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SHORT COMMUNICATION

Litter decomposition and arthropod composition under different ultraviolet levels following prescribed burn in a subtropical pastureland

Wei Huang[1,2,3] · Grizelle González[4] · María Fernanda Barberena-Arias[5] · Xiaoming Zou[1,2]

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Abstract

Reduction in faunal diversity is suggested to reduce litter decomposition, whereas increases in ultraviolet (UV) radiation may directly enhance or indirectly retard litter decomposition. Here we examined the effect of soil arthropods and UV radiation on litter decomposition in burned and unburned plots during a 469-day field experiment in a subtropical pastureland of Puerto Rico. Prescribed burn reduced soil arthropod diversity and increased UV radiation during the initial period of 240 days following the burn, and consequently reduced plant litter decomposition. The density of predators was lower in the burned than in control treatment. UV radiation reduced total arthropod density and diversity by retarding the recolonization of soil arthropods in the burned plots with reduced abundance of predators after 344 days post-burn incubation. Prescribed burn slowed down plant litter decomposition through direct reduction in arthropod diversity immediately after fire and through increase in UV radiation that retards the recolonization of arthropods in later stages after the prescribed burn in the subtropical pastureland.

Keywords Fire · Invertebrate · Litter decay · Puerto Rico · UV radiation

Introduction

Litter decomposition is a biogeochemical process fundamental to element cycling in terrestrial ecosystems (Bradford et al. 2016). Burning can mediate decomposition processes through changes in litter quality and quantity, decomposer community, and abiotic characteristics of the post-burn habitat (e.g. temperature, moisture, and solar irradiation) (O'Lear et al. 1996; Podgaiski et al. 2014). Burning causes a shift in the relative contribution of these three drivers to the pace of decomposition (Brennan et al. 2009). With more frequent burns, there is a marked increase in the functional importance of meso- and macroinvertebrate assemblages to litter decomposition (Brennan et al. 2009). Most studies have been concerned with the influence of changes in arthropod abundance post-burn incubation on litter decomposition (Brennan et al. 2009; Davies et al. 2013; Podgaiski et al. 2014). Furthermore, fire disturbances induce greater impact to soil arthropod diversity than to its abundance (Pressler et al. 2019). Several studies have shown empirical evidence on the relationship between terrestrial soil faunal diversity and litter decomposition rate (Cragg and Bardgett 2001; González et al. 2014; González and Seastedt 2000; Tresch et al. 2019), and greater arthropod species richness has been associated with faster decomposition in forests (Gessner et al. 2010).

Burning grass and woody plant canopies may increase solar radiation reaching the underlying litter on soil surface (Throop et al. 2017), resulting in changes in soil temperature, moisture, and ultraviolet (UV) radiation (Butler et al. 2019;

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✉ Xiaoming Zou
xzou2011@gmail.com

[1] College of Biology and the Environment, Nanjing Forestry University, 159 Longpan Road, Nanjing 210037, Jiangsu, China

[2] Department of Environmental Sciences, College of Natural Sciences, University of Puerto Rico, P.O. Box 70377, San Juan, PR 00936-8377, USA

[3] Key Laboratory of Coastal Basin Environment, Fujian Polytechnic Normal University, Fuqing 350300, Fujian, China

[4] International Institute of Tropical Forestry, USDA Forest Service, Jardín Botánico Sur, 1201 Calle Ceiba, Rio Piedras, PR 00926-1119, USA

[5] School of Sciences and Technology, Universidad Ana G. Méndez–Recinto de Gurabo, Gurabo, PR 00778, USA

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Podgaiski et al. 2014). The effects of UV radiation on litter decomposition can be directly through photochemical oxidation (Austin and Vivanco 2006; Lee et al. 2012) and indirectly through partially degrading litter and making it more vulnerable to biotic decomposition (King et al. 2012; Lin et al. 2015). The effects of UV radiation on decomposition rates also can be biotic by altering microbial and faunal communities and activities (Baker and Allison 2015; Smith et al. 2010; Verhoef et al. 2000). Although UV radiation is known as a dominant control of litter decay in arid and semiarid ecosystems (Bosco et al. 2016; Gliksman et al. 2017; Lin and King 2013), literature refers scarcely to mesic areas where soil fauna can sometimes exert pronounced influence on litter decomposition. Moreover, we found no studies on the contribution of UV radiation to litter decomposition in post-burn grassland ecosystems. Despite recent advances of photolysis and microbial decomposition by UV radiation (Baker and Allison 2015; Brandt et al. 2009; Brandt et al. 2010), the invertebrate-mediated litter decomposition under different UV levels has been largely ignored. To our knowledge, changes of soil arthropod diversity under different UV levels have not been reported for mesic grassland ecosystems in the subtropics.

We asked the following questions: (1) will plant litter decomposition in subtropical pastureland be affected by burn and UV radiation? (2) how may burn and UV radiation alter soil arthropod community composition? and (3) how do change in soil arthropod community affect plant litter decomposition after burning? We used litterbags to examine the process of litter decomposition responses to two levels of UV radiation in burned and unburned field sites over a period of 469 days in a subtropical mesic pastureland. We hypothesized that (1) prescribed burn will reduce soil arthropod diversity and increase site UV radiation; (2) the elevated UV radiation following prescribed burn will reduce arthropod density and diversity; and (3) reduction in soil arthropod diversity will slow down plant litter decomposition.

Materials and methods

Site description

The study was conducted in a pastureland of a USDA Forest Service Research Area in Guayama, located in southeastern Puerto Rico. The average annual temperature was 23 °C, and the average annual precipitation was 1693 mm. Soils are shallow Typic Haplustalfs (Muñoz et al. 2017), with pH 7 and bulk density of 1 g/cm^3. The clay loam soil (Boccheciamp 1977) contained 3.91% organic C and 0.32% total N in 15 cm surface layer. The study site was located on a relatively uniform slope of 3–5 degrees. The original vegetation in this area was subtropical moist forest. But this area, with an approximate area of 100 × 60 m, was deforested prior to 1937 and has been used as pastureland for horses from the nearby village since then. Periodic burning with a 1–5 years interval was typically practiced in this area over the last hundred years with the last event occurring in 2006. Two non-native grasses, *Megathyrsus maximus* (Jacq.) B.K.Simon & S.W.L.Jacobs and *Dichanthium annulatum* (Forssk.) Stapf, dominate the pastureland vegetation with a relative cover of 87% and 13% and standing biomass of 775 ± 196 g/m^2 and 357 ± 83 g/m^2, respectively. Some trees, shrubs, herbs, and vines occur sporadically in the pastureland (Supplementary Site description).

Field manipulation

We established eight 20 × 10 m rectangular plots in the pastureland. Four unburned plots were randomly assigned as control and four as burn treatment. The distance between each plot was around 5 m. Firebreaks (2 m width) around each plot were set up to avoid fire spread into the vegetation outside burn plots. The prescribed burn was carried out in the morning of 31 March 2017. Fire was ignited by fire gun. The plots were burned homogeneously; burn temperature was 537.5 °C at the litter layer. Aboveground shoots of herbs, grasses, shrubs, and vines were burned to death, but stems of trees remained alive. Regrowth of grasses was rapid in the post-burn raining season (April–August) with little regrowth of herbs, shrubs, and vines. There was no tree shading in the experimental plots during our experiment.

In each of the eight plots, we experimentally manipulated ultraviolet radiation (UV) using a pair of UV-blocking (UVB) and UV-passing (UVP) plastic panels (240 × 120 cm) sitting on aluminum frames at the height of 20 cm aboveground. The UVB treatment effect was achieved by using a polycarbonate panel which blocks 90% of UV-A and UV-B, optically equivalent to Lexan XL-1 (GE, Pittsfield, Massachusetts, USA). The UVP treatment effect was achieved by using a UV transparent acrylic panel which passes 90% of the solar spectrum, including UV-A and UV-B (Solacryl SUVT, Spartech Polycast, Stamford, Connecticut, USA). The UV manipulation can effectively pass or block UV radiation without substantially affecting temperature and photosynthetically active radiation (Brandt et al. 2007). To allow for penetration of precipitation to the covered ground, thirty-six holes of 1 cm diameter were drilled on each plastic panel 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). To minimize edge effects, we used a central 100 × 200 cm area under the plastic panels for the litterbag decomposition study.

Litterbags and arthropod collection

We constructed litterbags of 20 × 20 cm with three different mesh sizes. Small mesh size bags were made of cloth and had openings of 0.1 × 0.15 mm in size that were designed to allow microfauna (e.g. juvenile Oribatida) to enter and leave the bags. It also allowed a penetration of > 79% solar radiation (Supplementary Measure solar radiation penetration of litterbags). Medium mesh size bags were made of fiberglass and had openings of 1.5 × 1.5 mm in size that allowed micro- and mesofauna (e.g. Collembola and Hymenoptera) to enter and leave the bags with > 80% solar penetration. Large mesh size bags were made of fiberglass and had openings of 6 × 6 mm in size that allowed micro-, meso-, and macrofauna (e.g. some Blattodea and Orthroptera) to enter and leave the bags with a penetration of > 95% solar radiation. Litterbags of small and medium mesh sizes did not exclude meso- and macrofauna of juveniles successfully in this study; thus, we present our data by pooling data from all three mesh sizes for all analyses.

Lignin content of *M. maximus* and *D. annulatum* was around 10% and 7%, respectively (Fortes et al. 2016; Meyer and Brown 1985; Oliveira et al. 2018; Ramírez et al. 2005). Carbon concentration and C/N were significantly greater for *M. maximus* than *D. annulatum* ($P < 0.05$); C/P, N/P, and C/Ca of *D. annulatum* were significant higher than those of *M. maximus* ($P < 0.05$); N concentration did not differ between these two species (Table S1). For the initial setup of the experiment, aboveground shoots of *M. maximus* and *D. annulatum* were collected from the study site in November 2016, then grass material was cut into segments of approximately 20 cm in length and air-dried. Each litterbag was filled with 10 g of *M. maximus* or *D. annulatum*. Stem and leaves (both blades and sheaths) from these two grass species were put in litterbags. We placed 48 litterbags under each UV panel in each plot 3 days after the prescribed burn (3 April 2017). Two nails were used at opposite corners of each bag to secure it to the ground and to ensure direct contact with soil surface. Litterbags were recovered after 0, 15, 31, 59, 133, 237, 344, and 469 days in the field. At each collection, 12 bags per plot were retrieved with 6 litterbags representing the two grass species and three mesh sizes in the UV blocking and 6 litterbags in the UV passing treatments for a total of 96 bags/collection with eight collections. An initial (day 0) collection was used for correction of handling loss.

After each collection, the litter sample was removed from each litterbag and placed in Tullgren funnels for arthropod extraction (González and Seastedt 2001). All collected arthropods were counted, measured for body size, and identified to morphospecies. Morphospecies were assigned to broad trophic groups, based on the known biology of the taxa (Borror et al. 1989; Dindal 1990; Hoy 2009; McAlpine et al. 1981). Trophic groups were defined as detritivores (comminuters of litter), microbivores (feeding on fungi, bacteria, protozoa, and small detrital particles), herbivores, predators, scavengers, and omnivores. Shannon–Wiener Index and Simpson's reciprocal index were used to indicate arthropod diversity (Richardson et al. 2010; Wang et al. 2015). After arthropod extractions, the litter samples were oven dried at 65 °C for 5 days to obtain mass remaining and prepare for chemical analysis. Soil on the surface of litter was cleaned by brushing before weighting remaining mass. Arthropod densities were standardized to abundance per gram of dry litter.

Microclimatic measurements

We placed one data-logging temperature and relative humidity (RH) sensor (I-button, Dallas Semiconductor) hanging underneath each UVB and UVP panel to record air temperature and RH once at hourly interval. We used a UV radiometer (UV-X, UV Products, Upland, California, USA) to measure UV levels above litterbags under UVB and UVP panels of each plot between 10:00 am and 11:00 am everyday of litterbag collection.

Chemical analysis

Litter samples were dried at 65 °C, then ground to pass through an 18-mesh sieve (González et al. 2014). Total C and N for the litter samples were determined using the macro dry combustion method by means of the LECO TruSpec CN Analyzer (González et al. 2014) at the USDA IITF Chemistry Laboratory in Río Piedras, PR.

Statistical analysis

A nested, repeated measures ANOVA model was used to assess the effects of prescribed burn (burn vs. control), UV treatment (UVB vs. UVP), litter species, and time on percent mass remaining (PMR), percent of remaining C and N, C/N, microclimate, arthropod density, arthropod diversity indices, and density of trophic groups. We used subplot as a random effect, nested within prescribed burn and UV treatment. The effect of prescribed burn and UV treatments on percent mass remaining (PMR), percent C and N remaining, litter C/N, and arthropod communities at one sampling date were tested by two-way ANOVA. All data were tested for homogeneity of variance by using the Levene's test of equality of error variances and skewness. Log transformations were employed when the data did not meet the assumptions of normality. All ANOVA and Levene's test were conducted using JMP Pro 14.0 (SAS Institute, Cary, USA).

We used structural equation modeling (SEM) to disentangle linkages and relative contribution to decomposition by three main drivers: litter quality (C/N), physical environment (microclimate, UV radiation), and biota (arthropod diversity and trophic groups). We constructed two sets of SEM models

to compare the relative importance of different drivers during the initial 18–240 days post-burn and after 240 days post-burn incubation (i.e., after exposing litter for 344 days to UV) for litter PMR (Supplementary Statistical Analysis). All SEM analyses were performed with Amos 24.0 (Amos Development Co., Armonk, NY, USA).

Results

Litter decomposition

Litter decomposition was accelerated after 133 days in the field in mid-August, thus did not fit the simple negative exponential model (Fig. 1a). There was a significant effect of burn × time and UV × time for PMR in litterbags (Table S2, $P < 0.05$). Starting 31 days in the field, PMR was less in control plots than in burned plots ($P < 0.05$), and this reduced PMR in the control plots remained unchanged over the next two sampling dates. Litter PMR was overall not significantly affected by UV treatment, but greater mass was found in UVP treatment than in UVB treatment after exposing litter to UV for 344 days ($P < 0.05$). There was a significant effect of burn × UV for litter PMR at the last collection ($P < 0.05$). Litter PMR of the last collection was significantly higher in UVP than in UVB treatment in control plots ($P < 0.05$), but was not affected by UV in burned plots.

Microclimate

Burning increased UV radiation by 296% immediately after the burn. The higher UV levels in the burned plots lasted 136 days, except for day 59 collection (Fig. 1e, $P < 0.05$). There was a significant interaction between the burn and UV treatment (Table S3, $P < 0.05$), with burn + UVP having the highest UV level, whereas the control + UVB had the lowest UV level. There were no significant differences in air

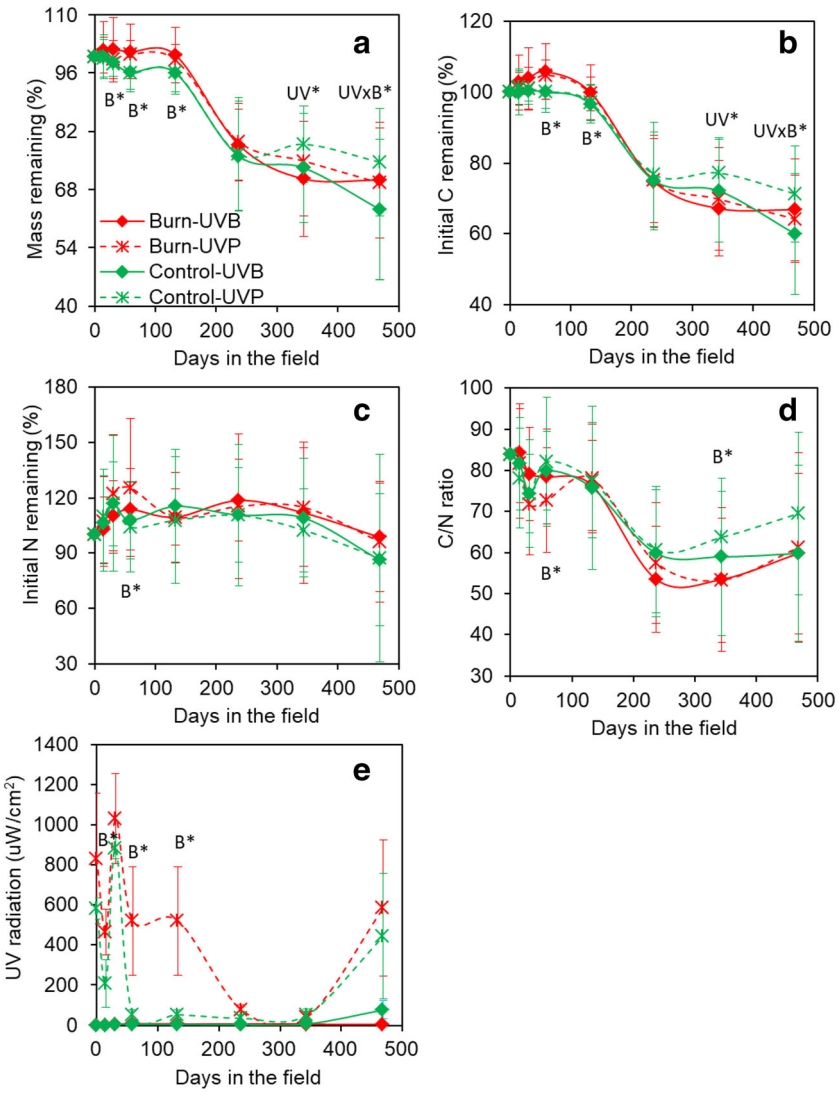

Fig. 1 The mean percentage of **a** mass remaining, **b** C and **c** N remaining, **d** C/N of the litter, and **e** UV radiation levels through time in the field after prescribed burn (mean ± standard deviation, $n = 24$; UVB: UV block, UVP: UV pass). Asterisks indicate significant differences among treatments for a given sample date (B-prescribed burn, UV-UV treatment, $P < 0.05$)

temperature and air RH between the control and burn treatments or between the UVB and UVP treatments (Fig. S1).

Litter quality

Litter PMR-C was affected by the interaction between burn and time (Table S2, $P < 0.01$), with significantly higher PMR-C in burned than in control plots at days 59 and 133 in the field (Fig. 1b, $P < 0.05$). Litter PMR-C and PMR-N were overall not affected by UV treatment (Table S2). Although on the 344th day collection, litter PMR-C was significantly lower in the UVB than in the UVP treatment (Fig. 1b, $P < 0$ .05). There was a significant effect of burn × UV for litter PMR-C at the last collection ($P < 0.05$). Litter PMR-C of the last collection was significantly higher in UVP than in UVB treatment in the control plots ($P < 0.05$), but was not affected by UV treatment in the burned plots. Litter PMR-N was overall not affected by burn, although it was higher in the burned than in the control treatment at day 62 post-burn (Fig. 1c, $P < 0.05$). Litter C/N during the process of decomposition was significantly affected by litter species (Table S2, $P < 0.01$). Overall litter C/N was not affected by burn and UV treatments. But at 62 and 347 days post-burn incubation, litter C/N was higher in the control than in the burned treatment (Fig. 1d, $P < 0.05$).

Litter arthropod communities

Burning had no overall effect on arthropod density and diversity indices, but significantly reduced the abundance of predators (Table S4 and Fig. 2d, $P < 0.05$). Lower predator density was found in the burned than in the control plots on the 240 days post-burn ($P < 0.05$). The UVP treatment had a negative effect on total arthropod density and Shannon–Wiener index (Table S4 and Fig. 2a, b, $P < 0.05$). Total arthropod density was significantly lower in the Burn-UVP than the Burn-UVB treatments at the last two collections ($P < 0.05$). There was a significant interaction between burn and time and between UV and time for Shannon–Wiener and Simpson's reciprocal index (Table S4, $P < 0.05$). Between 34 and 240 days post-burn incubation, litter arthropod Shannon–Wiener and Simpson's reciprocal index were higher in the control plots than in the burned plots; but towards the end of post-burn incubation, litter arthropod Shannon–Wiener and Simpson's reciprocal index were higher in the burned plots than in the control plots (Fig. 2 b and c, $P < 0.05$). Ultraviolet radiation had significantly negative effect on arthropod Shannon–Wiener and Simpson's reciprocal index after exposing litter to UV for 344 days. Levels of UV also significantly decreased arthropod Shannon–Wiener index at days 59, 133, 344, and 469 in the field (Fig. 2b, $P < 0.05$). At 34 days post-

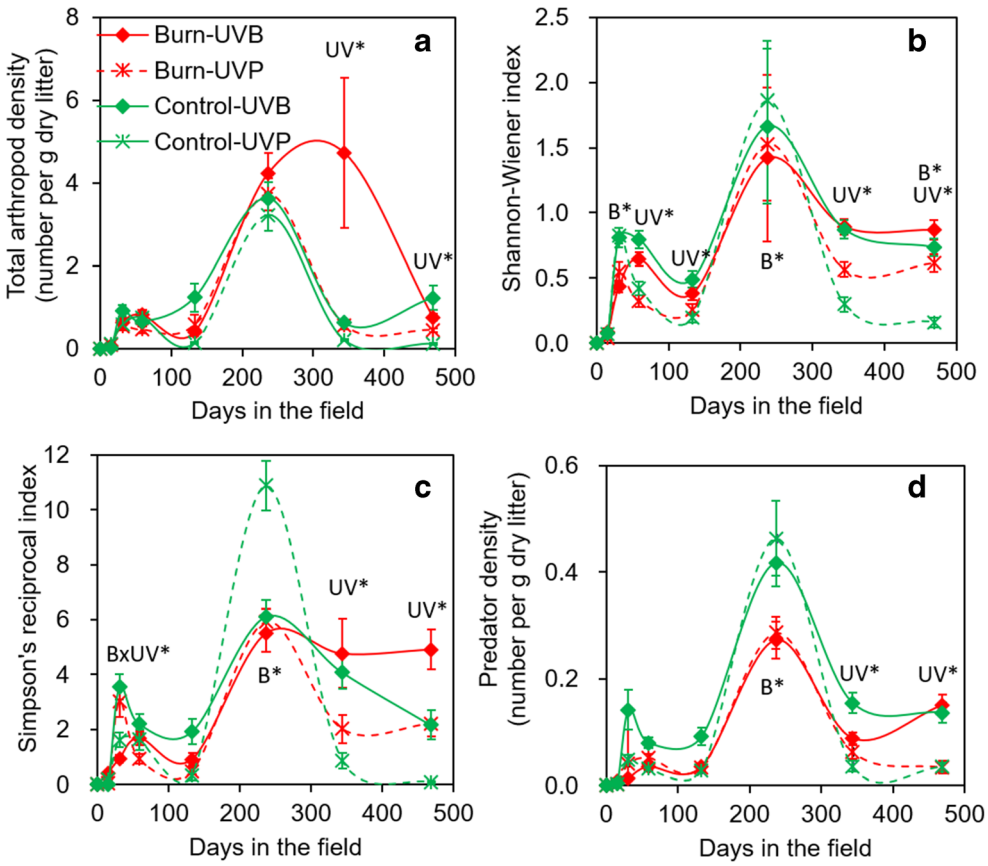

Fig. 2 Effect of prescribed burn and UV treatment on total arthropod **a** density and **b**, **c** diversity, and **d** predator density (number of per gram dry litter) over time (mean ± standard deviation, $n = 24$). Asterisks indicate significant differences among treatments for a given sample date (B-prescribed burn, UV-UV treatment, $P < 0.05$)

burn, there was a significant interaction between burn and UV for Simpson's reciprocal index ($P < 0.05$); Simpson's reciprocal index was significant higher in control than in burned plots under UVB treatment ($P < 0.05$), while Simpson's reciprocal index was not affected by burn under UVP treatment ($P < 0.05$). Predator density was lower at UVP than UVB treatment after exposing litter to UV for 344 days (Fig. 2d, $P < 0.05$).

The relative importance of microclimate, litter quality, and litter arthropod communities for litter decomposition

The two structural equation models were separately constructed for the periods for 18–240 days post-burn incubation and after 240 days post-burn incubation (Fig. 3). These two models explained about 56% of the variance in litter PMR between days 18–240 post-burn incubation (Fig. 3a) and 48% in litter PMR after 240 days post-burn incubation (Fig. 3b). During the initial period between days 18–240 post-burn incubation, arthropod Shannon–Wiener index ($r = -0.28$) and microbivores densities ($r = -0.30$) accounted for the most variation in litter PMR (Fig. 3a; Table S5). Higher arthropod Shannon–Wiener index and microbivore densities corresponded with lower litter PMR. Herbivore density was positively related with litter PMR. Microbivore, herbivore, and predator density indirectly and negatively affected litter PMR through their positive link with arthropod Shannon–Wiener index (Fig. 3a). Litter C/N had direct and positive influence on litter PMR and was also indirectly linked with litter PMR through its negative effect on arthropod Shannon–Wiener index and microbivore and predator densities. Direct and negative air RH effect on litter PMR was considerably lower than its indirect and negative effect on litter PMR through changing arthropod Shannon–Wiener index, densities of microbivore and predator, and litter C/N (Fig. 3a; Table S5). After 240 days post-burn incubation, UV radiation ($r = -0.10$), microbivore density ($r = -0.12$), and litter C/N

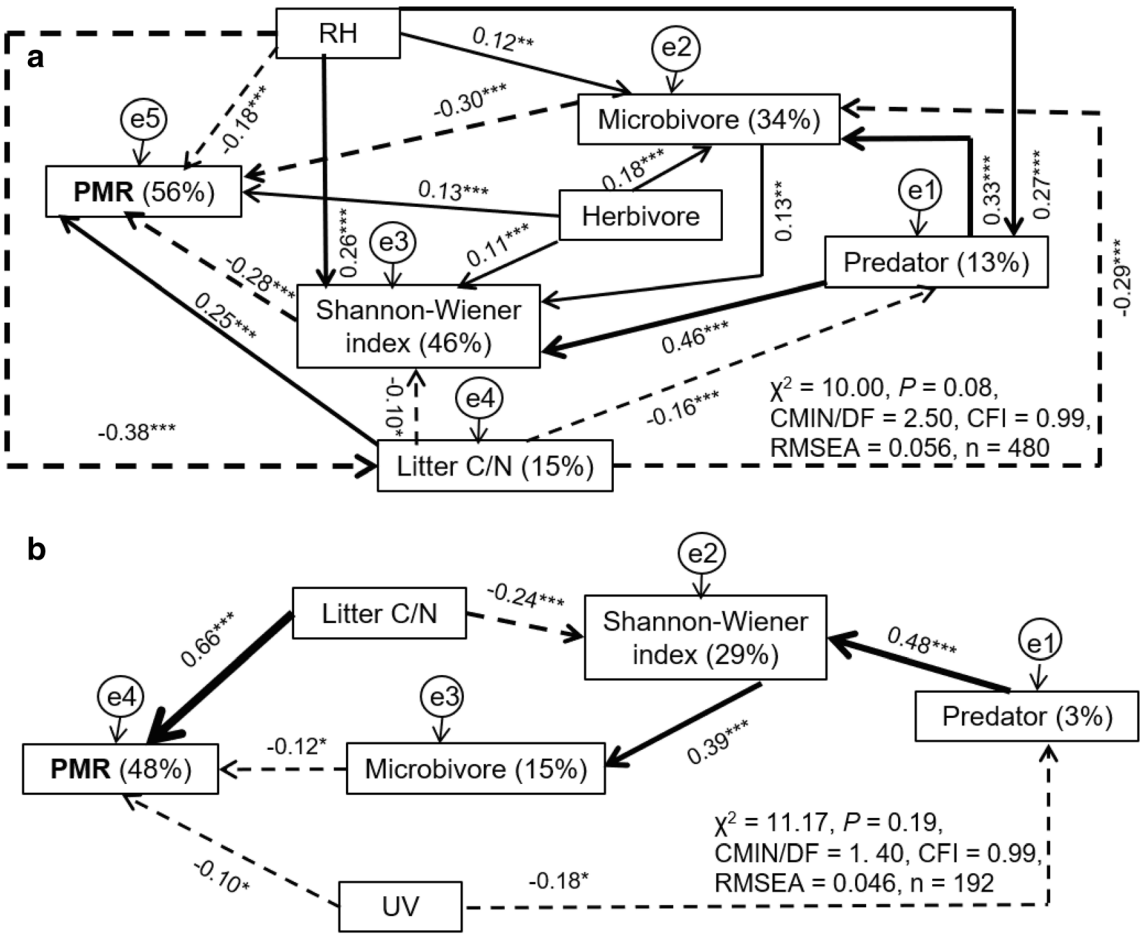

Fig. 3 Structural equation model depicting the direct and indirect influences of relative humidity, litter C/N, arthropod diversity, and densities of arthropod trophic groups on litter percent mass remaining **a** during 18–240 days post-burn incubation and **b** after 240 days post-burn incubation (i.e., after exposing litter 344 days to UV). Boxes indicate measured variables; circles indicate error terms of endogenous variables. Continuous and dashed arrows represent positive and negative relationships, respectively. The widths of the arrows are proportional to the strengths of the path coefficients. Numbers on the arrows are standardized regression weights. Percentages in parentheses near endogenous variables are the variances explained by the model (R^2). *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$

($r = 0.66$) accounted for the most variation in litter PMR (Fig. 3b). UV radiation also had an indirect and positive effect on litter PMR through decreasing predator density (Fig. 3b; Table S5). Predator density had indirect and negative influence on litter PMR through increasing arthropod Shannon–Wiener index. Arthropod Shannon–Wiener index had an indirect and negative influence on litter PMR by increase microbivore density. Microbivore density negatively affected litter PMR.

Discussion

Although there was lack of overall impact of burning on arthropod density and diversity, prescribed burn reduced arthropod diversity on days 34 and 240 post-burn incubation. Furthermore, prescribed burn reduced predator density. Thus, we can only partially accept our first hypothesis that prescribed burn reduces arthropod diversity. The lack of apparent burning effect on arthropods might attribute to that (1) soil arthropods have the ability to move into soil pore spaces during burning (Pressler et al. 2019) and (2) the placement of litterbags in burned plots may provide habitats attracting arthropods from surrounding area (in addition to the litterbag covered area) to colonize. Consistent with our first hypothesis, prescribed burn increased site UV radiation in the initial 136 days post-burn with the removal of vegetation canopy.

Supporting our second hypothesis, UV played an important role in controlling both arthropod density and diversity, especially during later stage of litter decomposition. Burning increases UV radiation after the removal of vegetation canopy. The elevated UV radiation can suppress biotic activity and diversity (Baker and Allison 2015; Lee et al. 2012). We found that UV radiation reduced the abundance and diversity of soil arthropods in the control plots as well as inhibited the recolonization of arthropods in the burned plots, and shading from UV radiation was found to increase arthropod abundance. High doses of ultraviolet A radiation are usually harmful to insects, inducing reactive oxygen species (ROS) damage and apoptosis (González et al. 2008; Meng et al. 2010; Zhang et al. 2011). Direct exposure of arthropods to ultraviolet B radiation usually affects their behavior and induces stress responses that can result in changes in their physiology and biochemistry (Jung et al. 2011). Therefore, direct exposure of arthropods to high dose of UV often induces an avoidance behavior (Ben-Yakir and Fereres 2016). Thus, arthropod species diversity and density significantly decreased after exposing for 344 days to UV. Thus, we accept our second hypothesis that the elevated UV radiation following prescribed burn will reduce arthropod density and diversity.

In line with our third hypothesis, the reduced litter arthropod diversity following the prescribed burn and elevated UV radiation attributed to the decrease of litter decomposition. However, there was a temporal variation in the relative effect of burning and UV radiation on arthropod diversity. While burning reduced arthropod diversity at the initial stage following the prescribed burn (< 240 days), UV radiation reduced arthropod diversity during later stage of greater than 240 days post-burn. Our results coincided with the results of Brennan et al. (2009) in Coastal Blackbutt (*Eucalyptus pilularis*) forest, whose study indicated that the decreased decomposition following burn were attributed to the declines in invertebrate decomposers. Burning can not only directly reduce arthropod diversity, but also indirectly through food web response to the altered predators. Schneider and Maraun (2009) reported that increased predator density resulted in a decrease in the densities of dominant groups of soil arthropods in a laboratory experiment. In our study, predator density was significantly higher in control than in burned plots at 237th day collection in the field, which may lead to the lower arthropod density in control than in burned plots at 344th day collection where UV radiation was blocked. After 240 days post-burn, arthropod diversity was not significantly lower in the burned than the control plots; thus, litter PMR was not significantly affected by burn after 240 days post-burn. Instead, UV radiation played a pronounced role in reducing arthropod diversity and consequently litter decomposition during the later (> 240 days) stage of post-burn incubation. We therefore accept our third hypothesis.

Our analyses of abiotic (RH, UV radiation, litter C/N) and biotic (arthropod composition) controls revealed only around 50% variation in litter decomposition. This suggests the important role of soil microbes and other litter chemical quality (e.g. lignin/N) in regulating decomposition processes that was not the focus of this study. Soil microbial abundance and activities was reduced by burn (Holden et al. 2012), facilitated (Baker and Allison 2015) or inhibited (Hughes et al. 2003) by UV radiation. Microbial activity can also be indirectly simulated by soil fauna (Hattenschwiler et al. 2005). Soil fauna consume and break up litter in the early decomposition stages (Coûteaux et al. 1995). Thus, the effect of arthropod Shannon–Wiener diversity on litter PMR was relatively direct and more important in the early stage than later stage of litter decomposition as shown in our structural equation models. Similar results were obtained by Liu et al. (2019), who found that soil fauna promoted litter carbon release within the first 212 decay days.

Conclusions

We demonstrated that burn and UV radiation are important controls of litter decomposition through their mediation on soil arthropods in this mesic subtropical pastureland of Puerto Rico. These two factors control litter mass loss during different stages of decomposition. Burning slowed litter mass

loss during the initial stage of 18–240 days post-burn through decreasing species diversity of litter arthropods. The increased UV radiation following the burning hampered litter mass loss after 240 days post-burn (i.e. after exposing litter for 344 days to UV) by inhibiting the recolonization of arthropods and by decreasing litter arthropod density and species diversity. Future studies should address whether changes in UV radiation differ under different fire regimes and how these changes in UV radiation might alter soil diversity (both soil microbes and fauna) and biogeochemical processes.

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Authors' contributions Zou X and González G designed the experiment. Huang W and Zou X conducted the field and lab work. Barberena-Arias helped identify arthropods. Huang W analyzed the data and wrote the manuscript. All authors reviewed the manuscript.

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Compliance with ethical standards

Competing interests The authors declare that they have no conflict of interest.

References

Austin AT, Vivanco L (2006) Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442:555–558. https://doi.org/10.1038/nature05038

Baker NR, Allison SD (2015) Ultraviolet photodegradation facilitates microbial litter decomposition in a Mediterranean climate. Ecology 96:1994–2003. https://doi.org/10.1890/14-1482.1

Ben-Yakir D, Fereres A (2016) The effects of UV radiation on arthropods: a review of recent publications (2010–2015). Acta Hortic: 335–342. https://doi.org/10.17660/ActaHortic.2016.1134.44

Boccheciamp RA (1977) Soil survey of the Humacao area of eastern Puerto Rico. NRCS USDA Publishing PhysicsWeb. Ttps://www.nrcs.usda.gov/Internet/FSE_MANUSCRIPTS/puerto_rico/PR689/0/Humacao.pdf. Accessed January 1977

Borror DJ, Triplehorn CA, Johnson NF (1989) An introduction to the study of insects. Saunders college publishing, Philadelphia

Bosco T, Bertiller MB, Carrera AL (2016) Combined effects of litter features, UV radiation, and soil water on litter decomposition in denuded areas of the arid Patagonian Monte. Plant Soil 406:71–82. https://doi.org/10.1007/s11104-016-2864-7

Bradford MA, Berg B, Maynard DS, Wieder WR, Wood SA, Cornwell W (2016) Understanding the dominant controls on litter decomposition. J Ecol 104:229–238. https://doi.org/10.1111/1365-2745.12507

Brandt L, Bohnet C, King J (2009) Photochemically induced carbon dioxide production as a mechanism for carbon loss from plant litter in arid ecosystems. J Geophys Res-Biogeo 114:114. https://doi.org/10.1029/2008JG000772

Brandt LA, King JY, Milchunas DG (2007) Effects of ultraviolet radiation on litter decomposition depend on precipitation and litter chemistry in a shortgrass steppe ecosystem. Glob Chang Biol 13:2193–2205. https://doi.org/10.1111/j.1365-2486.2007.01428.x|

Brandt LA, King JY, Hobbie SE, Milchunas DG, Sinsabaugh RL (2010) The role of photodegradation in surface litter decomposition across a grassland ecosystem precipitation gradient. Ecosystems 13:765–781. https://doi.org/10.1007/s10021-010-9353-2

Brennan KEC, Christie FJ, York A (2009) Global climate change and litter decomposition: more frequent fire slows decomposition and increases the functional importance of invertebrates. Glob Chang Biol 15:2958–2971. https://doi.org/10.1111/j.1365-2486.2009.02011.x

Butler OM, Lewis T, Rezaei Rashti M, Maunsell SC, Elser JJ, Chen C (2019) The stoichiometric legacy of fire regime regulates the roles of micro-organisms and invertebrates in decomposition. Ecology 100: e02732. https://doi.org/10.1002/ecy.2732|

Coûteaux MM, Bottner P, Berg B (1995) Litter decomposition, climate and liter quality. Trends Ecol Evol 10:63–66. https://doi.org/10.1016/S0169-5347(00)88978-8

Cragg RG, Bardgett RD (2001) How changes in soil faunal diversity and composition within a trophic group influence decomposition processes. Soil Biol Biochem 33:2073–2081. https://doi.org/10.1016/S0038-0717(01)00138-9

Davies AB, van Rensburg BJ, Eggleton P, Parr CL (2013) Interactive effects of fire, rainfall, and litter quality on decomposition in savannas: frequent fire leads to contrasting effects. Ecosystems 16: 866–880. https://doi.org/10.1007/s10021-013-9657-0

Dindal DL (1990) Soil biology guide. Wiley, New York

Fortes D, Valenciaga D, Garcia C, Garcia M, Cruz AM, Romero A (2016) Evaluation of three varieties of *Megathyrsus maximus* in the dry period. Cuban J Agr Sci 50:131–137

Gessner MO, Swan CM, Dang CK, McKie BG, Bardgett RD, Wall DH, Hattenschwiler S (2010) Diversity meets decomposition. Trends Ecol Evol 25:372–380. https://doi.org/10.1016/j.tree.2010.01.010

Gliksman D, Rey A, Seligmann R, Dumbur R, Sperling O, Navon Y, Haenel S, Angelis PD, Arnone JA III, Grünzweig JM (2017) Biotic degradation at night, abiotic degradation at day: positive feedbacks on litter decomposition in drylands. Glob Chang Biol 23:1564–1574. https://doi.org/10.1111/gcb.13465

González G, Seastedt TR (2000) Comparison of the abundance and composition of litter fauna in tropical and subalpine forests. Pedobiologia 44:545–555. https://doi.org/10.1078/S0031-4056(04)70070-0

González G, Seastedt TR (2001) Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology 82:955–964. https://doi.org/10.1890/0012-9658(2001)082[0955:sfapld]2.0.co;2

González G, Huang CY, Shu-Chun C (2008) Earthworms and post agricultural succession in the Neotropics. In: Myster RW (ed) Post-agricultural succession in the neotropics. Springer, Berlin, pp 115–138

González G, Lodge DJ, Richardson BA, Richardson MJ (2014) A canopy trimming experiment in Puerto Rico: the response of litter decomposition and nutrient release to canopy opening and debris deposition in a subtropical wet forest. Forest Ecol Manag 332:32–46. https://doi.org/10.1016/j.foreco.2014.06.024

Hattenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. Annu Rev Ecol Evol S

36:191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

Holden SR, Gutierrez A, Treseder KK (2012) Changes in soil fungal communities, extracellular enzyme activities, and litter decomposition across a fire chronosequence in Alaskan boreal forests. Ecosystems 16:34–46. https://doi.org/10.1007/s10021-012-9594-3

Hoy MA (2009) A manual of acarology. Texas Tech University Press, Lubbock

Hughes KA, Lawley B, Newsham KK (2003) Solar UV-B radiation inhibits the growth of Antarctic terrestrial fungi. Appl Environ Microb 69:1488–1491. https://doi.org/10.1128/AEM.69.3.1488-1491.2003

Jung I, Kim TY, Kim-Ha J (2011) Identification of *Drosophila* SOD3 and its protective role against phototoxic damage to cells. FEBS Let 585:1973–1978. https://doi.org/10.1016/j.febslet.2011.05.033

King JY, Brandt LA, Adair EC (2012) Shedding light on plant litter decomposition: advances, implications and new directions in understanding the role of photodegradation. Biogeochemistry 111:57–81. https://doi.org/10.1007/s10533-012-9737-9

Lee H, Rahn T, Throop H (2012) An accounting of C-based trace gas release during abiotic plant litter degradation. Glob Chang Biol 18:1185–1195. https://doi.org/10.1111/j.1365-2486.2011.02579.x|

Lin Y, King JY (2013) Effects of UV exposure and litter position on decomposition in a California grassland. Ecosystems 17:158–168. https://doi.org/10.1007/s10021-013-9712-x

Lin Y, King JY, Karlen SD, Ralph J (2015) Using 2D NMR spectroscopy to assess effects of UV radiation on cell wall chemistry during litter decomposition. Biogeochemistry 125:427–436. https://doi.org/10.1007/s10533-015-0132-1

Liu Y, Wang L, He R, Chen Y, Xu Z, Tan B, Zhang L, Xiao J, Zhu P, Chen L, Guo L, Zhang J (2019) Higher soil fauna abundance accelerates litter carbon release across an alpine forest-tundra ecotone. Sci Rep 9:10561. https://doi.org/10.1038/s41598-019-47072-0

McAlpine JF, Peterson BV, Shewell G, Teskey H, Vockeroth J, Wood D (1981) Manual of nearctic Diptera. Research Branch Agriculture Canada, Ottawa

Meng J, Zhang C, Lei C (2010) A proteomic analysis of *Helicoverpa armigera* adults after exposure to UV light irradiation. J Insect Physiol 56:405–411. https://doi.org/10.1016/j.jinsphys.2009.11.015

Meyer MW, Brown RD (1985) Seasonal trends in the chemical composition of ten range plants in south Texas. J Range Manag 38:154–157. https://doi.org/10.2307/3899260

Muñoz MA, Lugo WI, Santiago C, Matos M, Ríos S, Lugo J (2017) Taxonomic classification of the soils of Puerto Rico. https://dire.uprm.edu/handle/20.500.11801/817 Accessed 23 Jan 2018

O'Lear H, Seastedt T, Briggs J, Blair J, Ramundo R (1996) Fire and topographic effects on decomposition rates and N dynamics of buried wood in tallgrass prairie. Soil Biol Biochem 28:323–329. https://doi.org/10.1016/0038-0717(95)00138-7

Oliveira RL, Ribeiro OL, Bagaldo AR, Borja MS, Correia BR, Lima LS, Alba HDR, Leite VM, Bezerra LR (2018) Nutritional composition and fermentative characteristics of Massai grass silage added with licuri (*Syagrus coronata*) cake. Semina: Ciênc Agrár 39:1189. https://doi.org/10.5433/1679-0359.2018v39n3p1189

Podgaiski LR, Silva Goldas C, Ferrando CPR, Silveira FS, Joner F, Overbeck GE, Mendonça MS Jr, Pillar VD (2014) Burning effects on detritivory and litter decay in Campos grasslands. Austral Ecol 39:686–695. https://doi.org/10.1111/aec.12132

Pressler Y, Moore JC, Cotrufo MF (2019) Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. Oikos 128:309–327. https://doi.org/10.1111/oik.05738

Ramírez RG, González-Rodríguez H, García-Dessommes G, Morales-Rodríguez R (2005) Seasonal trends in chemical composition and digestion of *Dichanthium annulatum* (Forssk.) Stapf. J Appl Anim Res 28:35–40. https://doi.org/10.1080/09712119.2005.9706784

Richardson BA, Richardson MJ, González G, Shiels AB, Srivastava DS (2010) A canopy trimming experiment in Puerto Rico: the response of litter invertebrate communities to canopy loss and debris deposition in a tropical forest subject to hurricanes. Ecosystems 13:286–301. https://doi.org/10.1007/s10021-010-9317-6

Schneider K, Maraun M (2009) Top-down control of soil microarthropods – evidence from a laboratory experiment. Soil Biol Biochem 41:170–175. https://doi.org/10.1016/j.soilbio.2008.10.013

Smith WK, Gao W, Steltzer H, Wallenstein MD, Tree R (2010) Moisture availability influences the effect of ultraviolet-B radiation on leaf litter decomposition. Glob Chang Biol 16:484–495. https://doi.org/10.1111/j.1365-2486.2009.01973.x

Throop HL, Abu Salem M, Whitford WG (2017) Fire enhances litter decomposition and reduces vegetation cover influences on decomposition in a dry woodland. Plant Ecol 218:799–811. https://doi.org/10.1007/s11258-017-0730-1

Tresch S, Frey D, Le Bayon R-C, Zanetta A, Rasche F, Fliessbach A, Moretti M (2019) Litter decomposition driven by soil fauna, plant diversity and soil management in urban gardens. Sci Total Environ 658:1614–1629. https://doi.org/10.1016/j.scitotenv.2018.12.235

Verhoef HA, Verspagen JM, Zoomer HR (2000) Direct and indirect effects of ultraviolet-B radiation on soil biota, decomposition and nutrient fluxes in dune grassland soil systems. Biol Fert Soils 31:366–371. https://doi.org/10.1007/s003749900181

Wang S, Tan Y, Fan H, Ruan H, Zhen A (2015) Responses of soil microarthropods to inorganic and organic fertilizers in a poplar plantation in a coastal area of eastern China. Appl Soil Ecol 89:69–75. https://doi.org/10.1016/j.apsoil.2015.01.004

Zhang CY, Meng JY, Wang XP, Zhu F, Lei CL (2011) Effects of UV-A exposures on longevity and reproduction in *Helicoverpa armigera*, and on the development of its F1 generation. Insect Sci 18:697–702. https://doi.org/10.1111/j.1744-7917.2010.01393.x