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Urban street lighting differentially affects community attributes of airborne and ground-dwelling invertebrate assemblages

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ABSTRACT

1. The introduction of artificial light at night (ALAN) into natural and urbanised landscapes is a known and highly pervasive disruptor of invertebrate communities. However, the effect of variation in intensity and spectra of ALAN on invertebrate communities inhabiting different spatial niches is little understood. Further, the remarkable ability of ALAN to continue to disrupt biodiversity even in chronically-illuminated urban landscapes is not often acknowledged.
2. Here, we simultaneously sampled airborne and ground-dwelling invertebrate assemblages under and between urban streetlights to explore the effects on community composition and abundance of a) proximity to decadal (i.e long-illuminated) nocturnal street lighting and b) variation in the spectral output of light.
3. The two assemblages responded differently. For airborne invertebrates, night-time abundance doubled, and night-time assemblage composition was significantly different for traps under, compared with between, streetlights. These differences in abundance were not affected by streetlight intensity, and were absent in day samples, suggesting that even weak ALAN may be causing short-term redistribution of nocturnal invertebrates. Further, the abundance (but not composition) effects of ALAN on airborne invertebrates increased when the streetlights emitted a higher proportion of short-wavelength light.
4. In contrast, for ground-dwelling invertebrates, we found only marginal effects of proximity and spectrum of lighting on abundance and no effect on assemblage composition. However, more intense streetlighting reduced abundance and altered composition at traps both under and between lights.
5. *Synthesis and Applications:* Public lighting managers must consider ALAN impacts on invertebrate communities not only when introducing ALAN to naïve environments, but also when changing lighting in areas that are highly urbanised and exposed to decades of artificial light at night. Further, lighting proposals and environmental monitoring of invertebrate communities must take into account effects on both ground-dwelling and airborne assemblages, as these may respond very differently to the presence, intensity and spectrum of ALAN.

KEY WORDS: Artificial light at night (ALAN); Community effects; Correlated Colour Temperature (CCT); Insects; Light emitting diode (LED); Light pollution; Public lighting

INTRODUCTION

The global shift in the intensity and distribution of artificial light at night (ALAN) is one of the most visible and pervasive anthropogenic stressors on the planet (Longcore & Rich 2004; Hölker *et al.* 2010; Gaston, Visser & Hölker 2015; Falchi *et al.* 2016). ALAN is recognised as a significant community-level stressor of invertebrate assemblages and is linked to local- and landscape-scale shifts in abundance and community composition (Davies *et al.* 2017; Manfrin *et al.* 2017; Owens & Lewis 2018; Desouhant *et al.* 2019). Moreover, the ecological impact of the presence of ALAN appears to extend beyond the nocturnal environment, driving comparable taxa-wide shifts in diurnal communities (Davies, Bennie & Gaston 2012; Knop *et al.* 2017). Most recently, it has been linked to global declines in invertebrate biodiversity (Hölker *et al.* 2010; Boyes *et al.* 2020; Owens *et al.* 2020).

Exploring the effects of ALAN at the community level is necessary for a greater understanding of the broader ecological consequences of light pollution, but is also challenging (Sanders & Gaston 2018). Invertebrate studies typically sample from a single spatial stratum (Davies, Bennie & Gaston 2012; Knop *et al.* 2017; Wakefield *et al.* 2018; van Grunsven *et al.* 2019); rarely are both airborne and ground-dwelling assemblages sampled simultaneously at a given site (but see Manfrin *et al.* 2017). If distinct assemblages vary in their response to ALAN, this may mask the scale of its impact. For example, airborne invertebrates suffer direct and often proximate exposure to a light source, such as a streetlight, leading to behavioural responses including disorientation and attraction/repulsion (Longcore & Rich 2004), or increased mortality through exhaustion, predation, heat or collision (Eisenbeis 2006). In contrast, ground-dwelling invertebrates (including flying invertebrates at rest) are typically further from a light source. Thus, for this group, disorientation or attraction effects are likely to be muted, and direct light-related mortality potentially lower. If ground-dwelling individuals are also shaded by the filtering effects of vegetation and/or terrain (Endler 1993) such effects may be further reduced.

The spectral characteristics of a light are also important. Invertebrate taxa differ in their spectral sensitivities and associated behavioural responses (Briscoe & Chittka 2001; Davies *et al.* 2013; Donners *et al.* 2018) which may in turn promote spectra-related shifts in the composition of the communities in which they reside (Pawson & Bader 2014; Longcore *et al.*

2015; van Grunsven *et al.* 2019). Lights emitting a high proportion of short wavelengths typically elicit a stronger invertebrate phototactic response (both in terms of the number of individuals attracted to a light source and the number of taxa affected) compared with lights emitting a higher proportion of long wavelengths (Huemer, Kühtreiber & Tarmann 2010; Pawson & Bader 2014; van Grunsven *et al.* 2014; Wakefield *et al.* 2018). ALAN-associated behavioural shifts may promote spectra-mediated differences in the abundance and composition of invertebrate communities (Davies *et al.* 2017; van Grunsven *et al.* 2019). However, the technology of lighting (i.e. the type of light source) is not the sole determinant of its spectral characteristics. Even within a single light source, the spectra of individual lights may vary greatly due to age and manufacturing variances (see Appendix S1: Table S1 in Supporting Information). To broaden understanding of the effect of ALAN on urban wildlife, including invertebrates, it is therefore critical that the actual spectral outputs of lighting are incorporated along with other (more anthropocentric) parameters such as measures of illuminance (illumination weighted by the spectral sensitivity of the human eye).

Here, we assessed simultaneously the effect of the proximity and spectral characteristics of streetlighting on the composition and abundance of ground-dwelling and airborne invertebrate assemblages. Over three-day periods in 2016 and 2017, we sampled invertebrate assemblages under (illuminated) and between (darker) streetlights (adapted from Davies, Bennie & Gaston 2012) in three suburban streetscapes in Melbourne, Australia that have been lit by artificial streetlighting nocturnally for decades. Despite the long-term presence of streetlighting, we predicted that invertebrate assemblage composition and abundance would still differ under and between streetlights (Davies, Bennie & Gaston 2012), and that such differences may affect both diurnal and nocturnal communities (*sensu* Davies, Bennie & Gaston 2012; Davies *et al.* 2017; Knop *et al.* 2017). We predicted that the effects of ALAN would increase with lighting intensity and would be more subtle for ground-dwelling compared with airborne invertebrates due to the differing distances from the light (and variation in potential ground cover). Finally, due to the known variation in phototactic responses of invertebrates with respect to different light spectra, and the preponderance of invertebrate taxa with sensitivity to short-wavelength (UV, blue, green) light (Briscoe & Chittka 2001), we predicted that lights emitting a higher proportion of short wavelengths would elicit the strongest responses (Huemer, Kühtreiber & Tarmann 2010; Wakefield *et al.* 2018).

MATERIALS AND METHODS

Study locations

We sampled a single row of 10 streetlights (mean ± SE distance between streetlights = 58.28 ± 5.91m), at each of three suburban locations (Brunswick, Glenroy, Gowanbrae; Appendix S1: Table S1, Fig. S1) in Melbourne, Australia. The locations had a comparable 20-year history of 80-watt, UV-shielded, mercury vapor (MV) streetlighting, but were each in a different phase of a local council roll-out of 18-watt LED lights. Changes from MV to LED at some streetlights, routine bulb replacement and manufacturing variances meant that the intensity and spectral characteristics of lighting varied substantially within and between sites and years, including between streetlights employing the same technology (Table S1; full spectral data in Lockett *et al.* 2021). Each location was adjacent to a heavily modified minor watercourse with street-side vegetation comprising low herbaceous cover dominated by exotic grasses, and scattered trees, dominated by native Eucalypts and Acacias (see Appendix S1: Vegetation characteristics).

Invertebrate sampling

We sampled airborne and ground-dwelling invertebrates in 2016 (30 Mar – 2 Apr) and 2017 (4 Apr - 7 Apr). These trapping periods were almost exactly 12 months apart, shortly after the equinox, towards the middle of the lunar cycle, and over a 72-hour period with <1mm total precipitation.

Trap type – We used aerial intercept traps (modified from Young 2005; Fig. S2a) to sample airborne invertebrates and standard pitfall traps (modified from Woodcock 2005; Fig. S2b) to sample ground-dwelling invertebrates (see Appendix S1: Trap characteristics). Pitfall traps consisted of a 90mm diameter plastic pipe set 125mm into the ground. Both trap types funnelled invertebrates into a 70mL vial containing 20mL of diluted soapy (unscented) water.

Trap placement – We deployed a pair of aerial intercept and pitfall traps beneath each of the 10 streetlights (traps ‘under lights’; mean ± SE horizontal distance from luminaire = 2.70 ±

0.14m) and a second pair of aerial and pitfall traps between this streetlight and the next nearest streetlight (traps 'between lights'; horizontal distance from luminaire = 22.35m ± 0.85m; see Appendix S1: Trap characteristics). Traps 'under lights' were offset slightly to avoid dead or dying invertebrates falling from the luminaire into the trap. To ensure we were testing only the effects of light (rather than variation in heat), we placed aerial intercept traps 1m above the ground (several vertical metres from the luminaire) rather than suspended directly under the luminaire. We repeated this deployment in 2016 and 2017, ensuring that traps were reset as precisely as possible between years. One 'between lights' trap was moved 0.95m due to mulch covering its 2016 position.

Sampling procedure – We sampled traps in the hour before sunrise and the hour before sunset (following Davies, Bennie & Gaston 2012) over a 72-hour period each year, resulting in a total of 720 aerial and 720 pitfall trap samples (two trap placements x two daily sampling periods x three days x two years x 10 streetlights x three locations), half of which were collected under and half between streetlights. At each sampling event, captured individuals were preserved in 70% ethanol. We sampled all locations simultaneously using three coordinated teams. To minimize possible bias related to sampling time within a location, we reversed the order in which vials were collected within a given location every 24 hours. Two streetlights at each location were excluded following repeated loss of vials due to damaged traps.

Assessment of lighting

At each streetlight in each year, we took three measures of light: illuminance (lux; SKL300 light meter; Skye Instruments, Llandrindod Wells, UK), correlated colour temperature (CCT; UPRtek® MK350 LED Spectrometer; United Power Research Technology Corporation, Zhunan, Taiwan) and photon flux (μmol photons m^{-2} s^{-1}; Jaz Irradiance spectrometer; Ocean Optics, Largo FL, USA). Readings were taken at 1m above ground directly under the luminaire, on a cloudless night, after astronomical twilight and prior to moonrise. Illuminance was also measured 1m above the ground at all aerial traps and 0.1m above ground at all pitfall traps to confirm that traps under and between lights differed substantially in light levels. We used illuminance and CCT as, while they are calibrated to the human visual system and thus less appropriate when assessing other animal species (Endler 1990), they are commonly used in lighting industry standards (see e.g. International Electrotechnical

Commission 2014; VicRoads 2016; Standards Australia 2018). To provide an unweighted measure of the intensity and spectral output of each light, we measured the total photons emitted ('photon flux', μmol photons m^{-2} s^{-1}) across the UV and visible spectrum (250nm-750nm – 'total photon flux'), as well as across four 125nm bins of light comprising the UV (250-375nm), blue (375-500nm), yellow (500-625nm) and red (625-750nm) spectra. The photon flux in each bin was then divided by total photon flux and defined as 'proportion UV', 'proportion blue', 'proportion yellow' and 'proportion red', respectively. All light measurements were taken with the instrument sensor facing towards zenith.

Identification of invertebrates

Samples were reviewed under dissecting microscopes, with specimens identified to family (82%) or higher taxonomic level (18%) using published taxonomic keys (Appendix S1: Table S2). The effects of daily variation were minimised by aggregating each of the three sampling days and nights to give one 'day' sample and one 'night' sample per trap, per year (following Davies, Bennie & Gaston 2012; aggregated sample sizes: n = 192 (aerial traps) + 192 (pitfall traps)).

Analysis

Analyses were conducted in R version 3.5.0 (R Core Team 2018; R code in Appendix S3). Collembola (n = 255,850) and Acari (n = 15,676) were excluded as they were unlikely to be responding to ALAN conditions: the former mostly moving through the soil profile, and the latter trapped as parasites on larger invertebrates. Separate analyses confirmed that neither Collembola nor Acari abundance responded to variation in ALAN (Appendix S2: Table S3). The structure of the remaining data (numerous taxa, each with relatively few specimens) precluded analysis of the abundance of individual taxa; accordingly, taxon-level responses to ALAN were explored through compositional analysis. Consistent with our experimental aims, and the order of magnitude difference in individuals collected in pitfall compared with aerial traps, we analysed the two trap types separately.

Abundance – We assessed variation in abundance using generalised linear mixed effects models (packages *lme4* and *lmerTest*; Bates *et al.* 2015; Kuznetsova, Brockhoff & Christensen 2017). Aerial trap data were analysed using GLMMs with an assumed Poisson error distribution; pitfall trap data were over-dispersed (*DHARMa* package; Hartig 2021) and accordingly analysed in GLMMs with a negative binomial distribution. All abundance statistics are reported on the model (log) scale. As illuminance levels under and between lights were strongly bimodal (Appendix S1: Table S1) we treated this as a categorical variable (trap placement: 'between' (baseline) and 'under'). To assess whether proximity to streetlighting affected invertebrate abundance comparably during the day and at night we assessed variation across all samples (including trap placement, sampling period, and trap placement x sampling period interaction term) as fixed effects in the model. In a second set of models, we restricted analyses to night samples only to first assess whether the intensity and spectral characteristics of individual lights affected abundance (including illuminance, CCT and their interactions with trap placement). We then corroborated this analysis using total photon flux and proportion UV, proportion red and proportion yellow. Proportion blue and red were highly negatively correlated (r = -0.74, p = <0.0001). Where proportion red had a significant effect, the model was re-run with proportion blue instead. In all models, we added location, year and streetlight ID as random effects. Initial models comprised all possible combinations of the main effects and their interactions ranked by corrected Akaike information criterion (AICc). We applied model averaging (package MuMIn, Bartoń 2018; see Appendix S1: Model averaging) to calculate effect sizes and a 95% confidence interval for each fixed effect (confint, stats package; R Core Team 2018). Effects where the 95% CI did not straddle zero were considered supported. Supported interactions were assessed using post-hoc contrasts or slope estimates (*emmeans* package, Lenth 2019) derived from the top model. Predicted values for plotting were generated from final averaged models using the *predict()* function (R Core Team 2018).

Community composition – We explored the composition of ground-dwelling and airborne invertebrate assemblages separately using permutational multivariate analysis of variance (PERMANOVA: *adonis* function, *vegan* package; Oksanen *et al.* 2019). The main model comprised trap placement, sampling period (day, night) and their interaction, stratified using a combined 'location x year' blocking factor (Oksanen *et al.* 2019). Models were refined through sequential removal of terms where p > 0.10, and comparison of model AICc scores. Trap placement was of interest and retained even where not significant. Where we identified an effect of trap placement on composition (p-value < 0.05), we performed permutational (n = 10000) pairwise comparisons of 'under' versus 'between' streetlight samples to identify the contribution of each taxon to the average between-group Bray-Curtis dissimilarity (*simper* function, *vegan* package; Bray & Curtis 1957; Oksanen *et al.* 2019). As with the abundance analysis, we then repeated analyses with night samples only to assess whether the intensity and spectral characteristics of individual lights affected composition.

RESULTS

We analysed a total of 1152 vials which, when aggregated per trap, per three-day period, resulted in 192 aerial and 192 pitfall trap samples, with equal numbers in day and night traps and between years. Excluding the 255,850 Collembola and 15,676 Acari (see Methods above), we collected 2074 specimens representing 119 taxa in aerial traps (2016 = 1256 specimens; 2017 = 818 specimens), and 13,082 specimens representing 130 taxa in pitfall traps (2016 = 8294 specimens; 2017 = 4788 specimens; full data set in Lockett *et al.* 2021).

Abundance

All samples - The abundance of invertebrates captured in both aerial and pitfall traps was higher during the day than at night, however in aerial traps this was dependent upon trap placement (Table 1a, Fig. 1a). In the night samples, abundance in aerial traps placed under lights was twice that of abundance in aerial traps placed between lights (post hoc contrast of under versus between: $P < 0.0001$). In contrast, abundance in day samples was comparable regardless of whether the trap was placed under a light or between lights (post hoc contrast: $P = 0.44$; Table 1a, Fig. 1a). Abundance in pitfall traps was consistently higher for day compared with night samples but there was no effect of trap placement (Table 1b, Fig. 1b; mean abundance ± SE = 109.5 ± 69.5 for day samples; 26.8 ± 26.4 for night samples).

Night samples only - Restricting our analyses to night samples, we found main effects of CCT and trap placement for aerial traps, and an interaction between them (Table 2a, Fig. 2a). Abundance in aerial traps was negatively related to CCT between streetlights, but CCT had no effect under streetlights (post hoc estimated slopes: between = -0.25 ± 0.09; under = -0.04 ± 0.07). Our analyses further suggest that airborne invertebrate abundance increased with the proportion of longwave 'red' light (625-750nm) between, but not under, streetlights (interaction of trap placement x proportion red; post hoc estimated slopes: between = 4.44 ± 1.70; under = -2.80 ± 1.45; Table 2b, Fig. 2b). When proportion blue replaced proportion red in the model, we saw the opposite trend (post hoc estimated slopes: between = -4.45 ± 1.70; under = 2.80 ± 1.45; Appendix S2: Table S4).

Abundance in pitfall traps decreased with increasing total photon flux of the nearest streetlight: this effect was observed regardless of trap placement (no interaction between total photon flux and trap placement; Table 2b, Fig. 2c). Abundance at pitfall traps between (but not under) streetlights was also negatively related to the proportion of UV light (250-375nm) emitted by the nearest streetlight (interaction of trap placement x proportion UV; post hoc estimated slopes: between = -13.66 ± 4.16; under = 2.84 ± 3.95; Table 2b, Fig. 2d). These effects on abundance in pitfall traps were not observed when modelled using illuminance and CCT (Table 2a).

Table 1: Model estimates and 95% confidence intervals for the effects of sampling period (day/night) and trap placement (under/between streetlights) on total invertebrate abundance for (a) aerial traps (n = 96 traps in 2016, 94 traps in 2017) and (b) pitfall traps (n= 96 traps in 2016, 96 traps in 2017). Effects for which the 95% confidence interval did not straddle zero are in bold.

	Model-averaged coefficients (± SE)	**95% CI** (Lower and upper bounds)	
a) Aerial traps			
Intercept	2.65 ± 0.15	2.18	3.13
Sampling period	**-1.15 ± 0.08**	**-1.30**	**-1.00**
Trap Placement	0.04 ± 0.05	-0.06	0.14
Sampling period x Trap Placement	**0.65 ± 0.10**	**0.46**	**0.84**
b) Pitfall traps			
Intercept	4.61 ± 0.20	4.22	5.00
Sampling period	**-1.47 ± 0.08**	**-1.62**	**-1.32**

Table 2: Model estimates and 95% confidence intervals for the effects of (a) illuminance, correlated colour temperature (CCT) and their interactions with trap placement; and (b) total photon flux, photon flux proportions (UV, red, yellow) and their interactions with trap placement, on night-time abundance for aerial (n = 48 traps in 2016, 48 traps in 2017) and pitfall traps (n= 48 traps in 2016, 48 traps in 2017). Effects for which the 95% confidence interval did not straddle zero are in bold.

a) Trap placement x Illuminance, CCT			
Aerial traps			
Intercept	1.19 ± 0.39	0.41	1.97
Trap Placement	**0.68 ± 0.08**	**0.51**	**0.84**
CCT	**-0.22 ± 0.10**	**-0.43**	**-0.02**
Illuminance (lux)	0.01 ± 0.01	-0.01	0.04
Trap Placement x CCT	**0.25 ± 0.10**	**0.06**	**0.45**
Pitfall traps			
Intercept	3.96 ± 0.21	3.42	4.38
Illuminance (lux)	**-0.05 ± 0.01**	**-0.08**	**-0.03**
b) Trap placement x total photon flux, photon flux proportions			
Aerial traps			
Intercept	0.54 ± 0.41	-0.28	1.36
Trap Placement	**1.89 ± 0.32**	**1.26**	**2.52**
Proportion Red	**4.98 ± 1.42**	**2.16**	**7.80**
Proportion UV	-3.92 ± 3.77	-11.4	3.52
Trap Placement x Prop. Red	**-7.01 ± 1.63**	**-10.3**	**-3.77**
Trap Placement x Prop. UV	-6.82 ± 5.29	-3.59	17.2
Pitfall traps			
Intercept	5.91 ± 1.41	3.11	8.70
Trap Placement	-3.84 ± 1.98	-7.74	0.07
Total photon flux	**-2.75 ± 0.60**	**-3.95**	**-1.55**
Proportion UV	**-13.6 ± 3.99**	**-21.5**	**-5.67**
Proportion Yellow	-3.43 ± 2.09	-7.56	0.71
Trap Placement x Prop. UV	**16.3 ± 5.50**	**5.44**	**27.2**
Trap Placement x Prop. Yellow	5.73 ± 2.98	-0.14	11.6

Community composition

The composition of day and night samples was significantly different for both aerial and pitfall traps. Sampling period explained approximately 11% of the variance in composition in aerial trap samples, and 16% of variance in pitfall trap samples (Table 3). There was also an effect of trap placement on composition in aerial traps, but this explained <1% of the variance across samples (Table 3). There was no comparable effect of trap placement for pitfall traps and no significant sampling period x trap placement interaction regardless of trap type.

Post-hoc analyses suggest variation in the composition of airborne samples captured under and between streetlights was driven strongly by Diptera, Hemiptera, Hymenoptera and Coleoptera (contribution to dissimilarity index: Diptera families = 0.25; Hemiptera families = 0.19; Hymenoptera families = 0.12; Coleoptera families = 0.10; Appendix S2: Table S5).

In night samples, there was a significant difference in composition between aerial traps placed under and between streetlights (Table 4), which explained approximately 2.3% of the variation between samples. Effects of lighting intensity and spectrum were inconsistent and depended on which measures were used (compare Table 4a and b). In pitfall traps, composition was not significantly affected by trap placement, however the intensity of the nearest streetlight (whether measured as illuminance or total photon flux) explained approximately 4.5% of the variation in composition (Table 4a, b).

The composition of airborne samples captured at night under and between streetlights was driven strongly by Diptera, Coleoptera, Hymenoptera and Lepidoptera (contribution to dissimilarity index: Diptera families = 0.30; Coleoptera families = 0.16; Hymenoptera families = 0.10; Lepidoptera families = 0.06; Appendix S2: Table S6).

Table 3: Summary of results of Permutational Multivariate Analysis of Variance (PERMANOVA) of the effects of sampling period and trap placement on composition of trap samples for (a) aerial traps (n = 96 (day) + 96 (night)) and (b) pitfall traps (n = 96 (day) + 96 (night)). Significant effects (α = 0.05) are in bold.

	F statistic	R^2	P
Aerial traps			
Trap placement	**$F_{1,189}$ = 2.01**	**0.009**	**0.011**
Sampling period	**$F_{1,189}$ = 22.45**	**0.106**	**<0.0001**
Sampling period x trap placement	$F_{1,189}$ = 1.32	0.006	0.137
Pitfall traps			
Trap placement	$F_{1,191}$ = 1.59	0.007	0.089
Sampling period	**$F_{1,191}$ = 36.60**	**0.161**	**<0.0001**
Sampling period x trap placement	$F_{1,191}$ = 1.49	0.007	0.112

Table 4: Summary of results of Permutational Multivariate Analysis of Variance (PERMANOVA) of the effects of (a) illuminance, correlated colour temperature (CCT) and their interactions with trap placement; and (b) total photon flux, photon flux proportions (UV, red, yellow) and their interactions with trap placement, on composition of night-time aerial (n = 48 traps in 2016, 46 traps in 2017) and pitfall trap samples (n= 48 traps in 2016, 48 traps in 2017). Significant effects (α = 0.05) are in bold.

	F statistic	R^2	P
a) Trap placement x Illuminance, CCT			
Aerial traps			
Trap placement	**$F_{1,89}$ = 2.29**	**0.023**	**0.004**
Illuminance	$F_{1,89}$ = 3.05	0.031	0.071
CCT	$F_{1,89}$ = 1.61	0.016	0.596
Trap placement x CCT	**$F_{1,89}$ = 2.03**	**0.021**	**0.014**
Pitfall traps			
Trap placement	$F_{1,93}$ = 1.48	0.014	0.093
Illuminance	**$F_{1,93}$ = 4.47**	**0.045**	**0.001**
b) Trap placement x total photon flux, photon flux proportions			
Aerial traps			

Trap placement	**$F_{1,90} = 2.34$**	**0.023**	**0.003**
Total photon flux	$F_{1,90} = 5.36$	0.054	0.222
Trap placement x Total phot. flux	**$F_{1,90} = 2.40$**	**0.024**	**0.003**
Pitfall traps			
Trap placement	$F_{1,93} = 1.48$	0.015	0.099
Total photon flux	**$F_{1,93} = 4.43$**	**0.045**	**0.011**

DISCUSSION

Our data provide three key insights regarding the impact of ALAN for invertebrate assemblages. First, it confirms that even in an urban streetscape, with more than a 20-year history of exposure to artificial night lighting, the abundance and composition of invertebrate communities continues to be shaped by the presence, intensity and spectral characteristics of lights. Second, through simultaneous sampling of both ground-dwelling and airborne invertebrate assemblages, we demonstrate that the presence of ALAN affected the two assemblages differently: the nocturnal airborne invertebrate assemblage was characterised by differences in abundance and composition between samples collected under versus between streetlights. In contrast, we found little 'under versus between' difference in ground-dwelling invertebrates, but a decline in abundance and variation in composition were both related to brighter streetlights. A point to note is that while we used two distinct sampling methods, we do not conclude that the airborne and ground dwelling invertebrate assemblages are themselves separate communities. Given the significant overlap of taxa in the two assemblages (44% (72 out of 163) of families identified were found in both assemblages), and the significant number of alate individuals in pitfall traps (MTL, pers obs), it is probable that the two assemblages form a single ‘biological’ community. Thus, the observed effects of ALAN likely include indirect effects; that is, ALAN impacts on one assemblage may have cascading effects on the community structure of the other. Finally, our data highlight the importance of the spectral composition of lighting: the abundance of nocturnal airborne invertebrates captured under lights was positively related to colour temperature (i.e. 'whiter' lights attracted more invertebrates). Conversely, the abundance of airborne invertebrates captured in the darker traps (placed between lights) was negatively related to colour temperature and positively related to the proportion of red light emitted by the nearest streetlight.

Urban street lights continue to fragment invertebrate communities

There has been remarkably little acknowledgment of the power of ALAN to continue to disrupt biological diversity even after long term exposure (i.e. decadal or longer). Our data are broadly consistent with the pivotal pitfall study of Davies, Bennie and Gaston (2012) in that we found a clear effect of proximity to street lighting on the abundance and (to a much lesser extent) community composition of an invertebrate assemblage. In contrast to their study, we found only weak effects of ALAN on invertebrate composition, possibly due to the greater taxonomic complexity of our samples (163 here versus 60 taxa in Davies *et al*. 2012). In addition, the ground dwelling assemblage in our study was not affected by proximity to lighting, but its abundance decreased at all traps, and composition shifted, as lighting intensity increased. In both studies differences were linked to a small number of key taxa that included the Hymenoptera and Coleoptera (although differences in the sampled assemblages meant that we also detected significant shifts in Diptera, Hemiptera and Lepidoptera, while Davies *et al*. (2012) reported shifts in Opiliones, Isopoda and Amphipoda). An important question is whether these differences are comparable to, or different from, the initial shifts in community structure following introduction of lights to the environment and are thus sustained and permanent changes. A growing body of short-to-medium term experimental studies suggests analogous changes following exposure to night lighting that appear to persist for multiple generations (Davies *et al.* 2017; van Grunsven *et al.* 2019). However, the degree to which these differences are indicative of broadscale fitness declines is largely untested. If streetlighting acts as a persistent ecological trap then it is likely that species that are disproportionately attracted will likely decline over time (Knop *et al.* 2017; Owens *et al.* 2020), but trophic interactions may also modify impacts (Perkin, Hölker & Tockner 2014; Bennie *et al.* 2015; Bennie *et al.* 2018). For example, for predators or scavengers, light-attraction may provide trophic benefits that outweigh sub-lethal ALAN impacts (Willmott *et al.* 2019).

ALAN affects airborne and ground dwelling assemblages differently

A simultaneous exploration of airborne and ground dwelling assemblages provides broader insight into the potential fitness impact of streetlights. Notably, the assemblages responded differently: nocturnal abundance and overall composition were affected by the proximity of lights for aerial but not pitfall traps. As hypothesised above, this may have arisen through behavioural differences associated with how these assemblages experience and respond to light. In relatively open streetscapes, strong attraction/avoidance and disorientation behaviours might be expected by airborne invertebrates that have a clear line of sight to a luminaire (Longcore & Rich 2004). Under this scenario, airborne taxa are drawn towards streetlights and away from the darker spaces in between (akin to phototactic redistribution, *sensu* Eisenbeis 2006). The absence of this response for ground-dwelling species may be related to the fact that light at pitfall traps was on average 18% less intense than at the aerial traps and thus not as attractive (Appendix S1: Table S1), and the reduced mobility of walking versus flying invertebrates. However, the overall intensity of light from nearby streetlights significantly affected pitfall trap abundance: nocturnal ground-dwelling invertebrates in both illuminated (under) and darker (between) spaces were less abundant when the nearest streetlight was more intense (i.e. a higher total photon flux). This effect was not detected when modelled using illuminance (lux) —a measure weighted to the human spectral sensitivity—potentially underlining the importance of considering all parts of the spectrum when exploring effects on non-human biota. The composition of nocturnal ground-dwelling invertebrates also shifted with variation in streetlight intensity, regardless of proximity to the light. The less localised effect of intense light on ground-dwelling invertebrate abundance may indicate more gradual fitness impacts, perhaps through sub-lethal effects such as reduced fecundity (McLay, Green & Jones 2017; McLay *et al.* 2018) or impaired immune function (Durrant *et al.* 2015). These effects might disproportionately affect less mobile species or species with reduced geographic ranges and thus could have greater impact on ground-dwelling compared with airborne assemblages.

Spectral composition impacts even 'dark' spaces

Aside from behavioural changes associated with the intensity of streetlights, our data corroborate the need to consider spectral composition (Davies *et al.* 2013; Longcore *et al.* 2015). The abundance of nocturnal airborne invertebrates in the darker traps (placed between lights) was negatively related to colour temperature. Similarly, the abundance of airborne invertebrates at traps between lights was positively related to the proportion of red light emitted by the nearest streetlight. Both outcomes suggest that shorter-wavelength 'white' lights are more efficient at attracting invertebrates away from darker spaces. This result may be attributable to the preponderance of invertebrate taxa with spectral sensitivity peaks in the UV/blue/green part of the spectrum (Briscoe & Chittka 2001; Davies *et al.* 2013). The absence of clear spectrum-mediated compositional effects (Table 4a, b) suggests that, rather than partitioning invertebrate assemblages along spectral sensitivity lines, few airborne taxa at our study sites were immune to short-wavelength-mediated phototactic effects. This suggests sensitivity to at least part of the UV/blue/green spectrum is highly conserved, even in those taxa able to exploit longer wavelength light (Davies *et al.* 2013: their table S1). Thus, notwithstanding the diversity of spectral sensitivities in invertebrate communities, shifting the spectral composition of lights towards longer wavelengths may ameliorate the behavioural impacts of their presence for most species. Given the increasing evidence from across multiple animal taxa (including invertebrates) highlighting the biological relationship between blue light and physiological processes (Durrant *et al.* 2015; McLay, Green & Jones 2017; McLay *et al.* 2018; Grubisic *et al.* 2019), spectrum shifting may assist invertebrates on multiple levels. Disentangling the relative importance of the behavioural and physiological effects of exposure to streetlighting in terms of individual fitness is a critical next step to understand the mechanisms underpinning recent evidence for broadscale population declines (Knop *et al.* 2017; Boyes *et al.* 2020; Sanders *et al.* 2020; Senzaki *et al.* 2020).

Management implications

There is an emerging consensus around best practice for minimising the effect of ALAN on wildlife and biodiversity (Gaston *et al.* 2012; Longcore & Rich 2017; International Dark Skies Association 2018). Our study provides further empirical support for these guiding principles, namely that: (i) the presence of ALAN is linked to shifts in community abundance, composition and spatial distribution (sensu Sanders & Gaston 2018); (ii) even moderate amounts of short-wavelength light may impact airborne invertebrate communities (Davies *et al.* 2017). Our data add further cautionary notes: even in long-illuminated, highly-modified urban landscapes, street lighting continues to alter the abundance, spatial distribution and composition of invertebrate communities. Accordingly, public lighting managers and policy-makers must take care not only in introducing ALAN to light-naïve environments, but also in changing or augmenting existing public lighting. Further, invertebrate assemblages occupying different spatial niches may respond differently to ALAN: proposed lighting installations and environmental monitoring of invertebrate communities must consider both ground-dwelling and airborne assemblages to capture the full nature and scale of effects. Finally, changing legacy lighting to now-common 4000K LED luminaires will do nothing to ameliorate the behavioural effects of ALAN on airborne invertebrates around streetlights; instead it might exacerbate the impact.

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AUTHOR CONTRIBUTIONS

TMJ, MAE, KJG, MEV & GRH conceived the project, TMJ, GRH & MTL designed the project and carried out data analysis and interpretation of results. Fieldwork and specimen identification was carried out by MTL and GRH. MTL, GRH and TMJ wrote the manuscript; MAE, KJG, MEV edited the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sbcc2fr6s (Lockett *et al.* 2021).

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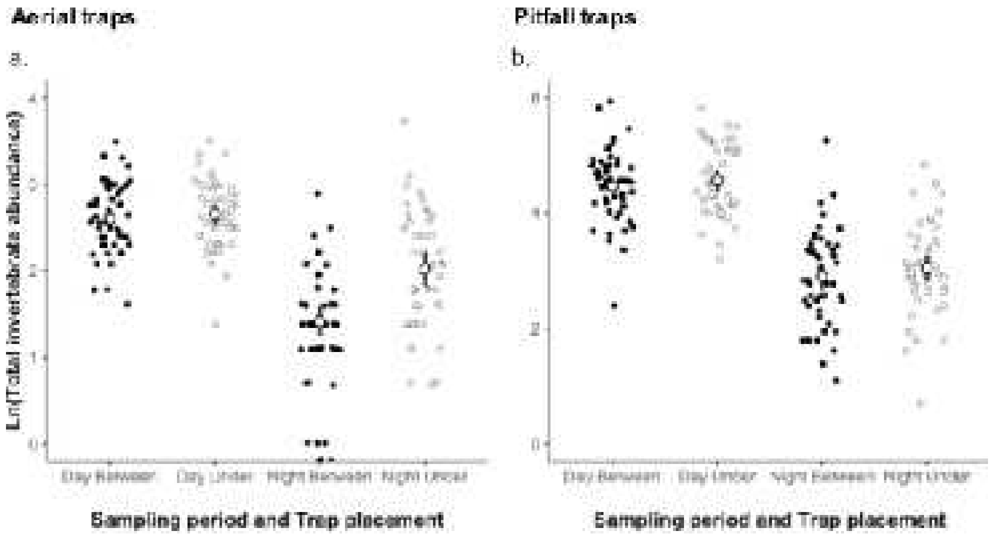
Figure 1: The relationship between sampling period (Day or Night), trap placement (Under or Between streetlights) and invertebrate abundance for (a) aerial and (b) pitfall traps. Points = observed data. Circle and whiskers = mean and 95% confidence interval. Note that datapoints are jittered to avoid overlap.

Figure 2: The effects of trap placement (Under or Between streetlights) and streetlight characteristics on night-time invertebrate abundance. *Aerial traps:* (a) the effect of trap placement and correlated colour temperature of nearest streetlight; (b) the effect of trap placement and proportion of 'red' photons emitted by nearest streetlight. *Pitfall traps:* (c) the effect of intensity (total photon flux) of nearest streetlight; (d) the effect of trap placement and proportion of ultra-violet light emitted by nearest streetlight. Points = observed data; lines = smoothed final averaged model predictions with 95% confidence interval.



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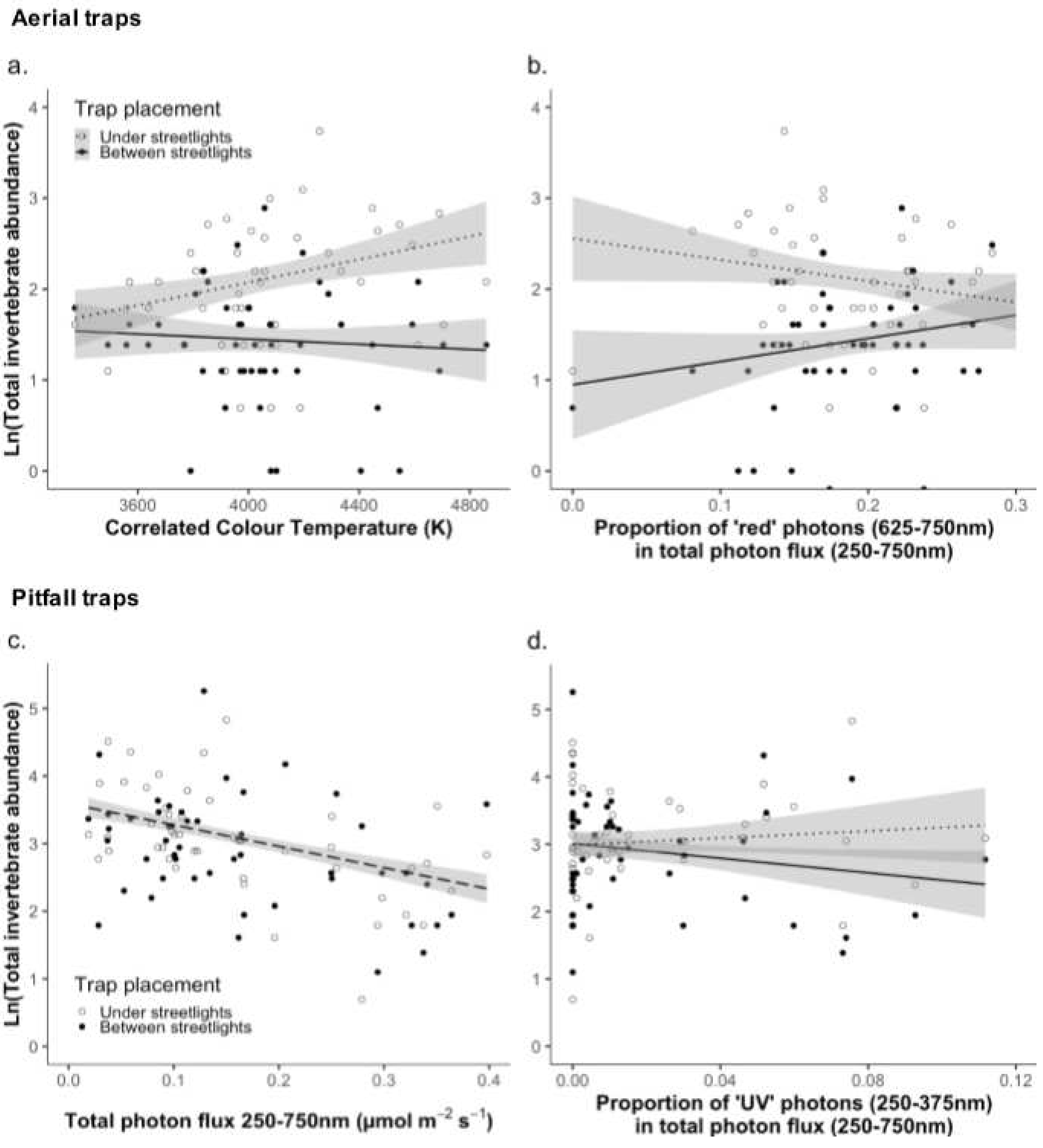

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