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Article

Rapid Shifts in Soil Nutrients and Decomposition Enzyme Activity in Early Succession Following Forest Fire

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Received: 3 August 2017; Accepted: 13 September 2017; Published: 15 September 2017

Abstract: While past research has studied forest succession on decadal timescales, ecosystem responses to rapid shifts in nutrient dynamics within the first months to years of succession after fire (e.g., carbon (C) burn-off, a pulse in inorganic nitrogen (N), accumulation of organic matter, etc.) have been less well documented. This work reveals how rapid shifts in nutrient availability associated with fire disturbance may drive changes in soil enzyme activity on short timescales in forest secondary succession. In this study, we evaluate soil chemistry and decomposition extracellular enzyme activity (EEA) across time to determine whether rapid shifts in nutrient availability (1–29 months after fire) might control microbial enzyme activity. We found that, with advancing succession, soil nutrients correlate with C-targeting β-1,4-glucosidase (BG) EEA four months after the fire, and with N-targeting β-1,4-*N*-acetylglucosaminidase (NAG) EEA at 29 months after the fire, indicating shifting nutrient limitation and decomposition dynamics. We also observed increases in BG:NAG ratios over 29 months in these recently burned soils, suggesting relative increases in microbial activity around C-cycling and C-acquisition. These successional dynamics were unique from seasonal changes we observed in unburned, forested reference soils. Our work demonstrates how EEA may shift even within the first months to years of ecosystem succession alongside common patterns of post-fire nutrient availability. Thus, this work emphasizes that nutrient dynamics in the earliest stages of forest secondary succession are important for understanding rates of C and N cycling and ecosystem development.

Keywords: carbon; decomposition; disturbance; ecosystem process; extracellular enzymes; exoenzymes; forest fire; nitrogen; soil enzymes; succession

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1. Introduction

Global change pressures have increased the prevalence of forest fires in western North America [1–3]. Therefore, a better understanding of the connection between resulting perturbations in environmental factors and ecosystem processes, such as decomposition, will be vital to modeling ecosystem responses in the wake of such disturbance [4–7]. Microbial production of extracellular enzymes (EEA) involved in decomposition is regulated by quantity and quality of substrate that can change strongly after forest fires, although other factors such as moisture and pH are known to impact EEA as well [8–10]. In particular, fire disturbances dramatically alter soil pH, water holding capacity, and carbon (C) and nitrogen (N) pools [11,12], which may all continue to change through succession. These factors may thus affect microbial investment in both C- and N-targeting decomposition enzymes across short time scales of ecosystem recovery (e.g., months).

Past studies in post-fire forest soils have evaluated changes in edaphic properties, microbial communities, and related EEA over decadal time scales [13,14], while shorter-term successional dynamics are less well characterized. However, research has more recently shown the importance of changes in microbial function across short timescales of succession [15–17]. Work in similar forest ecosystems relating to mountain pine beetle kill has shown not only long-term effects of such disturbance, but also immediate, short-timeframe impacts on microbial function, such as respiration [17]. Altogether, this body of work has demonstrated that even when succession is considered over just months to years after a disturbance, shifts in nutrient pools—such as in ammonium (NH_4^+) and C availability—can have strong effects on microbial function [16–18]. Indeed, immediately after fires, burning of soil organic matter leads to alteration of soil C pools; fires can both burn-off C and alter its chemistry [12,19]. For N pools, a pulse of inorganic N occurs immediately after severe burns, which may either be rapidly exported from the ecosystem or persist into the first year following the fire [11,12]. Thus, even on a timescale of months to years after disturbance, these rapid and profound shifts in nutrient pools may influence microbial processes, such as the production of extracellular enzymes, which are central to nutrient cycling and ecosystem dynamics.

Here, we chose to examine early succession on a timescale of months after a high-severity forest fire to understand how soils and microbial enzyme production may change during this time period [20–23], with putative implications for the trajectory of ecosystem development [24,25]. Importantly, we focus on high-severity wildfires that are increasingly prevalent in montane forests of the U.S. Intermountain West [2] and can elicit particular responses in soil edaphic properties and microbial communities that are different from lower-severity burns; studies have shown that burn severity can differentially influence soil nutrient pools, C chemistry transformations, soil physical properties, and microbial community composition (for example [6,18,26]). While past work has evaluated shifts in EEA [14] and environmental controls on enzyme potential across secondary succession in general [27], our study examines how relationships between edaphic properties and decomposition enzyme activity may change within the first years of succession following a severe forest fire. We contrast these relationships between the fire-disturbed (burned) soils and undisturbed (reference) forest soils to highlight the effect of fires versus a control, as well as elucidate successional vs. seasonal patterns.

Specifically, we assessed edaphic properties, nutrient pools, and microbial enzyme activities relating to C and N cycling of soils across three time points in the initial stages of succession spanning 29 months after a major forest fire. We characterized the soil C and N resource environment and β-1,4-glucosidase (BG) and β-*N*-acetylglucosaminidase (NAG) decomposition enzymes that target these resources [9]. Across a global scale, BG and NAG both show strong positive relationships to soil organic matter, NAG shows strong negative relationship with pH, and BG is weakly related to mean annual precipitation [9]. As such, we assessed the activities of these enzymes alongside nutrient pools, pH, and moisture. Enzyme potential and soil nutrient pools are well suited for examining successional patterns as they may broadly persist over inter-seasonal time scales [28] and thus reflect successional patterns beyond seasonal variability.

We hypothesized that on month to year scales of forest secondary succession, changes in soil enzyme activity occur given rapid alterations to edaphic properties after fire disturbance. We further hypothesized that correlations between nutrient pools and EEA would vary between burned and reference soils given the different roles of nutrient limitation (such as stronger C limitations in burned soils); and, that the strength of correlations between BG and NAG with nutrient pools would change over time to reflect common post-fire shifts in nutrient availability in burned soils. Accordingly, for burn soils we hypothesized that enzyme dynamics would reflect rapid shifts in nutrients that occur after fires: initially low C and high N pools would drive correlations between nutrient pools and BG, whereas with accumulating C and reductions in N over time, correlations between nutrient pools and NAG activity would become more prominent [29,30].

2. Methods

2.1. Site and Soil Properties

Samples were collected in the Fourmile Canyon, Boulder County, CO, USA. Samples were collected at 1 month (October 2010), 4 months (January 2011), and 29 months (June 2013) after a major, high-severity wildfire, which ignited on 6 September 2010. At all sample times, replicate samples were taken from both undisturbed (reference) forest soils and adjacent fire-disturbed (burned) soils. These sites were ~300 m apart and sampling areas fell within 650 m^2 landscapes at similar slope-aspect (northeastern facing mountainside slope) and elevation (~2100–2300 meters above sea level) within the extent of the Fourmile Fire (latitude: 40.036153, longitude: -105.400537) (Figure 1). Sample areas were free of tree mortality from bark beetles and fungi. Prior to the burn, this contiguous study area had similar soil conditions across the landscape given consistent topographical and vegetative features (Figure 1). Metamorphic and igneous parent material has resulted in coarse, poorly developed, sandy soils in Fourmile Canyon [31]. Soils are stony sandy loams of the Fern Cliff-Allens Park-Rock outcrop complex as per National Cooperative Soil Survey (NCSS) classification. Annual precipitation averages 475 mm and occurs primarily as snow in winter/spring [31]. Both reference and burned sites were dominated by *Pinus ponderosa* var. *scopulorum* and *Pseudotsuga menziesii* var. *glauca*; details of location vegetation and fire history as well as the Fourmile Canyon Fire dynamics have been previously described [31,32]. Photos and maps of the fire's extent and response to/control of the Fourmile Canyon Fire have been made available by the U.S. Department of Agriculture [31]. Trees in the burned site were severely burned (completely charred) and dead. Unlike the 1- and 4-month soils that were void of vegetation, 29-month soils were revegetated with understory herbaceous plants by seeding, dominated by sterile wheat.

Ten replicates for both burn and forested undisturbed soils were collected at each time point. Sampling locations within each treatment were 1 m from the base of a tree (burned or alive, respectively), and at least 3 m but no more than 25 m between individual trees used for sampling. At each sample location three 130.5 cm^3 soil cores of mineral soil at a depth of 5 cm were taken and bulked to constitute a single replicate. We avoided/removed belowground plant material. In reference site samples, the organic layer was removed prior to sampling; no organic layer was present in burned soils. One-month soils included an ash layer of <0.5 cm.

Within 2 h of sampling, soils were transported to the lab and then sieved through a 2 mm mesh, subsampled, and stored in a -70 °C freezer for molecular analysis or refrigerated at 4 °C for soil chemistry and enzyme assays. All samples were processed according to the methods enumerated in Ferrenberg et al. (2013), from which 1- (October 2010) and 4-month (January 2011) samples from the burned site, and 4-month samples from an undisturbed, unburned, forested site were also used. Soil moisture, pH, total dissolved nitrogen (TDN), extractable, non-purgeable, organic carbon (NPOC), and ammonium (NH_4^+) were evaluated.

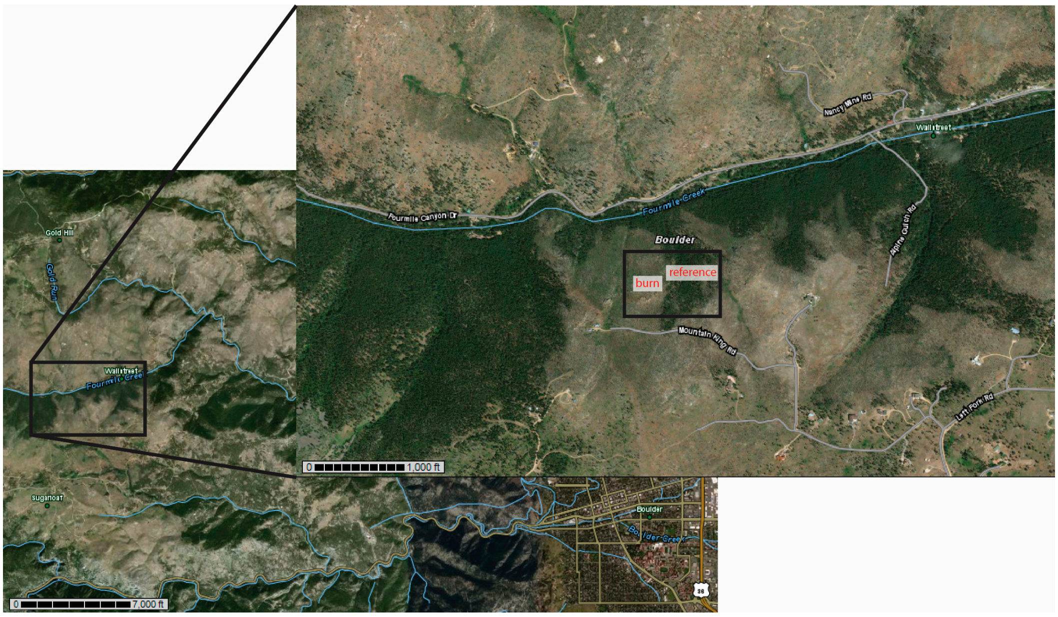

Figure 1. Maps of Boulder and Fourmile Canyon and surrounding region, with sample area demarcated in inset map. Maps are from the U.S. Department of Agriculture Natural Resources Conservation Service.

A subsample of each soil was dried at 100 °C for 48 h to determine gravimetric soil moisture; subsequent edaphic properties were calculated on a dry weight basis. Dried soils of all samples were ground and 50 mg were packed into tin capsules for %C and %N analysis using a Thermo Finnigan EA 1112 Series Flash Elemental Analyzer; (Thermo Fisher Scientific, Inc., Waltham, MA, USA) [33].

Immediately following collection, 8 g of soil were extracted for 1 h in 40 mL of 0.5 M K_2SO_4 and filtered with Whatman No. 1 paper (Whatman Incorporated, Florham Park, NJ, USA). Extract filtrate was frozen until analysis of NH_4^+, TDN, and NPOC. Filtrates were analyzed for NH_4^+ on a BioTek Synergy 2 Multidetection Microplate Reader (BioTek, Winooski, VT, USA) and TDN/NPOC, were measured on a Shimadzu TOC-V CSN Total Organic Carbon Analyzer (Shimadzu TOCvcpn, Kyoto, Japan). TDN, NPOC, and NH_4^+ analysis was completed for all 4 and 29 month soils. Soil pH was measured on soil slurries with a ratio of 2 mg dry soil: 4 mL water, which were shaken at 250 rpm for one hour and allowed to equilibrate for an hour before measuring.

2.2. Enzyme Analysis

Enzyme activities for β-1,4-glucosidase and β-1,4-*N*-acetylglucosaminidase were evaluated to assess microbial investment in C and N acquisition, the cycling of these nutrients, and connections with edaphic properties. BG and NAG enzymes are useful indicators of C and N cycling as they are produced across a wide variety of fungi and bacteria and importantly have been used widely in past research to assess microbial investment in C vs. N acquisition and the limiting nature of these nutrients in post-fire forest ecosystems [9,18,30]. While all ten replicates were used from 29-month samples, due to limited availability of samples, eight replicates of reference forested soils (4 months) and seven replicates of burned soils (1 and 4 months) were included for enzyme analysis. Enzyme activity was measured via fluorometric microplate methods [34,35]. The methods of Weintraub et al. [34,35] were used based on a 96-well assay plate method with 1 M sodium acetate buffer titrated to a pH of 7.0, and 4-methylumbelliferone standards. ~1 g of refrigerated soil was used from each sample [36]. Each sample (every experimental replicate) was run with 16 analytical replicates, quench corrections, standards, and negative controls for each enzyme assay. Fluorescence was measured using a microplate reader (Thermo Labsystems, Franklin, MA, USA) at 365 nm excitation and 460 nm emission to calculate nmol activity h^{-1} g $soil^{-1}$.

2.3. Statistical Analysis

The *pgirmess* package in the R statistical environment [37] was used to evaluate changes in edaphic properties within reference and burn soils across the various time points using Kruskal–Wallis contrasts. Enzyme activity was also analyzed as a BG: NAG ratio and tested for statistical differences across time within both burned and reference forest soils. Pearson product moment correlations were calculated between environmental factors of total C, total N, pH, C:N ratio, and percent moisture and BG/NAG activity both in burned and reference plot samples across all time points. Data were checked for normality and if nonconforming were transformed to achieve normality before correlation analysis.

2.4. Data Availability

All metadata have been made available at figshare [38].

3. Results

3.1. Extracellular Enzyme Activities

In burned soils, BG activity was significantly higher in 29-month soils than one- and four-month soils (Table 1), denoting a trend for increasing activity through time, becoming more comparable to reference soil activity levels. In contrast, NAG activity showed significant declines from 4- to 29-month soils. BG:NAG ratios exhibited a strong partitioning between the 1-/4-month and 29-month time points (Table 1). For instance, in burned samples, 29-month soils had significantly higher BG:NAG ratios than one- and four-month soils.

BG activity at all times was higher in reference soils than burned soils. While BG showed significantly higher activity in 29-month soils than four-month soils, no differences in NAG activity or BG:NAG ratios over time were observed in reference soils (Table 1).

3.2. Soil Properties

Burned soils showed patterns of change over time in ammonium (NH_4^+), total dissolved nitrogen (TDN), and percent moisture (Table 1). Significant decreases in NH_4^+ and TDN were observed between 4- and 29-month burned soils. Moisture declined from 1-month to 29-month time point; soil moisture at one month was significantly higher than at 29 months in burned soils. No significant changes were observed in total C and N pools as measured via %N, %C, or C:N ratio across any of the time points in burned soils.

Unburned reference soils showed declines in soil moisture over time with 4- and 29-month soils have significantly lower soil moisture than one-month soils. pH showed significant differences month to month (Table 1).

3.3. Soil Properties and Extracellular Enzyme Activity

In burned soils, EEA was uncorrelated to edaphic factors initially (i.e., at one month post-fire) but began to strongly relate to nutrient pools (%C and %N) at four months (r of >0.8) and onward (Table 2). These burned soils showed strong correlations between BG (but not NAG) and %C and %N. In contrast, the reference plots at this time point showed correlations of both NAG and BG with edaphic properties including C and N pools. By 29 months, both BG and NAG correlated with C and N pools, while no correlations were observed in reference plots (Table 2). Taken together, these analyses demonstrate that BG activity in burned soils correlated with soil nutrient pools during the 4–29-month post-fire interval, while NAG correlated with these same factors later in successional time only (e.g., at 29 months) (Table 2). In reference soils, both BG and NAG correlated with nutrient pools at four months and showed no correlation at 1- and 29-month time points.

Table 1. Mean (standard deviation) edaphic properties for reference/post-fire successional samples.

Category	**pH**	**% Moisture**	**% N**	**% C**	**NH4 (mg/kg Soil)**	**NPOC (mg/g Soil)**	**TDN (mg/g Soil)**	**BG (nmol Activity/h/g Soil)**	**NAG (nmol Activity/h/g Soil)**	**BG:NAG Ratio**
BURN										
1-month	7.21 (0.30) ^{AB}	9.93 (4.55) ^{BA}	0.14 (0.04)	2.43 (0.95)	N/A	N/A	N/A	53.94 (12.02) ^{C}	78.53 (31.46) ^{AB}	0.74 (0.23) ^{B}
4-months	8.08 (0.41) ^{A}	8.55 (2.36) ^{ABC}	0.11 (0.04)	2.33 (1.07)	48.94 (14.95) ^{A}	0.30 (0.16)	0.06 (0.02) ^{A}	76.38 (27.67) ^{BC}	107.54 (43.07) ^{A}	0.75 (0.18) ^{B}
29-months	7.00 (0.28) ^{B}	2.16 (0.80) ^{C}	0.12 (0.03)	2.48 (0.66)	2.30 (1.33) ^{B}	0.31 (0.30)	0.02 (0.02) ^{B}	127.00 (27.57) ^{A}	44.41 (14.61) ^{B}	3.01 (0.71) ^{A}
REFERENCE										
1-month	6.44 (0.67) ^{B}	19.74 (10.17) ^{A}	0.27 (0.08)	6.21 (2.01)	N/A	N/A	N/A	N/A	N/A	N/A
4-months	7.08 (0.46) ^{A}	6.35 (3.50) ^{C}	0.24 (0.17)	6.59 (5.08)	2.39 (1.40)	0.26 (0.18)	0.02 (0.01)	147.83 (54.97) ^{B}	136.29 (63.12)	1.17 (0.38)
29-months	6.63 (0.34) ^{AB}	8.40 (6.12) ^{BC}	0.24 (0.08)	5.20 (2.19)	1.24 (0.60)	0.09 (0.04)	0.01 (0.004)	254.41 (86.14) ^{A}	251.77 (116.38)	1.13 (0.38)

Letters denote significant differences across timepoints ($p < 0.05$) as per Kruskal-Wallis contrasts within Burn/Reference categories.

Table 2. Correlations between β-1,4-glucosidase (BG) and β-1,4-*N*-acetylglucosaminidase (NAG) enzyme activity and edaphic properties. Significant ($p < 0.05$) correlations (Pearson's r) shown for burned and reference soils across all time points.

		BURNED PLOTS		REFERENCE PLOTS	
Time	**Factors**	**BG**	**NAG**	**BG**	**NAG**
1-month post-fire October	pH	NS	NS	N/A	N/A
	moisture	NS	NS	N/A	N/A
	C	NS	NS	N/A	N/A
	N	NS	NS	N/A	N/A
	C:N	NS	NS	N/A	N/A
4-months post-fire January	pH	NS	NS	NS	NS
	moisture	NS	NS	0.9	0.76
	C	0.83	NS	0.81	0.79
	N	0.9	NS	0.78	0.72
	C:N	NS	NS	0.77	NS
29-months post-fire June	pH	NS	NS	NS	NS
	moisture	NS	NS	NS	NS
	C	0.69	NS	NS	NS
	N	NS	NS	NS	NS
	C:N	NS	0.69	NS	NS
33-months post-fire October	pH	NS	NS	NS	NS
	moisture	0.64	NS	NS	NS
	C	NS	NS	0.84	0.84
	N	NS	0.66	0.96	0.86
	C:N	NS	0.74	NS	NS

NS = not significant N/A = not available.

4. Discussion

Changes in edaphic properties and EEA of post-fire landscapes have been shown to occur across successional stages at decadal timescales [13,14,30,39,40]. Strikingly, we found that microbial EEA related to C and N acquisition varied significantly over a relatively short time span of 29 months of succession. Our results indicate that even within three years of succession [23] enzyme activity changes alongside rapid shifts in nutrient availability that are characteristic of post-fire succession. While microbes in early succession may be co-limited by both C and other macronutrients such as N [41–43], increasing BG:NAG ratios observed within the first 29 months of post-fire forest succession may reflect increasing C availability (e.g., revegetation) and a relative increase in microbial investment in C acquisition. Reference soils, however, showed no significant changes over time in BG:NAG ratios. Our work is consistent with past research in post high-severity forest fire soils that shows BG:NAG ratios of 2–3 at just over a year into succession, while lower disturbance environments displayed BG:NAG ratio around 1–1.5 [18]. In total, the observed shift demonstrates that within three years of succession EEA activity is responsive to the unique soil nutrient environment of burned soils and shows distinct dynamics from reference forest soils.

We more directly examined the relationship between edaphic properties and EEA within each stage of the burned landscape in contrast to corresponding reference soils. Within these stages of secondary succession, we observed a shift from correlations between only BG EEA and nutrient pools to correlations between NAG EEA and nutrient pools in the 29-month time point as well (Table 2). Although controls on microbial production of extracellular enzymes may vary, it is well known that the quantity and quality of available substrates can induce and structure the production/activity of both C and N acquiring enzymes [9,10]. The observed correlations indicate that even within the first years of secondary succession, nutrient limitation may control BG activity with eventual shifts toward more prominent connections between nutrient pools and NAG activity. This dynamic may reflect a relative shift from C to N limitation (or relative changes in co-limitation) and is consistent with general patterns in nutrient dynamics across succession in post-fire landscapes [11,12,43–45]. Specifically, research has commonly observed that post-fire landscapes are characteristically low in C and experience a pulse of inorganic N in the form of ammonium and nitrate after severe wildfires, while slightly later successional soils may be more constrained by N with the buildup of soil C [11,12]. Accordingly, we witnessed evidence of a pulse of NH_4^+ and TDN in the four-month post-fire soils and a strong drawdown in these N pools at the 29-month time point (Table 2), consistent with a vast body of literature which notes a pulse of inorganic N immediately after a fire, but drawdowns in this pool on a timescale of months to years [11,12]. While C pools do not show significant increases over time in soils at the scale measured in this study, past work has shown that fires can strongly influence the composition of soil organic matter without significant impact on total stock [26]. For example, fires can alter C chemistry in forest soils, including the humification of C compounds which can influence substrate availability for microbial decomposition [18,19,46]. Changes in C pools over successional time with plant colonization (29-month soils) may also be in terms of composition and quality, not just quantity [27,47,48].

While we acknowledge that seasonality can influence variation in EEA [49], the observation that strong correlations between EEA and soil N and C pools correspond with common post-fire dynamics, such as a drawdown in inorganic N, likely reflects successional dynamics. Additionally, the fact that these observed patterns in EEA of successional soils are different from reference soils shows that such patterns are specific post-burn soil dynamics in the first months after a fire, illustrating EEA responses to geochemistry even within 4–29 months post-disturbance.

While pH and moisture have well-described successional dynamics, such as an immediate increase in pH after fire and decreases over time, or increases in water holding capacity with the buildup of soil organic matter over time [11,12], these factors may also vary on a seasonal basis. In the case of this study, we interpret moisture changes, for example, as largely a seasonal shift. Over 29 months, there is little change in soil organic matter and water holding capacity, and shifts in soil moisture occur in a similar manner in both successional and reference soils. This pattern of change is not unique to successional soils, but rather a seasonal dynamic true of reference forests as well. However, neither soil moisture nor pH correlated with enzyme activity in post-burn successional soils. While future work should seek to address how seasonality versus succession influences these ecosystems in the first months after fire, significant increases in BG:NAG ratios over time and correlations between C and N pools with BG/NAG EEA are different from patterns in reference soils and demonstrate dynamics that are unique to post-burn successional soils within the first three years following a severe wildfire.

Additionally, enzymes are well suited to studying inter-seasonal dynamics as they persist in the soil [28] and are assayed for enzyme potential (at controlled temperature, moisture, and pH) rather than in situ enzyme activity. Enzyme potential assays, such as those completed in the lab, may therefore reflect successional dynamics rather than seasonal ones where variable in situ temperature, pH, and moisture can strongly affect enzymatic activity.

Altogether, our work leads to a conceptual model of patterns in the coupling of nutrients and decomposition enzyme activity on short timescales after fires (Figure 2). Because of characteristic changes in nutrient pools over the first years in post-fire succession, and the role of C and N availability as a control on enzyme production, we propose that the initial limitation in C availability results in a connection between BG activity and the resource environment. Likewise, in subsequent stages where C pools begin to build and N is more limited in availability (though C and N may be co-limiting), NAG activity shows connections with the resource environment (Figure 2). Here, in particular with plant colonization and the accumulation of C, BG:NAG ratios increase, reflecting improved availability of C substrates (Figure 2). It is important to note that these dynamics are envisioned for short timescales within the first years of succession, as N limitation alone across longer timescales can yield declines in BG:NAG ratio [30] and more dramatic variation in other important controls such as pH and soil moisture may also become more influential.

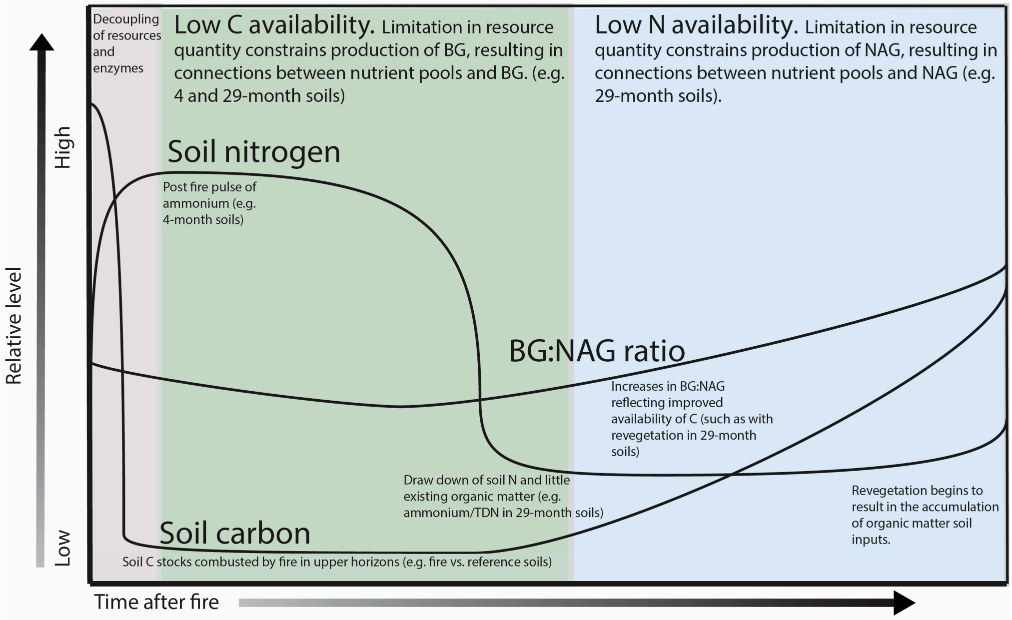

Figure 2. Soil resource and extracellular enzyme dynamics on a short timescale (<3 years) after a forest fire.

5. Conclusions

We found evidence for a connection between rapid shifts in nutrient pools and microbial decomposition enzyme activity in the first several years of secondary succession. We show that within 29 months of post-fire succession relative increases in BG:NAG ratios occur. These shifts are distinct from reference soils, and may represent rapid successional responses to changing nutrient dynamics. Our work demonstrates that soil nutrients first correlate with BG activity (C-targeting) and then correlate additionally with NAG activity (N-targeting) within 29 months of succession. This shift is likely driven by changes in substrate availability and quality as post-fire landscapes first show reductions in C pools, followed by reductions in NH_4^+/TDN pools over the timeframe examined in this study. Built on the empirical findings of this and other studies, our conceptual model suggests when and why we may expect to observe changes in nutrient–enzyme relationships across the initial stages of post-fire succession (Figure 2).

Despite the use of a single site in our research, such study systems and sampling schemes have traditionally been used in the study of ecosystem succession with great success in advancing the field empirically and theoretically [14,44,50,51]. Nonetheless, the research conducted herein represents samples from a single fire disturbance and thus we are limited in our ability to generalize such findings. We also note that scales of disturbance should be explicitly considered in future work and constrain the conclusions of this study, which were based on a high-severity fire. Past work has shown that high- vs. low-severity fires, for example, can modulate ecosystem responses in terms of soil chemistry and EEA [6,18].

We present our conceptual model as a hypothesis for further work (Figure 2). While this work describes shifts in EEA potential and the linkage between nutrients and soil enzyme activity within the first years of succession, future work should more closely examine the possible ecological mechanisms that underlie these patterns, such as how specific changes in microbial communities may be driving the observed differences in biogeochemical potential with EEA. Past work at this site in which bacterial communities were sequenced at each time point showed no correlation between bacterial community structure and EEA in the post-fire successional soils (data not shown); however, fungal communities are dominant drivers of EEA as well and further research may reveal to what extent microbial data can explain variation in soil EEA that is responsible for the cycling of C and N in these ecosystems [5].

Acknowledgments: This work was supported by the National Science Foundation of the USA through grant DEB-1258160 to D.R.N. and S.K.S. We also acknowledge support from the Microbiomes in Transition (MinT) Initiative at Pacific Northwest National Laboratory, operated by Battelle for the U.S. Department of Energy (DE-AC05-76RL01830). We thank Duaba and Sean O'Neill for assistance in the establishment of the field site and Janet Prevéy for botany insights at the field site. We appreciate the expertise of Holly Hughes in analytical chemistry and the comments of two anonymous reviewers on the manuscript. Diana Nemergut—a superbly creative and innovative scientist—guided and worked on this manuscript. Diana continues to impact not only the scientific community and ongoing research but also far wider, diverse communities of people who she forever shines upon with her generous and beautiful life.

Author Contributions: J.E.K., D.R.N., S.K.S., E.B.G. and S.F. conceived and designed the experiments; J.E.K., D.R.N., S.K.S., E.B.G., S.F., and J.D. performed field work; J.E.K., E.B.G., S.F., A.L., and A.L. performed laboratory work; J.E.K. analyzed the data; and J.E.K. wrote the paper with the assistance of D.R., S.K.S., E.B.G., and S.F.

Conflicts of Interest: The authors declare no conflict of interest.

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