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Does artificial light at night alter moth community composition?

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Ecological studies investigating the effects of artificial light at night (ALAN) have primarily focused on single or a few species, and seldom on community-level dynamics. As ALAN is a potential cause of insect and biodiversity declines, community-level perspectives are essential. We empirically tested the hypothesis that moth species differentially respond to ALAN and that these responses can cause shifts in community composition. We sampled moths from prairie fragments in Colorado, USA. We tested whether local light sources, sky glow, site area and/or vegetation affected moth community diversity. We found that increased sky glow decreased moth abundance and species richness and shifted community composition. Increased sky glow shifted moth community composition when light and bait traps were combined; notably this result appears to be driven entirely by moths sampled at bait traps, which is an unbiased sampling technique. Our results show that ALAN has significant effects on moth communities and that local light sources have contrasting effects on moth community composition compared to sky glow. It is imperative that we better understand the contrasting effects of types of ALAN to comprehend the overall impacts of light pollution on biodiversity declines.

This article is part of the theme issue 'Light pollution in complex ecological systems'.

1. Introduction

More than half of the world's population lives in urban or suburban areas and this development has caused over 20% of the terrestrial Earth's night skies to be affected by anthropogenic light [1,2]. Importantly, the effects of light pollution, especially sky glow, have been found to extend over long distances even outside urban areas [3]. At night, artificial lights function to extend human activities and promote safety [4]. However, artificial light at night (ALAN) also has consequential impacts on species within and adjacent to urban areas [5,6]. ALAN has been shown to influence behaviours of many vertebrates including bats, birds, frogs, humans and turtles (e.g. [7–22]) and affect the physiology and development of plants (e.g. [23–25]). Studies examining the impacts of ALAN have often focused on single or a few species but recently there have been calls in the literature for studies to investigate how the effects of ALAN vary more broadly across taxa, and how it may influence population dynamics and the structure of communities [5,11,26–36].

Studies of community-level responses owing to ALAN are uncommon compared to studies of single species [37–39], yet community composition is likely to be altered given that species vary in their responses to lights (e.g. [22,40–42]). Moreover, ALAN comes in two forms which may differentially impact community responses—light from a point source (e.g. streetlights) and sky glow, which is a measure of how bright objects appear or how much light is reflected off an object. Most studies of ALAN study only point sources of light or do not tease apart the effects of point sources of light from sky glow. However, sky glow has been shown to affect insect behaviour; for example, Foster *et al.* [43]

demonstrated that sky glow negatively affected dung beetle orientation behaviours. Changes in behaviours important to fitness may negatively affect population dynamics. Firebaugh & Haynes [44] also showed that ALAN can act as a demographic trap for populations wherein immigration exceeds emigration to light-polluted sites. If ALAN has significant effects on individual species by creating demographic traps for species attracted to lights, it follows that it may have important implications for community dynamics by altering community composition.

One group of organisms that are well known for their response to artificial lights is moths, and ALAN has been suggested as one of the potential causes for declines in their species richness and abundance [6,45–47]. Moth species and families vary in their degree of attraction to light [48,49]. ALAN can have negative impacts on moth individuals [50–52], populations [49], and there is evidence that it may lead to evolutionary change in the form of reduced phototaxis [53]. Grenis & Murphy [51] found that ALAN negatively affected the performance of a lepidopteran herbivore both directly and indirectly via altered host plant quality. Furthermore, moths found near artificial lights can be depredated by insectivores [20] and suffer from reduced vision capabilities [54]. There are also potential negative impacts yet to be tested, like fitness costs associated with light attraction; moths circling lights may have reduced energy stores or be unable to find suitable oviposition sites, resulting in fewer, smaller larvae under streetlights. However, whether and to what degree the individual and species-level responses and effects of ALAN cascade to affect the structure of an entire terrestrial community has been understudied.

Moth community responses to ALAN, if present, would occur at large spatial scales, and thus it is important to simultaneously account for other landscape factors that could drive community responses. A few studies have investigated how moth community abundance and species richness are affected by habitat fragmentation (e.g. [55–58]), but all of these studies occurred within forest fragments surrounded by agricultural fields, not urban development that introduces new and different pressures, like ALAN (see Merckx & Van Dyck [59] for evidence that urbanization in general affects moth diversity). These fragmentation studies within agricultural areas found that moth communities respond predictably to plant richness [56,58], but interestingly do not follow the typical species-area pattern commonly found for other organisms. Abundance and species richness both generally decline with decreases in habitat size for most organisms [60]; indeed, many other species that were tested at some of our same urban study sites follow the predicted declines in abundance and richness with decreases in habitat size (e.g. butterflies [61], bees [62] and grasshoppers [63]). However, whether moth abundance and richness are unaffected by habitat size in urban systems, as was found in the fragmentation studies in agricultural systems, or whether changes in habitat area influence abundance and species richness patterns of moths in urban ecosystems is unknown. Species richness patterns of moths may also be influenced by vegetation diversity, since most herbivorous insects are dietary specialists and therefore depend heavily on the types of plants present [64,65]. Previous studies on moths have found that increases in plant diversity within a habitat patch positively affect moth species richness [55,58], but plant diversity is not always dependent on patch size, particularly in urban and suburban landscapes [62,66,67].

Here, we empirically test the hypothesis that ALAN can cause shifts in community composition of moth species that are differentially impacted by their attraction to light. Specifically, we test whether ALAN affects communities of moths inhabiting fragmented prairie patches within an urban matrix. Many ecological studies test ALAN as a categorical variable (light or no light) or measure only the brightness of a point source of light, but insects are likely affected by both point sources and sky glow. We therefore measure ALAN as continuous measures of both local light sources and sky glow, and these two metrics allow us to explore the potentially differential effects of types of ALAN on the abundance and richness of moth species in an urban habitat. Based on the previous literature, we hypothesized that both types of ALAN (local light sources and sky glow) would have negative effects on the abundance and species richness of moths, decreasing overall diversity. We also test whether habitat size and vegetation affect moth community diversity as these variables have been shown to be important drivers of community diversity in other systems. Most species follow the species-area pattern in which species abundance and richness increase with greater habitat area [60]; however, previous studies on moths have found that they respond to changes in the plant community, but not to changes in habitat area [56,58]. We therefore hypothesized that moth community diversity would be unaffected by habitat size and positively affected by vegetation. Ours is, to our knowledge, the first study to test the effects of both local light sources and sky glow on an entire taxonomic community.

2. Methods

(a) Study sites

We surveyed moth communities at 23 prairie fragments along the Front Range of Colorado, USA. We selected sites in four general areas in the Denver-metro area across five counties (electronic supplementary material, table S1). We chose sites bordered by at least 75% residential/suburban development. The native ecosystem at all of the sites is shortgrass steppe with infrequent patches of tallgrass and native trees along riparian and mesic areas. To ensure that sites were not dispersed unequally by size (e.g. all the large sites in one county) and to have a representative sample of habitat sizes, we designed our sampling scheme such that each county contained at least five fragments with one small site (less than 5 ha), three to five medium sites (5–15 ha) and one large site (greater than 15 ha). Overall, site areas ranged between 2.4 and 73.7 ha. We determined site area using digital data from city and county records.

(b) Artificial light measures

At the time of our study, all streetlights in our study areas were high-pressure sodium lights. We measured sky glow to the 0.01 magnitudes per square arcsecond using a Sky Quality Meter (Unihedron, Grimsby, Ontario, Canada; range of measures = 11.20–19.99) pointed at zenith to measure sky brightness at zenith (converted later to the SI unit cd m^{-2}); this is a measure of the amount of light coming into the sensor from a narrow angle of sky directly overhead. For a wider angle of measure that includes light from local light sources around the perimeter of the site, we used an Extech EA33 Luxmeter measured to the nearest 0.01 lux (Extech Instruments Corporation, Nashua, NH, USA; range or measures = 0.1–12.82), which allowed us to measure light pollution in a full 360° around each point. Although lux is a

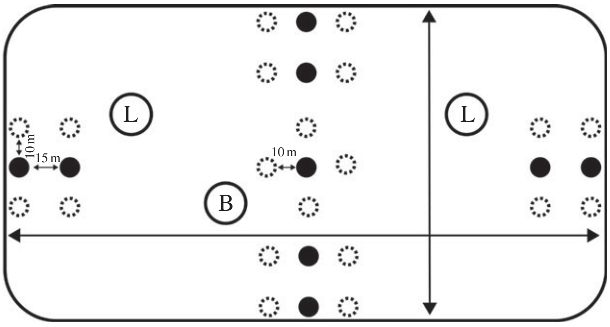

Figure 1. Layout of ground cover survey and point measurements of light intensity at a theoretical site. The long double-headed arrows are the north-south and east-west transects. Open circles represent the transect around each trap location; the central open circle surrounds the bait trap location (B) and the two other open circles surround the light trap locations (L). We used a point-line intercept method to quantify ground cover at each site. Dark circles indicate the focal spot for light readings along the edges and 15 m into the patch (north, east, south, west) as well as at the centre locations. The surrounding dashed circles show the position of additional light readings (10 m from focal location along the edge and 15 m into the patch).

measure of human photopic vision and does not necessarily measure moth photopic perception, we use it as our light measure because this is the measure used by city planners and land managers to make decisions about the amount of artificial light illuminating a given area when designing lighting systems (following [68,69]). To measure relative light levels across the entire site, we measured ALAN at 29 positions within each site, with 24 positions along the edge and five positions in the centre, and we averaged them together for a site mean (figure 1). All of our light measurements were taken without the light traps (see below) in the fields, prior to our experiments. We took measurements after astronomical twilight on clear nights within 3 days before and after the new moon between the hours of 20.00 and 2.00 to reduce the influence of natural moonlight on our measurements.

(c) Lepidoptera survey methods

To characterize the moth communities at each site, we sampled moths on nights between 20.00 and 2.00 without rain or wind and with less than 1 h of natural moonlight during five collection periods over the summers of 2011 and 2012. However, we did not sample all sites in all collections owing to weather, permitting, and safety (electronic supplementary material, table S1). We sampled sites haphazardly based on county location so that multiple sites could be visited in the same night. To sample the abundance and diversity of moth species attracted to lights, we used two Universal Black Light Traps (Bioquip Products, Rancho Dominguez, CA, USA) to collect moths during each survey; these light traps sample local moth communities [48]. However, ALAN can influence the effectiveness of light traps in catching moths [70]. Thus, we also sampled using bait traps, where the efficiency of the trap has not been linked to ALAN [71]. We used a pop-up butterfly bait trap (Bioquip Products, Rancho Dominguez, CA, USA) provisioned with a beer-based bait [72] and hung from a standing frame [73]. To minimize the degree to which all traps competed with nearby streetlights, we placed each trap at least 15 m from the site edge (figure 1). During three of our collection periods (July and August of 2011 and June of 2012), we visited traps every other hour and emptied them so that we could improve our rarefaction curves for estimates of species richness (see below). After collection, we froze and stored all the collections in the laboratory until we could count, pin, and identify macromoths to species with the assistance of local taxonomic experts (D. Bettman and C. Harp). We vouchered specimens in the zoology collections at the Denver Museum of Nature and Science.

(d) Vegetation measures

Previous studies have shown that moth communities are dependent on the type of vegetation present [56,58,74]. Given the difficulty in taxonomically identifying prairie grasses to species when not in flower, we measured the proportion of the ground covered by grasses, forbs and bare ground every 0.3 m across five point-intercept line transects at each site as a proxy for plant diversity. The transects we used to estimate ground cover plant types spanned the longest north-south and east-west distances in each site (figure 1). We also measured ground cover at a 3 m radius (18.85 m circumference) surrounding each trap location to account for vegetation within trap attraction range [75] (figure 1). To account for differences in site area and shape, we used proportion ground cover to standardize measurements for analyses.

(e) Statistical analyses

To evaluate differences in species richness and abundance across sites, we used four separate multiple regressions; for moths caught at light traps, we did one multiple regression for abundance and one for species richness, and then for moths caught at bait traps, we similarly did one multiple regression for abundance and one for species richness. Each of these four multiple regressions had local light sources, sky glow, site area, and proportion grass, as independent variables because these variables were not found to be correlated with each other. Initially, we included both proportion grass and proportion forb in the models, but using correlation values and tolerance, we found that proportion grass and proportion forb were highly correlated at 0.97, so we dropped proportion forb from the analyses and only used proportion grass because many of our species are grass feeders. We tested for normality and equality of variances for all independent variables and to meet the normality assumptions we log transformed site area and square root transformed local light sources and sky glow. Owing to the well-established relationship between species abundance and richness, we rarefied by abundance to estimate species richness; we re-scaled species richness with sample-based rarefaction curves by individuals to adjust for differing densities of sampled individuals across sites [76], but were only able to do this for samples caught at light traps where we had sufficient sample sizes. Using Ecosim 7.0 [77], we constructed individual-based rarefaction curves (1000 iterations) to calculate expected species richness when we sampled a similar number of individuals from light traps at each site. We scaled our estimate of species richness to the lowest number of individuals caught at a site ($n = 13$). Thus, for light traps, we used another multiple regression for estimated macromoth species richness that used the same independent variables described for the first four multiple regressions above. We used JMP v. 11 to perform all five of the regressions described above (SAS Institute Inc., Cary, NC). If we did find differences in abundance between light and bait traps, we wanted to determine whether such differences would be amplified or diminished based on the overall light conditions at a site. In other words, moths might not be as attracted to light traps when there is more light pollution at a site. To examine whether any differences we found in abundance between light and bait traps were affected by either the overall sky glow in an area (cd m^{-2}) or point light sources (lux), we ran a Poisson regression and compared a full model and reduced models using a chi-square test in R 4.1.1 [78].

We analysed moth community composition data using non-metric multidimensional scaling (NMDS), which is a robust

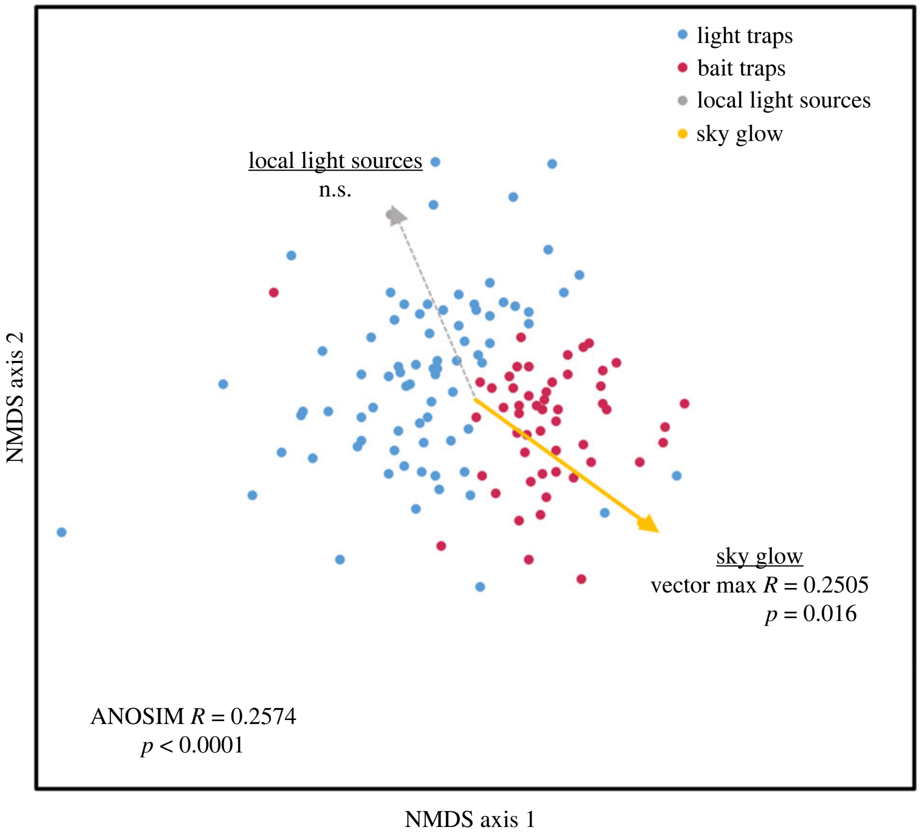

Figure 2. Impacts of light traps and bait traps on moth community composition. Compositional dissimilarity was based on 176 different moth species (electronic supplementary material, table S2). Shown is the two-dimensional representation of the moth community found in 128 collections. ANOSIM demonstrates that moth composition changed in light versus bait traps. Vector analysis (yellow arrow) indicates that differences in moth community composition were correlated with sky glow. While not significant, the vector for local light sources was included for a comparison with patterns for sky glow. (Online version in colour.)

ordination technique for community analysis [79–81]. We used NMDS to create a dissimilarity matrix among the sites with the Bray–Curtis dissimilarity coefficient [82]. Using stress levels obtained by fitting the dissimilarities to distance, we chose a two-dimensional solution as the best representation of the dissimilarities among sites. We tested for differences in community composition among light and bait traps using analysis of similarity (ANOSIM, [83]). We then performed vector analysis to determine the maximum correlation between site characteristics (site area, local light sources measured as lux, sky glow measured as cd m^{-2}, proportion grass, and proportion forb) and the configuration of points (i.e. the moth community at each site) in the ordination. We determined significance using 1000 random permutations of the data to determine if the observed vector fit was significantly different than that owing to chance alone [81,84]. Since light and bait traps might be differentially affected by site characteristics, we also performed NMDS ordination and vector analysis on data from light traps (bait traps excluded) and bait traps (light traps excluded). We performed NMDS and subsequent ANOSIM and vector analysis using DECODA (database for ecological community data [85]) and PRIMER-7 [86].

3. Results

(a) Community composition

We collected 3107 individual macromoths and identified 182 unique species in the 82 collections from 23 sites (electronic supplementary material, tables S1 and S2). Using ANOSIM, we found that moth community composition differed among light and bait traps (ANOSIM $R = 0.2574$, $p = 0.0001$; figure 2). There were only eight species (each with only a single individual) found exclusively at bait traps, while there were 126 species representing 998 individuals that were found exclusively at light samples. We found 48 species that were shared between light and bait samples. Importantly, vector analysis demonstrated that moth community composition changed according to light characteristics. When we examined both light and bait traps together, we found a significant correlation between sky glow and moth community composition (vector max $R = 0.2505$, $p = 0.016$), and this significant relationship seems to have been driven by results from our bait traps (see below). Notably, in the combined dataset, we did not find a correlation between moth community composition and any other site attributes: area (vector max $R = 0.155$, $p = 0.205$), local light sources (measured as lux, vector max $R = 0.0424$, $p = 0.88$), proportion grass (vector max $R = 0.0766$, $p = 0.693$), or proportion forb (vector max $R = 0.0579$, $p = 0.802$). This pattern was driven by community-wide responses; the negative impacts of sky glow on moth abundance could be seen for many of the most common species and were particularly strong for *Apantesis phalerata* (the harnessed tiger moth) and *Leucania multilinea* (the many-lined wainscot). To determine whether our significant results from our combined dataset were driven by moths captured at the light or bait traps, we examined light and bait traps separately and found that sky glow and lux differentially impacted moth communities depending on whether samples were collected from light or bait traps. Moth community composition at light traps was impacted by lux (vector max $R = 0.3752$, $p = 0.001$) and proportion forb (vector max $R = 0.2973$, $p = 0.032$), but sky glow did not impact moth community

Table 1. Multiple regressions of area, proportion grass, local point sources (lux), and sky glow (cd m^{-2}) on macromoth abundance, individual-based estimates of species richness, and estimates of total species richness for moths caught at light and bait traps. (Each dependent variable (macromoth abundance, macromoth species richness, and estimated macromoth species richness) represents a separate model for both light and bait traps. Estimated macromoth species richness is calculated only for moths caught at light traps where there were sufficient numbers to estimate species richness. Predictor variables were independent and were transformed to meet the normality assumption (see methods). Italicized predictor variables are significant.)

dependent variables	predictor variables	d.f.	*F*-stat	*p*-value	coefficient (s.e.)
light traps					
macromoth abundance	area	1,18	0.96	0.33	−31.3 (31.9)
	proportion grass	1,18	0.59	0.45	−51.7 (67.0)
	local point sources	*1,18*	*4.43*	*0.0495*	*97.2 (46.1)*
	sky glow	*1,18*	*7.12*	*0.0157*	*−1741.9 (652.9)*
macromoth species richness	area	1,18	0.86	0.37	−6.3 (6.8)
	proportion grass	1,18	0.002	0.96	0.7 (14.2)
	local point sources	*1,18*	*11.83*	*0.0029*	*33.7 (9.8)*
	sky glow	*1,18*	*12.62*	*0.0023*	*−492.5 (138.6)*
estimated macromoth species richness	area	1,18	1.79	0.20	−0.8 (0.6)
	proportion grass	1,18	0.01	0.93	−0.1 (1.3)
	local point sources	*1,18*	*5.28*	*0.0337*	*2.0 (0.9)*
	sky glow	*1,18*	*4.77*	*0.0424*	*−26.8 (12.3)*
bait traps					
macromoth abundance	area	1,18	0.42	0.53	12.6 (19.6)
	proportion grass	1,18	2.12	0.16	60.0 (41.2)
	local point sources	1,18	0.37	0.55	17.4 (28.4)
	sky glow	1,18	1.82	0.19	−541.2 (401.6)
macromoth species richness	area	1,18	0.02	0.90	0.3 (2.5)
	proportion grass	1,18	0.47	0.50	3.6 (5.2)
	local point sources	1,18	0.83	0.37	3.3 (3.6)
	sky glow	1,18	2.16	0.16	−74.5 (50.7)

composition at light traps (vector max $R = 0.0636$, $p = 0.871$). Conversely, moth community composition at bait traps was not affected by lux (vector max $R = 0.1751$, $p = 0.451$), but was instead marginally affected by sky glow (vector max $R = 0.3074$, $p = 0.083$). Importantly, for the combined data, sky glow was the only factor impacting the change in moth community composition, and this trend seems to be driven by the bait traps and not the light traps. Finally, area and proportion grass did not affect community composition when we examined moth communities from the light and bait traps separately.

(b) Species abundance and richness

The multiple regression for light traps using species richness was the only significant overall model ($F_{4,18} = 4.06$, $p = 0.02$; table 1). Our multiple regressions for light traps using abundance and estimated species richness were not significant (abundance: $F_{4,18} = 2.18$, $p = 0.11$; estimated species richness: $F_{4,18} = 1.82$, $p = 0.17$) nor were the multiple regressions for bait traps using abundance and species richness (abundance: $F_{4,18} = 1.44$, $p = 0.26$; richness: $F_{4,18} = 0.79$, $p = 0.54$). While our overall models were often not significant, and in all five multiple regressions there was no relationship between either site size or proportion grass on moth abundance, richness, or estimated richness, coefficients related to ALAN in the models were significant (table 1). In all three multiple regression analyses using data from our light traps, we found greater moth abundance (figure 3*a*) and species richness (figure 4*a*) with increasing local light sources (lux), but increased sky glow (cd m^{-2}) negatively affected both moth abundance (figure 3*c*) and richness (figure 4*c*) (table 1). Notably, moths that were found only at light traps (not bait) were not solely responsible for this relationship between abundance and lux ($R^2 = 0.028$, $p = 0.124$), it was the combination of moths found only at light traps, or both light and bait traps (only eight species were found exclusively at bait traps and only a single individual of each of these species was sampled). For the multiple regression analyses using data from the bait traps, moth abundance (figure 3*b*,*d*) and species richness (figure 4*b*,*d*) were not significantly related to local point sources or sky glow, but followed the same patterns as the light trap data; this is probably because our sample sizes for the bait traps were much smaller than for our light traps. Moreover, when we examined abundance patterns for species that were shared between light and bait traps using our Poisson regression, we found that the contrast in abundance between the two types of traps was greatest when overall levels of sky glow at a site (cd m^{-2}) were lower (deviance $= -40.344$, $p = 2.13 \times 10^{-10}$). Thus, when overall

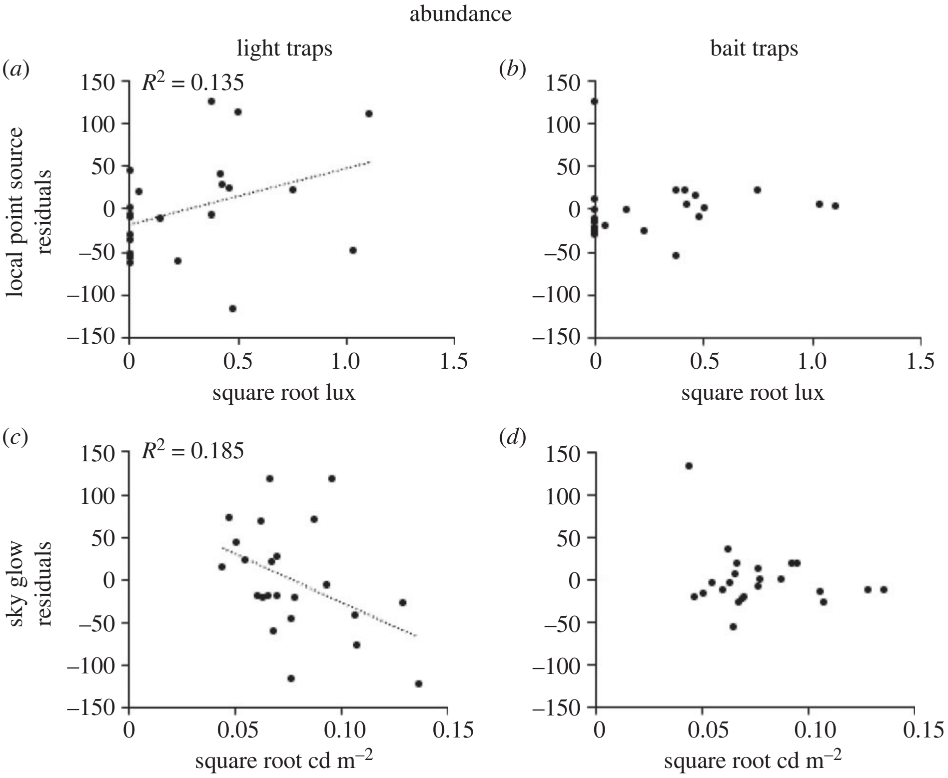

Figure 3. Partial regression plots of moth abundance versus lux (point sources of light; (*a*), (*b*)) or cd m^{-2} (sky glow; (*c*), (*d*)) (both square root transformed). For lux, we first performed a regression between moth abundance and all predictor variables except lux (cd m^{-2}, habitat size, and proportion grass), saved the residuals and then graphed the residuals against lux. For cd m^{-2}, we first performed a regression between moth abundance and all predictor variables except cd m^{-2} (lux, habitat size, and proportion grass), saved the residuals and then graphed the residuals against cd m^{-2}. Points represent individual sites and the lines of best fit are shown with their respective R^2 values.

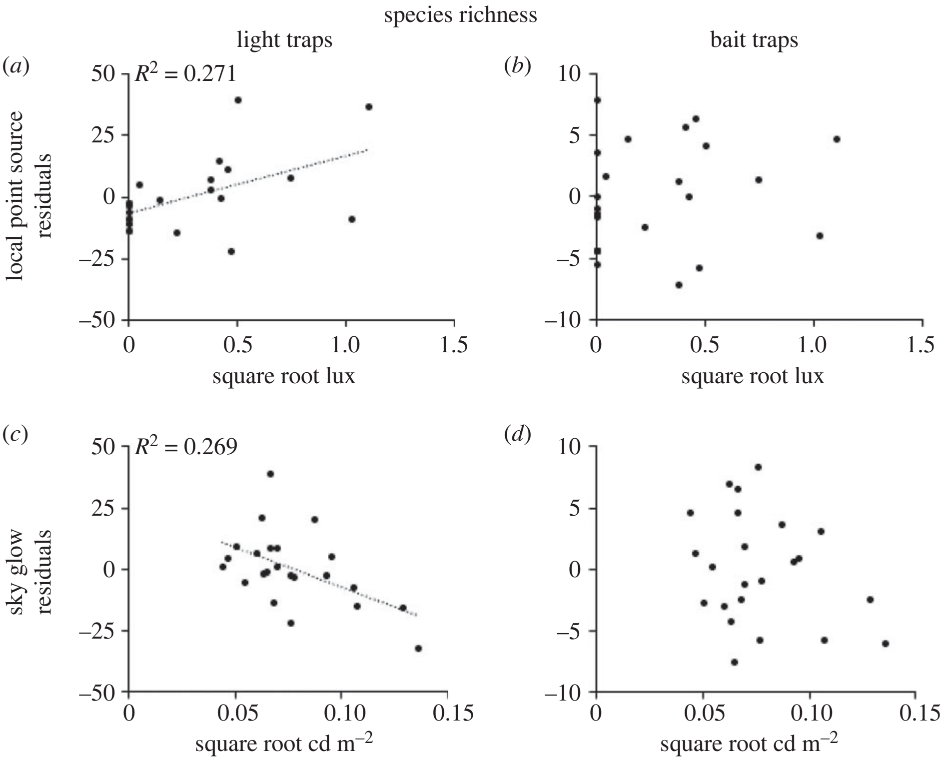

Figure 4. Partial regression plots of moth species richness versus lux (point sources of light; (*a*), (*b*)) or cd m^{-2} (sky glow; (*c*), (*d*)) (both square root transformed). For lux, we first performed a regression between moth species richness and all predictor variables except lux (cd m^{-2}, habitat size, and proportion grass), saved the residuals and then graphed the residuals against lux. For cd m^{-2}, we first performed a regression between moth species richness and all predictor variables except cd m^{-2} (lux, habitat size, and proportion grass), saved the residuals and then graphed the residuals against cd m^{-2}. Points represent individual sites and the lines of best fit are shown with their respective R^2 values.

levels of sky glow were higher at a site, there was less of a difference between light and bait traps. However, local light sources (lux) had no effect on the abundance of shared species (deviance = −0.10459, $p = 0.7464$).

4. Discussion

Light pollution has previously been shown to affect individual species, and here we show that ALAN can also significantly alter composition of an entire taxonomic community of nocturnal Lepidoptera. Furthermore, we found that different measures of ALAN (local light sources versus sky glow) have contrasting effects on community composition, which has not, to our knowledge, been previously reported. We found sky glow affected overall moth community composition, but this result differed depending on whether moths were collected from light or bait traps. At light traps, moth community composition was affected by local light sources (e.g. streetlights), but not sky glow, but it is important to recall that local light sources did not have a significant effect on community composition when all samples were considered together. Conversely, moth community composition at the bait traps was marginally impacted by sky glow, and not impacted at all by local light sources, yet sky glow was the only factor that drove community composition when all samples were considered together. These results are important because ALAN can influence the effectiveness of light traps in catching moths [70], but the efficiency of bait traps is not linked to ALAN [71]. Because using light traps to examine the impacts of ALAN on moth communities can be problematic, it is also imperative that future studies use unbiased trapping methods such as bait traps. Our study found that moth communities attracted to light traps were compositionally different from those found at bait traps, and two different aspects of ALAN (local light sources and sky glow) had completely opposite effects on moth communities found at light and bait traps.

There are several explanations for these patterns. In our study, areas with increased sky glow received indirect light because they were adjacent to areas with high numbers of artificial lights but did not actually contain as many of these point sources of light. These areas may have suffered decreased diversity because indirect light at these sites may make moths more visible to predators or disrupt circadian development and reproductive behaviours, with cascading effects on reproductive fitness (e.g. [52,87–89]). Interestingly, a recent study by Wilson *et al.* [90] found that increased sky glow had a positive fitness effect in a tightly co-evolved, specialist plant-pollinator system (yuccas and yucca moths) where they found increased recruitment and fruit set in areas of high sky glow. In our study, the shift in community composition indicates that moth responses to sky glow varied by species and unlike Wilson *et al.* [90], most species in our community-wide analysis did not respond positively. Our finding illustrates that the impact of ALAN on moths is not simply at the scale of an individual streetlight, but that the indirect effects of these point sources of light may extend across a larger spatial scale and have important conservation implications.

Local light sources (e.g. streetlights) impacted moth communities, but only at light traps where the trapping method and light source may be confounded [70]. Using our light trap data, we found a positive relationship between increased local light sources and moth species richness and abundance, and these light sources also altered moth community composition. Macgregor *et al.* [91] also found an increased abundance of moths flying aerially near streetlights but found fewer species at illuminated sites. It is difficult to compare our studies, however, because they did not measure sky glow, which in our system decreased species richness, similar to their results, and had a stronger negative effect on moth diversity than the positive effect of local light sources. We suggest that point sources of ALAN (e.g. streetlights) may act as an ecological or demographic trap for moths. Ecological traps are anthropogenic changes in the environment that cause organisms to make decisions based on formerly reliable cues that now negatively affect their fitness [92,93]. Under natural regimes, large-scale environmental changes usually occur over evolutionary time, which allows time for populations to adapt; however, the term ‘ecological trap’ more appropriately attributes this new maladaptation directly to human impacts in an ecological time frame that can drastically reduce population sizes [93–96]. Moths that occur in brighter areas are subject to higher rates of predation from vertebrate predators like birds and bats [20,50], but how such predation affects moth community composition and may create an ecological trap warrants future investigation.

Moth presence in illuminated areas also has consequences that go beyond increased predation for individual moths attracted to bright lights. Surviving moths found in areas of high local light probably continue their life cycle by mating and ovipositing in these brighter areas. In some habitats, streetlights actually increase the number of ground-dwelling predators [37,97] and therefore may increase predation on larvae; however, our previous research showed that predation rate for lepidopteran larvae is not affected by streetlights in our system [98]. Notably, we have also found that ALAN negatively affects larval performance both directly and indirectly via the altered quality of host plants that grow under streetlights [51]. Additionally, van Langevelde *et al.* [49] found significant population declines in light-attracted moth species and van Geffen *et al.* [52] found that ALAN negatively affected reproductive behaviours and timing of life-history events in moths. Thus, because artificial lights increase moth diversity locally but also increase predation rate on moths and decrease larval performance, there is evidence that ALAN may induce a demographic trap for nocturnal insects. Given the importance of many nocturnal Lepidoptera as pollinators, these effects then also cascade to negatively affect plant fitness [99] via reduced pollen transport by moths in lit areas [91].

Interestingly, we found no relationships between moth abundance, species richness, or community composition with habitat area. The lack of a decline in moth abundance and species richness with decreases in habitat size is notable given that this pattern is so commonly found in other systems and even with other species collected from our same sites (e.g. grasshoppers, bees, and butterflies, [61–63]). It appears that moths may be an exception to the species-area rule as some other studies on moths have also found no relationship between species abundance/richness and habitat area (but see [100]), for a discussion of the effects of habitat and traits; [74]; e.g. [56,58]). For moth species at our sites, ALAN was the only factor to explain changes in diversity.

Recent reports of an ‘insect apocalypse’ are debated [101–104] but may suggest that insect taxa are declining worldwide [105,106]. Among the many anthropogenic disturbances that have been suggested as contributors, ALAN is often not considered other than as a part of urbanization (e.g. [107]), but there are calls in the literature for ALAN to receive increased attention [5,29,46]. Using results from a multi-year study which captured 182 unique moth species, we demonstrate that ALAN from streetlights and other local light sources has different impacts on communities than wide ranging, pervasive ALAN across degraded night skies. Many ecological studies of ALAN only consider local light sources to be important [8,14,22,41,91,108], but sky glow can affect insect behaviour and thus also have population-level effects [43]. Our findings suggest that sky glow may have significant effects on insect communities, but these effects are rarely studied. If we had measured local light sources alone and sampled only with light traps, we would have concluded that streetlights positively affect moth abundance and species richness, which ignores the indirect negative effects of ALAN on moth species richness, abundance, and composition in areas adjacent to artificial lights. Furthermore, when considered with our prior research on the negative effects of streetlights on larval performance, it becomes clear that streetlights may act as an ecological trap and are probably deleterious to moth populations. The attraction of moths to highly lit areas, paired with the decrease in moth abundances and richness from increased sky glow, may play an important role in observed declines in worldwide moth diversity [45,46].

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data are archived from the Zenodo repository: https://doi.org/10.5281/zenodo.8349596.

Compiled species data is included in the supplementary material [109].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. K.G.: data curation, investigation, methodology, project administration and writing—original draft; C.N.: investigation, methodology and writing—review and editing; G.M.W.: data curation, formal analysis, writing—original draft, writing—review and editing; S.M.M.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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