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Investigating the impact of street lighting changes on garden moth communities

Kate E. Plummer,^{1,*} James D. Hale,^{2,3} Matthew J. O’Callaghan,^{2,4} Jon P. Sadler² and Gavin M. Siriwardena¹

¹British Trust for Ornithology, The Nunnery, Thetford, Norfolk, UK, ²School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, UK, ³Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland and ⁴School of Applied Sciences, University of South Wales, Pontypridd, UK

*Corresponding author. E-mail: kate.plummer@bto.org

Abstract

Night time illumination of cities is undergoing radical change through the adoption of new street lighting technologies, but the impacts of these large-scale changes on biodiversity have not been explored. Moths are of particular concern because of their nocturnal ‘flight-to-light’ responses. Here we examine *in situ* effects of (1) street lamp replacement and (2) the spatial distribution of local street lighting on garden moth communities in Birmingham, UK, to determine whether current shifts in street lighting infrastructure are leading to an increased attraction of moths into suburban areas. Using a unique before-after-control-impact survey, we show that switching from narrow (low-pressure sodium) to broad spectrum (high-pressure sodium) lamps significantly increases the diversity of macro-moths in suburban gardens. Furthermore, we demonstrate the complex ways in which the moth community differentially responds to variation in street lighting characteristics. In particular we found that macro-moth attraction was greatest at high lamp densities, whilst micro-moth families responded more strongly to street lamp proximity and the density of UV-emitting lamps specifically. Our findings indicate that moths are attracted to suburban gardens with closer, more dense and more spectrally diverse local street lighting, and suggest that suburban areas could represent ecological traps for moth communities if they have insufficient resources to support moth survival and reproduction. Further research is now needed to determine whether street lighting is progressively damaging moth communities, and to understand whether these impacts could be mitigated through changes to street lighting regimes or through the provision of ecologically important habitats in urban landscapes.

Key words: artificial light; ecological trap; Lepidoptera; light pollution; street lamps; urbanisation.

1. Introduction

Artificial night lighting is undergoing a rapid global expansion in its spatial distribution and intensity (Cinzano et al. 2001; Holker et al. 2010), with the potential to have a profound effect on ecological systems (Longcore and Rich 2004; Rich and Longcore 2006; Gaston et al. 2012). Recent research has demonstrated diverse impacts of anthropogenic light on behaviour,

reproduction, community composition and ecosystem function across a range of taxa (e.g. Davies et al. 2012; Dominoni et al. 2013; Meyer and Sullivan 2013; Hale et al. 2015; Minnaar et al. 2015). In addition, changes to lighting policy, predominantly aimed at improving energy efficiency, have initiated a shift towards new lighting technologies such as light-emitting diode (LED) lamps (Hölker et al. 2010). Although this presents an

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opportunity to promote 'ecologically friendly' lighting practices, it simultaneously reveals an important research priority. The landscape scale implications of street lighting changes for biodiversity are currently unknown (but see Stone et al. 2015), and as such must be carefully monitored to inform about the potential emergence of new threats to already impacted ecosystems (Hölker et al. 2010).

Of prominent concern is the increase in spectral heterogeneity that is likely to result from changes to street lighting (Gaston et al. 2012, 2013; Stanley et al. 2015). Different forms of artificial lighting exhibit unique spectral signatures, which characterise the colour and 'quality' of light perceived by the human eye (Elvidge et al. 2010). Some lighting types have emission spectra that extend out of the visible lighting spectrum, producing ultraviolet (UV) radiation that is detectable by a variety of species (Perkin et al. 2011; Gaston et al. 2013). Street lighting in Britain has traditionally been provided using low-pressure sodium (LPS) lamps, which emit an orange hue due to a strong narrow peak at 589 nm within the visible spectrum, although dominant lamp types vary within and between urban areas. However LPS lamps, which are likely to have a relatively limited effect on nocturnal animal behaviour (Eisenbeis 2006; Davies et al. 2013), are now being replaced with lamps that emit light over a much broader spectrum and have a greater luminous flux, such as high-pressure sodium (HPS), white LED and metal halide (MH) types (e.g. AMEY 2012; Stone et al. 2015). At the landscape scale, this leads to a complex patterning of artificial light sources, which also varies with land-use class and built density (Hale et al. 2013). The intensity of light emitted by a street lamp at particular wavelengths may play a critical role in determining its biodiversity impact, as species differ in their sensitivity to various parts of the light spectrum (e.g. Briscoe and Chittka 2001). Therefore, although the newer broad spectrum lighting technologies improve colour rendering for humans (as they emit more natural 'white light') and may reduce carbon emissions, they have the potential to elicit behavioural responses in a large number of species across all taxa (Davies et al. 2013; Pawson and Bader 2014; Minnaar et al. 2015). The current trend towards diverse, bright and broad spectrum street lighting and the use of lamps whose emission spectra extend into the UV, in particular, may have far-reaching consequences for biodiversity and ecosystem function (Gaston and Bennie 2014; Macgregor et al. 2014; Stanley et al. 2015).

The possible implications of artificial night lighting for moth diversity have been highlighted as a particular cause for concern (Frank 1988; Eisenbeis 2006). UV light, which is emitted at wavelengths below 400 nm, acts as an important environmental cue for invertebrates (Tovée 1995). Many moth species are strongly attracted to UV light (emitted by MH and mercury vapour (MV) bulbs, but not LPS, HPS, or standard LED, Elvidge et al. 2010), as well as the shorter wavelengths of visible light that are present to varying degrees in all broad spectrum street lamps (van Langevelde et al. 2011; Somers-Yeates et al. 2013; Pawson and Bader 2014). Flight-to-light behaviour can disturb local foraging, settling activity and longer-distance dispersal movements, potentially leading to high levels of mortality and reduced reproductive success (Frank 1988; Eisenbeis 2006). This has raised the question of whether street lighting in urban landscapes might function as an ecological trap, encouraging moths into unsuitable habitats (Bates et al. 2014). For example, recent research also suggests that broad spectrum lamps can have a significant impact on losses of moths to predation by bats (Minnaar et al. 2015). It has been postulated, therefore, that

artificial night lighting is a contributing factor in the large-scale declines being observed in British macro-moth populations (Conrad et al. 2006; Fox 2012; Fox et al. 2013). As such, the consequences of rapid changes in lighting policy and infrastructure currently underway in many British cities require urgent examination.

The objective of our study was to test the hypothesis that current shifts to new lighting technologies and increased lighting infrastructure would result in greater attraction of moths into suburban areas. To address this, we examined the impacts of (1) street lamp replacement and (2) local street lighting composition on garden moth communities in suburban Birmingham, central England. Birmingham City Council embarked upon a 25-year highway infrastructure improvement and maintenance programme in 2010, in partnership with a public service contractor (AMEY 2012). Throughout the city, LPS and MV street lamps are gradually being replaced by LED lamps in residential areas and by HPS lamps on major traffic routes, with city-wide increases in bright, broad spectrum street lighting and local shifts in UV emissions. Using a before-after-control-impact design, first, we investigated moth community responses to street lamp replacement in two neighbourhoods, in which either broader spectrum lighting (LPS to HPS) or reduced UV-emissions (MV to LED) were introduced, compared with a third neighbourhood where no changes took place. Secondly, to better understand the consequences of changes in street lighting composition for moths, we examined the relationships between local street lighting characteristics and the total garden moth community composition after the lamp replacements were completed, including both macro- and micro-moths. Micro-moths, those which are tend to be smaller and more primitive, are poorly studied in comparison to the larger macro-moths species (New 2004; Fox 2012), but evidence of their attraction to artificial light suggests that their response to suburban street lighting variation requires investigation (Eisenbeis 2006).

2. Methods

2.1 Study sites and moth sampling protocols

The study took place across three Birmingham neighbourhoods in central England, each ~0.5 km² in size and at least 1 km apart (Fig. 1). The neighbourhoods (hereafter referred to as Sites A, B, and C) had a similar structural composition in terms of maturity of housing development, road cover and habitat characteristics (Supplementary Table S1), but contrasting street lighting profiles (further details below; Table 1; Supplementary Table S1). Within each neighbourhood, six gardens were selected for repeated moth sampling in 2011 and 2013. Gardens did not change noticeably in their characteristics between years. Where it became impossible to conduct repeat sampling within a garden (across or within years) due to access restrictions, they were replaced by a comparable neighbouring garden within an average radius of 49.25 m (\pm 3.99 SE) ($n=5$) and the corresponding environmental data for the combined gardens were averaged in further analysis.

To maximise the abundance and richness of moths sampled, we used Skinner traps with 125 Watt MV bulbs run off mains electricity and operated during darkness hours (Bates et al. 2013). This does not appear to have differentially bias trapping outcomes towards moths under MV street lamps, since moth abundance and richness recorded in neighbourhoods with MV street lamps (sites B and C) was not consistently different to the

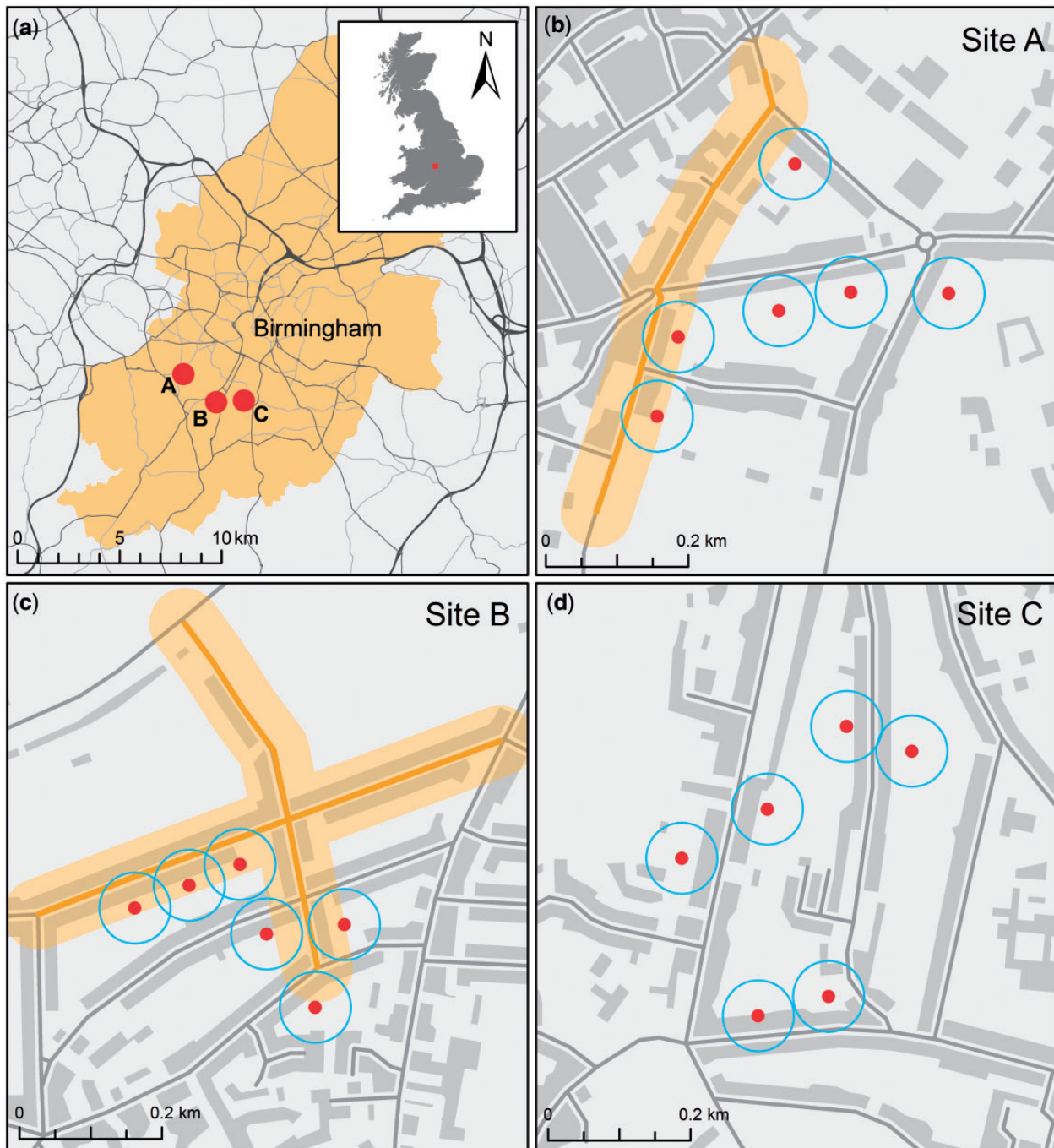


Figure 1. Maps of (a) the relative locations of three neighbourhoods surveyed in Birmingham, UK, and the positions of individual gardens surveyed (red) in (b) Site A, (c) Site B and (d) Site C. Where gardens required replacement with a comparable neighbouring garden, the location with the greatest number of visits is shown; see text for details. Garden 50m buffers used to measure surrounding lighting and land cover characteristics are illustrated in blue. Orange lines mark the extent of the street lamp replacement areas, with the surrounding 50m buffers used to identify gardens in close proximity to the lighting change (<50m); see text for further details. Contains Ordnance Survey data © Crown copyright and database right (2015).

neighbourhood without MV street lamps (site A) (see Fig. 2). Traps assumed a standardised central position within gardens on repeated visits, with up to four gardens sampled per night (mean \pm SE: 2011 = 2.14 ± 0.13 , 2013 = 3.63 ± 0.08). Estimates of surface illuminance, derived from aerial night photography (Hale et al. 2013), averaged $4.87 \pm 0.11 \text{ lx m}^{-2}$ across all surveyed gardens (range: $2.47\text{--}5.57 \text{ lx m}^{-2}$). Nights with bright moonlight, heavy rain and/or low temperatures were avoided (Bowden

1982; Eisenbeis 2006). Identification and release took place *in situ* at ca. 08:00 h on the morning after trapping.

2.2 Before-after-control-impact survey

2.2.1. Street lamp replacement. As a result of the city-wide lamp replacement programme, street lamps within Sites A and B underwent replacement between late 2011 and early 2013, while

Table 1. Street lighting characteristics, before and after street lamp replacement, of each Birmingham neighbourhood surveyed

	Before (2011)		After (2013)		Lighting change
	Lamp types	Spectral profile	Lamp types	Spectral profile	
Site A	HPS, LPS	Amber light, low UV	HPS	Amber light, low UV	LPS to HPS: Narrow to broad spectrum
Site B	MV	White light, high UV	MV, LED	White light, moderate UV	MV to LED: Reduced UV emission
Site C	HPS, MV, MH	Amber/white mix, high UV	HPS, MV, MH	Amber/white mix, high UV	No change

Lamp types are given in order of prevalence. The information is summarised for all street lamps within a 100 m radius of surveyed gardens.

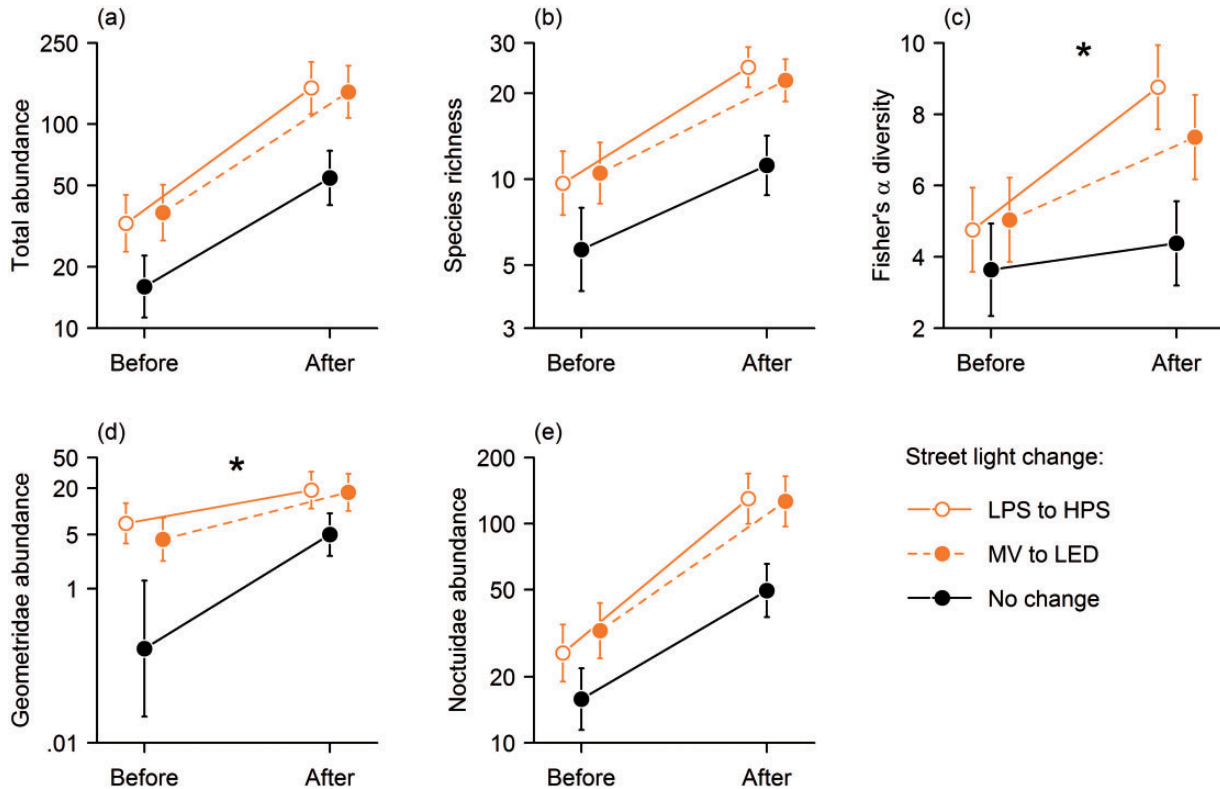


Figure 2. Interaction plots to show the effect of street lamp replacement, compared with an area of no lighting change, on macro-moth community measures: (a) total abundance, (b) species richness, (c) Fisher's α diversity, (d) Geometridae abundance and (e) Noctuidae abundance. Points represent parameter estimates \pm 95% confidence intervals for each neighbourhood before (2011) and after (2013) street lamps were changed, with abundance and species richness values (a, b, d, and e) plotted on the log scale. Significance stars are shown for significant interaction terms, see Table 2 for corresponding values.

lamps within Site C remained the same (Fig. 1), enabling an unreplicated before-after-control-impact (BACI) survey design to be employed. Absolute differences in the spectral profiles of all street lamp types present within the survey area in 2011 and 2013 are shown in Supplementary Figure S1. The lighting change at Site A can be summarised as a 'broad spectrum increase', with HPS lamps introduced along the western edge of the neighbourhood in place of the LPS bulbs previously present (Table 1; 36.0% of lamps within 100 m buffers of study gardens replaced). The lighting change at Site B can be summarised as a 'UV reduction', with LED lamps installed to replace some of the existing MV lamps (Table 1; 41.6% of lamps within 100 m buffers of study gardens). No lighting changes occurred at Site C during the course of the study. In addition to spectral changes, street lamp replacement is also likely to have resulted in changes in light intensity, shielding and/or the sphere of influence due to differences in bulb designs.

2.2.2 BACI moth community data. Baseline macro-moth sampling was conducted at each garden over two non-consecutive

nights in August–September 2011, prior to the large-scale street lighting replacement. Sampling was repeated at each garden on similar dates in 2013, following street lighting replacement, to ensure consistency in survey effort between years (Supplementary Table S2). Trapping events at closely situated gardens were temporally separated to minimise the recapture of the same individuals. Moth communities were evaluated in terms of their total and family-specific abundances, observed species richness and Fisher's α diversity index. Fisher's α diversity is commonly used to estimate moth diversity, due to its low sensitivity to under-sampling (Kempton and Taylor 1974; Thomas and Thomas 1994; Fuentes-Montemayor et al. 2012). Moth community measures were estimated for each garden before and after street lamp replacement by combining data from the two moth-trapping events conducted in 2011 and 2013, respectively.

2.2.3 BACI statistical analysis. To test for the impacts of street lamp replacement, macro-moth community variables were fitted as a function of a neighbourhood \times year interaction term

within separate generalised linear models ($n=36$). Post-hoc Student's *t* tests were then used to compare the significance of the differential change in moth communities (i.e. regression slopes) between neighbourhoods, therefore allowing the effects of street lamp replacement to be separated from those of temporal variation. The importance of garden proximity to street lamp replacement at Sites A and B was also evaluated by comparing the change in moth communities at gardens within 50 m of the street lamp replacement areas (see Fig. 1) to those further away. Variability in moth responses between gardens was not sufficient to warrant incorporating garden identity as a random effect. Appropriate link functions and error distributions were fitted for each response: total and family abundances used log links and negative binomial errors due to evidence of data overdispersion, species richness used a log link and Poisson errors and Fisher's α diversity was fitted using an identity link and a Gaussian distribution.

2.3 Street lighting composition survey

2.3.1 Street lighting and habitat characteristics. Garden moth communities could respond to street lighting in a number of different ways. For example, the local lighting spectral profile could be important, but equally garden moths might also be affected by the proximity of an individual lamp or by different lamp densities. Therefore in addition to examining the effects of the neighbourhood lighting profile (see Table 1), we also calculated three measures of street lighting variation for all gardens surveyed: (1) proximity to the nearest lamp, (2) total street lamp density (50 m^{-2}), and (3) high-UV emitting street lamp density (50 m^{-2}) (see Supplementary Table S1). Since moth abundance and richness in gardens are known to be influenced by local land cover (Bates et al. 2014), we also considered the effects of habitat variation in our analyses, using the percentage covers (50 m^{-2}) of vegetation and road land-cover parcels. Lamp density and percentage land cover data were accessed at a 50 m scale to capture the likely attraction distances of moths to local lighting infrastructure (Eisenbeis 2006).

Lighting and habitat characteristics were summarised for each garden using ArcGIS 9.2 (ESRI 2006) and Hawth's Analysis Tools (Beyer 2004). Street lamp position and lamp type data were provided by Birmingham City Council/AMEY and ground-truthed using visual inspections. Aerial night photography (Hale et al. 2013) was also used to identify additional lamps such as domestic security lights. Vegetation data were generated using colour and near-infrared photography (2007) (Bluesky International Limited, UK) and roads were identified using Ordnance Survey MasterMap (2008) polygons.

2.3.2 Moth community assessment. A comprehensive assessment of garden moth communities, including both macro- and micro-moths, was conducted following the street lamp replacements in June to September 2013. All gardens were visited six to eight times for repeated moth sampling (mean \pm SE: 6.94 ± 0.19); this incorporated two visits also being used for the BACI survey (described above). Garden visit order was randomised and two visits were conducted each month, where possible, to limit temporal bias within the sampling regime. All macro- and micro-moths were counted and identified to species level. Genus was recorded for any micro-moths that could not be identified to species level ($n=152$). Family-specific data were examined for micro- ($n=6$) and macro-moth families ($n=2$) with a total of >50 captured individuals (see Supplementary Table S3). Amongst these, four micro-moth families had a high proportion

($>40\%$) of zero captures and were therefore assessed using presence/absence.

2.3.3 Street lighting composition statistical analysis. To model the effect of suburban street lighting composition and configuration on contemporary garden moth communities we applied generalised additive mixed models to moth responses recorded at each 2013 trapping event ($n=112$). Garden identity was included as a random effect, to account for repeated sampling within gardens.

A likelihood ratio test was used to determine whether moth abundance responses should be fitted using either a Poisson or negative binomial error structure (Zuur et al. 2009: 238). Family presence/absence data were modelled using binomial errors, and species richness and Fisher's α were modelled using the same link functions and error distributions used in the previous BACI analyses. There was no evidence of spatial autocorrelation in overall total abundance (Moran's *I* test, $P=0.26$) or Fisher's α diversity ($P=0.26$) recorded in surveyed gardens, but limited evidence for species richness ($P=0.06$) suggests that power to detect significance for this response could potentially be artificially inflated due to pseudoreplication.

We created seven competing models to describe the different patterns of moth responses to the surrounding local environment and used an information theoretic analytical approach to directly compare their relative explanatory power. Temporal variation was modelled as a thin-plate regression spline smooth of trapping date in all models except the null (i.e. models 1–6), as in-flight moth numbers vary non-linearly across the season in response to changes in the lunar phase and species-specific differences in flight periods. While accounting for the date smooth, the first four models described the relationships between moth metrics and our four measures of street lighting composition: (1) neighbourhood class [\approx lighting profile], (2) distance to nearest lamp, (3) total lamp density, (4) high-UV lamp density. The fifth model examined whether moth differences might be better explained by variation in local habitat, by fitting vegetation and road percentage covers together as additive predictor terms while also accounting for the date smooth. There was no evidence of collinearity between these two predictors ($r=0.12$) and modelling them separately did not substantially improve model fit; therefore only the combined habitat model is presented. The sixth model included only the date smooth, whilst the seventh (null) model removed the smooth term such that only the intercept was fitted. Together, these seven models formed a set of candidate models which were fitted separately for each moth community response. The candidate models were ranked using ΔAICc and Akaike weights (w). Models with the lowest AICc value (i.e. top ranked models) were considered to be the most parsimonious, but models which differed by ≤ 2.0 AICc units were considered to have an equivalent level of support from the data (Burnham and Anderson 2002). All statistical analyses were conducted in R version 3.2 (R Core Team 2015).

3. Results

3.1 BACI: impacts of street lamp replacement on macro-moths

All moth community measures varied significantly among neighbourhoods and were consistently higher in 2013, across both the replacement and control locations (Table 2; Supplementary Table S4; Fig. 2). To account for this natural spatial and temporal variation, the impacts of street lamp replacement were therefore directly assessed by testing the

Table 2. Results of the BACI study to test the effects of street lamp replacement within two neighbourhoods, compared with a third neighbourhood with no street lighting changes

Response	Neighbourhood			Year			Neighbourhood × Year interaction		
	χ^2	df	P	χ^2	df	P	χ^2	df	P
Total abundance	36.03	2	<0.001***	103.93	1	<0.001***	0.87	2	0.649
Species richness	43.65	2	<0.001***	76.10	1	<0.001***	1.23	2	0.540
Fisher's α diversity	17.44	2	<0.001***	17.37	1	<0.001***	7.53	2	0.023*
Geometridae abundance	27.17	2	<0.001***	26.32	1	<0.001***	6.26	2	0.044*
Noctuidae abundance	33.51	2	<0.001***	120.15	1	<0.001***	2.63	2	0.268

significance of the differential change in moth communities among neighbourhoods between time periods (i.e. Neighbourhood × Year interaction term). Street lamp replacement did not influence total abundance or species richness (Table 2; Fig. 2a and b). However, exchanging LPS for HPS bulbs in Site A resulted in a significantly greater increase in Fisher's α diversity compared with both Site B ($t_{29}=3.84$, $P < 0.001$) and the control site ($t_{29}=4.83$, $P < 0.001$; Table 2; Figure 2c). Furthermore, within Site A, the proportional increase in Fisher's α diversity was greatest for gardens within 50m of the street lamp replacement area (see Fig. 1), compared with those further away ($F_{1,4}=23.68$, $P=0.008$; Fig. 3). By comparison, switching MV bulbs to LEDs did not result in a differential change in Fisher's α diversity at Site B, compared with the control site ($t_{29}=0.91$, $P=0.369$).

Street lamp replacement also influenced the numbers of moths from the Geometridae family recorded in gardens (Table 2). Interestingly, the proportional change in geometrid numbers was significantly lower at Site A ($t_{30}=2.39$, $P=0.023$) and Site B ($t_{30}=2.62$, $P=0.014$), where lighting had changed, compared with the control site (Fig. 2), suggesting a reduction in geometrid attraction. There was no difference in the proportional change in geometrid abundance between Sites A and B ($t_{30}=0.50$, $P=0.624$; Fig. 2), and there was no evidence that gardens closest to the areas of street lamp replacement (within 50 m, Fig. 1) in either neighbourhood had a reduced proportional change in abundance compared with those further away (>50 m, $P > 0.75$). Streetlamp replacement did not have a significant effect on Noctuidae abundance (Table 2; Fig. 2).

3.2. Influence of street lighting composition on garden moths

A total of 8820 individuals, representing 254 species, including 2859 micro-moths (92 species) and 5809 macro-moths (162 species), were sampled in suburban Birmingham over the 2013 flight season (Supplementary Table S3). Species richness was highly correlated with total abundance ($r=0.84$, $P < 0.001$) and Fisher's α diversity ($r=0.69$, $P=0.002$) within the 18 gardens monitored, but relationships with the predictor variables nevertheless differed considerably (Table 3).

Model comparison results indicate that variation in the composition of local street lighting was a good predictor of differences in garden moth communities (Table 3; Supplementary Table S5). Notably all street lighting models had a ΔAICc value of <2 when total abundance was considered as the response, highlighting the complex nature in which the local lighting environment can contribute to the numbers of moths visiting suburban gardens. However the different street lighting models had varying levels of support in describing other aspects of the moth community. The Lamp Distance model featured in the confidence set for eight of the eleven responses tested and was the best supported model in

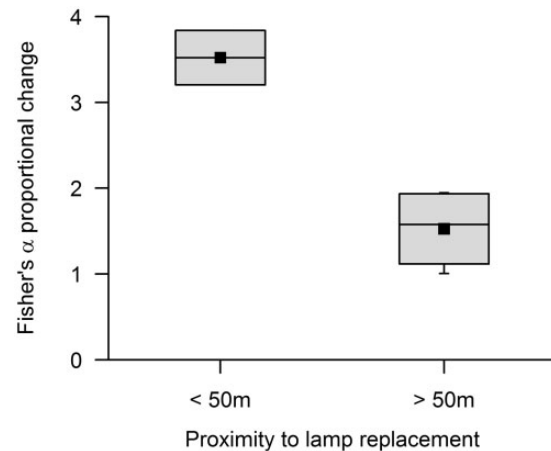


Figure 3. The quantitative effect of proximity to street lamp replacement at Site A (LPS to HPS) on Fisher's α diversity proportional change. Proportional change is estimated using 2013 diversity/2011 diversity per site ($n=6$). Boxes represent 25th, 50th (median), and 75th percentile and solid squares illustrate the means.

explaining variation in species richness and Tortricidae micro-moth abundance. Both species richness and Tortricidae numbers increased in gardens closer to street lamps (Fig. 4a and b). The Neighbourhood model had a similar level of support, indicating that broad differences in the overall lighting environment may be an important factor in explaining garden moth communities (Table 3). The two lamp densities models, however, highlighted differences between macro- and micro-moth street lighting responses. For example, Geometridae abundance was strongly influenced by increasing total lamp density (Fig. 4d), but the density of UV-emitting lamps was not an important predictor of macro-moth abundance more generally. By comparison, the High UV Lamp Density model featured in the confidence set for a number of micro-moth families (Table 3). In particular, Blastobasidae micro-moth presence was significantly greater in gardens within a higher density of UV-emitted lamps (Figure 4c). When considering the alternative models tested, as expected moth communities were shown to be strongly influenced by seasonal variation, with the Date Smooth model forming an equally or more parsimonious model for eight of moth response measures (Table 3; Supplementary Table S5). By comparison, the Habitat model was only well supported when explaining Fisher's α diversity ($\Delta\text{AICc}=0$) and Oecophidae micro-moth presence ($\Delta\text{AICc}=0.93$; Table 3; Supplementary Table S5).

4. Discussion

The aggregation of moths, and other nocturnal insects, around street lamps has been widely documented via both scientific

Table 3. Model selection results testing the effects of local street lighting composition on garden moth community responses

Moth response	Model Akaike weight						
	(1)	(2)	(3)	(4)	(5)	(6)	(7)
	Neighbourhood	Lamp distance	Lamp density	High UV density	Habitat	Date smooth	Null
Total abundance	0.134	0.169	0.140	0.135	0.062	0.359	0.000
Species richness	0.069	0.374	0.106	0.116	0.037	0.298	0.000
Fisher's α diversity	0.191	0.092	0.103	0.096	0.404	0.115	0.000
Micro-moth presence							
Gracillariidae	0.153	0.202	0.111	0.157	0.062	0.316	0.000
Yponomeutidae	0.060	0.209	0.146	0.137	0.045	0.404	0.000
Oecophoridae	0.245	0.092	0.082	0.135	0.154	0.245	0.046
Blastobasidae	0.216	0.067	0.088	0.504	0.020	0.105	0.000
Micro-moth abundance							
Tortricidae	0.023	0.677	0.055	0.052	0.038	0.156	0.000
Crambidae	0.166	0.162	0.113	0.175	0.059	0.325	0.000
Macro-moth abundance							
Geometridae	0.024	0.190	0.410	0.108	0.077	0.191	0.000
Noctuidae	0.431	0.075	0.073	0.166	0.032	0.223	0.000

All models except the null (i.e. models 1–6) include the date smooth. We report the Akaike weights (model probabilities) for all models. Models with $\Delta AIC < 2$ are highlighted, and top models are in bold.

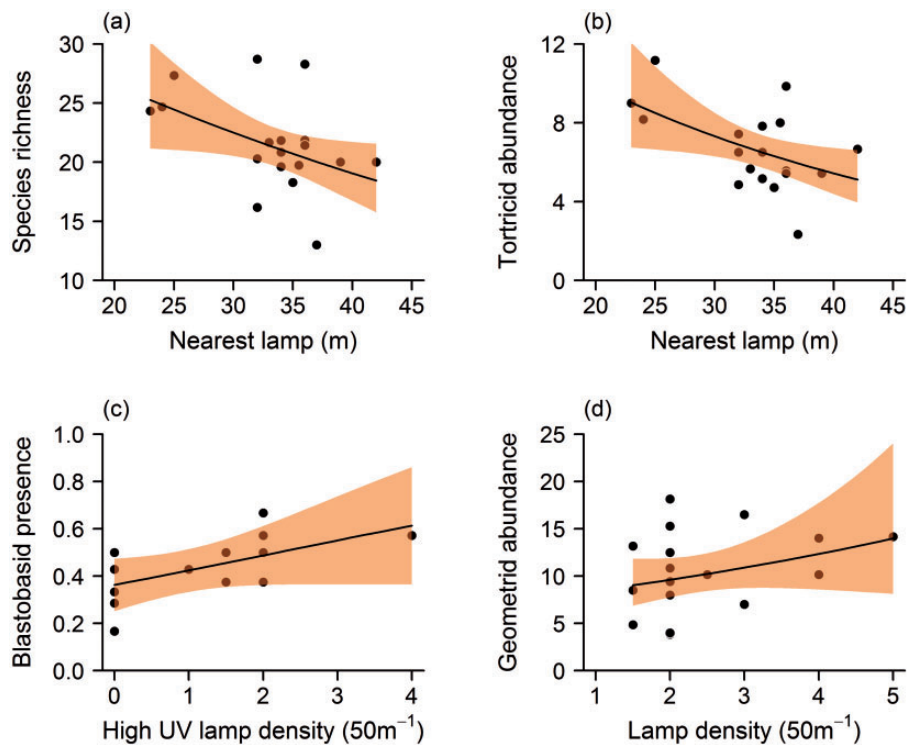


Figure 4. The effect of local street lighting characteristics on garden moth community metrics, including (a) species richness, (b) Tortricidae abundance, (c) Blastobasidae presence and (d) Geometridae abundance. Mean values per garden are plotted and lines (\pm 95% CI) are predicted from the most parsimonious models with the effect of the date smooth removed.

and anecdotal evidence (e.g. Frank 1988, 2006; Eisenbeis 2006; Somers-Yeates et al. 2013); however little is known about how street lighting variation influences the composition of moth communities within a suburban context. Here we examine *in situ* effects of street lighting changes and spatial characteristics on moth communities in gardens, highlighting the complex way in which different components of the moth community differentially respond to specific aspects of the lit environment. Broadly, our findings suggest that moth attraction into gardens

is greatest where street lamps are more spectrally diverse, in closer proximity and at higher densities. Further research is now needed to understand if these behavioural responses are a precursor for negative biological impacts on moths, and to reveal strategies through which such impacts could be reduced.

In relation to the current shifts in global lighting policy (Hölker et al. 2010), our findings show that replacing LPS with HPS lamps can lead to a significant increase in local moth diversity in nearby gardens. Although HPS lamps do not emit UV

they are still reported to be highly attractive to some moths and other insects (Somers-Yeates et al. 2013; Perkin et al. 2014). In contrast, attraction to LPS lamps is considered to be minimal, due to their much narrower spectral range (see Supplementary Fig. S1) (Eisenbeis 2006). In this study, the newly installed HPS lamps in Site A appear to have stimulated flight-to-light behaviour in a greater range of species, thereby drawing a larger diversity of moths into the neighbourhood from surrounding areas. Furthermore, the pattern was most pronounced in gardens closest to the area where street lamps were replaced. Interestingly, we also show that the replacement of MV bulbs with white LED lamps appears to have led to a reduction in the attraction of geometrid macro-moths to Site B. Geometridae species have a varied sensitivity to light of both low (381.8 nm) and high (597.1 nm) wavelengths (van Langevelde et al. 2011). Although white LED street lamps emit light over a broad spectrum, and as such have the potential to increase the ecological impacts of street lighting (Stone et al. 2012; Pawson and Bader 2014; Stanley et al. 2015), they do not emit UV light. Our findings imply that the reduction in UV emissions that resulted from replacing some MV lamps within the neighbourhood may have been enough to reduce geometrid attraction. These findings could potentially have important implications for moth populations, since flight-to-light behaviour can disrupt movements, reduce foraging activity and inhibit reproduction, as well as have a direct impact on survival (Frank 1988, 2006; Eisenbeis 2006). As such, the new, broader spectrum HPS lamps could potentially act as ecological traps (Battin 2004), if they are encouraging moths into unsuitable habitats (e.g. Kolligs 2000). On the other hand, at least for geometrids, using LEDs in place of UV-emitting lamps may reduce the potential for these negative impacts by encouraging fewer moths into gardens. Although we have not demonstrated that moths affected by street lamp changes have altered productivity or survival in this study, this is undoubtedly an important area for future research.

The results of the street lighting composition survey indicate that garden moth communities respond to street lighting spatial characteristics in a broadly similar way as they do to changes in street lamp types. However, notably, gardens positioned near to street lamps had greater moth species richness, suggesting that the close proximity of a street lamp, potentially irrespective of its spectral profile, is likely to be an important determinant of the total range of moth species attracted into a garden. Perhaps most striking was the differential importance of each aspect of the street lighting environment for different moth families, suggesting that differences in physiological and life-history characteristics are likely to be underpinning moth responses to street lighting variation. For example, for macro-moth families the neighbourhood and total street lamp density were found to be the best predictors of increased abundance. By comparison, we show that the distance of gardens to nearby street lamps and the density of UV-emitting (MV and MH) lamps were important influences on increased presence and abundance of micro-moth families. Therefore it seems that micro-moths may be most sensitive to lower wavelengths specifically, while macro-moths are perhaps more strongly affected by the heterogeneous nature of suburban street lighting regimes. Further interpretation of why response patterns differ across the moth community would purely be speculation at present, but could be achieved through a better understanding of species-level behaviours across a range of macro- and micro-moths. However, these findings suggest that lower density lighting as well as reduced use of UV-emitting lamps could potentially benefit a broad variety of moth species.

Our findings contradict previous suggestions that moth attraction to street lamps may be reduced at high lamp densities due to the general overall increase in the level of illumination in the surrounding landscape (Eisenbeis 2006). Although greater amounts of artificial night lighting can create moth sampling bias by reducing the efficacy of moth traps through increased light competition (Bowden 1982), this does not appear to have influenced the outcomes of the present study since attraction was greatest at higher values of our street lighting metrics. Therefore we assume that the moth traps were equally effective, or at least subject to consistent catching biases, regardless of the ambient light environment. We propose that further research is required to explore whether lamp density thresholds exist for flight-to-light behaviour and to determine the spatial extent over which these behaviours occur in, and around, artificially lit areas.

Unexpectedly, the switch from LPS to broad spectrum HPS lamps at Site A appears to have led to a decrease in geometrid abundance compared with the control neighbourhood. This could conceivably be a result of the of the lamp design. The LPS lamps within the study areas were poorly shielded, so although they emit light within a narrow part of the visible light spectrum, they may illuminate a wide area and be visible as a point source of light even above the horizon. In comparison, the new HPS had greater levels of shielding, which may have been effective in reducing the zone of attraction for geometrids. As such, these findings highlight the importance of considering street lamp design features, beyond just light spectrum, when addressing the ecological implications of various street lighting regimes.

Host plant availability is known to be important in influencing the distributions of other Lepidoptera species in Britain (Curtis et al. 2015). As such it is likely that subtle, small-scale differences in garden habitats will have important consequences for moth attraction. Although such fine-scale differences were not assessed here and the findings are purely correlative, there was little evidence that moth responses could be better explained by local habitat characteristics than by the street lighting environment. Furthermore, since street lighting metrics did not co-vary with vegetative cover, the findings are likely to be a true reflection of street lighting effects rather than an artefact of local habitat variation. Therefore, a plausible explanation of our findings is that moths are attracted to gardens with closer, more dense, and more spectrally diverse local street lighting. The risk is that these gardens may be acting as ecological sinks if they have insufficient resources to support moth survival or reproduction, in combination with any direct mortality that occurs through attraction to light (Schlaepfer et al. 2002; Gilroy and Sutherland 2007). Indeed, recent research has identified a general reduction in moth species abundance and richness in more urbanised locations (Bates et al. 2014). This is perhaps because street lighting provides an unreliable cue about habitat quality, facilitating the dispersal of moths from wide rural areas into urban sink habitats (Eisenbeis 2006; Bates et al. 2014). Comparison with surrounding non-urban, 'natural' habitats that are not subject to lighting changes would be required to determine whether this potential 'vacuum cleaner effect' is progressively damaging the integrity of the moth community in the local area.

In a broader context, our findings illustrate that there is unlikely to be a 'one size fits all' solution to curb the on-going impacts of artificial lighting on moth communities. We show that the potential consequences of changing street lighting regimes, both in terms of actual lamp replacement and variation in

spatial composition, vary for different components of the total moth community. Moths have an important functional role as pollinators, herbivores and prey for a variety of avian and mammalian predators. As such, changes to their abundance and diversity resulting from artificial lighting could have significant downstream effects on ecosystem service provision and at multiple trophic levels (e.g. Macgregor et al. 2014). Although we can be fairly confident that street lamp replacement and spatial characteristics can lead to changes in moth communities given our present findings, understanding the exact mechanisms driving moth response patterns will require a combination of both natural experiments, as reported here, and further controlled experimental manipulation studies (e.g. Spoelstra et al. 2015). This will allow separation of street lamp attraction properties such as lamp spectrum, brightness and total radiation, and thereby improve our ability to assess the potential implications of future broad-scale re-lighting projects.

It is unlikely that the switch to new technologies could be halted on ecological grounds; particularly given their advantages in terms of their reduced energy costs. However, if the policy priority is to reverse moth declines, our results suggest that the energy savings and safety improvements from new lighting technologies need to be traded off against the benefits for biodiversity that would result from lower street lamp densities. Alternative strategies to limit the adverse effects of street lighting on moths, and other biodiversity, are also worthy of investigation. For example, whilst our findings suggest that street lamps could potentially turn urban areas into ecological traps for moths, the severity of these effects could be reduced by providing ecologically important habitats in gardens and urban green spaces (Goddard et al. 2010). As traditional lamps continue to be replaced and new lighting regimes spread and intensify, further opportunities for 'natural experiment' research will emerge. It is therefore important that lighting engineers, city planners, ecologists and policy makers continue to work together to optimise artificial light at night while neutralising the impacts on ecological systems.

5. Data accessibility

Data for this article are available from Zenodo, <https://zenodo.org/record/56453> (Plummer et al 2016).

Conflict of interest: None declared.

Supplementary data

Supplementary data is available at JUECOL online.

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