Population to ecosystem level impacts of artificial light at night

Melissa H. Hey Richmond, Virginia

Bachelor of Science, College of William & Mary, 2015

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Abstract

Humans drive global change in a myriad of ways (Nelson et al. 2006), one of which is the introduction of artificial light at night (ALAN, Gaston et al. 2014). The intrusion of ALAN into nighttime environments is likely to have profound ecological consequences as a result of disruption to natural variations in light availability (Gaston et al. 2013; Gaston et al. 2014). Recent efforts have begun to uncover the ramifications of ALAN for populations, communities, and ecosystems. However, research on the ecological effects of ALAN is still relatively novel. Researchers studying ALAN face the additional challenge of chasing a moving target, as new lighting technologies emerge with time. In this dissertation, I explore the ways in which ALAN from increasingly popular broad-spectrum light emitting diodes affect populations, communities, and ecosystem processes. Despite their reliance on light as both an energy and information source (Gaston et al. 2013), relatively little work has addressed the effects of ALAN on plants in nature. In my second chapter, I tested the interactive effects of ALAN, intraspecific competition, and soil moisture on the growth and anti-herbivore defense of an herbaceous perennial. I found that ALAN affected plant growth, as well as had interactive effects with both competition and soil moisture on plant growth. These results highlight the complex ways ALAN may affect wild plants. ALAN is known to affect ground-dwelling arthropod community composition and trophic structure (Davies et al. 2012; Davies et al. 2017; McMunn et al. 2019; Heiling 1999). Terrestrial arthropod communities contribute to decomposition, an ecosystem process by which nutrients are returned to the soil, and which is affected by trophic structure of litter layer invertebrates (Wall & Moore 1999; Moore et al. 2004). Therefore, in my third chapter I tested the effects of ALAN on the litter-layer invertebrate community and whether these impacted the breakdown of plant litter. My results confirmed the findings of others that ALAN increases local abundances of secondary and tertiary consumer arthropods (Davies et al. 2012; Davies et al. 2017; McMunn et al. 2019; Yuen & Bonebrake 2017; Miller et al. 2017), however this did not depress the rate of decomposition under ALAN conditions. Another way in which terrestrial arthropods can influence nutrient dynamics is via dispersal (Yang & Gratton 2014; Hu et al. 2017; McInturf et al. 2019), because nitrogen in arthropods, and in particular insects, is quickly returned to the soil (Yang & Gratton 2014; Behie & Bidochka 2013). Attraction of arthropods to sources of ALAN may alter their dispersal (Eisenbeis 2006) and subsequently nutrient distribution. In my fourth chapter I tested the effects of ALAN on net fluxes (measured as attraction - repulsion) and local abundances of terrestrial arthropods. I found that some flying insects demonstrated net attraction to ALAN sources and effects of ALAN on local abundances varied substantially among arthropod taxonomic groups. Taken in totality, the work presented in my dissertation furthers our understanding of how ALAN affects plants and arthropods at population and community levels, new insights on impacts of ALAN-induced shifts in trophic structure and spatial redistribution of nutrients on ecosystem processes.

Doctoral Dissertation Committee

Kyle Haynes (Advisor) Department of Environmental Sciences Blandy Experimental Farm

Howard Epstein Department of Environmental Sciences

Jim Galloway Department of Environmental Sciences

> Deborah Roach Department of Biology

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Chapter 1

Introduction

One of the many ways in which humans drive global change is through the introduction of artificial light at night (hereafter ALAN), a widespread sensory pollutant which currently spans nearly a quarter of earth's terrestrial surface (Falchi et al. 2016). Because ALAN obstructs natural cycles of light and dark, it presents a novel environmental challenge by interfering with biological processes which have evolved in response to daily and seasonal variations in the availability of light (Gaston et al. 2013). The presence of ALAN has long been recognized as a nuisance to astronomers whose observations using telescopes are negatively impacted by its presence (Garstang 1989). A few seminal works summarized early knowledge about how the presence of ALAN impacts an array of organisms (Longcore & Rich 2004; Rich & Longcore 2013), however most of the interest in ALAN has grown in the last two decades. As our understanding of how many biological processes are organized by natural cycles of light has grown (Gaston et al. 2013), so too has the body of literature regarding the effects of ALAN on organisms, populations, and communities.

As photomorphogenic organisms that rely on light as both a source of energy and information, plants are likely to be affected by the introduction of ALAN (Briggs 2006; Gaston et al. 2013; Bennie et al. 2015, Bennie et al. 2016). However, most of the existing literature surrounding the effects of artificial light on plants is agricultural in nature and was conducted in greenhouses or growth chambers. Much less work has been dedicated to understanding the impacts of ALAN on wild plants (Cathey & Campbell 1975; Bennie et al. 2015; Bennie et al. 2016). However, there is some evidence for bottom-up effects of ALAN on invertebrate

populations through direct effects on plants. These include changes to plant-herbivore interactions (Bennie et al. 2015; 2018; Grenis & Murphy 2019) as well as tri-trophic interactions between plants, herbivores, and parasitoids (Sanders et al. 2015) under ALAN. Changes to both bottom-up and top-down trophic interactions can reverberate through entire food webs, with impacts on ecosystem processes (Gruner 2004; Wilkinson and Sherratt 2016).

In addition to changing trophic interactions involving plants, ALAN has also been found to affect terrestrial arthropod community trophic interactions as well as trophic structure. For example, higher abundances of predatory arthropods have been observed near sources of ALAN compared to unlit areas (Davies et al. 2012; Davies et al. 2017; McMunn et al. 2019; Heiling 1999), though one study found the opposite (Meyer & Sullivan 2013). Insects often suffer increased predation under ALAN from both vertebrates (Minnaar et al. 2015; Rydell 1992; Rydell 2006) and invertebrate (Willmott et al. 2019; Yuen & Bonebrake 2017; Adams 2000; Bennie et al. 2018) predators. Terrestrial arthropods contribute to a number of ecosystem processes including decomposition and nutrient cycling (Price et al. 2011; Schowalter et al. 2016; Schowalter et al. 2018). Additionally, predatory arthropods are capable of initiating topdown control over decomposition by either reducing or deterring detritivore populations (Hawlena et al. 2012; Schmitz et al. 2010; Lawrence & Wise 2000; Kajak 1995), thereby influencing the rate of nutrient returns to the soil. Therefore, findings that predatory arthropods are found in higher local abundances near sources of ALAN (Davies et al. 2012; Davies et al. 2017; McMunn et al. 2019; Heiling 1999) suggest the potential for cascading effects on ecosystem processes in which terrestrial arthropods are important, such as decomposition and nutrient cycling. To my knowledge, no one has yet studied the influence of ALAN on decomposition in terrestrial systems.

Few studies have how ALAN influences the directionality of invertebrate movement, in particular, quantifying both attraction to, and repulsion from, sources of ALAN (Meyer & Sullivan 2013; Manfrin et al. 2017). Net fluxes of invertebrates may have implications for both local abundances and community composition for recipient systems (Polis et al. 1997; Baxter et al. 2005). For example, Manfrin et al. (2017) and Perkin et al. (2014) found that ALAN increases the flux of emerging invertebrates from riparian to terrestrial patches. Terrestrial patches under sources of ALAN receiving an influx of aquatic invertebrates also had greater abundances of predatory arthropods, demonstrating the potential for ALAN effects on invertebrate fluxes to alter the trophic structure of recipient communities (Manfrin et al. 2017). Further research is needed to provide clarity on the effects of ALAN on the net flux (attraction - repulsion) of invertebrates across landscapes, as well as whether ALAN affects trophic structure and ecosystem processes (e.g. decomposition) via its effects on dispersal. For example, terrestrial insects represent a pool of nitrogen easily that is broken down during decomposition (Behie & Bidockha 2013), therefore spatial fluxes of insects may impact nutrient distribution across landscapes.

Over the past few years, I sought to quantify the direct effects of ALAN on plant growth and defenses, as well as direct and indirect effects of ALAN on terrestrial invertebrates, decomposition, and nutrient redistribution across the landscape.

Chapter Summaries

Despite a large body of literature concerning how plants respond to their light environment, direct effects of unintentional illumination of plants from ALAN remains largely unexplored. Plants exposed to ALAN in nature are likely to experience it in concert with a variation in a myriad of other abiotic and biotic factors. Therefore, in chapter 2, I tested whether the effects of ALAN on plant growth and anti-herbivore defenses depend on other factors which are both variable in nature and known to affect plant growth and fitness. In a field experiment using a split-plot factorial design, I studied the effects of ALAN, soil moisture, and plant density on the growth and anti-herbivore defenses of common milkweed, *Asclepias syriaca*.

In chapter 3, I studied the effects of ALAN on the litter-layer invertebrate community, and whether ALAN-induced changes in litter-layer invertebrate assemblages affected the decomposition of plant litter. While previous studies have explored effects of ALAN on grounddwelling invertebrates (Davies et al. 2012; Davies et al. 2017), this is the first experiment I am aware of testing the effects of ALAN on decomposition in terrestrial habitat. To parse out effects of ALAN on the litter-layer invertebrate community and the consequences of any such effects on the breakdown of plant litter, I conducted an experiment in which I manipulated presence of ALAN and invertebrate community using litterbags with various mesh sizes, which excluded invertebrates based with body sizes greater than the mesh size. In a second experiment, I quantify the effects of ALAN on the structure of invertebrate community assemblages, while controlling for potential effects of ALAN on vegetation structure.

In light of the fact that many insects display positive phototaxis (Eisenbeis et al. 2009), I explored the potential for ALAN of varying spectrums to create energy and nutrient sinks on the landscape via effects on terrestrial invertebrate movement (Chapter 4). In order to accomplish this, I carried out a field study in which I experimentally manipulated the presence and spectrum of ALAN and quantified the net attraction of herbivorous and carnivorous arthropods. To enhance my ability to measure the responses of a wide variety of terrestrial invertebrates to sources of ALAN, I used three different trap types common in entomological research. I estimated the potential for ALAN to affect biogeochemical redistribution through its effects on

invertebrate movement by measuring the biomass and nutrient content of taxa that were captured in high numbers.

In my concluding chapter, I argue that my research provides substantive contributions to our understanding of how ALAN affects population and community dynamics, as well as ecosystem processes. For example, I found evidence that ALAN interacts with both an abiotic factor (soil moisture) and a biotic factor (plant density) to affect plant growth, suggesting that the effects of ALAN on plants in nature are likely to be complex as plants face variable conditions regarding both abiotic resources and biotic interactions (Chapter 2). While I did find that predatory arthropods occurred in greater numbers under ALAN compared with unlit conditions, consistent with previous studies, I found no evidence that this lead to increased top-down control of decomposition (Chapter 3). Finally, I demonstrated that ALAN of varying spectra can affect local abundances of a number of terrestrial arthropod taxa, and that phylogeny may better determine arthropod responses to ALAN than trophic level (Chapter 4). Together, these findings shed light on the effects of ALAN on population, community, and ecosystem processes that have received very little attention to date, and underscore the need for further consideration of ecological ramifications of this sensory pollutant.

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Chapter 2

Interactions between artificial light at night, soil moisture, and plant density affect the growth of a perennial wildflower¹

Abstract

Artificial light at night (ALAN) has been shown to alter aspects of plant growth, but I am not aware of any studies that have examined whether the effects of ALAN on plants depend upon the backdrop of variation in other abiotic factors that plants encounter in field populations. I conducted a field experiment to investigate whether ALAN affects the growth and anti-herbivore defenses of common milkweed, Asclepias syriaca, and whether the effects of ALAN are influenced by plant density or soil moisture content. Artificial light at night, soil moisture, and plant density were manipulated according to a split-plot factorial design. Although increasing soil moisture by watering had no significant effects on latex exudation, attributes of plant growth generally responded positively to watering. The basal stem diameter (BSD) and height of plants were affected by ALAN × soil moisture interactions. For both of these variables, the positive effects of ALAN was greater for plants that were not watered than for plants that were. Basal stem diameter was also affected by an ALAN × plant density interaction, and the positive effect of ALAN on BSD was greater in the low-density treatment than in the high-density treatment. My results demonstrate that the effects of ALAN on plant growth can be altered by soil moisture and plant density. Consequently, the effects of ALAN on plants in nature may not be consistent with existing frameworks that do not account for critical abiotic variables such as water availability or biotic interactions between plants such as competition.

¹ This study was conducted in collaboration with Elizabeth DiBiase, David Carr, Deborah Roach, and Kyle Haynes.

Introduction

Artificial light at night (ALAN) currently affects nearly a quarter of Earth's terrestrial surface (Longcore & Rich 2004; Falchi et al. 2016). Over the past decade, there has been growing interest in understanding the biological and ecological effects of this pervasive sensory pollutant (Gaston et al. 2013; Falchi et al. 2016). It has adverse effects on animal behavior, for instance redirecting sea turtle hatchlings towards build structures rather than the ocean (Witherington 2000) and reducing foraging behavior in New Zealand weta (Farnworth et al. 2018). ALAN also changes local abundances of terrestrial invertebrates (Davies et al. 2012, Davies et al. 2017). Effects of ALAN on demographic processes in animal populations have also been found (Firebaugh & Haynes 2019). Much less is known about the effects of ALAN on wild plants (Gaston et al. 2013, Bennie et al. 2016) despite the fact that as photomorphogenic organisms, ALAN is likely to exert wide-ranging effects on plant growth, physiology, and phenology (Briggs 2006; Gaston et al. 2013; Bennie et al. 2013; Bennie et al. 2015, Bennie et al. 2016).

For plants, many of the ecological consequences of ALAN that have been found involve the alteration of biotic interactions. In contrast, little is known about whether the effects of ALAN depend upon variation in other abiotic factors that are critical to the performance of plants in nature, such as temperature or soil moisture. Some previous research suggests that interactive effects between ALAN and moisture availability should be explored. For example, plants exposed to continuous light exhibit loss of proper stomatal functioning (Kwak et al. 2017, Kwak et al. 2018). Improper stomatal functioning can decrease plant water use efficiency, making plants more susceptible to drought-related stress (Lawson & Blatt 2014). Moreover, the effects of continuous light on plant stomata may be particularly strong in the presence of broad-

spectrum LED lights, because plant photoreceptors triggered by blue light are associated with stomatal movements (Kami et al. 2010, Hart 1988, Briggs 2006). Such an effect of ALAN on plant stomata might adversely impact plant growth or survival.

ALAN has been shown to affect a number of biotic interactions. These include plantherbivore interactions (Bennie et al. 2015, 2018, Grenis & Murphy 2019), plant-pollinator interactions (Knop et al. 2017, Macgregor et al. 2017), and tri-trophic interactions between plants, their herbivores, and parasitoids (Sanders et al. 2015). In a multi-year field experiment, Bennie et al. (2017) found that ALAN altered plant species composition in a semi-natural grassland. While they emphasized that the shifts in species composition could be explained by direct effects of ALAN on plant physiology that influence growth form, resource allocation, and phenology, they did not rule out indirect effects mediated by biotic interactions. Furthermore, Bennie et al. (2016) argued that there is a need for more study on whether ALAN can affect plant communities through alteration of competition and other biotic interactions. Given that ALAN can directly induce plants to increase above-ground vegetative growth (Cathey & Campbell 1976), it is plausible that ALAN could intensify competition among neighboring plants for access to sunlight. Direct effects of ALAN on vegetative growth could, in turn, also increase plant demands for water and other soil nutrients, which could further increase competition among neighboring plants. Studying the vegetative growth of plants grown under ALAN at different densities and resource availabilities would be an important first step in understanding the potential effects of ALAN on competition in plants.

My objective was to test for potential interactive effects of ALAN with soil moisture and plant density on plant growth and defense. I selected common milkweed, *Asclepia syriaca*, as my model organism because it is an herbaceous perennial with a range that overlaps many of the

areas in the contiguous United States with the highest intensities of ALAN. As it often occupies recently disturbed habitats, *A. syriaca* is common along transportation networks (Nichter & Gregory 2018) and therefore is exposed to ALAN from roadway lighting and automobile headlights.

My objective was achieved using a manipulative field experiment. I manipulated ALAN (present or absent), plant density (one or three plants per pot), and soil moisture (plants provided supplemental water or received only ambient precipitation) and then monitored several attributes of plant growth over four weeks. I also measured exudation of latex, an anti-herbivore defense, during the third week of exposure to the treatments and biomass per plant at the conclusion of the experiment. I predicted that ALAN would have a positive effect on plant growth but a negative effect on plant defenses. Specifically, I expected that ALAN would stimulate plants to grow taller than their unlit counterparts, due to the stem-elongation response of some plants to continuous light (Cathey & Campbell 1975). I expected that ALAN-induced increases in growth would be weaker in plants grown at the higher density because competition for limiting resources would constrain growth. I also predicted that providing supplemental water would increase plant size, but that the effects would be smaller under ALAN because I expected ALAN-induced changes in stomatal functioning (Kwak et al. 2017; Kwak et al. 2018) to increase water stress (Greenham & McClung 2015; Robertson et al. 2009). Based upon growth-defense tradeoff theory (Lind et al. 2013; Huot et al. 2014; Zust & Agrawal 2017), I anticipated that increased aboveground plant growth due to ALAN would lead to a weakening of plant defenses. Finally, because latex production in common milkweed is known to increase with soil moisture availability (Couture et al. 2015), I anticipated that increased water loss due to ALAN would counteract positive effects of watering on latex production.

Methods

Study System

Common milkweed, *Asclepias syriaca*, is defended from herbivore attack by both physical and chemical defensive mechanisms and is therefore typically attacked only by a small group of specialist insect herbivores. Its physical defenses consist of non-glandular leaf trichomes and latex, a sticky substance exuded when aboveground tissues are damaged. The species' secondary metabolites (cardenolides) serve as a chemical defense as they are highly toxic cardiac glycosides capable of triggering cardiac arrest (Agrawal & Malcolm 2002; Agrawal 2009).

Experimental Design

The field experiment was carried out in 2017 at University of Virginia's Blandy Experimental Farm (Boyce, VA) in 10 1-m diameter plots that were created in 2016. I manipulated ALAN, soil moisture, and plant density according to a split-plot factorial design, with ALAN manipulated at the level of the plots, and plant density and soil moisture manipulated at the level of pots within the plots. Artificial light at night (from dusk to dawn) was added to half of the 10 field plots (chosen at random). In plots assigned to receive ALAN (hereafter ALAN plots), the light was emitted by a single broad-spectrum (4922 K) 12W LED (Bullet®, RAB Lighting Inc., Northvale, New Jersey, USA) suspended 3 m above the ground on a light post (Appendix A, Figures A1-2). Dummy light posts with no LED were installed over the plots receiving only ambient light. Based on light-meter (Extech LT300, FLIR® Systems, Inc., Wilsonville, Oregon, USA) measurements taken between civil twilight and dawn at a height of 1 m above the ground (roughly 60-80 cm above the plant canopy), illumination was 52.75 ± 4.41 (mean \pm SD) lux in the ALAN plots, which approximates light intensities experienced under streetlights (Bennie et al. 2016, Jin et al. 2017). Because light intensity was measured above the plant canopy, I can assume illumination of the experimental plants by the LEDs was somewhat lower than the recorded measurements. Illuminance in the ambient-lit plots was 1.2 \pm 0.14 lux.

To examine whether intraspecific competition among plants alters the effects of ALAN, seedlings were grown in pots (11.3 L) at two different densities, one (low-density treatment) or three plants (high-density treatment) per pot, with plants randomly assigned to each density treatment. The plants used in the experiment were grown from seeds collected at Blandy Experimental Farm in fall 2016, cold stratified during the winter, and germinated in May 2017. After growing in a greenhouse for 7 weeks, the plants were transplanted to the pots, which were filled with moistened soil (Sungrow Horticulture Professional Growing Mix, Sungrow Horticulture, Sun Gro®, Agawam, Massachussetts, USA). Four pots, two from each of the two plant density treatments, were randomly assigned to each of the 10 field plots. The pots were sunk into pre-drilled holes so that the soil surface within each pot was flush with the surrounding soil surface.

Soil moisture was manipulated with weekly additions of approximately 3.8 liters of water to one of the two pots per density treatment in each plot. The other pots received no supplemental water.

Data collection

I assessed the effects of ALAN, plant density, and soil moisture on plant growth based on measures of plant height, basal stem diameter, and area of the newest fully extended leaf taken for every experimental plant once per week over 4 weeks. Because the leaves are roughly

triangular in shape, leaf area was estimated as $\frac{1}{2} \times l \times w$, where *l* was the length of a leaf *w* was its maximum width.

I also evaluated the effects of the experimental factors on total (aboveground + belowground) biomass per plant. This was measured via destructive harvesting at the conclusion of the experiment, after 4 weeks of exposure to the experimental manipulations. For each individual, I cut the stem at the soil level and then cleared the soil from roots first by gentle brushing with a paintbrush, followed by rinsing with water. The roots and shoots were dried at 40°C for 66 hours and then weighed to determine the total biomass of each individual.

To examine effects of the experimental factors on plant defenses, I measured the amount of latex exuded (grams, dry weight) by one leaf on each plant during the third week of the experiment. The amount of latex present in milkweed leaves has previously been linked to plant water status (Agrawal et al. 2014). The experiment was carried out during a particularly wet season at BEF, July rainfall was approximately 19.05 cm, 7.62 cm higher than the average recorded over the previous ten years at the site. Latex was collected only once from each plant to limit damage to the plants. Latex was collected from each plant's youngest fully extended leaf following methods outlined in Agrawal et al. (2014). The leaf was cut 5 mm from the tip with scissors and latex was allowed to flow onto pre-weighed filter paper (1 cm²) until flow stopped, about ten seconds. After air drying the filter papers at room temperature for 2 days, they were weighed a second time to determine latex dry weights.

During week 2 of the experiment, I noticed foliar damage on some of the experimental plants. Beginning that week, I assigned each plant a damage score every week for the remainder of the experiment. The damage score ranged from 0 to 100% in increments of 20%; 0% damage

was recorded when there was no visible damage to any foliar tissue and 100% damage was recorded when nearly all leaves were severely damaged or removed.

Statistical Analyses

To avoid pseudoreplication due to the non-independence of the multiple plants growing within the same pot in the high-density treatment (three plants per pot vs. one plant per pot in the low density treatment), all statistical analyses used only the mean value of a response variable within each high-density pot (e.g., mean height of the three plants). For attributes of plant growth or defense that could be sampled non-destructively, I used a repeated-measures statistical design because it provides greater statistical power for a given number of study subjects than does a design in which each subject is only sampled once, such as at the conclusion of the experiment Guo et al. (2013).

Repeated measures analyses using linear-mixed-effects (LME) models were used to test the interactive effects of ALAN with soil moisture and plant density on plant height, BSD, and leaf area. The fixed effects in the models included ALAN, soil moisture, plant density, ALAN × soil moisture, ALAN × plant density, and week. I also included herbivore damage score (average score in each pot) as a covariate in my models. I modeled the random effect of plot across time (the interaction between plot and week) using uncorrelated random intercepts and slopes. Models with more complex random effects structures (e.g., correlated intercepts and slopes) failed to converge. To normalize the LME model residuals and to reduce heterogeneity of variance, basal stem diameter and leaf area were log(x + 1) transformed. Plant height was Box-Cox transformed, using an exponent (λ) of 0.88. The effects of ALAN, soil moisture, plant density, and ALAN \times soil moisture, ALAN \times plant density interactions on latex exudation and total biomass per plant were also assessed using LME models. Herbivore damage score was included as a covariate. I modeled the random effect of plot as random intercepts. Prior to the analyses, latex dry mass and total biomass were log(x +1) transformed to improve normality of the model residuals.

Given that I observed herbivore damage starting in the second week of the experiment, I also examined whether the presence/absence of herbivory was affected by the experimental factors (ALAN, soil moisture, and plant density) and their two-way interactions (ALAN × Soil Moisture, ALAN × Plant Density) in a repeated measures analysis using data from weeks 2 to 4. The analysis was conducted using a generalized linear mixed effects model using a binomial distribution for the response variable and the logit link function. Week was included as a fixed effect. I modeled the random effect of plot across time using uncorrelated random intercepts and slopes.

All statistical analyses were carried out using R (R Core Team, 2019). The LME model fitting was carried out using the package 'lme4' (Bates et al. 2014). To test the statistical significance of the fixed effects, degrees of freedom were estimated using via Satterthwaite's method using the package 'lmerTest' (Kuznetsova et al. 2017).

Results

My repeated-measures analyses of effects of ALAN, watering, plant density, and their interactions revealed a variety of effects on different attributes of plant growth. Both plant height and BSD were affected by the ALAN × watering interaction (Tables 1-2). Plant height was 14% higher, on average, under ALAN than under ambient light and 12% higher, on average, in pots

that were watered than in pots that were not watered (receiving only ambient precipitation; Figure 1, Table 2). The mean effect of watering on plant height was greater for plants under ambient light (20% increase) than those under ALAN (4% increase). Under ambient light, watering increased BSD by 13%, whereas watering only increased BSD by 5% under ALAN. Basal stem diameter was also affected by a significant ALAN × plant density interaction. The mean effect of ALAN on BSD was greater in the low-density treatment (8%) than in the highdensity treatment (2%). Leaf area was significantly increased by watering (Table 3, Figure 1, Appendix Figure A3) and was the only growth variable where I found a significant negative relationship with herbivore damage.

Total (aboveground + belowground) biomass per plant at the conclusion of the experiment was increased by watering by an average of 25% ($t_{21.1} = 2.291$, P = 0.032; Figure 2a, Table 4). However, plant biomass was not significantly affected by the other experimental factors or herbivore damage (Table 4).

Despite the fact that the dry mass of latex exuded was 40% higher on average from plants exposed to ALAN than from plants exposed to ambient light, latex exudation was not significantly affected by ALAN (Appendix Table A1), likely due to high variability in this measure (Figure 2b). Furthermore, I found no significant effects of any experimental factor or herbivore damage on latex exudation (Appendix Table A1).

Discussion

This study revealed that ALAN can interact with soil moisture and plant density to affect aboveground plant growth. Consistent with my prediction, based on studies showing that ALAN can adversely affect stomatal functioning (Kwak et al. 2017, Kwak et al. 2018), I found that positive effects of increasing soil moisture on plant growth (specifically basal stem diameter and plant height) were weaker under ALAN than under ambient light (Figure 1a-b). Improper stomatal functioning can decrease plant water use efficiency (Lawson & Blatt 2014), the ratio of net carbon assimilation to transpiration. If ALAN inhibited proper stomatal functioning in my experiment, decreased efficiency in carbon assimilation could potentially explain why increasing soil moisture had a weaker positive effect on plant growth in plants under ALAN than ambient light. One caveat to this argument is that I did not observe the same interactive effects on total (aboveground + belowground) plant biomass. Nonetheless, these findings suggest there is a need to study the effects of ALAN on the water use efficiency of plants given the inextricable link between water use efficiency and primary productivity.

Latex exudation is associated with anti-herbivore defensive ability in common milkweed (Agrawal & Fishbein 2006; Van Zandt & Agrawal 2004). In my study, the mean dry weight of latex exuded from plants exposed to ALAN was 40% higher than from plants exposed to ambient light, but latex exudation was highly variable (Fig. 2b) and not significantly affected by ALAN or any other experimental factor. Herbivory might help explain the high variability in latex exudation. Van Zandt and Agrawal (2004) demonstrated not only that latex production by common milkweed increases following herbivory, but also that the strength of the induced response in latex production differs between different specialist herbivores. It is possible that the variability in latex exudation that I observed was due to differences among the experimental plants in the intensity of herbivory or differences in the composition of attacking herbivore species. Given that latex exudation was only sampled at one point in time (week three), differences in the timing of the herbivory that occurred prior to my survey of latex production

may also have inflated the variability in latex exudation as induced defenses in common milkweed have been shown to attenuate over time (Malcolm and Zalucki 1996).

Bennie et al. (2016) highlighted the need to explore interactions between ALAN and biotic interactions, including competition between plants. One mechanism whereby ALAN may affect competition in plants is promotion of vegetative growth. In some plant species, exposure to ALAN leads to increased vegetative growth (Cathey & Campbell 1975, Goins et al. 1998; Darko et al. 2014). Plants that exhibit increased stem elongation (increased height) in response to ALAN, as I observed for common milkweed (Fig. 1, Table 2), may gain a competitive advantage over plants in the absence of ALAN because the former would be less likely to become shaded by neighboring plants. Further research is needed to improve understanding of how ALAN interacts with the intra- and inter-specific competitive interactions of plants and to discern the key underlying mechanisms.

In my study, BSD responded more positively to ALAN in plants grown at low density than in plants grown at high density. This is consistent with my prediction that ALAN-induced increases in growth would be weaker in plants grown at the higher density because per-capita resource availability would decrease with increasing density. This interpretation would be more compelling if the same pattern was observed across multiple measures of plant growth, however, this finding suggests further study of interactions between ALAN and competition among plants is warranted. In light of previous research demonstrating that ALAN-induced changes in the growth and reproduction of vegetation can have bottom-up effects on consumers (Bennie et al. 2015, Grenis and Murphy 2019), it stands to reason that interactions between ALAN and competition among plants could plausibly influence food web structure.

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Table 1. Results of linear mixed effects model on the effects of artificial light at night (ALAN), soil moisture, plant density, week (time since planting), herbivore damage, and some two-way interactions on the basal stem diameter (mm) of common milkweed.

| Source of variation | Estimate | S.E. | df | t | р |
|---------------------|----------|-------|--------|--------|------------|
| ALAN (A) | 0.049 | 0.032 | 70.62 | 1.523 | 0.132 |
| Soil moisture (S) | 0.141 | 0.021 | 135.16 | 6.716 | < 0.001*** |
| Density (D) | -0.017 | 0.021 | 132.54 | -0.792 | 0.430 |
| Week | 0.128 | 0.013 | 90.48 | 9.851 | < 0.001*** |
| Damage | 0.010 | 0.011 | 136.04 | 0.899 | 0.370 |
| $A \times S$ | -0.081 | 0.030 | 134.68 | -2.720 | 0.007 ** |
| $A \times D$ | 0.075 | 0.029 | 132.72 | 2.557 | 0.012 * |

* Significant at the a = 0.05 confidence level ** significant at the a = 0.01 confidence level

*** significant at the a = 0.001 confidence level

Table 2. Results of linear mixed effects model on the effects of artificial light at night (ALAN), soil moisture, plant density, week (time since planting), herbivore damage, and some two-way interactions on plant height (cm).

| Source of variation | Estimate | S.E. | df | t | р |
|---------------------|----------|-------|---------|--------|------------|
| ALAN (A) | 1.068 | 0.419 | 25.460 | 2.552 | 0.017 * |
| Soil moisture (S) | 1.286 | 0.285 | 136.390 | 4.507 | < 0.001*** |
| Density (D) | -0.311 | 0.286 | 134.680 | -1.088 | 0.279 |
| Week | 0.399 | 0.159 | 136.810 | 2.514 | 0.013 * |
| Damage | -0.161 | 0.145 | 137.340 | -1.112 | 0.268 |
| $A \times S$ | -1.036 | 0.400 | 135.900 | -2.589 | 0.011* |
| A 	imes D | 0.685 | 0.399 | 134.620 | 1.719 | 0.088 |

* Significant at the a = 0.05 confidence level

** significant at the a = 0.01 confidence level *** significant at the a = 0.001 confidence level

Table 3. Results of linear mixed effects model on the effects of artificial light at night (ALAN), soil moisture, plant density, week (time since planting), herbivore damage, and some two-way interactions on leaf area (cm²).

| Source of variation | Estimate | S.E. | df | t | р |
|---------------------|----------|-------|--------|--------|-----------|
| ALAN (A) | 0.011 | 0.147 | 18.03 | 0.071 | 0.944 |
| Soil moisture (S) | 0.239 | 0.098 | 131.33 | 2.442 | 0.016 * |
| Density (D) | -0.121 | 0.097 | 130.01 | -1.247 | 0.215 |
| Week | 0.193 | 0.059 | 54.73 | 3.275 | 0.002 ** |
| Damage | -0.173 | 0.051 | 132.07 | -3.371 | 0.001 *** |
| $A \times S$ | -0.083 | 0.137 | 131.41 | -0.603 | 0.548 |
| $A \times D$ | 0.142 | 0.136 | 130.36 | 1.043 | 0.299 |

* Significant at the a = 0.05 confidence level ** significant at the a = 0.01 confidence level *** significant at the a = 0.001 confidence level

Table 4. Results of linear mixed effects model on the effects of artificial light at night (ALAN), soil moisture, plant density, herbivore damage, and some two-way interactions on biomass (shoot + root mass, g) per plant.

| Source of variation | Estimate | S.E. | df | t | р |
|---------------------|----------|-------|--------|--------|---------|
| ALAN (A) | 0.113 | 0.144 | 19.719 | 0.783 | 0.443 |
| Soil moisture (S) | 0.250 | 0.109 | 21.120 | 2.291 | 0.032 * |
| Density (D) | -0.075 | 0.103 | 19.809 | -0.727 | 0.476 |
| Damage | -0.088 | 0.044 | 23.477 | -2.002 | 0.057 |
| A 	imes S | -0.189 | 0.143 | 20.747 | -1.324 | 0.200 |
| $A \times D$ | 0.217 | 0.145 | 19.941 | 1.498 | 0.150 |

* Significant at the a = 0.05 confidence level ** significant at the a = 0.01 confidence level *** significant at the a = 0.001 confidence level



Figure 1. Effects of artificial light at night (ALAN), plant density, and soil moisture on a) basal stem diameter, b) height, and c) leaf area in the final week of data collection. Bars are means ± 1 SE.



Figure 2. Effects of artificial light at night (ALAN), plant density, and soil moisture on a) total plant biomass (g) and b) latex exudation (mg dry weight). Bars are means ± 1 SE.
Chapter 3

Artificial light at night impacts the litter layer invertebrate community with no cascading effects on decomposition²

Abstract

Artificial light at night (ALAN) can impact the trophic structure of assemblages of ground-dwelling invertebrates, but the consequences for decomposition of plant litter, an important ecosystem service provided by these organisms, are unknown. I sought to answer whether ALAN affects decomposition via its effects on the community of ground-dwelling arthropods. To untangle the indirect effects of ALAN on decomposition of plant litter via the effects of ALAN on the litter-layer invertebrate community, I conducted a field experiment in which I manipulated the presence of ALAN and invertebrate communities following standard litterbag protocols. The rate of plant litter breakdown increased with the mesh sizes of litterbags, suggesting that the presence of larger arthropod secondary and tertiary consumers can affect plant litter decomposition via top-down effects on primary consumers (detritivores). In a second field experiment carried out to examine the effects of ALAN on the trophic structure of litterlayer invertebrate communities, while controlling for potential effects of ALAN on vegetation, I found that ALAN increased the abundances of secondary and tertiary consumers, but not primary consumers. Despite the effects of ALAN on the trophic structure of litter-layer invertebrate communities, I found no significant effects of ALAN on the decomposition of plant litter in either experiment. My findings show that larger assemblages of ground-dwelling secondary and tertiary consumer invertebrates under ALAN do not slow decomposition, suggesting ALAN may disrupt predator-prey interactions or increase the feeding activity of detritivores.

² This study was conducted in collaboration with Howard Epstein and Kyle Haynes.

Introduction

Artificial light at night (ALAN) is a widespread sensory pollutant which currently affects nearly a quarter of the terrestrial surface of our planet (Falchi et al. 2016; Falchi et al. 2019; Gaston et al. 2014; 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 (Gaston et al. 2013; Gaston et al. 2014; Longcore and Rich 2004). Most research documenting effects of ALAN has occurred at the organismal and population levels (Longcore & Rich 2004; Hölker et al. 2010; Gaston et al. 2015; Sanders & 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 (Grenis and Murphy 2019; Meyer and Sullivan 2013; Bennie et al. 2018a). For example, Bennie et al. (2018a) found that abundances of insect prey are reduced both through predator density and behavior. However, potential effects of ALAN on many ecosystem processes such as nutrient transfer and decomposition have yet to be explored.

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 (Heneghan et al. 1998; Moran et al. 1996; Hawlena et al. 2012; Schmitz 2009; 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 (Hawlena et al. 2012; Schmitz et al. 2010; Lawrence and Wise 2000; Kajak 1995). Artificial light at night is known to impact the composition of invertebrate assemblages (Manfrin et al. 2017; Meyer and

Sullivan 2013; Davies et al. 2017; Desouhant et al. 2019) and their trophic dynamics (Sanders and Gaston 2018; Sanders et al. 2015; Sanders et al. 2018; Bennie et al. 2018a). 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; Davies et al. 2017; Willmott et al. 2019; Manfrin et al. 2017; Sullivan et al. 2018). 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 grounddwelling predatory invertebrates are capable of initiating trophic cascades (Moran et al. 1996; Schmitz 2007; Schmitz 2009; Hawlena et al. 2012) and that (b) greater numbers of these are observed in light-polluted conditions (Davies et al. 2012; Holzhauer et al. 2015; Davies et al. 2017; Wolff 1982), 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; Sullivan et al. 2018), 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; Hättenschwiler et al. 2005; García-Palacios et al. 2016; Wardle et al. 2004). 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 (Beare et al. 1992; Vossbrinck et al. 1979; 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 (Ruess and Ferris 2004, Santos et al. 1981). In some cases, tertiary consumers can enhance the activity of microbial decomposers when their prey are mainly secondary consumers (Hedlund and Ohrn 2000). More commonly, tertiary consumers found in the litter layer slow decomposition by exerting top-down effects on detritivores (Lawrence and Wise 2000; Hawlena et al. 2012; Kajak 1995).

I explored the effects of ALAN on the breakdown of plant litter in a temperate grassland ecosystem through its effects on litter-layer fauna. To untangle potential multitrophic effects of ALAN on decomposition (e.g., trophic cascades), I carried out a field experiment in which I manipulated the presence of ALAN and the size classes of soil fauna. I did this by quantifying rates of litter decomposition 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 members of the invertebrate community belonging to various size classes influence decomposition (Bradford et al. 2002; Vossbrinck et al. 1979; Setälä et al. 1996), as invertebrate species richness within litter increases with mesh size (Bradford et al. 2002; Cole et al. 2006). I also carried out an experiment to examine the effects of ALAN on litter decomposition and invertebrate assemblage structure, while controlling for potential effects of ALAN on aboveground vegetation. Based on previous findings documenting high abundances of grounddwelling predatory invertebrates under ALAN compared with unlit areas (e.g., Davies et al. 2012, Davies et al. 2017), and that tertiary consumers can slow decomposition (Hawlena et al. 2012; Kajak 1995; Lawrence and Wise 2000), I predicted that ALAN would reduce rates of litter decomposition indirectly via increased top-down control of primary consumers by secondary and/or tertiary consumers.

Methods

Experiment 1: Untangling effects of ALAN and trophic structure on decomposition

To examine the effects of ALAN on the composition of litter layer invertebrates and the breakdown of plant litter, a field experiment was conducted in the Native Plant Meadow at Blandy Experimental Farm (BEF) in Boyce, Virginia, USA (39.0640° N, 78.0652° W) in the fall of 2017. Dominant vegetation in the meadow consisted of warm season, C₄ 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). Each ALAN plot was illuminated from dusk to dawn by four broad-spectrum (4922 K) 12W LED (Bullet®, RAB Lighting Inc., Northvale, New Jersey, USA) floodlights. The emission spectrum of this LED model is provided in the electronic supplementary material (Appendix B

Figure B1). 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, I installed identical posts without floodlights at the center of ambient-light plots. Within a pair, plots had a minimum distance of 10-m between edges, and pairs were a minimum of 20-m apart. The plots were originally established in 2015 (Firebaugh & Haynes 2016), and ALAN was manipulated throughout the summers of 2015 and 2016. For this study, ALAN was manipulated from the spring through the fall (April – October 2017).

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

To obtain standardized litter for the experiment, I 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 (Appendix B2). I harvested green leaf material on August 12, 2017 by trimming blades to the collar, and then oven dried it at 40°C for ~72 hours. Prior to placing the leaf material into the litterbags, all leaf material was intermixed to

maximize homogeneity among samples. I placed 0.72 ± 0.25 g of dried leaf material into each litterbag (W×L, 9 x 9 cm). The edges of the bags were sealed using a heat sealer.

To examine what trophic levels mediated ALAN-induced changes in decomposition, I manipulated the size classes of fauna that could gain access to the litter by using litterbags with three different mesh sizes: 0.1 mm, 2 mm, 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 (Swift et al. 1979, Wallwork 1970, 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, Swift et al. 1979, Wallwork 1970) include (but are not limited to) Collembolans (springtails), Acari (mites), Isoptera (termites) and other larval organisms (Cole et al. 2006, Wall and Moore 1999). Mesofauna are responsible for modification of the microbial community, comminution, and in some instances predation (Vossbrick 1979, Swift et al. 1979, Scheu & Setälä 2002). Macrofauna (body size > 2 mm, Swift et al. 1979, Wallwork 1970) 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 (Scheu & Setälä 2002, Briones 2014).

I 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). I expected that primary, secondary, and tertiary consumers would all gain access into the litterbags with the 2 mm 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, Cole et al. 2006; Swift et al. 1979; Bradford et al. 2002).

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

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; Bennie et al. 2018b; Grenis and Murphy 2019). I 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 my experimental plots on plant growth, I estimated the density of aboveground grass biomass (g/m²) in each plot from the mean biomass harvested from five 0.3m² quadrats placed randomly within each plot. The biomass was harvested in early August, 2017, dried for five days at 55°C, and subsequently weighed.

To examine the effects of ALAN on decomposition over time, I retrieved half of the litterbags from each plot after 31 days, and the remaining half after 61 days. Immediately after retrieval, I then removed invertebrates from the litterbags using Tulgren extraction carried out over 24 hours. Following extraction of the invertebrates, I dried the litter at 50°C for 24 hours and removed any residual soil or debris by hand. I estimated the proportion of litter decomposed as [1 - mass_{final}/mass_{initial}]. I then pulverized the litter samples into fine powder using a ball mill (Cianflone Scientific LLC, Pittsburgh, PA, USA) and performed combustion analysis to

determine final nitrogen content (Flash 2000 Elemental Analyzer, Fisher Scientific[™], Hampton NH, USA). To obtain initial litter nitrogen content, 0.3 g sub-samples of the litter placed into each litterbag were collected for combustion analysis.

I tested the effects of ALAN and litterbag mesh size on the mean proportion of litter decomposed 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. Nitrogen content in remaining litter was log(x+1) transformed 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 2017). I did not capture sufficient numbers of invertebrates from the litterbags in this experiment to examine how their abundances were affected by the experimental manipulations.

Experiment 2: Effects of ALAN on decomposition and litter-layer invertebrates while controlling aboveground vegetation

Because ALAN can affect vegetation (Bennie et al. 2018b; Grenis and Murphy 2019; Bennie et al. 2016), which could potentially affect invertebrate assemblages or litter decomposition, I 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), I measured rates of plant litter decomposition in litterbags; however, in the second experiment I took two steps to minimize differences across plots in the structure and biomass of aboveground vegetation. 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, I mowed all plots two 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 a distance of 5 m between adjacent plots. Half of the plots were selected at random to receive ALAN, while the other half received ambient light only. A plot was exposed to ALAN by one broad-spectrum 12W 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). At the ground level, the average nighttime light intensity in the ALAN plots was 126.8 \pm 7.32 lux (mean \pm 1 SD) in the ALAN plots and 0.4 \pm 0.21 lux in the ambient-light plots.

In this experiment, I intended to use plant litter that more closely resembled the mixed litter occurring in the grasslands at my study site. To accomplish this, rather than using green leaf material collected from greenhouse-propagated grass as in the 2017 study, I collected senesced leaves from standing C₄ grasses in the BEF Native Plant Meadow in August of 2018. The nitrogen content of the collected leaf litter was 1.02 ± 0.33 (% of total mass mean \pm SD). I collected leaf litter from plants located > 50 m from sources of ALAN. The leaf litter was dried at 50°C for five days, homogenized, and then placed into litterbags.

To increase my ability to characterize effects of ALAN on trophic structure, I took two steps to increase the numbers of invertebrates captured. First, I used a mesh size (4 mm) that excluded only large macrofauna. Second, I used larger litterbags (W×L, 10 x 20 cm) containing more plant material (3.0 ± 0.05 g) than in the 2017 experiment (0.72 ± 0.25 g).

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

I tested the effects of ALAN on the mean proportion of material decomposed [1 - mass_{final}/mass_{initial}] and mean nitrogen content of remaining litter using one-way ANOVAs.

I examined the effect of ALAN on the ground-dwelling invertebrate community, which was broken down into three trophic groups: primary consumers, secondary consumers, and secondary/tertiary consumers. Because of non-independence of potentially interacting trophic levels, I tested for a multivariate effect of ALAN on abundances of the three trophic groups using MANOVA. In the event of a significant multivariate effect, I 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 & Norberg 2010). I ran this test using the "manova" function in the "stats" package in R (R Core Team).

Results

Experiment 1: Untangling effects of ALAN and trophic structure on decomposition

The proportion of leaf litter decomposed tended to be higher under ALAN than under ambient light; however this difference was not statistically significant (p = 0.07, Table 1, Figure 1). The proportion of material that decomposed 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 sixty days, there was approximately a 20% difference in proportion decomposed in the largest mesh size compared with the smallest mesh size. I also observed a marginally significant interactive effect of ALAN and mesh size on the proportion of litter decomposed (p = 0.06, Table 1), potentially reflecting a stronger effect of ALAN on the proportion of litter decomposed 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). There was no effect of aboveground grass biomass on the proportion of litter that decomposed (p = 0.14, Table 1).

The average initial nitrogen content the litter for this experiment was 3.36 ± 0.32 (% of total mass) and the average nitrogen content of the litter remaining over 30 and 60 days was 3.25 ± 0.46 (% of total mass). I found no evidence that nitrogen content of remaining litter was affected by any of my experimental factors (Table 2, Figure 2).

Experiment 2: Effects of ALAN on decomposition and litter-layer invertebrates while controlling aboveground vegetation

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

I captured 348 invertebrates from my litterbags. 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 ($F_{1,8}$ = 5.561, p = 0.046) than litterbags exposed to ambient light regimes. In contrast, there was no significant effect of ALAN on the abundance of primary consumers ($F_{1,8}$ = 0.134, p = 0.724).

Discussion

To my knowledge, this is the first study to evaluate the effects of ALAN on decomposition of terrestrial vegetation. 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). I observed that the proportion of leaf litter that decomposed was, on average, 11% higher rates under ALAN compared with ambient-lit plots in 2017 (although this effect was not significant, p = 0.07; Figure 1). The lower rate of decomposition in 2018 is likely the result of the lower nutritional quality of the litter (1.02 ± 0.33 %N of total mass, mean \pm SD) than in 2017 (3.36 ± 0.32). Litter of poor nutritional quality, or having lower nitrogen content, is known to decompose more slowly (Smith and Bradford 2003). The lower amounts of decomposition in 2018 may have reduced my ability to detect potential effects of ALAN on litter decomposition in the second experiment. Lower foliar nitrogen has been reported for C₄ plants

(like those used in both of my experiments) compared with C₃ plants under the same fertilizer regime (Sage & Pearcy 1987). It is possible that ALAN may be more likely to affect the decomposition of nutrient-rich than nutrient-poor plant tissues, but further research is needed to resolve this question.

I found that the rate of decomposition of plant litter within litterbags increased with litterbag mesh size (Table 1, Figure 1). This phenomenon is consistent with prior research and is thought to be caused by increased abundance, diversity, and food web complexity of litterdwelling fauna in litterbags with larger mesh sizes (Bokhorst and Wardle 2013, Liu et al. 2019, Bradford et al. 2002, Smith 1979, Vossbrinck et al. 1979). Although these studies have demonstrated that increasing the access of a greater variety of arthropod consumers (including secondary and tertiary consumers) to litter-layer communities leads to increased rates of plant litter decomposition, I found no significant effects of ALAN on litter decomposition despite the fact that ALAN, like increases in litterbag mesh size, increased the abundances of arthropod secondary and tertiary consumers in litter-dwelling communities in my second experiment (Fig. 3).

Consistent with previous research on effects of ALAN on trophic structure within ground-dwelling arthropods (Davies et al. 2012; Sullivan et al. 2018), I found that ALAN increased the abundances of arthropod secondary and/or tertiary consumers, but had no effect on the abundance of primary consumers (Figure 3). My prediction that ALAN would reduce rates of litter decomposition indirectly via increased top-down control of primary consumers by secondary and/or tertiary consumers was not supported by my results. My findings suggest that ALAN may have increased rather than decreased the rate at which plant litter decomposed (Table 1, Figure 1); however, the effect of ALAN on decomposition was not significant (P =

0.07). One possible explanation is that detritivore feeding activity was increased by ALAN. Clearly, the ALAN-induced increases in abundances of arthropod secondary and tertiary consumers did not lead to a trophic cascade in which increased top-down control of primary consumers slowed the decomposition of plant litter. Finke & Denno (2005) found that aggregations of predators can sometimes lead to increased intraguild predation releasing primary consumers from top-down control. Higher intraguild predation under ALAN could potentially explain the lack of an effect of ALAN on primary consumer abundance in my study.

The greater total number of invertebrates in plots exposed to ALAN compared to plots exposed only to ambient light could have resulted in greater frass deposition under ALAN. Insect frass is high in organic nitrogen (Frost and Hunter 2007) and represents an important input of nitrogen return to soil (Frost and Hunter 2007; Behie and Bidochka 2013), as nitrogen can be leached directly to the soil, or organic nitrogen can be assimilated by microbial communities (Behie and Bidochka 2013). As invertebrate predators have higher N content than their prey (Fagan et al. 2002; Denno and Fagan 2003), their excrement may likewise have more N, though this has not been explored in the literature to my knowledge. I have focused on the breakdown of plant litter in my study, but recommend that future work on the effects of altered grounddwelling invertebrates under ALAN is expanded to consider other pathways (e.g., frass deposition) of nutrient return to the soil.

This work confirms the findings of others (Davies et al. 2017; Davies et al. 2012) that ALAN leads to higher local densities of ground-dwelling predaceous invertebrates (but see Manfrin et al. 2017). Contrary to my prediction, I found that the effect of ALAN on local abundance of arthropod secondary/tertiary consumers does not suppress the decomposition of plant litter. This indicates that detritivores in the litter layer may not be subjected to increased

predation under ALAN. This would align with the positive effect of increased trophic complexity on the rate of decomposition in my first experiment. Further work is needed to elucidate the activities of predaceous ground-dwelling invertebrates under ALAN, for example by investigating potential disruption of predator-prey interactions. There is increasing recognition that the effects of ALAN on invertebrate communities has implications for ecosystem processes like pollination (Knop et al. 2017; Macgregor et al. 2017) as well as aquatic to terrestrial fluxes of organisms and energy (Meyer & Sullivan 2013; Manfrin et al. 2017) and I propose that decomposition is another function which warrants further consideration.

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Figures & Tables

Table 1. Results of a linear mixed effects models to investigate the interactive effects of light treatment (ALAN or ambient) and litterbag mesh size on litter decomposition. Proportion decomposed was calculated as (1 - Final Mass/Initial Mass).

| Source of variation | S.S. | M.S. | df | Den. DF | F Value | р |
|----------------------|------|------|----|---------|---------|-------------|
| ALAN (A) | 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 *** |
| $A \times Mesh Size$ | 0.01 | 0.01 | 2 | 33.89 | 3.13 | 0.06 * |

* Significant at the a = 0.05 confidence level ** significant at the a = 0.01 confidence level

*** significant at the a = 0.001 confidence level

| Source of variation | S.S. | M.S. | df | Den. DF | F Value | р |
|----------------------|--------|--------|----|---------|---------|------|
| ALAN (A) | 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 |
| $A \times Mesh Size$ | 90.83 | 45.42 | 2 | 37.98 | 0.41 | 0.67 |

Table 2. Results of a linear mixed effects models to investigate the interactive effects of light

 treatment (ALAN or ambient) and litterbag mesh size on remaining nitrogen in litter.



Figure 1. Effect of litterbag mesh size and artificial light at night (ALAN) on the proportion of leaf litter (g) lost (mean \pm 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).



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.



Figure 3. Effects artificial light at night (ALAN) on numbers of invertebrate primary consumers, secondary consumers, and secondary/tertiary consumers (mean \pm SE) recovered from litterbags.

Chapter 4

Effects of artificial light at night spectrums on spatial fluxes of terrestrial arthropods: experimental examination of consequences for trophic structure and nutrient redistribution³

Abstract

There is mounting evidence that artificial light at night (ALAN) changes population dynamics, community structure, and trophic interactions for terrestrial arthropods. Few studies, however, have explored how ALAN affects the net attraction (attraction – repulsion) of these organisms to lights, or whether ALAN-induced changes to arthropod dispersal may influence local trophic structure or spatial biogeochemical fluxes. I sought to measure the net attraction of terrestrial arthropods in response to broad-spectrum LEDs with two different spectrums and quantified the effects of ALAN on net attraction at two different trophic levels to understand how local trophic structure may be impacted by ALAN. To inform whether ALAN may influence biogeochemical fluxes via effects on arthropod movements, I also measured biomass and nitrogen of common taxa. Herbivores captured in flight intercept traps demonstrated net attraction to ALAN, whereas I found no effects of ALAN on the net attraction of carnivores. Effects of ALAN on redistribution of energy or nutrients via insect movements appeared to be driven primarily by effects on larger bodied arthropods including scarabaeid beetles and moths. These results highlight the need to explore the mechanisms underlying ALAN-induced changes in trophic structure (increased abundances of carnivores) that have been observed in previous studies. Important avenues for future research include investigation of changes in *in situ* trophic dynamics caused by ALAN and the effects of arthropod attraction to ALAN on the ecosystem processes to which they contribute.

³ This study was done in collaboration with Lauren Okafor and Kyle Haynes.

Introduction

Disruption of nocturnal landscapes by artificial light at night (ALAN) is becoming progressively more common in terrestrial environments, as urbanized areas expand and the brightness of ALAN increases (Kyba 2018). ALAN is typically bright enough to mask natural nighttime lights such as the moon, light reflected by water, and stars (Falchi et al. 2016; Horváth et al. 2009). Positive phototaxis, or movement towards light, facilitates navigation by many insects under ambient light conditions (Jander 1964; reviewed in Shimoda & Honda 2013 and Owens & Lewis 2018). Insects attracted to sources of ALAN may quickly experience mortality due to exhaustion (Eisenbeis 2004), increased predation (McMunn et al. 2019; Minnaar et al. 2015; Czaczkes et al. 2018; Yuen and Bonebrake 2017; Wakefield et al. 2015), or collision with the sources (Gaston and Holt 2018). Consequently, the positive phototactic response of many insects may contribute to allochthonous inputs of nutrients to patches representing areas with high levels of ALAN that are embedded within areas that are dark at night.

ALAN is pervasive both in spatial and spectral extent (Kyba 2018; Kyba et al. 2017). The emissions spectra of light-emitting diodes (LEDs), which are increasingly popular for both outdoor and indoor use, tend to be much broader than older bulb types such as high-pressure sodium or metal halide. Artificial light sources that vary in their spectral properties elicit different responses of insects. For example, van Grunsven et al. (2019) found that LEDs rich in amber light were less attractive to insects (other than Hymenopterans) than mercury vapor lights. Longcore et al. (2015) demonstrated that the spectra of LEDs significantly impacted the number of arthropods captured in pan traps under sources of ALAN. Many insects are strongly attracted to high-energy, short-wavelength light including ultraviolet and blue light (O'brien and Wolfe 1964; Barghini and Souza de Medeiros 2012). However, some invertebrates exhibit a negative

phototactic response to ALAN rich in blue (Kim et al. 2013) and amber (Reisenman & Lazzari 2006; Reisenman et al. 1998) light. A transition from white LEDs, which are rich in blue light, to amber LEDs with spectra richer in longer wavelengths, has been proposed as a conservation strategy, as white lights are known to be more attractive to more arthropods than amber lights (Gaston et al. 2012; van Langevelde et al. 2011; Longcore et al. 2015). Further work examining the effects of LEDs of differing spectral properties on local abundances of arthropods as well as directionality of their movements (attraction vs. repulsion to ALAN sources) would help determine the effectiveness of transitioning from use of white LEDs to amber LEDs for outdoor lighting.

A small but growing body of literature addresses the ways in which ALAN impacts arthropod populations, trophic interactions, and communities (Sanders & Gaston 2018; Owens & Lewis 2018). Both top-down (Yuen & Bonebrake 2017; Sanders et al. 2018) and bottom-up (Bennie et al. 2015) trophic effects involving arthropods can be altered by ALAN (Bennie et al. 2018). The trophic structure of arthropod communities can also be altered by ALAN; higher abundances of ground-dwelling carnivorous species are often found near ALAN compared with areas with ambient light only (Davies et al. 2017; McMunn et al. 2019). These studies do not address the mechanism for this effect, which could be a result of attraction of such organisms to sources of ALAN, or changes to *in situ* trophic dynamics leading to higher relative abundances of carnivores under ALAN.

The mounting evidence for effects of ALAN on trophic structure in arthropod assemblages suggests that ecosystem dynamics may also be impacted by this sensory pollutant. In terrestrial ecosystems, arthropods strongly contribute to biogeochemical fluxes (Schowalter 2016; Schowalter et al. 2018). Their movement represents an important way in which energy and

nutrients are exchanged across ecotones (Baxter et al. 2005; Polis et al. 1997). For example, ALAN has been found to alter exchanges of arthropods across stream-riparian boundaries (Meyer & Sullivan 2013). However, relatively little is known about how ALAN influences the spatial fluxes of energy and nutrients across landscapes via its effects on arthropod movement.

My primary objective was to measure the net attraction of invertebrates in response to ALAN of different spectrums. I predicted that ALAN would increase net attraction of invertebrates, and that white LEDs would elicit greater net attraction than amber LEDs. My second objective was to explore the effects of ALAN on the trophic structure of terrestrial invertebrates. Prior research demonstrating high local abundances of ground-dwelling predators and scavengers under ALAN sources (Davies et al. 2017; McMunn et al. 2019) led me to predict stronger net attraction of carnivorous than herbivorous invertebrates toward ALAN. I also explored whether energy and/or nutrient sinks may form around sources of ALAN via the effects of ALAN on invertebrate dispersal. After identifying captured specimens to trophic level based on their taxa, I measured the biomass and nitrogen content of taxa for which the collected specimens provided sufficient biomass for determination of nitrogen content.

To achieve my objectives, I carried out a field experiment in which I tested the effects of ALAN from broad-spectrum LEDs of two different spectra (white and amber) on the net attraction of the terrestrial invertebrate community. To estimate net attraction to a source of ALAN, I used traps that selectively captured individuals as they moved toward or away from an ALAN source. Individuals captured in the former traps were assumed to be attracted to the source of ALAN, while individuals captured in the latter traps were assumed to be repulsed by the source of ALAN. To capture a wide variety of arthropod types, I used three different types of trap. I trapped arthropods which are primarily ground dwelling, such as spiders, beetles,

springtails, and others using pitfall traps. I also used flight intercept and malaise traps to capture flying insects.

Methods

Field Experiment

I carried out a field experiment in early stage successional fields at Blandy Experimental Farm (BEF) in Boyce, Virginia, USA (39.0640° N, 78.0652° W) in the summer of 2017. I set up three 12-m diameter plots, which were positioned at least 100 meters apart to prevent spillover effects of ALAN treatments between plots. To my knowledge, the early successional fields had not been previously exposed to artificial nighttime lighting prior to this experiment. All experimental plots were mowed in May of 2017 to minimize differences in vegetation structure across plots. In the center of each plot I installed a 2-m tall lamp post, which could be fitted with a 7W LED. The LED bulbs were each powered by a battery charged daily by a solar panel, and controlled by a conversion system (Solar Illuminations, FL 100 Solar Light Bulb Conversion System) stored in a box at the base of the solar panel. Solar panels were mounted on a second 2m tall post positioned 1-m to the west of the lamp post. Because I was interested in testing the effect of differing ALAN spectra, my ALAN treatments consisted of two spectral types: (1) broad-spectrum white LED and (2) broad-spectrum amber LED. A third treatment with no LED served as an unlit control. I characterized the emission spectra of the LEDs using a microspectrometer (STS-VIS-L-50-400-5MA, Oceanoptics[©], Winter Park, Florida, Appendix C Figure 1).

I conducted twelve experimental trials between June-August 2017. All three ALAN treatments were represented within each trial period (one plot received white ALAN, one

received amber ALAN, and one was an unlit control). Within four sets of three trials (trials 1-3, 4-6, 7-9, and 10-12), the treatments were randomly assigned, without replacement, to the plots ensuring that each plot was subjected to each treatment in each set of trials. Each trial ran for a six-hour period beginning at civil twilight (when the sun is 6° below the horizon). Trials were separated by a minimum of 72 hours. Trials were conducted on evenings when rainfall was unlikely and the minimum predicted temperature was >12.8° C.

To assess the effects of ALAN on the movement of a large portion of the terrestrial invertebrate community at the study site, I used three different types of trap. I employed malaise (Bioquip, model 2875AG), flight intercept, and pitfall traps. I used flight intercept traps (with a panel design) to capture flying insects which respond to colliding with barriers by dropping to the ground (many Hemiptera and Coleoptera; Bland & Jacques 2010, Lamarre 2012), pitfall traps to collect primarily ground-dwelling (including Coleoptera, Collembola, Isopoda, Araneae, and others, Epsky et al. 2008), and malaise traps to capture primarily flying insects which respond to impact with a barrier by moving in an upwards direction (Diptera, Hymenoptera, and Lepidoptera; Malaise 1937, Van Achterberg 2009, Bland & Jacques 2010). The flight intercept traps could potentially capture or impede the movements of both flying and crawling arthropods, because the collection pans rested on the ground, so I deployed the flight intercept traps only in June-July (trials 1-6) and then malaise and pitfall traps (concurrently) in July-August (trials 7-12, see Appendix C Figure 2 for trap layouts within each plot). Thus, I deployed each trap type in 6 replicate trials. I considered trials and plots as blocks to account for random temporal and spatial variation, respectively.

Each flight intercept trap consisted of a 1.2 m \times 1.4 m ($W \times L$) transparent plastic sheet suspended over a 1.2 m \times 1.2 m wooden frame, with collection pans placed at the base of the

frame. An individual flight intercept trap was oriented either to capture insects moving towards or away from the central lamp post, to quantify the numbers of insects that were attracted to, or repelled by, ALAN, respectively. The plastic sheet was held taut by anchoring it under the collection pans, which rested on the ground on one side of the trap. I deployed eight flight intercept traps per plot. To examine the distances over which ALAN influenced insect movement, the traps were deployed at two distances from the central lamp post (3 m and 6 m). At the 3-m distance, the traps were positioned to the north, south, east, and west of the lamp post. At the 6-m distance, the traps were positioned to the northeast, southeast, northwest, and southwest. At each distance, half of the traps were oriented to capture insects that were attracted and the other half were oriented to capture insects that were repelled. For simplicity, I refer to a trap oriented to capture insects moving towards the lamp post as an "attraction trap" and a trap oriented to capture insects moving away from the lamp post as a "repulsion trap". The traps were paired such that for any given flight intercept trap, the trap on the opposite side of the lamp post faced in the opposite direction, i.e., one was an attraction trap and the other was a repulsion trap. This design was adopted to account for possible directional biases in insect movement due to uncontrolled factors such as wind. For example, a moderately strong easterly wind would be predicted to cause higher captures of insects both for an attraction trap oriented to capture insects moving to the west, as well as the repulsion trap on the opposite side of the lamp post. In each trial, the orientation of each trap was selected at random, without replacement, so that half of the traps at each distance were attraction traps and the remaining half were repulsion traps.

Similarly, two malaise traps were positioned on opposite sides of the central lamp post, with one modified to be an attraction trap and the other to be a repulsion trap. Insects intercepted

by a malaise trap were collected in a container at the top of trap. Upon entering the container, the insects were killed by Dichlovoros released by insecticidal strips (Vaportape II).

Unlike the flight intercept and malaise traps, which were unidirectional, the pitfall traps were bidirectional, separately storing invertebrates moving towards versus away from the lamp post. Pitfall traps consisted of a 15 cm tall X-shaped barrier constructed from Plexiglas (to prevent shading) with two 10-cm diameter plastic collecting cups on opposite sides of the barrier, to capture ground-dwelling arthropods moving towards and away from the center post. I sunk the collecting cups into the ground with their rims flush with the soil surface. Prior to each trial, I added 2-oz of soapy water to the cups to prevent escape.

To investigate the possibility that ALAN, or particular ALAN spectra, had differing effects on the net attraction of herbivores and carnivores (predators, parasites, parasitoids, and scavengers), I identified specimens to order or family level, depending on which was needed to determine trophic level (for all identified orders, families, and their trophic levels, see S2). Prior to identification, specimens were stored in 70% ethanol (for flight intercept and pitfall traps) or in a freezer (malaise traps). In total, I identified 6,359 out of the 6,476 invertebrates captured; 117 were too damaged to identify. Of those identified, 4,466 were classified as either herbivores or carnivores. The remaining specimens belonged to families dominated by omnivores or detritivores, or contained species at differing trophic levels.

To assess whether energy and nutrient sinks may be created near sources of ALAN due to the net attraction of terrestrial invertebrates, I measured the biomass and nitrogen content of representative samples from eight taxonomic groups that comprised 61.5% of the identified invertebrates (Appendix C Figure 3). These taxa included orders Araneae and Lepidoptera, as well as families Scarabaeidae (Coleoptera), Aphidae, Cicadellidae, Derbidae, and Psyllidae

(Hemiptera), and Formicidae (Hymenoptera). To estimate biomass and N content, I air dried the specimens for one week, and then dried them in a drying oven at 40°C for 48 hours to remove any residual moisture from water or ethanol. After drying, I first weighed individuals to determine body mass, and then pulverized and homogenized all samples within each taxon using a mortar and pestle. I determined the average carbon and nitrogen content of each taxon using combustion analysis (Flash 2000 Elemental Analyzer, Fisher Scientific[™], Hampton NH, USA).

Statistical Analyses

Effects of ALAN on overall net flux of arthropods

I tested whether ALAN and ALAN spectrum impacted the net attraction of terrestrial invertebrates [calculated as log₁₀(number attracted) - log₁₀ (number repelled)] using linearmixed-effect (LME) models. Because all three trap types were not deployed concurrently, the data from each trap type were analyzed separately. The models for flight intercept trap and pitfall trap data included ALAN treatment and distance (from the central lamp post) as interacting fixed effects. For each trial and plot, the numbers of invertebrates attracted and repelled were pooled (summed) across all traps at each distance. The only fixed effect in the model for the malaise trap data was ALAN treatment because all malaise traps were 8 m from the central lamp post. Initially, the random effects in these models were trial (1-12) and plot, but the random effect for plot was removed to improve model parsimony after log-likelihood ratio tests showed that removal of plot did not significantly affect the fit of the models (Pinheiro & Bates 2006).

Many arthropods demonstrate positive phototaxis towards artificial light sources (Eisenbeis 2006). However, some flying insects exhibit erratic spiraling flight patterns in the
vicinity of sources of ALAN (Muirhead-Thompson 1991; Wakefield et al. 2015). Furthermore, arthropod responses and movements in the presence of ALAN can vary by taxa (Owens & Lewis 2018; Desouhant et al. 2019). Therefore, to explore whether my trapping design could successfully measure net fluxes, i.e., accurately estimate the difference between the number of individuals attracted and the number repulsed, I also examined the effect of ALAN on the total number of invertebrates captured in each trap type. I deemed that my trapping design could correctly characterize the net flux of invertebrates if I recorded both net attraction (number attracted > number repulsed) and higher total captures of invertebrates under a given ALAN treatment compared to the unlit controls. Conversely, if I recorded net repulsion under a given ALAN treatment, I expected total captures of invertebrates to be lower under ALAN compared to the unlit controls. I analyzed the effect of ALAN on total number of individuals captured using a LME model using the same fixed effects for each trap type as described in the previous paragraph. I included a random effect for trial modeled as a random intercept rather than trial and plot because log-likelihood ratio tests showed that removal of plot did not significantly affect the fit of the models (Pinheiro & Bates 2006). The number of invertebrates was log transformed to improve normality of the model residuals.

Trophic-level effects of ALAN on net attraction

To examine whether ALAN could influence local trophic structure by affecting the net fluxes of different trophic groups differently, I tested the effect of ALAN on the net attraction of herbivores and carnivores using LME models for each trap type. For the flight intercept and pitfall traps, I tested the effects of ALAN, distance from ALAN source, and their interaction on net attraction [calculated as log₁₀(number attracted +1) - log₁₀ (number repelled+1)] of carnivores and herbivores. For the malaise traps, I tested the effect of ALAN on net attraction of herbivores and carnivores $[log_{10} (number attracted+1) - log_{10} (number repelled +1)]$. I also replicated these analyses to investigate the effects on total captures for each trophic group. For all of these LME models, trial and plot were included in the models as random effects, which were modeled using random intercepts.

ALAN impacts on dispersal-mediated nutrient fluxes

I used the proportion of individuals (within a taxonomic group but pooled across trap types) that were attracted to, and repelled from, the central lamp post to estimate the effects of ALAN on the spatial fluxes of biomass (mg) and nitrogen (mg). The total biomass of a taxon was calculated as the mean biomass per individual × number of individuals captured across all trap types and ALAN treatments. The total nitrogen content represented by each taxonomic group was calculated as N content (%) × total biomass (mg).

I also evaluated the effects of ALAN on the net attraction of the eight dominant taxonomic groups (pooled across trap types) using generalized linear mixed effects models. Of these, seven models converged. I included ALAN treatment as a fixed effect, and random effects for trial and plot, with the random effects modeled as random intercepts. I specified a Poisson distribution and the log-link function.

I carried out all statistical modeling using the R programming language (R core Team 2018). I conducted linear and generalized linear mixed effects models using the package 'lme4' (Bates et al. 2015), generated p-values for LME and GLME models using the package 'lmerTest' (Kuznetsova et al. 2020), and ran post-hoc pairwise comparisons based on least-squares means using a Tukey p-value adjustment using the package "emmeans" (Lenth et al. 2019).

Results

Effects of ALAN on overall net flux of arthropods

I observed significant effects of ALAN and the ALAN × distance interaction on the overall flux of invertebrates captured in flight intercept traps (Table 1). Post-hoc comparisons demonstrated that effects of ALAN treatment on overall net attraction varied based on distance of traps from the lamp post. At a distance of 3m from the lamp post, net attraction was 30% higher in plots with an amber LED compared to unlit control plots, and 20% higher in plots with a white LED compared with unlit control plots (Figure 1). However, at a distance of 6m from the lamp post, net attraction was not significantly affected by ALAN from either LED (Figure 1). Net attraction of invertebrates was not significantly affected by ALAN treatment or distance from the ALAN source for arthropods captured in pitfall traps. There was also no significant effect of ALAN on the net attraction of arthropods captured in malaise traps (Table 1). The total number of invertebrates caught was not significantly affected by ALAN treatment, distance, or their interaction (for flight and pitfall traps) or ALAN treatment alone (for malaise traps, Table 1).

Trophic-level effects of ALAN on net attraction

ALAN had a significant positive effect on the net attraction of herbivores captured in flight intercept traps (p = 0.049, Table 2). Post-hoc comparisons showed that for herbivores captured in flight intercept traps, there tended to be greater net attraction to the amber LED at a distance of 3 m compared to the unlit control, although this was non-significant (p = 0.06). Distance of trap from the central lamp post did not affect net attraction for carnivores or

herbivores captured in flight intercept traps. However, distance from the source of ALAN affected the total numbers of both herbivores and carnivores captured in flight intercept traps (p = 0.001 and p = 0.009, respectively, Table 2). I captured more herbivores in flight intercept traps 3m from the lamp post than at 6m from the lamp post for all ALAN treatments. The number of herbivores captured was 30%, 87% and 52% higher at 3 m from the lamp post than at 6 m from the lamp post in plots with no LED (unlit control), an amber LED, and a white LED, respectively (Figure 2). Distance from the center post tended to have the same effect for carnivores caught in flight intercept traps, though this was only significant in plots receiving the amber LED treatment. In plots with an amber LED, I observed nearly a five-fold increase in carnivores captured in flight intercept traps at 3 m, compared to 6 m, from the lamp post (Figure 2). In the pitfall traps, net attraction and total number of invertebrates captured were not significantly affected by ALAN treatment or distance from the central lamp post in either trophic group (Table 3). Similarly, in the malaise traps, I found no significant effect of ALAN on net attraction or total number of invertebrates captured for either trophic group (Table 4).

ALAN impacts on dispersal-mediated nutrient fluxes

Nitrogen content (%N) did not differ substantially among taxonomic groups (Table 5). The group with the highest average nitrogen content was Cicadellidae (10.7%) and the lowest was Aphidae (8.5%). However, the estimated total nitrogen (mg) from common taxa in my study ranged over 3 orders of magnitude, with Aphidae comprising the lowest amount of total nitrogen (3.94 mg) and Scarabaeidae comprising the largest amount of nitrogen (2,379.54 mg).

Of the eight common taxa I examined, ALAN had a significant effect on the total number of invertebrates captured in five groups: Cicadellidae and Derbidae (Hemiptera), Formicidae (Hymenoptera), Scarabaeidae (Coleoptera), and Lepidoptera (Table 6). ALAN of the amber-LED spectrum increased the number of individuals belonging to Cicadellidae caught by 20% relative to the unlit controls (Figure 3). For Derbidae and Lepidoptera, the average number of individuals captured under both LED treatments was significantly higher than in the unlit controls (Figure 3). The mean number of Derbidae captured in plots with a white LED or an amber LED was 830% and 730% greater than unlit control plots, respectively. The average number of Lepidoptera captured was 10% greater in plots with a white LED compared with unlit-control plots, and 20% greater in plots with an amber LED compared with unlit-control plots. Formicidae and Scarabaeidae were both captured in greater numbers in plots with a white LED relative to plots with an amber LED. On average, the number of Scarabaeidae was 80% higher in plots with a white LED compared to plots with an amber LED, and six times as many Formicidae were captured in plots with a white LED compared to plots with an amber LED.

Discussion

This study demonstrates that broad spectrum LEDs can cause net attraction of some terrestrial arthropods regardless of spectrum. Based on previous studies promoting the use of amber LEDs to minimize effects of ALAN on arthropods (Gaston et al. 2012; van Langevelde et al. 2011; Longcore et al. 2015), I predicted that arthropods would demonstrate net attraction to both LEDs, but that the effect would be greater in plots with a white LED compared with an amber LED. This was partly supported by my results. I found that both white LEDs and amber LEDs caused net attraction of arthropods captured relative to unlit conditions for one trap type (flight intercept), and this effect was larger nearer to the source of ALAN, however there was no evidence for the white LED causing greater net attraction than the amber LED.

There has been little work using field studies to measure the unintended effects of ALAN on the directionality of arthropod movements (but see Meyer & Sullivan 2013). However, interest in the effects of artificial lights on the dispersal and movements of insects dates back several decades (Verheijen 1960; Jander 1963). Although many insects exhibit positive phototaxis towards sources of ALAN (Eisenbeis 2006, reviewed in Owens & Lewis 2018 and Desouhant et al. 2019), the responses of terrestrial arthropods towards light has been found to vary by taxa, and in some cases movements paths near lights are erratic and non-linear (Muirhead-Thompson 1991; Wakefield et al. 2015). Spiraling or circuitous movement paths near lights could mask signals of net attraction, measured as the numbers of individuals captured moving towards a light minus the numbers of individuals moving away from a light. For example, an individual that exhibited highly directional movement towards a light over a long distance only to spiral around the light upon reaching it could be captured as it spirals away from the light. Therefore, to assess whether my trap design could accurately measure net fluxes, I analyzed the effects of ALAN and ALAN spectra on total abundances of arthropods. I found evidence for an effect of ALAN on the net attraction of all arthropods caught in flight intercept traps, however there was no significant effect of ALAN on the total number of arthropods captured (Table 1). In herbivores, however, I found that ALAN caused a significant increase in net attraction (as measured using flight intercept traps) and a consistent, but not significant, increase in the number of herbivores captured (p = 0.097, Table 2). This mixed evidence suggests that measurements of net attraction to sources of ALAN using directional traps should be interpreted with caution. Interpreting the effects of ALAN on spatial net fluxes of

invertebrates may be best achieved by interpreting measurements of net attraction in concert with measurements of total captures near the source of ALAN.

I predicted that net attraction towards ALAN would be greater for carnivorous than herbivorous arthropods. Contrary to this prediction, I found no evidence for net attraction of carnivores towards ALAN. Instead, I found that ALAN increased the net attraction of herbivores. Herbivores captured in flight intercept traps demonstrated net attraction towards ALAN with an amber rich-spectrum compared to that with a white spectrum or the unlit control, and this effect was stronger with increased proximity to the light source. There also tended to be more herbivores caught in flight intercept traps in plots receiving ALAN from the amber LED, though this was not significant (Figure 2). Net attraction of herbivores to ALAN may lead to increased herbivory (McMunn et al. 2019), prey for predators (McMunn et al. 2019; Minnaar et al. 2015; Yuen & Bonebrake 2017; Wakefield et al. 2015), or cadavers for scavengers if individuals tend to perish from exhaustion or collision with lights (Eisenbeis 2004; Gaston & Holt 2018). I did not observe net attraction of carnivores to ALAN or significant differences in total abundances of carnivores to ALAN with either spectrum, unlike previous findings that found greater relative abundances of predators and scavengers to herbivores in ALAN conditions (Davies et al. 2017; McMunn et al. 2019). One explanation for why I did not observe net attraction of carnivores may be that my trial periods were too short to measure their dispersal, as previous studies documenting higher local abundances of carnivores measured long-term effects of ALAN (Davies et al. 2012; Davies et al. 2017). Long term effects of ALAN may be driven by changes in in situ trophic dynamics, which is suggested by findings from previous studies wherein changes to fluxes of insects across stream-riparian boundaries exposed to ALAN (Meyer & Sullivan 2013) benefitted predaceous arthropods (Manfrin et al. 2018; Sullivan et al. 2019).

ALAN influenced the number of individuals captured in five of seven common taxonomic groups (the statistical model for one of the eight major taxonomic groups did not converge). I observed significant effects of ALAN treatment on the numbers of Cicadellidae, Derbidae, Formicidae, Scarabaeidae, and Lepidoptera captured. However, these five groups did not exhibit a uniform response to the ALAN treatments. While four taxa demonstrated increases under at least one ALAN spectrum relative to the unlit controls, captures of Formicidae were lower in plots treated with amber LEDs relative to both the unlit control and white LED treatments (Figure 3). There were greater abundances of both Scarabaiedae and Formicidae in plots receiving the white LED compared to the amber LED, but no difference between the white LED and unlit control plots. Unlike Formicidae, however, there were not lower abundances of Scarabaiedae under the amber LED compared with control conditions. The number of individuals from Cicadellidae was greater under the amber LED compared with the unlit control plots. Two groups, Derbidae and Lepidoptera, were caught in higher abundances in plots receiving both LED treatments relative to the unlit control, though was not a difference for abundances between the different LED treatments. Together, these results suggest that effects of ALAN on the local abundance of arthropods may be strongly dependent on phylogeny.

I did not detect an effect of ALAN on insects captured by malaise traps, which are particularly suited to capturing Lepidoptera, an order with many members that exhibit positive phototaxis towards short wavelength light (van Langevelde et al. 2011, Somers-Yeates et al. 2013). Because I found evidence that the effect of ALAN is stronger closer to ALAN sources in flight intercept traps, the nearest of which were at a distance of 3 m from the source of ALAN, and malaise traps were positioned 8 m from the central lamp post, my ability to detect effects of ALAN using malaise traps may have been limited. When I pooled Lepidoptera captures across

trap types, I found that larger numbers were captured in plots exposed to both white and amber ALAN compared to the unlit control plots (Table 5, Figure 4). ALAN attracts many adult moths (Degen et al. 2016, Wakefield et al. 2015) and this effect is more pronounced in macro-moth families (Wilson et al. 2018). Contrary to previous findings that ALAN rich in shortwave emissions is more attractive to moths than ALAN rich in longer wavelength emissions (Langevelde et al. 2011), amber LEDs did not attract fewer Lepidoptera than white LEDs in my experiment. Attraction of adult moths to ALAN has important implications for biodiversity given that long-term declines in abundance have occurred in Lepidoptera species that exhibit positive phototaxis (Conrad et al. 2006; Macgregor et al. 2017; Langevelde et al. 2018). My findings suggest that transitioning to amber LEDs may not alleviate the problem of attraction of moths to ALAN.

My analyses of taxa that were numerically dominant in my captures support the notion that phylogeny is important in predicting the potential for energy and/or nutrient sinks to form around sources of ALAN via invertebrate dispersal. The potential for energy and nutrient redistribution via dispersal was more dependent on differences in average body mass per individual (mg) than number of individuals captured. For example, estimated total nitrogen in the Derbidae captured in my experiment was three orders of magnitude smaller than that of Scarabaeidae or Lepidoptera, despite having caught over 100 more individuals belonging to Derbidae than Scarabaiedae, and only 100 fewer individuals belonging to Derbidae than Lepidoptera. Together, the captured individuals in these two taxa amounted to an estimated 3.77 g of total nitrogen (captures pooled across all ALAN treatments and trials). In some taxa such as Araneae, Coleoptera, Orthoptera, and Lepidoptera, larger-bodied organisms are found in greater numbers near sources of ALAN compared with unlit areas (McMunn et al. 2019). However,

recent findings indicate that selective pressures may change the responses of terrestrial arthropods to ALAN (Altermatt & Ebert 2016; Czaczkes et al. 2018). For example, the attraction of moths towards ALAN can vary, with moths from urban areas demonstrating lower attraction towards ALAN compared to their counterparts from unlit regions (Altermatt & Ebert 2016). I predicted that ALAN would create local nutrient sinks via increased net attraction and increased local mortality. My results indicate that effects of ALAN and ALAN spectra on nutrient distribution via dispersal are likely to vary based on local arthropod community composition. My finding that larger-bodied arthropods are more abundant near sources of ALAN provides preliminary evidence that ALAN may create nutrient sinks in terrestrial systems. The responses of arthropods to ALAN may change over time (Altermatt & Ebert 2016; Czaczkes et al. 2018), highlighting the need for long-term field studies which manipulate the presence and type of ALAN to further our understanding of its effects nutrient redistribution via arthropod dispersal.

My findings suggest that net fluxes of arthropods pooled by trophic level are inadequate measures for understanding the effects of ALAN on terrestrial arthropod communities, and that the effects of ALAN on arthropods depend strongly on taxonomy. It seems likely that phylogenetic constraints affecting vision systems strongly influence how arthropods respond to ALAN. Invertebrates are important members of terrestrial ecosystems as they contribute to a variety of critical processes (Price et al. 2011; Showalter et al. 2018), including energy and nutrient transfers either through dispersal or trophic interactions. The potential for creation of nutrient sinks via arthropod attraction towards ALAN is likely influenced by the local community composition, and in particular taxonomic composition of larger-bodied arthropods.

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Tables & Figures

Table 1. Results of a linear mixed effects models testing the effect of artificial light at night (ALAN) treatment (amber LED, white LED, unlit control) on the net attraction (log_{10} number attracted – log_{10} number repelled) and total (log-transformed) number of invertebrates captured for each trap type.

| | · | Source of | | | | | | |
|------------------|---------------------|--------------|------|------|----|--------|---------|-------------|
| Trap Type | Model | Variation | S.S. | M.S. | Df | Den.DF | F value | р |
| | | ALAN A | 2.94 | 1.47 | 2 | 321.57 | 9.88 | < 0.0001*** |
| Elight Intergent | Net Attraction | Distance D | 0.01 | 0.01 | 1 | 322.11 | 0.05 | 0.83 |
| Fight Intercept | l | $A \times D$ | 2.53 | 1.26 | 2 | 321.87 | 8.48 | < 0.001*** |
| | | ALAN A | 2.75 | 1.37 | 2 | 326.00 | 0.67 | 0.51 |
| | Total Invertebrates | Distance D | 0.80 | 0.80 | 1 | 326.00 | 0.39 | 0.53 |
| | | $A \times D$ | 1.36 | 0.68 | 2 | 326.00 | 0.33 | 0.72 |
| | Net Attraction | ALAN A | 0.46 | 0.23 | 2 | 176.88 | 1.82 | 0.17 |
| | | Distance D | 0.01 | 0.01 | 1 | 180.27 | 0.09 | 0.77 |
| Pitfall | | $A \times D$ | 0.46 | 0.23 | 2 | 177.24 | 1.82 | 0.17 |
| | Total Invertebrates | ALAN A | 1.10 | 0.55 | 2 | 178.27 | 0.84 | 0.43 |
| | | Distance D | 0.01 | 0.01 | 1 | 179.21 | 0.01 | 0.92 |
| | | $A \times D$ | 1.05 | 0.52 | 2 | 178.35 | 0.81 | 0.45 |
| NC 1 * | Net Attraction | ALAN | 0.07 | 0.04 | 2 | 72.98 | 0.27 | 0.76 |
| Ivialaise | Total Invertebrates | ALAN | 2.76 | 1.38 | 2 | 75 | 0.78 | 0.46 |

* Significant at the a = 0.05 confidence level

** significant at the a = 0.01 confidence level

*** significant at the a = 0.001 confidence level

Table 2. Results of linear mixed effects models testing the interactive effects of artificial light at night (ALAN) treatment (amber LED, white LED, unlit control) and distance from the central lamp post on the net attraction [calculated as log_{10} (number attracted +1) - log_{10} (number repelled+1)] and log(x+1)-transformed number of herbivores and carnivores captured in flight intercept traps.

| Response | Source of | | | | | | | |
|-------------------|---------------|--------------|-------|-------|-------|--------|---------|---------|
| Variable | Trophic level | Variation | S.S. | M.S. | Df | Den.DF | F value | р |
| Net Attraction | Herbivores | ALAN A | 0.719 | 0.360 | 2 | 25.000 | 3.408 | 0.049* |
| | | Distance D | 0.037 | 0.037 | 1 | 25.000 | 0.351 | 0.559 |
| | | $A \times D$ | 0.609 | 0.305 | 2 | 25.000 | 2.886 | 0.075 |
| | Carnivores | ALAN A | 0.663 | 0.331 | 2 | 24.022 | 2.113 | 0.143 |
| | | Distance D | 0.001 | 0.001 | 1 | 24.095 | 0.008 | 0.931 |
| | | $A \times D$ | 0.819 | 0.410 | 2 | 24.090 | 2.611 | 0.094 |
| | Herbivores | ALAN A | 0.526 | 0.263 | 2.000 | 25.000 | 2.564 | 0.097 |
| | | Distance D | 1.591 | 1.591 | 1.000 | 25.000 | 15.501 | 0.001** |
| Number of | | $A \times D$ | 0.177 | 0.088 | 2.000 | 25.000 | 0.861 | 0.435 |
| Invertebrates | | ALAN A | 0.950 | 0.475 | 2.000 | 23.177 | 1.316 | 0.288 |
| | Carnivores | Distance D | 2.976 | 2.976 | 1.000 | 23.063 | 8.243 | 0.009** |
| | | $A \times D$ | 1.201 | 0.601 | 2.000 | 23.063 | 1.663 | 0.211 |

* Significant at the a = 0.05 confidence level

** significant at the a = 0.01 confidence level

*** significant at the a = 0.001 confidence level

Table 3. Results of linear mixed effects models testing the effects of artificial light at night (ALAN) treatment (amber LED, white LED, unlit control) and distance from the central lamp post on the net attraction [calculated as log_{10} (number attracted +1) - log_{10} (number repelled+1)] and log(x+1)-transformed number of herbivores and carnivores captured in pitfall traps.

| Source of | | | | | | | | |
|----------------------------|------------|--------------|-------|-------|-------|--------|---------|-------|
| Response Variable | e Guild | Variation | S.S. | M.S. | Df | Den.DF | F value | р |
| | | ALAN A | 0.001 | 0.000 | 2 | 24.159 | 0.003 | 0.997 |
| | Herbivores | Distance D | 0.044 | 0.044 | 1 | 24.191 | 0.386 | 0.540 |
| Net Attraction | | $A \times D$ | 0.015 | 0.008 | 2 | 24.076 | 0.067 | 0.935 |
| | Carnivores | ALAN A | 0.698 | 0.349 | 2 | 23.001 | 3.336 | 0.053 |
| | | Distance D | 0.058 | 0.058 | 1 | 23.157 | 0.551 | 0.465 |
| | | $A \times D$ | 0.453 | 0.226 | 2 | 23.259 | 2.164 | 0.137 |
| | Herbivores | ALAN A | 0.522 | 0.261 | 2.000 | 25.000 | 1.149 | 0.333 |
| | | Distance D | 0.096 | 0.096 | 1.000 | 25.000 | 0.423 | 0.522 |
| Number of Invertebrates | | $A \times D$ | 0.632 | 0.316 | 2.000 | 25.000 | 1.391 | 0.267 |
| inverteorates | | ALAN A | 1.096 | 0.548 | 2.000 | 23.000 | 1.154 | 0.333 |
| | Carnivores | Distance D | 0.957 | 0.957 | 1.000 | 23.000 | 2.015 | 0.169 |
| | | $A \times D$ | 1.081 | 0.541 | 2.000 | 23.000 | 1.138 | 0.338 |

Table 4. Results of linear mixed effects models testing the effects of artificial light at night (ALAN) treatment (amber LED, white LED, unlit control) and distance from the central lamp post on the net attraction [calculated as log_{10} (number attracted +1) - log_{10} (number repelled+1)] and log(x+1)-transformed number of herbivores and carnivores captured in malaise traps.

| Response Variable | Guild | Source of Variation | S.S. | M.S. | Df | Den.DF | F value | р |
|-------------------|------------|---------------------|-------|-------|----|--------|---------|-------|
| Not Attraction | Herbivores | ALAN | 0.034 | 0.017 | 2 | 10.000 | 0.204 | 0.819 |
| Net Attraction | Carnivores | ALAN | 0.261 | 0.130 | 2 | 7.972 | 1.882 | 0.214 |
| Number of | Herbivores | ALAN | 0.005 | 0.002 | 2 | 10.000 | 0.02 | 0.98 |
| Invertebrates | Carnivores | ALAN | 1.84 | 0.92 | 2 | 15 | 3.49 | 0.13 |

Table 5. Measured and estimated variables used to infer potential nutrient distribution via arthropod dispersal. Number of individuals trapped, mean \pm SD mass per individual (mg), and average N% are measured values, whereas total mass (mg) and total nitrogen (mg) are estimated values. These were calculated using measured values [Total Mass (mg) = # Trapped × Mean Mass per individual] and [Total Nitrogen = Total Mass (mg) × Average N%].

| Taxonomic Group | # Trapped | $Mean \pm SD$ $Mass$ (mg) | Average N% | Total Mass (mg) | Total Nitrogen (mg) |
|----------------------------|-----------|-----------------------------|---------------|--------------------|---------------------|
| Hemiptera Aphidae | 274 | 0.17 ± 0.1 | 8.5 | 46.58 | 3.94 |
| Hemiptera Cicadellidae | 962 | 0.4 ± 0.25 | 10.7 | 384.80 | 40.98 |
| Hemiptera Derbidae | 415 | 0.13 ± 0.07 | 10.5 | 53.95 | 5.68 |
| Hemiptera Psyllidae | 361 | 0.26 ± 0.16 | 10.2 | 93.86 | 9.61 |
| Hymenoptera Formicidae | 1012 | 0.275 ± 0.23 | 10.1 | 278.30 | 28.02 |
| Coleoptera Scarabaeidae | 282 | 85.37 ± 36.76 | 9.9 | 24073.40 | 2379.54 |
| Araneae | 75 | 13.82 | 10.0 | 1036.50 | 103.54 |
| Lepidoptera | 528 | 30.7 ± 14.33 | 8.6 | 16209.60 | 1387.58 |

Table 6. Results of generalized linear mixed effects models to investigate the effects of artificial light at night (ALAN) treatment (amber LED, white LED, unlit control) on the total number of individuals captured in the eight dominant taxonomic groups.

| Group | Source of Variation | χ^2 | Df | р |
|----------------------------|---------------------|----------|----|-------------|
| Hemiptera Aphidae | ALAN | 2.65 | 2 | 0.27 |
| Hemiptera Cicadellidae | ALAN | 6.29 | 2 | 0.043 * |
| Hemiptera Derbidae | ALAN | 78.47 | 2 | < 0.001 *** |
| Hemiptera Psyllidae | ALAN | 1.58 | 2 | 0.45 |
| Hymenoptera Formicidae | ALAN | 14.67 | 2 | 0.001 ** |
| Coleoptera Scarabaeidae | ALAN | 10.84 | 2 | 0.004 ** |
| Araneae | ALAN | NA | NA | NA |
| Lepidoptera | ALAN | 9.01 | 2 | 0.01 * |

* Significant at the a = 0.05 confidence level ** significant at the a = 0.01 confidence level

*** significant at the a = 0.001 confidence level



Figure 1. Effect of artificial light at night (ALAN) treatment (unlit control, amber LED, white LED) on the net attraction [calculated as log_{10} (number attracted) - log_{10} (number repelled)] of arthropods captured in flight intercept traps. Means significantly different are marked by different letters (p < 0.05, based on Tukey adjusted least-squares means comparisons).



Figure 2. Effect of artificial light at night (ALAN) treatment (unlit control, amber LED, white LED) on the number (mean \pm SE) of (a) herbivores and (b) carnivores captured in flight intercept traps. Within a trophic level, means significantly different based on treatment are marked by different letters (*p* < 0.05, based on Tukey adjusted least-squares means comparisons).



Figure 3. Effect of artificial light at night (ALAN) treatment (unlit control, amber LED, white LED) on the mean number of individuals (log-transformed mean \pm SE) belonging to common taxonomic groups for which generalized mixed effects models converged. Within a taxonomic group, means significantly different based on treatment are marked by different letters (p < 0.05, based on Tukey adjusted least-squares means comparisons).

Chapter 5

Conclusions

These studies demonstrate that the effects of ALAN occur across multiple levels of organization including populations and communities, with consequences that can impact ecosystem processes. Despite a large body of literature addressing how plant growth, reproduction, and phenology respond to light (Hart 2012), we have a limited understanding for how ALAN will affect plants in nature (Bennie et al. 2015). I used a manipulative field experiment to study the interactive effects of ALAN, soil moisture, and plant density on the growth and anti-herbivore defenses of common milkweed (Chapter 2). I found that one attribute of plant size, basal stem diameter, responded positively to ALAN. This effect was smaller in plants experiencing intraspecific competition, indicating that increases in growth under ALAN are likely to be limited by resource availability. These findings suggest that bottom-up effects of ALAN on herbivores may be stronger where competition among plants is weaker.

In my third chapter, I predicted that as a consequence of higher local abundance of, and interception of prey by, predatory arthropods under ALAN (Davies et al. 2012; Davies et al. 2017; McMunn et al. 2019; Yuen & Bonebrake 2017; Miller et al. 2017), the rate of decomposition of leaf litter would be curtailed by increased top-down control over detritivores under ALAN. Contrary to my prediction, decomposition rates tended to be higher under ALAN. This finding suggests that detritivores in the litter layer may not be subjected to increased predation under ALAN, and that increases in predatory arthropods under ALAN does not limit the rate of decomposition (Chapter 3). This highlights the need for improved understanding of the effects of ALAN on trophic interactions in the detrital food web. We have a limited understanding of the contribution to litter breakdown by litter-layer invertebrates, but the rate of return of nutrients to the soil via their actions is known to have significant impacts on community and system structure (Wall and Moore 1999; Moore et al. 2004).

ALAN has been predicted to have a "fixation" effect on many insects, characterized by high immigration to sources of ALAN with low emigration away from ALAN sources (Eisenbeis 2006). Previous studies attribute increased abundances of some invertebrates near ALAN to attraction of insects (Davies et al. 2012; Davies et al. 2017). However, in very few studies were the effects of ALAN on the directionality of invertebrate movements measured. I measured both attraction and repulsion of terrestrial invertebrates to ALAN and found that some flying insects, particularly herbivores, did in fact demonstrate net attraction to ALAN (Chapter 4). This effect was greater at traps located closer to the sources of ALAN. My results confirm that ALAN can alter the spatial fluxes of insects (Chapter 4; Meyer and Sullivan 2013). Movement of insects represents an important avenue for biogeochemical exchange across systems (Schowalter et al. 2018; Baxter et al. 2005). Moreover, because nitrogen in insects is easily returned to the soil (Yang & Gratton 2014; Behie & Bidochka 2013), and effects of ALAN on spatial fluxes of nutrients were likely to be driven by larger bodied arthropods such as many scarab beetle and moth species, which were found in greater abundances near ALAN sources (Chapter 4), my work provides preliminary evidence for the creation of nutrient sinks under sources of ALAN. Our understanding of the ecosystem-level effects of ALAN would benefit greatly from long-term experiments measuring nutrient inputs by ALAN-induced attraction of insects. This would allow us to confirm whether net attraction of herbivores to sources of ALAN may create local nutrient sinks driven by allochthonous inputs of nitrogen.

My findings demonstrate that the introduction of ALAN affects plant growth (Chapter 2) as well as terrestrial arthropod movement and trophic structure (Chapters 3, 4). Plants are integral to primary productivity and nutrient cycling, and movement and trophic dynamics of terrestrial arthropods can influence decomposition and biogeochemical fluxes (Price et al. 2011; Showalter et al. 2018). One potential biogeochemical consequence of ALAN could be an increase in the magnitude and speed of nutrient cycling near sources of ALAN, and decreases in nutrient deposition in surrounding areas with lower intensities of ALAN. There are likely to be two non-mutually exclusive mechanisms through which addition of an ALAN source may create a local nutrient sink. First, a local nutrient sink may be created through the decomposition of arthropod carcasses under sources of ALAN. Eisenbeis (2004) estimated that a large fraction of nocturnal insects that are attracted to light sources die soon after reaching a light source. This could explain observations of increased abundances of scavenger arthropods under sources of ALAN (Chapter 3, Davies et al. 2012; Davies et al. 2017). While I did not detect an effect of ALAN on net attraction of carnivorous arthropods in the experiment described in Chapter 4, the duration of the experimental trials may have been too short to observe an effect on scavengers. Scavenger densities may increase under sources of ALAN if they are attracted to increased numbers of herbivore carcasses, or if the population growth rates of scavengers under sources of ALAN are boosted by long-term subsidies of herbivore carcasses. Second, arthropods drawn to sources of ALAN may create relatively nutrient-rich patches under ALAN sources through increased deposition of frass due to aggregation of positively phototactic insects under sources of ALAN. Nitrogen is much more readily leached to the soil from frass than from leaf litter (Hollinger 1986), therefore net attraction of herbivores (Chapter 4) to sources of ALAN could possibly increase nitrogen leaching to the soil from frass deposited by herbivores. Both of these

potential avenues for enhanced nitrogen deposition, and subsequent increased nitrogen availability in the soil, would likely enhance primary production under sources of ALAN. To my knowledge, this hypothesis has not yet been tested. In conclusion, my findings underscore the need for further research studying ways in which long-term exposure of habitats to ALAN affects community structure and fundamental ecosystem processes such as nutrient cycling and primary productivity.

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Appendix

Appendix A: Interactions between artificial light at night, soil moisture, and plant density affect the growth of a perennial wildflower1 (Chapter 2)



Figure A1: Absolute spectral irradiance (μ W/cm²) for the bulbs used in the experiment for Chapter 2 over the wavelengths (nm) in which they emit light.



Figure A2: Diagram of an experimental field plot (a) during the day and night. Of the six available spaces (holes) in each plot, potted plants were sunk into four randomly chosen spaces (b).



Figure A3: Effects of artificial light at night (ALAN), plant density, and soil moisture on (a) basal stem diameter, (b) height, and (c) leaf area over the four weeks of data collection. Bars are means \pm SE.

| Source of Variation | Estimate | S.E. | df | t | р |
|---------------------|----------|-------|--------|--------|-------|
| ALAN (A) | 0.114 | 0.113 | 18.677 | 1.010 | 0.325 |
| Soil moisture (S) | 0.011 | 0.086 | 19.444 | 0.133 | 0.895 |
| Density (D) | -0.003 | 0.082 | 17.731 | -0.034 | 0.974 |
| Damage | 0.020 | 0.035 | 22.095 | 0.558 | 0.582 |
| $A \times S$ | -0.074 | 0.113 | 19.088 | -0.655 | 0.520 |
| $A \times D$ | 0.001 | 0.114 | 18.014 | 0.006 | 0.995 |

Table A1. Results of linear mixed effects model to investigate the interactive effects of artificial light at night (ALAN), plant density, and soil moisture on latex weight (mg).





Figure B1. Spectral irradiance (μ W/cm²) of lights used for both experiments over the wavelengths (nm) in which they emit.

B2. Methods

To obtain uniform plant tissue for examining effects of ALAN on plant-tissue decomposition, we grew switchgrass, *Panicum virgatum* in the greenhouse at Blandy Experimental Farm over the summer of 2017. We scarified switchgrass seeds using 16.8 M H₂SO₄ for 10 minutes with 1 g of seeds per 25 mL solution, then rinsed seeds under cool running water for 20 minutes. Seeds were then planted at a density of 90 seeds/pot in 3.8 liter pots in Sungro Horticulture potting soil (Sungrow Horticulture Professional Growing Mix, Sungrow Horticulture, Sun Gro®, Agawam, Massachusetts, USA). All pots were initially fertilized using ½ tablespoon of slow-release fertilizer (Osmocote Plus, 15:9:12 N:P:K, Osmocote® Smart-Release® Plant Food, The Scotts Company LLC, Marysville, Ohio, USA) and grown in the greenhouse at Blandy Experimental Farm, Boyce, VA, USA, for 3 months before blade material was harvested on August 12, 2017. Pots were randomized with respect to location in the greenhouse and watered weekly. Immediately after harvesting the blade material, and oven dried at 40°C for ~72 hours before being placed into litterbags.

Appendix C: Effects of artificial light at night spectrums on spatial fluxes of terrestrial arthropods: experimental examination of consequences for trophic structure and nutrient redistribution (Chapter 4)



Figure C1. Spectral irradiance (μ W/cm²) of light emitting diodes (LEDs, Amber and White) used for both experiments over the wavelengths (nm) in which they emit.



Figure C2. Schematic diagram depicting trap locations for (a) flight intercept and (b) pitfall traps, and distance from the center of the plot for (c) malaise traps. Flight intercept traps were deployed during trial periods 1-6, while pitfall and malaise traps were deployed concurrently during trial periods 7-12.



Figure C3. Taxonomic profile of the number of invertebrates trapped in across all traps and treatments. The number identified (x axis) is represented on a logarithmic scale for clarity.

| Order | Family | Trophic Level | Source |
|------------|-----------------|----------------------|---------------------|
| Aranae | (all) | Carnivore | Price 2011 |
| Coleoptera | Anthicidae | Other | Evans 2014 |
| Coleoptera | Cantheridae | Herbivore | Evans 2014 |
| Coleoptera | Carabidae | Carnivore | Evans 2014 |
| Coleoptera | Cerambycidae | Herbivore | Borrer & White 1970 |
| Coleoptera | Chrysomelidae | Herbivore | Evans 2014 |
| Coleoptera | Cleridae | Other | Borrer & White 1970 |
| Coleoptera | Coccinellidae | Carnivore | Evans 2014 |
| Coleoptera | Corylophidae | Herbivore | Borrer & White 1970 |
| Coleoptera | Cryptophagidae | Herbivore | Evans 2014 |
| Coleoptera | Curculionidae | Herbivore | Evans 2014 |
| Coleoptera | Elateridae | Herbivore | Evans 2014 |
| Coleoptera | Endomychidae | Herbivore | Borrer & White 1970 |
| Coleoptera | Haliplidae | Other | Evans 2014 |
| Coleoptera | Histeridae | Carnivore | Evans 2014 |
| Coleoptera | Laemophloeidae | Herbivore | Evans 2014 |
| Coleoptera | Lampyridae | Carnivore | Evans 2014 |
| Coleoptera | Latriidae | Herbivore | Evans 2014 |
| Coleoptera | Leiodidae | Other | Borrer & White 1970 |
| Coleoptera | Monotomidae | Other | Evans 2014 |
| Coleoptera | Mordellidae | Other | Liu et al. 2018 |
| Coleoptera | Nitidulidae | Herbivore | Evans 2014 |
| Coleoptera | Oedemeridae | Herbivore | Evans 2014 |
| Coleoptera | Phalacridae | Herbivore | Evans 2014 |
| Coleoptera | Ptinidae | Other | Borrer & White 1970 |
| Coleoptera | Scarabaeidae | Herbivore | Evans 2014 |
| Coleoptera | Scirtidae | Herbivore | Evans 2014 |
| Coleoptera | Staphylinidae | Carnivore | Evans 2014 |
| Diptera | Agromyzidae | Herbivore | Borrer & White 1970 |
| Diptera | Anthomyzidae | Herbivore | Borrer & White 1970 |
| Diptera | Asilidae | Carnivore | Borrer & White 1970 |
| Diptera | Calliphoridae | Herbivore | Borrer & White 1970 |
| Diptera | Cecidomyiidae | Other | Dorchin 2008 |
| Diptera | Cecidomyiidae | Herbivore | Borrer & White 1970 |
| Diptera | Ceratopogonidae | Carnivore | Boorman 1993 |
| Diptera | Chironomidae | Herbivore | Borrer & White 1970 |

Table C1 Trophic delineations for invertebrates identified in net attraction study. Carnivores include predators, scavengers, parasites, and parasitoids. Herbivores include invertebrates which are either generalists or specialists of any plant tissue. All else are listed as Other.

| Diptera | Chloropidae | Herbivore | Borrer & White 1970 |
|-----------|-----------------|-----------|------------------------------|
| Diptera | Culicidae | Carnivore | Borrer & White 1970 |
| Diptera | Dolichopodidae | Carnivore | Borrer & White 1970 |
| Diptera | Drosophilidae | Herbivore | Bahder e al. 2015 |
| Diptera | Lauxaniidae | Herbivore | Borrer & White 1970 |
| Diptera | Lonchopteridae | Other | Borrer & White 1970 |
| Diptera | Muscidae | Herbivore | Borrer & White 1970 |
| Diptera | Mycetophilidae | Herbivore | Kerr 2008 |
| Diptera | Otitidae | Herbivore | Borrer & White 1970 |
| Diptera | Phoridae | Other | Borrer & White 1970 |
| Diptera | Sciaridae | Herbivore | Borrer & White 1970 |
| Diptera | Sphaeroceridae | Other | Borrer & White 1970 |
| Diptera | Syrphidae | Herbivore | Borrer & White 1970 |
| Diptera | Tephritidae | Herbivore | Borrer & White 1970 |
| Hemiptera | Acanaloniidae | Herbivore | Slater & Baranowski 1978 |
| Hemiptera | Aleyrodidae | Herbivore | Pappas et al. 2018 |
| Hemiptera | Alydidae | Herbivore | Borrer & White 1970 |
| Hemiptera | Anthocoridae | Carnivore | Borrer & White 1970 |
| Hemiptera | Aphididae | Herbivore | Borrer & White 1970 |
| Hemiptera | Berytidae | Herbivore | Borrer & White 1970 |
| Hemiptera | Cercopidae | Herbivore | Cryan & Svenson 2010 |
| Hemiptera | Cicadellidae | Herbivore | Dietrich 2005 |
| Hemiptera | Cixiidae | Herbivore | Holzinger et al. 2002 |
| Hemiptera | Corimelanenidae | Herbivore | Borrer & White 1970 |
| Hemiptera | Corixidae | Herbivore | Borrer & White 1970 |
| Hemiptera | Cydnidae | Herbivore | Borrer & White 1970 |
| Hemiptera | Delphacidae | Herbivore | Cook & Denno 1994 |
| Hemiptera | Derbidae | Herbivore | Gossner & Damken 2018 |
| Hemiptera | Flatidae | Herbivore | Souliotis et al. 2018 |
| Hemiptera | Issidae | Herbivore | Denno & Perfect 2012 |
| Hemiptera | Lygaeidae | Herbivore | Burdield-Steel & Shuker 2014 |
| Hemiptera | Membracidae | Herbivore | Borrer & White 1970 |
| Hemiptera | Mesoveliidae | Carnivore | Borrer & White 1970 |
| Hemiptera | Miridae | Herbivore | Slater & Baranowski 1978 |
| Hemiptera | Nabidae | Carnivore | Slater & Baranowski 1978 |
| Hemiptera | Pentatomidae | Herbivore | Slater & Baranowski 1978 |
| Hemiptera | Phymantidae | Carnivore | Slater & Baranowski 1978 |
| Hemiptera | Psyllidae | Herbivore | Borrer & White 1970 |
| Hemiptera | Pyrrhocoridae | Herbivore | Borrer & White 1970 |
| Hemiptera | Reduviidae | Carnivore | Slater & Baranowski 1978 |
| | | | |

| Hemiptera | Rhopalidae | Herbivore | Borrer & White 1970 |
|-------------|----------------|-----------|---------------------|
| Hemiptera | Saldidae | Carnivore | Borrer & White 1970 |
| Hymenoptera | Aphelinidae | Carnivore | Borrer & White 1970 |
| Hymenoptera | Braconidae | Carnivore | Borrer & White 1970 |
| Hymenoptera | Eurytomidae | Other | Borrer & White 1970 |
| Hymenoptera | Formicidae | Other | Borrer & White 1970 |
| Hymenoptera | Ichneumonidae | Carnivore | Borrer & White 1970 |
| Hymenoptera | Platygastridae | Carnivore | Borrer & White 1970 |
| Hymenoptera | Scelionidae | Carnivore | Gupta 2008 |
| Hymenoptera | Sphecidae | Carnivore | Gupta 2008 |
| Hymenoptera | Tenthredinidae | Herbivore | Boevé 2008 |
| Hymenoptera | Tiphiidae | Carnivore | Pate 1947 |
| Isopoda | Armadillidae | Herbivore | Price 2011 |
| Isopoda | Porcellionidae | Herbivore | Price 2011 |
| Ixodida | Argasidae | Carnivore | Price 2011 |
| Lepidoptera | (all) | Herbivore | Price 2011 |
| Mantodea | (all) | Carnivore | Price 2011 |
| Orthoptera | (all) | Herbivore | Price 2011 |