0.14
HIGH	OPEN	0.69 ±0.05	0.81 ±0.14
HIGH	SHRUB	0.79 ±0.05	0.55 ±0.14
HIGH	CANOPY	0.68 ±0.05	0.83 ±0.14
LOW		0.75 ±0.03	0.65 ±0.08
MID		0.64 ±0.03	0.95 ±0.08
HIGH		0.72 ±0.03	0.73 ±0.08
	OPEN	0.65 ±0.03	0.92 ±0.08
	SHRUB	0.77 ±0.03	0.58 ±0.08
	CANOPY	0.68 ±0.03	0.83 ±0.08