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Scale dependence in functional equivalence and difference in the soil microbiome

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ABSTRACT

Climatic history can shape the functioning of soil microbial communities and thus rates of ecosystem processes such as organic matter decomposition. For example, broad spatial scale differences in climatic history, such as contrasting precipitation regimes, have been shown to generate unique microbial functional responses to contemporary moisture conditions. Yet it is an open question as to whether local differences in soil microclimate similarly influence the functional potential of decomposer communities. Here, we use a multi-scale approach within and among two temperate forest field sites to investigate this question. Soils from fifty-four microsites, that vary in their soil moisture climate-regimes, were used as inocula for a common leaf litter (*Quercus rubra* L.) in a controlled, laboratory microcosm study. Microcosms were placed under dry, mesic and wet lab-moisture conditions and the rate of carbon (C) mineralization of the litter was measured over 202 days. Our results reveal differences in decomposition rates under controlled conditions that highlight broad-scale functional differences between the soil communities at each site. Specifically, we found that C mineralization differed by as much as two-fold for soil communities when compared between the sites. Our results also show that functional differences of soil communities are observable within one site but not the other. In the site where local-scale functional legacies were apparent, the historical soil moisture microclimate-regimes generated as much as an 89% change in C mineralization rates of the leaf litter under the same contemporary, lab-imposed moisture conditions. A similar pattern was not observable in the other site; instead, laboratory moisture conditions explained almost all variation in C mineralization. Notably, for the site with pronounced local-scale functional legacies, there was much greater within-site variation in field-soil microsite moisture than at the site which did not exhibit functional legacies, suggesting that the extent of local-scale variation in microclimate may act as control on whether local-scale functional legacies are observed. Regardless of whether this mechanism does explain our findings, our observations do confirm those from prior studies where regional-scale moisture-regime differences shape microbial function, and extend this prior work by providing evidence that pronounced local-scale differences in soil moisture microclimate-regimes are associated with microbial functional legacies.

1. Introduction

Soil heterotrophic microorganisms produce carbon dioxide as they metabolize decomposing organic material for energy and growth (Swift et al., 1979). As biological agents that mediate decomposition, their activities contribute substantially to the fluxes of carbon (C) from terrestrial ecosystems to the atmosphere (Falkowski et al., 2008; Bond-Lamberty and Thomson, 2010). Soil temperature, moisture, and litter quality are important controls on decomposition rates (Aerts, 1997; Parton et al., 2007) and are consequently represented in soil biogeochemical models. These models are used to understand and project how decomposition rates respond to changing environmental conditions, and the inclusion of microbial biomass and community traits as additional controls on organic matter decomposition reflect growing evidence that their influence on decomposition rates extends beyond those mediated directly by abiotic controls (Glassman et al., 2018;

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Maynard et al., 2018). These modeling efforts have revealed that the way in which microbes are represented can strongly influence projected changes in soil organic matter flux rates and pool sizes (Schimel and Weintraub, 2003; Wang et al., 2013; Wieder et al., 2015b; Abramoff et al., 2018; Fatichi et al., 2019).

There is now a wealth of empirical evidence that the abiotic environment shapes both the structure and function of microbial communities. In experimental manipulations and across environmental gradients, past abiotic regimes of temperature (Karhu et al., 2014; Romero-Olivares et al., 2017), moisture (Evans and Wallenstein, 2012, 2014; Hawkes et al., 2017), and litter input quality (Keiser et al., 2011) have been observed to shape contemporary microbial function (Strickland et al., 2015; Crowther et al., 2019). Additionally, the abiotic historical legacies of these regimes on microbial community function can be persistent. For example, Hawkes et al. (2020) showed that within a regional precipitation gradient, 4.5 years of manipulated rainfall did not significantly shift microbial community function. Instead, soil respiration responses to the rainfall manipulation continued to reflect the community's 'climate origin'. These findings suggest that persistent functional legacies in biotic communities may constrain local ecosystem responses to environmental change, yet it is unclear in which environments and at which scales these legacies manifest (Baveye et al., 2018; Ladau and Eloe-Fadrosh, 2019).

Climatic variables are known to vary at both macro- and microscales. For instance, soil moisture regimes often vary substantially in space both across and within sites. In forests, spatial variation in soil moisture at local scales (m to km) can be equal in magnitude, or even exceed, variation in site-mean soil moisture among sites arrayed across regional climate gradients (Bradford et al., 2014, 2017; Loescher et al., 2014). Variables including topography, soil properties and plant traits interact to produce microscale heterogeneity in moisture (Vanderlinden et al., 2012), but how microclimatic variation imprints historical legacies on the functioning of microbial communities appears largely unknown. Yet within-site moisture regimes have been linked to patterns in fungal composition and function (van der Wal et al., 2015; Šťursová et al., 2016), enzyme activities (Baldrian et al., 2010; Baldrian, 2014) and litter decomposition (Bélanger et al., 2019) suggesting that microclimate, as well as macroclimate, regimes may influence how microbial community function responds to contemporary and future variation in environmental conditions.

In this study we take an experimental approach to disentangle whether the climatic regime influences decomposition rates via direct effects on microbial activities only, or additionally via indirect effects mediated by functional legacies that are embedded within the climate regime. We first look for evidence that site-level macroclimate regimes generate microbial communities that function distinctly. Second, we test competing hypotheses, the first of which is based on the idea that microclimate variation within sites does not generate functional legacies because they would be overwhelmed by rates of local dispersal of microbes and/or materials (e.g., decomposing leaves; Allison and Martiny 2008; Nemergut et al., 2013). Alternatively, high within-site heterogeneity in microclimate could allow functional legacies to manifest at local scales, generating microbial communities with distinct functional responses to contemporary moisture conditions. Our laboratory microcosm approach established and controlled three contemporary soil moisture regimes, imposed on a common leaf litter inoculated with soil microbial communities sourced from local-scale spatial gradients in soil moisture regime found within two forest sites within a regional climate gradient. We repeatedly measured carbon mineralization of the litter for 202 days.

2. Materials and methods

2.1. Microsite characteristics and sampling

We worked at two forest sites, ~650 km apart, that are part of the National Ecological Observation Network (NEON), which splits the continental United States into 20 ecoclimate domains to monitor ecosystems under environmental change across time and space (Keller et al., 2008). Both sites are temperate deciduous forests that spanned from the mid-Atlantic domain (SCBI: Smithsonian Conservation Biological Institute, Front Royal, VA) to the Northeast domain (HARV: Harvard Forest, Petersham, MA). The two sites have different climate and soil characteristics (Table 1) and differ in the degree to which soil moisture varies within each site (Fig. 1). Within each forest site we established twenty-seven microsites (1 m^2) around the perimeter of the eddy-flux tower footprint, which covers about 1.3 km^2.

Microsites were on average 46 m apart from the next nearest microsite with the closest two microsites being 18 m apart and the two microsites furthest from one another being 1389 m apart within a site. We chose microsites that varied in topographic position (e.g., ridge versus valley bottom) to capture heterogeneity in microsite conditions. Microclimate measurements were taken at three discrete time points over a 10-month period from December 2019 to September 2020. Temperature was measured at 5 cm depth for soil and 1 cm depth for the litter layer using a hand-held thermometer. Soil volumetric moisture was measured in the field using a time domain reflectometry (TDR) probe, inserted at a 45° angle to ~5 cm depth, in addition to gravimetric moisture measured in the lab. These discrete point measurements were intended to capture relative differences in soil characteristics over space, specifically for soil moisture, which has often been described as temporally stable where relative moisture differences in sampled locations persist over time (Vachaud et al., 1985; Brocca et al., 2010; Penna et al., 2013). In our study, temporal stability calculated through Spearman's rank-order correlation reveals high temporal stability in gravimetric soil moisture ($r_s > 0.73$) for the three point measurements over the year, confirming that point measurements are useful for characterizing spatial patterns in soil variables such as relative moisture regimes (Vanderlinden et al., 2012).

Leaf litter was collected at peak litter fall in November 2019 across all of the microsites. Due to its presence across both sites, northern red oak (*Quercus rubra* L.) litter was pooled to create a common litter substrate and air dried. The *Q. rubra* leaves were ground to 2 mm using a Wiley mill, further mixed to homogenize the sample, and then autoclaved twice at 121 °C at 15 psi for 20 min, following the approach of

Table 1
Site characteristics. Soil data are from the microsites within each site. Values represent the mean of the microsites and standard deviation is displayed in parentheses for %C, %N, C:N, Soil Moisture, Soil pH, and Microbial Biomass.

	Unit	Harvard Forest, MA (HARV)	Smithsonian Conservation Biological Institute, VA (SCBI)
Coordinates		(42.54, −72.17)	(38.89, −78.14)
Elevation	m a.s.l.	351	361
Mean Annual Temperature	°C	8	13
Mean Annual Precipitation	mm	976	1054
Soil C	%	23.9 (11.9)	8.0 (3.2)
Soil N	%	0.9 (0.4)	0.6 (0.4)
C:N	unitless	26.8 (3.1)	14.4 (1.8)
Soil Moisture	%	57.4 (15.0)	37.6 (7.2)
Soil pH	unitless	4.2 (0.3)	6.8 (0.5)
Microbial Biomass	μg CO_2-C hr^{-1} g^{-1} dry soil	9.0 (4.2)	8.7 (6.4)
Dominant Tree Species		Red oak (*Quercus rubra*), White pine (*Pinus strobus* L.), Red maple (*Acer rubrum* L.)	Red oak (*Quercus rubra*), Tulip poplar (*Liriodendron tulipifera* L.), Pignut hickory (*Carya glabra* Miller)
Soil Order		Spodosol, Inceptisol, Entisol	Alfisol
n		27	27

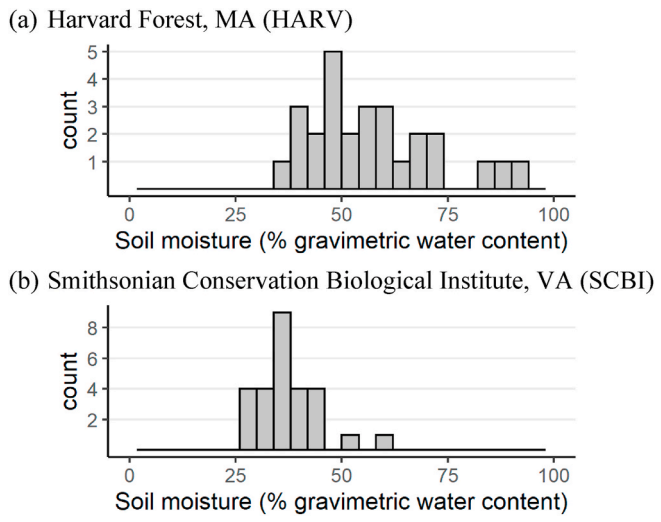

Fig. 1. Soil moisture variation in sampling points from HARV (a) and SCBI (b) from Spring 2020. Values represent point measurements representative of the spatial range in moisture regimes. Histogram represents the number of microsites, binned at 2.5% intervals with n = 27 per site.

Strickland et al. (2009a, b; Keiser et al., 2011) to sterilize the litter. The top 5 cm of soil was sampled with a 2-cm dia. corer at each microsite in December 2019 for HARV and January 2020 for SCBI. Five to ten cores were taken per microsite, passed through a 4-mm sieve, then homogenized and stored at 4 °C until their use as the microbial community inoculum (see next section).

Soils were similarly sampled at each microclimate measurement point. Specifically, gravimetric soil moisture (GWC) was measured by drying soils for 24 h at 105 °C and is reported as the percent water contained in field fresh soil. Water holding capacity (WHC) was measured for the soils and sterilized litter by allowing saturated samples to drain for 2 h in Whatman #1 filter paper and then to dry for 24 h at 105 °C. Soil pH was measured by placing soil in deionized water (1:1 volumetric ratio), followed by measurement of the supernatant with a benchtop pH meter after 10 min. Microbial biomass was assayed using a modified substrate induced respiration (SIR) method (Fierer et al., 2003; Strickland et al., 2010) whereby 5 mL of soil was incubated at 20 °C with autolyzed yeast. After 1 h of gentle shaking, headspaces were flushed with CO_2-free air, and then accumulated headspace CO_2 was measured after 4 h with an infrared gas analyzer (IRGA; Model LI-7000, Li-Cor Biosciences, Lincoln, Nebraska, USA). SIR biomass is reported as maximum CO_2 production normalized by dry weight equivalent of soil. Volume, as opposed to mass, was used to determine the amount of soil for the SIR incubations because of marked differences in soil organic matter contents (which causes similar masses to have very different volumes). Total soil carbon and nitrogen were measured on air-dried soils by grinding, packing in tins and combusting them on an NA1500 CHN Analyzer (Carlo Erba Strumentazione, Milan, Italy).

2.2. Microcosm set-up

Our microcosm design followed published approaches (Strickland et al., 2009a, b; Keiser et al., 2011; Cleveland et al., 2014) that introduce a small amount of soil, to serve as a microbial inoculum, to a litter environment which serves as the dominant organic substrate across the incubation. The approach then standardizes the substrate (i.e., the litter) and varies the microbial community inoculum, to tease out whether communities function similarly or differently once placed in a standard environment. Specifically, we used 50-mL centrifuge tubes with 0.25 g of dry weight equivalent soil from each microsite, which was thoroughly mixed with 1-g dry-weight equivalent and ground *Q. rubra* litter. Soil-only controls were constructed that contained ~6 g dry-weight equivalent soil, which were used to correct C mineralization fluxes from the leaf litter by subtracting the C mineralized throughout the experiment from the soil. The estimated respiration from the soil in the soil-litter microcosms was, at most, 10.6% and the mean was 2.3 ± 1.6% (SD) of the cumulative CO_2 respired per microcosm.

Three treatments were applied to the soil only and soil + litter microcosms to create constant moisture regimes ('Lab Moisture') that spanned from drier (35% WHC) to mesic (60% WHC) to wet (100% WHC) conditions. WHC for the litter + soil mixtures was obtained by measuring WHC for the ground litter and soils as described above and calculating target moisture content based on the dry mass equivalents for the litter and soil. In total, 162 unique soil-litter mixtures were created (2 sites × 27 composite soils from each microsite × 3 lab moisture treatments) and were maintained at target moisture by mass adjustments with weekly DI-water additions. The additional 162 soil-only microcosms were also incubated under the same three lab moisture regimes. All microcosms were kept at 20 °C over the course of the experiment. Carbon mineralization was measured over 202 days by measuring CO_2 production in each microcosm over 24 h at 17 time points (day 1, 6, 9, 13, 20, 27, 34, 43, 50, 64, 78, 92, 105, 120, 141, 168, 202) with the frequency of measurement decreasing over the course of the experiment. At each time point, a cap with a rubber septum and O-ring was fitted to the top of the 50-mL tube and the headspace flushed with CO_2-free air. After 24 h of incubation, a 5-mL sample of gas was taken and used to flush a 1-mL sample loop that was then transferred for measurement on an IRGA.

To assess variability of C mineralization of the same litter-soil mix under different conditions, we captured the distribution of responses from a subset of the unique litter-soil mixes through high replication. This approach can be useful for representing error in measurements and for propagating parameter uncertainties into modeling frameworks (LeBauer et al., 2013). Here, one microsite was selected from dry and wet field moisture conditions at each site and replicated 7 times under each treatment (4 soils × 7 replicates × 3 lab moisture treatments = 84 microcosms). Together with the experimental units (164) and soil controls (164), we maintained 408 microcosms across the 202-day experiment.

2.3. Data and inferential analysis

Cumulative C mineralization rates were calculated using the area under the curve ('AUC') function in the DescTools package (Signorell, 2021) in the statistical freeware R (R Core Team, 2020). To estimate CO_2 evolved from *Q. rubra* litter, cumulative C mineralization from litter-soil microcosms were subtracted from soil-only controls for the corresponding microsite soil sample. Differences in cumulative C mineralization between the two sites and lab moisture treatment were analyzed using ANOVA and comparisons were assessed using Tukey's honest significance test.

To directly test the competing hypotheses that decomposer community response to contemporary moisture conditions are or are not modified by historical soil moisture microclimate, we used regression to model experimental moisture treatment with known controls on litter decomposition – via microbial functional legacies – such as field soil moisture, temperature, and soil pH (Table 2). This causal statistical inferential approach follows Holland (1986), where the focus is on identifying the conditional effect size of a causal variable relative to other known causes (see Bradford et al., 2021). Cumulative respiration response was natural-log transformed to meet assumptions of normality, but results were qualitatively the same with non-transformed data. We first ran a linear model including only gravimetric soil moisture ('Field Soil Moisture'), treatment ('Lab Moisture'), and their interaction (Reduced Model, Table S1). A second-order term for Lab Moisture was included because of the expectation that microbial communities will have a unimodal response, where mesic (60% WHC) conditions will have the highest mineralization rates (Howard and Howard, 1993). We

Table 2
Model results from a linear regression model of cumulative mineralization rates including laboratory treatments and microsite soil conditions from within HARV and SCBI sites. Lab moisture was treated as a continuous variable to allow comparison with field soil moisture. A second-order lab moisture term was included to capture the unimodal response where mesic moisture conditions resulted in higher respiration rates. Standardized coefficients with their standard error in parentheses are shown and were calculated by subtracting the mean and dividing by 2 × standard deviation (SD) when there were categorical predictors, and one SD when only continuous predictors were assessed. Unstandardized model results are presented in supplemental information (Table S2).

	Both Sites (Full Model)	HARV (Full Model)	SCBI (Full Model)
Predictors	Standardized Estimates	Standardized Estimates	Standardized Estimates
(Intercept)	**3.91** (0.05)***	**4.08** (0.03)***	**4.22** (0.05)***
Site [HARV = 0]	**0.48** (0.09)***	na	na
Lab Moisture	**−0.31** (0.04)***	0.01 (0.02)	**−0.30** (0.03)**
Lab Moisture^2	0.03 (0.11)	**−0.07** (0.03)**	**0.09** (0.04)**
Field Soil Moisture	**0.14** (0.05)**	**0.08** (0.02)***	0.03 (0.03)
Soil pH	0.04 (0.05)	0.02 (0.02)	0.01 (0.03)
Soil Temperature	−0.06 (0.09)	0.00 (0.02)	−0.02 (0.03)
Lab Moisture × Field Soil Moisture	**0.25** (0.07)***	**−0.04** (0.02)*	0.00 (0.03)
Observations	162	81	81
R^2/R^2 adjusted	52.7/50.5	36.7/31.5	62.8/59.8

*P < 0.05.
**P < 0.01.
***P < 0.001; na: not applicable.

ran 'Lab Moisture' as a continuous variable to allow comparison with 'Field Soil Moisture' at the same scale and assess relative effect sizes. Variables were standardized by subtracting the mean and dividing by one standard deviation to allow comparison of relative effects when adding variables with different units. When we included site in the models, variables were standardized by subtracting the mean and dividing by two standard deviations to assess continuous and binary predictors ('Site') on the same scale (Gelman, 2008).

Among the reduced and full models, we iteratively included and omitted interactions and non-correlated variables to explore the degree to which the effect sizes of our variables of interest ('Field Soil Moisture' and 'Lab Moisture') were influenced by model structure (Fig. S1). This sensitivity analysis approach is tailored to test the robustness of the absolute and relative causal effect sizes of the predictors of interest, in light of the fact that ecological outcomes are multi-causal and conditional, with plausible causative variables typically non-orthogonal (see Hobbs et al., 2012 and Bradford et al., 2019). The variables used in the model for both sites and for each site included soil pH, soil temperature, litter temperature, and soil bulk density. In addition to including variables that were not or only marginally correlated with field soil moisture, we examined how inferences about soil moisture regime might be influenced by related microsite conditions such as total soil organic C (TOC) concentration and microbial biomass that also can influence microbial function. Unstandardized model results and those of the sensitivity analyses are included in the supplementary material (; Table S2 Figs. S1-2). R package 'tidyverse' (Wickham et al., 2019) was used to process data and for visualization; 'jtools' (Long, 2020), 'interactions' (Long, 2019), and 'sjPlot' (Lüdecke, 2021) were used to report and visualize model analyses.

3. Results

3.1. Site comparisons

We found functional differences between soil communities from the two sites, but the strength of the difference was dependent on contemporary moisture conditions (Table 2). Specifically, cumulative C mineralization in the dry conditions was 110.3 ± 5.1 mg C g^{-1} litter (mean ± SE) for the SCBI soils, which is 97% higher than the cumulative mineralization observed for the HARV soil communities (55.7 ± 2.5 mg C g^{-1} litter; Fig. 2d). In mesic conditions, SCBI communities mineralized only 24% more litter C than the corresponding HARV communities (74.1 ± 3.5 mg C g^{-1} litter compared to 59.7 ± 2.0 mg C g^{-1} litter), whereas under the wet conditions, mean cumulative mineralization for SCBI was 4% higher than HARV (53.8 ± 1.4 mg C g^{-1} litter compared to 51.9 ± 1.3 mg C g^{-1} litter; Fig. 2f).

The differences between the sites and among the lab treatments were underlain by differences in temporal dynamics over the 202-day incubation, which translated to different cumulative mineralization rates (Fig. 2d–f). Carbon mineralization rates from leaf litter increased and peaked in all treatments across the first six to nine days of the incubations (Fig. 2). Decomposer communities from HARV across treatments exhibited a single peak respiration after six to nine days. SCBI communities exhibited a second, delayed increase in respiration that varied in magnitude and length depending on laboratory treatment: dry conditions produced a large response which began at day 43 and peaked at day 105 (Fig. 2a); mesic conditions exhibited a second, smaller peak at 27 days (Fig. 2b); and the wet conditions had a second peak at day 34 that was similar in magnitude to the first peak (Fig. 2c). These secondary peaks in C mineralization rates for the SCBI soils in the two drier lab treatments meant that the expectation that cumulative respiration rates would peak at 60% WHC – as they did for HARV soil inocula (Fig. 2d–f) – was not realized for the SCBI soil communities. Instead, the main effect of lab moisture treatment for the both-sites model was negative (Table 2). Notably, however, the standardized coefficient for the interaction between lab moisture and the field moisture conditions was approximately three-fourths the size of the lab moisture main effect (Both Sites, Table 2). This large interaction effect most likely arose because in the dry and mesic lab treatments, drier soils from SCBI resulted in higher cumulative mineralization than from wetter soils from HARV, whereas the wet treatment had similar cumulative fluxes when the two sites were compared (Fig. 2d–f). The large coefficient for Site was likely driven by these high cumulative mineralization rates for SCBI inocula in the dry and mesic lab-moisture treatments, which overall led to higher cumulative mineralization (across all lab treatments) for SCBI versus HARV inocula.

3.2. Harvard Forest, MA – HARV

Functional differences among the soil decomposer communities, associated with the field moisture conditions from where they were sourced, were similarly observed when the HARV data were considered independent of the SCBI data. Specifically, there was a main effect of field soil moisture and an interactive effect with lab moisture treatment (Table 2). The imposed lab moisture regime did not have a strong effect, but the relatively large, negative second-order Lab Moisture term reflects the observation that the highest cumulative mineralization rates were under mesic moisture conditions. The effect of field soil moisture and the interaction with lab moisture treatment drove the majority of variation in this site as indicated by the standardized coefficient terms. Notably, the 'Field Soil Moisture' terms reveal that the soil communities from across the different microsite moisture regimes at the HARV site are functionally distinct. Notably, these functional differences had a larger effect on the observed mineralization rates than the lab-imposed moisture conditions.

The interaction term appeared to be associated with the fact that soil communities sourced from drier microsites had lower cumulative mineralization rates under the drier lab moisture treatment, whereas for soil communities sourced from the wettest microsites cumulative mineralization was lowest under the wettest lab moisture treatment (Fig. 3a). These dynamics meant that the field moisture regime had a

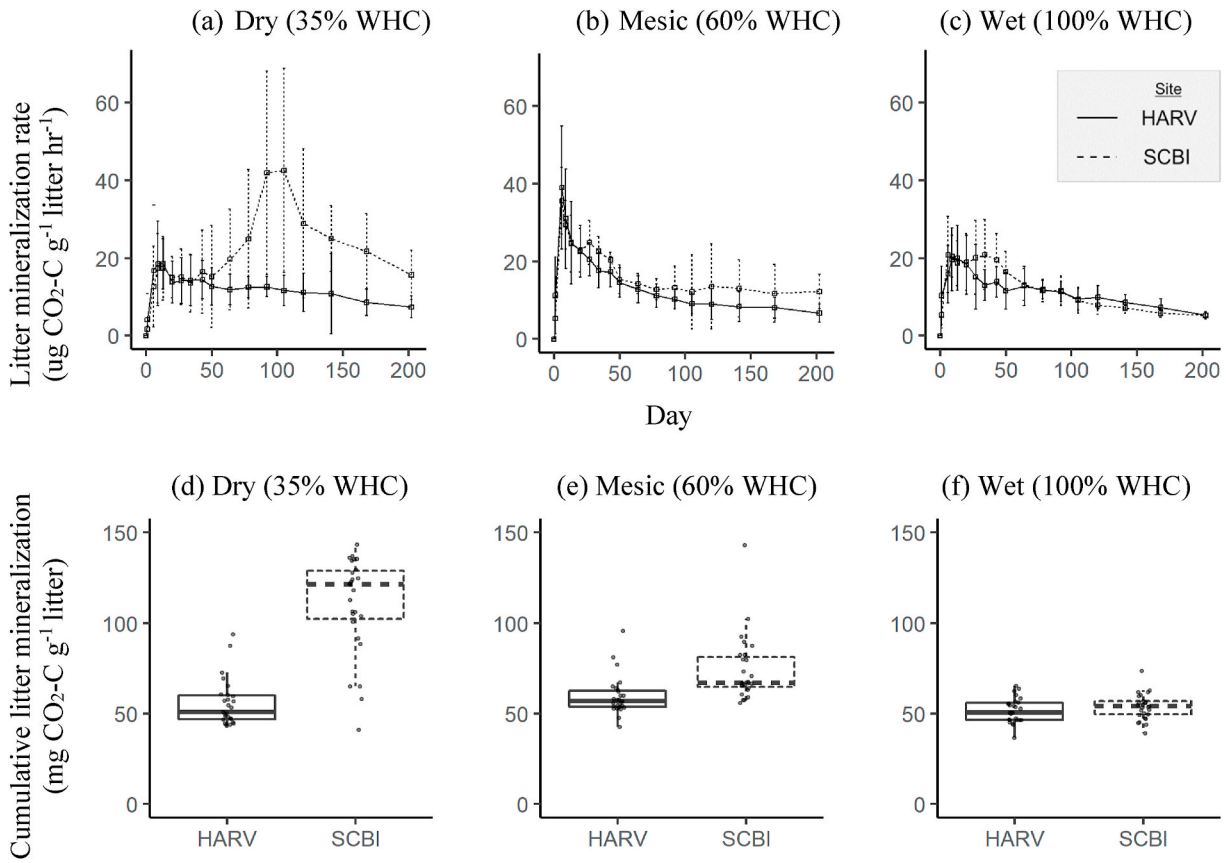

Fig. 2. Litter mineralization rates over 202 days. The upper panels (a–c) are shown here as the mean carbon mineralization rate (μg CO_2-C g^{-1} litter hr^{-1}) of each time point from litter microcosms comprised of *Quercus rubra* litter and decomposer communities from HARV (solid line) or SCBI (dashed line) sites. Laboratory treatments are presented from left to right of increasing moisture conditions. Error bars are ±SD (n = 27). Bottom panels (d–f) represent boxplots of cumulative mineralization over 202 days grouped by site. The median of each site is within the 25th and 75th percentiles (interquartile range, IQR) shown as horizontal lines with vertical lines extending to the first observation closest to but not exceeding 1.5*IQR. Each point represents an observation.

strong positive effect on cumulative respiration rates for the dry lab treatment, but a much shallower slope for the wet lab treatment (Fig. 3a). The slope for the mesic lab treatment was intermediate but, again, communities sourced from increasingly moist microclimate regimes had higher cumulative respiration rates than those sourced from drier field regimes (Fig. 3a). Using the regressions from Table 2 and Fig. 3, we estimated the effect size that history of soil moisture had on contemporary responses. In dry lab conditions (Fig. 3a), communities from the wetter end of the moisture gradient mineralized 89% more litter C than soils from drier microclimate regimes: 39.0 ± 3.7 mg C g^{-1} litter compared to 73.6 ± 3.9 mg C g^{-1} litter. Under mesic conditions (Fig. 3a), communities sourced from wetter microclimates mineralized 50% more than dry microclimates: 48.2 ± 2.8 mg C g^{-1} litter compared to 72.0 ± 2.9 mg C g^{-1} litter. The wet lab treatment (Fig. 3a, blue solid-line) resulted in soils from the wettest microclimates mineralizing 14% more C compared to soils from drier microclimates: 48.7 ± 3.9 mg C g^{-1} litter compared to 55.4 ± 4.2 mg C g^{-1} litter. Notably, the within-site variation across the field soil moisture gradient is comparable to the differences in mineralization rates between sites under dry conditions: 89% difference within HARV vs. 97% between sites. Further, the difference in cumulative respiration from the microsite communities that were incubated under mesic lab conditions were higher within the HARV site than between the two forest sites (50% variation within HARV microsites vs. 24% variation between HARV and SCBI sites).

3.3. Smithsonian Conservation Biological Institute, VA – SCBI

Decomposer communities from the SCBI site were not influenced by their local historical moisture regimes (Table 1, Fig. 3b). The slopes for cumulative respiration for lab moisture treatments were not significantly different suggesting that there were no within-site differences in microbial function. Standardized effect size estimates for field soil moisture ranged from 0 to 0.10 which indicates that there is potentially a positive association of field soil moisture regime with cumulative C mineralization, but the interaction between lab and field moisture essentially had a slope of zero (Table 2). As a result, the lab-based moisture treatments accounted for nearly all of the variation in cumulative C mineralization that was observed (SCBI: 'Lab Moisture', Table 2, Fig. 3b). Dry conditions resulted in mineralization rates of 110 ± 5.1 mg C g^{-1} litter (mean ± SE): 49% higher than mesic conditions (74.1 ± 3.5 mg C g^{-1} litter) and 105% higher than wet conditions (53.8 ± 1.4 mg C g^{-1} litter).

3.4. Model structural sensitivity

Given that the microsites from where we sourced the soil communities differed in more than moisture, we evaluated how other micro-environmental predictors that might influence microbial community functioning affected our interpretation of field moisture history as a causal variable. We explored how the addition of factors not strongly correlated with soil moisture, such as soil pH and soil temperature, affected the coefficient estimates of interest (Table 2). For the both site model, HARV, and SCBI models, coefficient sizes for 'Field Soil Moisture' remained relatively unchanged compared to a reduced model with only 'Field Soil Moisture' and 'Lab Moisture' (Table S1). Microbial biomass and TOC were highly correlated with field soil moisture (respectively, r

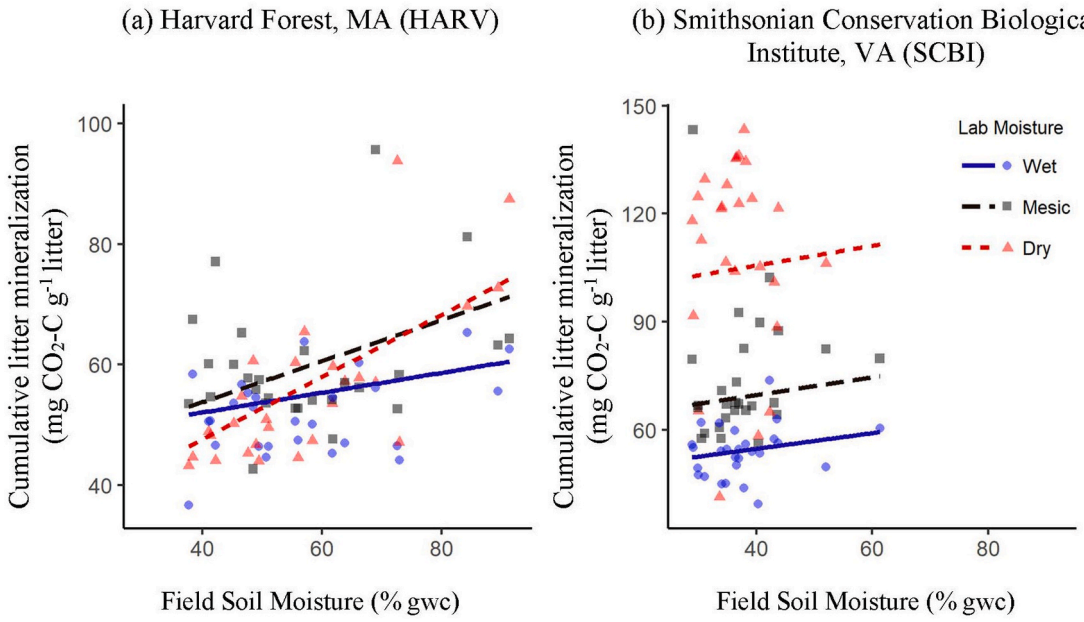

Fig. 3. Cumulative mineralization (reported as mg CO_2-C mineralized g^{-1} litter) for unique decomposer communities sourced from within the SCBI (a) and HARV (b) sites. Cumulative values (for the 202-day incubations) are plotted against microsite soil moisture conditions (% gravimetric soil moisture) from Spring 2020 and by the three laboratory moisture treatments that were imposed on each community. Points (n = 27 soil inocula per site) represent unique litter-soil microcosms subjected to 35% of maximum water holding capacity (Dry: red points and quick dashed line), 60% of maximum water holding capacity (Mesic: black points and long dashed line), and 100% of maximum water holding capacity (Wet: blue points and solid line). Note that the regression lines are not fit to the observations in a univariate manner. Instead, regression lines were calculated using unstandardized coefficients from the multiple regression models with non-log transformed cumulative respiration rates but otherwise are identical to models presented in Table 2. Note the different scales on the Y-axes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

= 0.67 and 0.89 for HARV and 0.68 and 0.91 for SCBI; SI Tables 3, 4), with variance inflation factors (VIF) > 2 when included in main effects models. For the models including both sites and only HARV, the inclusion of these variables continued to not affect the sign and magnitude of the 'Field Soil Moisture' effects (Fig. S1c). In the model specified for SCBI, the inclusion of TOC modified the coefficient for field soil moisture but it remained insignificant and close to zero (Fig. S1e). Across all models, we lastly substituted measures of field soil moisture taken at different times, and the mean value of these over the three time points. Soil moisture across sampled time points provided coefficient estimates that support our conclusions (Figs. S2a-e). In short, our results appeared relatively insensitive to model structural and parameter assumptions, suggesting that the coefficient estimates for 'Field Soil Moisture' and 'Lab Moisture' were robust.

To understand how unique experimental units might vary if they themselves were replicated, we replicated microcosms from one wet and one dry microsite within each site (4 microsites × 3 treatments × 8 replicates). Variation within these subsamples had a median coefficient of variation (COV) of 12%, which was consistently lower than the variation within treatments and site groupings except for a single highly-replicated SCBI community under dry conditions. Overall, within-replicate variation in C mineralization was about half that of within-site variation across treatments providing confidence that our conclusions about laboratory moisture treatment and microsite legacy effects are robust to potential within-replicate variation in observed C mineralization rates.

4. Discussion

Numerous studies report that soil communities sampled from sites with different precipitation regimes (and hence assumed differences in soil moisture regimes) exhibit functionally distinct responses to contemporary moisture conditions (Evans and Wallenstein, 2012; Hawkes et al., 2017). Our site-level findings contribute a further empirical example where our two sites, HARV and SCBI, had distinct C mineralization time-courses and cumulative fluxes across different lab-imposed moisture regimes (Fig. 2). This finding supports regional studies that observe that microbial responses to new conditions can be shaped by environmental history (Evans and Wallenstein, 2012; Averill et al., 2016; Hawkes et al., 2017; Glassman et al., 2018). We additionally asked whether these macroscale functional differences were exhibited at local, within-site scales. We found evidence for both of our hypotheses where, in one site (HARV), historical microsite conditions were associated with differences in cumulative C mineralization. Whereas in the other site (SCBI) only lab-imposed moisture conditions drove differences in C mineralization with no evidence of within-site differences in functioning.

Differences in microbial function emerge from multiple controls such as environmental history and contemporary conditions. We specifically asked how within-site heterogeneity in soil moisture regimes might generate microbial functional differences. In HARV, soils sourced from wetter microclimates mineralized more litter C than soils from drier microclimates across all lab-imposed moisture conditions (Fig. 3a). This effect was stronger for the dry and mesic lab moisture conditions compared to the wet lab conditions (Table 3; Fig. 3a). Results from this site suggest historical legacies of soil moisture shape the functioning of communities at local scales, reflecting similar functional patterns across regional precipitation gradients where historically wetter sites exhibit higher respiration rates (Hawkes et al., 2017, 2020). Whereas dispersal limitation, landscape heterogeneity and adaptation can play a role in functional divergence across broad spatial extents (Talbot et al., 2014; Strickland et al., 2015; Maynard et al., 2019), patterns revealed here also suggest that within-site, spatial heterogeneity in environmental conditions can generate functionally different microbial communities.

Drier moisture regimes can lead to lower microbial biomass but select for taxa that are more resistant to moisture stress and lead to higher functional ability under stressful conditions (Lennon et al., 2012; Maynard et al., 2019; Lustenhouwer et al., 2020). This broad scale

pattern was observed between the two sites, where the SCBI soil communities, that generally experience a drier soil moisture regime (Fig. 1), also exhibited much higher mineralization rates than the HARV soil communities under dry lab-moisture conditions (Figs. 2d and 3). However, the highest mineralization rates for the HARV soil communities were always observed for communities sourced from wetter microclimates, and the greatest among-community sensitivity to contemporary moisture conditions was observed under dry lab conditions (Fig. 3a). This within-site pattern observed at HARV was distinct from the within-site SCBI pattern (Fig. 3), and these within-site patterns were distinct from the patterns observed between sites. Collectively, our results suggest that functional differences observed among sites at regional scales do not necessarily translate to finer scales, raising the possibility that mechanisms that generate microbial functional differences at one scale might be distinct to mechanisms operating at another scale.

In contrast to the HARV observations, within the SCBI site we observed functionally equivalent decomposer communities where C mineralization rates were driven almost entirely by the lab moisture conditions (Table 2; Fig. 3b). Both forest sites experience similar amounts of annual precipitation, but the warmer mean climate of SCBI contributes to lower soil moisture values and a narrower spatial range in field-soil moisture regimes (Fig. 1, Table 1; CV = 0.191 for SCBI compared to 0.261 for HARV). Although results from SCBI do not show a strong effect of within-site moisture, as found at HARV, the effect size was still positive (Table 2). This positive coefficient suggests that there was also a positive effect of field soil moisture regime at this site, but it had only a small influence on mineralization rates. The microbial functional response of the SCBI soil communities to lab moisture conditions were, however, unexpected. Specifically, communities under dry lab conditions had higher C mineralization than communities under mesic and wet moisture lab conditions (Figs. 2 and 3b). This empirical result provides further evidence that microbial respiration does not always peak at mesic moisture conditions (Moyano et al., 2013). A potential explanation for the drier conditions under which we observed the peak is that, in leaf litter, constraints on C mineralization rates due to lower moisture may be smaller than in soil due to better gas and nutrient diffusion in dense litter packs. Nevertheless, the peak mineralization for the SCBI communities was still drier than for the HARV communities. Whereas we did not uncover the specific mechanisms explaining this observation, adaptation to drier conditions across the two sites and within SCBI reflect evidence from other systems where drier sites exhibit higher functional potentials. For example, Averill et al. (2016) found that enzyme potentials were linked to historical precipitation and soil moisture, with historically drier sites exhibiting stronger enzyme activity and sensitivity to moisture. Similarly, in our study, historical moisture regimes beget unique functional microbial responses that can lead to deviations from the typical unimodal response of mineralization to contemporary moisture conditions.

Models that represent explicitly how microorganisms mediate decomposition aim to explore how changes in environmental conditions affect microbes and in turn the rates of the biogeochemical processes they mediate (Wang et al., 2013; Wieder et al., 2013; Abramoff et al., 2018). These process-based models are an ideal framework for querying how functional legacies might affect rates. Our study is a starting point in addressing how functional legacies between and within sites might affect biogeochemical rates as moisture changes seasonally and interannually through climate change. For example, these models typically assume a unimodal moisture response, such that increasing moisture increases decomposition up to a threshold where decomposition rate decreases again (Davidson et al., 2012). We did observe this pattern at HARV, for the lab moisture treatments that were imposed, but not at SCBI suggesting that functional legacies create context-dependency in how contemporary moisture controls litter-C mineralization rates. Certainly, our data still support the assumption that contemporary moisture exerts strong direct control on mineralization rates, but equally our lab experiment provides further justification for field experiments that address how historical moisture regimes modify these contemporary responses. Experimental studies that tease out microbial functional effects from other environmental effects can help quantify the influence of functional microbial differences on contemporary biogeochemical process rates (Hawkes et al., 2017; Glassman et al., 2018). When partnered with process-based models that represent microbial functional differences, such experimental observations can help inform how functional differences might affect biogeochemical process rates under new conditions (Wieder et al., 2015a; Hall et al., 2018; Malik et al., 2020; Wang and Allison, 2021).

As more research focuses on the role of microbial biogeography, diversity and its relation to ecosystem function, our data reveal that the nature of these relationships are likely to be strongly scale- and context-dependent. Certainly, our data contribute to previous findings that historical contingencies shape contemporary functioning when sites are compared at regional scales. As such, they bolster expectations that measuring community functional potentials at the regional scale captures community adaptation to climatic drivers at similar scales (Strickland et al., 2015; Maynard et al., 2019). Yet our data also reveal that pronounced differences in field microclimate regime equally can affect microbial function under contemporary moisture conditions, in a manner distinct from those observed to arise because of macroclimate regimes. These scale dependencies might be expected to generate unique, non-linear, emergent responses of biogeochemical process rates to changing moisture conditions at regional scales, highlighting the importance of evaluating their influence on projections of climate change impacts on C cycling.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2021.108451.

Data availability and supplementary information

Data and code are available on DataDryad https://doi.org/10.5061/dryad.51c59zw8j.

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