



# Artificial Light at Night Impacts the Litter Layer Invertebrate Community With No Cascading Effects on Litter Breakdown

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Artificial light at night (ALAN) can impact the trophic structure of assemblages of ground-dwelling invertebrates, and changes in such assemblages can affect decomposition in terrestrial systems due to the various functional roles of these invertebrates, including microbial grazing, comminution of litter, and predation of other invertebrates, that can directly or indirectly affect plant-litter breakdown. Despite this, we are unaware of any studies that have evaluated the effects of ALAN on the breakdown of plant litter in a terrestrial ecosystem. We sought to answer whether ALAN affects litter breakdown via its effects on a community of ground-dwelling arthropods using two field experiments. In one experiment, we manipulated the presence of ALAN and the size classes of soil invertebrates that could enter mesh bags containing plant litter (litterbags). We found that the rate of plant-litter breakdown increased with the mesh size of litterbags but was unaffected by presence of ALAN. In a second field experiment carried out to examine the effects of ALAN on the trophic structure of litter-layer invertebrate communities, while controlling for potential effects of ALAN on vegetation, we again found that ALAN did not affect litter breakdown despite the fact that ALAN increased the abundances of secondary and tertiary consumers. Our finding that larger assemblages of ground-dwelling secondary and tertiary consumer invertebrates under ALAN did not slow litter breakdown through increased top-down control of detritivores suggests ALAN may disrupt predator-prey interactions in litter-layer communities.

**Keywords:** light pollution, ecosystem function, trophic structure, trophic cascade, grassland

## INTRODUCTION

Artificial light at night (hereafter ALAN) is a widespread sensory pollutant which currently affects nearly a quarter of the terrestrial surface of our planet (Gaston et al., 2014; Falchi et al., 2016, 2019; Kyba et al., 2017). It is widely considered to have extensive ecological consequences across levels of biological organization ranging from the organism (e.g., physiology and behavior) to the ecosystem (Longcore and Rich, 2004; Gaston et al., 2013, 2014). Most research documenting effects of ALAN has occurred at the organismal and population levels (Longcore and Rich, 2004; Hölker et al., 2010; Gaston et al., 2015; Sanders and Gaston, 2018). Perhaps the best evidence that ALAN

affects higher levels of organization are studies that have shown effects on multi-trophic structure or dynamics (Meyer and Sullivan, 2013; Bennie et al., 2018a; Grenis and Murphy, 2019; Sullivan et al., 2019). At the community level there is increasing recognition of the potential for ALAN to disrupt pollination (Knop et al., 2017; Macgregor et al., 2017; Giavi et al., 2020) as well as invertebrate food-web dynamics (Bennie et al., 2018a; Sanders et al., 2018; Maggi et al., 2019). However, effects of ALAN on the ecosystem processes of nutrient transfer and decomposition are largely unknown.

Decomposition is a critical ecosystem process driving nutrient transfer from dead organic matter to plant-available forms, which in turn can affect plant growth and carbon fixation (Bardgett, 2005). The structure and trophic dynamics of ground-dwelling invertebrate assemblages have profound effects on the decomposition of organic matter in terrestrial ecosystems (Moran et al., 1996; Heneghan et al., 1998; Schmitz, 2009; Hawlena et al., 2012; Tonin et al., 2018). For example, the presence of predatory invertebrates can slow decomposition by limiting the activity of detritivores, which break down plant material in the litter layer (Kajak, 1995; Lawrence and Wise, 2000; Schmitz et al., 2010; Hawlena et al., 2012). The opposite has also been found, wherein the absence of predatory invertebrates slows decomposition, which could be attributed to competition among prey invertebrates in the litter layer (Lawrence and Wise, 2004; Melguizo-Ruiz et al., 2020). Artificial light at night is known to impact the composition of invertebrate assemblages (Meyer and Sullivan, 2013; Davies et al., 2017; Manfrin et al., 2017; Desouhant et al., 2019) and their trophic dynamics (Sanders et al., 2015, 2018; Bennie et al., 2018a; Manfrin et al., 2018; Sanders and Gaston, 2018). Multiple studies have documented that ground-dwelling invertebrate assemblages under ALAN have higher abundances of predators such as arachnids and carabid beetles than those found in areas that are dark at night (Davies et al., 2012, 2017; Manfrin et al., 2017; McMunn et al., 2019; Willmott et al., 2019). The attraction of predators to ALAN-affected areas has been predicted to lead to increased top-down control (Sanders and Gaston, 2018). Given that (a) large ground-dwelling predatory invertebrates are capable of initiating trophic cascades (Moran et al., 1996; Schmitz, 2007, 2009; Hawlena et al., 2012) and that (b) greater numbers of these are observed in light-polluted conditions (Wolff, 1982; Davies et al., 2012, 2017; Holzhauser et al., 2015), ALAN may elicit indirect effects on decomposition by increasing the strength of top-down control over detritivores. Despite the observed effects of ALAN on trophic structure of ground-dwelling invertebrates (Davies et al., 2012, 2017; Meyer and Sullivan, 2013; Manfrin et al., 2017), the effects of ALAN on decomposition of organic matter in terrestrial systems are poorly understood.

Three interacting factors most strongly influence the rate of decomposition in terrestrial systems: abiotic conditions, litter nutritional quality (primarily nitrogen content), and the composition of soil fauna and microorganisms (Swift et al., 1979; Wardle et al., 2004; Hättenschwiler et al., 2005; García-Palacios et al., 2016). In the litter-layer food web there are typically up to three levels of consumers: primary, secondary, and tertiary. Primary consumers, including microorganisms (bacteria and

fungi) and invertebrate detritivores, feed directly on dead plant matter. Primary consumers drive most terrestrial decomposition (Swift et al., 1979; McGuire and Treseder, 2010). Detritivores enhance the activity of bacteria and fungi by fragmenting plant material, thereby increasing attackable surface area, and by depositing frass (Vossbrinck et al., 1979; Beare et al., 1992; Coleman et al., 2004). Secondary consumers, in contrast, can slow the breakdown of plant matter through their consumption of bacteria, fungi, or detritivores. In systems where decomposition is primarily driven by bacterial or fungal pathways, secondary consumers which regulate bacterial and fungal populations include protozoa, nematodes, and mites (Santos et al., 1981; Ruess and Ferris, 2004). Tertiary consumers can enhance the rate of decomposition by releasing microbial decomposers from predation from secondary consumers (Hedlund and Ohrn, 2000; Lawrence and Wise, 2004), and can also slow decomposition by exerting top-down effects on detritivores (Kajak, 1995; Lawrence and Wise, 2000; Hawlena et al., 2012).

We conducted two studies to explore the effects of ALAN on the breakdown of plant litter in a temperate grassland ecosystem through its effects on litter-layer fauna. First, to test for potential effects of ALAN on decomposition mediated by multitrophic interactions (e.g., trophic cascades), we carried out a field experiment in which we manipulated the presence/absence of ALAN and the size classes of soil fauna. We did this by quantifying rates of litter breakdown, or proportion decomposed over time, within litterbags of three different mesh sizes in plots that were exposed to ALAN or ambient light levels at night. Exclusion of soil organisms of different body sizes from plant litter has previously been used successfully to draw conclusions about how subsets of the invertebrate community belonging to different size classes influence decomposition (Vossbrinck et al., 1979; Setälä et al., 1996; Bradford et al., 2002). As litterbag mesh size is increased, the assemblages of invertebrates that establish within the litterbags increase in maximum organism body size, species richness (Bradford et al., 2002; Cole et al., 2006), abundance and diversity of secondary and tertiary consumers, and functional complexity (Setälä et al., 1996; Bradford et al., 2002; Smith and Bradford, 2003). A second field experiment was carried out to test effects of ALAN alone on the trophic composition of soil arthropods and plant litter breakdown, while controlling for potential effects of ALAN on vegetation (Bennie et al., 2016, 2018b; Grenis and Murphy, 2019), which could potentially affect invertebrate assemblages or litter decomposition. We manipulated the presence/absence of ALAN (as above), while controlling for potential effects of ALAN on above-ground vegetation by mowing all plots prior to the experiment. To characterize effects of ALAN alone on invertebrate trophic structure, we used litterbags of a single large mesh size. Based on previous findings documenting higher abundances of ground-dwelling predatory invertebrates under ALAN compared with unlit areas (e.g., Davies et al., 2012, 2017), and that tertiary consumers can slow decomposition (Kajak, 1995; Lawrence and Wise, 2000; Hawlena et al., 2012), we predicted that ALAN would reduce rates of litter breakdown indirectly via increased top-down control of primary consumers by secondary and/or tertiary consumers.

## MATERIALS AND METHODS

### Experimental Design

We conducted two experiments at Blandy Experimental Farm (BEF) in Boyce, Virginia, United States (39.0640°N, 78.0652°W). In the fall of 2017, we conducted an experiment to test the independent and interacting effects of ALAN and invertebrate size classes on decomposition of plant litter. The experiment was carried out in eight replicate plots, half exposed to ALAN and half receiving no added ALAN. Within each plot, we measured the decomposition of litter within mesh bags (litterbags), using litterbags with three different mesh sizes (0.1, 2, and 4 mm) to manipulate the size classes of fauna that could gain access to the litter. In the fall of 2018, we carried out a second experiment to for two primary reasons: (1) to control for potential effects of ALAN on vegetation (Bennie et al., 2016, 2018b; Grenis and Murphy, 2019), which could potentially affect invertebrate assemblages or litter decomposition, and (2) to test effects of ALAN on the trophic composition of soil arthropods. This experiment was carried out in ten replicate plots, five with ALAN added and five with no ALAN added. To control for potential effects of ALAN on vegetation, we minimized differences in vegetation height and biomass by mowing all plots prior to the start of the experiment. To examine the effects of ALAN on arthropod trophic composition, we deployed litterbags in the second experiment that would allow us to recover larger numbers of arthropods than we could in the previous experiment. This was accomplished by using litterbags that were larger, contained more litter, and had only the largest mesh size (4 mm).

### Experiment 1: Untangling Effects of Artificial Light at Night and Invertebrate Size Classes on Decomposition

This experiment was carried out in the Native Plant Meadow at BEF. Dominant vegetation in the meadow consisted of warm season, C<sub>4</sub> grasses including switchgrass (*Panicum virgatum*), Indian grass (*Sorghastrum nutans*), and big bluestem (*Andropogon gerardii*). Controlled burning is the primary management practice used to prevent succession of the meadow from grassland to forest. The most recent controlled burn prior to the experiment was carried out in the spring of 2017.

The experiment was carried out in eight 20-m diameter circular plots arranged in a paired design. Within each of four pairs of plots, one plot was randomly assigned to receive artificial light at night (hereafter ALAN plot). The other plot received no addition of ALAN, and thus only was lit with ambient diurnal sunlight, moonlight, and starlight (hereafter ambient-light plot). There were no barriers to restrict movement of invertebrates into, or out of, a plot. Within a pair, plots had a minimum distance of 10-m between edges, and pairs were a minimum of 20-m apart. Each plot represented a replicate. Each ALAN plot was illuminated from dusk to dawn by four broad-spectrum (4922 K) 12 W LED (Bullet®, RAB Lighting Inc., Northvale, New Jersey, United States) floodlights. The emission spectrum of this LED model is provided in the electronic (**Supplementary Figure 1**). Each LED floodlight was attached to the top of a 3 m post in

the center of the plot. All floodlights were aimed downward, with a slight deflection of 25° outward toward the edge of the plot. To hold physical structure constant across treatments, we installed identical posts without floodlights at the center of ambient-light plots. The plots were originally established in 2015 (Firebaugh and Haynes, 2016), and ALAN was manipulated throughout the summers of 2015 and 2016. For this study, ALAN was manipulated continuously beginning in the spring (April) through the fall including the study period, which ran from August through October 2017.

At the end of the growing season (August 17, 2017), we placed mesh bags (litterbags) containing litter within each plot. The litterbags were placed 1 m from the central post. At this distance from the central post, we measured nighttime light intensity 1 m above the ground to minimize the blocking of light by the vegetation canopy, recording intensities of  $193.16 \pm 5.0$  lux (mean  $\pm$  1 SD) in the ALAN plots and  $0.014 \pm 0.012$  lux in the ambient-light plots. The light levels in our plots were well within the range for canopy level Illuminance reported by Bennie et al. (2016) which extends from 30 to 1200 lux depending on vertical distance from the light source in question. Lower values have been reported elsewhere in the literature (Bennie et al., 2016; Grenis and Murphy, 2019), and we assume that the light levels reaching the litter layer were significantly lower and more variable than at 1 m above the ground.

We set out litterbags in groups of three, with one bag of each of the three mesh sizes per group. Within a group, we arranged litterbags so that none overlaid the other, and all were staked down to maintain contact with the soil surface. We placed six groups in each plot, with the direction of each group relative to the central pole chosen haphazardly.

To obtain standardized litter for the experiment, we grew switchgrass, *Panicum virgatum*, in a greenhouse at BEF during the summer of 2017. For a detailed description of the methods of grass propagation and growth (see **Supplementary Material Methods**). We harvested green leaf material on August 12, 2017, by trimming blades to the collar, and then oven dried it at 40°C for ~72 h. Prior to placing the leaf material into the litterbags, all leaf material was intermixed to maximize homogeneity among samples. We placed  $0.72 \pm 0.25$  g of dried leaf material into each litterbag (W  $\times$  L, 9  $\times$  9 cm). The edges of the bags were sealed using a heat sealer.

To explore which invertebrates mediated ALAN-induced changes in decomposition, we manipulated the size classes of fauna that could gain access to the litter by using litterbags with three different mesh sizes: 0.1, 2, and 4 mm. These mesh sizes exclude (in order) all macrofauna and mesofauna, all macrofauna, and some macrofauna (Setälä et al., 1996; Bradford et al., 2002; Smith and Bradford, 2003). Litter-inhabiting organisms with body sizes < 0.1 mm include bacteria, fungi, protozoa, and nematoda (Wallwork, 1970; Swift et al., 1979; Wall and Moore, 1999); these organisms directly (and indirectly in the case of protozoa and nematoda) effectuate nutrient cycling (McGuire and Treseder, 2010). Mesofauna (body size between 0.1 and 2 mm, Wallwork, 1970; Swift et al., 1979) include (but are not limited to) Collembolans (springtails), Acari (mites), Isoptera (termites) in addition to larval organisms (Wall and Moore, 1999;

Cole et al., 2006). Mesofauna are responsible for modification of the microbial community, comminution of litter, and in some instances predation of other invertebrates (Swift et al., 1979; Vossbrinck et al., 1979; Scheu and Setälä, 2002). Macrofauna (body size > 2 mm, Wallwork, 1970; Swift et al., 1979) include Araneae, Hymenoptera, and Coleoptera (larvae and adults), along with larvae and nymphs from other orders. Litter-dwelling macrofauna are responsible for comminution of litter and predation of secondary and tertiary invertebrates (Scheu and Setälä, 2002; Briones, 2014).

We expected that primary and secondary consumer microorganisms would gain access into the litterbags with the 0.1 mm mesh, but that arthropod tertiary consumers, along with arthropod secondary consumers whose body sizes exceeded 0.1 mm in diameter, would be excluded (Wallwork, 1970; Swift et al., 1979). We expected that primary, secondary, and tertiary consumers would all gain access into the litterbags with the 2 and 4 mm mesh sizes, but that fewer tertiary consumers would be excluded from the 4-mm mesh size litterbags than from the 2-mm mesh size litterbags (Wallwork, 1970; Swift et al., 1979; Bradford et al., 2002; Cole et al., 2006).

A small but growing body of literature highlights some of the effects of ALAN on plants in roadside or semi-natural conditions. ALAN from street-lighting has direct and indirect effects on the plant community and its herbivores (Bennie et al., 2018a,b; Grenis and Murphy, 2019). We therefore considered it plausible that ALAN-induced changes in plant biomass could affect the rate of plant litter decomposition. For example, increased density of standing senesced vegetation could attract detritivores or affect the litter-layer microclimate. To test for potential effects of ALAN in our experimental plots on plant growth, we estimated the density of aboveground grass biomass ( $\text{g/m}^2$ ) in each plot from the mean biomass harvested from five  $0.3\text{-m}^2$  quadrats placed randomly within each plot. The biomass was harvested in early August, 2017, dried for 5 days at  $55^\circ\text{C}$ , and subsequently weighed.

### Experiment 2: Effects of Artificial Light at Night on Decomposition and Litter-Layer Invertebrates While Controlling Aboveground Vegetation

Because ALAN can affect vegetation (Bennie et al., 2016, 2018b; Grenis and Murphy, 2019), which could potentially affect invertebrate assemblages or litter decomposition, we carried out a second field experiment in the fall of 2018 in a different set of plots at BEF. Like in the first experiment (carried out in 2017), we measured rates of plant litter breakdown in litterbags; however, in the second experiment we took steps to minimize differences across plots in the structure and biomass of aboveground vegetation via two means. First, the plots used in the 2018 experiment were not exposed to ALAN during the 2018 growing season; in the prior experiment, ALAN was manipulated throughout the growing season as well as during the fall decomposition experiment. In 2018, ALAN was not manipulated until August 16, 2 days before litterbags were placed in the plots. Second, we mowed all plots 2 days prior to the start of the 2018 experiment to further minimize differences in aboveground vegetation structure and biomass across plots.

This experiment was carried out in ten 1-m diameter field plots that were arrayed in a grid pattern with 5 m between adjacent plots. Half of the plots were selected at random to receive ALAN, while the other half received ambient light only. As with our first study, each plot represented a replicate. A plot was exposed to ALAN by one broad-spectrum 12 W LED (same model as in Experiment 1) floodlight, which was positioned on the underside of the horizontal arm of a light post at a height of 3 m and aimed directly downward over the center of the plot. Identical light posts were established for all plots (both ALAN-plots and ambient-light plots). There were no barriers to prevent movement in or out of plots. In this experiment, we were able to measure nighttime light intensity at ground level (the top of the litter layer) because the vegetation was mowed. Nighttime light intensity in the ALAN plots was  $126.8 \pm 7.32$  lux (mean  $\pm$  1 SD) and  $0.4 \pm 0.21$  lux in the ambient-light plots.

In this experiment, we intended to use plant litter that closely resembled litter occurring in the grasslands at our study site. Thus, we collected senesced leaves in August 2018 from standing *C4* grasses in the BEF Native Plant Meadow (> 50 m from sources of ALAN). The nitrogen content of the collected leaf litter was  $1.02 \pm 0.33$  (% of total mass mean  $\pm$  SD). The leaf litter was dried at  $50^\circ\text{C}$  for 5 days, homogenized, and then placed into litterbags.

To increase our ability to characterize effects of ALAN on invertebrate trophic structure, we took two steps to increase the numbers of invertebrates captured. First, we used a mesh size (4 mm) that excluded only large macrofauna. Second, we used larger litterbags ( $W \times L$ ,  $10 \times 20$  cm) containing more litter material ( $3.0 \pm 0.05$  g) than in the 2017 experiment ( $0.72 \pm 0.25$  g). The edges of the bags were sealed using a heat sealer, and all litterbags were staked down to maintain contact with the ground surface when deployed in the plots.

## Data Collection and Analysis

### Experiment 1: Untangling Effects of Artificial Light at Night and Invertebrate Size Classes on Decomposition

To examine the effects of ALAN on litter breakdown over time, we retrieved half of the litterbags from each plot after 31 days, and the remaining half after 61 days. Immediately after retrieval, we then removed invertebrates from the litterbags using Tulgren extraction carried out over 24 h. Following extraction of the invertebrates, we dried the litter at  $50^\circ\text{C}$  for 24 h and removed any residual soil or debris by hand. We estimated the proportion of litter broken down, or decomposed, as  $(1 - \text{mass}_{\text{final}}/\text{mass}_{\text{initial}})$ . We then pulverized the litter samples into fine powder using a ball mill (Cianflone Scientific LLC, Pittsburgh, PA, United States) and performed combustion analysis to determine final nitrogen content (Flash 2000 Elemental Analyzer, Thermo Fisher Scientific<sup>TM</sup>, Hampton NH, United States). To obtain initial litter nitrogen content, 0.3 g sub-samples of the litter placed into each litterbag were collected for combustion analysis.

Statistical analyses were run using the mean of response variables because plots were considered true replicates in our study. We tested the effects of ALAN and litterbag mesh size on the mean proportion of litter broken down and the nitrogen

content of remaining litter within each plot using linear mixed effects (LME) models. The fixed effects in the LME models were ALAN, mesh size, their interaction, time in the field, and aboveground grass biomass. The random effects of plot pairs were modeled using random intercepts. Mean change in litter nitrogen was transformed using a power transformation ( $x^3$ ) to improve normality of residuals (Williamson and Gaston, 1999). The LME models were fitted using the “lmer” package (Bates et al., 2015) implemented in the program R (R Core Team, 2018). *Post hoc* pairwise comparisons based on least-squares means with *p*-values adjusted using the Tukey method were carried out using the R package “emmeans” (Lenth et al., 2019). In this experiment, we did not recover a sufficient number of invertebrates from the litterbags to explore how their abundances were affected by the experimental manipulations.

### Experiment 2: Effects of Artificial Light at Night on Decomposition and Litter-Layer Invertebrates While Controlling Aboveground Vegetation

We deployed six litterbags in each of the plots on August 18, 2018, and collected them 116 days later. Upon retrieval from the field, invertebrates were extracted following the method used in Experiment 1. We identified invertebrates to order or family level, whichever was needed to determine their trophic position (primary consumers, secondary consumers, or secondary/tertiary consumers). We estimated the proportion of litter decomposed and nitrogen content using the same procedures described in Experiment 1.

We tested the effects of ALAN on the mean proportion of litter broken down ( $1 - \text{mass}_{\text{final}}/\text{mass}_{\text{initial}}$ ) and mean nitrogen content of remaining litter using one-way ANOVAs. We examined the effect of ALAN on the ground-dwelling invertebrate community in two ways. First, we tested for the effect of ALAN on the mean total number of invertebrates identified using a one-way ANOVA. Total number of invertebrates was  $\log(x + 1)$  transformed to reduce heterogeneity of variance. Second, we investigated the effect of ALAN on the three trophic groups present in our invertebrate community: primary consumers, secondary consumers, and secondary/tertiary consumers. Because of non-independence of potentially interacting trophic levels, we tested for a multivariate effect of ALAN on abundances of the three trophic groups using MANOVA. In the event of a significant multivariate effect, we tested the effects of ALAN on each of the trophic groups using univariate ANOVA (Quinn and Keough, 2002). Prior to these tests, the abundances of each trophic group were Box-Cox transformed to improve normality (Olivier and Norberg, 2010). We ran this test using the “manova” function in the “stats” package.

Given the proximity of the experimental plots (5 m between adjacent plots), it is possible that some litter-layer invertebrates may have visited litterbags in more than one experimental plot. This could potentially cause non-independence of the measures of invertebrate abundance from different plots. Through trophic interactions, non-independence in invertebrate abundance could translate into non-independence in measures of litter breakdown. We addressed these possibilities by testing for spatial autocorrelation in the residuals from

the MANOVA and each ANOVA model (Ver Hoef and Cressie, 1993). Moran’s *I* tests implemented in the “ape” package (Paradis and Schliep, 2019) showed there was no significant spatial autocorrelation in the residuals from any of the models.

## RESULTS

### Untangling Effects of Artificial Light at Night and Invertebrate Size Classes on Decomposition

Mean daily precipitation during this experiment (August 17 to October 17) was 3.18 mm. This is 11% higher than mean daily precipitation for this range of dates over the previous 30 years (1986–2016) at our study site.

We observed a marginally significant interactive effect of ALAN and mesh size on the proportion of litter broken down ( $P = 0.06$ , **Table 1**), potentially reflecting a stronger effect of ALAN on the proportion of litter broken down or removed in litterbags with the largest mesh size than with the intermediate and smallest mesh sizes (14, 8, and 6% higher under ALAN than under ambient light after 60 days, respectively, **Figure 1**). The proportion of material broken down differed significantly between litterbag mesh sizes ( $p < 0.001$ , **Table 1**), with the least loss of litter with the mesh size that excluded all but microorganisms (smallest mesh size) and the most breakdown in the mesh that excluded only large macrofauna (largest mesh size; **Figure 1**). After 60 days, there was a 20% difference in proportion broken down in the largest mesh size compared with the smallest mesh size. The proportion of leaf litter broken down tended to be higher under ALAN than under ambient light; however, this difference was not statistically significant ( $P = 0.07$ , **Table 1** and **Figure 1**). There was no significant effect of aboveground grass biomass on the proportion of litter that broke down ( $P = 0.14$ , **Table 1**).

Mean initial nitrogen content the litter for this experiment was  $3.36 \pm 0.32$  (mean  $\pm$  SE, % of total mass) and mean nitrogen content of the litter remaining after 30 and 60 days was  $3.25 \pm 0.46\%$ . We found no evidence that the nitrogen content of the remaining litter was affected by any of our experimental factors (**Table 2** and **Figure 2**).

### Experiment 2: Effects of Artificial Light at Night on Decomposition and Litter-Layer Invertebrates While Controlling Aboveground Vegetation

During the 120-day period of this experiment, mean daily rainfall was 4.75 mm. This is approximately 78% greater than during the previous 30 years.

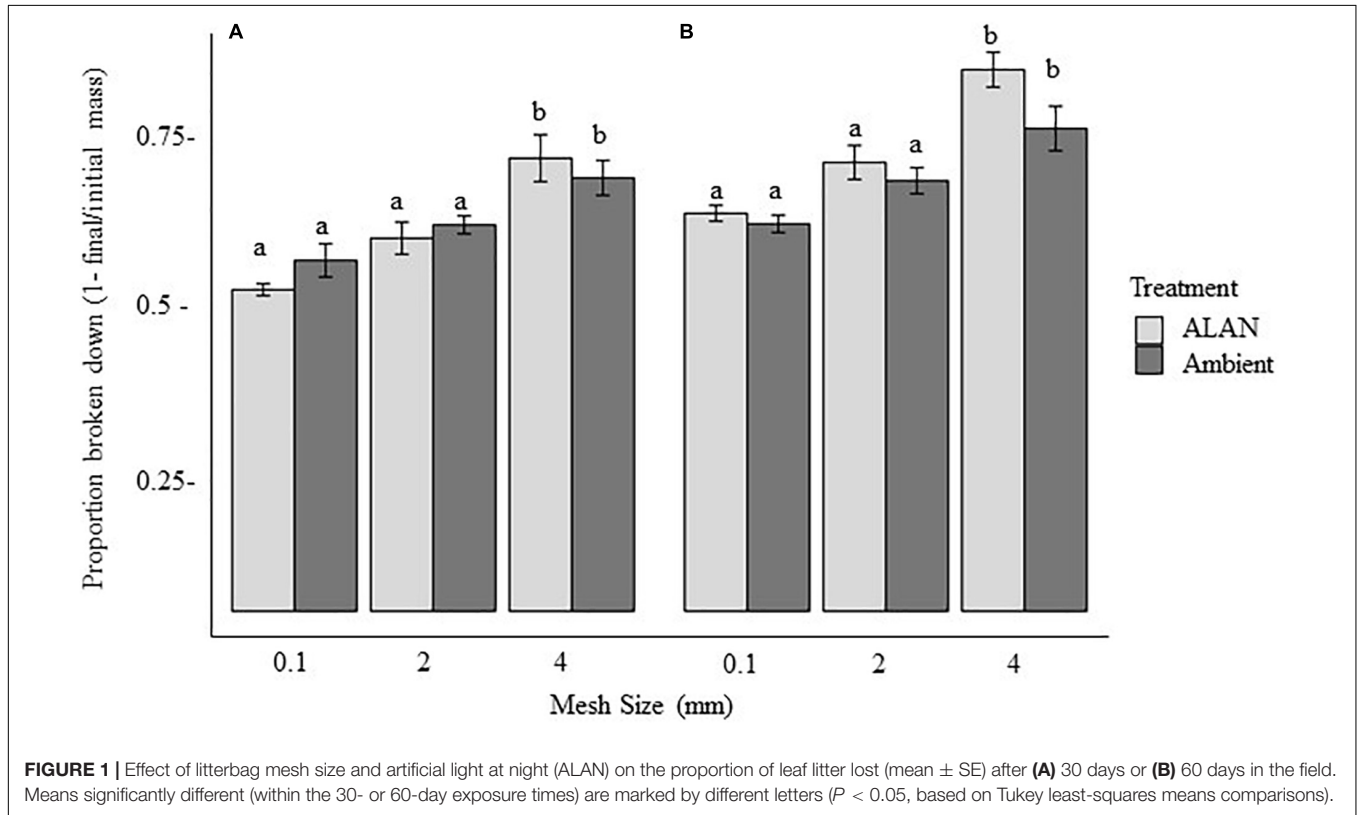
In the second experiment, we did not observe an effect of ALAN on the proportion of leaf litter that broke down after 120 days [ $F_{(1, 8)} = 0.648$ ,  $P = 0.44$ ]. The nitrogen content of the remaining litter was also not significantly affected by ALAN [ $F_{(1, 8)} = 1.544$ ,  $P = 0.249$ ].

We recovered and identified 348 invertebrates belonging to 7 orders from the experimental litterbags

**TABLE 1** | Results of a linear-mixed-effects model to investigate the interactive effects of artificial light at night (ALAN) and litterbag mesh size on litter breakdown.

Source of variation	S.S.	M.S.	Numerator DF	Denominator DF	F	P
ALAN	0.01	0.01	1	6.17	4.81	0.07
Mesh size	0.27	0.13	2	33.89	63.21	<0.001***
ANPP	0.01	0.01	1	4.32	3.33	0.14
Time	0.12	0.12	1	33.89	55.68	<0.001***
ALAN × Mesh size	0.01	0.01	2	33.89	3.12	0.06

Proportion broken down was calculated as  $(1 - \text{Final}/\text{Initial Mass})$ . \*\*\* Significant at the  $\alpha = 0.001$  confidence level. Other variables included in the model include aboveground net primary production (ANPP) and length of time in the field (time).



**FIGURE 1** | Effect of litterbag mesh size and artificial light at night (ALAN) on the proportion of leaf litter lost (mean ± SE) after (A) 30 days or (B) 60 days in the field. Means significantly different (within the 30- or 60-day exposure times) are marked by different letters ( $P < 0.05$ , based on Tukey least-squares means comparisons).

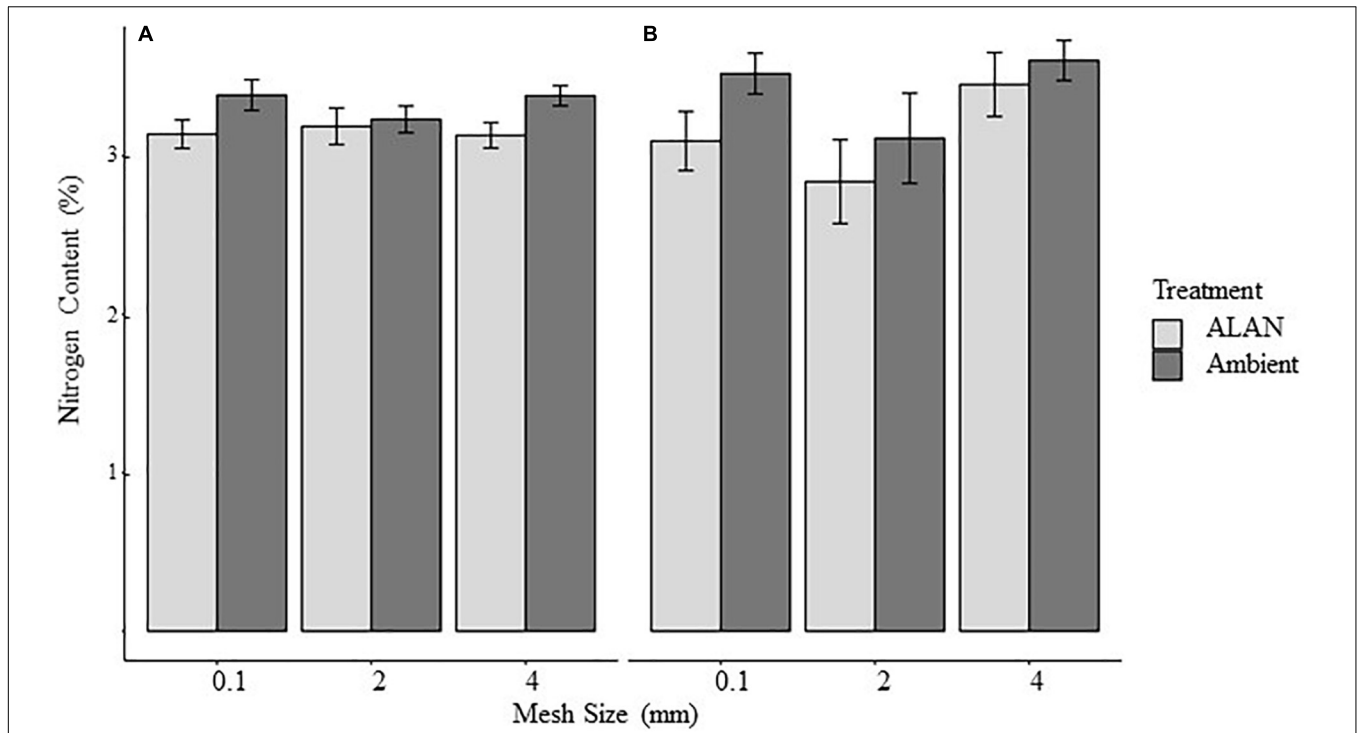
**TABLE 2** | Results of a linear-mixed-effects model to investigate the interactive effects of artificial light at night (ALAN) and litterbag mesh size on remaining nitrogen (%) in litter.

Source of variation	S.S.	M.S.	Numerator DF	Denominator DF	F	P
ALAN	344.24	344.24	1	8.78	3.12	0.11
Mesh size	607.92	303.96	2	37.98	2.76	0.08
ANPP	5.95	5.95	1	2.89	0.05	0.83
Time	91.95	91.95	1	37.98	0.83	0.37
ALAN × Mesh size	90.83	45.42	2	37.98	0.41	0.67

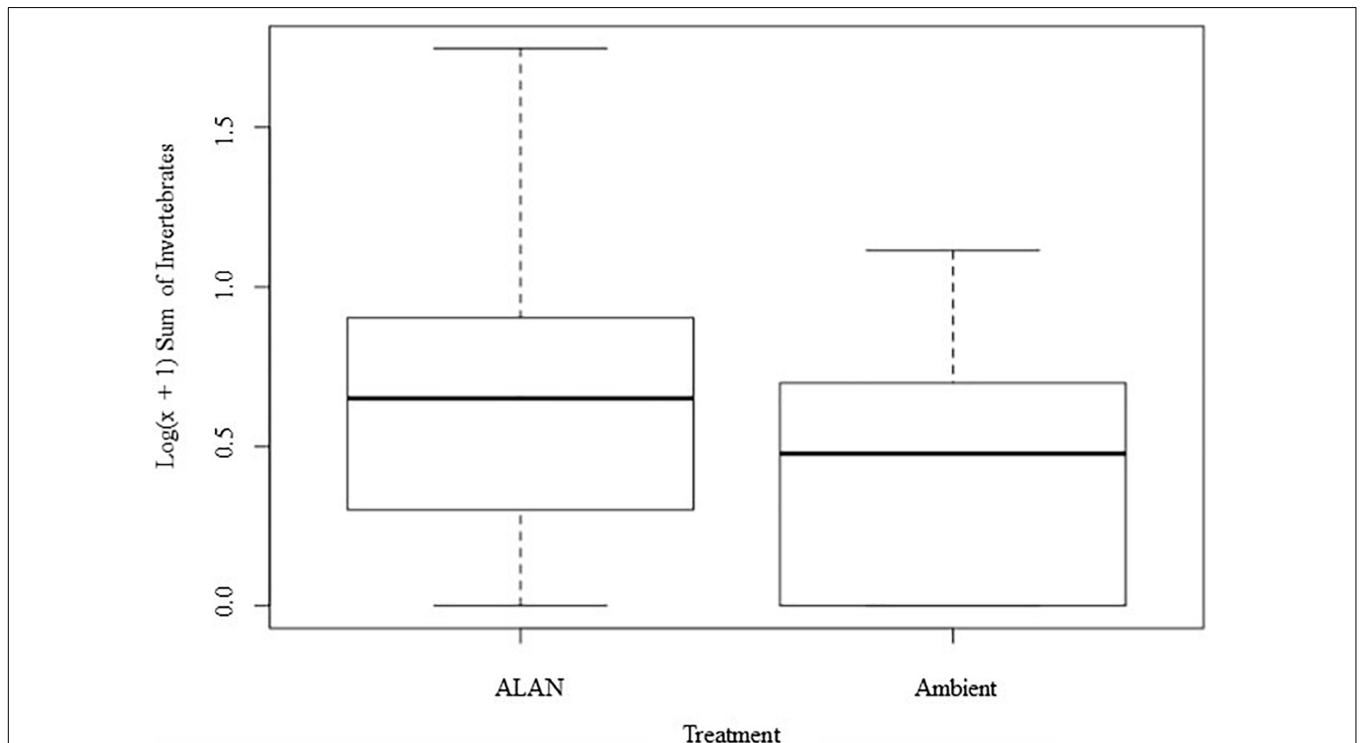
Other variables included in the model include aboveground net primary production (ANPP) and length of time in the field (time).

(Supplementary Figure 2 and Supplementary Table 1). On average there were 65% more invertebrates in litterbags exposed to ALAN compared to ambient light [ $F_{(1, 8)} = 12.33, P = 0.008$ , Figure 3]. There was a significant multivariate effect of ALAN on the abundances of primary, secondary, and secondary/tertiary

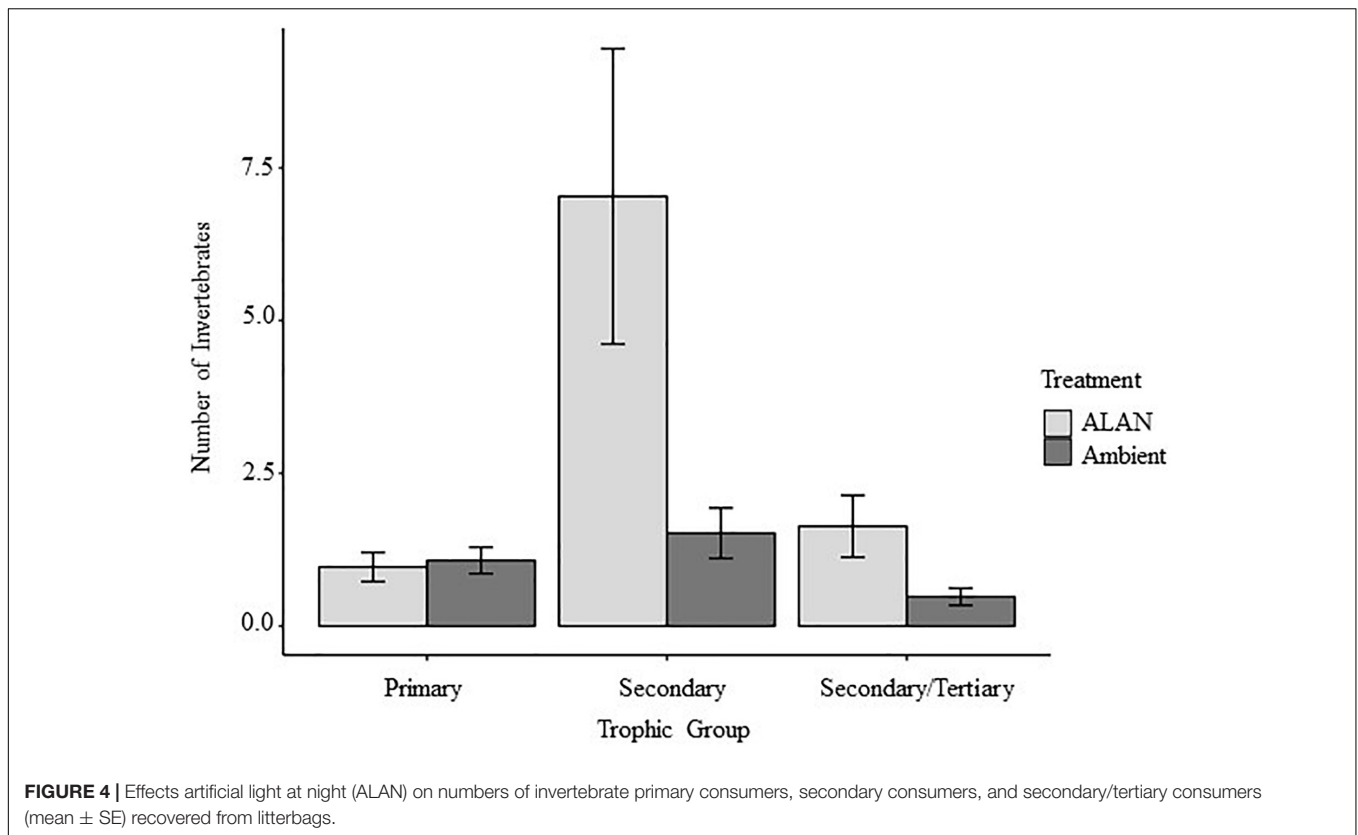
consumers (Pillai's trace = 0.75,  $F = 6.025, P = 0.031$ ). Litterbags exposed to ALAN contained 4.6 times more secondary consumers [ $F_{(1, 8)} = 6.688, P = 0.032$ ] and 3.5 times as many secondary/tertiary consumers [ $F_{(1, 8)} = 5.563, P = 0.045$ ] than litterbags exposed only to ambient light. In contrast, there was



**FIGURE 2 |** Effect of litterbag mesh size and artificial light at night (ALAN) on the nitrogen content of litter retrieved from the field after **(A)** 30 days or **(B)** 60 days. Nitrogen is expressed as percent of tissue (mean ± SE).



**FIGURE 3 |** Effect of artificial light at night (ALAN) on log-transformed number of invertebrates recovered and identified from litterbags for each light treatment. Data are represented in a box and whisker plot indicating the median, interquartile range, and minimum and maximum values.



no significant effect of ALAN on the abundance of primary consumers [ $F_{(1, 8)} = 0.134, P = 0.724$ ].

## DISCUSSION

To our knowledge, this is the first study to evaluate the effects of ALAN on the breakdown of plant litter in a terrestrial ecosystem. However, a recent study showed that ALAN-induced changes in microbial communities can impact the decomposition of plant litter in polluted streams (Pu et al., 2019). Consistent with prior research (Bradford et al., 2002), we found that the rate of breakdown of leaf litter within litterbags increased with mesh size (Table 1 and Figure 1). The phenomenon of greater litter breakdown with larger mesh sizes is thought to be caused by biotic factors including increased litter shredding and removal by detritivores as well as abiotic factors such as light, moisture, and temperature (Lecerf, 2017). We also observed that the proportion of leaf litter broken down was, on average, 11% higher under ALAN compared with ambient-lit plots in 2017 (although this effect was not significant,  $P = 0.07$ ; Figure 1). The proportion of litter broken down was 10% higher, on average, after 60 days in 2017 than after 120 days in 2018. This is likely the result of the higher nutritional quality of the litter used in 2017 ( $3.36 \pm 0.32\%N$ ) than in 2018 ( $1.02 \pm 0.33\%N$ ). Litter of poor nutritional quality, or having lower nitrogen content, decomposes slowly compared to nutrient-rich litter, which is favored by detritivores (Smith and Bradford, 2003; Hessen et al.,

2004). The lower amounts of breakdown in 2018 may have reduced our ability to detect potential effects of ALAN on litter breakdown in our second experiment. Lower foliar nitrogen has been reported for  $C_4$  plants (like those used in both of our experiments) compared with  $C_3$  plants (Sage and Pearcy, 1987). It is possible that ALAN may be more likely to affect the breakdown of nutrient-rich than nutrient-poor plant tissues, but further research is needed to resolve this question.

We detected greater abundances of invertebrates in litterbags exposed to ALAN compared with ambient light in our 2018 experiment ( $P = 0.008$ , Figure 3). Consistent with previous research on effects of ALAN on trophic structure within ground-dwelling arthropods (Davies et al., 2012, 2017), we found that ALAN increased the abundances of invertebrate secondary and/or tertiary consumers but had no effect on the abundance of primary consumers (Figure 4). Addition of ALAN may have slightly increased the rate at which plant litter decomposed (Table 1 and Figure 1); however, there was no significant effect of ALAN on litter breakdown ( $P = 0.07$ ). Thus, our prediction that ALAN would reduce rates of litter breakdown indirectly via increased top-down control of primary consumers by secondary and/or tertiary consumers was not supported. This prediction may have been based on an oversimplified view of food-web dynamics in the litter layer. Greater local abundance of predators can sometimes lead to increased intraguild predation, releasing primary consumers from top-down control (Finke and Denno, 2005). This might explain why litterbags with larger mesh sizes tend to have higher abundance, diversity, and food



web complexity of litter-dwelling fauna, but rates of plant litter decomposition tend to be high despite the presence of secondary and tertiary consumers (Swift et al., 1979; Vossbrinck et al., 1979; Bradford et al., 2002; Bokhorst and Wardle, 2013; Liu et al., 2019). Higher intraguild predation under ALAN could potentially explain the lack of an effect of ALAN on primary consumer abundance and litter decomposition in our study. However, experimental approaches that allow direct control over food web structure, combined with manipulations of ALAN, will likely be needed to fully understand how ALAN alters predator-prey interactions among soil fauna.

This work confirms the findings of others (Davies et al., 2012, 2017) that ALAN leads to higher local densities of ground-dwelling predaceous invertebrates. However, effects of ALAN on secondary and tertiary consumer invertebrates may differ by habitat type or depending on the taxa present. For example, Manfrin et al. (2017) found that, in a riparian environment, in contrast to the grassland ecosystem studied here, ALAN increased abundances of Araneae but decreased abundances of carabid beetles. Contrary to our prediction, we found that increased abundance of arthropod secondary/tertiary consumers under ALAN did not suppress the breakdown of plant litter. This indicates that detritivores in the litter layer may not be subjected to increased predation under ALAN. Further work is needed to elucidate the activities of predaceous ground-dwelling invertebrates under ALAN, for example by investigating potential increases in intraguild predation. In addition, trophic dynamics under point sources of ALAN takes place within a matrix of darker habitats. Although ALAN is known to influence the movement behaviors of many arthropod taxa (Degen et al., 2016; Manfrin et al., 2017; Duarte et al., 2019), little is known about how ALAN affects the net attraction of litter layer invertebrates. Determining how ALAN impacts net spatial fluxes of invertebrates of different trophic ranks will be critical for understanding the consequences of ALAN for ecosystem dynamics across landscapes.

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## DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## AUTHOR CONTRIBUTIONS

MH, HE, and KH conceived, designed the experiments, revised, and edited the manuscript. MH performed the experiments and wrote the initial manuscript. MH and KH analyzed the data. All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.748983/full#supplementary-material>

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