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The stoichiometric legacy after fire: multi-element shifts and arthropod community filtering in a subtropical grassland

Wei Huang[1], Grizelle González[2], Weili Liu[1] and Xiaoming Zou[3*]

Abstract

Background Fire is a disturbance that alters nutrient cycling, but its legacy is often reduced to shifts in carbon (C), nitrogen (N), and phosphorus (P). This C:N:P paradigm overlooks the vast suite of other elements critical to decomposer organisms. Post-fire changes in the abiotic environment—especially when interacting with co-occurring stressors such as ultraviolet (UV) radiation—may reorganize the entire multi-element stoichiometric network within litter, yet the direct implications for arthropod decomposer communities remain largely unknown.

Results In a 469-day factorial field experiment in a subtropical pastureland, we imposed prescribed burn and UV radiation treatments on litterbags. By quantifying 33 elemental ratios of litter, we revealed that abiotic environment change post fire acted as a reductive force, significantly decreasing 20 ratios (e.g., ln C:Fe by 6.89%, ln N:Fe by 8.76%) and enriching the litter with metals. In contrast, UV radiation decoupled potassium from litter, increasing ratios like K:P and K:Na. These reconfigured elemental landscapes of litter directly filtered the arthropod community, with diversity showing strong negative correlations with metal N, P and K constraints (e.g., N:Mn, N:Fe).

Conclusions We demonstrate that post-fire abiotic environmental change and UV rewire litter stoichiometry towards distinct, metal-enriched, and potassium-decoupled states. This multi-element network perspective moves beyond the C:N:P paradigm to reveal a powerful mechanism through which disturbances shape decomposer communities. Monitoring these stoichiometric networks provides a predictive framework for assessing the ecological legacy of fire in a changing world.

Keywords Arthropod community, Fire ecology, Litter decomposition, Multi-element stoichiometry, Nutrient cycling, Photodegradation, Stoichiometric niche

Resumen

Background El fuego es un disturbio que altera el ciclo de nutrientes, aunque su legado es frecuentemente reducido a cambios en el Carbono (C), el Nitrógeno (N), y el fósforo (P). Este paradigma de C:N:P, pasa por alto el vasto conjunto de otros elementos críticos para los organismos descomponedores. El cambio post fuego en el ambiente abiótico –especialmente cuando interactúa con estresores co-ocurrentes como la radiación ultravioleta (UV)- puede reorganizar completamente la red estequiométrica dentro de la broza, por lo que sus implicancias directas para las comunidades de artrópodos descomponedores permanecen, en gran medida, desconocidas.

*Correspondence:
Xiaoming Zou
xzou@jaas.ac.cn
Full list of author information is available at the end of the article

Resultados En un experimento factorial en una pastura subtropical que duró 469 días, realizamos una quema prescripta y tratamiento con rayos ultravioletas en bolsas con broza. Mediante la cuantificación de 33 relaciones entre elementos de la broza, revelamos que el cambio en el ambiente abiótico en el post fuego actuó como una fuerza reductora, decreciendo significativamente en 20 relaciones (i. e. en C:Fe en un 6,89%, y en N:Fe en un 8,76%) y enriqueciendo la broza con metales. En contraste, la radiación UV desacopló el potasio de la broza, incrementando las relaciones como entre K:P y K:Na. Este "paisaje" de elementos reconfigurados en la broza filtraron directamente la comunidad de artrópodos, con la diversidad mostrando grandes correlaciones negativas de metales con N, P y K (i. e. N:Mn, o N:Fe).

Conclusiones Demostramos que cambios en el ambiente abiótico post fuego y los rayos UV reconfiguran la estequiometría de la broza hacia algo diferente, enriqueciendo los metales y desacoplando el estado del potasio. Esta perspectiva de red de multi-elementos cambia desde el paradigma del C:P:N, revelando un poderoso mecanismo a través del cual los disturbios modelan las comunidades de descomponedores. El monitoreo de estas redes estequiométricas provee de un marco predictivo para determinar el legado ecológico del fuego en un mundo cambiante.

Introduction

Nutrient stoichiometry, the balance of elements in organic matter, is a fundamental constraint on ecological processes from decomposition to trophic interactions. For decades, the classic carbon (C), nitrogen (N), and phosphorus (P) framework has powerfully predicted decomposition rates and nutrient cycling across ecosystems (Hessen et al. 2013; Sardans et al. 2021). However, this paradigm is fundamentally incomplete. It overlooks a vast suite of other elements—such as potassium (K), calcium (Ca), magnesium (Mg), and metal micronutrients like manganese (Mn) and iron (Fe)—that are critical for organismal physiology and the enzymatic machinery driving decomposition (Berg et al. 2010; Kaspari & Powers 2016). A truly mechanistic and predictive understanding of how ecosystems respond to disturbance requires a multi-element stoichiometric perspective.

Prescribed burning is the most commonly used management practice in moist tropical areas, with the main focus of maintaining pasture vegetation, as well as reducing the risk of hazardous fire (Asada et al. 2025; Kohman et al. 2022). An improved understanding of the ecological effects of prescribed burning is therefore vital to achieving positive ecological outcomes while simultaneously reducing the risk of wildfires (Butler et al. 2018). Fire in tropical grasslands has well-documented impacts on C, N and P. It volatilizes labile C and N while depositing ash rich in non-volatile elements, such as P, K, and metals (Butler et al. 2019; Gray & Dighton 2006).

However, fire increasingly co-occurs with other anthropogenic pressures, such as intensified ultraviolet (UV) radiation. Over the past decades, human activities have significantly impacted global UV radiation levels by weakening the ozone layer (Barnes et al. 2019). Models project spatial overlaps between regions of intensified fire expansion and areas with heightened UV variability in the coming decades, particularly in tropical regions (Xie et al. 2023; González et al. 2025). Ultraviolet radiation acts as a photodegradative force, directly breaking down lignocellulose and altering the solubility of elements like K (Huang et al. 2021; Lin et al. 2015). Ultraviolet photodegradation is thought to take on added importance in grassland ecosystems. First, litter in grassy areas would have greatest solar radiation exposure (Throop et al. 2017). Second, in grassland ecosystems, litter is formed through the senescence of standing grass. This standing litter may be subject to photodegradation before it comes in contact with the soil microbial community (Baker and Allison 2015). Although the individual effects of these disturbances on C, N, and P dynamics are documented, their synergistic impact on a broader network of elemental couplings remains a critical unknown. Specifically, we lack understanding of how fire and UV reconfigure multi-element ratios such as N:Mn, N:Fe, and P:Ca, which may be more sensitive indicators of biogeochemical change and its ecological consequences.

These stoichiometric shifts are not merely chemical curiosities; they create the fundamental resource landscape for decomposer communities. Soil arthropods maintain strict physiological stoichiometry (e.g., high P in RNA, Ca in exoskeletons) and must selectively forage to meet their elemental demands (Zhang et al. 2022). Microbes, while more flexible, require balanced metal cofactors for key enzymes (e.g., Mn for lignin peroxidase, Fe for nitrogenase; Hofrichter 2002; Kim and Rees 1994). Therefore, disturbances that alter the availability and balance of a wide range of elements—shifting ratios like N:Mn, N:Fe, or P:Ca—can disrupt decomposer efficiency by exceeding homeostatic tolerances (Li et al. 2023), effectively acting as a stoichiometric filter that shapes the functional community. Although past work in this field has focused on the relationship between arthropods and C-coupling element or N:P ratios (Butler et al. 2021; Jochum et al. 2017; Ott et al. 2014), only the linkage

among beetles and the multi-element stoichiometry was explored (Butler et al. 2020). Relatively little attention has focused on the potential role of N-, P-, and C-coupling metal ratios on shaping communities of mites and springtails, which are dominant groups of litter micro- and meso-arthropods. These arthropods, which are mostly microbivores and detritivores (Stehr 1987; Borror et al. 1989), play a vital role in ecosystem biogeochemistry (Lakshmi et al. 2020).

Critical knowledge gaps persist: (1) How do fire and UV interact to alter integrated suites of elemental ratios, creating a new multi-element stoichiometric landscape in decomposing litter? (2) Do these shifted elemental couplings create stoichiometric niches that filter arthropod communities based on their specific nutritional requirements? We addressed these questions through a 469-day factorial experiment in a subtropical pastureland. We subjected litterbags of two dominant grasses to fire and UV treatments, quantifying 33 stoichiometric ratios and arthropod communities. We hypothesized that

- Fire would reduce C- and N-coupled ratios (e.g., C:Fe, N:Mg) due to volatilization losses but elevate ratios involving ash-enriched elements (e.g., P:Mn).
- UV radiation would amplify K-driven ratios (K:C, K:Mg) by inhibiting microbial K immobilization while enhancing photodegrading C loss.
- Arthropod diversity and composition would be most strongly correlated with multi-element constraints (e.g., C:Mn, K:Fe), reflecting stoichiometric niche partitioning driven by shifts in the broader elemental network.

By testing these hypotheses, we aim to establish multi-element stoichiometry as a central framework for predicting how interacting global change drivers rewire nutrient cycles and structure decomposer communities.

Materials and methods

Study site

The study was conducted in a 100×60 m subtropical pastureland in the USDA Forest Service Research Area, Guayama, Puerto Rico (18°N, 66°W), with a mean annual precipitation of 1693 mm and a mean annual temperature of 23 °C. Soils are shallow Typic Haplustalfs clay loam. The original vegetation here is subtropical moist forest. It was deforested before 1937. Then, the nearby village used it as pastureland for horses, and burned it every 1–5 years, with the last fire occurring in 2006. Vegetation is now dominated by the non-native grasses *Megathyrsus maximus* and *Dichanthium annulatum*, a variety of trees, shrubs, herbs, and vines occur sporadically throughout the pastureland (Huang et al. 2021, 2024).

Experimental design

Eight 10×20-m experimental blocks, separated by 5-m firebreaks, were established. Four blocks were randomly subjected to prescribed burning, with the remaining four serving as unburned controls. A low-intensity surface fire was ignited by fire guns at the study site on 31 March 2017, with flame lengths less than 120 cm and a temperature of 537.5 °C at the litter layer. Fires were homogeneous across every burn plot. Trees in the burned plots remained alive. Although fire consumed the aboveground biomass of herbs, grasses, shrubs, and vines completely, some grass regrew rapidly in the post-fire rainy season (April–August).

Ultraviolet radiation (280–400 nm) was manipulated over the litter layer at each plot using aluminum frames (240×120×20 cm, l×w×h) fitted with UV-pass or UV-block panel in a randomized complete block design. UV-transparent acrylic panels (90% UV-A/B transmission) were used for UV-pass treatments, and UV-absorbing polycarbonate panels (90% UV-A/B blockage) were used for UV-block treatments. Neither kind of panel substantially affects temperature or photosynthetically active radiation under panels. Every panel had 36 1-cm holes to permit precipitation flow, with nine holes parallel to the 240-cm edge and four holes parallel to the 120-cm edge (24 cm distance between every two adjacent holes; Huang et al. 2021). Use of a central 200 cm×100 cm area under the panels minimized edge effects. There was no tree shading in the experimental plots during our experiment.

Litterbag sampling

Litterbags were 20×20 cm, and were constructed with either large mesh size (6 mm fiberglass, >95% solar penetration), medium mesh size (1.5 mm fiberglass, >80% penetration), or small mesh size (0.1×0.15 mm cloth, >79% penetration). In November 2016, 5 months before the prescribed burn, aboveground shoots of *M. maximus* and *D. annulatum* were collected from the site. The grass material was cut into segments of 20 cm in length and air-dried. Ten grams of air-dried *M. maximus* or *D. annulatum* litter was put in each litterbag. Forty-eight litterbags (two species×three mesh sizes×eight collections) were placed under each UV panel, and attached to the ground in two corners with metal nails. A total of 768 litterbags were deployed on 3 April 2017, with samples collected at 0, 15, 31, 59, 133, 237, 344, and 469 days (4 replicates per treatment combination). Arthropods were extracted from these litterbags over 168 h using Tullgren funnels, stored in 70% ethanol, sorted, and identified to morphospecies using available keys (Borror et al. 1989; Dindal 1990). Morphospecies were assigned to broad trophic groups, based on the

known biology of the taxa (Stehr 1987; Borror et al. 1989; Merritt et al. 2008). Diversity was compared among treatments and over time using Simpson's Reciprocal and Shannon–Wiener Index (1/D), which accounts for species density (number per gram of dry litter) intoer arthropod extractions, litter was retained for chemical analysis.

Elemental and stoichiometric analyses

Litter samples were oven-dried (65 °C), ground, and analyzed for C and N via dry combustion (LECO TruSpec CN Analyzer), and P, sulfur (S), K, Ca, Mg, Mn, Fe, aluminum (Al), and sodium (Na) via ICP-OES (Spectro SpectroBlue) following HNO_3-H_2O_2-HCl digestion (Huang & Schulte 1985). Methods for elemental quantification and quality control (e.g., certified reference materials, moisture corrections) follow Huang et al. (2024). We computed 33 stoichiometric ratios on a mass basis: (1) Carbon-coupled ratios: C:P, C:S, C:Ca, C:Mn, C:Mg, C:Fe, C:Al, C:Na; (2) Nitrogen-coupled ratios: N:P, N:S, N:Ca, N:Mn, N:Mg, N:Fe, N:Al, N:Na; (3) Phosphorus-coupled ratios: P:S, P:Ca, P:Mn, P:Mg, P:Fe, P:Al, P:Na; and (4) Potassium-coupled ratios: K:C, K:N, K:P, K:S, K:Ca, K:Mn, K:Mg, K:Fe, K:Al, K:Na. Carbon, N, P and K were chosen as the numerators of the element ratios, because they are biogenic macro-elements for biota in the ecosystem (Wang et al. 2021). In previous studies, the change of micro-climate, UV radiation and biota, and deposition of ash after burn significantly altered the content of C, N, P and K (Kuzmina et al. 2024; Gao et al. 2025). Furthermore, the variation of C, N, P and K is tightly linked to metal elements through complexing to metal elements or biota activities (Gray & Dighton 2006; Butler et al. 2019).

Statistical analysis

We used a repeated-measures ANOVA (IBM SPSS Statistics 25) to test the effects of burn, UV, litter species, mesh size, and time on element concentration or each one of 33 stoichiometric ratios. Time was included as a within-subject factor; burn, UV, litter species, and mesh size were included as between-subject factors; and a full factorial model was used. Principal component analysis (PCA) on mean litter element concentrations was conducted in order to detect the relationship among them. Fire effects on the mean of each one litter stoichiometric ratios were also quantified as log-transformed response ratios:

$$R_B = \ln\left(\frac{X_{\text{burn}}}{X_{\text{control}}}\right) \quad (1)$$

where X_{burn} is the mean of one element stoichiometric ratio (e.g., C:Fe) in burn treatments, and X_{burn} is the mean of one element stoichiometric ratio (e.g., C:Fe) in control treatments. Values of $R_B > 0$ and < 0 indicate that element stoichiometric ratio values of burn treatments were larger and smaller, respectively, than the control treatments. Ultraviolet radiation effects on the mean of each litter stoichiometric ratio were also quantified as response ratios.

$$R_{UV} = \ln\left(\frac{X_{\text{UV-pass}}}{X_{\text{UV-block}}}\right) \quad (2)$$

where $X_{\text{UV-block}}$ is the mean of one stoichiometric ratio (e.g., K:Na) in UV-block treatments, and $X_{\text{UV-pass}}$ is the mean of one stoichiometric ratio (e.g., K:Na) in UV-pass treatments. Values of $R_{\text{UV}} > 0$ and < 0 indicate that element stoichiometric ratio values of UV-pass treatments were larger and smaller, respectively, than the UV-block treatments. Pearson correlations and redundancy analysis (RDA) tested associations between arthropod diversity and densities with element concentration or stoichiometric ratios. The PCA and RDA were conducted using CANOCO software, version 5.02 (Microcomputer Power, Ithaca, USA). Pearson correlation analysis was conducted using SPSS software (version 25). The differences of K:C, K:N, K:P, K:S, K:Mg, and K:Na among treatments at every sampling data were analyzed using two-way ANOVAs, with burn and UV treatments as factors. Stoichiometric ratio data were natural log-transformed before all statistical analyses and preparatory calculations (Isles 2020). The other data violating normality or homogeneity assumptions (Levene's test) were log-transformed. Significance was assessed at $P < 0.05$.

Results

Litter elemental concentrations

Fire significantly increased the concentrations of Mn, Mg, Fe, and Al, and decreased K concentration in decomposing litter (Table 1). We note here that the responses of these litter elements to prescribed burning at the same site from ambient grassland without UV-block or UV-pass planes have been reported previously; however, litterbags in this study were taken from a UV-block or UV-pass plane with different microclimates than the ambient grassland. Thus, effectively none of the litter element data presented here have been published elsewhere. UV radiation significantly increased litter K concentration (Table 1). Litter of *M. maximus* had significantly higher concentrations of P, S, Ca, Mg, and K than *D. annulatum* litter, which was richer in Mn, Fe, and Al (Table 1). Litterbag mesh size had a significant effect on the concentrations of all measured elements except P in decomposing litter. Concentrations of Al and Fe increased with the increase of litterbag mesh sizes, but Ca, Na, and S decreased with the increase of litterbag mesh sizes, and Mg and Mn concentrations were higher in medium than small and big mesh sizes. Potassium

Table 1 Repeated-measures ANOVA *P*-values for the effects of prescribed burn (B), ultraviolet radiation treatment (UV), litter species (S), litterbag mesh sizes (M), and days in the field (D) on litter P, S, Ca, Mn, Mg, Fe, Al, Na, and K concentrations

	B	UV	S	M	D	B×UV	B×D	U×D	Other interactions
P	0.311	0.776	**<0.001**	0.175	**0.025**	0.421	0.507	0.433	D×UV×S
S	0.990	0.564	**<0.001**	**0.005**	**<0.001**	0.231	0.522	0.421	D×UV×S, B×S
Ca	0.108	0.184	**<0.001**	**0.001**	**<0.001**	**0.001**	0.402	0.085	None
Mn	**0.001**	0.966	**0.001**	**0.013**	**<0.001**	0.120	**0.004**	1.000	D×M
Mg	**0.014**	0.843	**<0.001**	**0.032**	**<0.001**	**0.038**	0.119	0.880	None
Fe	**0.001**	0.930	**0.020**	**0.016**	**<0.001**	0.789	**0.001**	0.920	None
Al	**<0.001**	0.325	**0.002**	**0.015**	**<0.001**	0.375	**<0.001**	0.775	None
Na	0.313	0.520	0.085	**<0.001**	**<0.001**	0.453	**0.002**	0.725	D×M
K	**0.018**	**0.027**	**<0.001**	0.053	**<0.001**	0.235	0.907	0.261	None

Bold type highlights significant values ($P < 0.05$)

concentrations decreased significantly over the time of the study; all other element concentrations increased significantly over time. A burn×UV interaction significantly affected Ca and Mg concentrations of decomposing litter. Calium and Mg concentrations were increased by UV radiation in fire treatments, but were decreased by UV radiation in control treatments. The effect of fire on the concentrations of Mn, Fe, Al, and Na of decomposing litter changed over time (significant burn×time interaction). Prescribed burning increased the concentrations of Mn, Fe, Al at 347 days after fire, and increased Na concentration during 136–241 days after fire.

When we put all litter element concentrations into a PCA, the first principal component axis accounted for 45.6% of the variability in litter element concentrations, mainly dominated by K and P concentrations (Fig. 1). The load values of K and P concentrations for the first PC were 0.41 and 0.49, respectively. The second principal component axis accounted for 28.9% of the variability in litter element concentrations, which is mainly dominated by Al, Fe, Mn, and Mg concentrations (Fig. 1). The load values of Al, Fe, Mn, and Mg concentrations for the second PC were 0.46, 0.47, 0.43, and 0.47, respectively.

The relationship between litter elemental concentrations and arthropods

The concentrations of specific litter elements were strong predictors of arthropod community structure, with micronutrients like Mn and Fe acting as attractants while high potassium acted as a deterrent.

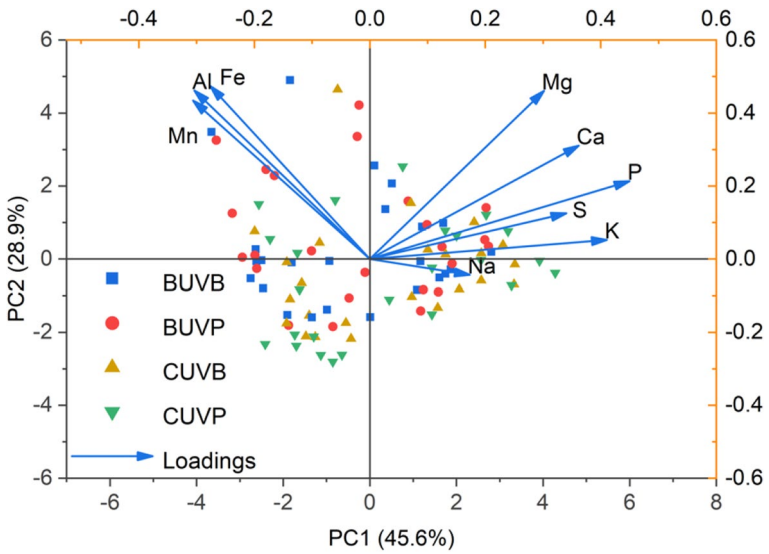

Fig. 1 Principal component analysis (PCA) of mean element concentrations in litter. BUVB, burn UV-block; BUVP, burn UV-pass; CUVB, control UV-block; CUVP, control UV-pass

Manganese concentration was positively correlated with total arthropod density, diversity (Shannon–Wiener Index), and the density of microbivores, detritivores, and predators (Table 2). Fe concentration showed positive correlations with total arthropod density, diversity, microbivore density, and detritivore density.

K concentration was negatively correlated with total arthropod density, diversity, and the density of microbivores and detritivores, but positively correlated with herbivore density (Table 2). Na concentration negatively influenced the density of total arthropods, microbivores, and detritivores. Ca concentration was positively correlated with the density of all arthropod groups (Table 2). P and S concentrations were negatively correlated with total arthropod density and diversity.

Litter elemental stoichiometry

Prescribed burning and UV radiation generated distinct and significant shifts in the multi-element stoichiometric network of decomposing litter. Fire significantly reduced 20 of the 33 elemental ratios ($P < 0.05$, Fig. 2, Table S1 and S2). This included substantial declines in ratios involving C, N, and P coupled with metals, such as ln C:Fe of *M. maximus* litter (decreased 6.9%), ln N:Fe of *D. annulatum* litter (decreased 11.3%), and ln P:Al (decreased 190.8%) (Table S2). All potassium-coupled ratios also decreased significantly by burning (e.g., K:P, K:Mn, K:Fe, K:Al, K:Na;

Table 2 Pearson correlation coefficients (*r*) (and two-tailed probability values) for the nutrient concentrations of litter and the density, diversity of litter arthropods in litterbags

	P	S	Ca	Mn	Mg	Fe	Al	Na	K
Total arthropod density	−0.101**	−0.104**	−0.087*	0.169**	0.019	0.120**	0.130**	−0.110**	−0.158**
Shannon–Wiener Index	−0.095*	−0.124**	−0.075	0.277**	0.124**	0.261**	0.269**	0.044	−0.241**
Simpson's Reciprocal Index 1/D	−0.098*	−0.096*	−0.064	0.210**	0.081*	0.215**	0.226**	0.002	−0.167**
Microbivore density	−0.111**	−0.120**	−0.050	0.229**	0.063	0.168**	0.189**	−0.173**	−0.223**
Detritivore density	−0.123**	−0.141**	−0.062	0.274**	0.081*	0.213**	0.236**	−0.188**	−0.248**
Predator density	0.033	0.014	0.003	0.090*	0.070	0.059	0.086*	−0.020	−0.013
Herbivore density	< 0.001	0.118**	−0.023	−0.068	−0.037	−0.060	−0.059	0.055	0.092*
Scavenger density	0.007	−0.001	0.013	0.021	0.026	0.025	0.023	−0.012	−0.011
Omnivore density	0.045	−0.054	−0.056	0.034	−0.029	0.015	0.015	−0.035	−0.045

$n = 672$, the asterisk "**" represents $P < 0.01$ and "*" represents $P < 0.05$

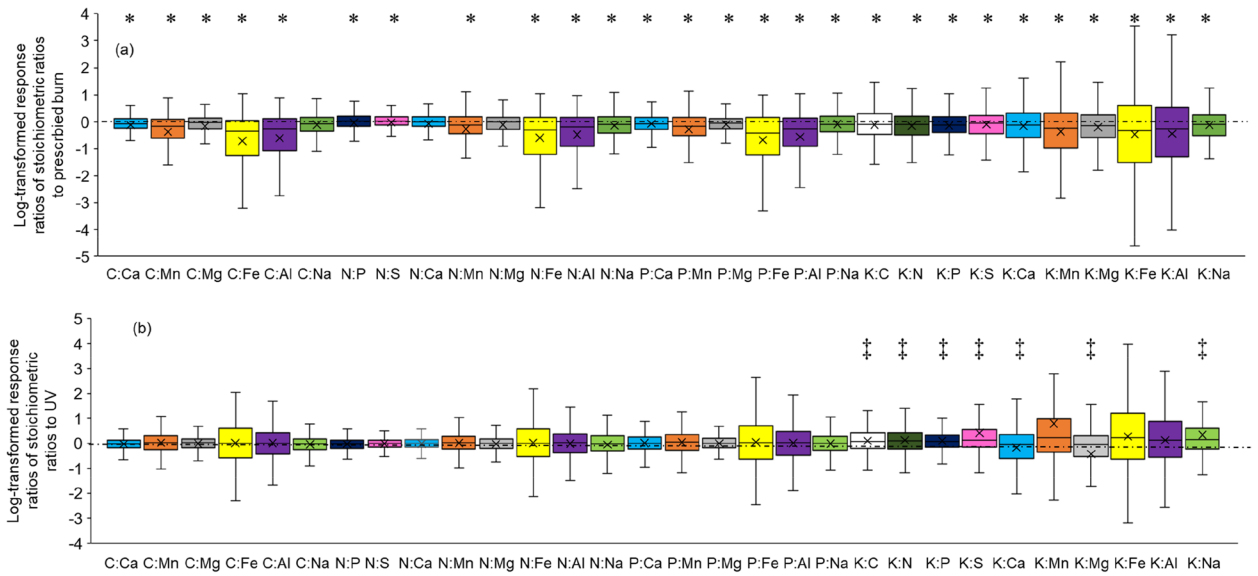

Fig. 2 Box and whisker plot showing response ratios of mean element stoichiometry in litter to prescribed burn (**a**) and UV (**b**) treatments. Means are displayed as a cross. Medians are displayed as solid lines inside boxes. Asterisks indicate the element stoichiometries were significantly affected by prescribed burning, and ‡ indicates the element stoichiometries were significantly affected by UV in the repeated-measures ANOVA analysis

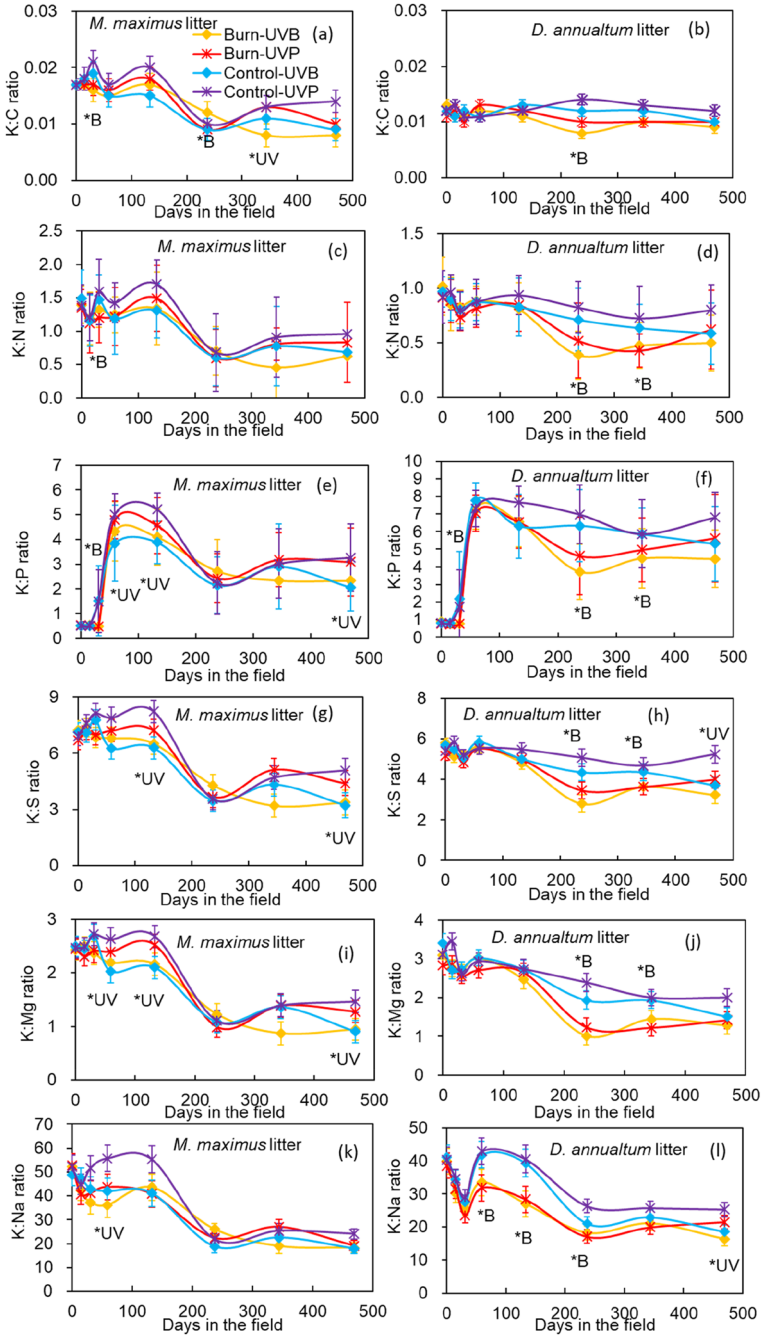

Fig. 3 Effect of prescribed burning and UV treatment on mean elemental stoichiometry of K:C (**a**, **b**), K:N (**c**, **d**), K:P (**e**, **f**), K:S (**g**, **h**), K:Mg (**i**, **j**), and K:Na (**k**, **l**) in *Megathyrsus maximus* (Jacq.) and *Dichanthium annulatum* (Forssk.) litter over time (UVB, UV-blocking; UVP, UV-passing, mean ± standard deviation, $n = 12$). Asterisks indicate significant differences among treatments for a given sampling date (B, prescribed burn; UV, UV treatment, $P < 0.05$)

all $P < 0.01$; Fig. 2, Table S1 and S2). UV radiation significantly increased K:P K:S, K:Mg and K:Na, such as ln K:Mg of *M. maximus* litter increased 39.6% (Fig. 2, Table S1 and S3). But K:C, K:N, and K:Ca were significantly decreased by UV radiation; ln K:Mg of *M. maximus* litter decreased 74.1% (Fig. 2, Table S1 and S3).

Litter of *Dichanthium annulatum* had significantly higher C:P, N:P, and K:Mg ratios than *Megathyrsus maximus* litter, whereas *M. maximus* litter exhibited higher ratios for metal-coupled pairs such as C:Mn, C:Fe, and K:Fe (Fig. 3, Table S1). Time had a significant effect on nearly all ratios. Carbon-coupled ratios increased during

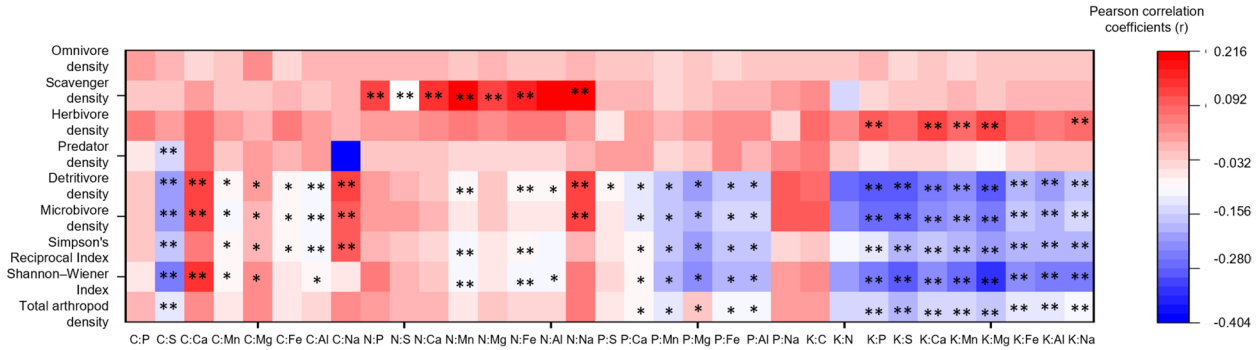

Fig. 4 Matrix of Pearson correlation coefficients (*r*) (and two-tailed probability values) for the element stoichiometry of litter and the density and diversity of litter arthropods in litterbags. $n = 672$, the asterisk "**" represents $P < 0.01$

the initial 62 days after fire, then declined. Nitrogen-coupled ratios increased during the initial 34 days after fire, then declined. The ratios of P:S, P:Mg, P:Fe, and P:Al decreased significantly over the time of the study, while ratios of P:Ca, P:Mn, and P:Na increased during the initial 62 days after fire, then declined. Potassium-coupled ratios reached the highest values at around 137 days after fire, then declined. Litterbag mesh size influenced several ratios. The ratios of C:Fe, C:Al, N:Mn, N:Fe, P:Mn, P:Mg, P:Fe, P:Al, and K:Fe were largest in small mesh size litterbags; the ratios of K:C, K:S, K:Ca, and KAl were largest in medium mesh size; the ratios of C:S, C:Ca, C:Na, N:Mg, N:Na and P:Na were largest in big mesh size. The ratios P:Ca, K:Ca, and K:Na were significantly affected by the interaction between fire and UV (burn × UV; $P < 0.05$; Fig. 3, Table S1).

Ultraviolet radiation significantly increased P:Ca, K:Ca, and K:Na ratios in the control treatment but did not affect these ratios under fire treatments. The effects of fire on most element ratios such as C:Ca, N:P, and N:Fe evolved over time (significant burn × time interaction; Table S1). These effects were explained by the significant decrease in C:Ca, C:Mn, C:Mg, C:Fe, C:Al, C:Na, N:Mn, N:Fe, N:Al, N:Na, P:Mg, P:Fe, P:Al, P:N, K:P, K:Mn, K:Fe, and K:Al and increase in N:P, N:S, and P:Mn by fire during 240–347 days after fire. The effects of UV radiation on K:N and K:S ratios evolved over time (significant burn × time interaction; Table S1), which were explained by the significant decrease in K:N and K:S ratios by UV around 136 and 347 days after fire.

The relationship between litter elemental stoichiometry and arthropods

The structure of the arthropod decomposer community was most strongly linked to the stoichiometric landscape, with multi-element ratios of litter explaining a substantial portion of the variation in arthropod density and diversity. The litter C:S ratio showed negative correlations with Shannon–Wiener index, Simpson's Reciprocal index, and the density of total arthropods, microbivores, detritivores, and predators (Fig. 4, Table S4). The C:Ca ratio was positively correlated with the Shannon–Wiener index and the density of microbivores, detritivores, and predators. The C:Mg ratios showed positive correlations with the Shannon–Wiener index and the density of detritivores. The C:Fe ratios negatively correlated with Shannon–Wiener index and Simpson's Reciprocal index but positively related to the density of herbivores. The C:Al and C:Na ratios showed negative correlations with Shannon–Wiener index and Simpson's Reciprocal index. The density of microbivores and detritivores showed negative correlations with the C:Al ratio but positive correlations with the C:Na ratio.

The N:P ratio showed positive correlations with the Shannon–Wiener index and the densities of total arthropods, microbivores, detritivores, and scavengers (Fig. 4, Table S4). The N:S ratio is positively related to the densities of total arthropods, microbivores, detritivores, and scavengers (Fig. 4, Table S3). The N:Ca ratio showed positive correlations with the densities of herbivores and scavengers. The N:Mn ratio was negatively correlated with the Shannon–Wiener index, Simpson's Reciprocal index, and the density of the densities of total arthropods, microbivores, detritivores and predators, but positively correlated with the densities of herbivores and scavengers. The N:Mg ratio was also negatively correlated with Shannon–Wiener index and Simpson's Reciprocal index but positively correlated with the densities of herbivores and scavengers. The N:Fe and N:Al ratios were negatively correlated with Shannon–Wiener index, Simpson's Reciprocal index, and the density of total arthropods, microbivores, detritivores, and predators, but positively correlated with the density of herbivores.

The P:Na ratio was positively correlated with microbivore, detritivore, and scavenger densities (Fig. 4, Table S3). The ratios P:Ca, P:Mn, P:Mg, P:Fe, P:Al, K:C, K:N, K:S, and K:Mg showed negative correlations with the densities of all arthropods, microbivores, and detritivores. The Shannon–Wiener index and Simpson's

Reciprocal index were also significantly negative correlated with the ratios P:Ca, P:Mn, P:Mg, P:Fe, P:Al, K:C, K:N, K:S, and K:Mg. The P:S ratio was negatively associated with the density of detritivores. The P:Na ratio shows a positive correlation with the densities of microbivores and detritivores. The K:P ratio is positively related to the Shannon–Wiener and Simpson's Reciprocal index, and the densities of microbivores and predators. The ratios K:S and K:Ca showed negative correlations with the Shannon–Wiener indes and Simpson's Reciprocal index, and the density of all arthropod microbivores and detritivores, but positively related to herbivore density. The K:Mn ratio was negatively associated with the Shannon–Wiener index and Simpson's Reciprocal index, and the densities of total arthropods, microbivores, detritivores, and predators, but positively associated with herbivore density. The ratios K:Fe, K:Al, and K:Na showed negative correlations with the diversity index of Shannon–Wiener and Simpson's Reciprocal, and the density of all arthropods, microbivores, detritivores, and predators, but positive correlations with herbivore density.

In the RDA, the 33 elemental ratios explained 39.5% of variation in densities and diversity of litter arthropods (Fig. 5, Table 3). The RDA also showed that the ratios N:Mn, N:Na, C:S, K:Ca, and N:Ca ($p < 0.05$) played key roles in structuring densities and diversity of litter arthropods (Table 3).

Discussion

Fire as a reductive force and potassium paradox

Partly consistent with our first hypothesis, fire acted as a broad reductive force for carbon- and nitrogen-coupled ratios. The large declines in carbon- and nitrogen-coupled ratios with metals reflect the well-documented dual pathway of volatile loss of labile C and N versus the ash enrichment of non-volatile elements (Gray & Dighton, 2006). The increase in litter N:S of our study is consistent with a long-term, frequent prescribed burning study in a wet eucalypt forest, indicating that S volatilizes more readily than N (Butler et al. 2020). However, the decrease of K in other element ratios in our study was contrary to the relatively enriched K relative to other elements in the wet eucalypt forest (Bulter et al. 2020). Potassium was expected to enrich from ash (Bulter et al. 2020), but its high solubility led to rapid post-fire leaching in this high-rainfall system, demonstrating that elemental couplings are more sensitive indicators of the ecosystem-specific legacy of fire than concentrations alone. P-to-metal element ratios were significantly decreased by fire in our study, which is inconsistent with our hypothesis and diverges from the higher P:Mg in burned than no-burn plots in wet eucalypt forest (Butler et al. 2020). A possible reason for this discrepancy may be that the magnitude of immobilization of Ca, Mn, Mg, Fe, Al, and Na during litter decomposition by microbes was more than that of P deposition from ash in burn treatments.

UV radiation: the photochemical decoupler of potassium

Our second hypothesis was partly supported, as UV radiation consistently amplified K:P, K:S, K:Mg, and K:Na. We posit a dual mechanism for this decoupling: the suppression of microbial activity by UV reduces biotic potassium immobilization, increasing soluble pools. This positions potassium as a keystone element in photodegradation

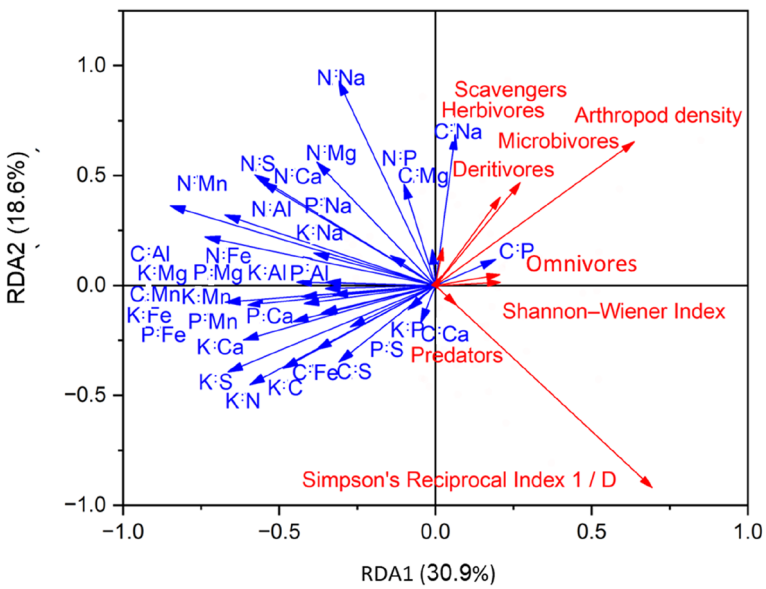

Fig. 5 Redundancy analyses (RDA) for the element stoichiometry of litter and the density and diversity of litter arthropods

Table 3 Results of redundancy analysis (RDA) showing the contribution of individual elemental ratios to explaining arthropod community variation

Variation	Litter elemental stoichiometry		
	Explanation (%)	Contribution (%)	*P*
N:Mn	6.8	17.3	0.002
N:Na	3.8	9.6	0.008
C:S	2.5	6.4	0.024
K:Ca	2.3	5.9	0.044
N:Ca	1.7	4.3	0.07
C:Fe	1.3	3.2	0.248
N:S	1.4	3.6	0.138
K:N	0.9	2.3	0.394
N:Al	1.0	2.6	0.374
K:C	1.0	2.5	0.362
K:Na	0.9	2.2	0.446
N:Mg	0.8	2.1	0.512
C:Mg	0.8	2.1	0.464
C:Mn	0.7	1.9	0.544
P:Al	0.7	1.8	0.572
K:Mg	0.7	1.9	0.576
K:S	0.7	1.8	0.618
C:Ca	0.8	2.4	0.436
K:P	0.6	2.6	0.346
N:P	0.8	1.9	0.526
P:Ca	1.0	2.1	0.346
C:Na	0.7	1.8	0.638
C:P	0.7	1.7	0.628
K:Al	0.9	2.0	0.362
P:Mn	0.8	1.9	0.55
P:Na	0.6	1.4	0.744
P:Mg	0.8	2.0	0.548
C:Al	0.4	1.1	0.832
K:Fe	0.9	2.1	0.374
N:Fe	1.0	2.2	0.23
P:Fe	0.6	1.5	0.732
K:Mn	0.6	1.5	0.708
P:S	0.2	0.5	0.99

cascades, although a decrease in K:C by UV radiation may be explained in part by inhibition of C loss by UV after 344 days of litter decomposing (Huang et al. 2021). Whereas previous studies have found that litter N:P and C:P ratios were higher in the presence of UV radiation (Ball et al. 2019), we found N:P and C:P ratios were not significantly affected by UV radiation. A possible reason for this discrepancy may be that P from ash deposition offsets the decline in P content by UV radiation.

Arthropod diversity is governed by stoichiometric niche filtering

Our most significant finding provides robust support for our third hypothesis: the reconfigured stoichiometric landscape acts as a powerful filter on the arthropod decomposer community after one year in subtropical pastureland. Our study is largely consistent with conclusions from subtropical eucalyptus forest that the responses of forest floor invertebrate communities to long-term fire regime are coupled with the shifts in the stoichiometry of basal resources (Bulter et al., (Butler, et al. 2021). The strong linkage between litter stoichiometry and arthropod communities may be explained by the greater mobility of invertebrates that should enable preferential grazing of more palatable litter components, as well as recolonization and community restructuring in response to changing nutrient availability (Butler et al. 2019). The important function of Ca, N, K, Na, and S in invertebrate structure and physiology may have contributed to the key roles of N:Na, C:S, K:Ca, and N:Ca in control of litter arthropod communities. First, Ca and N are essential for the structural components of the body tissues (Ott et al. 2014). Second, plants use K and animals use Na to maintain membrane gradients (Kaspari & Yanoviak, 2009). Third, S is a good indicator of S-rich defense structures and thus nutrient-rich plant material (Jochum et al. 2017).

The stoichiometric network legacy of interactive disturbances

Litter was collected from living grass prior to prescribed burning, and our study was conducted around 1 year after the fire. The rewiring of the multi-element stoichiometric network of decomposing litter mostly reflected (1) differences in immobilization of some metal elements by microbes between fire and control treatments, and (2) effects of the postfire abiotic environment; for example, litter bags were immersed in cation-rich ash deposited on the soil surface and UV radiation increased. Although in the long-term fire study, litter was collected from the forest floor several years after fire, shifts in litter stoichiometry were mainly caused by fire shifting plant nutrient cycling, for example the relative differences among elements in the energetic tradeoffs between acquiring that element from the environment (i.e., from soil or from the atmosphere in the case of C) versus re-absorbing that element from senescing tissue prior to leaf abscission (Butler et al. 2016, 2018, 2019, 2020, 2021).

Conclusions

Our study demonstrates that fire and UV radiation rewire litter stoichiometry towards metal-enriched, potassium-decoupled states, creating a stoichiometric filter that constrains the arthropod decomposer community. This underscores that moving beyond the C:N:P paradigm to a multi-element network perspective is crucial for a mechanistic understanding of how disturbances shape ecosystem processes. Furthermore, the diagnostic stoichiometric ratios we identified—such as N:Mn, N:Na, C:S, K:Ca, and N:Ca—serve as potential tools for land managers by providing quantifiable early-warning indicators of nutrient constraints and litter quality degradation following fire.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-026-00491-7.

Additional file 1.

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Statement on inclusion

Our study brings together authors from diverse national backgrounds, including scientists based in Puerto Rico who have long-term research experience in the response of tropical forests to disturbance. Every author was actively involved from the early stages of the study, and all contributed their perspectives. Relevant literature by local scientists was thoroughly cited, with additional efforts made to consider work published in the local language where appropriate.

Authors' contributions

Grizelle González and Xiaoming Zou designed the research. Wei Huang performed the experiment, analyzed the data, and wrote the manuscript. Grizelle González, Xiaoming Zou, and Weili Liu revised the manuscript.

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Data availability

Data will be made available on request.

Declarations

Ethics approval and consent to participate

Not applicable.

Competing interests

The authors declare no competing interests.

Author details

[1]Fujian Provincial Key Lab of Coastal Basin Environment, Fujian Polytechnic Normal University, Fujian 350300, China. [2]International Institute of Tropical Forestry, USDA Forest Service, Jardín Botánico Sur, 1201 Calle Ceiba, Río Piedras, San Juan, Puerto Rico 00926-1119, USA. [3]Jiangsu Academy of Agricultural Sciences, Institute of Agricultural Resources and Environment, Nanjing 210014, China.

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